Carabid Beetles as Bioindicators: Biogeographical, Ecological and Environmental Studies

Proceedings of the XIV European Carabidologists Meeting, Westerbork, 14–18 September, 2009

Edited by D. Johan Kotze, Thorsten Assmann, Jinze Noordijk, Hans Turin, Rikjan Vermeulen



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This book is dedicated to our late colleagues Konjev Desender (1956–2008) and Jean-Pierre Maelfait (1951–2009)

Contents

List of Participants of the European Carabidologists Meetings

I In memoriam: Konjev Desender (1956–2008) and Jean-Pierre Maelfait (1951–2009)

Gábor L. Lövei

- 37 Eucamaragnathus desenderi, a new ground beetle species from Africa (Coleoptera, Carabidae) Thorsten Assmann, Claudia Drees, Andrea Matern, Andreas Schuldt
- 47 Calleida desenderi, new species from Ecuador (Coleoptera, Carabidae, Lebiinae) Achille Casale
- 55 Forty years of carabid beetle research in Europe from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation

D. Johan Kotze, Pietro Brandmayr, Achille Casale, Emmanuelle Dauffy-Richard, Wouter Dekoninck, Matti Koivula, Gábor L. Lövei, Dietrich Mossakowski, Jinze Noordijk, Wilfried Paarmann, Roberto Pizzolotto, Pavel Saska, Axel Schwerk, José Serrano, Jan Szyszko, Angela Taboada, Hans Turin, Stephen Venn, Rikjan Vermeulen, Tullia Zetto

149 Sub-fossil beetle assemblages associated with the "mammoth fauna" in the Late Pleistocene localities of the Ural Mountains and West Siberia

Evgeniy Zinovyev

171 Predator feeding choice on conspicuous and non-conspicuous carabid beetles: first results

Teresa Bonacci, Pietro Brandmayr, Tullia Zetto Brandmayr

- 181 Predation of amphibians by carabid beetles of the genus Epomis found in the central coastal plain of Israel *Gil Wizen, Avital Gasith*
- **193** Current knowledge on exocrine glands in carabid beetles: structure, function and chemical compounds *Anita Giglio, Pietro Brandmayr, Federica Talarico, Tullia Zetto Brandmayr*
- 203 Morphometry of eyes, antennae and wings in three species of Siagona (Coleoptera, Carabidae)

Federica Talarico, Pietro Brandmayr, Anita Giglio, Alessandro Massolo, Tullia Zetto Brandmayr

- 215 Heavy metals in carabids (Coleoptera, Carabidae) Ruslan O. Butovsky
- 223 Using demographic data to better interpret pitfall trap catches Andrey V. Matalin, Kirill V. Makarov
- 255 When to sample in an inaccessible landscape: a case study with carabids from the Allgäu (northern Alps) (Coleoptera, Carabidae) Ingmar Harry, Claudia Drees, Hubert Höfer, Thorsten Assmann
- 273 A plea for using qualitative aspects in the interpretation of ecological field data as revealed by carabid beetle assemblages of a pristine salt marsh

Dietrich Mossakowski, Wolfgang Dormann

- 287 Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions Matti I. Koivula
- 319 Model of succession in degraded areas based on carabid beetles (Coleoptera, Carabidae) Axel Schwerk, Jan Szyszko

- 333 Poleward range expansion without a southern contraction in the ground beetle Agonum viridicupreum (Coleoptera, Carabidae) Claudia Drees, Pietro Brandmayr, Jörn Buse, Petra Dieker, Stephan Gürlich, Jan Habel, Ingmar Harry, Werner Härdtle, Andrea Matern, Hartmut Meyer, Roberto Pizzolotto, Markus Quante, Katharina Schäfer, Andreas Schuldt, Angela Taboada, Thorsten Assmann
- 353 Habitat disturbance and hydrological parameters determine the body size and the reproductive strategy of alluvial ground beetles Michael Gerisch
- 371 Ground beetle (Coleoptera, Carabidae) assemblages inhabiting Scots pine stands of Puszcza Piska Forest: six-year responses to a tornado impact

Jarosław Skłodowski, Paulina Garbalińska

- 393 Carabid beetle diversity and mean individual biomass in beech forests of various ages Lucija Šerić Jelaska, Vlatka Dumbović, Mladen Kučinić
- 407 Changes in salt-marsh carabid assemblages after an invasion by the native grass Elymus athericus (Link) Kerguélen Anita Georges, Philippe Fouillet, Julien Pétillon
- 421 Effects of ecological flooding on the temporal and spatial dynamics of carabid beetles (Coleoptera, Carabidae) and springtails (Collembola) in a polder habitat

Tanja Lessel, Michael Thomas Marx, Gerhard Eisenbeis

447 Assemblages of carabid beetles (Coleoptera, Carabidae) in humid forest habitats of different stages of succession in the Puszcza Knyszyńska Forest (northeastern Poland) Adam Kwiatkowski

46 I Belowground carabid beetle diversity in the western Palaearctic effects of history and climate on range-restricted taxa (Coleoptera, Carabidae)

Andreas Schuldt, Thorsten Assmann

- 475 Recent records of steppe species in Belarus, first indications of a steppe species invasion? Oleg Aleksandrowicz
- 487 How unique is the tiger beetle fauna (Coleoptera, Cicindelidae) of the **Balkan Peninsula?**

Radomir Jaskuła

- 503 Ground beetles of the Ukraine (Coleoptera, Carabidae) Alexander Putchkov
- 517 What do we know about winter active ground beetles (Coleoptera, Carabidae) in Central and Northern Europe? Radomir Jaskuła, Agnieszka Soszyńska-Maj
- 533 Calodromius bifasciatus and other Carabidae on 26 oak-trunks in a nature reserve in the Netherlands Ron Felix, Paul van Wielink
- 545 Historical ecology meets conservation and evolutionary genetics: a secondary contact zone between Carabus violaceus (Coleoptera, Carabidae) populations inhabiting ancient and recent woodlands in north-western Germany

Andrea Matern, Claudia Drees, Werner Härdtle, Goddert von Oheimb, Thorsten Assmann

565 Animals as an indicator of carbon sequestration and valuable landscapes

Jan Szyszko, Axel Schwerk, Jarosław Malczyk

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IN MEMORIAM



In memoriam: Konjev Desender (1956–2008) and Jean-Pierre Maelfait (1951–2009)

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It is about a year ago that Belgian biology lost, in quick sequence, two distinguished and internationally known representatives: Konjev Desender and Jean-Pierre Maelfait.

Before contemplating this sad loss, allow me to mention some facts, even if they are well known in these circles. Konjev Desender was born in 1956, and graduated in 1978 from the University of Ghent. In 1987, he received his PhD, and in 1990, he joined the Belgian Institute of Natural Sciences, where he remained until his untimely death from cancer at the age of 52. Originally interested in birds, Konjev's attention later turned to ground beetles, and after 1980, he mainly worked with invertebrates. The focus of his research was ground beetles, especially in relation to nature conservation, forestry, and population genetics. He took part in 6 expeditions to the Galapagos Islands (for which I envied him a great deal), has worked on salt marshes around Europe, but above all, worked and collected intensively in Belgium. His work was massive in terms of numbers of beetles collected, driven by keen curiosity, and he understood well that human activities have shaped even the invertebrate fauna of his country. I really liked his work on identifying beetle remains in old wells excavated by archeologists, giving a richer understanding of environments past. This was, however just one facet of his varied activities. He was a hard worker, and published over 350 papers, mostly in collaboration, guided numerous younger scientists, and was active in the Belgian entomological society. He also organised one of the European carabidologist meetings, in 1992, in collaboration with his friend Jean-Pierre Maelfait and other Belgian colleagues.

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Konjev Desender

Jean-Pierre Maelfait

I have first met both of them, I believe, at a soil zoology symposium in Louvainla-Neuve in 1982, and recall the intensity in Konjev's voice when he talked about his research, and the quiet presence of Jean-Pierre.

I remember Konjev mostly through our encounters at meetings like this one, where he has always been present (actually more frequently than myself), and I do not think there are many in this room who do not remember him as one of the central figures of our carabidologist meetings.

Jean-Pierre was a more relaxed, one could even say slower, but no less impressive personality. Jean-Pierre Maelfait was born in 1951, 5 years senior to Konjev, and spent most of his career at the University of Ghent and at the Institute for Nature Conservation and Forestry in Brussels (INBO). Like for many others who graduated from that university, he was also Konjev's teacher, later a colleague and friend. As a teacher, he will be long remembered – I believe there are several participants in this room who were Jean-Pierre's students, and I am sure he has made a profund influence on your knowledge and professional attitude. Jean-Pierre was also a productive scientist – his output,

3

some of which is still being published, amounts to ca. 300 items. These include numerous articles on ground beetles, but his speciality was arachnology, the venerable study of spiders. Jean-Pierre and Konjev shared a similar approach to science and nature, were very active in the conservation of their respective groups, and also their habitats; they also shared several projects. Both of them visited the Galapagos Islands several times, and published on their results from there over a period of more than a decade. Their first shared publications go back to 1980; altogether they are co-authors on 100 published papers. These concern surface-active organisms, papers on the inhabitants of Belgian sand dunes, forest invertebrates, ecological restoration, and so on.

Due to this shared interest and close relationship, Jean-Pierre was originally asked by the organisers of this meeting to talk about Konjev here. Then, suddenly and unexpectedly, he died. He was 57; hardly older than Konjev. And this is how this mantle, this not-so-light mantle fell on me.

I have had a very dear New Zealand friend, sadly also dead, by the name of John Bevan Ford. He was a respected and much loved New Zealand Maori artist. Once he was explaining to me the Maori attitude to life, its continuity and death. When someone dies, he said, people who knew him gather together to celebrate his or her life, and talk to him as someone still much present, even if unable to answer. If they had a quarrel, they mention it. If they have unsorted business, they lament that this can now never be laid to rest. And they mention how much they enjoyed when they did things together, and rejoice again. In this spirit I would like to remember these two colleagues of us. I think it is wise and very fitting. I, for one, can now never berate Konjev and convince him that one does not need to kill tens of thousands of beetles to illustrate an ecological phenomenon. He will not kill more beetles now, but I am not happy. And I smiled again, when I saw the photos of Konjev and Johan Kotze, at the conference party at Mols, Denmark, playing with empty beer glasses, and a few coins. That photo is so full of the joy of life...I am sure that we all carry similar memories of both of them.

So when we rember them now, I do not ask you to stand up and think silently about them, to show respect. Respect we have for them and respect we will continue to show them. But I would also like to quote a Japanese haiku, which says that a sumo wrestler shows respect for his teacher by winning over him on the wrestling mat. Science is not about fighting, but this, in a way, we shall also do – to build on their work, and proceed further. I know that they had no intention to stop and see only us advance, nor would they have withdrawn their support when younger colleagues were preparing to surpass them. We are only a little sad that they themselves were stopped.

Bearing such a loss is not easy. When I now turn to the families of Jean-Pierre and Konjev, I know that these words do not bring them back, and hearing these words may make their grief swell again. Jean-Pierre will not again silently, gently sit among us, and Konjev's sharp voice will not be heard again at future meetings. Nevertheless, I would still like, in the name of all of us, to say to you, that we are glad. We are glad to have known them, even if we met them only sporadically, and we thank you for providing support for them. None of us can function without this support. We, carabidologists are an odd race, in finding small, smelly creatures of strange habit fascinating, interesting, and well worth spending days (months) away from home, coming home late, and going into our workplace or field site even on weekends. This is all time taken from you, from our family. We mostly cannot help it and we can only ask for understanding. We are probably not party stars when it comes to our work, and I cannot imagine people with open mouths and jealous expressions when it comes to mentioning our work with carabids; yet we are always willing to talk about them. We hope you understood that neither Konjev, nor Jean-Pierre was odd nor slightly crazy – and hope you believe we are not, either. I hope both of them found time for you as well as carabids, spiders, and work, and that they were appropriate support and good company. Whatever they did in science, at the last count is not so important. If they managed to instill in their children, friends, and family, that life on Earth is wonderful, and studying it is worth spending a life with, then you, or we, cannot ask for more.

In closing this short remembrance, allow me to voice my gratitude that I, that we, have had Jean-Pierre and Konjev in our lives. I would like to thank the organisers for thinking about this remembrance which I feel is appropriate, and thank you for bearing with me. I hope the families of Jean-Pierre and Konjev will find some consolation to know how much we appreciated these two colleagues of ours as scientsts and human beings. May all of us, when the time comes, have left as rich and inspiring a legacy as Konjev and Jean-Pierre did, and be remembered this fondly.

Thank you.

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RESEARCH ARTICLE



Eucamaragnathus desenderi, a new ground beetle species from Africa (Coleoptera, Carabidae)

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Abstract

Eucamaragnathus desenderi **sp. n.**, a new ground beetle species of the tribe Hiletini, is described from eastern and southern Africa and dedicated to the recently deceased Belgian carabidologist Konjev Desender. The new taxon is known so far from localities in Zambia (Mukuku, southeast of Mansa) and in South Africa (Bothaville, south of Klerksdorp). The new species belongs to the *E. castelnaui* group and is characterized by shape of pronotum, smooth or sparsely punctate pronotal transverse impression, characters of male genitalia and elytral striae continued to the apex. Illustrations of the habitus, the median lobe and its internal sac and several other morphological features are presented. An updated identification key to the African *Eucamaragnathus* species is given.

Keywords

Coleoptera, Carabidae, Hiletini, new species, Zambia, South Africa, identification key

Introduction

The pantropically distributed ground beetle tribe Hiletini is only poorly known, mainly because its members are rarely represented in collections. Erwin & Stork (1985) describe in their revision 20 species arrayed in two genera. Since that time no further species have been described.

Consequently we were surprised to find a series of an *Eucamaragnathus* species among other ground beetles caught by the Czech coleopterologists Miroslav Snižek and Vladimír Tichý in southern and eastern Africa. The examination of the material revealed that the specimens belong to a new species. Here we describe the species and dedicate it to our deceased colleague and friend Konjev Desender due to his exceptional engagement in the fields of ground beetle ecology, evolutionary biology and taxonomy.

Material

The material examined is housed in the collections listed below:

- CAM Collection of the Africa Museum, Tervuren, Belgium
- **CAS** Working collection Th. Assmann, Bleckede, Germany (type material will be given to Zoologische Staatssammlung München)
- CFA Working collection Sergio Faccini, Modena, Italy
- CMA Working collection Werner Marggi, Thun, Switzerland
- **CSH** Working collection P. Schnitter, Halle, Germany
- CSS Working collection P. Schüle, Stuttgart, Germany
- **CST** Working collection W. Starke, Warendorf, Germany (type material will be given to Westphalian Museum of Natural History, Münster, Germany)
- CWR Working collection D.W. Wrase, Berlin, Germany

Methods

Measurements were made at a magnification between $12.5 \times \text{and } 50 \times$, using an ocular micrometer in a Leica MZ 95 stereobinocular microscope. The following measurements are used in the description: Total body length is measured from the tip of the mandibles to the apex of the right elytron as the maximum linear distance; the width of the head (HW) as the maximum linear distance across the head, including the compound eyes; the length of the pronotum (PL) from the anterior to the posterior margin along the midline; the length of the elytra (EL) from the basal margin to the apex of the right elytron as the maximum width of the pronotum (PW) and elytra (EW) at their broadest point; the width of the pronotal base (PBW) between the tip of the posterior angles; the width of the pronotal apex (PAW) between the tip of anterior angles.

Microsculpture was examined at a magnification of 100×

Dissections were made using standard techniques; genitalia were preserved in a mixture of polyvinylpyrrolidon, sorbitol and glycerol on acetate labels (Lompe 1989), and pinned beneath the specimens from which they had been removed. The photographs were taken with an Olympus E-330 digital camera in combination with a Leitz MZ 95. Post-processing was done in Adobe Acrobat Professional 7.0. To achieve sufficient depth of focus, up to 20 planes were captured which were copied to separate layers, and the out-of-focus planes were masked by a stacking programme (Combine Z5).

Description

Eucamaragnathus desenderi Assmann, Drees, Matern & Schuldt, sp. n. urn:lsid:zoobank.org:act:7F180D34-C5F8-4D79-AC05-E2F727CAD2E3 http://species-id.net/wiki/Eucamaragnathus_desenderi

Type material: Holotype male: "ZAMBIA NE. 2004 / 240 km SE Mansa / 25 km SE Mukuku / 29.11. Snižek, Tichý" (CAS). Paratypes: 13 males and 8 females, same as holotype (CAS, CFA, CST, CSH, CSS, CWR). 2 males and 4 females: "RSA, NW prov. 2001 / Klerksdorp, 20 km W / of Bothaville, Vaal riv. / M. Snižek lgt. 12.1." (CAS, CWR).

Diagnosis: A macropterous species of average size for the *Eucamaragnathus castelnaui* group, black, pronotum transverse, sides sinuate with posterior angles acute, transverse anterior impression punctulate, transverse posterior impression strongly punctate, elytral striae continued to apex. Habitus see Fig. 1.

Description: Body length 8.8 - 10.6 mm; width 3.6 - 4.0 mm (holotype 10 mm and 3.8 mm, respectively).

Colour: Black, without iridescence, not metallic; mandibels, mouth-parts, antennae, and tarsi partly infuscate.

Head (Figs 1 and 2) large, about one fourth less wide than pronotum (HW: 2.0 – 2.4 mm, holotype: 2.3 mm; ratio HW/PW: 0.75 - 0.78). Eyes fairly large, their diameter (seen in dorsal view) about four tenth of head width; protected posteriorly by lateral extension of the cranium. Antennae robust, scape longer than the following 4 antennomeres, antennomeres 5 - 11 with dense and fairly fine setae. Mesal edge of mandibles markedly serrate (mandible teeth triangular shaped). Two pairs of supraorbital furrows. Frons not punctate, except basal close to pronotal anterior margin.

Pronotum (Fig. 2) transverse (PW: 2.6 - 3.1 mm, holotype: 3.0 mm; PL: 1.9 - 2.2, holotype: 2.0 mm), widest prior to middle (basally of lateral seta). Pronotum at the base broader than at the apex (PAW: 2.2 - 2.6 mm, holotype: 2.5 mm; PBW: 2.3 - 2.8 mm, holotype: 2.7 mm). Anterior margin moderately straight; anterior angles pronounced, but rounded; lateral sides clearly sinuate; posterior angles acute, basal



Figure 1. Eucamaragnathus desenderi sp. n., habitus; holotype.



Figure 2. Eucamaragnathus desenderi sp. n., basal part of head, pronotum, basal part of elytra; holotype.

margin curved. Anterior transverse impression sparsely punctulate; lateral beads deep, not punctate; basal transverse impression deep, markedly punctate and connecting basal foveae; basal foveae deep, punctate and delimited externally by a keel-like carina without punctations.

Legs (Fig. 1) similar to those found in other Hiletini species. Males with small tooth on profemur. Single long guard seta of tarsus 5 much longer than claws. Males with spatulate adhesive setae beneath protarsi 1 - 3 and mesotarsus 1.

Elytra (Figs 1 and 3) with pronounced humeri, slightly enlarged to the end of the second third (EL: 4.8 - 5.9 mm, holotype: 5.75 mm; EW: 3.3 - 3.9 mm, holotype: 3.7 mm). Basal margin reduced, reaching 6th interval. Scutellar striae short; elytral striae deep and punctate, at the apex less impressed, but well visible; intervals flat, at the apex slightly convex. Discal setae of third stria in punctiform depressions.

Surface with microsculpture of irregular and weak mesh patterns, meshes mainly transverse; a clear micropunctation on head, pronotum and elytra (20× magnification); surface shiny.

Male genitalia (Figs 4 and 5). Median lobe with ostium dextral. Both parameres multisetiferous, the setae of the narrow right paramere are longer than those of the broad left one.

Comparisons: Due to form of mandible teeth and long single guard seta of last tarsomere the new species belongs to the genus *Eucamaragnathus* Jeannel, 1937. The small tooth of profemora in males, the dextral position of the ostium of the aedea-



Figure 3. Eucamaragnathus desenderi sp. n., apex of elytra; paratype.

gus and elytral striae continued to the apex place the new species in the *E. castelnaui* (Bocandé, 1849) group (cf. Erwin and Stork 1985) which is exclusively distributed in Africa.

The new species is similar to *E. castelnaui* and *E. fissipennis* (Ancey, 1882). The best character to separate *E. desenderi* sp. n. from the nominate species of the group is the shape of the pronotum and especially the weak punctation of the pronotal anterior impression which is markedly punctate in *E. castelnaui*. In comparison to the other species of the group, *E. desenderi* sp. n. has acute pronotal anterior angles, but they are less produced than in *E. oxygonus* Chaudoir, 1861. Moreover the median lobe, especially its internal sac structures, of *E. desenderi* sp. n. differs from all other species of the group. From *E. fissipennis* the new species can be easily distinguished by stronger punctation of posterior transverse impressions of pronotum (Figs 2 and 6), stronger punctation of elytral striae, which are weaker at the apex, but still well visible (Figs 3 and 7) and a microsculpture with stronger punctation.

From *E. bocandei* (Alluaud, 1914), which forms an own species group, the new species differs by its strong punctation of pronotal posterior impression and from *E. suberbiei* (Alluaud, 1914) it can be separated by the size of tooth on ventral surface of profemur in males.

For better distinction we present an identification key for the known members of the African *Eucamaragnathus* species (see below).

Etymology: It gives us great pleasure to dedicate this species to the memory of Konjev Desender, the well known Belgian carabidologist who recently deceased. We had many scientific meetings, excursions and productive collaborations with him, and we will honor his memory. An obituary is given by Lövei (2011) including a list of his publications.



Figure 4. *Eucamaragnathus desenderi* sp. n., male genitalia, left lateral aspect of median lobe (aedeagus); paratype.



Figure 5. Eucamaragnathus desenderi sp. n., male genitalia, ventral aspect of parameres; paratype.

Distribution: Up to now *E. desenderi* sp. n. is only known from the two sites in Zambia and South Africa. The population from Zambia (close to the border to Congo) lies in the tropical part of Africa fitting well to the main distribution area of the tribe in tropical Africa. In contrast, Bothaville in South Africa, the other site from where *E. desenderi* sp. n. is known, is located between the 27^{th} and 28^{th} degrees of southern latitude, doubtless in the subtropical realm, and seems to be the most southern known



Figure 6. Eucamaragnathus fissipennis, basal part of elytra.

record of a Hiletini species in Africa (and worldwide). The wide distribution of *E. desenderi* sp. n. in Africa is not unusual for a Hiletini species (cf. the large distribution areas of *Hiletus alluaudi* (Jeannel, 1937) and *E. fissipennis*, Erwin and Stork 1985).

Eucamaragnathus desenderi sp. n. seems to co-occur with *E. fissipennis* which is distributed in tropical East Africa and south-eastern Africa. *E. oxygonus* is known only from one locality in South Africa. All other African species of the genus *Eucamaragnathus* show – so far known – an allopatric distribution (*E. suberbiei* is an endemic of Madagascar, *E. castelnaui* and *E. bocandei* occur exclusively in tropical western Africa, Erwin and Stork 1985).

Habitat: The specimens were caught at light and habitat preferences are therefore unknown. Together with the holotype of *E. desenderi* sp. n., a single Hiletini specimen of *Hiletus katanganus* Basilewsky, 1948 has been found. We compared this specimen of the rarely recorded species with the type material preserved in the Africa Museum (collection of Basilewsky) and detected morphological differences. Without more material (especially males) it seems to be impossible to assign specimens conclusively to this species (see also the note in Erwin and Stork 1985: 431).

Key to the African species of Eucamaragnathus Jeannel

This new identification key is based on the one presented by Erwin & Stork (1985), but it is modified and illustrated additionally.



Figure 7. Eucamaragnathus fissipennis, apex of elytra.

_	Elytral striae 1 – 4 continued to apex (Fig. 3)2
2.	Pronotum with basal impression rugosely punctate. From continental Africa 3
_	Pronotum with basal impression smooth, no traces of punctation. From
	MadagascarE. suberbiei (Alluaud, 1914)
3.	Pronotum with anterior angles markedly produced, sides barely sinuate be-
	hind (Fig. 3h in Erwin & Stork 1985) E. oxygonus (Chaudoir, 1861)
_	Pronotum sides sinuate, more or less cordiform
4.	Male with tubercle on sternum VI E. bocandei (Alluaud, 1914)
_	Male without any specific character on sternum VI (except 1 pair of setae)5
5.	Pronotum with anterior transverse impression markedly punctate, puncta-
	tion similar to that of the posterior transverse impression of pronotum
	<i>E. castelnaui</i> (Bocandé, 1849)
_	Pronotum with anterior transverse impression with only few punctures,
	punctuation less strong than on the posterior transverse impression of prono-
	tum

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RESEARCH ARTICLE



Calleida desenderi, new species from Ecuador (Coleoptera, Carabidae, Lebiinae)

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Abstract

Calleida desenderi Casale, **sp. n.**, is described from Ecuador, Napo Province, surroundings of San Rafael. The new taxon is mostly characterized by the head and appendages rufous, the disc of elytra with marked metallic green reflection, the median lobe of aedeagus ring-like, and the endophallus with a long, twisted flagellum. A key for identification of the closer Neotropical species described so far is also provided.

Keywords

Coleoptera, Carabidae, Calleida desenderi, new species, Ecuador

Introduction

As I recently noted (Casale, 2008), Ecuador, in spite of its small surface area (283,561 square kms), is a South American country that includes a surprising variety of environments. Thanks to its geographical position crossed by the Equator, the occurrence of some of the highest peaks of Southern America, and the presence of tropical rain and cloud forests on both the Pacific and Amazon sides of the Andes, Ecuador is currently cited as one of the main hot-spots of biodiversity and endemism in the world, but also

as one of the areas more threatened by deforestation. However, its mainland insect fauna, with some exceptions (see Moret, 2005), is little known at present. Amongst carabid beetles, the genus *Calleida* Dejean 1825 (in the widest sense of Chaudoir, 1972), including nice, arboreal species mostly tied to wet forests, can be cited as a good example of scarce knowledge.

On the contrary, the Galapagos islands and their biodiversity offer a fantastic place for any student familiar with evolutionary biology, and have been investigated for many decades. Several contributions from these investigations include beetles (for a synopsis see Peck, 2006).

Konjev Desender and Jean Pierre Maelfait contributed greatly to the knowledge of the arthropod fauna of the Galapagos Islands: thanks to many travels, they had the opportunity to produce a series of highly interesting scientific contributions dedicated to this archipelago (see Lövei, 2011 for a list of Konjev's publications).

Thanks to Konjev, I had the opportunity to describe the only *Calleida* species known so far in Galapagos (*Calleida migratoria* Casale in Desender et al., 2002), a species introduced from Peru and now widely spread on several islands. Therefore, this is for me an honour – but also a great sadness - to dedicate to him this paper, and a very fine and interesting *Calleida* species from Ecuador, in memory of pleasant days spent with him in congresses, in the field, and at his Institute in Brussels.

Material and methods

The following data come from many specimens of Neotropical *Calleida* species examined so far (including type series), most of them received from different museums, institutes and colleagues. The type material of the new species here described has been offered to me for study by my good friend Giovanni Onore, former professor of Entomology at the Pontificia Universidad Catolica del Ecuador in Quito.

Male genitalia were dissected, dehydrated in ethanol, cleared in cold KOH, examined and illustrated, using standard techniques before their definitive inclusion on microscope slides. Line drawings were made using a camera lucida attached to stereomicroscopes Wild M-3 and Wild M-5, and a microscope Leitz Orthoplan. The photograph of habitus was obtained using a digital camera Canon G6 attached to stereomicroscope Zeiss Stemi 2000.

Acronyms:

- TL body Total Length, from the anterior margin of clypeus to the apex of elytra, measured along the suture.
- L overall Length, from apex of mandibles to apex of elytra, measured along the suture.
- **PL/PW** ratio Length of Pronotum, as linear distance from the anterior to the basal margin, measured along the midline/maximum Width of Pronotum, as greatest transverse distance.

EL/EW ratio Length of Elytra, as linear distance from the basal ridge to the apex, measured along the suture/maximum Width of Elytra.

Collections:

- **QCAZ** Zoology Museum, Departamento de Biologia, Pontificia Universidad Catolica del Ecuador, Quito (Ecuador)
- CCa Casale collection, University of Sassari (Italy)

Taxonomic treatment and morphological terms

In this contribution, the genus *Calleida* is treated in the narrow sense, i.e. as a unit including only American species, and excluding African and Asiatic taxa (*Callidiola* Jeannel, 1949, *Stenocallida* Jeannel, 1949, of authors), currently treated at subgeneric rank of *Calleida* (see, among others: Lorenz, 2005). In spite of this choice, the limits of these generic groups are not yet defined.

The median lobe of aedeagus is a synonym of phallus of some authors. Endophallus is synonym of inner sac of authors.

Calleida desenderi Casale, sp. n.

urn:lsid:zoobank.org:act:D9A8E5CC-04AB-4F26-AB9E-BAB0216BD3F8 http://species-id.net/wiki/Calleida_desenderi

Diagnosis. With the character states of the Neotropical *Calleida* species (see Erwin, 2004), but markedly characterised by the peculiar combination of the following morphological features: medium sized (L: 9.0–9.5 mm; TL: 8.5–9.0 mm); body and appendages rufous, contrasting in colour with the translucent, metallic green disc of elytra; pronotum slightly transverse, with lateral margins slightly sinuate in the basal fourth; elytra moderately elongate, depressed, with marked pre-apical callosity and apical margin not beaded, bent and prominent at the sutural angle. Abdominal sternum VII with two setae on each side in males, three setae in females.

Male genitalia as in Figs 3–5: median lobe of aedeagus ring-like, depressed at sides; apex short; endophallus with a long, twisted flagellum.

Close to *C. scyntillans* Bates, 1883 and *C. schumacheri* Steinheil, 1875, *C. desenderi* sp. n. is distinguishable from the closest Neotropical species for the features stressed below (see Key, in Relationships).

Type locality. Ecuador, Napo: San Rafael, 1400 m.

Type material. Holotype ♂: Ecuador, Napo: Reventador, San Rafael 1400 m, 10 Jan 1998 F. Maza, at light trap (QCAZ); paratype ♀: Ecuador, Sucumbios, Cascada San Rafael, 1150 m, 77°33'30"W 00°2'44"S, 30 Apr 2004, D. Cisneros (CCa).

Note: the male holotype presents some malformations (elytral intervals wrinkled, metatibiae asymmetrically curved). For this very reason, the female paratype is illustrated in Fig. 1.



Figure 1. Calleida desenderi sp. n., female paratype, habitus, dorsal aspect.

Etymology and dedication. It is a great honor for me to dedicate this new Ecuadorian species to the memory of Konjev Desender, the Belgian carabidologist who contributed greatly to the knowledge of carabids of the Galapagos Islands, the famous archipelago belonging to the Republic of Ecuador

Description. General features as in Fig. 1. Medium sized: L: 9.0 mm (male holotype) – 9.5 mm (female paratype); TL: mm 8.5 mm (male holotype) – 9.0 mm (female paratype).

Colour: Head, base of antennae, prothorax, pterothorax, abdomen, basal and lateral margins of elytra, and legs, concolorous pale rufous; apex of mandibles, apical half of antennomere 4, and antennomeres 5–11 markedly infuscated; disc of elytra translucent, light metallic golden green (but reddish at oblique light), with cupreous-purple reflections at apex and on the sutural interval.



Figures 2–5. *Calleida desenderi* sp. n., male holotype **2** abdominal segment IX, ring sclerite **3** male genitalia, median lobe of aedeagus and inner sac, dorsal-right aspect **4** male genitalia, median lobe of aedeagus and inner sac, lateral left aspect **5** male genitalia, left paramere.

Lustre and microsculpure: Head and pronotum shiny, with highly effaced microsculpture; elytra shiny, translucent, with fine, hardly visible reticulate sculpture and marked metallic lustre.

Head: wide, with moderate neck constriction; genae short, moderately swollen and regularly curved to the neck constriction, not contiguous with the posterior margin of eyes; frontal furrows sparsely punctuate; eyes very large and prominent; two supraorbital setae on each side.

Prothorax: subquadrate, slightly wider than long (ratio PL/PW: 0.9), with lateral sides shortly sinuate in the basal fourth. Lateral reflection moderate, more evident basally; lateral furrows wide, depressed, each with a series of deep punctures. Disc moderately depressed, with marked transversal wrinkles. Anterior angles rounded, not prominent; basal angles obtuse. Basal margin markedly oblique at the extreme lateral sides. One paramedial seta and one basolateral seta on each side present.

Elytra: moderately elongate (ratio EL/EW: 1.7), slightly widened at the apical third; disc depressed, with evident concavity at the middle on each elytron; striae superficial, shallowly punctuate; intervals flat. Post-humeral sinuation shallow, pre-apical outer callosity evident on intervals 7–8. Apical margin obliquely bent, markedly prominent at the sutural angle, not beaded. Interval 3 with two small discal and one apical setiferous pores; umbilicate series of 13 pores along stria 8.

Hind wings: fully developed.

Legs: femora robust, tibiae elongate, tarsomeres of slender form; only metatarsomere 1 grooved dorsally; metatarsomere 4 deeply bilobed, its lobes short, widened and truncate at apex. Tarsal claws denticulate, each with six long teeth on the inner side.

Abdominal sterna: sternum VII with two setae on each side in males, three setae in females; male abdominal segment IX as in Fig. 2.

Male genitalia: median lobe of aedeagus (Figs 3–4) ring-like, depressed at sides; apex short, distally rounded; endophallus with a long, twisted flagellum. Left paramere as in Fig. 5.

Female genitalia: not examined, owing to the fact that the abdominal sterna, in the only female specimen known so far, were not fully sclerotized.

Geographical distribution and ecology. *C. desenderi* sp. n. is known so far from Ecuador (Napo Province), surroundings of San Rafael, on the Amazon side of the Andes. The two specimens of the type series were obtained in January and April, in two different years, in secondary humid premontane forests at 1150–1400 m.

Relationships. The most interesting and curious fact is that *C. desenderi* sp. n. is very similar in external features to the sympatric species *C. vignai* Casale, 2008, this also known so far from only two individuals sampled in two different years. This datum confirms the well known occurrence, in arboreal canopies of tropical forests, of apparently rare sibling species belonging to different species groups, markedly isolated by pre-zygotic barriers thanks to different phenologies, habitat choices, and by completely different morphological features in genitalia.

In fact, *C. vignai*, for the character state of male genitalia (median lobe of aedeagus elongate and slender, endophallus with copulatory lamella composed by two pieces connected at the base), belongs to a group of taxa that I indicated as *lindigii* species group (Casale, 1998, 2008).

On the contrary, *C. desenderi* sp. n. belongs to another group of Neotropical species, that here I will indicate as *cupreocincta* species group. Diagnostic features of this group are: body and appendages rufous, elytra in part or fully metallic green; elytra moderately elongate, depressed, with apical margin not beaded. Abdominal sternum VII with two setae on each side in males, three setae in females. Male genitalia: median lobe of aedeagus ring-like, depressed at sides; endophallus with a long, twisted flagellum.

The group includes some not yet described species from Central and Southern America. The species described so far can be distinguished by the following key:

1 Genae markedly swollen, abruptly constricted to the neck. Elytral disc mostly dark rufous, with metallic green reflection only at base and on outer intervals 7-9. Elytral pre-apical callosity slightly distinct. Metatarsomeres 1-3 deeply grooved dorsally. Range: Brazil, Atlantic coast (Pernambuco, Rio de Janeiro)... C. cupreocincta Chaudoir, 1848 Genae swollen but regularly curved, not abruptly constricted to the neck. Elytral disc with metallic reflection extended to all intervals. Elytral pre-apical callosity markedly distinct on intervals 7-8. Metatarsomere 3 not grooved dorsally.....2 2 Pronotum elongate, constricted in front. Elytral disc with marked metallic green reflection, but with distinct reddish patch on the inner intervals, more evident at oblique light. Metatarsomeres 1-2 superficially grooved dorsally. Range: Central America (Panama) C. scyntillans Bates, 1883 Pronotum subquadrate or slightly transverse. Elytral disc fully metallic green Apical half of antennomere 1, and following antennomeres, markedly infus-3 cated. Apical margin and sutural interval of elytra with metallic cupreous-Antennae fully rufous. Sutural interval of elytra bright metallic green; apical margin of elytra yellow reddish, as the base and lateral margins. Range: Co-

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REVIEW ARTICLE



Forty years of carabid beetle research in Europe – from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation

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Abstract

'Carabidologists do it all' (Niemelä 1996a) is a phrase with which most European carabidologists are familiar. Indeed, during the last half a century, professional and amateur entomologists have contributed enormously to our understanding of the basic biology of carabid beetles. The success of the field is in no small part due to regular European Carabidologists' Meetings, which started in 1969 in Wijster, the Netherlands, with the 14th meeting again held in the Netherlands in 2009, celebrating the 40th anniversary of the first meeting and 50 years of long-term research in the Dwingelderveld. This paper offers a subjective summary of some of the major developments in carabidology since the 1960s. Taxonomy of the family Carabidae is now reasonably established, and the application of modern taxonomic tools has brought up several surprises like elsewhere in the animal kingdom. Progress has been made on the ultimate and proximate factors of seasonality and timing of reproduction, which only exceptionally show non-seasonality. Triggers can be linked to evolutionary events and plausibly explained by the "taxon cycle" theory. Fairly little is still known about certain feeding preferences, including granivory and ants, as well as unique life history strategies, such as ectoparasitism and predation on higher taxa. The study of carabids has been instrumental in developing metapopulation theory (even if it was termed differently). Dispersal is one of the areas intensively studied, and results show an intricate interaction between walking and flying as the major mechanisms. The ecological study of carabids is still hampered by some unresolved questions about sampling and data evaluation. It is recognised that knowledge is uneven, especially concerning larvae and species in tropical areas. By their abundance and wide distribution, carabid beetles can be useful in population studies, bioindication, conservation biology and landscape ecology. Indeed, 40 years of carabidological research have provided so much data and insights, that among insects - and arguably most other terrestrial organisms - carabid beetles are one of the most worthwhile model groups for biological studies.

Keywords

Carabidae, ground beetle, systematics, biology, life history, rhythms, seed feeding, ant feeding, ectoparasitism, predation on amphibians, dispersal, pitfall trapping, statistics, population dynamics, long-term research, bioindicators, conservation, habitat management, landscape ecology

Contents

1	Introduction	57
1.1.	General	57
1.2.	Basic knowledge	58
1.3.	European Carabidologists' Meetings (ECMs)	61
2	Systematics, phylogeny and evolution	65
2.1.	Overview	65
2.2.	General outline on systematics and phylogeny of the Carabidae	66
2.3.	Within-species diversity	66
2.4.	Species borders and hybridisation	67
2.5.	Speciation, radiation and biogeography	68
2.6.	Phylogeny based on different types of characters	70
3	Biology	74
3.1.	Life history strategies and rhythms	74
3.2.	Carabid beetle food	79
3.3.	Dispersal	84
4	Methods	87
4.1.	Methodological approaches	87
4.2.	Analysing pitfall-trapped carabid data	88
5	Population dynamics and long-term research	92
6	Bioindicators	95
7	Carabid conservation, protection and habitat management	97
8	Landscape ecology	103
9	Concluding remarks	109

I Introduction

1.1. General

Carabid beetles are one of the best-known taxa in entomology. These beetles have been studied intensively by generations of coleopterists, who have clarified the taxonomy and phylogeny, geographic distribution, habitat associations and ecological requirements, life history strategies and adaptations, especially in Europe (e.g. Holdhaus and Lindroth 1939; Palmén 1944; Lindroth 1945a, b, 1949; Thiele 1977; Ball 1979; Desender 1986, Desender et al. 1994a; Turin 2000; Luff 2007).

This wealth of basic information has fostered a plethora of quantitative ecological studies. Indeed, the first European Carabidologists' Meeting in Wijster, the Netherlands in 1969, touched upon one of the fascinating characteristics of carabid beetles – dispersal and dispersal power (Den Boer 1971). As a life history trait, dispersal has profound consequences for the dynamics and persistence of populations, the distribution and abundance of species and for community structure (Dieckmann et al. 1999).

Not surprisingly, a summary based on the 3rd International Carabidologists' Meeting emphasised the role of dispersal in increasingly fragmented landscapes, and argued that much more knowledge on the effects of habitat loss and fragmentation on carabid beetle population dynamics is needed if sensible decisions are to be made regarding conservation and land-use (Thacker 1996).

But why study carabid beetles? The reasons are diverse: relatively stable taxonomy, high species richness, occurrence in most terrestrial environments and geographical areas, the availability of easy collection methods, known sensitivity to environmental changes, and perceived role as beneficial in agriculture (see Darlington 1943; Lövei and Sunderland 1996; Rainio and Niemelä 2003). Armed with such a diverse wealth of knowledge, many ecologists and taxonomists have turned to carabid beetles to test ecological research questions. In this paper we emphasise progress in some of the major fields in carabidology since the first European Carabidologists' Meeting, 40 years ago.

1.2. Basic knowledge

Modern disciplines in carabid beetle ecology, such as bioindication, conservation and habitat management, landscape ecology and urban ecology rely heavily on the work done by professional and amateur carabidologists from the more traditional fields of natural history, systematics and taxonomy. This species-rich family occurs in most terrestrial habitats and is found in the vegetation as well as high up in the trees and the canopy, not only in the tropics (Arndt 2005). This is probably the main reason why carabids are relatively well represented in collections around the world. In many regions, information on labels from these collections has been gathered in large databases. Combined with data from systematic sampling, such datasets enable profound faunistic work. These databases are increasingly elaborated and published as annotated checklists, red lists, catalogues and/or atlases. In combination with a clear taxonomy, mainly identification literature, these provide a sound basis for biogeographical, biological, ecological and experimental studies. Table 1 shows an overview of the major publications for the European continent, which is covered well, although there is clearly need for updating in a few regions, mainly in the east (Romania, Hungary, Russia, Caucasus). In some cases, older works are mentioned in Table 1, which belong to antiquity and do not adequately cover the fauna of that region anymore (e.g. Ganglbauer 1892; Apfelbeck 1904; Porta 1923-1959). These older works are hardly in use for identification anymore. However, they still provide historical bases for modern identification works, which often have to be elaborated from numerous smaller keys or large revisions (e.g. Jeannel 1926-28; Breuning 1932-37), such as the keys to the Carabinae (Casale et al. 1982) and to the supraspecific taxa of Italy (Casale 2005).

A sound basic list of the Carabidae of the world is the recent checklist published by Lorenz (2005) and a catalogue with distributional data is available for the Palaearctic

region as a whole (Löbl and Smetana 2003). Furthermore, many recent checklists and catalogues are available (concerning Europe, see some examples in Table 1). In particular, Kryzhanovskij et al. (1995) provided detailed information on the carabid fauna of Russia and adjacent countries (including central-Asiatic). In the Western Hemisphere (the Americas), detailed information is available, especially for the regions north of Mexico (Lindroth 1961–1969; Ball and Bousquet 2001; Larochelle and Larivière 2003; Erwin 2007; Erwin and Pearson 2008), or will soon be (Erwin in preparation), but in many tropical areas of Central and South America, many genera and species remain undescribed. Other geographical areas are less well known. Asia, as a huge continent is relatively well-known in some parts, such as Siberia, Near and Middle East and especially Japan (e.g. Habu 1967, 1973, 1978), whereas immense areas are a "work in progress" (China, The Himalayas and South-East Asia). Africa is well-known in some northern countries, in particular Morocco, Algeria and Tunisia, thanks to the contributions of specialists like Antoine (1955–1962), Bedel (1899–1900) and Kocher (1963). Nevertheless, in spite of the numerous papers published by Alluaud, Basilewsky, Jeannel and others, the sub-Saharan (tropical) part of the continent needs more investigation. Australia, thanks to the C.S.I.R.O. has one of the best-organised services of insect collections, and is covered by catalogues and revisions, of which we highlight the catalogue by Lawrence et al. (1987). But also, recent investigations allowed the discovery of many new genera and species, including impressive, large sized Pamborus species.

Finally, remote islands and archipelagos such as like Madagascar, Papua-New Guinea and Galápagos, for instance, have been carefully investigated by specialists like Jeannel, Darlington and Desender, respectively, but produce many new discoveries every year.

In the world catalogues of Lorenz (1998, 2005) more than 35 000 ground beetle species have been listed. An estimated number of 40 000 species, which is more than 10 times the number of described mammals, has often been mentioned (Thiele 1977; Noonan 1985). Currently, approximately 38 600 valid names occur worldwide (based on Lorenz 2005 and an estimate of approximately 100 additional new species every year). For the Western Hemisphere only, the species count currently stands at 9 374 (Terry Erwin in litt.).

More in line with the meetings are a number of thematic treatments, but again the listed works are only examples. For a more complete and thematically arranged overview of significant work in carabidology, we refer to the excellent introduction to the proceedings of the Symposium on Phylogeny and Classification of Caraboidea by Ball et al. (1998). Worth mentioning for European carabidology are the publications of the German "Gesellschaft für Angewandte Carabidologie" (GAC) with special reference to habitat studies, such as carabid beetles in river meadow habitats (GAC 1999), in forests (GAC 2001) and in xerothermic habitats (GAC 2004). The GAC provides many carabidological papers in open access (see http://www.laufkaefer.de/gac). Other published thematic studies, often including compilations of numerous papers from various authors, concern, amongst others: biotopes (Heydemann 1962; Schjøtz-Christensen 1965), larvae (Brandmayr and Zetto Brandmayr 1982; Arndt 1991; Luff 1993), biol-

Country	Identification literature	Checklist/Catalogue	Atlas
Albania	Apfelbeck 1904	Guéorguiev 2007	
Austria	Müller-Motzfeld 2004	Mandl 1972, 1978; Müller- Motzfeld 2004	
Baltic	Haberman 1968; Müller- Motzfeld 2004	Haberman 1968; Barsevskis 2003; Alexandrovitch et al. 1996	Haberman 1968
Belgium/	Boeken et al. 2002; Müller-	Desender et al. 1995; 2008b	Desender et al. 2008a
Luxem- bourg	Motzfeld 2004; Muilwijk et al. (In prep.)		
Bulgaria	Apfelbeck 1904	Hieke and Wrase 1988; Guéor-	
		guiev and Guéorguiev1995; Guéorguiev et al. 1997	
Caucasus	lablokov-Khnzorian 1976	Krvzhanovskij et al. 1995	
Czech	Reitter 1908: Kult 1947: Hurka	Hurka 1996, Müller-Motzfeld	Skoupý 2004
Republic/ Slovakia	1996	2004	
Denmark	Hansen 1968; Müller-Motzfeld 2004	Bangsholt 1983	Bangsholt 1983
Fen- noscandia	Lindroth 1985-1986	Lindroth 1945a, 1960, 1985-86; Strand 1970	Lindroth 1945b
France	Jeannel 1941-1942, 1949; Forel	Jeannel 1941-1942, 1949; Forel	Coulon et al. 2000; Forel and
	and Leplat 1995, 2001, 2003, 2005	and Leplat 1995, 2001, 2003, 2005	Leplat 1995, 2001, 2003, 2005; Callot and Schott 1993
Germany	Reitter 1908; Müller-Motzfeld 2004; Wachmann et al. 1995	Müller-Motzfeld 2004	Gebert 2006
Great Britain	Luff 2007	Hyman and Parsons 1992; Luff 2007	Luff 1998
Greece	Apfelbeck 1904; Arndt et al. (in press)	Arndt et al. (in press)	
Hungary	Csiki 1946	Csiki 1946	
Iberia	Forel and Leplat 1998; Herrera and Arricibita 1990; Machado 1992 (Canary Islands); Ortuño and Tarihia 2005	Herrera and Arricibita 1990; Zaballos and Jeanne 1994; Serrano 2003; Machado 1992 (Canary	Herrera and Arricibita 1990; Ortuño and Toribio 2005
Iceland	Lindroth 1985, 1986; Luff 2007	Lindroth 1931; Larsson and Gigja	
Ireland	Anderson et al. 2000 Porta	Anderson et al. 2000 Luigioni	Anderson et al. 2000 Casale et
Italy	1923-1959; Casale et al. 1982; Casale 2005	1929; Magistretti 1965; Vigna Taglianti 1993, 2005	al. 1982, 2007; CK Map 2006
Moldova/ Romania	Csiki 1946	Kryzhanovskij et al. 1995; Necu- liseanu and Matalin 2000	
The Neth- erlands	Boeken et al. 2002	Brakman 1966; Turin 2000; Muilwijk and Felix 2010	Turin 2000
Poland	Müller-Motzfeld 2004	Burakowski et al. 1973-1974; Müller-Motzfeld 2004	
Russia/ Belarus	Kryzhanovskij 1983	Kryzhanovskij et al. 1995; Alexan- drovitch et al. 1996	
Switzer- land	Müller-Motzfeld 2004	Marggi 1992; Müller-Motzfeld 2004; Luka et al. 2009	Marggi 1992; Luka et al. 2009
Ukraine	Kryzhanovskij 1983	Kryzhanovskij et al. 1995; Putch- kov 2011	
Former Yugoslavia	Apfelbeck 1904	Drovenik 1999	
Europe, general	Ganglbauer 1892; Du Chatenet 1986; Trautner and Geigenmül- ler 1987; Eurocarabidae: http:// www.eurocarabidae.de	Turin 1981; Kryhanovskij et al. 1995; Löbl and Smetana 2003; Fauna Europea: http://www. faunaeur.org	European maps: Du Chatenet 1986 (189 European species); Turin 2000 (380 Dutch spe- cies), Turin et al. 2003 (<i>Cara- bus</i> : 135 species); Fauna Euro- pea; http://www.faunaeur.org

Table 1. Overview of publications concerning the faunistics of ground beetles in Europe.
ogy and periodicity (Larsson 1939), agroecology (Holland 2002), biogeography (Ball 1985; Noonan et al. 1992), dispersal ecology (Palmén 1944; Den Boer 1977; Baars 1982; Desender 1989b; Aukema 1995), morphology (Sharova 1981; Deuve 1993) and phylogeny (Ball et al. 1998). This listing is not exhaustive, especially in the fields of genetics and molecular biology, which are growing rapidly. We conclude with the classical works *Die Fennoskandischen Carabidae* (Lindroth 1945a, b, 1949, re-published in English as Lindroth 1988, 1992a, b) and *Carabid beetles in their environments* (Thiele 1977). These inspired many carabidologists and have been, for many students, the starting point of their enthusiasm.

1.3. European Carabidologists' Meetings (ECMs)

In 1959, Piet den Boer, a zoologist at the Biological Station in Wijster, started pitfall trapping at several locations in the Dwingelderveld, a large area of heathland. His purpose was to test the model proposed by Andrewartha and Birch (1954), in which animal populations could be thought of as sets of smaller local populations which periodically become extinct, their sites being subsequently reoccupied. This became known (and fashionable) under the term "metapopulation" (Levins 1970). By using carabid beetles as test organisms, Den Boer was able to show that in a large area many local populations or interacting groups fluctuate in numbers of individuals in space and time, developing his theory of 'spreading of risk' (Den Boer 1968). According to this theory, species occupying large areas survive more easily because the reproductive success of each separate (but interacting) group differs at different places. Dispersal between these interacting groups stabilises the number of individuals in the whole population through time. Local extinctions may occur but the chances of extinction of the entire population are minimised (Den Boer 1970). Den Boer eagerly wanted to discuss this topic with other carabid beetle specialists, in particular with Carl Lindroth from Sweden, who studied the significance of dispersal and Hans-Ulrich Thiele from Germany, who studied the reproduction of these animals. Consequently in 1969, a number of eminent European carabidologists were invited to Wijster. This select group of researchers focused on the topic of dispersal and the dispersal power of carabid beetles (Fig. 1a). In 1973, Thiele invited a number of carabidologists to Rees-Grietherbush, a field station of the University of Cologne. This second ECM appeared to be an informal one and no proceedings volume was published. However, it resulted in the organisation of a now official third ECM, also at Rees-Grietherbush, by Thiele and his colleague Friedrich Weber in 1978. Most participants were German or Dutch, though Pietro Brandmayr from Italy was also present. The proceedings entitled 'On the evolution and behaviour of carabid beetles' was dedicated to Lindroth, who passed away in early 1979. In 1981, Weber took the initiative and organised the fourth ECM at Haus Rothenberge (Münster), on the theme 'The synthesis of field study and laboratory experiments'. Thiele presented a lecture but his contribution for



Figure 1a. Participants of the first European Carabidologist Meeting in Wijster, 1969. From left to right: Vlijm, Van der Aart, Lindroth, Stein, Wijmans, Hengeveld, Palmén, Van Dijk, Richter, Venema, Mook, Thiele, Tjallingii, Den Boer, Haeck, Neumann, Meijer.

the proceedings was never received. The proceedings, dedicated to Thiele, was published after his death in 1983.

The first four meetings were followed by meetings organised across Europe (Table 2). As a result of political changes in Eastern Europe since the 1990s, the ECMs attained a more 'complete' European character. Not only did it become easier for scientists from Eastern Europe to attend these meetings, they also started to organise them. Even more noticeably during recent decades, carabidologists from beyond Europe regularly started to participate in the ECMs. Besides the official ECMs, there have been a few separate carabid beetle meetings in Europe (Table 2). Two of these (Hamburg in 1984 and Kauniainen in 1995) were not official ECM meetings, though they were mainly attended by the same carabidologists who regularly attend ECMs. The fourteen proceedings from the major ground beetle meetings that have been published before the present volume (see Fig. 1b-c, Table 2), comprise together more than 400 articles covering a wide range of topics. A rough classification of the articles leads to the following summary: Habitat preference, community ecology was the topic of 84 papers, Biology (development, preferences, etc.) of 55, Population biology - 46, Nature conservation - 35, Agro-ecology - 34, Dispersal ecology - 33, Evolutionary biology, phylogeny - 22, Morphology - 15, Ecology, general - 13, Genetics - 13, Biogeography - 11, Taxonomy - 11, Method-development - 10, Rest - 10, Faunistics - 9, and Palaeontology - 2. A similar series of meetings and proceedings started in America with the publication of the First International Symposium of Carabidology (Erwin et al. 1979). In 1999, a volume consisting mainly of taxonomic papers was published, dedicated to the memory of Oleg L. Kryzhanovskij (Zamotailov and Sciaky 1999).



Figure 1b. Front covers of the first European meetings, ECM 1–8 and that of Hamburg 1984 (centre cover) (see also Table 2).



Figure LC. Front covers of the last five ECMs and of a few major carabidology publications (Thiele 1977; Ball et al. 1998; Erwin et al. 1979; Noonan et al. 1992) (see also Table 2).

Year	Location	Proceedings
1969	Wijster, The Netherlands (ECM 1)	1971. Dispersal and dispersal power of carabid beetles
		(Den Boer)
1973	Rees-Grietherbush, Germany (ECM 2)	None
1978	Rees-Grietherbush, Germany (ECM 3)	1979. On the evolution of behaviour in carabid
		beetles (Den Boer et al.)
1981	Münster, Germany (ECM 4)	1983. The synthesis of field study and laboratory
		experiments (Brandmayr et al.)
1982	Stara Brda Pilska, Poland(ECM 5)	1986a. Feeding behaviour and accessibility of food for
		carabid beetles (Den Boer et al.)
1984	Hamburg, Germany (17 th International	1986b. Carabid beetles, their adaptations and dynam-
	Entomological Congress)	ics (Den Boer et al.)
1986	Balatonalmadi, Hungary (ECM 6)	1987. Proceedings of the 6 th ECM (Den Boer et al.)
1989	London, United Kingdom (ECM 7)	1990. The role of ground beetles in ecological and
		environmental studies (Stork)
1992	Louvain la Neuve, Belgium (ECM 8)	1994a. Carabid beetles, ecology and evolution (De-
		sender et al.)
1995	Kauniainen, Finland (3 rd International	1996b. Population biology and conservation of cara-
	Carabidology Congress)	bid beetles (Niemelä)
1998	Camigliatello, Italy (ECM 9)	2000. Natural history and applied ecology of carabid
		beetles (Brandmayr et al.)
2001	Tuczno, Poland (ECM 10)	2002. How to protect or what we know about carabid
	9	beetles (Szyszko et al.)
2003	Arhus, Denmark (ECM 11)	2005. European Carabidology 2003 (Lövei and Toft)
2005	Murcia, Spain (ECM 12)	2006. Proceedings of the XII ECM; ground beetles
		as a key group for biodiversity conservation studies in
		Europe (Serrano et al.)
2007	Blagoevgrad, Bulgaria (ECM 13)	2008. Back to the roots and back to the future.
		Towards a new synthesis between taxonomic, ecologi-
		cal and biogeographical approaches in carabidology
		(Penev et al.)
2009	Westerbork, Netherlands (ECM 14)	2011. Present volume (Kotze et al.)

Table 2. The year, location, title and editors of all the European Carabidologists' Meetings.

In 2009, the 14th ECM returned to the starting grounds in the Netherlands and was attended by five participants of the first ECM: Piet den Boer, Jaap Haeck, Rob Hengeveld, Jan Meijer and Theo van Dijk. The participants visited the permanent sampling plots in the Dwingelderveld and Mantingerveld, started 50 years earlier.

2. Systematics, phylogeny and evolution

2.1. Overview

Regular carabidologists' meetings have contributed significantly to our understanding of carabid phylogeny, evolution and systematics, as evidenced by the presentation of more than 60 papers on these topics. Progress has been made at different taxonomic ranks and in different fields of carabid systematics. At present, the integrative approach of combining morphology, molecular systematics, ethology, ecology, geographic distribution, etc., as well as the use of bioinformatics, is recognised as the best framework for solving the challenges still faced by carabidologists (Assmann et al. 2008), and by animal taxonomists in general.

What follows is a short overview of recent advances in carabid beetle systematics, concentrating on literature presented at ECMs and the international congresses mentioned above. As the main aim of this section is to present a general overview, only some of the main papers with a wide scope are cited.

2.2. General outline on systematics and phylogeny of the Carabidae

Ball (1979) showed that the classification of Carabidae is mostly based on morphological characters and that it includes both clade-based and grade-based criteria; classifications differ depending on the importance given to one or the other criterion. After this seminal revision, few advances have been made to unify the criteria to elect Caraboidea (splitters) or Carabidae (lumpers), and the same holds true for other high-ranked taxa. A practical synthesis of these ideas was presented by Nagel (1979a), while Ball et al. (1998) and Assmann et al. (2008) revised the issue in depth. These two last-mentioned papers highlighted the need for an integrative approach to morphology, morphometrics and molecular systematics as the appropriate way of finding rapid solutions for challenging problems.

2.3. Within-species diversity

An electrophoretic study on 14 Pyrenean populations of *Carabus punctatoauratus* (Assmann 1990) revealed that the Pyrenees probably hosts an isolated relict population for this species, and that bottlenecks have affected western, central and eastern populations differentially. Subtle differences at a micro-geographic scale have also been shaped by small bottleneck phenomena in this species with low dispersal power.

Range expansion of *Carabus auronitens* during the 19th century has allowed gene flow between populations in the surroundings of Münster, Germany, as evidenced by an electrophoretic study of 19 populations that showed a steep gradient of slow and fast alleles (Terlutter 1990). The high dispersal power of this species accounts for the observed allelic gradient (esterase-encoding gene) from source areas to recently colonised areas (Niehues et al. 1996). Assmann et al. (1994) showed that present-day populations of this species originated from three major refuges in southern France and that these putative core populations have contributed differentially to postglacial range expansion of the species.

Ashworth (1996) showed that Quaternary climatic oscillations did not lead to enhanced rates of extinction and speciation in carabids, as inferred from ¹⁴C-dated fos-

sil assemblages. The future responses of Carabidae to climate change will probably be similar to that of the past, with the exception that extinction rates are expected to be higher because of human-caused habitat fragmentation.

Rasplus et al. (2000) found that populations of the threatened species *Carabus solieri* consist of two distinct clusters corresponding to subspecies *bonnetianus* and *solieri*. These populations were probably isolated during the last glaciation and are worthy of protection as gene flow is restricted between these two groups. Moreover, molecular markers suggest that the subspecies *curtii* is a hybrid between *bonnetianus* and *solieri*.

Desender et al. (2000) investigated the genetic diversity and wing polymorphism of the salt-marsh beetle *Pogonus chalceus* in 30 populations from the Atlantic coast and nine populations from the Mediterranean Basin. These Mediterranean populations showed little differentiation associated with high dispersal power, a finding possibly related to habitat instability. A higher structuring was found in Atlantic populations, which showed varying degrees of wing polymorphism and dispersal power, possibly related to adaptation to particular conditions.

Kamer et al. (2008) investigated variation in the 12S RNA sequence in populations at different geographic scales, namely the Baltic coast, inland populations across Central Europe, and Central plus Western Europe. Population structure varied as a result of complex factors that include past history and present dispersal power, amongst others. Cryptic taxa or a lack of molecular differences among siblings were also found, showing the usefulness of landscape genetic analyses.

2.4. Species borders and hybridisation

Koch (1986) showed that *Pterostichus nigrita* and its sibling *P. rhaeticus* are distinct species according to habitat preferences, subtle details in male and female genitalia and karyotypic numbers. Both species are reproductively isolated, as shown by cross-breeding laboratory experiments. More recently, Angus et al. (2008) described a new cryptic species in the Iberian Peninsula, *P. carri*, and a new subspecies of *P. nigrita* from Anatolia. All taxa shared a basic 2n = 36 + X male karyotype, whereas marked variation in the number of accessory chromosomes was found within and between these taxa.

Vogler and DeSalle (1994) analysed the relationships of 17 populations of *Cicindela dorsalis* along a littoral transect from New England to Veracruz. These populations are currently ascribed to four subspecies which is difficult to ascertain. Mitochondrial DNA haplotypes showed that populations could readily be grouped into two major entities that represent well defined phylogenetic species without gene flow between them, one occupying the Atlantic coast, the other inhabiting the Gulf of Mexico. Within each of these entities, moderate diversification was found but without much geographic structure, probably because of moderate gene flow between populations.

Galián et al. (1996) studied the karyotypes and the RFLPs resulting from digestion of total DNA with endonuclease EcoRI in four populations ascribed to *Ceroglossus chilensis*. Differences between these populations in terms of chromosome number and molecular data led to the conclusion that there are three cryptic species living in sympatry.

A clear distinction between *Abax parallelepipedus* and *A. angustatus* (reported as a subspecies of the former) resulted from a morphological analysis of sympatric populations of both species, and a molecular study based on allozymes and mitochondrial DNA (Düring 2002). No molecular evidence of hybridisation between these two species was found.

Mossakowski et al. (1986) carried out a field study on the frequency of hybrids between species of the subgenus *Chrysocarabus*, *C. lineatus* and *C. splendens* in the Pyrenees. Reliable morphological characters allowed for determining the occurrence of hybrids. Both species may hybridise (up to 40% of individuals) when particular ecological conditions are met, which indicates that complete reproductive isolation has not yet been attained. However, a number of characters are fixed in each species allowing their classification as valid species. Furthermore, Düring et al. (2000, 2006) studied the mitochondrial haplotype in many *C. splendens* populations and found convincing evidence of introgressive hybridisation in *Chrysocarabus* (incongruence between mitochondrial and nuclear gene trees). In contrast, nuclear ITS-2 sequences showed that populations of *C. splendens* made up a monophyletic clade, which is sister to that made up by *C. lineatus* and *C. lateralis*. Shared haplotypes between *C. splendens* and *C. punctatoauratus* are probably the result of introgression of the latter into the former species. On the other hand, mitochondrial DNA of *C. rutilans* was probably acquired from *C. splendens* through introgression.

2.5. Speciation, radiation and biogeography

Juberthie (1979) analysed the evolutionary pathways of the genus *Aphaenops* (Trechinae) from putative epigean ancestors to specialised troglobionts, and noted that food must have been a major factor in promoting their morpho-functional characters. He also concluded that *Aphaenops* and other hypogean Trechinae are not living fossils but show highly derived characters, either regressive (loss of eyes and pigmentation) or positive (slender appendages, new chemoreceptors) with regard to ancestral epigean forms, with which they still share particular plesiomorphies.

Mossakowski (1979) postulated that habitat preference is an evolutionary process that can be reconstructed when matching it against a phylogenetic tree of particular taxa. He tested this hypothesis by considering the subgenus *Chrysocarabus* and concluded that there was an adaptive shift from Mediterranean to deciduous forests and a recent colonisation of alpine environments.

Liebherr (1986) constructed a phylogeny of the *Agonum extensicolle* group based on morphological quantitative characters and the allelic frequencies derived from the electrophoresis of soluble enzymes. The resulting tree was used to test the hypothesis of the vicariance effects of the Cochise filter/barrier separating the Sonoran and Chihuahuan deserts in SW North America. He argued that the zone between the deserts has probably caused vicariant events between particular pairs of species and species groups, and also between subspecies of *A. decorum* 6.5 to 2.8 million years ago. This barrier has probably led to the same phenomena in other carabid taxa.

Desender et al. (1990) studied speciation of the genus *Pterostichus* in the Galápagos using multivariate morphometric analysis and ecological data. They concluded that a combination of allopatric (stepping stone model) and parapatric events (segregation in altitude of two species inhabiting the same island) may explain radiation of the genus from ancestors related to *Pterostichus peruviana*, a species presently found in South America.

Andersen and Skorping (1990) presented a conclusive model of sympatric speciation of the genus *Bembidion* (and in particular in the subgenus *Chysobracteon*), in which habitat selection and the effects of parasites may give rise to disruptive selection that promotes reproductive isolation and in turn speciation. Habitat shifts in riparian carabids may have evolved in sympatry, whereas allopatry would have produced new taxa showing mere variations of the same ecological theme.

Baehr (1994) constructed a cladistic analysis of the Pseudomorphinae based on morphological characters that solved relationships of the main lineages within the subfamily. He postulated that the subfamily has an Australian-South American origin, and that it has recently spread to North America and SE Asia.

Brandmayr and Zetto Brandmayr (1994) presented an elaborated hypothesis on the evolutionary history of the genus *Abax*, based on characters of male genitalia (inflated median lobe), larval morphology, type of parental care and larval behaviour, habitat preferences and geographic distribution. Ancestors of this genus possibly inhabited lowland forests during the late Miocene, whereas most recent taxa are found in alpine grasslands and mountain forests. This suggests that there has been a major colonisation trend towards mountains during the last geological periods. A predominantly allopatric pattern was inferred for the radiation of *Abax*.

The supertribe Carabitae poses major evolutionary problems because many character states are difficult to interpret due to homoplasy, and the biogeographic patterns of tribes are not congruent at first glance with relationships derived from molecular and morphological data. A synthesis of different studies (Prüser and Mossakowski 1998; Kamer et al. 2002; Mossakowski 2002) based on the analysis of morphological characters (adults and larvae) plus molecular data, indicates that Cychrini is sister to all other tribes, and that Carabini is sister to a clade made up of tribes Ceroglossini and Pamborini. This hypothesis also postulates a Laurasian origin of Carabitae and a single migration event across the tropics. A corollary of this hypothesis is that the *Cychrus*-like mandible of *Pamborus* is a homoplasy that would result from an adaptation to feed on snails ('cychrisation').

Of the four *Calosoma* species inhabiting the Galápagos, only *C. granatense* is widespread among islands and altitudinal habitats. In spite of its high dispersal power and morphological stability, this species shows substantial genetic differentiation between populations on different islands and volcanoes (Desender and Verdyck 2000). There was probably a single colonisation event from the mainland and a stepping-stone model of island colonisation. However, gene flow must have been enough to prevent speciation events. The other three *Calosoma* species of the Galápagos are endemic to localities at high altitudes on a single island, which suggests that they have originated by convergent habitat shifts.

The phylogenetic relationship of three *Carabus* species inhabiting the Tenerife and Gran Canaria (subgenus *Nesaeocarabus*) was investigated by a phylogenetic analysis based of the mitochondrial *nd5* gene (Prüser et al. 2000). The hypothesis of a close relationship between *Nesaeocarabus* and the subgenus *Eucarabus* was rejected. Instead, Canarian taxa were closely related to the subgenus *Eurycarabus* from northern Africa, southern Italy, Sardinia and Sicily. Diversification of *Nesaeocarabus* in the Canaries was congruent with the geological history of the archipelago, with a diversification of ancestors beginning 14–7 million years ago.

The subgenus *Platycarabus* includes five species living in the Alps and adjacent areas. Casale et al. (1998) tested the hypothesis of a close relationship of these species with the subgenus *Hygrocarabus*, both included in the genus *Chaetocarabus* sensu Ishikawa (1984). Separate and combined analyses of 26 adult and larval characters, and of sequences of the *nd1* gene, rejected this hypothesis, as *Platycarabus* is a robust monophyletic lineage distantly related to *Chaetocarabus*, and is even farther from *Hygrocarabus*.

Mossakowski (2005) revised the proposal of Imura (2002) of grouping the genus *Carabus s. l.* into 29 sections and 137 genera, based on molecular data (see also Casale and Mossakowski 2003). Analysis of the inflated median lobe of the male endophallus and the reassessment of DNA sets with stringent criteria of bootstrap values showed that (i) relationships of the subgenera of *Carabus* were poorly solved, (ii) the results do not support the hypothesis of an explosive radiation of the ancestors of this genus, and (iii) these uncertainties do not favour the ranking of subgenera to genera proposed by Imura (2002).

2.6. Phylogeny based on different types of characters

Ethology

Brandmayr and Zetto Brandmayr (1979) found that the genus *Abax* shows different stages between a pure pre-social condition of merely laying eggs with a well-developed ovipositor, and the advanced construction of a chamber, laying the eggs in capsules and taking care of brood until hatching and pigmentation of the larvae. It was concluded that behavioural characters are difficult to interpret in a phylogenetic context due to convergence. However, in some instances they provide valuable clues to reconstruct the evolution of a group and give a good phylogenetic signal.

Morphology

Wing folding mechanisms have been suggested to be a character with phylogenetic value at higher taxonomic ranks (Hammond 1979). Differences in the structure (presence of patches of microtrichia) and mechanism (abdominal movements helping with folding) of wing folding among lineages of Carabidae are not congruent with phylogenetic inferences derived from other characters. The Trachypachidae is a lineage distinct from carabids, a conclusion congruent with recent molecular (Maddison et al. 2009) and karyotypic data (Martínez-Navarro et al. 2011), whereas *Gehringia* was close to other carabids, as currently accepted. The basis for investigating the phylogenetic value of wing venation within Adephaga and Carabidae was outlined by Ward (1979). This topic has received little attention, perhaps because there is a generalised model in Carabidae that shows a relatively low degree of variation within particular lineages at the tribal or generic level.

Higher-ranked taxa were considered by Beutel (1998) when analysing the relationships of Trachypachidae, based on morphological and functional characters of adults and larvae. He concluded that the family Gyrinidae is sister to all other Adephagan groups. Of these clades, Haliplidae was sister to the remaining families; these were in turn split into two main clades, one made up of Carabidae (including Rhysodini and Cicindelitae), the other made up of (Trachypachidae) + (Noteridae(Amphizoidae+ Dytiscidae)). These results contradict Beutel and Haas (1996), who found Trachypachinae to be sister to Carabidae; Beutel and Haas' hypothesis has recently received support from molecular analyses (Maddison et al. 2009). Ancestors of Adephagan beetles were probably associated with riparian habitats and it has been postulated that independent colonisations of aquatic habitats gave rise to the families Gyrinidae, Haliplidae and Dytiscidae.

Liebherr and Will (1998) studied the phylogenetic value of characters of the female reproductive tract at an inclusive scale that covered the whole family Carabidae. Surprisingly no character defined the Carabidae as a monophyletic taxon; instead the Isochaeta appeared as the adelphotaxon of Anisochaeta (that included Gehringiini and Rhysodini). In turn, the Anisochaeta was divided into two clades separated by the evolution of a secondary spermatheca. Less inclusive clades within these two major groups of Anisochaeta showed relationships that agreed with previous hypotheses in some cases.

Arndt (1998) analysed the phylogenetic relationships derived from larval morphology in 44 tribes of Carabidae. He found support for a monophyletic Carabidae+ Tachypachidae+Dytiscidae clade. The family Carabidae was also a monophyletic clade if Rhysodidae were excluded. The Cicindelitae was also monophyletic and showed several autapomorphies. Metriitae and Paussitae made up a monophyletic clade. The subfamily Harpalinae ("higher" carabids) appeared to be a monophyletic clade but relationships of Brachinitae were ambiguous and remain a major challenge for future studies; a close relationship with Harpalinae is unlikely. The phylogenetic relationships among basal grade Carabidae was revisited by Kavanaugh (1998) who showed that Trachypachidae is sister to all carabid taxa examined (which confirms similar conclusions reported in former works), that the supertribe Nebriitae is a grade rather than a clade (Nebriini is separated from related tribes), and that cicindines are related to Carabini, Cychrini, Cicindelini and Omophronini.

Cladistic analyses based on different data sets (morphology, ethology, geographic distribution), were carried out to investigate the phylogeny of Paussinae (Nagel 1979b), Ozaenini plus Metriini and Paussini (Vigna Taglianti et al. 1998), the *Agra cayennensis* group (Erwin 1996), the supertribe Nebriitae (Kavanaugh 1996), the subtribe Calleidina (Lebiini; Casale 1998), the Western Hemisphere Pseudomorphini (Erwin and Geraci 2008), the tribe Rhysodini (Bell 1998; which is likely a highly specialised predator of slime moulds rather than a primitive Adephagan stock), the subfamily Broscinae (Roig-Juñent 1998), and the subfamily Psydrinae (Baehr, 1998). These studies either corroborated previous ideas about relationships of taxa or shed light on new and unsuspected hypotheses about the phylogeny and classification of taxa, including the erection of new high-ranked taxa.

Defence substances

Characterisation of chemical compounds used for defence and the phylogenetic interest of this trait was summarised by Moore (1979). The review showed that (i) compounds can be grouped into at least nine categories according to their chemical nature, (ii) there probably occurred a convergent development of the same substances in distantly related lineages, (iii) diversification of chemical types occurred within some subfamilies (e.g. Pterostichinae) whereas others (Harpalinae, Lebiinae) are much more uniform; (iv) the phylogenetic signal of this trait is valuable at tribal level or higher ranks; some compounds seem to vary in particular lineages (Australian Panagaeninae) and could be useful for assessing relationships at lower ranks; and (v) further insight into this trait would result from the study of biochemical synthetic pathways, fine structure of defensive glands and the detection of more subtle compounds.

Karyotypic evolution

A number of contributions have addressed the question on the ancestral karyotype of Adephaga and the Carabidae, and its main patterns of evolutionary change (Nettmann 1986; Serrano 1986; Serrano and Galián 1998), or referred to the karyotypic evolution of particular taxa (Harpalini: Serrano et al. 1994). The family Carabidae (915 taxa analysed) is characterised by a notable variation of the diploid number (2n = 4 - 69), the occurrence of high chromosome numbers in comparison to Polyphagan beetles, and a

repeated karyotypic formula in well-studied lineages (e.g. 2n = 26 + XY in Carabini; 2n = 22 + XY in Bembidiini; 2n = 36 + X in Harpalini).

The ancestral karyotype of Coleoptera, still present in many Polyphagan lineages, $2n = 18 + Xy_p$, had probably undergone significant changes in the ancestors of carabids, since neither this number of autosomes nor the particular Xy_p sex chromosomes are found in any carabid. The ancestral condition of a 2n = 36 + X0 male karyotype is widespread in many lineages and may be notably diversified in particular carabid lineages. The occurrence of this formula in some dytiscids and in trachypachids (Martínez-Navarro et al. 2011) provided further support to this hypothesis. However, it has not been found in lineages showing plesiomorphic morphological characters, which suggests that it has evolved rapidly in earlier offshoots of the Carabidae.

Karyotypic data have been shown to be valuable for understanding carabid systematics though it seems that karyotypic changes are not a main driving force for speciation in carabids. This is not to deny the role of karyotypic changes in reinforcing isolation mechanisms in recently originated taxa, regardless of the occurrence of speciation processes under conditions of geographic isolation or in lowland areas (Serrano 1992).

Serrano et al. (1994) summarised the karyotypic data of members of the tribe Harpalini, and found that ancestors likely had a 2n = 36 + X male karyotype. Constraints to numerical variations within this tribe are similar to those found among other carabid tribes. The Ditomina are peculiar because they show high chromosome numbers, which corroborates its ranking as a separate subtribe.

Molecular data

The number of molecular studies have increased since the 1990s, either based only on molecular data or (more recently) combined with other data sets. Inferred relationships have corroborated relationships derived from traditional taxonomy but also often contradicted these, thus emphasising the need of more holistic approaches aimed at obtaining robust and congruent phylogenies.

Maddison et al. (1998) published the first comprehensive DNA-based phylogeny of Carabidae. They studied the nuclear small subunit (18S) ribosomal DNA, sequenced in 35 carabid genera representing 26 tribes. All higher-level clades were monophyletic except for the Scrobifera (scaritines plus clivinines); the Trechitae was sister to Patrobines; *Morion* and Pseudomorpha were members of Harpalinae; *Psydrus* and elaphrines were sisters and both were sister to trechites plus patrobines; there was a grade including scaritines immediately below Harpalinae.

A combined analysis of larval morphological characters and molecular data of Cicindelitae showed a number of inferences that contradict current systematics: Omina had a basal position, Megacephalini was a polyphyletic taxon, and Cicindelinae was not monophyletic (Vogler and Barraclough 1998). Use of the resulting inferences showed that there are differential diversification rates among major lineages (e.g. a high rate of diversification was found at the base of megacephalines and collyrines, and another at the base of cicindelines).

Düring and Brückner (2000) investigated the phylogeny and history of lineages of Molopina using molecular analysis based on the sequence of two mitochondrial DNA fragments. Representatives of the genera *Percus, Molops* and *Abax* were included, as well as *Pterostichus* and *Carabus* as outgroups. These three genera made up a monophyletic clade, and *Molops* and *Abax* were sister taxa. In a further step, Brückner and Mossakowski (2006) investigated the phylogeny of the genus *Percus* by integrating previous molecular, morphological and biogeographic characters with those of nuclear 28S rRNA. This genus is likely a monophyletic taxon divided into three main clades. Relationships among the Tyrrhenian taxa remained unresolved probably as a result of recent diversification and low mutation rates of the molecular marker.

A molecular study of the tribe Harpalini based on the mitochondrial *cox1* gene (Martínez-Navarro et al. 2005) showed that (i) Pelmatellina should be included within Stenolophina, (ii) subtribe Harpalina is polyphyletic, (iii) Ditomina is a valid subtribe, and (iv) Selenophori should be ranked as a valid subtribe closely related to the Aniso-dactylina.

An analysis based on sequences of 28S and *wingless* genes of *Ildobates neboti* (a rare hypogean species inhabiting a few caves in eastern Spain) and related taxa showed that tribes currently included in Dryptitae (Dryptini, Galeritini and Zuphiini) made up a monophyletic clade, and that *Ildobates neboti* is a member of the Zuphiini (Ribera et al. 2006).

Vogt et al. (2005) studied the relationships of African Anthia and Termophilum, and the related Cypholoba chaudoiri, based on the sequence of the mitochondrial nd5 gene. Taxa of Anthia made up a monophyletic clade in which C. chaudoiri was unexpectedly included. Taxa of Termophilum made up two distinct clusters, which suggests paraphyly of this genus.

Current division of the genus *Calathus* (Sphodrini) was investigated on molecular grounds by sampling a *cox1-cox2* fragment in 44 taxa (Ruiz and Serrano 2006). The monophyly of the subgenus *Calathus* was corroborated, as well as the distinctness of the monotypic subgenera *Bedelinus* and *Iberocalathus*. The subgenus *Neocalathus* is polyphyletic and needs taxonomic revision and the same holds true for the Canarian *Lauricalathus*. The latter subgenus should be divided into two subgenera, and one of these should include *Trichocalathus*.

3 Biology

3.1. Life history strategies and rhythms

Land animals evolve strategies to optimise and synchronise their life cycle with seasonal changes of the environment. For example, reproduction usually takes place under optimal conditions, while metabolism may be reduced if conditions are suboptimal (e.g. dormancy, which in carabids has thus far only been observed for larval and adult stages).

Ultimate (limiting) factors regulating ground beetle life histories

Ultimate factors determining beetle life cycles include variation in temperature and rainfall. Optimal development of the immature stages requires an estimated temperature range of 4–35°C. Rainfall, in combination with temperature, affects soil humidity, which is critical because eggs absorb water from their surroundings to complete embryonic development (Paarmann 1986) and larvae are sensitive to desiccation (Paarmann 1973).

Food can also be critical. Reproduction of, for example, seed-feeding carabid species may be governed by ripe seeds that usually appear at the end of the wet or warm season. Only very few habitats offer suitable conditions for polyvoltine development throughout the year, for example, lake shores, swamps and some lowland rainforests with very short dry spells.

The only ultimate factor determining carabid beetle life cycles in the Arctic, Subarctic and Antarctic, as well as in montane habitats of the temperate zone is temperature (e.g. Thiele 1977). In the summer, only a short time window exists for reproduction and development. All species in these habitats are summer developers. Species with rapid larval development, such as *Pterostichus adstrictus* (Paarmann 1994), are true summer breeders with adult hibernation only. Species with slow larval development hibernate as larvae as well as adults and require more than one season to complete their life cycle (Kaufmann 1971; Davies 1972; Matalin 2008). In the mountains of temperate Europe (altitude of 2200-2600 m) the favourable season is reduced to 3-4 months. In forest Pterostichines, especially in the large genus Pterostichus and in the Molopines Abax and Percus, cycles are often biennial (Brandmayr 1977). In the genus Molops, where embryonic development can last for more than one month and the eggs are guarded in a subterranean hole, the females disappear from the soil surface during summer, and reappear in the autumn. The subterranean larvae are active during winter, and the new generation requires a further year to reach maturity (Brandmayr and Zetto Brandmayr 1991).

Larsson (1939) recognised different reproductive strategies in carabid beetles of the temperate zone by studying museum material. He divided them into Frühlingstiere (spring breeders) and Herbsttiere (autumn breeders). Spring breeders reproduce during the spring and hibernate as adults only. Autumn breeders reproduce during the autumn and hibernate mainly as larvae. In a number of species, adults may hibernate after reproduction to enter a second reproductive period (Gilbert 1956; Vlijm et al. 1968; Schjøtz-Christensen 1968; Krehan 1970). Schjøtz-Christensen (1965, 1966) showed that in some *Harpalus* species spring and autumn breeding populations cooccure in the same habitat. Other examples include *Abax parallelepipedus* (Löser 1970), *Poecilus lepidus* (Paarmann 1990), *Pseudophonus rufipes* (Matalin 1997a) and *Harpalus affinis* (Matalin 1998). A third breeding category – spring-autumn breeder (Matalin 1997b) – is found in the genus *Stenolophus*. In 1990 Den Boer and Den Boer-Daanje, summarising the life history strategies of 68 common carabid beetles in Drenthe (the Netherlands), found a continuum of reproduction from early spring to late autumn, and seven of them reproduced during winter. Den Boer and Den Boer-Daanje distinguished species with summer larvae (summer developers, 40 species) and species with winter larvae (winter developers, 28 species). Drenthe is located in an area with Atlantic climate: warm winters and wet summers, thus offering a broad reproductive window. In areas with a continental climate, however, this window is much narrower.

Cave environments are buffered against climatic variation and can have (i) a constant temperature throughout the year, or (ii) distinct seasonality. Trechines living in caves are mostly autumnal reproducers with winter larvae. The rhythms of *Aphaenops* and related genera may show distinct seasonality at least in the activity of adults, influenced by the cave's air humidity (Juberthie 1969), and sometimes with two distinct annual peaks (Cabidoche 1963, 1966). Reproduction may coincide with a peak in food, as found between *Neaphenops tellkampfi* and the eggs of the orthopteran *Hadenoecus subterraneus* (Kane et al. 1975).

The seven winter breeding species found in the Netherlands (see above) connect the carabid fauna of the temperate zone with the life history strategy typical for the subtropics with winter rain. In Palestine, Bodenheimer (1934) only caught beetles from October to June. Winter breeding (rainy season breeding) is a typical reproductive strategy in habitats that are dry in the summer, such as North Africa (Paarmann 1970, 1975). In specific habitats with moist soil during the dry summer period, propagation and reproduction occur throughout the year (Paarmann 1975, 1976d). *Thermophilum sexmaculatum* and *Graphipterus serrator*, with specialised larvae that feed on ants and their brood, reproduce in the summer (Paarmann 1985; Paarmann et al. 1986; Dinter et al. 2002), but only in sandy soil that acts as a moisture trap.

In Mediterranean Europe, which is also dry in the summer, some seed-feeding carabids - the ditomines *Carterus calydonius*, *Ditomus clypeatus*, and harpaline carabid beetles that provide *Daucus* or *Plantago* seeds to their larvae (Brandmayr and Zetto Brandmayr 1974; Schremmer 1960) - show summer reproduction. Other seed-feeders (*Ophonus*, *Pseudoophonus*) are adapted to more humid soils and normally reproduce in the autumn (winter larvae; Zetto Brandmayr 1983a, b).

No information is available on the reproductive strategies of Carabinae from the subtropics with summer rain. However, it seems reasonable to suggest that they show rainy season propagation (summer breeding) in habitats which are dry during winter. A number of studies on carabid beetle life histories are available from the tropics. In Central Africa (Kivu district), which is characterised by low variation in median air temperature (0.9 °C) and low rainfall from June-August (Walter and Lieth 1960), the majority of species avoid reproduction during and around the dry season (Paarmann 1976b). Dry season propagation was only found in two species, one living in a swamp and one in a cultivated area. North Sulawesi (Indonesia) is without a dry period, yet the appearance of gonad dormancies was widespread among 155 carabid beetle species: 65% had at least one dormant female (Paarmann and Stork 1987; Stork and Paarmann 1992). Females of the canopy dweller *Colpodes buchanani* also synchronise reproduction with annual temperature changes typical of the subtropical climate (Paarmann and Paarmann 1997).

Along the Amazon River in Brazil, forests are often inundated for up to seven months of the year. This flooding is independent of the rainy season in central Amazonia. During flooding, carabid beetles occur on tree trunks or in the canopy in the inundated site, reproducing when the water level is low (Adis et al. 1986; Adis et al. 1990). In lowland rainforests, carabids aggregate in areas with an accumulated amount of organic matter, such as fruit falls (Erwin 1979b). These fruit falls are unpredictable in space and time, lasting only for a few weeks. Fig fruit falls play an important role in these rainforests, as they occur virtually throughout the year. Distinct carabid assemblages have been found at fig fruit falls in lowland rainforests of the Amazon basin (Paarmann et al. 2001), Brunei (Borcherding et al. 2000), Australia and Africa (Paarmann et al. 2006). Female gonad maturation starts immediately after locating a fruit fall, with some females carrying ripe eggs combined with the undeveloped ovaries. These 'transport eggs' can be deposited directly after arrival at the fruit fall, providing larvae more time for development. While moving between patches of fruit fall, females experience short gonad dormancy induced by food shortages (Paarmann et al. 2001; Arndt and Kirmse 2002).

Proximate factors and endogenous rhythms

During unstable temperatures, soil humidity and resources, proximate factors and endogenous rhythms play a major role in controlling carabid beetle life cycles. At temperate latitudes, many species, especially species with summer larvae, use photoperiodic changes to synchronise gonad maturation (Thiele 1977). Autumn breeding species display thermic parapause (Müller 1970): an obligatory dormancy at a genetically fixed developmental stage, where the phase of induction cannot be recognised. Larval development can only be completed after passing a certain period of time at low temperatures. Larvae of other species with winter larvae, such as *Abax ovalis* and *Abax parallelepipedus*, only pass a thermic quiescence (Müller 1970): a facultative delay or suspension of development. This may also be the case for species with winter larvae at higher latitudes (and montane regions): Subarctic populations of *Pterostichus nigrita* were still under photoperiodic control in terms of gonad maturation, yet displayed a shift of the response curve to longer day lengths (Ferenz 1975).

Annual day length amplitudes decrease from higher latitudes to the equator, as does the importance of photoperiodic changes as a proximate factor. However, day length changes of 1 h can control imaginal diapause (Norris 1959, 1965). Two carabid species from North Africa synchronise their life cycle with annual rainfall, triggered by a decrease in temperature and a decline in the photoperiod (Paarmann 1974, 1976c). This control mechanism in a rainy season breeder (or winter breeder) of the subtropics with winter rain shows marked similarities with temperate autumn breeders and aestivation (Thiele 1977).

In the Kivu region, Central Africa (see Paarmann 1976b), the maximum change in daylight is 16 min only, and the maximum annual temperature change is 0.9°C.

Under such climatic conditions, temperature plays a role as a proximate factor. The temperature of the upper soil layers and the soil surface is influenced by the water content of the soil. With water loss in the upper soil layers, daily temperature fluctuations increase. Some hours of higher temperatures per day induce gonad dormancy. With the onset of rainfall, temperature fluctuations decline and dormancy is terminated. Synchronised maturation is stimulated by the increase in average temperatures (Paarmann 1986).

Endogenous control of gonad dormancies

The synchronisation of gonad maturation with seasonal change in ultimate factors is possible only if proximate factors influence the endocrine system controlling this maturation. Emmerich and Thiele (1969) and Hoffmann (1969) were the first to study the hormonal control of gonad maturation in spring breeders. They found a connection between proximate factors, neurosecretions and the activity of the *corpora allata*, which produces juvenile hormones (JH). JHs are necessary to complete gonad maturation in males (Ferenz and Hölters 1975). In females, only previtellogenesis is controlled by JHs. To complete ovarian maturation, the production of a second hormone is postulated. Applications of JHs to dormant beetles of the winter breeder *Orthomus barbarus* have confirmed a similar control mechanism for this breeding type (Paarmann 1976a). The same application to dormant beetles of the summer breeder *Pogonus chalceus* resulted in complete maturation of both sexes, even complete gonad maturation in females, meaning that either complete maturation is controlled by JHs only, or high temperatures suppress only the production of JHs but not of vitellogenic hormones.

Endogenous rhythms are involved in gonad maturation. Under constant environmental conditions gonad maturation is controlled by an endogenous rhythm, synchronised by an external cue such as soil temperature (Paarmann 1986). In the desert-dwelling carabid beetle *Thermophilum sexmaculatum* thermoregulational behaviour is controlled by a circannual rhythm, resulting in lower body temperatures at the end of the optimal reproductive period, which causes an inactive stage of the gonads (Erbeling and Paarmann 1986).

As part of the taxon pulse theory (Erwin 1979b), ground beetles from tropical areas undergo latitudinal and altitudinal expansion, leading to climatic specialisation, including the development of dormancy to survive unfavourable climatic conditions. If all carabid beetle dormancies are based on a uniform hormonal system, manifold convergent evolution is possible. The use of gonad dormancies to synchronise life cycles with changing environmental conditions is widespread among tropical carabid beetles. Only one *Abacetus* species, living under stable humidity and temperature conditions (the shore of Lake Kivu, Central Africa), seems to develop without dormancy. With the exception of short gonad dormancies, triggered by food shortages in the seed-feeding guild, all studied gonad dormancies are under the control of temperature as a proximate factor.

Specialisation along riparian habitats (pathway i) leads to a synchronisation of the life cycle with seasons with stable moisture conditions, especially along riverbanks.

Specialisation in seasonally dry habitats (pathway ii) leads to a synchronisation of the life cycle with the period of optimal soil humidity, e.g. rainy season propagation (Paarmann 1979). While larvae of winter breeders in the subtropics with winter rainfall are adapted to comparable temperatures, a small group requires high temperatures for successful development. These specialists, whose larvae feed on ants and ant brood, have evolved along pathway (ii) in the subtropics with summer rainfall and spending the winter in gonad dormancy. Such species have yet to be reported in the temperate zone.

Larsson (1939) found no autumn breeders among 21 studied species of the old genus *Agonum*. These species are possibly all descendants of one common ancestor that reached the temperate zone along pathway (i) after which some descendant species adapted to non-riparian habitats. One member of this group, namely *Platynus (Agonum, Limodromus) assimilis* is a spring breeder, but its gonad dormancy is controlled in a fundamentally different way than in other spring breeders, by a photoperiodic quiescence (Neudecker and Thiele 1974).

Gaps in our current understanding of carabid beetle life history strategies include (i) a lack of knowledge on life history strategies in the subtropics with summer rainfall, in the tropics with long dry seasons and in areas with unpredictable rainfall, (ii) whether canopy dwelling carabid beetles in tropical rainforests display seasonal patterns, and (iii) a detailed study on the hormonal control of dormancies in carabid beetles, as no such studies have been performed since Ferenz (1977).

3.2. Carabid beetle food

Carabid beetles are generally considered polyphagous predators. However, in line with their enormous species richness and diversity in body shapes and biotopes they inhabit, a whole range of trophic specialisations occurs in the Carabidae (Hengeveld 1980a; Zetto Brandmayr et al. 1998b). Although carabid feeding ecology and biology has been studied frequently (also during ECM meetings), it is surprising how many basic questions on carabid food remain unanswered. Except for Larochelle (1990), who mentioned food preferences of 1054, mainly North-American, European and Japanese species, basic information on food preferences or requirements is often lacking, even for many common species. This chapter does not attempt to review all trophic specialisations of Carabidae; it has been done before (Thiele 1977; Hengeveld 1980a; Toft and Bilde 2002). Instead, it focuses on recent advances in the domains of seed and ant feeding, as well as unique life history strategies, such as ectoparasitism and the predation of amphibians.

Seed feeding

Carabid beetles accept a variety of plant foods such as leaves, fruits, pollen, seeds and fungi (Toft and Bilde 2002 and references therein). Seed feeding, or granivory, occurs in many species including polyphagous ones that prefer animal prey (Lund and Turpin 1977;

Hengeveld 1980b; Toft and Bilde 2002). True granivory, i.e. where seeds are central to the species' food budget, has evolved in two tribes of Carabidae, Zabrini and Harpalini. The ecology of granivorous carabids is of great interest since granivory required the evolution of morphological, physiological and behavioural adaptations associated with crushing, digesting and foraging for seeds. To crush hard seeds, adults and larvae of granivorous species have evolved broad mandibles with massive adductors (Zetto Brandmayr et al. 1998b; Paarmann et al. 2006). Sclerotised structures in the adult proventriculus are then used for fine grinding of the ingested seed fragments (Evans and Forsythe 1985). Behavioural adaptations have involved, for example, climbing plants and storing seeds in burrows (Thiele 1977). Physiological adaptations to seed feeding are understudied but recent evidence shows that digestion of seeds is facilitated by endosymbionts (Lundgren and Lehman 2010).

The amount of seeds eaten by carabids in the field may be substantial. Based on seed losses of artificially exposed seeds, Honek et al. (2003) estimated that up to 4000 seeds $m^{-2} d^{-1}$ may be removed by carabid beetles in arable fields in the Czech Republic. Honek et al. (2005) reported that carabids, mainly *Amara montivaga*, destroyed about 83–88% of the annual seed production of *Taraxacum officinale* spp. agg., and Kjellsson (1985) showed that approximately 65% of the annual seed production of *Carex pilulifera* L. was consumed by a single species, *Harpalus solitaris*. However, individual capacity for eating seeds varies with season (Honek et al. 2006) as a result of natural phenological changes (transition from dormancy to reproduction, dispersal, breeding and searching for overwintering sites). Consumption is also affected by temperature (Saska et al. 2010). Clearly, carabid beetles may have an important impact on the reproductive success and dispersal of plant species, but more research is needed on how these affect the population dynamics of plants in the longer term. Larvae should also be considered in these studies, as their consumption of seeds can be comparable to that of adults (Klimeš and Saska 2010).

The consumption of particular seed species is ultimately determined by the preferences of the carabids in question. During the last 30 years, a number of authors have investigated carabid preferences for seeds in the laboratory using choice (cafeteria) experiments (Lund and Turpin 1977; Brust and House 1988; Jørgensen and Toft 1997a). Most studies, however, have established preferences based on a limited number of seed species (usually 2-5). Only Honek et al. (2003, 2006, 2007) tested seed preferences in carabids using 64 or 28 species of herbaceous seed. Honek et al. (2003, 2007, 2011) demonstrated that the preference for seeds correlates with carabid body size: on average, smaller species prefer smaller seeds, and vice versa. Larger carabids also consume a greater variety of seed species and Harpalini are less specialised than Zabrini (Honek et al. 2007). However, there are other characters such as seed shape, thickness of the testa (Lundgren and Rosentrater 2007) and nutrient content of the seed that affect preference. Similarly to other seed-cracking organisms (e.g. Diaz 1994), mandible size and shape determine the seed preferences of Notiobia species occupying fruit fall sites in tropical forests (Arndt and Kirmse 2002; Paarmann et al. 2006), and these preferences are consistent throughout the season (Honek et al. 2006).

Taxonomic affiliation constrains the preferences for food in many insect groups. Earlier research as well as direct field observations have indicated that species of certain genera had specific affinities with respect to their seed preferences. For example, Brandmayr and Zetto Brandmayr (1987) and Zetto Brandmayr (1990) suggested that most Ditomina and Ophonus (both Harpalini) are associated with Apiaceae, while Harpalus (Harpalini) is unspecialised in this sense (Zetto Brandmayr 1990). Hurka (1996) reported that species of the subgenus Zezea (Zabrini: Amara) may be associated with Poaceae. The existence of a taxonomic constraint has been experimentally confirmed by Honek et al. (2007), who carried out a cafeteria experiment that included 28 seed species and 30 carabid species. They demonstrated that species of Zabrini mostly prefer seeds of *Taraxacum*, while species of Harpalini prefer seeds of *Cirsium* and Viola. Carabids not only distinguished seeds from different families, but they were also able to discriminate between seeds at a finer taxonomic scale, i.e. seeds of different sections of the Taraxacum officinale species complex (Honek et al. 2011). The origin of seeds plays a role in some carabid species. For example, Honek et al. (2011) fed Czech carabids with Italian and Czech seeds of the same plant species and found that the beetles preferred the latter. It is likely that the existence of specialisation on particular seeds reduces the competition for food and allows the coexistence of species in the same habitat.

Seeds are nutritious, but their value as food for carabids has not been appropriately recognised until recently. The value of food is best defined by its contribution to the fitness of the consumer (Toft and Bilde 2002). Fitness parameters that are commonly used as criteria for the evaluation of food quality are female fecundity, survival and duration of larval development, and the attainable body size. Zetto Brandmayr (1976) showed better survival in larvae of several species of the genus Ophonus when provided with seeds of Apiaceae compared to other seeds or insects. Although Jørgensen and Toft (1997a, b) stimulated further research on this topic (mainly in Europe and Japan), information on how seed diet affects fitness is only available for a small number of species. Adaptations to granivory have evolved to varying degrees in different taxa, and even closely related species may show different strategies (for Amara, subgenus Amara, compare e.g. Jørgensen and Toft 1997b; Saska and Jarošík 2001; Hurka and Jarošík 2003; Fawki and Toft 2005; Saska 2008; for Amara, subgenus Curtonotus, compare e.g. Saska 2005; Sasakawa 2007; 2009); for Notiobia, see Arndt et al. 1996; Paarmann et al. 2001; Arndt and Kirmse 2002). More interestingly, particular seed diets may have contrasting effects on different fitness traits (Fawki and Toft 2005). The effects of maternal diet (Saskawa 2009) or diet of the previous generations (Hurka and Jarošík 2003) on larval performance are poorly studied. Also, worthy of mention here is the scoring system of Paarmann (2002) used to evaluate larval performance under different dietary regimes. In general, larvae are more specific in their food preferences than adults (Thiele 1977) because of increased selection pressures on larvae (Sasakawa 2007) and due to morphological constraints on the suitability of the available food during the early stages of development (Paarmann et al. 2006). Klimeš and Saska (2010) argued that this selection pressure is highest in the first instar larva and decreases in older instars, with increasing the head width/seed size ratio in larvae and widening the range of edible food items.

Ant feeding

Ants are the most abundant group of organisms on Earth in terms of biomass (Hölldobler and Wilson 1990). Not surprisingly they represent an important food source for many other taxa, including carabid beetles. Polyphagous carabid species frequently prey on ants (Thiele 1977; Hengeveld 1980b), and several clades have adapted to ant feeding with some having evolved the highest degree of specialisation, i.e. myrmecophily. In general, biological information is very limited and needs systematic study.

Species that have adapted to feeding on ants have evolved interesting behavioural and morphological adaptations, including chemical mimicry that reduces the risk of being attacked by their hosts (Zetto Brandmayr et al. 2000a; Dinter et al. 2002). Larvae of *Sphallomorpha* (Pseudomorphini) form burrows close to ant nests and attack ants that pass by (Moore 1974). Associations with ants and termites seem to be a joint character for the entire tribe of Pseudomorphini, though evidence is limited (Baehr 1994). Species of the Siagonini also prey on ants (Zetto Brandmayr et al. 1998a, 2000b). Species of the genus *Siagona* inhabit crevices in the soil near ant nests and attack ants both as adults and larvae, but do not seem to enter ant nests frequently (Bauer et al. 2005). The larvae of some Ozaeini use so-called terminal disks (modified last abdominal segments) for attracting and capturing ants (Di Giulio and Vigna Taglianti 2001; Moore and Di Giulio 2006).

Adults of the North African Anthiini and Graphipterini are free-living but larvae enter ant nests where they prey upon ants to complete their development (Paarmann 1985; Paarmann et al. 1986). The larva of *Thermophilum* (Anthiini) moves freely in the nest after it gains chemical mimicry from ants it has previously attacked (Dinter et al. 2002), and consumes both ants and ant brood (Paarmann and Erbeling 1986). In contrast, the larva of *Graphipterus serrator* forms a chamber inside the ant nest where it stores ant brood before consumption, and hides against ant attacks (Dinter et al. 2002). Species of *Thermophilum*, as well as *G. serrator*, show preferences for particular ant species, *Graphipterus* being the least selective (Dinter et al. 2002).

True myrmecophily (and perhaps termitophily) evolved in the tribe Paussini, in which morphological and behavioural adaptations are prominent in both adults and larvae (Nagel 1979b; Di Giulio and Moore 2004; Moore and Di Giulio 2006). Although this association is well known, data on food requirements or trophic associations are known for a limited number of taxa only, and this requires further investigation.

Unique life history strategies – ectoparasitism and the predation of amphibians

The variety of life history strategies in carabid beetles includes ectoparasitoidism, a strategy otherwise rare in beetles. Parasitoids are insects whose larvae develop at the expense of a single prey individual (a host), which ultimately dies as a result of parasitoid feeding (Vinson 1976). Ectoparasitoid larvae attach to the host body and feed externally on it, while their adults are free-living (Vinson 1976).

Ectoparasitoidism has been described from four carabid genera: *Brachinus* (Brachinini), *Pelecium* (Peleciini), *Lebia* and *Lebistina* (both Lebiini) (Weber et al. 2008), but several related genera show tendencies towards parasitoidism (Erwin 1979a; Frank et al. 2009). The life cycle of a typical carabid ectoparasitoid includes (i) a female depositing eggs in the host habitat when hosts are present; (ii) mobile early instar larva searching for and attaching to a suitable host; (iii) after attachment, a short physogastric feeding phase, typically with rapid ingestion; and (iv) a distinct pre-pupal "resting" phase during which the host is consumed.

Despite the early discovery of ectoparasitoidism in Carabidae (e.g. Wickham 1893; Silvestri 1904), known host associations are few. With one known exception, beetle pupae are the hosts. Larvae of *Lebia* (five species known to be parasitoids) and *Lebistina* (one species) parasitise leaf beetle (Chrysomelidae) pupae (Weber et al. 2008). Larvae of a single undetermined species of *Pelecium* have been observed developing on chrysomelid pupae and millipedes (Salt 1928). Nearctic wetland species of *Brachinus* (seven species) parasitise the pupae of water beetles (Dytiscidae, Gyrinidae, Hydrophilidae) (Saska and Honek 2004). Despite suggestions proposed by Jeannel (1942), the discovery of the hosts for dryland species of *Brachinus* from Europe was only made 60 years later. Saska and Honek (2004, 2005) successfully reared two species (*B. explodens* and *B. crepitans*) on the pupae of another carabid genus, *Amara*, a finding that has recently been confirmed for *B. elegans* by Makarov and Bokhovko (2005).

Besides direct observations, host-parasite associations have frequently been suggested simply on the basis of co-occurrence of the carabid parasitoid and potential host species. In some cases, however, these observations have led to erroneous predictions (Jeannel 1942; Perez-Zaballos 1985), subsequently refuted because the life cycles of the two suggested partners are not synchronous. Such synchrony has so far been demonstrated only for *B. explodens* and *B. crepitans* (Saska and Honek 2008). Thus, when looking for hosts of Mastax or Aptinus (both Brachinini) or wetland Palaearctic Brachinus species, both co-occurrence and synchrony should be taken into account. More discoveries are probably to be made in the tropics, as that climatic zone contains a vast diversity of lebiine carabids (Ober and Maddison 2008). Research is also needed on the ecology of ectoparasitic carabids to determine the adaptive significance of life history traits of this peculiar strategy. In most cases, available information relates to a brief description of development; only a few species have been studied in detail (Erwin 1967; Juliano 1985; Saska and Honek 2004, 2005, 2008; Weber et al. 2006). Host selection, food utilisation or the adaptive significance of variation in the number of instars (2-5 instead of the typical 3) could produce interesting results. Mimetic complexes have been described between adults of *Lebia* and chrysomelids, including species for which parasitoidism is unknown (Hemenway and Whitcomb 1967), suggesting further trophic associations between the two groups. Focusing on taxa representing transitional evolutionary steps to parasitoidism (Erwin 1979a; Frank et al. 2009) may shed light on the evolution of parasitoidism in Carabidae and in Coleoptera in general.

Carabid beetle larval and adult predation on amphibians has recently been described in Israel. Elron et al. (2007) have shown that larvae of the carabid *Epomis de-* *jeani* preyed upon two amphibian species (*Bufo viridis* and *Hyla savignyi*), confirming an earlier brief note by Moore (1971) from Australia. Subsequently, Wizen and Gasith (2011) performed laboratory experiments, and showed that adults of the two sympatric *Epomis* species in Israel, *E. dejeani* and *E. circumscriptus*, prey upon five and four amphibian species, respectively. Wizen and Gasith (2011) argue that little is known about the feeding habits of sympatric congeneric insects, and that the partial food overlap of these *Epomis* species warrants further investigation.

3.3. Dispersal

Carabid beetles found a rich niche in ecological research through the peculiarities of their dispersal power. Sahlberg (1868) recognised that carabid species exhibit a variety of wing attributes, including wing dimorphism, and that this has implications for their powers of dispersal. Darwin was probably the first to consider the evolutionary and ecological implications of wing polymorphism in Coleoptera after recording high proportions of flightless beetles on the island of Madeira. He hypothesized that flight ability might be evolutionarily disadvantageous for species from insular populations, as they would be more likely to get carried away from the island (Darwin 1859). A few decades later, Darlington turned his attention to the low proportions of macropterous carabids in isolated locations such as islands and mountain tops, and concluded that wing reduction must confer enhanced viability (Darlington 1936, 1943). Lindroth (1988, 1992a, b) studied the wing morphology of carabid assemblages from islands in the Baltic Sea in comparison to control assemblages from nearby mainland sites. He found that the proportions of brachypterous and macropterous species were both lower in insular than in mainland assemblages, even whilst macropterous species were predominant in all of the studied assemblages (see also Ås 1984, Kotze et al. 2000). Dimorphic species, on the other hand, were more numerous in insular than in mainland faunas (Lindroth 1988, 1992a, b). These observations were of fundamental importance to Lindroth's epic zoogeographical studies, published posthumously in 1992 (Lindroth 1988, 1992a, b). After determining the frequencies of the different wing morphologies in populations of wing-dimorphic carabid species across the Fennoscandian region, Lindroth was able to estimate the relative ages of these populations. On that basis, he theorised about the routes of post-glacial colonisation of Fennoscandia by different species. He was subsequently able to divide the fauna into three elements: Wűrm hibernators, immigrants from a southern route to the west of the Baltic Sea and immigrants from the east. Both Lindroth (1988, 1992a, b) and Den Boer (1970) came to the conclusion that macropterous specimens dominate in recently established populations of dimorphic species, which gradually shift to an increasing proportion of brachypterous individuals as these populations grow older. Observations of pioneering populations of the invasive species *Pterostichus melanarius* in Canada support this model (Niemelä and Spence 1991).

85

Largely thanks to the work of Piet den Boer and colleagues, subsequent to the Dutch land reclamation projects of the late 1950s, research interest in the dispersal of carabid beetles flourished, and this provided the theme for the first meeting of European carabidologists in Wijster in 1969, which Piet den Boer hosted (see above). Dispersal power was also the theme of the subsequently published proceedings volume, edited by Den Boer (1971, see also Table 2).

Lindroth was keen to determine the genetic mechanism behind wing dimorphism and conducted breeding experiments with the wing-dimorphic species Pterostichus anthracinus (Lindroth 1988, 1992a, b). The results he obtained, supported by similar results from studies of other coleopteran taxa, led him to conclude that wing dimorphism is inherited in a simple Mendelian pattern, in which brachyptery is dominant. The late Konjev Desender, in whose honour the 14th ECM was held, performed similar breeding experiments using the wing polymorphic species Pogonus chalceus. In this species, crosses between macropterous and brachypterous adults produced offspring with intermediate wing length, suggesting that the genetic control of wing length in this species is polygenic (Desender 1989a). Desender also conducted an exhaustive biometric study of wing development in 300 carabid species indigenous to Belgium and demonstrated that, in addition to brachypterous individuals, also a large proportion of macropterous individuals do not possess functioning flight muscles and are therefore incapable of flight. In the wing-polymorphic Pterostichus vernalis, for instance, some populations are entirely macropterous, with functional flight (but see below) muscles even in relatively short-winged individuals, whereas in some other populations even macropterous individuals lack functional flight muscles (Desender 1989b, see also Nelemans 1987). Desender also studied wing morphology in the genus *Calosoma* after research trips to Easter Island and the Galapagos archipelago. Three endemic species appeared to be brachypterous, whereas the supposedly introduced species, Calosoma granatense, appeared to be wing polymorphic (Desender et al. 2000).

Berend Aukema conducted breeding experiments with the Calathus melano*cephalus* group to shed further light on the inheritance of dispersal characteristics. Aukema (1990) demonstrated that these species show a simple Mendelian pattern of inheritance of wing morphology, as described by Lindroth, i.e. simple inheritance with brachyptery dominant over macroptery for the two wing dimorphic species Calathus cinctus and C. melanocephalus. However, he also demonstrated that certain environmental factors, such as temperature and food supply, influence expression, with higher temperatures and better food availability resulting in both greater proportion of macropterous individuals (Aukema 1990), and the development of flight muscles (Nelemans 1987). Moreover, long-winged females of these two species had greater fecundity than short-winged females, both in terms of quantity of egg production and duration of egg production (Aukema 1991). This result was somewhat counterintuitive, as a number of other studies of wing dimorphic insects, e.g. Roff (1986) found that brachypterous females are generally more fecund, suggesting that the advantage conferred by brachyptery is enhanced fecundity for females. Furthermore, macropterous females of Pogonus chalceus have greater fecundity, suggesting

that long wings and functional flight muscles are associated with large body size (Desender 1989b; Aukema 1991).

Work from other invertebrate taxa has suggested that there is a cost in terms of reproductive capacity for flight, with some macropterous females lysing their flight muscles and shedding their wings prior to reproduction, resulting in enhanced reproductive capacity. Among carabids, *Amara plebeja* autolyses its wings and can subsequently regenerate them to facilitate migration between breeding and over-wintering habitats (van Huizen 1977, 1979). This is supported by Matalin's (1994) observation that reproductive females from window traps invariably have fewer ova than those from pitfall traps. Matalin (1994) also concluded that the choice between flying and walking varies considerably between species and with different stages in the life cycle, with flight activity being favoured by dispersive young adults, shortly after emergence and, in *Harpalus rufipes* and *H. calceatus*, by mature males. Mature adults exhibit the highest walking activity during the breeding season, apparently being the favoured form of locomotion when seeking a mate (Matalin 1994).

Wing morphology alone is not sufficient to describe dispersal ability in carabids. Desender (2000) and Matalin (2003) studied the phenology of carabids in relation to flight muscle development. Desender (2000) investigated the trade-off between dispersal and reproduction in female carabids from the Belgian fauna, and most of the species he studied supported the oogenesis-flight syndrome, i.e. females with ripe ovaries tend not to possess functional flight musculature. This phenomenon was most pronounced for species that reproduce in late summer or autumn and emerge in late spring (Desender 2000). Matalin (2003) concluded that in females of large species, wing muscles decline during a period of increasing body mass, after development of the gonads.

In addition to the wealth of material on dispersal by flight, carabidologists have also investigated running activity, demonstrating that larger *Carabus* species run slower than smaller carabids, though in Pterostichinae and Harpalinae, larger species are faster (Mossakowski and Stier 1983). Temperature has a significant effect on running activity in *Carabus auronitens* (Althoff et al. 1994). Clearly the expression of dispersal ability in carabid beetles is highly complex, being governed by environmental and life cycle factors, in addition to genetic control. It is equally clear that there are still many unresolved issues regarding the dispersal of carabids and we are likely to see studies on this topic at future ECMs. In particular, ongoing land-use change and habitat fragmentation, exacerbated by the influence of climate change, mean stronger selective advantages for species with better powers of dispersal. A major challenge for the scientific community will be to discern evolutionary changes in response to this selective pressure. In conservation, the main challenge will be to develop strategies for the conservation of species with poor powers of dispersal.

4 Methods

4.1. Methodological approaches

Methods influence the way we approach, perceive, and understand the world. All methods have strengths and weaknesses, which make certain things to be easily noticed while others remain hidden or un-emphasised – and such effects of the methods on knowledge often go unnoticed or are unappreciated by researchers. Carabid research has long been dominated by observation and description, but there still remains much to be observed and described about carabids. However, the prevalence of certain methods in carabid research (e.g. pitfall trapping as a collection method, see below) has put a strong stamp on the amount and structure of our knowledge about carabids. Some of the resulting biases are mentioned below; this list is illustrative, not exhaustive.

Prevalence of knowledge about adults: Due to the epigaeic activity of the adults, and the fact that they are more easily collected, manipulated and kept in the laboratory, there is an overwhelming disparity about our knowledge on the ecology of the different life stages of carabid beetles. Our knowledge on carabids was (Lövei and Sunderland 1996) and remains primarily determined by knowledge about adults. A search on Web of Science with the term "carabid* OR ground beetl*" between 2000–2009 yield-ed 3186 papers, only 460 remaining when this was combined with the term "larv*" (search made by G Lövei, on 4 February 2011).

Geographical unevenness in the origin of our knowledge: This is a general phenomenon: we know that the tropics is more species rich, in general, than the temperate region (already mentioned by Darwin 1859), yet most of our research effort is still directed towards temperate ground beetles. Of the above computer search on ground beetles, only 80 of the original 3186 papers remained when the additional term "tropic*" was introduced. We can safely predict important new understanding emerging from more detailed studies performed in more southerly regions; many of the techniques formerly restricted to developed countries can now be usefully employed in more tropical areas.

Biased perception of carabids as predators: Predators and predation keep us fascinated, possibly because early humans have been both hunters and hunted. However, this colours our perception of the world (see *Carabid beetle food* above). In the case of carabids, the fact that many species will attack prey offered to them, especially in the laboratory, and that many beetles are indeed fast-moving predators, has led to a widelyheld belief that carabids are predators. Carabidologists (mostly) know better, but we have been a bit lax to actively dispel this notion among ecologists, natural historians, and the general public. In relatively recent literature, one still comes across this perception (Braun et al. 2004), and in some cases, elaborate theories are built on such shaky grounds (Lövei and Magura 2006).

The rarity of testable hypotheses: Due to a history of descriptive studies, there seems to be a general rarity of precisely formulated, testable hypotheses. Many studies have

the only justification that "we do not yet know, so let's find out". With increasingly fierce competition for funding and publication, such arguments do not carry much weight. An additional advantage of formulating hypotheses is that it forces us to think ahead: what is to be expected? Why? However, hypotheses should be well formulated (see Ford 2009; Underwood 2009). In the literature (not only in carabidology) one often encounters the "null hypothesis" formulated as "we expect no differences will be found". Do researchers really expect that "nothing will happen"? If so, why is the experiment worth performing? Indeed, in the real world the null hypothesis is rarely if ever true as there will always be differences between effects. What is of importance is the magnitude, i.e. effect size, and precision, i.e. confidence interval of the effect (Nakagawa and Cuthill 2007; Läärä 2009). The careful separation of hypothesis formulation vs. the Popperian way of arriving at scientific evidence should not be confused – but often is.

The overall task is unchanged: to understand what made carabids such an evolutionarily successful group. In order to answer this question, one has to quantitatively continue to document the patterns of occurrence of members of this group – this is a logistical, not a methodological challenge. Among the promising "methodological approaches", modern population genetical toolkits are well used, with several interesting results – it would be good to take these and use them in extra-European habitats as well. Gene expression study methods have recently developed and simplified considerably (Ouborg and Vriezen 2007), and facilitate the study of some interesting ecological questions, such as reaction to such factors as stress and food selection. Modern methods, such as those of ecological immunity, also allow a more refined characterisation of ground beetle reactions to habitat quality.

4.2. Analysing pitfall-trapped carabid data

Pitfall trapping is the best-known collection method used by carabidologists, especially in ecological studies (Lövei and Sunderland 1996). The method, originally described nearly 80 years ago (Barber 1931) and later often referred to as Barber traps (Thiele 1977), is cheap, easy to use and once set up, operates by itself. It allows for adequate replication in field-based studies, and collects large samples (see Fig. 2 for examples of a few commonly used pitfall traps).

One of the most convenient features of pitfall trapping is also its main disadvantage, because the resulting catch, although beguilingly countable, is not a measure of density, but of activity density. Carabidologists have recognised this and other drawbacks of pitfall trapping, which have often been discussed in the literature from Greenslade (1964), Thiele (1977) and Lövei and Sunderland (1996) to Holland (2002) and regularly at ECMs. However, the method has not been subject to rigorous, thorough testing, nor to a systematic review, and consequently, most carabidologists tip their hat at the problem, then proceed to ignore it, and often use sophisticated evaluation methods to answer important research questions. Need-



Figure 2. Different pitfall types. **A** = Jar or yoghurt can. **B** and **C** = traps with an outer can to make collecting of the sample easier. **B** = funnel trap with small jar. **C** = trap for moist biotopes (the outer can contains gravel or stones to prevent the can from being pushed up by groundwater). **V** = preservative (usually formaldehyde 3–4% or propylene glycol), **S** = stones or gravel.

less to say that if these drawbacks in pitfall-trapped samples remain unresolved, this brings into question any analysis using assemblage data, such as ordination techniques, diversity indices, the determination of dominance structure and any ecological analysis or testing of theory.

While the sharpening of research questions before starting trapping is a salutary piece of advice, which will also influence the type and arrangement of traps, some problems associated with pitfall traps for general carabid beetle studies have reached a general consensus. Several of the aspects below are, however, still ignored but could be easily fixed. These include that (i) an odourless preservative is preferred, because formalin, for example, seems to attract some species and repel others (Thiele 1977); (ii) the traps should have a cover to prevent flooding, desiccation, scavenging and bycatch – a funnel to prevent escape and reduce bycatch also helps (Lange et al. 2011); (iii) traps should preferably not be used solitarily, but placed in series of at least three to five traps at distances of less than 10 m apart in order to optimise the catch and to overcome occasional trap losses; (iv) distances between sampling plots (single traps or trap groups) should be large enough to allow for sample independence (this distance will, of course, depend on the dispersal power of the focal species, see e.g. Digweed et al. 1995); and (v) the question of missing samples that inevitably occur when large numbers of traps are used over long time periods (see below). Important challenges that await study and resolution are: (i) that trap numbers and length of the trapping period do not contribute equally to the catch (Lövei and Magura 2011); (ii) how to reliably minimise the impact of trapping on assemblages and protected species (the methods of partial seasonal samples and pulsating samples, for example, have been suggested: Sapia et al. 2005);

and (iii) the challenge of non-destructive carabid sampling (Bowie and Frampton 2004), such as radiotelemetry (see Negro et al. 2008).

The arrangement of pitfall traps in the field depends on the research question asked. The most popular research questions include: (i) Faunistic investigations intended to obtain an accurate species list of a given area. Here many pitfall traps should be used, also along gradients and at biotope edges; it seems that the spatial aspect is more important than the temporal one, i.e. it is better to have many traps for shorter periods of time than fewer traps for longer time periods (Lövei and Magura 2011). (ii) Community or gradient studies intended to investigate the (typical) fauna of different biotopes or at different positions along a gradient. In this case series of traps per biotope or gradient position can be used (Fig. 3a) with independent replicates (with sufficient distances between the series, see above). An example of this is the Globenet project (Niemelä et al. 2002). In some cases a row design with repeats will generate more precise information (Fig. 3b), especially when short-term movements of species along gradients are expected. The same holds for different treatments in an experimental design, such as (iii) Biological studies investigating e.g. the periodicity of one or more species within a year, to be eventually compared with different biotopes or years in phenological and/or climate studies (e.g. do species reproduce earlier or later during warmer periods or in different biotopes?). In the case of (iv) Biological studies investigating diurnal rhythms or movements of adults and larvae, a grid or matrix design (Fig. 3c) is recommended; and (v) *Population studies* intended to investigate the response of populations to biotic and abiotic environmental factors. Here, estimates of population densities are required and, as such, pitfall-trapped data need to be interpreted with caution.

The fact that pitfall catches are a function of the species' true population size and its activity (activity-density: Greenslade 1964; Thomas et al. 1998), creates specific statistical problems. Continuous sampling over the whole activity period can cause a potential-



Figure 3. Examples of pitfall trap placements across a forest edge.

ly serious problem when the catch is analysed. Trap losses can occur at any time during the activity period and have traditionally been dealt with by standardising the catch to 100 trapping days without taking into account variability in activity across the season (Kotze and Niemelä 2002; Niemelä et al. 2002). For example, some species are more active in the spring or autumn (see *Life history strategies and rhythms* above), while others are active throughout the summer months. As such, a trap lost at the beginning of the continuous sampling period will have a different effect on the estimated activity-density of a spring-active species, for example, than if the trap is lost at a later stage when activity is low. When the research question involves study of the response of separate species to an environmental gradient, statistical models in which seasonality (or visit) is added as a free factor and sampling effort (number of trapping days per visit) as an offset term, and in which the response variable is specified as following a negative binomial distribution, seem to correct for seasonality and trap losses appropriately.

The reason for specifying activity-density (or abundance) data as following a negative binomial distribution (and not a Gaussian distribution, as is often done) is that ecological field data (here counts of individuals or species) seldom follow the assumptions of classical parametric statistics (Dalthorp 2004). Carabid beetles (both in terms of abundance and species) are often aggregated in space (Niemelä et al. 1986, 1992; Thomas et al. 1998) and sampling them is likely to produce an expected variance that is greater than the expected mean. Such 'clumped' counts data appear to be most appropriately analysed by models that incorporate extra variation, such as the negative binomial distribution (see White and Bennetts 1996; Dalthorp 2004), or quasi-Poisson methods (Ver Hoef and Boveng 2007; e.g. Elek et al. 2010). Another important advantage of using methods designed for dealing with count data (negative binomial, Poisson) is that the response variable (number of individuals or species) does not need to be transformed to comply with the assumptions of parametric test statistics, such as analysis of variance, t-test or linear regression. Surprisingly, abundance and species richness data are often log-transformed for subsequent use in parametric test procedures, even though textbooks on statistical methods in ecology (Sokal and Rohlf 1995; Crawley 2003) recommend the use of the square-root transformation to normalise count data. Nevertheless, neither square root nor log-transformed count data (for use in parametric tests) performed as well as *non*-transformed data (for use in a negative binomial model) (O'Hara and Kotze 2010). A possible reason for this is that count data often contain many zero values, which have to be fudged (when a log transformation is performed) by adding 0.1 or 1 to every observation - which may have unforeseen effects on estimates.

Another problem occurs when the activity density results for different species are compared. Since each species reacts differently to pitfall traps, their "catchability" will also differ, subsequently with more or less incomparable results between species. A possible solution, suggested by Den Boer, is to standardise the catches per species over the sampling sites (Turin et al. 1991). After standardisation, with the obtained "relative abundances", multivariate methods (calculating (dis)similarities, clustering and ordination) can be used to analyse the data. Similar classifications have been carried out for Britain (Luff et al. 1989; Eyre and Luff, 1990; Mccracken 1994; Anderson et al. 2000). Although the approach of correcting and standardising the data was quite different from the Dutch method, the results for classification of the carabid habitats in the Netherlands and Britain were very similar. A study of the carabid fauna of Trento, Italy (Bonavita and Chemini 1996) in a deviating trans-alpine fauna, revealed highly corresponding results for the classification of the 48 (out of 57) species common to Italy and northern Europe. A relatively simple and flexible method developed by Dufrêne and Legendre (1997) to classify a Belgian dataset (the IndVal procedure), has the advantage that it is insensitive to the relative abundances of species. We contend that the problems associated with the comparison of assemblages sampled by pitfall trapping are still not fully resolved, but the above confirm that this method has merit in many types of investigations.

5 Population dynamics and long-term research

Since the 1960s the population dynamics of carabid beetles has been subject to the study of population persistence. During this time, discussion has revolved around how the size of populations and their fluctuations have been established, resulting in two popular theories. The first theory postulates that population sizes are balanced within narrow limits by density dependent processes, a feedback mechanism in which predators, parasites, competitors for food and other biotic aspects of the environment are involved, resulting in the regulation of population size (see Nicholson 1958). The second theory argues that the founding and re-founding of local populations take place, driven by dispersal, small population size and extinction, heterogeneity of the environment, the distinction between local (sub) and natural (entire) populations, and the genetic plasticity of species in relation to different components of the environment and to fluctuations of population size (Andrewartha and Birch 1954). Den Boer tested the latter theory by using carabid beetles as a model group. In 1959 he started pitfall trapping at several locations in the Dwingelderveld, a large area of heathland in the Netherlands, which he regarded as home to large natural populations of several carabid species. This founding/re-founding theory, the concept of metapopulation, states that natural populations consist of many local populations or colonies. Indeed, Den Boer was able to show that in a large area many local populations or interacting groups of carabids fluctuated in numbers of individuals in space and time. From these results the "spreading of risk" theory was derived (Den Boer 1968, see European Carabidologists' Meetings (ECMs) above).

The significance of dispersal in founding, re-founding and establishment of populations was confirmed during the first ECM (see Introduction). However, the role of density dependent processes was not resolved. In 1970 in Oosterbeek, the Netherlands, an entire symposium on the *Dynamics of Populations* (Den Boer and Gradwell 1971) was devoted to whether or not populations were regulated. Some contributors showed examples in which density-dependent processes seemed to govern the abundance of a species, whereas others showed the opposite, so the discus-

sion continued. Later on, again using carabid beetles, several studies were conducted to test the density dependence hypothesis. For instance Baars and Van Dijk (1984) were able to show that the number of eggs in the ovaries of females was negatively correlated with the mean density around pitfall traps. However, later on Van Dijk and Den Boer (1992) demonstrated that egg and larval mortality were too high to compensate for egg production. It was concluded that the density dependent relationship could hardly play an important role in the dynamics of the populations of Calathus melanocephalus, as shown by Baars and Van Dijk (1984). In Pterostichus oblongopunctatus the amount of food available affects the number of eggs laid. Heessen (1981) suggested that this would regulate population dynamics of this species. However, Szyszko (1981) and Den Boer (1986) observed that population explosions of certain prey species lead to a strong decline in some carabids. Vermeulen and Szyszko (1992) were able to show that in order to maintain a high level of egg production, P. oblongopunctatus has to switch prey. Presumably the right mixture of amino acids and the quality of nitrogen (White 1993) are essential for a high level of egg production. Another study on regulation in carabid populations was carried out by Brunsting et al. (1986). They showed that cannibalism occurs between larvae of *P. oblongopunctatus* and suggested that this phenomenon would regulate population size. However, Vermeulen (1986) could not find differences in raising P. oblongopunctatus under circumstances in which cannibalism was included and excluded, suggesting that larvae may not be actively searching for other larvae of the same species to feed upon. Cannibalism might take place only under extremely high, unnatural densities. Also, the role of competition in the population dynamics of carabid beetles has not been convincingly demonstrated so far. For example, Loreau (1990) found only weak evidence for competitive regulation in Abax ater populations. He suggested that competition might only be significant in dominant species. On the other hand, Den Boer (1980, 1985) and Niemelä (1993) showed that competition hardly plays any role in determining population size. The discussion on whether or not regulation plays an important role in population dynamics led to a second symposium on population dynamics, this time held in Poland in 1992 (Den Boer et al. 1993). However, again only a discussion for and against regulation resulted. After this meeting the subject quickly went out of fashion and was not discussed in this way again. In 1996, Den Boer and Reddingius wrote a book in which they reviewed all the population dynamic theories so far.

At present, it is generally accepted that the persistence of carabid populations depends on the availability of sufficient suitable habitat over long periods of time, as well as on habitat quality. The latter was nicely illustrated in the Dwingelderveld, the Netherlands. These heathlands have nitrified from the 1970s onwards, associated with an almost complete disappearance of *Carabus nitens* there. A few years after the removal of the nutrient-rich topsoil layer by sod cutting, however, this species was again recorded in high numbers (Van Essen 1993). A similar recovery is now seen in the Mantingerveld, the Netherlands, for the same species since 2007 (Rikjan Vermeulen, pers. obs.). Because of the turnover in local populations, dispersal is necessary for a given species to (re)colonise areas where habitat patches are small. The classical technique for investigating these processes has been mark and recapture. Using modern techniques, e.g. simulation programmes (Persigehl et al. 2004) and genetic techniques (e.g. Drees et al. 2011), the relationships between populations can be demonstrated more easily.

Permanently set-up pitfall traps give an impression of the activity of different species during different seasons and between years, and produce relative estimates of population fluctuations for a particular species. In 1959, several series of permanent pitfall traps were initiated in the Dwingelderveld and later, in 1963, in the Mantingerveld (Den Boer and Van Dijk 1994). Carabid beetles from these series were collected on a weekly basis. Results from the first 6-7 years showed considerable fluctuations in the total number of individuals of a particular species collected per series between successive years. This fluctuating pattern was also different between each separate catching series within an area in the same year. These observations of asynchronous fluctuations in catches of a particular species were instrumental in the development of the "spreading of risk" theory by Piet den Boer (see above). Environmental conditions since the establishment of these series also changed. At the end of the 1960s the ground-water table gradually receded and during the 1970s the effects of air pollution became apparent: increasing acidification and eutrophication of the upper soil layers and the subsequent replacement of both Calluna and Erica by grasses. At the end of the 1980s, the local nature management authority started to artificially raise the water table, which subsequently reached its pre-1960s level during 2010-2011. At the same time the grassy vegetation, together with the polluted top soil layer, was removed by sod cutting, and grazing by cows and sheep has subsequently been introduced. Moreover, the average temperature of the area had increased by 1 °C in the last few decades. Both the increase in temperature and the hours of sunshine appear to be significant from 1988 onwards (Prins et al. 2007).

Since the establishment of these series of pitfall traps, the composition of the carabid beetle fauna has changed continuously. In the beginning of the 1970s species such as Agonum krynickii, Carabus cancellatus, Cicindela sylvatica and C. germanica disappeared completely from the catches, followed by Amara quenseli and A. praetermissa. During the same period, species such as Carabus nitens, Harpalus solitaris and Amara *infima* decreased significantly in numbers. The climate did not change significantly during this period, and it can be speculated that changes in the environment, as mentioned above, and habitat fragmentation (in the case of Hullenzand, Mantingerveld) may be responsible for these local extinctions and changes in population numbers. From the end of the 1990s, species such as Agonum ericeti, Cymindis vaporariorum and *C. macularis* disappeared from the catches. This may be a consequence of climate change, since during this period environmental conditions in the heathlands improved. This is well illustrated for *Carabus nitens*, which became rather abundant during this period, as well as for C. arvensis, Nebria salina and H. solitaris. From 1990 to 2004, ten species not previously recorded from these areas have been collected (Vermeulen et al. 2004). Recently, two records of Agonum viridicupreum can be added to this list (Rikjan Vermeulen pers. obs.). Apart from one, all of these newly recorded species have their

center of distribution south of the Netherlands, suggesting that their appearance is related to climate warming. Similarly, the virtual disappearance of the northern species, *A. ericeti*, may be related to this phenomenon. Adequate management may, to a limited extent, compensate for the effects of climate change. The northerly distributed *C. nitens* that almost disappeared from both the Mantinger- and Dwingelderveld, made a rapid comeback after top-soil removal and sod-cutting.

However, the dramatic decline and extinction of the highly hygrophylic *Carabus clatratus* in Italy may not be entirely related to climate change. *Carabus clatratus* is one of the most localised and endangered carabid species in Europe, and its disappearance from Italy, and possibly also France, is possibly a consequence of the colonisation of its wet biotopes by the alien red swamp crayfish, *Procambarus clarkii*, which preys on adults of *C. clatratus* (Casale and Busato 2008).

Long-term data on weekly catches can also be used to monitor phenological changes in species. For example, compared to the period prior to 1988, the activity of *Amara equestris*, *C. arvensis*, *Poecilus lepidus* and *P. versicolor* started earlier in the season.

As far as the consequences of climate change, management and other environmental changes are concerned, it is of great importance to continue long-term observational studies of carabid beetles, such as that in Drenthe, so that future changes can be monitored and possibly explained. Such long-term sampling programmes for carabid beetles are also known from Poland, Germany and Italy.

6 Bioindicators

Carabids are excellent model organisms for research on ecological and conservation theory. These beetles readily respond to abiotic and biotic variation, and to disturbances and management (e.g. Lövei and Sunderland 1996; Rainio and Niemelä 2003). This evidence has led many to suggest carabids to function as 'indicators'. An indicator is a taxon or a structure "*whose characteristics* (...) *are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest*" (Landres et al. 1988). However, using this definition many, if not most, of carabid 'indicator' studies appear to only demonstrate individualistic responses to environmental variation. But instead of investing resources for finding new indicator taxa, environmental managers should test and select taxa that are already well known and easily sampled, and that cover multiple dimensions of biodiversity (Taylor and Doran 2001), and critically evaluate their indicator functioning (Langor and Spence 2006). Carabids fulfil the former but the latter aspect requires further attention.

European carabids have certain qualities that make them good candidates for indicators. They are taxonomically well known, with relatively stable systematics, and their ecology has been widely studied (Lövei and Sunderland 1996). Variation in carabid morphology, life history strategies and small-scale abiotic and biotic requirements are extensively documented (e.g. Lindroth 1961–1969, 1985, 1986). Carabids also respond predictably to not only small-scale but also to landscape- and even continent-level phenomena (e.g. Hengeveld 1987; Kotze and O'Hara 2003; Koivula and Spence 2006). Moreover, they are relatively easy to collect in high numbers using standard methods. But can carabids reflect environmental variation in ways useful for conservation assessment purposes? Knowledge of carabid indicator functioning, using the categories listed in Lindenmayer et al. (2000), is briefly summarised below (see Koivula 2011 for a complete evaluation).

i. Taxon indicators. The presence of a taxon indicator reflects the presence of a set of other species, and its absence indicates the lack of the entire set of species. Perfect multi-taxon richness overlaps may be rare (e.g. Jonsson and Jonsell 1999; Sætersdal et al. 2005; Similä et al. 2006), which highlights the importance of using multiple taxa in environmental assessments (Taylor and Doran 2001; Duelli and Obrist 2003). Carabid functioning as taxon indicators mostly relies on weak correlations among taxa.

ii. Keystone indicators. These species affect their environment disproportionately strongly relative to their abundance. In field and laboratory conditions, carabids forage on slugs and pest insects (e.g. Kromp 1999). Hance (1987) showed that, using enclosures with different carabid densities, carabids have the potential to significantly prey on pest insects foraging on crop plants with economic benefits.

iii. Pollution indicators. These taxa reflect human-altered abiotic conditions. Heavy metals in the soil negatively affect carabids (e.g. Maryański et al. 2002; Ermakov 2004), and in agro-ecosystems, pesticides and fertilizers affect carabids, at least in the short term (e.g. Huusela-Veistola 1996; Kromp 1999).

iv. Dominant indicators. These taxa make up much of the total biomass or the number of individuals in an area of interest and predict particular ecosystems or assemblages. Many common carabid species are succession and habitat-type generalists (Lindroth 1985, 1986; Niemelä et al. 2007), so their numbers may not indicate aspects useful for conservation or management. Mean Individual Biomass (MIB), on the other hand, links carabid biomass to succession without considering species entities (Szyszko et al. 2000). However, the 'behaviour' of MIB along succession should be examined in detail before applying it in conservation and management.

v. Environmental indicators. These should reliably reflect particular environmental conditions. Although carabids have the potential to reflect soils, wetness and habitat-type variation (e.g. Thiele 1977; Lindroth 1985, 1986), they cannot currently compete with plants as indicators of these factors.

vi. Early-warning signallers (true bio-indicators). These taxa are extremely sensitive to changing environmental conditions. Carabid evidence is scarce, but some carabids have apparently undergone shifts of tens of metres in altitude over 10–20 years (Assmann 2009; Pizzolotto 2009, David Kavanaugh, pers. comm.), coinciding with climate warming (Parry et al. 2007, see *Population dynamics and long-term research*
above). These observations suggest good potential in, for example, climate-change and urban-spread research.

vii. Disturbance indicators. These taxa reflect natural and human-caused disturbances. Carabids readily respond to agriculture and forestry (for reviews, see Lövei and Sunderland 1996; Kromp 1999; Niemelä et al. 2007). Their indicator functioning may hold at a general level: they respond similarly to environmental change as many other taxa do (e.g. Barbaro et al. 2005). But indicators should not be used for self-evident patterns: the ecological impact of clear-cutting, for example, does not require an indicator.

Clearly, carabids have good potential for becoming useful indicators for conservationists and environmental managers. Certain obstacles still need to be overcome. First, the functioning and accuracy of carabids to predict habitats or species requiring conservation action should be critically evaluated. According to the indicator definition of Landres et al. (1988), none of the above examples indicate that carabids function as particularly useful indicators. Thus, for a conservationist, carabid responses should be considered as individualistic as long as there is no evidence for their responses to reliably predict responses of threatened taxa or particular, difficult-to-observe conditions. This is important because there is very little room for error if threatened species or habitats are at stake. Strict tests must thus be applied to evaluate indicator functioning (Langor and Spence 2006). Second, the relationship between carabid responses and other taxa should be considerably clarified (Rainio and Niemelä 2003) before using these beetles in environmental assessments. Third, it is unclear whether carabids reflect aspects not attainable using other indicators (apart from their individualistic response) and whether conditions exist under which carabids really are the most cost-efficient indicator taxon. Currently widely used, easy-to-use, relatively cheap and economic tools for assessing the state of the environment include vegetation, habitat structural elements, satellite and aerial photos, as well as weather and land-use inventory data.

The focus of carabidologists should perhaps be changed from total species richness to the indicator potential of single species, groups of specialists or functional groups. We lack an explicitly defined 'niche' of these beetles in environmental assessment protocols. Cases for carabids fulfilling the conservationists' definition for a useful indicator (Landres et al. 1988) will possibly be documented in the near future, but their indicator functioning may always remain context specific.

7 Carabid conservation, protection and habitat management

Conservation may mean protecting particular species or patches of habitat against alteration, generally human-caused, but the term may also include operations characterised by an active human role (e.g. Freitag and Kavanaugh 1993; Den Boer and Van Dijk 1994; Sutherland 1998; Gaston and Spicer 2004). Examples include the maintenance of areas of high natural value, the restoration of patches to a state they are presumed to once have represented (often referred to as 'natural' state), and the artificial conversion of one habitat type to another. The latter may be required in landscapes where habitat for a threatened species has become rare (see Negro et al. 2008) and new habitat patches are unlikely to appear through natural processes. Such cases might be found, for example, within urban areas. These active operations of patch maintenance, restoration and creation are collectively called 'conservation management'.

Insect conservation management is a relatively new research discipline, both generally and in the context of carabid beetles (e.g. Lewis et al. 2007; Leather et al. 2008; New 2010). The restoration and artificial creation of habitats - two elements of conservation management - have been important components of carabid conservation since the 1980s (e.g. Thomas 1990; Främbs 1990; Blake et al. 1996). Conservation became an important topic for the ECMs since the Hungarian meeting in 1986. Before that meeting, conservation issues were only occasionally discussed, but from then on, both conservation in general (e.g. identifying diversity hotspots and gathering data on endemic and rare species) and practical conservation management in particular have been among key topics and have altogether consistently made up over 20% of papers in the proceedings. Generally, almost any piece of knowledge on carabid ecology can be applied in conservation-management policy and action to support these beetles and associated epigaeic fauna. In Europe and North America, information necessary for efficient conservation - on carabid ecology and threats - is readily available (Maelfait et al. 1994; Lövei and Sunderland 1996; see also national lists of threatened species). However, the functioning of active management for the benefit of threatened carabid species urgently demands critical evaluation and detailed information. For instance, according to Desender et al. (2010), the decline of carabid beetles in Belgium between the period <1950 and 1950–1985, had halted for a considerable number of species. During the period 1986–2008, however, 60% of these species still had not reached the same distribution area as in the first half of the 20th century, notwithstanding many initiatives and large scale active management. Most of these species now only occur in large and high-quality nature reserves with the last remnants of semi-natural biotopes and have, at present, little or no possibilities to further increase their distribution range.

Here the advances in conservation management, mostly as derived from the proceedings of the previous ECMs are discussed under four topics: (i) Which species characteristics are particularly associated with threatened species? (ii) In which habitat types can conservation of carabids best be realised? (iii) What do we know about habitat connectivity as a way to conserve carabids? (iv) How does conservation management of habitats affect carabids?

i. Ecological and habitat characteristics of threatened species. To study which ecological and habitat characteristics of carabids are associated with species being threatened, national species lists and their IUCN categories for five countries are used as examples: Belgium, Sweden, Denmark, Norway and Finland (respectively Desender et al. 2008a, b; Gärdenfors 2005; Pedersen and Wind 2009; Kålås et al.

2006; Rassi et al. 2001). This dataset is complemented with four regional lists of threatened species from Niedersachsen and Bremen, Germany; Nordrhein-Westfalen, Germany; Wadden Sea area; and a preliminary red list for Drenthe, the Netherlands (respectively Assmann et al. 2002; Schüle and Terlutter 1998; Mahler et al. 1996; Noordijk and Vermeulen 2009). For analytical purposes, species characteristics were collected from Lindroth (1985, 1986), Desender (1986), Turin and Den Boer (1988), Desender and Turin (1989), Turin (2000), Anonymous (2006) and Desender et al. (2008a). Several characteristics were evaluated, such as the roles of body size, wing morphology, and associations with shadiness and moisture. This evaluation was done by calculating percentages per size, wing morphology, shadiness and moisture classes for all species (for the five countries), for species classified as threatened by IUCN categories NT (Near Threatened), VU (VUlnerable), EN (ENdangered), CR (CRitically endangered) and EW (Extinct in the Wild; also RE, i.e. Regionally Extinct, in some national lists), and also the proportion of threatened species over all species within a given class. Occasionally, certain information for some species was lacking and these were (partly) removed from the analysis. For example, if for a certain species information was unavailable on wing morphology, it was omitted from the wing morphology analysis but retained in other analyses.

Carabids mostly fell into mid-size classes (43–46% of all species were 4.1–8.0 mm and 28–31% were 8.1–16.0 mm), were macropterous (64–71%) and were associated with open areas (63–64%), but were quite evenly distributed among moisture-association classes (see columns "All" in Table 3). Carabids classified as being threatened roughly complied with these figures (columns "IUCN" in Table 3): also these species were mostly mid-sized (26–50% were 4.1–8.0 mm and 24–39% were 8.1–16.0 mm), macropterous (64–81%) and open-area associated (63–79%; very shady habitats had only 2–12%). However, threatened species were more often associated with either very wet (34–53%) or very dry habitats (32–47%) than with "average" or moist/dryish conditions (12–30%). This dichotomous association with both very dry and very wet habitats was much more pronounced in the four Nordic countries and in the two areas in Germany than in Belgium or in Drenthe (Table 3).

The proportion of threatened species over all species in the five countries revealed some important issues (columns "% IUCN" in Table 3). First of all, relative to the total number of species per category, larger species tended to be more often threatened than smaller species (see Kotze and O'Hara 2003). For size classes 8.1–16.0 mm and >16 mm, the proportions of threatened species were 21–39% and 12–50%, respectively, whereas for the size classes 0.1–4.0 mm and 4.1–8.0 mm, they were 10–18% and 7–25%, respectively. After pooling species into larger (>8.1 mm) and smaller (0.1–8.0 mm) size classes, proportions of these were between 19–40% (mean 28%) and 8–23% (mean 16%), respectively. Regarding wing morphology, the proportions of threatened species were rather even among the categories. In this respect, wing morphology was not clearly related to species being threatened, except for the slight tendency of wing-polymorphic species being proportionally more frequently threatened in Denmark and brachypterous species in Norway. Regarding shadiness associations, open-area species

Table 3. Morphological and habitat-association characteristics of all carabid species found in a given area ("All" columns; % of species), of species classified as threatened according to the IUCN ("IUCN"; categories NT, EN, VU, CR and EW pooled; % of species), and proportion of threatened species of all species within a given category ("% IUCN"). For example, the value "50" for BEL % IUCN >16 mm indicates that in Belgium, of all species with body size >16 mm, 50% are considered threatened. Values for "All" and "IUCN" columns make up 100% for each area/country. BEL = Belgium; SWE = Sweden; DEN = Denmark; NOR = Norway; FIN = Finland; Niede = Niedersachsen and Bremen, Germany; Nordr = Nordrhein-Westfalen, Germany; Wadde = Wadden Sea area; and Drent = Drenthe, the Netherlands (proposed Red Data list). For the last four areas, only species classified as threatened according to the IUCN are shown. For species and their characteristics data, see text.

		BEL			SWE			DEN		
			%			%			%	
Classes	All	IUCN	IUCN	All	IUCN	IUCN	All	IUCN	IUCN	
Body size										
0.1-4.0 mm	18	13	18	19	16	14	19	9	13	
4.1-8.0 mm	44	40	25	44	31	11	43	38	25	
8.1-16.0 mm	31	35	31	29	40	23	30	41	39	
>16 mm	7	12	50	8	13	28	8	12	46	
Wing morpho	logy									
Macropt	71	69	23	68	69	15	66	68	29	
Poly/dimo	16	18	26	19	19	14	14	16	33	
Brachypt	13	13	23	13	12	13	20	16	23	
Shadiness										
Shady (forest)	11	8	24	11	11	17	11	10	25	
Generalist	26	23	29	25	11	7	25	26	29	
Open	63	69	36	64	78	20	64	64	28	
Moisture					1					
Water/wet	39	35	29	38	35	15	37	42	32	
Moist-dryish	29	23	26	30	18	10	31	22	20	
Dry	32	42	43	32	47	24	32	36	30	
		NOR			FIN		Niede	Nordr	Wadde	Drent
			%			%				
Classes	All	IUCN	IUCN	All	IUCN	IUCN	IUCN	IUCN	IUCN	IUCN
Body size										
0.1-4.0 mm	18	13	13	18	15	10	19	17	19	16
4.1-8.0 mm	46	38	15	45	26	7	44	40	50	33
8.1-16.0 mm	28	36	24	31	53	21	30	34	24	39
>16 mm	8	13	30	6	6	12	7	9	7	12
Wing morpho	logy							-		
Macropt	64	63	16	70	81	12	71	74	74	64
Poly/dimo	21	16	13	17	15	9	17	14	21	21
Brachypt	15	21	23	13	4	3	12	12	5	15
C1 1.										
Shadiness	I		1							
Shadiness Shady (forest)	10	9	15	10	3	4	6	7	2	12
Shady (forest) Generalist	10 26	9 21	15 15	10 27	3 21	4 9	6 28	7 30	2 19	12 21
ShadinessShady (forest)GeneralistOpen	10 26 64	9 21 70	15 15 20	10 27 63	3 21 76	4 9 15	6 28 66	7 30 63	2 19 79	12 21 67
ShadinessShady (forest)GeneralistOpenMoisture	10 26 64	9 21 70	15 15 20	10 27 63	3 21 76	4 9 15	6 28 66	7 30 63	2 19 79	12 21 67
Shadiness Shady (forest) Generalist Open Moisture Water/wet	10 26 64 37	9 21 70 47	15 15 20 22	10 27 63 40	3 21 76 47	4 9 15	6 28 66 46	7 30 63 51	2 19 79 53	12 21 67 31
Shadiness Shady (forest) Generalist Open Moisture Water/wet Moist-dryish	10 26 64 37 32	9 21 70 47 17	15 15 20 22 10	10 27 63 40 30	3 21 76 47 12	4 9 15 14 5	6 28 66 46 16	7 30 63 51 17	2 19 79 53 14	12 21 67 31 30

included proportionally slightly more threatened species than did species of very shady habitats or shadiness generalists. Regarding moisture associations, species associated with very dry habitats included proportionally more threatened species (17–43%) than wet-habitat species (14–29%) or moist/dryish-habitat species (5–26%).

To the extent one can generalise from these figures, in northern and western Europe (see also Casale and Busato 2008 for southern Europe) particular attention should be paid to large carabids, species associated with very dry, open habitats (e.g. sand dunes, heathlands and calcareous meadows; see national Red Lists) and water-associated species (e.g. freshwater stream specialists and salt-marsh species; see national Red Lists). However, as is evident from the variation in percentages presented in Table 3, particular targets of conservation and management (habitat types and species) should vary from one area to another. Below, research-based evidence on how to protect these carabids by the application of conservation management is reviewed.

ii. Habitat selection for conservation efforts. Undisturbed mature ecosystems, particularly nature reserves, are vital for the conservation of many carabid species (e.g. Desender 2005; Skłodowski 2006). Also edge habitats and habitat mosaics may be important for carabid conservation (e.g. Kotze 2000; Falke et al. 2000; Hatteland et al. 2005; Andorkó and Kádár 2006). The scarcity of certain habitat types has increased the need for active maintenance of remaining patches. For example, Bérces et al. (2008) used field and museum data, original research and communication among entomologists, and showed that *Carabus hungaricus* can best be protected by active management of open meadows. Due to the on-going loss of natural and semi-natural areas and the intensification of agricultural practices in many countries, also particular anthropogenic habitats have become important for carabid conservation. Examples include roadside verges, former agricultural fields, urban waste-grounds, and sand and gravel pits (Plachter 1986; Eversham et al. 1996; Telfer and Eversham 1996; Schwerk 2000; Versteirt et al. 2002; Koivula and Kotze 2005).

iii. Habitat connectivity. Habitat-patch isolation and fragmentation may be of major concern for carabids (De Vries 1994; Kinnunen et al. 1996; Noordijk et al. 2006; Hendrickx et al. 2009). A number of means of reducing the impact of fragmentation have been suggested (Vermeulen et al. 2002). For forested environments, Terlutter (1990) discovered for *Carabus auronitens* two different gene flows from two old forest remnants into a recent, regenerated forest-field mosaic. Later on, Petit (1994) underlined the importance of hedgerow networks for forest carabid assemblages. However, more recent hedges may be sub-optimal for this purpose (Thiele 1971; Gruttke 1994). For open areas, on the other hand, Vermeulen and Opsteeg (1994) showed that roadside verges might be used either as habitat or as movement corridors connecting heathland patches. Both purposes may be served by roadsides, as shown by Koivula (2002a, 2005) for Finnish forest roads and Noordijk (2009) for highway verges in the Netherlands. Moreover, Vermeulen and Spee (2005) stressed the importance of source habitats for nature restoration sites. Hence, the remaining patches of natural

habitat, corridors of similar, often man-made environments, and artificially created, larger patches may together form an efficient patch network for carabid conservation.

iv. Habitat management. Because many important natural processes (wildfire, flooding, wind, grazing and insect outbreaks) are effectively prevented in many areas, particularly in urban environments, active maintenance is considered necessary to preserve certain vegetation types. Carabids respond varyingly to these efforts (Versteirt et al. 2002; Cuesta et al. 2006; Taboada et al. 2006a). The effects of grassland management were discussed in depth by Rushton et al. (1990) who found that some species avoid intensively managed sites, some are favoured by these, while others showed intermediate or no detectable responses. Similarly, Blake et al. (1996) showed that vegetation management in wildflower meadows resulted in a decrease in large species and an increase in xerophilous species, while species characteristic of areas with 'natural' conditions were absent. Like mowing, grazing also profoundly affects carabids: its intensity determines assemblage composition (McFerran et al. 1994). Cole et al. (2006) showed that intensive grazing decreases the abundance of large Carabus species more than less intensive grazing. These studies indicate that variation in management leads to variation in carabid beetle assemblages. In riparian environments, Fuellhaas (2000) showed that raising the water-table level increases the number of hygrophilic species. Främbs (1990) studied regenerating peat bogs and found that although carabid diversity increased, the peat-bog specialist Agonum ericeti remained absent. Drees et al. (2007) argued that this might be related to habitat quality, in this case the lack of peat-producing vegetation.

To summarise, (i) Carabid conservation should give special attention to very large species, and species associated with both very wet and very dry, exposed conditions, (ii) Old and undisturbed natural areas are important for many specialists, but conservation of pioneer or open-habitat species can be realised in many anthropogenic areas as well (Fig. 4), (iii) Fragmentation potentially isolates local populations, but its effects can be decreased by maintaining large, inter-connected areas, corridor networks, and designing restoration areas near potential source areas, and (iv) Guidelines for active management of carabid habitats are difficult to draft, as some species respond negatively to any disturbance, including conservation management. However, many species urgently need small-scale management that keeps habitats constantly at some preferred successional phase; most of these species are subject to severe stress in modern, fragmented landscapes.

The conservation of carabids and their habitats is far from perfect. This issue is complicated by the fact that, due to these beetles' mobility, occupation of varyingly sized habitat patches, varying degrees of specialisation, and development through numerous developmental phases, their ecological requirements vary in time and place. As habitat patches of carabid assemblages usually include several vegetation types and/or physical structures, a conservation approach targeted for maintaining only particular vegetation types or high plant diversity may not always be appropriate for the conservation of arthropod assemblages (Panzer and Schwartz 1998; Dennis et al. 2007). Moreover, the



Figure 4. Cylindera germanica (Photo by Jinze Noordijk)

high number of carabid species, each with specific demands, makes it difficult to define a single conservation strategy. Protection of whole landscapes with mosaics of distinct habitat types may prove efficient for carabid conservation. Simultaneously, the natural variety of successional stages should be conserved, as particular stages can be crucial for certain species (cf. Niemelä et al. 2007). Moreover, some species – such as *Amara plebeja* (van Huizen 1977) – possibly require more than just one habitat type and/or successional stage to persist in a landscape ('landscape species'; Szyszko 2004; Szyszko et al. 2011; Axel Schwerk, pers. comm.). Habitat patches within these mosaics should include particular structures, such as micro-relief, patches of bare sand, stony patches, small water bodies, heaps of decaying plant material, and dead wood, features that are often of no special importance for plants and vertebrates and therefore often ignored if conservation management is based on vegetation data alone. Thus, a broad landscape approach, supplemented by these small-scale structures, may produce good results for the conservation of carabid beetles (Kirby 1992; New 1995, 2010; Samways 2005, 2007; Haslett 2007).

8 Landscape ecology

How carabid beetles perceive space may influence habitat selection, home ranges, the dispersal of individuals and the dynamics and distributions of populations. Furthermore, the amount, extent and spatial arrangement of suitable habitats within a land-scape (i.e. landscape composition and configuration) may affect long-term population

persistence. Thus, although the spatial distribution of carabid beetles may be primarily determined by microhabitat conditions and biotic interactions at the local scale, identifying general patterns of carabid responses to landscape features may help us to understand how species, functional groups and assemblages effectively distribute, and to predict how they will cope with current and future land-use and climatic changes. As such, the spatial context related to a species' distribution patterns is an essential component when studying how global changes affect carabid species conservation.

Over the last 40 years, investigations of ground beetle landscape ecology have demonstrated that landscape features influence not only the spatial distribution of these beetles, but also their population dynamics (Matalin 1997c; Bommarco 1998) and genetic structure (Brouat et al. 2003; Keller et al. 2004; Desender et al. 2005; Sander et al. 2006). From the late 1950s until the mid 1970s, contributions to carabid beetle ecology aimed at characterising the structure and composition of communities occurring in specific types of landscapes, which were, at that stage, considered as homogeneous entities (e.g. forested vs. open landscapes; see Thiele 1977). Research developed in the 1980s and 1990s confirmed the significance of heterogeneity within landscapes and thus addressed the role of singular landscape elements or habitat types for the carabid fauna in a variety of either natural or highly-modified and simplified landscapes. In tests of the application of the theory of island biogeography (MacArthur and Wilson 1967) to carabid communities, it has been shown that local communities are not simply a passive random sample of the regional species pool, but that species are filtered according to the association of their life history traits to habitat quality, configuration and biotic interactions (e.g. Ranta and Ås 1982; Niemelä et al. 1985; De Vries et al. 1996). Studies that have looked for an island effect in carabid assemblages of patches of terrestrial habitats have generally concluded that such patches are not sufficiently isolated to represent islands, due to the strong dispersal capacity of many carabid species (Davies and Margules 1998; Magura et al. 2001; Brose 2003). Studies have also been conducted on carabid assemblages of real islands, and these too have concluded that a simple species-area relationship explains the differences in carabid species richness between islands of different size better than distance from mainland populations (Kotze and Niemelä 2002; Zalewski 2004).

In recent literature, studies on the importance of the landscape context in determining the occurrence of carabid species based on different aspects of landscape composition, configuration, connectivity, history, land-use type and intensity have proliferated (e.g. Purtauf et al. 2004; Bräuniger et al. 2010; Gardiner et al. 2010; Nabe-Nielsen et al. 2010; Woodcock et al. 2010). Many studies analysed the influence of the landscape context on overall carabid beetle activity density and species richness, often finding no statistically significant effect. Mostly, changes in landscape features have been related to shifts in carabid species composition, and variations in the activity density of individual species and ecologically meaningful groups (e.g. Niemelä 2001; Kotze and O'Hara 2003; Niemelä et al. 2007; Niemelä and Kotze 2009).

Agricultural landscapes in particular, driven by daily, seasonal and annual fluctuations, soon became the subject of many carabid beetle surveys, followed by an extensive number of publications to date (e.g. Kinnunen et al. 2001; Holland 2002). In general, the basic composition of the carabid fauna of agricultural mosaic landscapes appears to be surprisingly similar across countries (Luff 2002), dominated by eurytopic species, which are highly tolerant to disturbance. However, the size, amount, isolation and spatial arrangement of agricultural patches, the composition of the arable mosaic, as well as the occurrence of permanent landscape elements (e.g. hedgerows, field margins, natural woodlands and grasslands), affect carabid beetle assemblages (Kinnunen et al. 1996, 2001; Burel et al. 1998; Petit and Usher 1998; Fournier and Loreau 2001; Millán de la Peña et al. 2003; Aviron et al. 2005; Purtauf et al. 2005; Griffiths et al. 2007; Hendrickx et al. 2007; Saska et al. 2007).

In forest ecosystems, natural and anthropogenic disturbances create a dynamic mosaic of successional habitat patches for carabids (e.g. Bouget and Duelli 2004 for windstorm disturbance). Each forest successional stage is characterised by a specific carabid assemblage, in terms of species composition as well as ecological group composition, with the greatest differences between early and advanced stages (e.g. Szyszko 1990; Niemelä et al. 1996; Butterfield 1997; Koivula et al. 2002; Du Bus de Warnaffe and Lebrun 2004; Richard et al. 2004; Magura et al. 2006; Taboada et al. 2008). Changes in population dynamics and morphological traits also take place through succession (e.g. Szysko et al. 1996 for Pterostichus oblongopunctatus, Table 4). Changes in the carabid fauna are possibly correlated with the amount of carbon accumulation in the forest system, i.e. in the wood, litter and mineral soil (Szyszko 2010; Szyszko et al. 2011). The increase of carbon in the mineral soil is related to the decomposition of litter by the macrofauna. For pine stands in Poland, Szyszko (1986a) demonstrated that biomass of the macrofauna is correlated with parameters of the carabid fauna, such as species number and Mean Individual Biomass (MIB). MIB increases as succession progresses (Szyszko 1986b; Szyszko et al. 2000; Szyszko 2004), suggesting that this measure functions as a good indicator of the state of succession (see Bioindicators above). The rate at which species composition changes during succession and the successional trajectory followed by the carabid assemblages depends on environmental conditions, such as soil properties (Szyszko 1986b, 1990; Schwerk 2008), dominant tree species (Du Bus de Warnaffe and Lebrun 2004), and the type of disturbance that initiated the succession (Du Bus de Warnaffe and Lebrun 2004). Indeed, the larger the newly-created gap is and the fewer trees retained, the more severe the perturbation for carabid assemblages (Koivula 2002b following timber harvest; Bouget 2005 and Skłodowski and Garbalińska 2010 following windthrow gap). As a consequence, the maintenance of a variety of successional phases of the forest cycle results in increased heterogeneity at the landscape level and, therefore greater regional carabid diversity (e.g. Mullen et al. 2008; Taboada et al. 2008). Thus, the effects of forest landscape features on the carabid fauna have also been extensively addressed as regards to landscape heterogeneity, the occurrence, composition and spatial configuration of either natural or human-modified habitats (e.g. proportion of deciduous vs. coniferous forests, age and extent of exotic plantations, forest edge density and permeability), the role of particular landscape elements (e.g. retention tree groups), and the landscape context

Table 4. Changes in carabid fauna, interaction groups and populations of *Pterostichus oblongopunctatus* with changes in habitat (according to Szyszko et al. 1996, reprinted and modified with permission from Aarhus University Press).

Comparatively early stage of succession				Comparatively late stage of succession							
Carabidae fauna											
low state of development of fauna	\rightarrow			high state of development of fauna							
high number of species		\rightarrow	low number of species								
small individuals	\rightarrow			large individuals							
low mean individual biomass (MIB)	\rightarrow			high mean individual biomass (MIB)							
Interaction group of Pterostichus oblongopunctatus											
long period of activity		\rightarrow	short period of activity								
long survival of adults		\rightarrow	short survival of adults								
complicated age structure		\rightarrow	simple age structure								
small individuals (imago)	\rightarrow			big individuals (imago)							
high proportion of males	\rightarrow			high proportion of females							
low number of eggs in ovaries	\rightarrow			high number of eggs in ovaries							
high number of eggs laid?	\rightarrow			low number of eggs laid?							
good food situation for adults?	\rightarrow			bad food situation for adults?							
bad food situation for larvae?	\rightarrow			good food situation for larvae?							
unable to fly?	\rightarrow			able to fly?							
uneconomic life strategy	\rightarrow			economic life strategy							
Populations of Pterostichus oblongopunctatus											
asynchronously fluctuating interaction groups	\rightarrow	synchronously fluc- tuating interaction groups	\rightarrow	asynchronously fluctuating interaction groups							
low probability of high fluc- tuations of numbers	\rightarrow	high probability of high fluctuations of numbers	\rightarrow	low probability of high fluc- tuations of numbers							
resistant population	\rightarrow	not very resistant population	\rightarrow	resistant population							

resulting from historical and/or recent management practices (Koivula et al. 2002; Bouget 2004; Barbaro et al. 2005; Matveinen-Huju et al. 2006; Taboada et al. 2006b; Barbaro et al. 2007; Niemelä et al. 2007; Fuller et al. 2008; Pawson et al. 2008; Barbaro and van Halder 2009).

Much effort has been devoted to investigating how carabid beetles are distributed in fragmented landscapes and insular environments (for reviews, see Niemelä 2001 and Kotze 2008, respectively). Carabid responses to fragmentation depend on the geographical context, are species specific and, to a great extent, relate to species' life history traits and habitat associations (e.g. Koivula and Vermeulen 2005; Gaublomme et al. 2008). In a fragmented landscape context, mobility is crucial for persistence, especially for specialist and scarce species (De Vries 1994; De Vries et al. 1996). In general, good dispersers and abundant species are expected to maintain populations in small and isolated patches through recolonisation of empty patches, whereas poor colonisers and scarce species may not be able to do so (Den Boer 1977; Niemelä 2001). Hostile types of matrix or linear elements in the landscape can act as dispersal barriers for specialist species. For instance, some forest species are reluctant to cross highways (Mader 1984; Koivula and Vermeulen 2005) or open habitats (Plat et al. 1995; Riecken and Raths 1996), while other stenotopic species effectively move along hedgerows (Burel 1989; Plat et al. 1995; Charrier et al. 1997) and roadside verges (Vermeulen 1993, 1994; Vermeulen and Opdam 1995), which function as movement corridors for such species. Dirt roads in forested landscapes may serve as dispersal corridors for open habitat species (Koivula 2002a), and roadsides overgrown with poplars have been suggested to serve as corridors for forest species with low dispersal power (Dymitryszyn et al. 2003). Attempts to improve the connectivity of landscape elements by means of corridors may have contrasting effects on different carabid species according to their habitat requirements and, hence, new approaches regarding this matter are now under evaluation, such as semi-open corridors (Eggers et al. 2010) and innovative, small scale forest harvesting techniques (Koivula et al. 2002, see also Carabid conservation, protection and habitat management above).

Further studies have investigated the responses of ground beetles to anthropogenic or human-modified landscapes and urban environments (e.g. Czechowski 1982; Klausnitzer and Richter 1983; Šustek 1987, 1992; Niemelä et al. 2002). These investigations have identified distinct sets of species associated with the urban cores or city centres (but see Niemelä et al. 2002). However, for a considerable number of these species, urban populations may be dependent on recruitment from populations in the urban periphery (Klausnitzer and Richter 1983). The possible effects of urbanisation on carabid population genetics (i.e. genetic diversity and differentiation) remain unclear (Desender et al. 2005). In general, the overall abundance and species richness of carabids decrease with increasing urbanisation (Niemelä and Kotze 2009; but see Magura et al. 2010). Also, large species tend to be relatively scarce in urban habitats, resulting in a decline in average body size in urban areas compared to less disturbed ones, both for forest assemblages (Niemelä et al. 2002; Ishitani et al. 2003; Sadler et al. 2006; Elek and Lövei 2007) and those of open habitats (Czechowski 1982; Šustek 1987; Venn 2007). Flightless species also tend to be relatively scarce in urban assemblages (Venn et al. 2003; Sadler et al. 2006). Other responses detected in carabid assemblages (either in the proportion of species or the number of individuals) to urbanisation include (i) a decrease in species with restricted geographical ranges, along with the enhancement of those distributed over broad ranges; (ii) a decline in oligotopic, stenotopic and specialist species, whilst eurytopic, polytopic and generalist ones increase; (iii) a decrease in forest species and associated increase in open habitat species; (iv) an increase in xerophilic and mesohygrophilous species at the expense of more hygrophilous species; and (v) an increase in omnivorous species and a corresponding decrease in zoophagous species. Whilst stenotopic and specialist species generally decline with

increasing urbanisation, some extremely harsh urban habitats accommodate these species, such as populations of *Amara equestris* in central reservations of a busy ring road in Helsinki, Finland (Koivula et al. 2005). In fact, Eversham et al. (1996) reported that more than 35% of Britain's rare and scarce carabids are to be found from manmade sites, *Omophron limbatum* and *Dyschirius obscurus* exclusively so. Subsequent to numerous urbanisation studies from single cities, the GLOBENET project (Niemelä et al. 2000; http://www.helsinki.fi/science/globenet) was established to apply a standard urbanisation gradient approach in cities across the globe (nine cities located in Europe, Japan and Canada). The main findings indicated that the carabid fauna of urban forested habitats display uniform patterns of response to the degree of urbanisation of the 'concrete' matrix (Niemelä and Kotze 2009; Magura et al. 2010).

In the BIOASSESS project (http://www.nbu.ac.uk/bioassess), global patterns in carabid responses to a land-use intensity gradient from old-growth or unmanaged forests to arable crop-dominated landscape across ten countries, have so far reported effects on overall species richness, number of individuals, ecological groups and species composition (Grandchamp et al. 2005; Schweiger et al. 2005; Vanbergen et al. 2005, 2010; Hendrickx et al. 2007; Martins da Silva et al. 2008). Similarly, changes in landscape structure over time (i.e. landscape history) have been addressed when investigating carabid population declines or range-size modifications in human-altered landscapes (Turin and Den Boer 1988; Desender et al. 1994b; Petit and Burel 1998; Kotze and O'Hara 2003). Additionally, these investigations have related contemporary distribution patterns of carabid endemism, rarity and habitat specialisation across landscapes to landscape history.

Even now, the spatial scale at which carabid beetles relate to resources across landscapes is not completely understood. Future studies should accomplish multiscale approaches that consider a wide range of fine and coarse grains at which each carabid species may perceive the landscape, depending on its mobility and body size (e.g. Burel et al. 2004; Aviron et al. 2005; Janssen et al. 2009). The spatial distribution of carabid species in a given landscape is nearly always aggregated at some scale (see e.g. Niemelä et al. 1996; Thomas et al. 2002), which suggests that spatial autocorrelation should always be taken into account (Barton et al. 2009). Additionally, the use of multiple habitats by carabid species in mosaic heterogeneous landscapes (e.g. for feeding, reproducing and overwintering; van Huizen 1977), and the importance of particular habitat combinations for a species' survival at the landscape level remain unclear (Barbaro et al. 2007). Moreover, since many of the reported carabid responses to landscape features are species specific, more attention should be devoted to the individual species level, and not only for species of present conservation concern but also for common and widely distributed species, as well as to the ecological group level. Nonetheless, sampling strategies that avoid confounding effects are needed to clearly assess the respective weights of local and landscape factors and, at the landscape scale, the respective importance of composition and configuration on a species'

survival. Indeed, experimental landscapes (Davies and Margules 1998) or mensurative experiments (Hurlbert 1984) would be useful to disentangle these gradients that tend to be naturally correlated (Niemelä 2001; Fahrig 2003). Attention should also be paid to discrepancies between carabid species' responses to landscape features across countries, possibly denoting that the impact of landscape structure on a particular species is likely to differ over its distribution range. Finally, in the current context of continuous landscape transformation, more emphasis should be given to the role of newly created habitats and abandoned areas across countries regarding carabid distribution, as well as to singular expanding elements and surrogate habitats, such as golf courses or private gardens in urban environments (Tanner and Gange 2005; Saarikivi et al. 2010), roads (Koivula and Vermeulen 2005; Melis et al. 2010; Yamada et al. 2010), power lines (Hollmen et al. 2008) and biomass crops (coppice with short and very-short rotation) in either open or forested landscapes. Eventually, potential mechanisms could be investigated by confronting the empirical data with models of dispersal and survival in heterogeneous landscapes (see e.g. Vermeulen and Opsteeg 1994; Pichancourt et al. 2006).

9 Concluding remarks

Carabids are among the most species-rich families of beetles, which has made them a natural focus of entomological research. Carabidologists are busy studying this evolutionarily successful group at several levels, from sub-cellular to supra-individual. Indeed, from the discovery of a pH receptor on the antennae of carabid beetles (Merivee et al. 2005; Milius et al. 2006) to cross-continental, landscape related research (Niemelä and Kotze 2009; Magura et al. 2010; Vanbergen et al. 2010) "carabidologists do it all". They are helped by a reasonably solid taxonomy, even if evolutionary relationships are still undetermined.

Carabidology has contributed to several prominent ecological theories, including metapopulation theory (pioneering work by Piet den Boer and colleagues), and provides one of the best examples of a consistent, systematic study of the effects of urbanisation on biodiversity (Niemelä et al. 2002, and subsequent studies). These somewhat ad hoc examples are still powerful in the argumentation to encourage the use of carabids in ecological, evolutionary and behavioural studies.

Even from a subjective summary as this article admittedly is, it is obvious that carabids have contributed in a major way to our understanding of invertebrate adaptations, phylogeny and ecology. Accepting Hutchinson's analogy that on the world stage an ecological play is being played out in the evolutionary theatre (Hutchinson 1965), watching and describing the peculiarities of one of the star players, ground beetles, will certainly advance our understanding of nature. In an age in which the earth is dominated by humans, this will provide important knowledge on how to maintain the richness of life on Earth, and with it, extend the lifespan of our own species.

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RESEARCH ARTICLE



Sub-fossil beetle assemblages associated with the "mammoth fauna" in the Late Pleistocene localities of the Ural Mountains and West Siberia

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Abstract

The distribution of beetles at the end of the Middle Pleninglacial (=terminal Quaternary) was examined based on sub-fossil material from the Ural Mountains and Western Siberia, Russia. All relevant localities of fossil insects have similar radiocarbon dates, ranging between 33,000 and 22,000 C14 years ago. Being situated across the vast territory from the southern Ural Mountains in the South to the middle Yamal Peninsula in the North, they allow latitudinal changes in beetle assemblages of that time to be traced. These beetles lived simultaneously with mammals of the so-called "mammoth fauna" with mammoth, bison, and wooly rhinoceros, the often co-occurring mega-mammalian bones at some of the sites being evidence of this. The beetle assemblages found between 59° and 57°N appear to be the most interesting. Their bulk is referred to as a "mixed" type, one which includes a characteristic combination of arcto-boreal, boreal, steppe and polyzonal species showing no analogues among recent insect complexes. These peculiar faunas seem to have represented a particular zonal type, which disappeared since the end of the Last Glaciation to arrive here with the extinction of the mammoth biota. In contrast, on the sites lying north of 60°N, the beetle communities were similar to modern sub-arctic and arctic faunas, yet with the participation of some sub-boreal steppe components, such as Poecilus ravus Lutshnik and Carabus sibiricus Fischer-Waldheim. This information, when compared with our knowledge of synchronous insect faunas from other regions of northern Eurasia, suggests that the former distribution of beetles in this region could be accounted for both by palaeo-environmental conditions and the impact of grazing by large ruminant mammals across the so-called "mammoth savannas".

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Keywords

Carabidae, Coleoptera, sub-fossil beetles, fauna change, insect assemblages

Introduction

One of the main tasks of any zoological investigation is the study of the influence of environmental factors on the structure of communities, including changes in insect faunas. These changes may be estimated from modern faunas. But it is necessary to study such factors, which could define the specific structure of insect communities in the past.

With respect to research on palaeo-entomological processes, it is extremely difficult to estimate the character of external influences on the structure of communities, because there are no real opportunities to inspect them directly. It is only possible to make reconstructions, which are based on the analysis of sub-fossil insect assemblages found in Quaternary strata. The term "sub-fossil" means, that insect remains are presented in these layers by isolated chitin fragments not yet fossilized. Present ecological requirements of these species can be extrapolated to the period of the past investigated; the conclusions of which can be compared with results of palaeo-botanical analysis and studies of mega and small mammals. The comparison of these conclusions allows a reconstruction to be made of palaeoenvironmental conditions prevailing in the given territory in the analyzed period of the past.

The aim of this study is to try to explain peculiarities of the insect faunas in relation with the paleoenvironmental conditions of the terminal phase of the Late Pleistocene and estimate the factors possibly determining the composition of insect species in the past, including the influence of the large herbivorous mammals.

Materials

To this end, I took some synchronous sites situated in the vast territory from the Jamal peninsula in the North up to vicinities of Ekaterinburg city in the South. Radiocarbon dating confirmed the synchrony of these sites. The period of investigations covers the end of the Late Pleistocene including terminal phase of Middle Pleninglacial period and the beginning of the Late Pleninglacial or Late Glacial Maximum (LGM). Chronologically this time corresponds to the end of Maritime Isotope Stage (MIS) 3 and the beginning of MIS 2; 33,000–22,000 years Before Present (BP). This period is considered by geologists as the most severe time of the Late Pleistocene and characterized by a cooler-than-present climate which fluctuated heavily on time scales of a few thousand years (Adams et al. 1999; Adams and Faure 1999; Arkhipov and Volkova 1994; Astakhov 2009; Bos et al. 2004).

The work is based on sub-fossil material obtained from 13 sites scattered over the large territory of the Ural Mountains and West Siberia (Figure 1; Table 1). Sub-fossil

insect remains were found in deposits exposed both in quarries and in river banks. Field sampling was done using the standard techniques in Kiselev (1987). Geologists provided geological descriptions of the sites and their provisional dating; most samples were radiocarbon-dated (Table 1). Laboratory treatment and the subsequent identification of fossil specimens were performed at the Institute of Plant and Animal Ecology in Ekaterinburg. The classification of the sub-fossil insect faunas used is that proposed by the author (Zinovyev 2006).

Results

All studied insect faunas occurred in the interval between 33,000 and 22,000 C^{14} yr. BP (Table 1), the terminal phase of the Middle Pleninglacial (MIS 3). These studies cover the vast territory between 67° and 57°N. I tried to trace elements of latitudinal zonality and estimate factors affecting natural ecosystems and insect faunas.

According to the classification by Zinovyev (2006), the studied faunas can be referred to as arctic, sub-arctic, "mixed" and boreal types.

Only faunas of the arctic type were found at the sites lying north of 61°N latitude (sites 1–3 in Table 1). The main characteristics of these faunas are:

- 1. Dominance or sub-dominance of arctic species *Curtonotus alpinus*, *Pterostichus costatus*, *P. sublaevis* and the rove beetle *Tachinus* cf. *arcticus* (Table 2).
- 2. Dominance or sub-dominance of sub-arctic species of the sub-genus *Cryobius* and the species *Pterostichus pinguedineus*, *P. ventricosus*, *Diacheila polita*, *Curtonotus torridus* (Table 2).
- Single occurrences of sub-boreal steppe species Carabus sibiricus, leaf beetles Chrysolina perforata, Ch. aeruginosa. Only one elytrum of a specimen of Poecilus ravus was found in the Aganskyi uval-1290/2 site (61°22'N, 76°45'E).

Entomo-complexes referred to as "arctic" allow the reconstruction of severe environmental conditions similar to the modern arctic tundra, characterized by a cold climate with temperatures of July +12°C, January -27°C, the distribution of open landscapes and the absence of wood.

Between 61° and 59°N, the fossil beetle faunas of the sub-arctic type are similar to the recent communities of the south tundra and forest tundra (sites 4–7 in Table 1). The main characteristics of these faunas are:

- 1. Presence of arctic species *Curtonotus alpinus, Pterostichus costatus* and the rove beetle *Tachinus* cf. *arcticus* (but in fewer quantities than in arctic faunas).
- 2. Dominance of sub-arctic species presented by the sub-genus *Cryobius* of genus *Pter-ostichus*, *Pterostichus pinguedineus*, *Curtonotus torridus*, *Diacheila polita* (Table 2).
- 3. Occurrence of sub-boreal steppe species *Carabus sibiricus, Poecilus ravus,* the weevil *Stephanocleonus eruditus,* and the carrion beetle *Aclypaea sericea.*



Figure 1. Geographical location of the study sites in the Ural Mountains and Western Siberia. Numbers of sites: 1 Syoyakha-Mutnaya 2 430 km from Ob 3 Aganskiy uval-1290/2 4 Mega 5 Lokosovo 6 Kul'egan-2247 Point I 7 Kul'egan -2247 Point II 8 Skorodum 9 Andriyshino 10 Nizhnyaya Tavda 11 Mal'kovo 12 Nikitino 13 Shurala.

- Borders of vegetation types, reconstructed for the beginning of MIS 2 on the basis of palynological data: I periglacial tundra II periglacial steppe and forest-steppe III boreal forest and parklands (after Grichuk and Borisova 2009) 4. Presence of single xylophagous beetles associated with larch or spruce, the weevil *Callirus albosparsus*, and the bark beetle *Phoelotribus spinulosus*.

Insect assemblages referred to as belonging to the "sub-arctic" type, are similar to modern insect faunas from the southern part of the contemporary Sub-arctic. Presumably, reconstructed landscapes look like modern south tundra or forest tundra with the presence of single trees, such as larch or spruce. The thermal regime is probably characterized by several temperatures: July $+13^{\circ} - +14^{\circ}$ C, January $-25^{\circ} - -26^{\circ}$ C. These reconstructions are confirmed by palaeo-botanical data.

The faunas from sites situated south of 59°N are of a "mixed" type characterized by species combinations not presently found together; insect complexes of the majority of these localities resemble each other, with main features:

- 1. Dominance or sub-dominance of weevils Otiorhynchus similar to O. politus.
- 2. Presence of arctic and sub-arctic species *Pterostichus (Cryobius)* spp., *Curtonotus alpinus*, the carrion beetle *Aclypaea sericea*.
- 3. Presence of sub-boreal steppe and sub-alpine insects *Poecilus (Derus)* spp., *Cy-mindis mannerheimi, Pseudotaphoxenus dauricus.*
- 4. Occurrence of some halophylous beetles *Pogonus* spp., darkling beetles *Belopus* spp.
- 5. Occurrence of xylophagous beetles (e.g., the bark beetle *Phoelotribus spinulosus*).

These faunas have no analogues among modern insect complexes, and may be classified as indicative of tundra steppe, although their species composition differs from that known from relict tundra steppe communities found today in Eastern Siberia and described by Berman (2001).

Discussion

Interpretation of the beetle communities

At first, these faunas suggest cooler than present climatic conditions, which is confirmed by the occurrence of sub-arctic species (*Pterostichus* (*Cryobius*) cf. *pinguedineus*, *P. ventricosus*, *Curtonotus torridus* and the arctic species (*Curtonotus alpinus*). This shows their southward distribution relative to their modern ranges.

As evidence of the lack of dense forest, is an absence of such typically boreal beetles as *Calathus micropterus*, *Pterostichus adstricus*, *P. oblongopunctatus* and others inhabiting the forest litter; at present they are widely distributed in the vast territories of West Siberia. Single boreal species are rare in the "mixed" faunas and are represented mainly by bark beetles (for example, *Phoelitribus spinulosus*, associated with spruce). The presence of sub-boreal beetles, inhabiting modern East-Siberian steppes (*Poecilus ravus*, *P. hanhaicus*) and sub-alpine grasslands (*Cymindis mannerheimi*) could indicate open landscapes. An abundance of weevils of the genus *Otiorhynchus* may be explained by the

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Sites wh	nere sub-fossil in	rsect faunas were found	Coord	linates	Radiocarbon dat	a, years before present (yr. BP). The
			Z	щ	abbreviation of (organization and laboratory number of
					this data are give	n in parenthesis
1.	Syoyakha-Muti	naya (V.I.Nazarov, unpublished data)	72°25'	66°48'	$30,700\pm1100$	(DPI-716)
2.	430 km of Ob		64°25'	70°50'	$24,000\pm1500$	(IPAE-63)
3.	Aganskiy uval-	1290/2	61°22'	76°45'	23,300±575	(IPAE-95)
4.	Mega-2172		60°56'	72°20'	$33,100\pm 2300$	(IOAN 132)
			60°56'	72°20'	26,285±590	(SOAN 982)
5.	Lokosovo		$60^{\circ}40'$	71°32'	22,930±650	(SOAN 956)
6.	Kul'egan-2247	Point I	60°25'	75°50'	$21,815\pm 225$	(SOAN-6837)
7.	Kul'egan -2247	7 Point II	60°25'	75°50'	26,730±250	(LOIA-8663)
8.	Skorodum		57°47'	70°58'	26,500±550	(SOAN 4538)
9.	Andriyshino		57°41'	66°08'	approximately 30	,000 C14 yr. BP
10.	Nizhnyaya Tav	da	57°41'	66°12'	27,400±335	(SOAN 4534)
			57°41'	66°12'	24,820±750	(SOAN 4535)
11.	Mal'kovo		56°25'	$66^{\circ}10'$	$31,800\pm350$	(GIN-5338)
12.	Nikitino		57°34'	63°17'	24,480±550	(SOAN 4537)
			57°34'	63°17'	$28,460\pm800$	(SOAN 4536)
13.	Shurala	Plant detritus	57°28'	60°15'	27,600±150	(Ki-15505)
		Mammalian bone	57°28'	60°15'	36,700±250	(Ki-15512)

Table 1. Chronological position of the study sites dated by the end of the Middle Pleninglacial period and associated with the "mammoth fauna".

wide distribution of herbal meadow vegetation. These faunas differ from contemporary insect steppe communities by the lack of darkling beetles, occurring in modern steppes and forest steppes (*Oodescelis polita, Crypticus quisquilius, Platyscelis hypolita, Opatrum riparium* etc.); it is possible that their absence was a result of cold climatic conditions.

At the same time, the presence of halophylous species, such as ground beetles of the genus *Pogonus*, darkling beetles of the genus *Belopus*, may indicate local soil salinity. At present these halophilic species are distributed southwards from 56–57°N and are very rare between 57–58°N, situated in sites with "mixed" faunas. Moreover, I am not aware of the presence of halophilic species of the genera Pogonus and Belopus in Central and East Siberia.

It may be assumed that such faunas inhabited open communities which can be defined as "cool grasslands" with a presence of rarefied forests or of single trees and local soil salinity. Similar conclusions have been drawn from palaeo-botanical data obtained at the same sites: they show a dominance of herbal vegetation with an abundance of cereals, wormwoods and chenopodiaceous plants.

The occurrence of some boreal faunas in single sites (Niznyaya Tavda, C^{14} 27,400 ± 335 yr. BP) do not contradict the overall distribution of open landscapes, and show the presence of isolated patches of forest vegetation, like in modern forest steppes.

Therefore, entomological data show that at the time of the terminal phase of Middle Pleninglacial the following types of landscapes were distributed in the territories of the Ural Mountains and West Siberia: the northern part of the region north of 61°N was dominated by open landscapes similar to modern tundra, between 64 and 62°N similar to forest tundra and between 59 and 57°N – non-analogue landscapes, which may be defined as "open grasslands" or savannas with a presence of rarefied forests.

The main influence on the natural ecosystems came from palaeo-environmental factors. The Middle Weichselian Interstadial was characterized by a continental and a cooler-than-present climate with low winter temperatures and a wide distribution of permafrost; the resulting development of large ice sheets caused a strong drying effect. Decreasing sea levels provided the opening of sea shelves and the connection between Europe and the British Isles, and the Beringian Bridge between Siberia and Alaska. Cold and dry climatic conditions reconstructed for main territories of Europe, even for the Mediterranean region (Adams and Faure, 1997) may have caused a wide distribution of open landscapes such as tundra steppes of grasslands corresponding with the periglacial zone or "hyperzone" (Velichko 1973). Palaeoenvironmental reconstructions of "mixed" insect faunas from localities situated in the Ural Mountains and West Siberia show the presence of landscapes similar to savannas with rarefied woody vegetation. According to palaeo-botanical data (Stefanovsky et al. 2007), these "mixed" faunas correspond with open plant associations with an abundance of herbal vegetation.

It is necessary to define which factors might prevent the distribution of woods in the period of the Late Pleistocene studied. The main environmental factor is climate as a combination of thermal regime, precipitation, insulation, etc. At present I can suggest that severe climatic conditions similar to the palaeo-environment of the terminal phase end of the Middle Pleninglacial in the Central part of North Eurasia between 59° and

Type of	Taxon					Si	tes (s	see T	able	1)				
range*		1	2	3	4	5	6	7	8	9	10	11	12	13
	COLEOPTERA:										1			
	Carabidae:													
a-sb	Carabus sibiricus FW.						+	+					+	
a-sb	C. cf. sibiricus FW.		+											
	C. (Trachycarabus) sp.									+				
a	C. truncaticollis Esch.			+										
a	C. cf. truncaticollis Esch.		+											
sa	C. cf. odoratus FW.		+											
	C. (Morphocarabus) sp.							+						
	C. sp.		+	+					+	+			+	+
р	Nebria rufescens Sturm						+							
sa	N. nivalis Payk.							+	+					
	N. sp.	+												
sa	Pelophila borealis Payk.		+				+	+	+	+	+	+	+	
р	Elaphrus riparius L.		+											
p	Notiophilus cf. aestuans Motsch.													+
p	N. cf. aquaticus L.			+		+	+	+	+	+			+	
b	N. reitteri Spaeth								+		+			
b	N. biguttatus F.								+					
	N. sp.							+	+	+	+		+	
sa	Blethisa catenaria Brown.		+		+		+	+						
р	<i>B. multipunctata</i> L.				+									
sa	Diacheila polita Fald.	+	+	+	+		+	+	+	+	+	+	+	
sa	D. arctica Gyll.				+					+				
р	Elaphrus riparius L.				+			+	+				+	
sa	E. lapponicus Gyll.								+					
b	<i>E. angusticollis</i> R. F. Sahlb.						+	+	+					
b	<i>E.</i> cf. <i>angusticollis</i> R. F. Sahlb.								+					
	E. sp.						+			+				
р	Lorocera pilicornis F.													+
p	Clivina fossor L.							+		+				+
p	Dyschiriodes cf. globosus Hbst.													+
_1	<i>D.</i> sp.								+	+			+	
b	Trechus secalis Payk.										+			
b	T. rivularis Gyll.						+	+						
b	Bembidion striatum F.								+				+	
b	B. velox L.								+					
sa	B. captivorum Net.						+							
sa	B. scandicum Lindr.						+							
b	B. ovale Motsch.						+							
sa	B. umiatense Lindr.								+					
sa	B. cf. umiatense Lindr.							+	+	+				
				1			1	. ·	· ·	· ·				L

Table 2. Species of beetles found in the study sites associated with the "mammoth fauna".

range* 1 2 3 4 5 6 7 8 9 10 11 12 13 b B. infuscatum Dej. Image <
b B. infuscatum Dej. I
b B. cf. infuscatum Dej. + + + + + sa B. grapei Gyll. + + + + + sa B. cf. grapei Gyll. + + + + + b B. scopulinum Kby. + + + + + b B. deletum Serv. + + - - + + - b B. cf. deletum Serv. - + + - - - + + - - - +
sa B. grapei Gyll. + + + + sa B. cf. grapei Gyll. + + + + b B. scopulinum Kby. - + + - b B. deletum Serv. - + + - - b B. cf. deletum Serv. - - + - - p B. cf. tetracolum Say - + + - - B. (Ocydromus) sp. - + + + + + + sa B. cf. fellmanni Mnnh. - + + + + + sa B. (Plataphodes) sp. - + + + + + p B. obliquum Ol. - - + + + B. (Bembidionetolitzkya) sp. - - + + + B. sp. + + + + + + + b Pogonus cf. punctatulus Dej. - - + + - - </td
sa B. cf. grapei Gyll. + + + + - - + - - + - - + - - + - - + - - + - - + - - + - - + - - + - - - + - - - + - - - + - - - + - - - + - - - + - - - - + - - - - + - - - - - + + - - - - - - - - + + + + + - - - - - - + + + - - - - + - - - - - + - - - - + - - -
b B. scopulinum Kby. + + + b B. deletum Serv. + + - b B. cf. deletum Serv. + + - - p B. cf. deletum Serv. + + - - p B. cf. tetracolum Say + + + - B. (Ocydromus) sp. + + + + + sa B. fellmanni Mnnh. + + + + sa B. cf. fellmanni Mnnh. + + + + B. (Plataphodes) sp. + + + + + p B. obliquum Ol. + + + + B. (Bembidionetolitzkya) sp. + + + + B. sp. + + + + + sb Pogonus cf. punctatulus Dej. + + + + sb P. cf. umanus Lutschn. + + + + sb P. cf. transfuga Chaud. + + + +<
b B. deletum Serv. + + - + - - b B. cf. deletum Serv. - + + - + + + - - - - +
b B. cf. deletum Serv. + + - - p B. cf. tetracolum Say + + + + + B. (Ocydromus) sp. + + + + + + + sa B. fellmanni Mnnh. + + + + + + sa B. cf. fellmanni Mnnh. + + + + + + sa B. cf. fellmanni Mnnh. + + + + + + sa B. (Plataphodes) sp. + + + + + + p B. obliquum Ol. + + + + + + B. (Bembidionetolitzkya) sp. + + + + + + B. sp. + + + + + + + sb P ogonus cf. punctatulus Dej. + + + + + sb P. cf. transfuga Chaud. + + + + + p Patr
pB. cf. tetracolum Say++++B. (Ocydromus) sp.++++++saB. fellmanni Mnnh.+++++saB. cf. fellmanni Mnnh.+++++saB. cf. fellmanni Mnnh.+++++ $B. (Plataphodes)$ sp.+++++ P B. obliquum Ol.++++ $B. (Bembidionetolitzkya)$ sp.++++ $B. sp.+++++B. sp.+++++B. sp.+++++B. cf. cumanus Lutschn.++++sb<$
B. (Ocydromus) sp. + + + + + + + + + + + + + + + + + + +
sa B. fellmanni Mnnh. + + + + sa B. cf. fellmanni Mnnh. + + + + + B. (Plataphodes) sp. + + + + + + p B. obliquum Ol. + + + + + B. (Bembidionetolitzkya) sp. + + + + + B. sp. + + + + + + B. sp. + + + + + + sb Pogonus cf. punctatulus Dej. + + + + + sb P. cf. cumanus Lutschn. + + + - - sb P. cf. transfuga Chaud. + + + + - - sb P. sp. + + + + + + + p Patrobus septentrionis Dej. + + + + + + sb Poecilus major Motsch. + + + +<
saB. cf. fellmanni Mnnh.+++B. (Plataphodes) sp.+++pB. obliquum Ol.+++B. (Bembidionetolitzkya) sp+B. sp.++++B. sp.++++b< Pogonus cf. punctatulus Dej.
B. (Plataphodes) sp. + + + + p B. obliquum Ol. - - + + B. (Bembidionetolitzkya) sp. - - + + B. Sp. + + + + + B. Sp. + + + + + b. Orgonus cf. punctatulus Dej. - - + + sb<
p B. obliquum Ol. - - + B. (Bembidionetolitzkya) sp. - - + + B. sp. + + + + + sb Pogonus cf. punctatulus Dej. - - + + sb P. cf. cumanus Lutschn. - + + - sb P. cf. neridionalis Dej. - + + - sb P. cf. transfuga Chaud. - + + - sb P. sp. - + + + + p Patrobus septentrionis Dej. + + + + + p P. assimilis Chd. - + + + + sb Poecilus major Motsch. - + + + +
B. (Bembidionetolitzkya) sp. + <td< td=""></td<>
B. sp. +
sb Pogonus cf. punctatulus Dej. + + + sb P. cf. cumanus Lutschn. + + - - sb P. cf. neridionalis Dej. + + - - - sb P. cf. meridionalis Dej. + + + - - sb P. cf. transfuga Chaud. + + + + - sb P. sp. + + + + + + p Patrobus septentrionis Dej. + + + + + p P. assimilis Chd. + + + + + sb Poecilus major Motsch. - + + + +
sb P. cf. cumanus Lutschn. + - - sb P. cf. meridionalis Dej. + + - - sb P. cf. meridionalis Dej. + + - - sb P. cf. transfuga Chaud. + + + + + sb P. sp. + + + + + + p Patrobus septentrionis Dej. + + + + + p P. assimilis Chd. + + + + + sb Poecilus major Motsch. + + + + +
sb P. cf. meridionalis Dej. + + + - - sb P. cf. transfuga Chaud. + + -
sb P. cf. transfuga Chaud. + + - sb P. sp. + + + + p Patrobus septentrionis Dej. + + + + p P. assimilis Chd. + + + + sb Poecilus major Motsch. + + + +
sb P. sp. - + </td
p Patrobus septentrionis Dej. + + + + + p P. assimilis Chd. + + + sb Poecilus major Motsch. + + +
p P. assimilis Chd. + + sb Poecilus major Motsch. + +
sb Poecilus major Motsch.
sb P. cf. major Motsch.
sb <i>P. ravus</i> Lutshn. + + + + + + + +
sb P. cf. ravus Lutshn.
sb <i>P. hanhaicus</i> Tsch. +
sb P. cf. hanhaicus Tsch.
sb <i>P. (Derus)</i> sp. + +
t <i>P. lepidus</i> Leske +
<i>P. (s.str)</i> sp. + + +
p Pterostichus nigrita F. + +
b <i>P. mannerheimi</i> Dej. +
b <i>P. maurusiacus</i> Mnnh +
b P. cf. maurusiacus Mnnh +
sa <i>P. parens</i> Tsch. +
P. (Eosteropus) sp. + +
sa <i>P. montanus</i> Motsch. + +
sa <i>P. cf. montanus</i> Motsch. +
sa <i>P. kokeili</i> ssp. archangelicus Popp. +
sa <i>P. tundrae</i> Tsch. + + + + +
sa P cf. tundrae Tsch.
sa P. cf. abnormis I.R.Sablb.
P. (Petrophilus) sp. + + + + +

Type of	Taxon	Sites (see Table 1)												
range*		1	2	3	4	5	6	7	8	9	10	11	12	13
sa	P. agonus Horn.		+				+							
a	P. vermiculosus Men.	+	+	+	+		+	+						
a	P. cf. cancellatus Motsch.		+											
a	P. costatus Men.		+	+	+		+	+						
a	P. sublaevis J.R.Sahlb.		+	+			+	+						
sa	<i>P. tareumiut</i> Ball.					+								
sa	P. cf. tareumiut Ball.						+							
sa	P. theeli Maekl.					+								
sa	P. cf. theeli Maekl.						+							
sa	P. middendorfii J.Sahlb.						+	+						
sa	P. cf. middendorffi J.R.Sahlb.							+	+	+				
sa	P. ventricosus Esch.			+			+	+					+	
sa	P. cf. ventricosus Esch.		+	+									+	
sa	P. pinguedineus Esch.	+				+								
sa	<i>P.</i> cf. <i>pinguedineus</i> Esch.		+	+				+	+	+			+	
sa	P. cf. nigripalpis Popp.	+		+										
sa	P. negligens Sturm.			+			+	+		+		+	+	
sa	P. cf. negligens Sturm		+							+				
sa	P brevicornis Kby			+		+	+	+		+			+	
sa	P. cf. brevicornis Kby		+				-		+					
sa	P (Cryobius) sp.	+	+	+	+		+	+	+	+	+		+	+
b	P. diligens Sturm						+	+	+				+	· ·
b	P. cf. diligens Sturm								+	+				
b	P. cf. strenuus Panz.									+				+
	P (Phonias) sp.				+			+		+				
	P sp.		+	+					+	+			+	+
sa	Stereocerus haematopus Dei		+	+			+	+		+				
sa	S. cf. haematopus Dei						· ·	+						
sa	S. rubrities Motsch							+						
<u>sa</u>	S of rubripes Motsch						+	+						
<u>- 52</u>	S sp													
34	Platamus sp						т		+	-				
60	Agonum alpinum Motsch								т	т				
5a	A of normation Sturm												т	
<u>Р</u>	A aricati Pana												+	
<u>Р</u>	A migane Nic				Ŧ		-							
<u>р</u>	A. micans INIC.								+					
р	A. CI. gracue Gyll.						+							
	A. (<i>Luropnius</i>) sp.								+					
1	A. sp.	+		+			+	+		+	+			
D	Synuchus vivalis Payk.			+										
sb	Pseudotaphoxenus dauricus FW.									+				
sa	Amara quenseli Shoenh.						+						+	
а	A. glacialis Mnnh.						+	+						
sa	A. erratica Duft.							+		+				

Type of	Taxon	Sites (see Table 1)												
range*		1	2	3	4	5	6	7	8	9	10	11	12	13
b	A. minuta Motsch.							+						
sa	A. interstitialis Dej.						+	+	+		+			
b	A. brunnea Gyll .			+				+		+			+	+
b	A. cf. brunnea Gyll.							+						
	A. (Bradytus) sp.								+					
-	A. (Celia) sp.								+					
	A. sp.						+	+	+	+			+	
sa	Curtonotus hyperboreus Dej.								+					
a	C. alpinus Payk.		+	+		+	+	+		+				
a	C. cf. alpinus Payk.									+				
sa	C. torridus Panz.					+		+	+	+			+	
sa	C. cf. torridus Panz.		+					+	+	+				
sb	C. dauricus Motsch.									+				
	<i>C.</i> sp.		+	+				+	+	+	+			
sa	Harpalus nigritarsis C.R.Sahlb.							+	+	+			+	
sa	H. cf. nigritarsis C.R.Sahlb.								+				+	
sb	H. cf. pulvinatus Men												+	
	H. sp.								+	+				
sa	Dicheirotrichus mannerheimi R.						+	+	+	+				
	F. Sanib.													
SD	Cyminais mannerneimi Gebl.									+		+	+	
<u>sa</u>	C. macularis FW.								+	+				
D	C. cf. <i>rivularis</i> Motsch.									+				
	Cyminais sp.								+	+				
	Carabidae indet.			+			+	+						
	Dytiscidae:													
	Agabus (Gaurodytes) sp		+	+	+		+	+					+	
	Agabus sp.							+	+	+			+	+
	Hydroporus sp.	+					+		+		+			
	Dytiscidae indet.						+	+						
	Gyrinidae:													
	<i>Gyrinus</i> sp.			+					+					
	Hydrophilidae:										1			
р	Hydrobius fuscipes L.			+				+	+					
р	Helophorus ct. nubilis F.	+												
sa	H. obscurellus Popp.						+							
sa	H. ct. obscurellus Popp.								+					
	H. sp.		+				+	+	+	+	+		+	
	<i>Helophorus</i> sp.							+						
	<i>Cercyon</i> sp.				+		+	+	+	+	+		+	
	Histeridae:										,			
	Margarinotus sp.								+					
	Catopidae:	1			1					1	1			
	<i>Catops</i> sp.		+	+		+	+	+	+		+			

Type of	Taxon					Si	tes (see T	able	1)				
range*		1	2	3	4	5	6	7	8	9	10	11	12	13
	Colon sp.									+				
	Silphidae:												•	
sb	Aclypaea sericea Zoubk.								+					
sb	A. bicarinata Gebl.								+		+			
р	A. opaca L.						+	+	+	+	+		+	
-	Thanatophilus sp.			+			+		+					
	Liodidae:													
	Agathidium sp.			+			+		+	+	+		+	
	Anisotoma sp.			+										
	<i>Liodes</i> sp.							+	+	+	+			+
	Staphylinidae:													
р	Acidota crenata Mnnh.										+			
р	A. cf. cruentata Mnnh.						+							
-	<i>A</i> . sp.										+			
	Olophrum sp.			+			+		+					+
	Omaliinae gen. sp.	+	+	+				+	+	+	+		+	
а	Tachinus cf. arcticus Maekl.	+	+	+		+	+	+	+					
	Omaliinae gen. sp.													
	Ocypus sp.									+				
	Oxythelinae gen. sp.									+	+			
	Tachinus sp.			+	+			+	+	+			+	
-	?Mycetoporus sp.								+					
	? Philonthus sp.		+											
	Tachyporinae gen. sp.			+							+			
	Stenus sp.			+			+	+	+					
	Lathrobium sp.			+			+				+			+
	Paederinae gen sp.			+					+		+			
	Quedinus sp.			+					+					+
р	Scaphisoma sp.						+							
-	Staphylinidae indet.			+	+	+	+	+						
	Scarabaeidae:												1	
t	Aphodius distinctus Müll.								+					
t	A. cf. distinctus Müll.						+	+	+				+	
t	A. cf. melanostictus W.Schm.							+		+	+			
t	A. cf. fossor L.								+		+			
t	A. cf. brevis Er.								+		+			
t	A. cf. rufipes L.												+	
	A. sp.			+			+	+	+	+	+		+	
р	Aegialia abdita Nikritin							+	+	+	+		+	
. 1	Helodidae:										1			
	Cyphon sp.							+			+			
	<i>Cyphon</i> sp.													
	Dermestidae:										1			. <u> </u>
	Dermestidae indet.								+					
	Byrrhidae:													

range* 1 2 3 4 5 6 7 8 9 10 11 12 13 Byrrhus sp. + - - - +	Type of	Taxon					Si	tes (s	see T	able	1)				
Byrrhus sp.+++ <th< th=""><th>range*</th><th></th><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th><th>9</th><th>10</th><th>11</th><th>12</th><th>13</th></th<>	range*		1	2	3	4	5	6	7	8	9	10	11	12	13
sb Porcinolus murinus E. I <td></td> <td><i>Byrrhus</i> sp.</td> <td>+</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>+</td> <td></td> <td>+</td> <td></td> <td>+</td> <td></td>		<i>Byrrhus</i> sp.	+							+		+		+	
sa Morychus viridis Kuzm. et Kor. +	sb	Porcinolus murinus F.								+	+				
sa M. cf. viridis Kuzm. et. Kor. +	sa	Morychus viridis Kuzm. et Kor.			+			+	+			+			
M. sp. + <td>sa</td> <td>M. cf. viridis Kuzm. et. Kor.</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>+</td> <td></td> <td></td> <td></td> <td></td> <td></td>	sa	M. cf. viridis Kuzm. et. Kor.								+					
Simplocaria sp.+++++++Carinopsis sp.++Byrthida gen. sp.+++Anobiidae:-+++PCaenocara bovistae Hoffm.++++Heteroceridae:-+ <td></td> <td><i>M.</i> sp.</td> <td></td> <td>+</td> <td></td> <td></td> <td></td> <td></td> <td></td> <td></td> <td>+</td> <td></td> <td></td> <td>+</td> <td></td>		<i>M.</i> sp.		+							+			+	
Curimopsis sp. + -		<i>Simplocaria</i> sp.			+	+		+	+	+				+	
Byrrhidae gen. sp. +		Curimopsis sp.			+										
Anobiidae: +		Byrrhidae gen. sp.			+					+					
p Caenocara bovistae Hoffm. + + + - Heteroceridae: - - - - - Heteroceris sp. + - - - - - P Hypnoidus cf. rivularis Gyll. + - + - + - - - - - - - - - - - - - - - - - -		Anobiidae:													
Heteroceridae: Heteroceris sp. Elateridae: p Hypnoidus cf. rivularis Gyll. H. sp. Nitidulidae: Nitidulidae: Vitidulidae: Vitidulidae: Cryptophagidae: Cryptophagidae: Cryptophagidae: Cryptophagidae: Cryptophagidae: Coccinellidae: b Scpmnus sp. sa Hippodamia arctica Schneider b C. cf. hieroglyphica L. b C. sp. Latridiidae: U Latridiidae: Latridiidae: Oedemeridae: Oedemeridae: Dedemeridae: Dedemeridae: Dedemeridae: Donacia sp. + - b Chrysolina perforata Gebl. + - b Ch. cf. aruginosa Fald. + - Anthicidae Esh. Donacia sp. + b	р	Caenocara bovistae Hoffm.			+			+							
Heteroceris sp.+Elateridae:pHypnoidus cf. rivularis Gyll.H. sp.H. sp.Nitidulidae:Nitidulidae:Cryptophagidae:Cryptophagidae indet.Erotylidae:Erotylidae:Erotylidae:Erotylidae:bScymmus sp.saHippodamia arctica SchneiderbC. cf. hieroglyphica L.bC. sp.Latridiidae:Latridiidae:Latridiidae:Voedemeridae:Codemeridae:Dedemeridae:Dedemeridae:SbBelopus sp.Anthicidae gen.sp.Anthicidae:Chrysomelidae:Donacia sp.tt <td></td> <td>Heteroceridae:</td> <td></td>		Heteroceridae:													
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a <i>Ch. cf. subsulcata</i> Esch. + +	30	Ch. cf. actigand I D Sahlh		+											
a 07. cl. suosuuuu Escli. + +		Ch. cf. cubigera J.K.Sallib.		+											
so Ch septentrion dis Men	a	Ch. sattantrian die Mon		+	+										
sa Ch. schentrionalis Men	3d	Ch. of ceptentrianglis Mon		+											

Type of	Taxon					Si	tes (s	see T	able	1)				
range*		1	2	3	4	5	6	7	8	9	10	11	12	13
р	Ch. cf. graminis L.								+					
-	Ch. sp.		+	+			+	+	+	+				
a	Chrysomela cf. taimyrensis L.		+											
	Medv.													
	Ch. sp.			+		+	+	+		+	+		+	
sb	Colaphellus sophiae Schall.								+	+	+			
р	Hydrothassa hannoverana F.												+	
	<i>Phaedon</i> sp.		+							+				
р	Plagoiodera versicolora Laich.		+						+					
	<i>Crosita</i> sp.							+	+					
	<i>Phratora</i> sp.			+										
	Chalcoides sp.								+					
	<i>?Chalcoides</i> sp.								+					
	<i>?Chaetocnema</i> sp.								+					
	Altica sp.			+										
	Alticinae gen. sp.			+										
	Chrysomelidae indet.			+		+								
	Erirhinidae:													
р	Tournotaris bimaculatus F.			+			+	+	+	+	+	+	+	+
b	<i>T. ochoticus</i> Kor.						+	+						
b	T. cf. ochoticus Kor.													+
р	Notaris aethiops F.						+	+		+	+			+
-	<i>N.</i> sp.	+					+		+				+	
	Curculionidae:		L											1
sb	Otiorhynchus unctuosus Germ.										+			
b	<i>O. politus</i> Gyll.									+	+	+		+
b	O. cf. <i>politus</i> Gyll.								+	+	+	+	+	+
sb	O. wittmeri Legalov									+				
sb	O. cf. <i>wittmeri</i> Legalov									+				
sa	O. cf. arcticus F.		+											
p	O. ovatus L.										+			
<u>р</u>	O. cf. ovatus L.										+			
11	<i>O</i> . sp.						+		+	+	+		+	+
sa	Sitona cf. ovipennis ssp.borealis		+				+							
	Kor.													
	S. sp.	+									+			
b	Chlorophanus cf. sibiricus Gyll.										+			
	Ch. sp.						+							
?p	Phyllobius cf.crassipes Motsch et			+										
T	maculicornis Germ.													
	Ph. sp.						+	+	+	+	+		+	
-	Strophosoma sp.							+						
sb	Eusomus ovulum Germ.													+
a-sb	Coniocleonus ferrugineus Fahr										+		+	+

Type of	Taxon	Sites (see Table 1)												
range*		1	2	3	4	5	6	7	8	9	10	11	12	13
a-sb	C. cf. ferrugineus Fahr		+											
-	<i>C.</i> sp.		+							+				+
a-sb	Stephanocleonus eruditus Fast.						+							
-	S. sp.										+		+	
sb	Bothynoderes foveocollis Gebl.										+			
	Cleoninae indet.					+	+	+	+	+			+	
р	Hypera rumicus L.							+						
p	H. cf. ornata Cap.		+				+	+						
p	<i>H. elongata</i> Pk.			+										
-	<i>H.</i> sp.			+	+	+	+	+	+	+	+		+	+
sa	Lepyrus nordenskjoldi Faust.						+	+						
sa	L. cf. nordenskjoldi Faust		+	+										
sa	L. cf. arcticus Pk.	+												
	L. sp.					+	+	+					+	
b	Trichalophus maeklini Faust		+											
	T. sp.													+
р	Phytobius cf. velaris Gyll.		+		+									
b	Callirus albosparsus Boh.						+							
b	<i>C.</i> sp.										+			
b	Pissodes sp.							+			+			
	Bagous sp.						+			+				
	?Limnobaris sp.								+					
b	?Magdalis sp.												+	
b	Rhyncholus ater L.										+			
	Anthonomus sp.									+	+			
р	Dorytomus cf. imbecillus Faust							+						
	D. sp.							+		+	+			+
р	Ceutorrhynchus cf. erysimi F.						+							
-	<i>C.</i> sp.						+	+					+	
р	Isochnus saliceti Müll	+												
sa	<i>I. arcticus</i> Kor.			+				+						
-	<i>Rhynchaenus</i> sp.		+		+				+	+	+			
	Curculionidae indet.						+	+						
	Brentidae:													
sa	Hemitrichapion tschernovi TM.			+	+		+	+						
-	<i>H.</i> sp.													
р	Mesotrichapion cf. punctirostre						+	+						
-	Gyll.													
р	Betulapion simile Kby									+			+	
р	B. cf. simile Kby.			+										
	<i>Cyanapion</i> sp.									+				
	Brentidae gen.sp.	+	+	+			+	+		+	+		+	
	Scolytidae:													
b	Phoelotribus spinulosus Rey.							+	+		+		+	
b	Polygraphus sp.								+					

57°N are presented in the inner parts of Central and East Siberia. However, the modern conditions of cool and continental climate cannot avert the present distribution of woodland vegetation in this area. I suggest that not only climatic factor prevented of the distribution of woods in the central part of northern Eurasia between 59° and 57°N. Apart from climate, other factors might influence Pleistocene ecosystems; these factors may have impeded reforestation and stimulate the distribution of open landscapes.

The influence of mammoths and other large herbivorous mammals representing the "mammoth fauna" is probably large. It is known that vast areas of the continent were occupied by mammals belonging to the mammoth complex at that time (Markova et al. 2008).

Evidence for the co-occurrence of insects with mega mammals of the "mammoth" fauna

Firstly, in many sites fossil insects were found along with mammoth remains (*Mammuthus primigenius*) and other large herbivorous mammals (teeth, tusks, fragments of cranium, etc.) (Borodin et al. 2001).

Secondly, in the majority of sites fragments of dung beetles of the genus *Aphodius*, were found which suggests the presence of mammoths and other large herbivorous mammals in the same landscapes (Sher and Kuzmina 2007).

According to the literature, mammoths and other mega mammals such as woolly rhinoceros (*Coelodonta antiquitatis*), giant deer (*Megaloceros giganteus*), reindeer (*Rangifer tarandus*), wild ox (*Ovibos moschatus*), primitive bison (*Bison priscus*) and some others may be considered as an additional factor, which influenced Late Pleistocene ecosystems (May 1993; Puchkov 2001).

Mammoths and other mammals were indicators of certain communities, and preserved specific ecosystems (Puchkov 2001):

- 1. Destruction of undergrowth and feeding impeded reforestation and might preserve herbal communities.
- 2. The hooves of mammoths destroyed the moss turf; as a result, moss cover disappeared in the territories of modern taiga and tundra zones, being replaced by mezo- and xerophylous herbal vegetation.

That is, mammoths and other mega mammals could rarefy forests and promote the distribution of zoogenic herbal vegetation consisting of cereals (Stuart and Hibbard 1986; Stuart 1991; May 1993; Puchkov 2001).

Consequently, Pleistocene forests were rare, and meadow and steppe plants were significant in the Siberian ecosystems.

I therefore suggest that the species composition of insects was affected by two important factors:

1. Cool and dry climate which caused low winter temperatures and a wide distribution of permafrost. 2. Pasture of large herbivorous mammals (mammoth and accompanying species) which caused the formation of «pasture» savannas with an abundance of herbal vegetation and rare forests.

Do these factors define the composition of insect complexes as "mixed" faunas at 59°–56°N?

Firstly, cool and dry climate may cause a southward advance of arctic and sub-arctic species (*Diacheila polita*, *Curtonotus alpinus*, *C. torridus*, *Pterostichus* (*Cryobius*) spp.). As such, the warming and drying of local habitats (such as slopes with a southern exposition) in dry and cold climatic conditions and their subsequent salinity may cause the occurrence of some halophilic beetles.

Secondly, the pasture of mammoths and other mega mammals may cause the distribution of grasslands with a dominance of cereals and an abundance of weevils of the genus *Otiorhynchus*. The presence of sub-boreal steppe and sub-alpine species (*Poecilus ravus*, *Cymindis mannerheimi*, *Chrysolina perforata*) may have been caused by both environmental conditions and pasturable load. Rarefaction of woods may explain the lack of species inhabiting forest litter (*Calathus micropterus*, *Pterostichus oblongopunctatus* etc.); presence of single trees - occurrences of xylophagous beetles (bark beetle *Phoelotribus spinulosus* etc.). The fertilization of the soil may have caused the occurrence of coprophagous beetles (dung beetles of the genera *Aphodius*).

A combination of these factors may have caused the distribution of several landscapes. In the control and northern parts of the radius parts of 50° N, the cold climate and

In the central and northern parts of the region north of 59°N, the cold climate and corresponding mammoth pasture formed communities similar to modern tundra and forest tundra. South of 59°N and up to 57°N, specific landscapes and according insect faunas were formed. These conclusions do not contradict literature data on the palaeo-geography of that period (Arkhipov and Volkova 1994; Volkova et al. 2005; Astakhov 2009).

It may be assumed, that ground beetles of the species *Carabus sibiricus, Poecilus ravus, Pterostichus pinguedineus, Cymindis mannerheimi* and others have been widely distributed in the territories of the central part of Northern Eurasia, so that these insects may form an integral part of the landscapes containing the "mammoth faunas".

Factors leading to the disappearance of the "mammoth faunas"

At the beginning of the Holocene (10,000 yr. BP) in the Northern Hemisphere significant climatic changes took place, modifying all natural communities, and the final degradation of "mammoth faunas" took place. The largest mammals, mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), and giant deer (*Megaloceros giganteus*), having the greatest effect on terrestrial ecosystems, died out about 10–8,000 years ago, and the ranges of other species, such as reindeer (*Rangifer tarandus*), musk ox (*Ovibos moschatus*)) shifted either northwards to the

tundra and forest tundra, or southwards, to the steppes, such as the saiga antelope (*Saiga tatarica*).

The subsequent Early Holocene warming and humidification of climate, the extinction of mammoths and its consequent failing of the "pasture load" caused the reforestation and water logging of vast territories, the formation of the boreal belt, the transformation of the flora and fauna, and the wide distribution of conifer forests.

Therefore, climatic changes and the extinction of the large mammals happening between the Pleistocene and Holocene caused the disappearance of the "mixed" or nonanalogue insect faunas. However, the insect species did not die out, but only changed the location of their ranges. At that time the "mixed" insect faunas disintegrated into groups of single species, shifting their ranges northwards (*Curtonotus alpinus, Pterostichus (Cryobius*) spp.), southwards (*Pogonus* spp., *Cymindis mannerheimi*) or eastwards (*Poecilus (Derus) hanhaicus, P. (Derus) ravus, P. (Derus) major, Pseudotahoxenus dauricus, Amara minuta*). These species only left the territories studied but could survive these environmental changes in other regions of northern Eurasia, such as Mongolia, Eastern Siberia, or the Pamir Mountains, where environmental conditions are more compatible to their ecological requirements.

Comparison with other regions of North Eurasia

The "mixed" or non-analogue faunas of the central part of North Eurasia were compared with synchronous insect faunas as described for East Siberia (Sher et al. 2005, Kuzmina and Sher, 2006; Sher and Kuzmina, 2007). Significant differences between these regional faunas were found. Firstly, in the Late Quaternary insect complexes of Northeastern Siberia with remains of the pill beetle Morychus viridis were found in large quantities. Moreover Sher and Kuzmina claimed that Morychus viridis is "... a real symbol of the Pleistocene biota in Northeastern Siberia" (Sher and Kuzmina, 2007, p. 105). Remains of Morychus similar to M. viridis were found in "mixed" faunas from the Ural Mountains and West Siberia, although these insects were not so numerous here. The MIS 3 insect assemblages of the study area characterized by an abundance of fragments of weevils of the genus Otiorhynchus and morphologically similar to O. politus did not occur in the East Siberian sub-fossil insect faunas. The steppe assemblages of fossil insects from East Siberia belong to species, which are not found in the "mixed" insect faunas of the Ural Mountains and West Siberia, such as weevils of the genus Stepanocleonus (S. eruditus, S. fossulatus), Poecilus nearcticus, Harpalus vittatus. Tundra steppe beetles, such as Troglocollops arcticus, and Galeruca interrupta circumdata were not found in the insect assemblages of the Ural Mountains and West Siberia. An important feature of these "mixed" faunas of the Central part of North Eurasia is the presence of halophilic beetles which indicates local soil salinity, which may be explained by a strong aridity of the climate and by an external biogenic influence (pasture load) on the landscapes. No halophilic insects were found in fossil insect assemblages in Central and East Siberia. However, in East Siberian MIS 3 faunas

remains of dung beetles of the genus *Aphodius* were found, which are considered to indicate the presence of herbivorous mammals (Sher and Kuzmina, 2007).

Sub-fossil insect assemblages from Northeastern Siberia may reflect the existence of tundra steppe landscapes which have no analogue among modern ecosystems (Sher et al. 2005). The climate forming these communities can be considered as a main factor, but by cutting and trampling of grasses herbivores including large mammals made their own contribution to the formation of these ecosystems. For a long time pasture load allowed the perpetuation of grazing ecosystems (Zimov et al. 1995, Sher et al. 2005).

Insect faunas at the end of the Middle Pleninglacial in Western Europe (Bos et al. 2004) differ strongly from our faunas by the lack of steppe, by the absence of halophilic species and by the occurrence of the pill beetle of the genus *Morychus*. Weevils of the genus *Otiorhynchus* from European sites belong to *O. dubius*, which is not found in West Siberian faunas.

It is possible that these faunas, belonging to the "mixed" type, were distributed mainly in the Central part of North Eurasia (including West Siberia and the Ural Mountains) during the Late Pleistocene (MIS 4-MIS 2). So, similar faunas were found in the Gornova site, situated in the South Ural Mountains, near Ufa city (data given by F.G.Bidashko (Kazakhstan)). These assemblages are characterized by abundance of remains of the genus *Otiorhynchus* (similar to *O. politus*), the presence of *Poecilus ravus, Pogonus* spp., *Belopus* spp. and other species, with the presence of some endemic forms (*Nedria uralensis*).

Conclusions

- Sub-fossil insect assemblages allow us to reconstruct several elements of the natural zonality which existed in the central part of Northern Eurasia during the terminal phase of the Middle Pleninglacial (MIS 3). In the northern and central parts of the region north of 59°N, the cold climate and the corresponding mammoth pasture formed communities similar to modern tundra and forest tundra. In the southern part of the study area between 57° and 59°N, specific landscapes and corresponding insect faunas formed, known as "mammoth savannas".
- 2. Insect faunas of a "mixed" type of the Ural Mountains and West Siberia differ from East Siberian sub-fossil insect assemblages found in synchronous layers with the presence of numerous fragments of weevils *Otiorhynchus* which are morphologically similar to *O. politus*, as well as the halophilic beetles of the genera *Pogonus* and *Belopus*. Steppe beetles, such as weevils of the genus *Stepanocleonus* did not establish assemblages in West Siberia. Significant differences between insect assemblages from the central part of northern Eurasia and Western Europe were marked too. These faunas cannot be identified both as forest tundra nor tundra steppe and differ even from modern insect communities of East Siberia relict tundra steppes.
- 3. The species composition of insect complexes was determined not only by climate, but by pasture pressure of mammoths and other herbivorous mammals as well. A pasture load occurred in all territories of the Ural Mountains and West Siberia,

but is defined differently in different parts of the study area. In the central and northern parts of the region north of 59°N, a combination of these factors formed communities similar to modern tundra and forest tundra in accordance to the southward advance of arctic and sub-arctic insect complexes relative to contemporary faunas. In those territories lying during the terminal phase of MIS 3 between 59° and 57°N insect faunas existed without any analogues among modern insect complexes and included sub-arctic, sub-boreal steppe species, halophilic insects and weevils of the genus *Otiorhynchus* and similar to *O. politus*.

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RESEARCH ARTICLE



Predator feeding choice on conspicuous and non-conspicuous carabid beetles: first results

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Abstract

Insects use various types of behaviour, chemical defences, mimetic, aposematic or cryptic appearances as anti-predatory strategies. Among insects, carabid beetles of the genus *Brachinus* are distasteful prey because they discharge an irritating "cloud" of quinones when threatened. These beetles live in aggregations and adopt warning (conspicuous pattern) colours and chemicals to create a template that is easily learnt by predators. Another carabid beetle, *Anchomenus dorsalis*, mimics the colours and cuticular profile of *Brachinus* and is usually found in *Brachinus* aggregations. In this paper we report results from laboratory observations on feeding choice of the following natural predators - *Crocidura leucodon* (Insectivora: Soricidae), *Ocypus olens* (Coleoptera: Staphylinidae) and *Podarcis sicula* (Reptilia: Lacertidae) - on carabid beetle species. Comparing the number of attacks of predators towards aposematic and non-aposematic prey, there was a statistically significant preference towards non-aposematic prey.

Keywords

Brachinus, Anchomenus, anti-predatory strategies, warning signals, Coleoptera, Carabidae, laboratory tests

Introduction

Visual and chemical anti-predatory strategies influence trophic webs, as defensive substances (such as semiochemicals or ecomones) (sensu Pasteels 1977, 1982) play an important role (Pasteels et al. 1983) as deterrents against predators. A considerable amount of work has been done in evaluating anti-predatory strategies and in the identification of defence compounds in arthropods (Eisner 1970; Edmunds 1974; Guilford 1990; Alatalo and Mappes 1996; Gamberale and Tullberg 1998). Many animals use warning colours (or aposematism) to signal their unpalatability to potential predators (Cott 1940; Guilford 1990). In insects, aposematic colouration often co-occur with gregariousness (Edmunds 1974) increasing the effect of the aposematic signal (Poulton 1890; Cott 1940; Rowe and Guilford 1999; Riipi et al. 2001).

In Europe, Anchomenus dorsalis (Pontoppidan 1763), which produces methylsalicylate from its pygidial gland (Schildknecht 1970) as well as other chemicals (Bonacci et al., work in progress), is often found with species of the bombardier beetle genus Brachinus Weber, 1801 (Wautier 1971; Juliano 1985; Zaballos 1985; Bonacci et al. 2004a; Mazzei et al. 2005; Zetto Brandmayr et al. 2006) and, like Brachinus, is brightly coloured (green-blue and red-brown). In terms of chemical defence, bombardier beetles are amongst the best protected insect taxa. When attacked, these beetles eject jets of fluid (with a loud popping sound) from a pair of gland openings on the tip of the abdomen, aiming their discharge with accuracy towards the threat. The active compounds of the secretion are 1,4-benzoquinones, p-benzoquinone and 2-methyl-p-benzoquinone, which are mixed explosively at the moment of ejection, and discharge at 100°C with an audible detonation (Schildknecht 1961; Aneshansley et al. 1969; Eisner 1970; Eisner and Aneshansley 1999; Eisner et al. 2005; Bonacci et al. 2008). A number of predators have been shown to be repelled by bombardier beetles, including ants, carabid beetles, praying mantids, spiders, frogs and toads (Eisner 1958, 2003; Eisner and Dean 1976; Thiele 1977; Dean 1980a, b; Bonacci et al. 2004a, b, 2006).

In this study we report results from laboratory observations on the number of attacks of natural insect predators: *Crocidura leucodon* (Hermann, 1780) (Insectivora: Soricidae), *Ocypus olens* (Müller, 1764), (Coleoptera: Staphylinidae) and *Podarcis sicula* Rafinesque, 1810 (Reptilia: Lacertidae) towards some species of carabid beetles.

Material and methods

The lizard Podarcis sicula

Eleven hand collected adult male lizards (*Podarcis sicula*) were used in this study (collected from Cosenza province, southern Italy). Lizards were kept in the laboratory under natural daylight conditions. They were maintained in plastic cages (55 cm length \times 34 cm width \times 33 cm height) with opaque sides. Prey used were four species of carabid beetles, two of which were conspicuous: *Brachinus sclopeta* (Fabricius, 1792) (N = 11), *Anchomenus dorsalis* (N = 11); and two non-conspicuous: *Amara anthobia* A. Villa & G. B. Villa, 1833 (N = 11), *Amara aenea* (De Geer, 1774) (N = 11). The carabid beetles were collected by hand in the Crati Valley, Cosenza province, southern Italy.

Lizards were tested individually in an open arena (size: 28 cm length \times 18 cm width \times 16 cm height) with a lamp on a white plaster substrate. During the experiment temperature was maintained at 24–26°C. The trials were performed from June to July 2006. Each lizard was tested once by offering one individual of four prey species (*B. sclopeta, A. dorsalis, A. aenea, A. anthobia*) at the same time. Each carabid beetle was tested once. Before the beginning of the trial, each lizard was not fed for two days. The lizard to be tested was kept in the arena for 10 minutes before starting the trial. The trial began when the four prey individuals was put into the arena and lasted when the prey was ingested. If no predation occurred, the trial lasted for 30 minutes after the prey was put into the arena.

The behaviour of each lizard during the trial was recorded using a digital camcorder (Sony HDV 1080i). Attack delay and whether the carabid beetles were killed or refused were also recorded. Differences between the occurrences of attacking the different prey species were evaluated using the Chi-square test. Attack delay was evaluated using Mann-Whitney and Kruskal-Wallis tests, using the SPSS v.12.0 statistical package.

The staphylinid beetle Ocypus olens

Ten adult male staphylinid beetles, *Ocypus olens*, were collected by hand in the field (Cosenza Province, Italy). Each beetle was kept in the laboratory in a climate chamber at 18–24°C under L/D: 18/6 photoperiod. Each individual was maintained in a plexiglas container (10×8×6 cm) with 2 cm of clayey soil. The trials were performed between September 2003 and July 2004. Each beetle was collected four days before the experiment and maintained until the end of the experiment.

The beetles were not fed the day before the trial. Each beetle was individually tested in the laboratory. During each trial, one staphylinid beetle was placed in an arena $(10\times8\times6$ cm), followed immediately by adding one of eight carabid prey species (see below). The observation period started immediately and lasted for 10 minutes (for a total of 80 minutes per staphylinid specimen) without a rest period between the interactions.

The order in which the different carabid beetle prey species were introduced to the arena was random. The trials were video-recorded with a Panasonic digital video-camera. We counted the number of attacks towards the different prey species. The model prey consisted of eight species of carabid beetles. Three species possess warning colours and chemical defences (*Brachinus sclopeta, Anchomenus dorsalis* and *Chlaenius velutinus* (Duftschmid, 1812)) and five are without these characteristics (*Steropus melas* (Creutzer, 1799), *Calathus fuscipes* (Goeze, 1777), *Pseudophonus rufipes* (De Geer, 1774), *Poecilus cupreus* (Linné, 1758), and *Amara anthobia*). Attack frequency differences between species that possess warning colours and chemical defences, and those who do not possess these characteristics were evaluated using the Chi-square test in SPSS v.12.0.

The shrew Crocidura leucodon

Two adult specimens of the shrew, *Crocidura leucodon* (1 male and 1 female), were collected by long worth traps (Pollino mountain, Calabria, 1200 m a.s.l.) in October 2002. The shrews were kept under laboratory conditions in plastic cages (55 cm length \times 34 cm width \times 33 cm height) with opaque sides under natural daylight conditions. Nine carabid species were used as prey; *Scybalicus oblongiusculus* (Dejeani, 1829), *Parophonus hispanus* (Rambur, 1838), *Steropus melas* and *Calathus montivagus* Dejeani, 1831 (without warning colours and chemical defences) and *Chlaenius chrysocephalus* (Rossi, 1790), *Anchomenus dorsalis, Brachinus brevicollis* (= *peregrinus*) (Apfelbeck 1904), *B. sclopeta* and *B. crepitans* (Linné, 1758) (with warning colours and chemical defences). Shrew were tested individually in an open arena (size: 25 cm length \times 15 cm width \times 18 cm height) with plaster as a substrate and with low-light. Before the start of the trial, each shrew was starved for two days. The order in which the different carabid beetle prey species were introduced into the arena was random. The trials were video-recorded and the number of attacks towards the prey species was evaluated using the Chi-square test.

Carabid beetle nomenclature follows Vigna Taglianti (1993).

Results

We found a statistically significant preference towards non-conspicuous prey by the lizard *Podarcis sicula. Amara anthobia* and *A. aenea* were attacked with high frequency (Fig. 1a), while *Brachinus sclopeta* and *Anchomenus dorsalis* with low frequency ($X^2 = 23.76$, DF = 3, P < 0.001). Non-conspicuous prey were captured and eaten without difficulty, but when *Brachinus sclopeta* or *Anchomenus dorsalis* were captured, lizards always tossed their heads and then rubbed their snouts on the soil. This is most likely because of the unpalatability of aposematic prey (Bonacci et al. 2008; Bonacci et al., work in progress).

The staphylinid beetle *Ocypus olens* reacted differently to chemically protected and unprotected carabids. Aposematic and chemically protected species (*Brachinus sclopeta, Anchomenus dorsalis* and *Chlaenius velutinus*) were attacked with lower frequency ($X^2 = 23.56$, DF = 1, P < 0.001) than species without these characteristics (*Poecilus cupreus, Pseudophonus rufipes, Calathus fuscipes, Steropus melas* and *Amara anthobia*). Larger carabid species (*C. velutinus* and *S. melas*) were attacked quicker than smaller-sized species (Fig. 1b) (Bonacci et al. 2006).

The shrew *Crocidura leucodon* attacked and consumed all non-conspicuous and unprotected species of carabids, such as *Scybalicus oblongiusculus*, *Parophonus hispanus*, *Steropus melas* and *Calathus montivagus* (Fig. 1c). *Chlaenius chrysocephalus*, *Brachinus peregrinus*, *B. crepitans*, *B. sclopeta* and *Anchomenus dorsalis* were attacked infrequently ($X^2 = 35.25$, DF = 1, P < 0.001) and with difficulty (Fig. 2) (Bonacci et al. 2004b).



Figure I a Consumption of *Amara anthobia* by the lizard *Podarcis sicula* **b** attack on *Calathus fuscipes* by the staphylinid *Ocypus olens* **c** consumption of *Campalita maderae* by the shrew *Crocidura leucodon*.

Discussion

Our results support the hypothesis that conspicuous colouration and defence chemicals in gregarious carabid beetles can produce a sufficient aposematic signal to limit the attack by ambush and active predators. We found a statistically significant preference of predators for non-aposematic prey. Animals protected by chemical defence are often conspicuously coloured (Alcock 1979), since unpalatability is frequently coupled with warning signals (aposematic colours and odours) (Cott 1940; Tullberg et al. 2000). As such, edible prey may exploit the aversion of predators to warning-coloured species and evolve to resemble the model (Joron and Mallet 1998). Moreover, it is likely that unpalatability selects for gregariousness (Alatalo and Mappes 1996). Carabid beetles belonging to *A. dorsalis* use warning colouration and an odour pattern similar to that of *Brachinus sclopeta* (Bonacci et al. 2008; Bonacci et al. work in prep.) to trigger aversion in predators. In Müllerian mimicry, similarity does not necessarily need to be complete (Huheey 1988; Ihalainen et al. 2007), as in the case of *Anchomenus dorsalis* and *Brachinus sclopeta* (Fig. 3), which are quite similar in body size and colour pattern and live in conspicuous aggregations. These results suggest that colouration and chemi-



Figure 2. Percentage of attacks by *Crocidura leucodon* (Insectivora: Soricidae) on conspicuous and nonconspicuous carabid beetles. Black bars represent conspicuous species; grey bars represent non-conspicuous species.

cals (multimodal signals) used by the gregarious carabid beetles *Brachinus* spp. and *A. dorsalis* are an efficient anti-predatory strategy. In this case the quinones excreted by *Brachinus sclopeta* and other *Brachinus* species and the methylsalicilate (and probably other warning chemicals) produced by *Anchomenus dorsalis* can act as predator repellents. All predators tested here showed aversion towards *Brachinus* spp. and *A. dorsalis* individuals compared to non-conspicuous species (*Poecilus cupreus, Pseudophonus rufipes, Calathus fuscipes, Calathus montivagus, Steropus melas, Amara anthobia A. aenea, Scybalicus oblongiusculus, Parophonus hispanus*).

As suggested by many authors, Müllerian mimicry may influence the diversity of defensive secretions of a species (Rettenmeyer 1970; Edmunds 1974; Pasteels et al. 1983) and in this case, *A. dorsalis* benefits from the different defence systems of *Brachinus* individuals. A similar anti-predatory system has been reported in several reviews concerning insect defence chemistry (Brower 1969; Blum 1981; Nishida 2002); also, Müllerian mimics are sympatric aposematic species that share the same or similar warning patterns (Wickler 1968). The anti-predatory strategies of *Brachinus* spp. and *A. dorsalis* appear to be supported by a combination of conspicuous colouration, defence chemicals and a gregarious habit.

Future chemical and behavioural work should attempt to determine whether species of conspicuous and chemical defense systems are recognizable by the constant emission of odours or by the emission of chemicals after contact with predators (Bonacci et al. work in progress).



Figure 3. Interspecific aggregation of *Brachinus sclopeta* **a** *Anchomenus dorsalis* **b** and individuals of *Poecilus cupreus* **c**. Scale bar = 2 mm.

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RESEARCH ARTICLE



Predation of amphibians by carabid beetles of the genus *Epomis* found in the central coastal plain of Israel

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Abstract

The genus *Epomis* is represented in Israel by two species: *E. dejeani* and *E. circumscriptus*. In the central coastal plain these species are sympatric but do not occur in the same sites. The objective of this study was to record and describe trophic interactions between the adult beetles and amphibian species occurring in the central coastal plain of Israel. Day and night surveys at three sites, as well as controlled laboratory experiments were conducted for studying beetle-amphibian trophic interaction. In the field we recorded three cases of *E. dejeani* preying upon amphibian metamorphs and also found that *Epomis* adults share shelters with amphibians. Laboratory experiments supported the observations that both *Epomis* species can prey on amphibians. Predation of the three anuran species (*Bufo viridis, Hyla savignyi* and *Rana bedriagae*) and two urodele species (*Triturus vittatus* and *Salamandra salamandra infraimmaculata*) is described. Only *E. dejeani* consumed *T. vittatus*. Therefore, we conclude that the two species display a partial overlap in food habit.

Keywords

Epomis, Carabidae, amphibians, predation, feeding behavior, congeneric difference in food habit

Introduction

Invertebrates are known predators of juvenile and adult amphibians. The majority of reports list arachnids (e.g. Formanowicz 1981; McCormick and Polis 1982; Dehling 2007) and aquatic hemipterans (e.g. Hinshaw and Sullivan 1990; Haddad and Bastos

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1997; Toledo 2005) as the main arthropod predators. A few studies report predation by ants (Freed and Neitman 1988; Zuffi 2001; Ward-Fear et al. 2009) and by adult beetles (McCormick and Polis 1982; Hinshaw and Sullivan 1990; Jung et al. 2000). The latter involves mostly carabid beetles (Littlejohn and Wainer 1978; Ovaska and Smith 1988; Robertson 1989).

Following Brandmayr et al. (2010) we rank *Epomis* as a separate genus and not as a subgenus of *Chlaenius*. The genus *Epomis* belongs to the Chlaeniini tribe in which about 20 species are known, mainly from tropical Africa and south and south-eastern Asia. Five species are known from the Palaearctic region (Kryzhanovskij 1983).

So far, to the best of our knowledge, predation of an amphibian by an adult *Epomis* beetle was reported in a single note, describing the predation of a juvenile *Rana ni-gromaculata* by *E. nigricans* Wiedemann 1821, in Japan (Toshiaki 2006). Recently, predation of juveniles of two amphibian species (*Bufo viridis* and *Hyla savignyi*) by larvae of the carabid beetle *Epomis dejeani* Dejean & Boisduval 1830, was reported (Elron et al. 2007). Until 2007 only *E. dejeani* was known from Israel (Elron et al. 2007); however, while conducting this study we discovered an additional species, *E. circumscriptus* Duftschmid 1812 (identified by Pietro Brandmayr). In the central coastal plain we found the *Epomis* beetles in clay type and sandy soils around the banks of rain-pools (Elron et al. 2007). Rain-pool habitats are the major breeding sites of amphibians in Israel. Here we report on the food habit and predation behavior of adults of the two *Epomis* species in Israel.

Methods

Distribution

During the period of 2007 – 2009 we conducted 103 daytime surveys at 26 sites along the central coastal plain (from south of Tel-Aviv to north of Hadera) in order to examine the presence of *Epomis* species close to freshwater bodies where amphibians are usually present. The specimens observed were identified and recorded. Selected specimens were deposited in the Natural History Collection, Tel-Aviv University.

Field observations

We conducted daytime and night surveys at three sites in the central coastal plain (Table 1). The location of the study sites is shown in Figure 1. Outside this study, observations on *E. circumscriptus* life history dynamics were conducted in two additional sites in the central coastal plain (Qadima and Kfar Netter, Table 1).

During daytime surveys we searched for adult beetles under natural and artificial shelters. The former consisted of any local wooden debris or rocks of various sizes.

Site name	Coordinates	daytime surveys	night surveys	
Dora	32°17'30"N	27	5	
	34°50'48"E			
Berekhat Ya'ar	32°24'16"N	37	11	
	34°54'61"E			
Samar	32°26'23"N	15	11	
	34°53'01"E			
Qadima	32°27'25"N	-	-	
-	34°89'64"E			
Kfar Netter	32°28'65"N	-	-	
	34°87'28"E			

Table 1. Location and number of daytime and night surveys conducted in the study sites.

For artificial shelters we used 40×40 cm cement tiles. At night we used white-light flashlights (Hyundai, Search Finder 1×10^6 candle power) to locate adult beetles and amphibians and to record their activity outside shelters. Each survey (day or night) lasted for two hours. When predation interaction was encountered, the entire event was recorded.

Laboratory observations

We supplemented the field observations of predation interactions with controlled experiments in the laboratory, in which we exposed a known species of amphibian to one or other species of *Epomis*. The encounter experiments were conducted in one liter plastic containers (10.5cm high; 14.5cm diameter) with moist peat-moss as substrate in which an individual beetle was reared. A randomly selected metamorph of one out of five amphibian species occurring in the coastal plain was added to the container with the beetle. These metamorphs were measured (snout-vent for anurans; snout-end of tail for urodeles) with a caliper (± 0.05mm) and weighed using an analytical scale (± 0.001g). For each experiment we used a naive amphibian and beetle. Beetles presented with crushed house crickets (Acheta domestica) served as a control for feeding interaction. The beetles are used to this food because we routinely feed them with crushed crickets once a week. We fed the amphibian metamorphs daily with live house crickets. Food was not presented to the beetle or the amphibian on the day of the experiment. All observations were made under natural light. We documented the predation encounter using a Canon powershot SX10 video camera. The video recording started 10 seconds before releasing the amphibian into the beetle's container, and was carried out in 10 minute clips until the interaction ended. In addition, we documented the interaction with still photographs (DSLR, Canon EOS 20D and Canon EOS 50D). Distribution records and observations of predation behavior did not require statistical analysis.



Figure 1. Distribution of *Epomis* species in the study area, central coastal plain, Israel, 2007–2009 (square in left corner shows location of study area).

Results

Distribution

In 103 surveys conducted in 26 sites in the coastal plain, *Epomis* beetles were recorded in four sites only, all within a radius of 18km (Table 2). The two species were never found in the same site (Fig. 1); *E. dejeani* was found in Berekhat Ya'ar and Samar, whereas *E. circumscriptus* was found in Dora, Qadima and Kefar Netter (west of Qadima).

Field observations

We observed three events of adult beetles, *E. dejeani* only, preying on *Bufo viridis* metamorphs (two in March, one in July), all during night surveys. On seven out of

	Dora	Qadima	Berekhat Ya'ar	Samar
Dora	-			
Qadima	5.1	-		
Berekhat Ya'ar	14.4	14.8	-	
Samar	16.3	17.4	2.8	-

Table 2. Distances (in km) between the surveyed sites, central coastal plain, Israel.

79 daytime surveys we recorded adult beetles co-occurring with amphibians (metamorphs, juveniles and an adult) under the same shelters (Table 3; URL: Amphibian - Adult *Epomis* interaction). In all these cases a single adult beetle (male or female) was sharing a shelter with amphibians. Co-occurrence with *E. circumscriptus* was recorded in March and April and with *E. dejeani* in February, March and May. Although we did not observe predation interaction in the above cases we did find in one case the remains of three devoured metamorphs of *B. viridis* (URL: Amphibian - Adult *Epomis* interaction). One of the authors observed similar remains of *B. viridis* under a shelter occupied by *E. circumscriptus* at another site (Qadima, Fig. 1).

Laboratory experiments

In the laboratory we found that *E. dejeani* preyed on all five amphibian species presented to it in 38 experiments (100% predation occurrence, Table 4). In the case of *E. circumscriptus* predation occurred in 78% of 37 experiments. In all the experiments involving *Triturus vittatus* and *E. circumscriptus*, predation did not take place (Table 4).

Predation behavior

On March 26th, 2008 at ca. 10 pm we observed at the Berekhat Ya'ar site, ca. 50m from the pond, an *E. dejeani* female biting a *B. viridis* metamorph on the lower back area and dragging it for a short distance (ca. 20cm). We then observed the female devour-

Table 3. Developmental stage and number of individuals of amphibians (Adl.= Adult; Juv.= Juvenile; Met.= Metamorph; in parentheses, number of records) recorded co-occurring with adult *Epomis* beetles in the field under the same shelter.

	E. circumscriptus			E. dejeani			
Amphibian species	Adl.	Juv.	Met.	Adl.	Juv.	Met.	
Bufo viridis	0 (45)	1 (2)	30 (1)	0 (72)	0 (72)	0 (72)	
Hyla savignyi	0 (45)	0 (45)	0 (45)	1 (1)	1 (1)	2 (1)	
Rana bedriagae	0 (45)	0 (45)	4 (1)	0 (72)	0 (72)	0 (72)	

Amphibian species	Mean	Mean	Epomis		Epomis	
	weight	length	circumscriptus		dejeani	
	±SD (g)	±SD (mm)	Predation (%)	n	Predation (%)	n
Bufo viridis	0.38±0.11	16.3±1.5	100	17	100	18
Hyla savignyi	0.24±0.03	15.8±1.0	100	5	100	5
Rana bedriagae	1.24±0.32	23.4±1.4	100	5	100	5
Triturus vittatus	0.21±0.03	33.0±1.9	0	8	100	8
Salamandra	1.19±0.36	54.7 ± 4.1	100	2	100	2
salamandra						
infraimmaculata						

Table 4. Comparison of predation of juveniles of five amphibian species by adult beetles of two *Epomis* species. Weights and lengths (anurans – snout-vent; urodeles - snout-end of tail) of the amphibians and shown. n indicates number of experiments.

ing the metamorph for a period of 27 minutes, starting at the back area, and leaving only the fore and hind limbs. Twenty minutes later, at a distance of ca. 250m from the pond, we observed a different *E. dejeani* female feeding on a *B. viridis* metamorph in a crevice in the ground. On July 6th, 2008 at 7 pm we observed on the pond bank at the Samar site a male *E. dejeani* feeding on a *B. viridis* metamorph. The beetle was chewing on the rear legs of the metamorph. Upon our approach it abandoned the site, leaving its prey behind.

In all of the laboratory experiments involving B. viridis, H. savignyi and S. salamandra infraimmaculata metamorphs, adults of both Epomis species demonstrated a similar response of immediately jumping on the amphibian's back, biting at the lower back area (Fig. 2a). This caused the amphibian metamorph to jump, trying unsuccessfully to shake the beetle off. Using its mandibles, the beetles made a horizontal incision in the lower back of the amphibian (Fig. 2b) causing it to cease moving within ca. 1-2minutes. Subsequently the beetle started chewing on the back and sides of the metamorph (Fig. 2c). Within an hour (H. savignyi and S. salamandra infraimmaculata) to an hour and a half (*B. viridis*), only the amphibian's limbs and head remained (Fig. 2d). In all these cases the beetle's abdomen swelled noticeably (Fig 2e). In some cases (B. viridis n=5; H. savignyi n=4; S. salamandra infarimmaculata n=2) the beetle continued feeding, consuming the amphibian's eyes as well. In all cases (n=5 for *E. dejeani*; n=5 for *E. circumscriptus*), predation of *Rana bedriagae* metamorphs started with the beetle biting at one of the rear limbs. Despite the vigorous jumping of the Rana metamorph the beetle hung on successfully. Within ca. 40 seconds the metamorph ceased to struggle and the beetle changed position to the posterior venter where it initiated chewing. Feeding continued for ca. two hours.

Four out of the five amphibian species were consumed by the two *Epomis* species, whereas *T. vittatus* was consumed only by *E. dejeani*. In all cases, predation of *T. vittatus* started by biting at the central venter (Fig. 2f). Feeding lasted for 27–34 minutes, and when it ended only a few bones remained. In contrast, most *E. circumscriptus*



Figure 2. Predation of amphibians by adult *Epomis*: **a** *B. viridis* juvenile by *E. circumscriptus* **b** *Hyla* savignyi juvenile by *E. circumscriptus* **c** *B. viridis* juvenile by *E. circumscriptus* **d** *S. s. infraimmaculata* metamorph by *E. dejeani* **e** *H. savignyi* juvenile by *E. circumscriptus* **f** *T. vittatus* metamorph by *E. dejeani* (photographs by Gil Wizen).

(n=5) completely avoided any encounter with *T. vittatus*. In two cases of *E. circumscriptus* the beetle jumped on the newt but did not initiate biting, and within ca. 10 seconds turned away from the amphibian. It then moved its forelegs and antennae through its mouth parts; this display appeared as cleaning behavior. In one case *E. circumscriptus* clasped *T. vittatus* by its neck using its mandibles and carried it for a short distance (ca. 10cm). The beetle then dropped the newt on the ground and ceased biting. The beetle was restless, repeatedly moving its forelegs and antennae through its mouth parts as described above.

The amphibian-*Epomis* predation interaction is demonstrated in photos and short videos (URL: Amphibian - Adult *Epomis* interaction).

Discussion

Two *Epomis* species occur in the central coastal plain of Israel. In the course of this study, they were recorded in four sites only, within a radius of <20 km, but never in the same site. Climate, soil type and vegetation were similar in the four sites in which the beetles occur. In the absence of neither a physical barrier nor an apparent habitat difference the segregation of the species to different sites may be a case of sympatric species that do not occur in the same sites (reviewed in Fitzpatrick et al. 2008). Except for a single observation from 1927 (O. Theodor) where the two species were collected at Hadera (no site information), sympatric distribution with no overlap is supported by all other records of the Natural History Collection, Tel-Aviv University.

Adults of the two *Epomis* species share shelters with amphibians during the day. The encounter between predator and prey is inevitable when the two become active at night. The outcome of this interaction is invariably fatal for the amphibian. Adult Carabidae are phytophagous, zoophagous and mixophagous (Kryzhanovskij 1983). The diet of predacious carabids is diverse, including insects, arachnids, gastropods, isopods and lumbricid worms (Lövei and Sunderland 1996), as well as injured and dead vertebrates (Littlejohn and Wainer 1978). Adult beetles of the Chlaeniini tribe are known to feed on various live and dead invertebrates as well as on carcasses of vertebrates (Kryzhanovskij 1983). The diet of *Epomis* species corresponds to the Chlaeniini food habit, with the addition of live amphibians as an optional food item in their diet. We examined *Epomis* interactions with five out of six amphibian species occurring in Israel. We avoided using the anuran *Pelobates syriacus* which is a rare species in Israel. The beetles' interaction with this species awaits examination. We describe the predation behavior of the two *Epomis* species based on laboratory observations. The behavior agrees with that described for *E. nigricans* in the field (Toshiaki 2006). Nevertheless, further observations in the field are required to support our laboratory observations.

In the field we have evidence for predation of *B. viridis* by the two *Epomis* species. In laboratory experiments we found that one of the *Epomis* species preyed upon three anurans and two urodeles while the other species avoided *T. vittatus*.

An in-depth investigation of predation of amphibians by *Epomis* species in Israel has revealed that the diet of the two sympatric congeners that do not occur at the same site overlaps only partially. Most reported studies on food habits demonstrate diet partitioning as well as overlap in congeneric sympatric species. These reports include vertebrates such as fish (Targett 1978; Yang and Livingston 1986; Correra et al. 2009), amphibians (Fraser 1976; Dolmen and Koksvik 1983; Griffiths 1986), reptiles (Rose 1976), birds (Schoener 1965; Holmes and Pitelka 1968), and bats (Arlettaz et al. 1997; Lopez and Vaughan 2007). Relatively little is known on food habits of sympatric congeneric insects, such as herbivorous coleopterans (Futuyma and Mitter 1996), lepidopterans (Chew and Renwick 1995; Menken 1996; Friberg and Wiklund 2008) and hymenopterans (Heatwole and Davis 1965). Most of the reports on insects discuss food overlap (e.g. Futuyma and Mitter 1996; Friberg and Wiklund 2008), and only a

few deal with congeneric species with a specialized diet (e.g. Heatwole and Davis 1965; Chew and Renwick 1995; Menken 1996). Among congeneric predacious adult insects that exhibit sympatric distribution but do not occur in the same site, we know of no other example of partial food overlap other than the *Epomis* species we studied. The reason for the partial overlap in the two *Epomis* species is still unknown. A possibility of anti-predator defensive mechanism seems less probable because the known defense responses of amphibian are not species specific (reviewed in Dodd 1976 and Dodd and Brodie 1976). Presently, we examine whether the same difference in food habit found for the adult beetles holds for the larval stages as well.

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SHORT COMMUNICATION



Current knowledge on exocrine glands in carabid beetles: structure, function and chemical compounds

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Abstract

Many exocrine products used by ground beetles are pheromones and allomones that regulate intra- and interspecific interactions and contribute to their success in terrestrial ecosystems. This mini-review attempts to unify major themes related to the exocrine glands of carabid beetles. Here we report on both glandular structures and the role of secretions in carabid adults, and that little information is available on the ecological significance of glandular secretions in pre-imaginal stages.

Keywords

antennal glands, pygidial gland, defensive secretion, carabid beetles

Introduction

Exocrine gland secretions in insects are involved in reproductive and defensive behaviour (Pasteels et al. 1983; Blum 1996), and are important in social integration and communication among members of the same colony (as in Hymenoptera) (Hölldobler and Wilson 1990). These exocrine glands have an ectodermal origin and morphological or functional classifications have been generally used to describe them. The location and morphology of these glands are directly related to their function (Billen 1998). Many glands are common to all insects, e.g. mandibular and salivary glands, male and female accessory glands associated with reproductive organs (Dallai et al. 1999; Viscuso et al. 2001) and defensive glands (Thiele 1977), whereas some glands are characteristic of a family or species (Grassé 1975; Quennedey 1998, 2000), especially in social insects (Cammaerts 1974; Bin et al. 1989; Hölldobler and Wilson 1990, also see reviews; Billen 1991; Delfino et al. 1991, 1992; Pedata et al. 1993; Bartlet et al. 1994; Isidoro and Bin 1995; Isidoro et al. 1996, 2000; Bot et al. 2001; Gobin et al. 2001, 2003; Torres et al. 2001).

Information on the chemistry of defensive secretions in many carabid species are available in Dettner (1987), Whitman et al. (1990) and Will et al. (2000). In this manuscript, carabid beetles are meant in the widest sense of the word, including the old lineage of Trachypachidae, the Rhysodidae and the Paussinae as a subfamily (as in Beutel and Leschen 2005). The nomenclature of palaearctic taxa follows Löbl and Smetana (2003).

Adult antennal glands

The cellular architecture of adult antennal glands has been investigated for *Platynus* assimilis (Paykull 1790) (Weis et al. 1999), Paussus spp Linnaeus 1775 (Di Giulio et al.2003, 2009; Nagel 1979) and Siagona europaea Dejean 1826 (Giglio et al. 2005). Structural analysis shows a great number of antennal glands that have been classified into the following main categories (Noirot and Quennedey 1991, Quennedey 1998): i) unicellular gland class 2, which is not in contact with the cuticle; ii) bi- and tricellular gland class 3, connected to the cuticle by a cuticular duct draining the secretions outside. The first type (class 2) includes unicellular glands known as oenocytes. They are located only within the antennal lumen of *S. europaea* and are not found in other carabid species (Giglio et al. 2005). Their role in cuticular hydrocarbons secretions is suggested by Lockey (1988) and Noirot and Quennedey (1991). The second type are tri-cellular glands, composed of a secretory, an intercalary and a duct cell, and are found in P. assimilis (Weis et al. 1999), Paussus favieri Fairmaire (Di Giulio et al. 2009) and S. europaea. Moreover, a large number of bi-cellular glands, composed of one gland and one duct cell, are located on the antennal surface of *P. favieri*. The structural variability and distribution of the antennal glandular apparatus on Paussini, such as the myrmecophilous *P. favieri*, are closely related to their symbiotic life style (Geiselhardt et al. 2007). Predators, such as P. assimilis and S. europaea, which have free-living life habits, show a more simple glandular apparatus. Exocrine gland class 3 of the myrmecophagous S. europaea produces secretions that protect the surface of the antennae and sensilla from wear.

Pygidial glands

Ground beetles possess a pair of abdominal glands known as pygidial glands, which produce defensive secretions. Their structure consists of two sets of secretory lobes, collecting canals, collecting reservoirs and has been well described for many species (Benn 1973; Forsyth 1970, 1972; Scott et al. 1975; Balestrazzi et al. 1985; Rossini et al. 1997; Eisner et al. 2000; Will et al. 2000, 2010; Attygalle et al. 2004). These glands are variable in structure and in the nature of the produced substances (Thiele 1977), and discharge the secretion products by oozing, spraying or crepitation. Oozing is probably the plesiotypic mode of discharge, with active spraying and crepitation as later refinements (Moore 1979). The main function of pygidial glands is probably in the defence against predators, but also in the facilitation of the penetration of defensive compounds into the predator's integuments, antimicrobial and antifungal activity, and in producing alarm messages (Evans and Schmidt 1990; Blum 1996).

A comparative study of the secretions of carabid pygidial glands was made by Schildknecht et al. (1968). Moore (1979) and Will et al. (2000) listed all the principal groups of secretions detected in carabid tribes: hydrocarbons, aliphatic ketones, saturated esters, formic acid, higher saturated acids, unsaturated carboxylic acids, phenols (m-cresol), aromatic aldehydes (salicylaldehyde) and quinones. Attygalle et al. (1991) showed that D_o-L-valine is incorporated into methacrylic and isobutyric acids in the pygidial defensive glands of Scarites subterraneus Fabricius 1775. The pygidial glands of Helluomorphoides clairvillei (Dejean 1831) females discharge a mixture of compounds including carboxylic acid, aliphatic esters and hydrocarbons (Attygalle et al. 1992). The taxonomic distribution of defensive secretions was reviewed by Will et al. (2000) for 47 tribes. Data have shown a close relationship between chemical classes and habitat diversification. Tribes with high species diversity in tropical-subtropical and steppe habitats use formic acid as primary chemical defences, while tribes with high diversity in temperate regions use carboxylic acids, phenols, quinone, aromatic aldeydes and ketones. This can be explained by the interaction of ground beetles with their predators and prey. Specifically, ants are hypothesized to have had a major influence on the evolution of ground beetle secretions in tropical species. Bombardier beetles of the genus Brachinus Weber 1801 are able to release irritating quinones, produced by the oxidation of hydroquinones in a double-chambered apparatus (Schildknecht 1961; Eisner and Meinwald 1966; Schildknecht et al. 1968; Aneshansely et al. 1969; Eisner and Aneshansely 1999; Eisner et al. 2000); a certain amount of heat and the explosion associated with the reaction reinforce the defensive effect. Predation on these beetles appears to be rare (Juliano 1985; Bonacci et al. 2006, 2008). From the literature it is known that Anchomenus dorsalis (Pontoppidan, 1763) produces toxic methylsalycilate from its pygidial glands (Schildknecht 1970). Tiger beetle species living in moist habitats produce benzaldehyde (Altaba 1991). The carabid beetle Galerita lecontei Dejean 1831 secretes, as a spray, a mixture of formic acid, acetic acid and lipophilic components (long-chain hydrocarbons and esters) (Rossini et al. 1997). Biosynthesis of tiglic and ethacrylic acids from isoleucine via 2-methylbutyric acid was demonstrated in Pterostichus californicus (Dejean 1828) (Attygalle et al. 2007). Complex mixtures of monoterpenes are found in the defensive secretions of Ardistomis schaumii Leconte 1857 and Semiardistomis puncticollis Dejean 1831. The presence of monoterpenes in beetle secretions is well known, yet it is not very common to find the opposite enantiomers in secretions in related species (Attygalle 2009).

Exocrine glands of larval and pupal stages

Although exocrine glands and their defensive secretions are well investigated in adults, hardly any information exists for the larval and pupal stages, which are the most vulnerable stages of the beetle's life cycle.

Glandular organs have been found in the larval stage of myrmecophilus *Pseudomorpha* sp. These glands are located on the head and thorax and secrete chemical compounds which repel ants (Erwin 1981). In Paussini larvae (*Paussus kannegieteri* Wasmann 1896) as well as in Metriini (*Metrius*) and Ozaenini, the modified terminal abdominal segments have glandular pores that secrete pleasant substances to attract their host ants (Arndt et al. 2005; Geiselhardt et al. 2007; Di Giulio 2008).

In the pupal stage of Carabus lefebvrei Dejean, 1826, Sturani (1962) described a "flavour humour" and suggested that this secretion has a waterproofing or an antipredatory function. Ultrastructural analyses have shown that this exudate is secreted by an acinose abdominal complex of exocrine glandular units (Giglio et al. 2009). The independent glandular unit consists of a single secretory cell, a duct and its associated cell and belongs to gland cell class 3 according to the classification of Quennedey (1998). In the cytoplasm, the secretory cell contains abundant rough endoplasmatic reticula, glycogen granules, numerous mitochondria and many well-developed Golgi complexes producing electron-dense secretory granules. Mitochondria are large, elongated and often adjoining electronlucent vesicles. Their close association with tracheoles suggests very high aerobic metabolism. Chemical analyses of the gland secretions revealed a mixture of low molecular weight terpenes as well as ketones, aldehydes, alcohols, esters and carboxylic acids, which in adults are regarded deterrents against predators. Monoterpenes, especially linalool, were the main chemical products produced by the pupal stage of *C. lefebvrei*. It is suggested that this gland secretion has both a deterrent function against predators and a prophylaxis function against pathogens.

Conclusions and future studies

The present manuscript summarized the main knowledge on the exocrine glands in ground beetles. The main characteristic of glandular secretions of each life stage is its diversity and dependence on interspecific relations in the ecological niches of species. Our main future aim is to accumulate data on defensive secretions to understand, i) the mode of action of chemical compounds, and ii) species-specific variation of glandular structures and chemical secretions, paying particular attention to morphological, phylogenetic and behavioural aspects. Moreover, the need for more detailed studies on larval and pupal stages has already been stressed. Presently, the pupal stages of carabid beetles are known not to possess any physical protection, thus chemical protection provided by the abdominal glands is very important. This stage is present in environments rich in bacterial and fungal microorganisms, some of which are possible insect

pathogens. Besides, the highly lipophilic nature of monoterpene compounds suggests that their principal targets are bacterial and/or fungal cell membranes.

To support this hypothesis additional research is needed to evaluate the range of activity of the secretions of pupal abdominal glands towards microorganisms and fungal entomopathogens.

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RESEARCH ARTICLE



Morphometry of eyes, antennae and wings in three species of Siagona (Coleoptera, Carabidae)

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Abstract

In carabid beetles, physiological and behavioural characteristics reflect specific habitat demands and there is a strong correlation between body form and habit in species with different life style. In this study, we compared the morphometry and compound eye characteristics of three species of the genus *Siagona: S. jenissoni, S. dejeani* and *S. europaea*. These carabids have a stenotopic lifestyle in Mediterranean clayey soils, inhabiting the ground fissure system formed during the dry season. All species have a Mediterranean distribution and are nocturnal olfactory hunters, and are strict ant predators. For morphometric measurements, we considered body length (mm), wing length (mm), antenna length (mm), head width (mm), trochanter length (mm), number of ommatidia, eye surface area (mm²), ommatidia density (number of ommatidia/ mm² of eye surface area), head height (mm), thorax height (mm) and abdomen height (mm). The data revealed intersexual and interspecific differences. The three species differ in relative length of the antennae, density and number of ommatidia and relative trochanter length. Significant differences occurred in wing sizes, which are well developed in *S. europaea*, the only species capable of flight. When eye size is compared with other ground beetles of various lifestyles, *Siagona* shows pronounced "microphthalmy" an adaptation to subterranean life in clayey crevices of tropical and subtropical climates with a marked dry season.

Keywords

Compound eyes, morphometric measurements, Siagona

Introduction

Carabid beetles vary in body form and size, annual rhythmicity and habitat choice. They also differ in many physiological and behavioural characteristics that reflect specific habitat demands (Thiele 1977; Den Boer 1986). As a consequence there is a strong correlation between body form and habit (e.g., feeding, locomotion, burrowing and flying) in carabid beetles with different lifestyles. Those living in restricted or confined habitats, such as fissures in the ground or burrows, tend to have narrower and flatter (shallower) bodies, with the prothorax similar in width to the hind body. It has been suggested that this type of body form minimizes friction by causing less obstruction when moving through confined spaces (Forsythe 1982, 1983, 1991; Evans and Forsythe 1985).

Moreover, most ground beetles with seemingly similar body shapes have speciesspecific morphological peculiarities that reflect the special demands of their niches (Bauer and Kredler 1993). For example, although variability in eye morphology may be small among closely related species, e.g. those of the same genus, variability do exist if there are divergent habitat preferences (Bauer et al. 1998). The morphometry and eye morphology in three species of the genus *Carabus (C. coriaceus, C. lefebvrei* and *C. presli*) were recently investigated in relation to habitat demands (Talarico et al., 2007). The three species are large-spectrum olfactory hunters, but their different lifestyles have influenced body and eye characteristics: the number of ommatidia is significantly higher in *C. coriaceus* than in *C. lefebvrei* and *C. preslii*, and the authors suggested that this could be habitat-related. As a consequence, *C. coriaceus* and *C. lefebvrei* can be included in the second group of Bauer and Kredler (1993), including species with no preferred activity period (i.e., active by day and night, but preferably at twilight), while *C. preslii* belongs to the third group of nocturnal species.

The genus *Siagona* (tribe Siagonini) should be placed among the less derived Carabidae (Carabinae, Caraboidea Simplicia of Jeannel 1941, the so called "lower carabids"), and a recent study by Ball and Shpeley (2005) reported marked differences from the very similar genus *Cymbionotum* Baudi di Selve.

The biology of siagonines is poorly known. Andrewes (1929) hypothesized relationships between the Siagonini tribe and termites. The same author collected adult beetles of four *Siagona* species from India during the rainy season in vegetable refuse surrounding rice fields. The genus has a wide geographic distribution, including India, Arabia, Africa and the Mediterranean region. Three species are present in Southern Europe, *S. jenissoni* Dejean, 1826, *S. dejeani* Rambur, 1837 and *S. europaea* Dejean, 1826 (Bauer et al. 2005). All siagonines have a strikingly flat body with a stalk-like constriction between the pro- and mesothorax and strong mandibles with large retinaculum. The flatness of the body and thoracic constriction are possible adaptations to life in narrow soil crevices. The short but strong mandibles are well-suited for grasping and chewing arthropod prey with tough and flexible cuticles (e.g. ants; Zetto Brandmayr and Pizzolotto 1994; Bauer et al. 2005).

S. europaea is exclusively myrmecophagous, both of adult ants and their brood (Zetto Brandmayr and Pizzolotto 1994; Zetto Brandmayr et al. 1998; Bauer et al.
2005). It has a Mediterranean distribution (Italy, Spain, Greece and North Morocco), preferring open, sclerophyllous habitats of the Mediterranean biome (Brandmayr and Pizzolotto 1990). In Southern Italy, *S. europaea* occurs in pastures and abandoned fields only in clayey soils up to an altitude of about 250 m a.s.l., while in Calabria it occurs up to ca. 450 m (Pizzolotto et al. 2005). In early spring, when soil moisture is high, the beetles are found under stones. From mid-April onwards, when the soil dries out and becomes deeply fissured, they retreat into deeper crevices, especially during the hot and dry hours of the day. Their activity is mainly nocturnal, as shown by recordings and by the structure of their compound eyes (Bauer et al. 2005), with a value of ommatidia/mm body length typical for nocturnal species (cf. Bauer and Kredler 1993).

Only fragmentary information is available for *S. jenissoni* and *S. dejeani*. They occur in southern Spain, between Cadiz and Malaga, in Portugal (Serrano 2003) and on the coast of Morocco (Andrewes 1929; Antoine 1955). The aim of this study was to acquire further knowledge on the biology of the three southern European *Siagona* species by morphometric investigations of intersexual and interspecific differences of some morphological features, such as the antennae, eyes and wings.

Methods

Animals

The sample consisted of 20 individuals (10 males and 10 females) for each species: *S. jenissoni, S. dejeani* and *S. europaea*. Specimens of *S. europaea* were collected in southern Italy (Calabria, Squillace, Catanzaro, 250 m a.s.l.) mostly by bait-traps in open fields and pastures during the spring of 2004, while *S. jenissoni* and *S. dejeani* were collected in southern Spain (Andalusia, between Algesiras and Cadiz) in March of 2005 (100–400 m a.s.l.).

Morphometric analyses

The animals were stored in alcohol (70%). Photographs were taken with a stereoscope (Zeiss Stemi SV 11Apo) and acquired by Matrox PC-VCR software (for Windows[®] 2000). For each individual, we measured body length (mm), wing length (mm), antenna length (mm), head width (mm), trochanter length (mm), number of ommatidia, eye surface area (mm²), ommatidia density (number of ommatidia/mm² of eye surface area), head height (mm), thorax height (mm) and abdomen height (mm).

Relative measures of antennal lengths, number of ommatidia and eye surface area were weighted against head width, while trochanter length, head height, thorax height and abdomen height were weighted against body length. To determine the number of ommatidia and cornea size, we softened the specimens in hot potash lye for a few minutes. The cornea was removed and fixed through the following stations: distilled water, acetone, ethanol (70%), absolute ethanol and xylol. It was then spread on a microscope slide and photographed. Measurements were taken using Sigma Scan Pro 5 Software (SPSS[®] Inc.).

Statistical analyses

Sexual dimorphism in each species was tested using the Mann-Whitney U test (Siegel and Castellan 1988), while the Kruskall-Wallis test was used to test for morphological differences among species (Sokal and Rohlf 1995). Pairwise comparisons (between species) were performed with the Mann-Whitney U test, and significance levels were corrected using the Dunn-Šidák significance level correction method: $a' = 1 - (1 - a)^{1/k}$, were *k* is the number of comparisons (Sokal and Rohlf 1995).

The probability level was computed using a complete randomisation method (permutation or exact test; P_{exact}) or by a Monte Carlo simulation based on 10 000 sampled tables ($P_{MonteCarlo}$) when computation was not possible (Mehta and Patel 1996; Good 2000).

The multivariate general lineal model (GLM) with species and sex as main factors was applied to sensorial structures, eye asymmetry and main body size measures to verify previously performed univariate hypothesis testing. Multivariate differences between factors were tested by Pillai's Trace, while univariate tests were computed using the type III sum of squares.

Means are reported with standard error of means (± SEM) throughout the text.

Statistical analyses were performed using the Statistical Package for Social Sciences 13.01 (SPSS[®] Inc.).

Results

The three species presented some sex differences related to size (Table 1, Fig. 1). Males of *S. dejeani* and *S. jenissoni* had significantly longer trochanters (relative to body length) compared to females (respectively U = 21.5, W = 76.5, $P_{Exact} = 0.029$ and U = 1.0, W = 56.0, $P_{Exact} < 0.001$), while in *S. europaea* females had wider heads than males (U = 23.0, W = 78.0, $P_{Exact} = 0.043$). Notably, there was no difference in the size of sensory structures (antennae and eyes) ($P_{Exact} > 0.05$); therefore, we evaluated specific differences in sensory structures with no concern for gender.

Ommatidia density differed significantly among species ($X^2 = 30.951$, d.f. = 2, $P_{Exact} < 0.001$), being significantly higher ($P_{Exact} < 0.05$) in *S. europaea* and lower in *S. dejeani* (Table 2, Fig. 2A). The weighted number of ommatidia in *S. europaea* was higher ($X^2 = 45.057$, d.f. = 2, $P_{Exact} < 0.001$), but there was no significant difference between *S. dejeani* and *S. jenissoni* (Fig. 2B). *S. dejeani's* antennae were significantly shorter than those of the other two species ($X^2 = 24.521$, d.f. = 2, $P_{Exact} < 0.001$) (Fig. 2C).

The GLM analysis confirmed these results, with the global morphological pattern differing among species (*Pillai's Trace* = 1.609, F = 16.822, d.f. = 22, P < 0.001), but not between the sexes (*Pillai's Trace* = 0.321, F = 1.894, d.f. = 22, P = 0.067).

Table 1. Sex differences in body and eye morphological characteristics (means and Standard Error of Means) in three species of *Siagona*. Mann-Whitney test results are shown, with significance levels estimated using a permutation procedure (P_{Exac}). Statistically significant results are in bold. L = left, R = right.

			Ger	nder		м	W/I ·	
Species		Fen	nale	M	ale	Mann	-Whitn	ey test
		Mean	SEM	Mean	SEM	U	W	P _{Exact}
Siagona	Body length (mm)	23.33	0.16	22.83	0.29	30.0	85	0.143
dejeani	Antenna length (mm)	12.58	0.15	12.82	0.25	43.0	98	0.631
	Head width (mm)	5.06	0.06	5.09	0.09	46.5	101.5	0.796
	Number of ommatidia L	407.80	25.21	404.10	14.77	49.0	104	0.971
	Number of ommatidia R	404.30	12.47	356.40	15.87	22.0	77	0.035
	Eye surface L (mm ²)	0.06	0.01	0.06	0.01	41.0	96	0.529
	Eye surface R (mm ²)	0.08	0.00	0.07	0.00	33.0	88	0.218
	Trochanter length (mm)	1.65	0.02	1.71	0.04	39.0	94	0.436
	Head height (mm)	2.80	0.08	2.76	0.08	44.5	99.5	0.684
	Thorax height (mm)	3.37	0.06	3.33	0.06	44.5	99.5	0.684
	Abdomen height (mm)	3.22	0.13	3.17	0.11	44.5	99.5	0.684
	Weighted antenna length	2.49	0.04	2.52	0.05	42.0	97	0.579
	Weighted trochanter length	0.07	0.00	0.07	0.00	21.5	76.5	0.029
	Weighted ommatidia L number	80.86	5.30	79.51	2.89	49.0	104	0.971
	Weighted ommatidia R number	80.03	2.68	69.95	2.65	15.0	70	0.007
	Weighted head height	0.12	0.00	0.12	0.00	49.0	104	0.971
	Weighted thorax height	0.14	0.00	0.15	0.00	48.0	103	0.912
	Weighted abdomen height	0.14	0.01	0.14	0.00	49.0	104	0.971
	Right ommatidia density	5019.71	252.49	4857.98	162.19	48.0	103	0.912
	Left ommatidia density	19964.03	9939.31	20421.65	10096.35	43.0	98	0.631
Siagona	Body length (mm)	11.73	0.22	11.16	0.18	26.5	81.5	0.075
europaea	Antenna length (mm)	6.96	0.16	7.03	0.11	50	105	1.000
	Head width (mm)	2.64	0.04	2.52	0.03	23	78	0.043
	Number of ommatidia L	528.60	28.98	564.90	25.03	40	95	0.481
	Number of ommatidia R	494.10	31.81	536.10	17.72	36	91	0.315
	Eye surface L (mm ²)	0.01	0.00	0.01	0.00	46	101	0.796
	Eye surface R (mm ²)	0.01	0.00	0.01	0.00	48.5	103.5	0.912
	Trochanter length (mm)	0.85	0.02	0.84	0.02	39	94	0.436
	Head height (mm)	1.36	0.05	1.25	0.04	27	82	0.089
	Thorax height (mm)	1.71	0.05	1.71	0.03	46.5	101.5	0.796
	Abdomen height (mm)	1.84	0.05	1.76	0.07	35.5	90.5	0.280
	Weighted antenna length	2.65	0.06	2.79	0.04	31	86	0.165
	Weighted trochanter length	0.07	0.00	0.08	0.00	37	92	0.353
	Weighted ommatidia L number	200.85	10.92	223.42	8.45	32	87	0.190
	Weighted ommatidia R number	187.94	12.24	212.58	7.25	32	87	0.190
	Weighted head height	0.12	0.01	0.11	0.00	47	102	0.853
	Weighted thorax height	0.15	0.01	0.15	0.00	28	83	0.105
	Weighted abdomen height	0.16	0.01	0.16	0.01	49	104	0.971
	Right ommatidia density	64068.08	9474.82	71412.86	7665.16	44	99	0.684
	Left ommatidia density	68827.82	8122.49	68715.15	5377.99	40	95	0.481

			Ger	nder				
Species		Fen	nale	Ma	ale	Mann	-Whitn	ey test
		Mean	SEM	Mean	SEM	U	W	P _{Exact}
Siagona	Body length (mm)	14.38	0.14	14.11	0.09	35	90	0.280
jenissoni	Antenna length (mm)	8.89	0.08	8.97	0.09	41.5	96.5	0.529
	Head width (mm)	3.20	0.04	3.31	0.03	25	80	0.063
	Number of ommatidia L	314.90	11.88	316.30	3.75	48	103	0.912
	Number of ommatidia R	346.50	9.23	363.00	15.99	42.5	97.5	0.579
	Eye surface L (mm ²)	0.04	0.00	0.04	0.00	45.5	100.5	0.739
	Eye surface R (mm ²)	0.04	0.00	0.03	0.00	41.5	96.5	0.529
	Trochanter length (mm)	0.99	0.01	1.03	0.01	23.5	78.5	0.043
	Head height (mm)	1.82	0.06	1.74	0.06	44	99	0.684
	Thorax height (mm)	2.09	0.06	2.20	0.07	38.5	93.5	0.393
	Abdomen height (mm)	2.24	0.13	2.28	0.12	48	103	0.912
	Weighted antenna length	2.79	0.03	2.71	0.03	24	79	0.052
	Weighted trochanter length	0.07	0.00	0.07	0.00	1	56	<0.001
	Weighted ommatidia L number	98.82	4.35	95.57	1.12	36	91	0.315
	Weighted ommatidia R number	108.83	3.87	109.71	4.89	49	104	0.971
	Weighted head height	0.13	0.01	0.12	0.00	50	105	1.000
	Weighted thorax height	0.15	0.01	0.16	0.00	31	86	0.165
	Weighted abdomen height	0.16	0.01	0.16	0.01	45	100	0.739
	Right ommatidia density	10786.08	1392.59	11925.89	1320.63	42	97	0.579
	Left ommatidia density	8943.47	1037.65	9130.10	821.02	43	98	0.631

Further investigation of the wing set showed that *S. dejeani* and *S. jenissoni* are brachypterous (respectively 1.93±0.03 mm and 0.94±0.03 mm wing lengths), while *S. europaea* has long wings (8.01±0.05 mm) folded under the elytra, and can thus be considered a macropterous species presumably capable of flight.

Discussion

The three *Siagona* species investigated presented sex and inter-specific differences. The sexes differ only in size: males of *S. dejeani* and *S. jenissoni* had significantly longer trochanters (relative to body length) than females, while in *S. europaea* females had wider heads than males.

These *Siagona* species are olfactory hunters and belong to the third group of nocturnal species described by Bauer and Kredler (1993), based on compound eye characteristics; laboratory recordings of activity of *S. europaea* have confirmed their nocturnal habit (Bauer et al. 2005). Nevertheless, eye parameters differed significantly among the species: the number of ommatidia is much higher in *S. europaea* (more than 500, see Table 2) than in the other two species (no more than 400 for *S. dejeani* and 300 for *S. jenissoni*). Presumably *S. europaea* has better visual capabilities than the others two species, even though all three species are nocturnal.



Figure 1. Measured traits between sexes in the three species: **A** weighted trochanter length (mm) in *S. dejeani* **B** head width (mm) in *S. europaea* **C** weighted trochanter length (mm) in *S. jenissoni.*

			Speci	es			Krusk	al-W	allis test
	Siagona	dejeani	Siagona	europaea	Siagona j	ienissoni			
	Mean	SEM	Mean	SEM	Mean	SEM	Chi-	df	P _{Monte Carlo}
							Square		
Body length (mm)	23.08	0.17	11.44	0.16	14.25	0.09	52.569	2	< 0.001
Antenna length (mm)	12.70	0.14	7.00	0.10	8.93	0.06	52.468	2	< 0.001
Head width (mm)	5.07	0.05	2.58	0.03	3.25	0.03	52.469	2	< 0.001
Number of ommatidia	405.95	14.23	546.75	19.10	315.60	6.07	44.612	2	< 0.001
Eye surface (mm ²)	0.06	0.01	0.01	0.00	0.04	< 0.01	28.722	2	< 0.001
Trochanter length (mm)	1.68	0.03	0.85	0.01	1.01	0.01	51.865	2	< 0.001
Head height (mm)	2.78	0.05	1.31	0.03	1.78	0.04	50.937	2	< 0.001
Thorax height (mm)	3.35	0.04	1.71	0.03	2.14	0.05	49.799	2	< 0.001
Abdomen height (mm)	3.19	0.09	1.80	0.04	2.26	0.09	43.233	2	< 0.001
Weighted antenna lenght	2.51	0.03	2.72	0.04	2.75	0.02	24.521	2	< 0.001
Weighted trochanter length	0.07	0.00	0.07	0.00	0.07	0.00	9.586	2	0.007
Weighted ommatidia number	80.19	2.94	212.13	7.20	97.20	2.22	45.057	2	< 0.001
Weighted head height	0.12	0.00	0.11	0.00	0.12	0.00	5.979	2	0.049
Weighted thorax height	0.15	0.00	0.15	0.00	0.15	0.00	2.977	2	0.228
Weighted abdomen height	0.14	0.00	0.16	0.00	0.16	0.01	9.667	2	0.007
Ommatidia density	20192.84	6895.16	68771.49	4740.88	9036.79	644.29	30.951	2	< 0.001

Table 2. Inter-specific differences in body and eye morphological characteristics (means and Standard Error of Means) in three species of *Siagona*. Kruskal-Wallis test results estimated with a permutation procedure ($P_{Monte Carbo}$) are reported.

S. europaea has a higher number of ommatidia, full-sized wings and a greater antenna vs. head ratio. These features are indicative of high dispersal powers, which is a good strategy for adapting to habitats such as pastures and fields, where natural or anthropogenic disturbances are frequent. Furthermore, it is likely that high powers of dispersal enhance the probability of finding new ant nests, which are often scattered rather than homogeneously distributed throughout the territory. Conversely, *S. dejeani* has shorter antennae, a lower number of ommatidia and smaller wings than the other two species. This is presumably related to a lesser need to search for a partner, as the beetles live in aggregation in which chemical cues easily allow males and females to meet.

In conclusion, the general morphometry of these three Mediterranean species of the genus *Siagona* is typical of beetles living in narrow spaces, presumably in darkness, for most of their life. As a consequence, eye morphology is well adapted to their habitat demands and to olfactory/tactile predation. Indeed, success in detecting ants or ant traces is assured by the complex sensory structure of the labial palps, which has been described in detail for *S. europaea* (Giglio et al. 2009). The antennae of male and female beetles are likely similar in their general structure in each of the three species (Giglio et al. 2007) and vary only in size. Conversely, some significant differences occur in the size of the wings, which are well developed only in *S. europaea*, the only species capable of flight. In this species, ecological demands are probably both for better vision for orientation in space and an enhanced antennal sensorial role in searching for a partner after dispersal by flight.



Figure 2. Measured traits: A ommatidia density (N/mm^2) B weighted ommatidia number C weighted antenna length.

Concluding remarks

The carabid genus *Siagona* is a stenotopic ground dweller that preys on ants in the deep fissures of clayey soil. In Fig. 3 we compared the eye sizes of the three European species with the "ommatidial indices" of the three groups of Bauer and Kredler (1993). The first group includes diurnally active species, many of them true "visual hunters", while the second group includes taxa with a less fixed or twilight activity period and the third includes nocturnally active carabids. The three *Siagona* species occupy a very unique position in this graph, similar to the more or less microphthalmic *Trechus alpicola* Sturm, 1825, a species living under stones in the Central Austrian Alps. The ommatidia/body length ratios of *S. jenissoni* and *S. dejeani* are particularly low (23 and 17, respectively), while the mean value of *S. europaea* is somewhat higher (43), indicating a pronounced adaptation to dark conditions of the habitat.

In conclusion, the European *Siagona* species exhibit a lifestyle thus far unknown in carabid beetles, i.e., a stenotopic adaptation to clayey soils of tropical and subtropical



Figure 3. Ommatidial index versus body length in the three Bauer-Kredler groups of carabids and comparison with European species of *Siagona* (this study). Y-axis: mean number of ommatidia per body length in mm. In order of decreasing ommatidial index, **Group 1:** *Cicindela campestris, C. hybrida, Elaphrus cupreus, E. riparius, E. ullrichi, E. aureus, Notiophilus biguttatus, Asaphidion flavipes, A. pallipes, A. caraboides, Bembidion quadrimaculatum.* **Group 2:** *Carabus granulatus, Agonum sexpunctatum, Poecilus cupreus, P. versicolor, Carabus auratus.* **Group 3:** *Carabus problematicus, C. lefebvrei, C. coriaceus, Leistus rufomarginatus, Nebria brevicollis, Pterostichus nigrita, Carabus preslii, Abax parallelepipedus, Patrobus atrorufus, Pterostichus burmeisteri, Trechus alpicola.*

climates marked by a long dry season. The adults probably enter fissures in the clay at the beginning of the dry phase and are able to exploit the rich trophic resources (ant workers and perhaps ant brood) in this three-dimensional subterranean space.

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RESEARCH ARTICLE



Heavy metals in carabids (Coleoptera, Carabidae)

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Abstract

Carabid beetles (Coleoptera, Carabidae) are one of the most studied soil groups in relation to heavy metal (HM) accumulation and use for bioindication of environmental pollution. Accumulation of Zn and Cu in carabid beetles was species-, sex- and trophic group-specific. No differences were found in HM contents between omnivorous and carnivorous species. The use of carabid beetles as indicators of HM accumulation appears to be rather limited.

Keywords

Heavy metals, carabid beetles, pollution, accumulation

Introduction

Because of the increasing impacts of chemicals on terrestrial and soil ecosystems, assessment of environmental quality by bioindicators is of particular interest.

Carabid beetles are traditionally used as bioindicators of anthropogenic stresses for a number of reasons. They inhabit most terrestrial ecosystems. The ecology and systematics of the group are well studied. Sampling methods are simple and universal. And the data collected by different researchers are comparable.

In soil trophic webs, carabid beetles play an extremely important role as non-specialized predators and 2nd order consumers.

There are numerous publications demonstrating structural changes in carabid communities due to different anthropogenic impacts caused by motorways, metallur-

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gic smelters, and recreation (see review by Butovsky 2001). In addition, several studies on heavy metal accumulation in carabid beetles have been performed in different ecosystems (see review by Butovsky 1997).

This paper reviews the literature data on heavy metal (HM) impacts on carabid beetle communities and also considers the use of carabids as indicators of HM accumulation.

Results and discussion

HM contents limits

The mean HM content in carabids decreased in the following sequence Fe > Zn > Cu > Mn > Pb > Cd (Butovsky 1997). The most toxic elements (Pb and Cd) were not accumulated in large quantities, in contrast to the accumulated Zn and Cu (Andrews and Cooke 1984; Beyer et al 1985; van Straalen and van Wensem 1986; Roth 1993; Jelaska et al. 2007).

The concentration ratios of Cd : Pb : Mn : Cu : Zn : Fe in an average carabid beetle were 1 : 2.5 : 7 : 17 : 29.5 : 93. In other words, an average carabid beetle may contain 93 times more Fe than Cd and 37 times more Fe than Pb (Butovsky 1997).

HM contents in different genera

Variation coefficients of HM in carabids were variable and dependent on the carabid genus and type of HM (Table 1). In *Carabus* spp. for Pb, Zn and Cu the coefficient was 17.9% (5.2–32.5%) and in *Pterostichus* spp. 29.9% (6.3–48.2%). (Table 1).

The analysis of 14 HMs in 28 carabid species revealed that the variability of HM in *Carabus* spp. was 26% and in *Pterostichus* spp. 42% (Stepanov et al. 1987). The authors aggregated all predacious carabids for bioindication as a uniform group, thus ignoring differences at species level.

HM contents in small, medium and large carabid species

A positive correlation between body mass and Pb content was found in beetles of the genus *Carabus* (Emets and Zhulidov 1983) and three other species: *Calathus melano-cephalus, Notiophilus biguttatus, N.rufipes* (but not for Zn or Cd) (van Straalen and van Wensem 1986).

I subdivided the collected carabids into three groups: (1) with body mass (B) less than 15 mg (genera *Agonum, Leistus, Loricera, Notiophilus, Calathus*); (2) with 15<B<50 mg (genera *Pseudophonus, Poecilus, Pterostichus, Abax, Harpalus*) and (3) with B>50 mg (genus *Carabus*) (Table 2).

Mean HM content (at least for Zn, Pb and Mn) was not dependent on the mass/ size of carabid beetles. Medium-sized species contained more Fe compared to small-

Genera	N			Heavy	y metals, ppm		
		Cd	Cu	Fe	Mn	РЬ	Zn
Abax	3	0.1*	15.9	N/A	N/A	3.1 <u>+</u> 1.7	62.8
Agonum	2	0	25.8 <u>+</u> 7.9	532.3	24.3	4.9 <u>+</u> 4.9	95.0 <u>+</u> 14.4
Calathus	4	1.0 <u>+</u> 0.3	57.2 <u>+</u> 30.8	58.7 <u>+</u> 49.0	29.1 <u>+</u> 9.3	6.7 <u>+</u> 1.9	89.2 <u>+</u> 21.1
Carabus	9	0.1 <u>+</u> 0.1	16.9 <u>+</u> 0.9	333.9	N/A	4.3 <u>+</u> 1.4	96.1 <u>+</u> 15.3
Harpalus	1	0	23.3	N/A	N/A	0	130
Leistus	2	2.9 <u>+</u> 1.1	30.1	N/A	N/A	7.8	118.6
Loricera	1	N/A	N/A	N/A	N/A	1.9	N/A
Notiophilus	2	1.7 <u>+</u> 0.3	27.5 <u>+</u> 1.3	117.1 <u>+</u> 109.9	29.2 <u>+</u> 2.8	1.7 <u>+</u> 0.3	77.9 <u>+</u> 10.5
Poecilus	2	0.1 <u>+</u> 0.1	16.3	N/A	N/A	4.2 <u>+</u> 4.2	118.7 <u>+</u> 30.7
Pseudo-ophonus	1	0	17.3 <u>+</u> 2.1	461.2	N/A	3.0 <u>+</u> 3.0	92.3 <u>+</u> 6.4
Pterostichus	5	0	29.5 <u>+</u> 10.4	436.3 <u>+</u> 37.3	N/A	2.9 <u>+</u> 1.4	116.2 <u>+</u> 7.4

Table 1. Inter-generic variability in HM contents (ppm) in carabid beetles (by different authors after Butovsky 1997).

N – number of species; ***** - one replicate; **N/A** - not available.

sized species and small species contained more Cd and Cu compared to medium-sized and large species.

HM contents in males and females

In most studies no clear pattern of HM contents in males or females of carabid species were observed (Roth 1993; Butovsky 1995, 2001).

In some species, males contained more metals (Pb, Zn, Cd, Cu, Mn, Fe, Co, Ni, Sr, Cr, Al) than females (Stepanov et al. 1987). In another study on ten species, males accumulated more Cu than females, which, in contrast, accumulated more Cd than males (Purchart and Kula 2007).

Sex-specific differences were found in six carabid species (*Poecilus cupreus*, *Pteros-tichus melanarius*, *P. niger*, *Pseudophonus rufipes*, *Carabus nemoralis* and *C. granulatus*), while females contained more Zn than males (Butovsky 1994).

Microelement (Na, Mg, K, Ca) concentrations were higher in females compared to males in populations of *Agonum dorsale* and *A. sexpunctatum* (Novak 1989).

Heavy metals		Body mass, mg	
	<15	15-50	>50
Cd	1.4 <u>+</u> 0.6	0.5 <u>+</u> 0.3	0.1 <u>+</u> 0.1
Cu	35.1 <u>+</u> 7.4	20.5 <u>+</u> 2.6	16.9 <u>+</u> 0.9
Fe	236.0 <u>+</u> 149.1	448.7 <u>+</u> 12.4	333.9
Mn	26.7 <u>+</u> 2.4	29.1	-
Pb	4.6 <u>+</u> 1.2	2.6 <u>+</u> 0.7	4.3 <u>+</u> 1.4
Zn	95.2 <u>+</u> 8.6	104.0 <u>+</u> 11.9	96.1 <u>+</u> 15.3

Table 2. Heavy metal content (ppm) and dry body mass of carabid beetles (Butovsky 1997).

HM in different species

No regular pattern was found in studies of HM contents in dozens of carabid species published by numerous authors (reviewed by Butovsky 2001). The contents were variable and species-specific.

HM and feeding behavior

Omnivorous species (*Harpalus* spp., *Amara* spp.) contained more Cu but less Zn than carnivorous species (*Pterostichus* spp., *Carabus* spp.) in roadside ecosystems (Butovsky 1995).

The effects of feeding ecologies were evident only for the essential elements: carnivores (*Calathus* spp., *P.cupreus, P.melanarius*) had significantly higher contents of Zn, Cu and Mn than omnivores (*Harpalus* spp., *P.rufipes*). No differences were found for Pb and Cd (Purchart and Kula 2007).

HM and seasonal changes

Seasonal differences in abundance, species composition, and age structure of invertebrates may lead to high variability in HM contents in carabid beetles, and the highest variability can be expected at highly polluted sites (Hunter et al. 1987).

Seasonal changes in Cd contents were not found for *N. biguttatus*, but higher concentrations were observed in *C. melanocephalus* in autumn, likely due to a peak of reproductive activity (Janssen 1991).

I found a decrease of Zn and Cu contents in the dominant species *P. cupreus* and *P. melanarius* in roadside ecosystems of the Moscow region at the end of the season (Butovsky 1994, 1995).

In roadside populations of *P. oblongopunctatus* the Zn contents of over-wintered beetles was higher than in newly hatched ones (Emetz and Kulmatov 1983).

In ten carabid species, Zn and Cu contents during the spring were higher than in autumn. The authors speculated that in the period of increased feeding activity (spring), the elements were stored in body fat, while during sexual activity and wintering they were mobilized and excreted. The composition of a population with regards to the fraction of juvenile specimens, active feeders, or reproducing individuals may have a considerable effect on the seasonal dynamics of the metals (Purchart and Kula 2007).

Bioaccumulation and biomagnification

Carabids are relatively poor accumulators of heavy metals, particularly the most toxic ones, such as cadmium or lead (Butovsky 1997). Among carabids the most active HM accumulators were represented by *Carabus* spp. (concentration factor, Cf = 5.2-6.7)

(Emetz and Zhulidov 1983). Less accumulation was observed in omnivorous species (Cf = 1.1-2.0) (Butovsky 1995).

In contrast, the highest concentrations of non-essential metals (Cd and Pb) were found in carnivorous carabid beetles together with earthworms and oribatid mites in the vicinity of a metallurgic smelter (van Straalen et al. 2001).

In putative trophic chains, carabids as non-specialized predators accumulated less copper and zinc (Cf = 0.54 and 0.21 respectively) than specialized predators (like *Coccinellidae*, *Syrphidae*) (0.67 and 0.99 respectively) and specialized parasitoids (*Alloxystidae*, *Pteromalidae*) (1.07 and 2.08 respectively). These differences probably reflected the increase of trophic adaptation to elevated concentrations of HM in non-specialized predators, specialized predators and parasitoids (Butovsky and van Straalen 1995).

Mechanisms of HM detoxification

As in other holometabolic insects, carabid beetles possess various detoxification systems, which can segregate metals and turn it into inactive forms (Hopkin 1989) although there has not been much research conducted on these systems in beetles. One may expect that HM are stored in metal-containing granules in the hindgut wall and can be excreted with the faeces.

Compared to other groups of soil invertebrates, carabid beetles are characterized by low accumulation and high excretion rates of cadmium (Table 3).

The concentrations of Pb differed between the exoskeleton and the soft tissues in the carabid body. Up to 63–82% of Pb was accumulated in the exoskeleton (Roberts and Johnson 1978). Additional data confirm that HM (in particular, Cd) were accumulated in the exoskeleton and lost during larval molts (Lindquist et al. 1995). That may explain the fact that in many studies, carabid larvae contained more metals than imagos (Carter 1983).

Females from contaminated sites have elevated activities of some enzymes (glutathione-S-transferase and carboxyl-esterase), but males do not (Stone et al. 2002).

High Cd contents	Low Cd contents
Isopoda	Orabitida (fam. Notaspididae)
Opiliones	Lithobiidae
Lyniphiidae	Collembola (Entomobriidae)
Pseudoscorpions	Carabidae
Gamasidea	Staphylinidae
Oribatida (fam. Camisiidae)	Gryllidae
Geophylidae	Tettigoniidae
Diplopoda	
Collembola (fam. Onychiroidea)	

Table 3. Cd "accumulators" and "disseminators" in soil invertebrate communities (van Straalen and vanWensem 1986; van Capelleveen 1987; Janssen 1991; Butovsky et al. 1999)

The fat concentration in carabids collected from polluted sites was lower when compared to reference sites. Presumably, HM excretion requires energy, thus restricting the accumulation of fat (Lindqvist and Block, 2001).

Adaptation (in terms of HM accumulation and excretion) did not occur in carabids inhabiting chronically polluted sites and obviously had no genetic basis (Lagisz and Laskowski 2007).

Conclusion

Carabid beetles constitute one of the most appropriate invertebrate groups for the study of "ecological" effects of different anthropogenic stressors of soil communities, and the changes in carabid community dominance, diversity, abundance, sex ratio etc. have been used as bioindicators in numerous studies (Butovsky 2001).

On the other hand, carabids are relatively poor HM accumulators (being both holometabolic insects and predators). They may contain elevated amounts of HM in polluted sites compared to referent sites, but results are variable and no accurate assessments of contamination levels can be made.

Our extensive research in roadside ecosystems showed that HM contents in carabids did not correlate with their relative abundance or distance from the motorway (Butovsky 1995) or a metallurgic smelter (van Straalen et al. 2001).

More research is obviously needed on HM stress on carabids, e.g. detoxification, genetic resistance, physiology and demography.

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RESEARCH ARTICLE



Using demographic data to better interpret pitfall trap catches

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Abstract

The results of pitfall trapping are often interpreted as abundance in a particular habitat. At the same time, there are numerous cases of almost unrealistically high catches of ground beetles in seemingly unsuitable sites. The correlation of catches by pitfall trapping with the true distribution and abundance of Carabidae needs corroboration. During a full year survey in 2006/07 in the Lake Elton region (Volgograd Area, Russia), 175 species of ground beetles were trapped. Considering the differences in demographic structure of the local populations, and not their abundances, three groups of species were recognized: residents, migrants and sporadic. In residents, the demographic structure of local populations is complete, and their habitats can be considered "residential". In migrants and sporadic species, the demographic structure of the local populations is incomplete, and their habitats can be considered "transit". Residents interact both with their prey and with each other in a particular habitat. Sporadic species are hardly important to a carabid community because of their low abundances. The contribution of migrants to the structure of carabid communities is not apparent and requires additional research. Migrants and sporadic species represent a "labile" component in ground beetles communities, as opposed to a "stable" component, represented by residents. The variability of the labile component substantially limits our interpretation of species diversity in carabid communities. Thus, the criteria for determining the most abundant, or dominant species inevitably vary because the abundance of migrants in some cases can be one order of magnitude higher than that of residents. The results of pitfall trapping adequately reflect the state of carabid communities only in zonal habitats, while azonal and disturbed habitats are merely transit ones for many species of ground beetles. A study of the demographic structure of local populations and assessment of the migratory/residential status of particular carabid species are potential ways of increasing the reliability of pitfall trap information.

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Keywords

Carabidae, abundance, community, resident, migratory, sporadic, residential habitats, transit habitats, labile component, stable component, zonal sites, azonal sites

Introduction

Pitfall trapping is one of the most commonly used techniques to quantify terrestrial arthropods (Barber 1931). The simplicity of the method and the possibility of data standardization are the main advantages of their application in numerous entomological studies. Pitfall trapping is easy, and as such arthropods can be captured in different places at the same time. This explains the extensive use of pitfall traps in ecological investigations of ground beetles (Scherney 1959; Skuhravý 1959; Novák 1964; Kabacik-Wasylik 1970; Tietze 1973; den Boer 1977; Brandmayr and Zetto Brandmayr 1986; Østbye and Hägvar 1996; Gryuntal 2008; Makarov and Matalin 2009).

However, doubts concerning the reliability of the obtained results were already expressed during the first pitfall trap studies and have been discussed subsequently (for example, see Adis 1979). Numerous factors have been found to affect pitfall trap catches, such as, the size of a trap and its inlet (Luff 1975; Waage 1985; Work et al. 2002; Koivula et al. 2003), the colour of a trap (Buchholz et al. 2010), the presence and type of preservative (Luff 1968; Feoktistov 1980; Gryuntal 1982; Karpova and Matalin 1992; Weeks and McIntyre 1997) and the ways of setting traps across habitats (Greenslade 1964; Perner and Schueler 2004; Korczycski and Sienkiewicz 2006). In addition, the mobility of beetles in relation to both their physiological condition and the environment vary widely in the course of a season and between seasons (den Boer 1977; van Huizen 1977, 1979; Baars 1979; Matalin 1994, 1997, 2003; Desender 2000).

Towards the second half of the 20th century it became clear that pitfall trapping reflected not as much the abundance as the locomotor activity of beetles. Numerous steps have been taken to increase the reliability of the results of catches: changes in trap construction (Reeves 1980; Boucher 1981; Kuschka et al. 1987; Loreau 1987; Dufrêne 1988; Makarov and Tshernyakhovskaya 1990; Karpova and Matalin 1992; Kuschka 1998) and in the type of preservative used (Louda 1970; Feoktistov 1980; Gryuntal 1982; Pekar 2002), exhaustive catches from enclosed areas (Kudrin 1971; Gryuntal 1981; Desender and Maelfait 1986), the calculation of correction coefficients from the re-trapping of marked specimens (Holland and Smith 1991; Raworth and Choi 2001), and the comparisons of dynamic (pitfall trapping) and static (standard soil fauna quadrate sampling) population densities (Kudrin 1966; Arnoldi et al. 1972; Desender and Segers 1985; Spence and Niemelä 1994). In spite of these important advances, standard pitfall trapping has 'de facto' become a standard technique used in synecological investigations of Carabidae.

At the same time, when pitfall-trapped data are interpreted, the beetles' migratory capacities are often ignored. This is because there is no universal technique for quantitatively estimating beetle locomotion (den Boer 1977; Prisnyi 1987). Interpretation of life cycles to evaluate the demographic structure of local populations can provide a new approach to solving this problem. For example, a significantly deficient demographic structure recently observed in some carabid species in agricultural or disturbed habitats shows that in many places the populations are represented only by certain 'age groups' (Borkowski and Szyszko 1984; Wallin 1989; Makarov and Tshernyakhovskaya 1989; Tshernyakhovskaya 1990; Khotuleva 1997). According to data obtained by Bokhovko (2006), five of the 11 dominant carabid species from arable soils in the Kuban Region, southern Russia, demonstrated high abundance levels, coupled with incomplete demographic spectra. For example, in semi-centennial forest belts as well as in alfalfa fields, about 80% of the dominants completed their development. On the other hand, in corn fields and in a forest belt with *Robinia*, about 75% of the carabid beetles did not complete their full life cycle.

The last case clearly illustrates the probable scales of migration in Carabidae, showing that populations are often incapable of reproducing in such environments. However, it still remains unclear whether this situation is general or not. We can assume that the proportion of species with incomplete demographic spectra represented in pitfall traps is higher in disturbed habitats, while in undisturbed or moderately disturbed habitats, the sex and age structures of the populations are more or less balanced.

In the present study, we highlight a key methodological problem that the actual community structure (e.g., the roles of individual species) cannot be understood based on pitfall counts alone. We also demonstrate how demographic analysis can be used to address this problem.

Materials and methods

Ground beetle communities in the Lake Elton region, Volgograd Area, south-eastern Russia (49°12.47'N, 46°39.75'E) were studied in 2006–2007. Lake Elton is situated within the Botkul-Bulukhta drainless desert depression, which belongs to the Caspian Lowland. A strongly pronounced salt-dome structure is characteristic of this region, and desert steppes are typical plant associations in most of the habitats present (Nekrutkina 2006; Safronova 2006). Dense reedbeds occur in the river valleys, in gullies at lakesides there are trees and shrubs, while lakesides near the mouth of most large rivers are characterised by salt-marshes. Near the village of Elton, all desert steppes are fragmented or transformed into pastures.

Pitfall trapping was conducted in 10 habitats: six zonal - characteristic of this particular biogeographical area, and four azonal - present in a variety of biogeographical areas (Walter 1973; Chernov 1975). Three selected habitats were located near the village of Elton, while seven were placed on the north-western shore of Lake Elton, on the right bank of the River Khara (for more details see Makarov and Matalin 2009). Zonal habitats were represented by sagebrush and sagebrush-grassland steppe with varying degrees of anthropogenic disturbances (strong near Elton village, moderate on the northern slope of Mt. Ulagan, and weak in the watershed of River Khara). Azonal habitats were chosen along salinity and solar irradiation gradients (strong in the lakeside salt-marsh, moderate in the salina on the floodplain terrace of River Khara, and weak in reedbeds along River Khara).

Plastic cups of 0.5 L capacity and 95 mm upper diameter containing 4% formaldehyde solution as a preservative were used. In each habitat, 10 traps were arranged along transects at 10 m intervals. The traps were checked every ten days from 10 May to 31 October in 2006 and from 1 April to 10 May in 2007.

All captured carabids were dissected. Based on gonad condition (Gilbert 1956, Skuhravý 1959, van Heerdt et al. 1976, Wallin 1989), as well as on the degree of wearand-tear of the mandibles, claws and cuticle (Houston 1981, Brandmayr and Zetto Brandmayr 1986, Butterfield 1986, Davies 1987), six physiological states in the adults of both sexes were distinguished.

Teneral. Recently emerged beetles with soft and pale cuticle; mandibles and claws sharp. Ovaries thin, white or translucent without any trace of developing oocytes; corpora lutea absent; lateral oviducts very thin. Testes thin and dull or relatively large and white; accessory glands always thin and poorly visible.

Immature. Cuticle fully hardened and coloured; mandibles and claws pointed. Ovaries compact, opaque and white, with or without distinctly visible oocytes, but always without ripe eggs; corpora lutea absent; lateral oviducts long and thin. Testes opaque and white; accessory glands no longer than half of the abdominal length, occupying less than a third of the abdominal space.

Mature of parental generation. Cuticle slightly worn; mandibles and claws hardly or distinctly dulled. Ovaries with ripe eggs; corpora lutea absent or yellowish, hardly visible; lateral oviducts wide. Testes large and white or cream-coloured; accessory glands long and white or light-yellow, filling more than three-quarters of the abdominal space.

Mature of ancestral generations. Cuticle clearly worn; mandibles and claws dull. Ovaries with ripe eggs; corpora lutea distinctly light or dark brown; lateral oviducts wide. Testes large and cream-coloured; accessory glands long and cream-coloured or light-brown, filling more than three-quarters of the abdominal space.

Spent of parental generation. Cuticle clearly worn; mandibles and claws as a rule distinctly dull. Ovaries compactly opaque and cream-coloured, without ripe eggs; corpora lutea clearly visible and dark brown, often deposited above last developing oocytes; lateral oviducts wide. Testes medium-sized or relatively small (regressed), opaque and cream-coloured or yellow; accessory glands thin opaque and yellow or light-brown, occupying less than a third of the abdominal space.

Spent of ancestral generations. Cuticle very worn; mandibles and claws blunt. Ovaries compactly opaque and cream-coloured or light-brown, without ripe eggs; corpora lutea clearly visible and dark brown, as a rule deposited under the developing oocytes; lateral oviducts wide. Testes medium-sized or relatively small (regressed), opaque and yellow or brown; accessory glands thin opaque and yellow, yellow-orange or brown, occupying less than a third of the abdominal space.

The separation between parental and ancestral generations was somewhat subjective and should be interpreted with caution. However, in most cases this separation was not required for the reasonable interpretation of demographic structures of the studied populations.

Results

Detection of the chronology of the maximum activity of the above-mentioned groups of specimens in the key stages of their life cycles as a result of feeding, reproduction or preparation for hibernation, forms the basis of our analysis. In such an approach, the quantitative recording of eggs, larvae, and pupae is not required. Moreover, we can evaluate the demographic spectra of a local population from small numbers (several dozen) of individuals.

In 'spring breeders' (Types 1 and 2 according to Thiele 1977), such a chronological series represents: immature of parental generation after hibernation \rightarrow mature of parental generation \rightarrow spent of parental generation \rightarrow teneral of new generation \rightarrow immature of new generation prior to hibernation (Fig. 1A). During this sequence, the abundance of species can be high or low. For example, in the reedbeds along the River Khara in early spring, peaks of abundance in the populations of *Pogonus transfuga* and *Brachinus hamatus* were observed. However, in the former species abundance reached 112–113 individuals in early April and early May (Fig. 2A), while in the latter species, abundance during April was less than 25 individuals (Fig. 2B). In spite of this, both species are characterised by a complete demographic spectrum.

In 'autumn breeders' (Type 4 according to Thiele 1977), the chronological series is as follows: teneral of parental generation \rightarrow immature of parental generation prior to aestivation \rightarrow immature of parental generation after aestivation \rightarrow mature of parental generation \rightarrow spent of parental generation prior to hibernation (Fig. 1B). In other 'autumn breeders' (Type 3 according to Thiele 1977), the same order of physiological conditions of the adults is observed, but without an aestivation parapause. As in the previous case, the abundance of species can vary widely. For example, in the grassforb steppe, the abundance of *Calathus ambiguus* was about 500 individuals in June and August (Fig. 3A), but in the sagebrush-grassland desert steppe, the abundance of *Pseudotaphoxenus rufitarsis major* was only 41 and 36 individuals at the end of September – beginning of October, respectively (Fig. 3B), yet the sex and age structure in the populations of both species was complete.

Importantly, in all these cases there are clear changes in successive waves of activity of different adult 'age' groups. It should be noted that in populations of many carabid species, the individuals of ancestral generations (which live and breed during two or more years) are often represented. In these cases the pattern of change in the physiological conditions can be blurred because separate successive waves of activity overlap each other.

Thus, it is not abundance, but rather a regular change in the physiological condition that allows for a reconstruction of the life cycle at the local population scale, and this must be regarded as the criterion for the successful existence and breeding of a



Figure 1. Chronology of changes in periods of activity of individual 'age' groups, characterised by female gonad condition, in 'spring' (**A**) and 'autumn' (**B**) breeding carabid beetles (T - teneral, Im - immature, M - mature, Sp - spent beetles).

population in a particular habitat. Species that meet these demands are considered 'residents' and their habitats 'residential'.

An incomplete demographic spectrum of a population means that the probability of a complete life cycle in a particular habitat is low to zero. Such a situation is often followed by extremely high abundance levels. In reedbeds from the end of June until the end of July, *Harpalus rufipes* was by far the most numerous carabid beetle collected, with abundance levels of 1753, 7047, 3770 and 2830 for successive ten-day periods. Without information on the physiological conditions of individuals, this species may be considered dominant in this habitat. However, mature females were completely absent from the demographic spectra in this local population of *H. rufipes*. Moreover, there were no successive waves of activity, because the peaks of abundance in teneral, immature and spent beetles were observed at the same time (Fig 4A). In these cases a reproductive phase in the demographic spectra of the local populations was absent.

Yet the presence of mature specimens is not necessarily evidence of successful breeding. For example, in lakeside salt-marshes, the demographic spectrum of *P. rufitarsis major* was mainly represented by mature specimens. The abundance of spent beetles was very low, while teneral and immature beetles were completely absent (Fig. 4B). The lack of young specimens in the demographic spectrum of this species provides evidence



Figure 2. Seasonal dynamics of activity, as well as the age structure of the populations of *Pogonus transfuga* (**A**) and *Brachinus hamatus* (**B**) from reedbeds along the River Khara, combined data for 2006/07 (*T* – teneral, *Im* – immature, *M* – mature, *Sp* – spent beetles; solid lines below graphs - parental generation, dashed lines below graphs – new generation; **N** (ex.) – number of specimens; **I**, **2**, **3** – first, second and third ten-day periods per month, respectively).



Figure 3. Seasonal dynamics of activity, as well as the age structure of the populations of *Calathus ambiguus* from grass-forb steppe with *Amygdalus nana* (**A**) and *Pseudotaphoxenus rufitarsis major* from sagebrush-grassland desert steppe on the northern slope of Ulagan Mountain (**B**), in 2006 (breaks in the periods of activity of immature specimens correspond to the time of aestivation parapause; see Figure 2 for further explanations).

of immigration of mature beetles. Species with incomplete demographic spectra are here considered 'migrants' and their habitats as 'transit'.

The spatial distribution of carabid species is determined by the availability both of habitats and landscape suitable for the complete realization of their life cycle. So the same habitat can be residential for one species and transit for another. Among the examples discussed above, reedbed is a residential habitat for *P. transfuga* (Fig. 2A), but a transit habitat for *H. rufipes* (Fig. 4A). At the same time, various habitats offer different living conditions to the same species. The sagebrush-grassland desert steppe on the northern slope of the Ulagan Mountain is a residential habitat for *P. rufitarsis major* (Fig. 3B), while the lakeside salt-marsh is a transit one for this species (Fig. 4B).

In summary, the demographic structures of 66 carabid species found in the Lake Elton region were analyzed. The other 109 carabid species were represented by only one or two individuals (Appendix). Considering the differences in abundance and demographic structure of the populations, three groups of Carabidae of the studied habitats can be distinguished:

Residents with their life cycles completed in a given habitat. In such species, migration forms only a facultative part of the life cycle. The catches of different species vary widely and sometimes differ by two orders of magnitude.



Figure 4. Seasonal dynamics of activity, as well as the age structure of the populations of *Harpalus rufipes* from reedbeds along the River Khara (**A**) and *Pseudotaphoxenus rufitarsis major* from the lakeside saltmarsh (**B**), in 2006 (see Figure 2 for further explanations).

Migrants that are characterised by relatively high numbers, yet rarely dominant, but with an incomplete demographic structure in particular habitats. Because their reproduction and development are observed in different habitats, their roles in specific assemblages would be minor. Migration forms both facultative and obligatory parts of their life cycles.

Sporadic species with very low numbers, probably not associated with a particular habitat, neither during migration nor reproduction.

Without question, residents interact both with their prey and with each other in a particular habitat. Sporadic species are hardly important to a carabid community because of their low abundance levels. The role of migrants in the local carabid community remains unknown, with possible interactions between the migrants and residents. First, even very high numbers of migrants in relatively small-sized habitats do not reflect the condition of the populations of other carabid species. For example, in reedbeds of an area of 1 km², more than 13 000 specimens of *H. rufipes* were trapped. This equates to a population density of about six individuals per square meter. This is a very high value. For example, the pest threshold of *Zabrus tenebrioides*, which is of the same size as *H. rufipes*, is two-three individuals per square meter. Hence, if the captured specimens of *H. rufipes* fed in this habitat and interacted with other species, we would expect changes in the demographic parameters of residents during this period. However, this is not the case, because the dynamics of the demographic structure in



Figure 5. Seasonal variation in abundance curves and reproduction aspects in four resident carabid species coupled with abundance of a migrant-species *Harpalus rufipes* from reedbeds, combined data for 2006/07 (**R** and **L** - right and left Y axis, respectively; **N** (**ex.**) – number of specimens).

the populations of resident carabid beetles failed to change during this period (Fig. 5). Second, relatively high numbers and species diversity levels of migrants were recorded at some seemingly unsuitable sites. These sites included the lakeside salt-marsh with high salt concentrations, poor vegetation and soil, as well as occasional floods. Under these conditions, only some specialist Carabidae: 17 species from the genera *Cephalotha, Calomera, Tachys, Bembidion, Pogonus, Pogonistes, Cardiaderus, Dyschiriodes, Poecilus, Daptus, Dicheirotrichus* and *Harpalus,* can survive. Among 66 species collected in this habitat, 75% can neither feed nor breed there (see Tables 1–2 and Appendix). Nonetheless, the catching efficiency of several migrants (for example the bothrobiont *P. rufitarsis major*) in this habitat was not lower compared to that in zonal sites.

"Stable" and "labile" components can be recognized in ground-beetles communities (Makarov and Matalin 2009). The former includes species whose life cycles are realized in certain habitats (residents), while the latter comprises species that are not capable of breeding in particular habitats (migrants and sporadic species).

The ratio of stable to labile components in the studied habitats varied strongly and was not always in favour of residents. Resident species comprised only 6–35% of the species list and 15–90% of total abundance. In zonal habitats, residents formed the dominant part of the assemblage. More than 65% of total abundance and 15–35% of total species diversity consisted of resident species. In azonal habitats the labile component prevailed. These species accounted for about 75% of the fauna and about 80%



Figure 6. Species diversity and the share of labile/stable components in particular habitats in the Lake Elton region, combined data for 2006/07 (black bars – labile component, white bars – stable component, line – number of species; **N (sp.)** – number of species).

of total abundance (Fig. 6). Only in zonal habitats did results from pitfall trapping adequately reflect the state of the carabid community while azonal and apparently disturbed habitats are only transit sites for many species of ground beetles.

Discussion

According to our data, the capture in a pitfall trap indicates only the fact that the beetle has moved across the trap area, but do not reflect true abundances. In some cases, errors occurring from direct interpretations of pitfall trapping data can be severe, and statistical techniques can not compensate for this. This is evident from cases in which high numbers of some carabid species are collected from seemingly unsuitable locations, for example from city dumps (Budilov 2002; Romankina et al. 2007), urban quarters (Khotuleva 1997; Sharova and Kiselev 1999), places with strong oil or chemical pollution (Avtaeva 2006) and along roads (Noordijk et al. 2008; Solodovnikov 2008). The



Figure 7. Numbers of the 10 most abundantly collected carabid species in reedbeds with regards to migrants (**A**) and residents only (**B**). Dominant species are in bold text, combined data for 2006/07; **N (ex.)** – number of specimens (after Makarov and Matalin 2009).

varying contribution of the labile component substantially distorts our knowledge of species diversity in carabid communities. Taking into account the contribution of the labile component can change conclusions based on pitfall trapping data considerably.

Firstly, criteria for determining the most abundant, or dominant species inevitably vary. The abundance of migrants in some cases is one order of magnitude higher than that of residents. Therefore, estimating the faunistic or community features based solely on abundant or dominant species, fail to solve the problem and can even worsen the situation. In reedbeds, for example, 36 migrant species made up about 83% of the total abundance. The complex of dominants in this community, as identified by the usual criterion (abundance exceeding 5%) while discarding the demography of individual species, contains only two polyzonal migrants *Harpalus rufipes* and *Harpalus distinguendus*. In fact, six thermophilic resident species form the main body of this community: *Calathus ambiguus, Pogonus transfuga, Broscus semistriatus, B. cephalotes, Curtonotus propinguus* and *Cylindera germanica* (Fig. 7).

Secondly, common information regarding the habitat preferences of particular species, as well as indicator species, is considerably altered. In our case, all studied habitats belong to two contrasting groups: dry desert steppes and riparian, more or less halophilic habitats. As such, variation in carabid populations is expected. When analyzing the habitat distribution of all dominants-subdominants, we find more or less eurytopic species inhabiting both zonal dry steppes on floodplain terraces and azonal alluvial salt-marshes. The grouping of dry steppes is very poor and contains one or two species



			Lakeside salt-marsh														
abitats	ntrazona habitats	terrace	Salina on floodplain of River Khara	-													
zonal h	<u> </u>	г Кһага	Reedbeds along Reve														
Α	Exclave habitat	ວາ	Riverine wood in "Biological" Ravir				-	1		1							2
		nk hara	стаss-torb steppe with Amygdalus сапа					1		1	1				1	1	2
		ıt ba er K	Grass-forb steppe	-										5			
bitats		Rigl of Riv	desert steppe Brassland Sagebrush-					1					1				
Zonal ha		Northern slope of Ulagan Mnt.	qesett stebbe Brassland Sagebrush-		1				1								
		<u> </u>	desert steppe														
		ban River Shay rogd	erassland Sagebrush-			-		-									
		Left of Bol Smc	desert steppe Sagebrush				1			1	1						
			opecies	Calathus ambiguus	^D seudotaphoxenus rufitarsis major	Harpalus rufipes	Harpalus distinguendus	Symindis lateralis	Curtonotus desertus	4mara ambulans	Carabus bessarabicus concretus	Sephalota atrata	Cicindela campestris	Harpalus anxius, H. picipennis	Amara aenea	Doecilus punctulatus	Calathus distinguendus, Cymindis lineata

				Lakeside salt-marsh					2					$\boldsymbol{\mathcal{N}}$
abitats	ntrazonal	habitats	terrace	Salina on floodplain of River Khara			2	1		6	1		7	
conal h	I		т Кћага	Reedbeds along Reve		1			2			10		
Az	Exclave	habitat	ət	Riverine wood in "Biological" Ravir	1		2							
			ank Khara	Grass-forb steppe with Amygdalus nana		1								
			çht b ver H	Grass-forb steppe										
bitats			Rig of Ri	desert steppe grassland Sagebrush-										
Zonal ha			Northern slope of Ulagan Mnt.	desert steppe grassland Sagebrush-										
			ta r k	desert steppe										
			t ban Rive I'shay oroge	Sagebrush-										
			Lef of Sm	desert steppe Sagebrush										
			Creater	socies	Harpalus zabroides	Amara ingenua	Broscus semistriatus, Harpalus calceatus	Dicheirotricus ustulatus	Pogonus transfuga, Chlaenius spoliatus	Cylindera germanica, Calosoma auropunctatum, Dyschiriodes luticola, Dolichus halensis, Curtonotus propinquus, Brachinus hamatus	Cephalota elegans	Clivina ypsilon, Broscus cephalotes, Bembidion aspericolle, Tachys scutellaris, Poecilus cupreus, Pterostichus niger, Amara littorea, A. similata, Anisodactylus poeciloides, A. signatus	Cephalota chiloleuca, Scarites tericola, Bembidion minimum, Pogonus meridionalis, Agonum gracilipes, Harpalus smaragdinus, Cymindis decora	Pogonus cumanus, Pogonistes convexicollis, P. rufoaeneus, Cardiaderus chloroticus, Daptus vittatus

which occur in one to three habitats, as a rule. In contrast, the inhabitants of saltmarshes are very diverse and peculiar. Interestingly, the woodland in the 'Biological' Ravine supports not only a native carabid beetle community, but also a peculiar species, *Harpalus zabroides* (Table 1). Results from an analysis of the habitat distribution based solely on residents are distinctly different. Only one species, *C. ambiguus*, can be labelled eurytopic because it reproduces in nine of the ten studied habitats. The communities of carabid beetles on floodplain terraces and in flood-plains are clearly isolated from each other. Each of them includes the main body of oligotopic species and a few stenotopic ones. Finally, the riverine woodland does not have a native carabid community and can be considered a transit habitat for practically all carabid species (Table 2).

As such, the contribution of migrants to the trophic structure of carabid communities is not apparent and requires further research. That a particular carabid species inhabits and breeds in, and even dominates a certain habitat, is only a hypothesis that needs corroboration each time. Species with high abundance levels and high frequency of occurrence in a particular habitat can belong to both labile and stable components. Thus, in the Lake Elton region, Calosoma auropunctatum, Dolichus halensis, Amara aenea, Harpalus calceatus, H. rufipes, H. distinguendus and Anisodactylus signatus belong to the labile component in all the habitats where they occur; Cephalota elegans comprises the main element of the stable component in several azonal habitats; while Calathus ambiguus, Cymindis lateralis and P. rufitarsis maior play the main role in the composition of the stable component in the majority of zonal habitats (Appendix). Overall, 65–75% of the species diversity of both individual habitats and the landscape as a whole comprised of non-residential species. It is important to note that almost half of the migrants (41 of 94 species) failed to breed in any of the studied habitats. Thus, the distances of their movements are substantially greater compared to the size of the site. So, the migrations of such species should be characterised at the landscape scale.

Conclusions

Because we have only very few examples that illustrate more or less close relations between ground beetles and their habitats, we are unable to assess the commonality of the situation described in the present study. However, it is conceivable that migrants in a carabid beetle community contribute to diversity estimates. Based on results from this study, some preliminary conclusions can be made.

A study of the demographic structure of local populations and an assessment of the migratory/residential status of particular carabid species are possible ways to increase the reliability of pitfall trapping information.

Up to 65–75% of species diversity, both of particular habitats and the landscape as a whole, can comprise of non-residential carabid species, i.e. migrants.

Results from pitfall traps adequately reflect the state of carabid communities only in zonal habitats. Azonal and apparently disturbed habitats are only transit sites for many species of ground beetles.

(combined data for $2006/07$).									
	Zonal I	abitats				Azonal h	abitats		
						Exclave habitat	Intra	zonal h	abitats
	Left ba of Rive Bol'sha Smorog	nk r ya şda	Northern slope of Ulagan Mnt.	Right l of Rive	oank sr Khara		рага	race	
Species	ssert steppe gebrush	ssert steppe sert steppe	ssert steppe sert steppe	ssert steppe igebrush-grassland	rass-forb steppe	iverine wood iverine wood "Biological" Ravine	eedbeds along Rever K	lina on floodplain ter River Khara	akeside salt-marsh
Calathus ambienus	p P S	p S	ep es	pp PS	9 9 _	м Я ni	ষ	io S	r
Cicindela campestris, Carabus bessarabicus concretus, Pseudotaphoxenus rufitarsis maior. Cartonotus desertus			4						
Japhoxenus gigas	1			-					
Cymindis lateralis		-			1				
Poecilus sericeus	1				1				
Cephalota atrata									
Ophonus minimus	1								
Harpalus cyclogonus, H. anxius		2			5				
Harpalus serripes				_					
Amara ambulans, A. diaphana, Brachinus costatulus			3						
Harpalus foveiger				1					
Harpalus picipennis, H. zabroides					2				

Table 2. Habitat preferences of individual species and the composition of carabid assemblages without the labile component - resident species only

	Zonal ł	nabitats				Az	onal ha	abitats			1
						Ex ha	clave bitat	Intra	conal h	abitats	1
	Left ba of Rive Bol'sha Smorog	nk tr tya gda	Northern slope of Ulagan Mnt.	Right b of Rive	ank r Khara			Thara	LYCE		1
Species	Gesert steppe Sagebrush	Sagebrush-grassland desert steppe	desert steppe Sagebrush-grassland	Sagebrush-grassland desert steppe	Grass-forb steppe	with Amygdalus nana Riverine wood	anivasa "lasigoloid" ni	Reedbeds along Rever K	Salina on floodplain ter of River Khara	Lakeside salt-marsh	
Poecilus punctulatus, Harpalus calathoides					2						1
Cymindis lineata						1					
Calathus distinguendus						1	1				1
Pogonus transfuga, Pogonistes rufoaeneus, Tachys scutellaris, Broscus semistriatus, Dyschiriodes salinus striatopunctatus									Ś		
Ojlindera germanica, Scarites terricola, Dischiriodes luticola, Poecilus nitens, Curtonotus propinguus, Dicheirotrichus ustulatus, Brachinus hamatus								7			
Cephalota elegans, Pogonus meridionalis, P. punctulatus, Daptus vittatus, Harpalus dispar splendens									5		
Chlaenius spoliatus								1		1	
Carabus clathratus, Clivina ypsilon, Broscus cephalotes, Bembidion aspericolle, Anisodactylus poeciloides, Acupalpus elegans, A. parvulus, Stenolophus mixtus, Dicheirotrichus discicollis, Chlaenius tristis								10			I
Cephalota chiloleuca, Dyschiriodes cylindricus hauseri, Amara abdominalis, A. parvicollis									4		
Calomera littoralis conjuctaepustulata, Dyschirius humeratus, Pogonus cumanus, Pogonistes convexicollis, P. angustus, Cardiaderus chloroticus										6	

Knowledge concerning the composition of carabid communities, as well as study techniques, need to be significantly updated. No statistical method is capable of correcting the errors inferred from direct interpretations of pitfall trapping results.

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Appendix

Classification of the carabid species from the Elton Lake region into migrant (M), resident (R) and sporadic (S) species, based on their abundance and demographic spectrum in each habitat type (combined data for 2006/07).

ts	habitats	Lakeside near the River Khara	Salt-marsh	Μ	S	R	М		R		S		Μ	М			
habita	razonal	Floodplain terrace of River Khara	snils2	Я		R	Σ	R		М			Μ	Μ	s		М
conal	Int	Bank of River Khara	Reedbeds	Ч		Μ				Σ			М	М		R	Σ
Az	Exclave	aniveA "lasigoloid"	Riverine wood										М	М	S	Μ	Μ
		Lantsug	ətebbe														
		Watershed of the Rivers Khara and	grassland desert Sagebrush-				R			Я							Я
		- 1, J- F- 12A	erass-torb steppe				7			~	_	S					~
		River Khara	EIIEII				~			_	_						—
	ubitats	Floodplain terrace of	Grass-forb steppe with Amygdalus	М			М			R		S	Μ	Μ			Я
	Zonal ha	Vorthern slope of Ulagan Mountain	steppe Srassland desert Sagebrush-							R			М				R
		River Bol'shaya Smorogda	steppe Brassland desert Sagebrush-				R			R							R
		Left bank of	steppe Sagebrush desert	Μ			К			R							R
		HABITATS	SPECIES	Cylindera (Cylindera) germanica germanica (Linnacus, 1758)	Cylindera (Eugrapha) contorta contorta (Fischer von Waldheim, 1828)	Cephalota (Taenidia) elegans elegans (Fischer von Waldheim, 1823)	Cephalota (Taenidia) atrata (Pallas, 1776)	Cephalota (Taenidia) chiloleuca (Fischer von Waldheim, 1820)	Calomera littoralis conjunctaepustulata (Dokhtouroff, 1887)	Cicindela (s. str.) campestris pontica Fischer von Waldheim, 1828	Cicindela (s. str.) maritima kirgisica Mandl, 1936	Notiophilus laticollis Chaudoir, 1850	Calosoma (Campalita) auropunctatum dzungaricum Gebler, 1833	Calosoma (Caminara) denticolle Gebler, 1833	Calosoma (Charmosta) investigator investigator (Illiger, 1798)	Carabus (Limnocarabus) clathratus clathratus Linnaeus, 1761	Carabus (Tomocarabus) bessarabicus concretus Fischer von Waldheim, 1823

SPECIES Annumber of the fame of the structure of the struct	6	labitats	Lakeside near the mouth of River Khara	Salt-marsh		Μ		R							R	Μ	S	R		М	R	0
SPBCIBS Stretches Bank of River Khara River Khara Tablities Subbinde (stret) Diperintele (stret) Binological ¹ Ravine Tablities Tablities Subbinde (stret) Diperintele (stret) Stretone Stretone Stretone Stretone Diperintele (stret) Diperintele (stret) Stretone Stretone Stretone Stretone Diperintele (stret) Diperintele (stret) Stretone Stretone Stretone Stretone Diperintele (stret) Diperintele (stret) Stretone Stretone Stretone Stretone Stretone Diperintele (stret) Stretone	habitat	azonal ŀ	Floodplain terrace of River Khara	snils2		R	М	Μ			S	s		S	R	R		R		М	R	
SPECIES SPECIES Sectoralistic (Paralishing) and control in the control of the first Kharar Naterior stepse Eliphine (s.st.) hynorial promits Sements, 1926 Sectoralistic (First Kharar and escent stepse Eliphine (s.st.) hynorial promits Sements, 1926 Sectoralistic (First Kharar and escent stepse Eliphine (s.st.) hynorial promits Sements, 1926 Sectoralistic (First Kharar and escent stepse Eliphine (s.st.) hynorial promits Sements, 1926 Sectoralistic (First Kharar and escent stepse) Depointed (Sector Sector) Sectoralistic (First Kharar and escent stepse) Depointed (Sector) Sectoralistic (First (Sector) Depointed (Sector) Sectoralistic (Sector) <th>onal</th> <th>Intr</th> <th>Bank of River Khara</th> <th>Reedbeds</th> <th>s</th> <th>К</th> <th>Ч</th> <th></th> <th></th> <th></th> <th></th> <th>s</th> <th>s</th> <th>S</th> <th>Σ</th> <th>R</th> <th></th> <th>К</th> <th>S</th> <th>R</th> <th>R</th> <th></th>	onal	Intr	Bank of River Khara	Reedbeds	s	К	Ч					s	s	S	Σ	R		К	S	R	R	
SPECIES SPECIES Maintail Signation of the standard description of the standar	Az	Exclave habitat	sniveA "Issigoloid"	Boow anitaviA	s					s								М		М	М	v
SPECIES MABITATIS Additional point of section steppe Elightrus (s. st.) hyporrial procession descrit steppe MABITATIS Additional point (s. st.) hyporrial procession (s. st.) hyporrial (s. st.) hyporrial procession (s. st.) hyporrial descrit province (s. st.) hyporrial procession (s. st.) hyporrial procession (s. st.) hyporrial descrit province (s. st.) hyporrial procession (s. st.) hyporrial procession (s. st.) hyporrial Dysolvirolet (s. st.) hyporrial (s. st.) hyporrial (s. st.) hyporrial procession (s. st.) hyporrial Dysolvirolet (s. st.) hyporrial (S. st.) hypor			Watershed of the Rivers Khara and Lantsug	stebbe Brassland desert Sagebrush-															S			
SPECIES Maintain SPECIES Structus Elliphrus (s.st.) hyperitai hyperita hyperihyperita hyperita hyperita hype				Grass-forb steppe																	Σ	
SPECIES HABITATS Condition SPECIES SPECIES Induction Induction <th></th> <th>ıbitats</th> <th>Floodplain terrace of River Khara</th> <th>oqqote drof-eeses with Amygdalus nana</th> <th></th> <th></th> <th></th> <th></th> <th>S</th> <th></th> <th>Μ</th> <th></th>		ıbitats	Floodplain terrace of River Khara	oqqote drof-eeses with Amygdalus nana					S												Μ	
SPECIES HABITATS HABITATS SPECIES BABITATS HABITATS SPECIES SPECIES Stepper Streat to logitation description Secontext Stepper School of extraction by procriate Semenov, 1926 Sagebrush- stepper Stepper Scarrites (Parallelonorphus) territolat territolat Bonelli, 1813 School of territolat territolat Bonelli, 1813 School of territolat territo		Zonal ha	Yorthern slope of Ulagan Mountain	steppe Grassland desert Sagebrush-																	М	
SPECIES HABITATS SPECIES HABITATS SPECIES SERECIES SPECIES Sagebrush descr Second Second Second Second <th></th> <th></th> <th>River Bol'shaya Smorogda</th> <th>steppe Grassland desert Sagebrush-</th> <th></th>			River Bol'shaya Smorogda	steppe Grassland desert Sagebrush-																		
HABITATS SPECIES SPECIES SPECIES SPECIES Elaphra (s.str.) hypocriat bypocriat Semenov, 1926 Elaphra (s.str.) hypocriat bypocriat Semenov, 1926 Scarites (Panillelomorphus) terricola Bonclli, 1813 Clivina yptilon Dejean, 1829 Dyschrinder (Eudischrinus) repicton terricola Bonclli, 1813 Dyschrinder (Eudischrinus) repicton 1850 Dyschrinder (Eudischrinus) refices (Descan, 1825) Dyschrinder (Eudischrinus) ruffner (Dejean, 1825) Dyschrinder (S. str.) humenture (Fleischer, 1898) Dyschrinder (S. str.) ruticola turicola (Copolos, 1927) Dyschrinder (S. str.) ruticola turicola (Chandoir, 1850) Dyschrinder (S. str.) ruticola turicola (Chandoir, 1826) Dyschrinder (S. str.) ruticola turicolar (Purceys, 1846) Dyschrinder (S. str.) ruticola turicolar (Purceys, 1846) Dyschrinder (S. str.) ruticolar turicolar (Purceys, 1846) Dyschrinder (S. str.) ruticolar (S. Str.) Browcus cerphalore (Linnaeus, 1781) Frowcus cerphalore (Linnaeus, 1781)			Left bank of	steppe Sagebrush desert																	М	
			HABITATS	SPECIES	Elaphrus (s.str.) hypocrita hypocrita Semenov, 1926	Scarites (Parallelomorphus) terricola terricola Bonelli, 1813	Clivina ypsilon Dejean, 1829	Dyschirius (s. str.) humeratus Chaudoir 1850	Dyschiriodes (Eudischirius) globosus (Herbst, 1783)	Dyschiriodes (Eudischirius) rufipes (Dejean, 1825)	Dyschiriodes (Chyridysus) euxinus (Znojko, 1927)	Dyschiriodes (Chyridysus) ruftmanus (Fleischer, 1898)	Dyschiriodes (s.str.) apicalis (Putzeys, 1846)	Dyschiriodes (s.str.) chalceus (Erichson, 1937)	Dyschirtiodes (s.stt.) cylindricus hauseri (Fleischer, 1898)	Dyschirriodes (s.str.) luticola luticola (Chaudoir, 1850)	Dyschiriodes (s.str.) pusillus (Dejean, 1825)	Dyschirtiodes (s.str.) salimus striatopunctatus (Putzeys, 1846)	Dyschiriodes (s.str.) tristis (Stephens, 1828)	Broscus cephalotes (Linnaeus, 1758)	Broscus semistriatus (Dejean, 1828)	Trechus (s. str.) auadrictriatus (Schrank. 1781)

	habitats	Lakeside near the mouth of River Khara	Salt-marsh	R	R	S	S		Μ					R	R	R	R	S	S		R
hahita	azonal	Floodplain terrace of River Khara	Salina	Я	Я			s		R	Μ	S			М	R	Я	S	S	S	R
onal	Int	Вапк оf River Khara	Reedbeds	Ч		s	S	s	М		R		S								R
Az	Exclave habitat	Biological" Ravine,	Riverine wood									S									
		Lantsug	əddəşs																		
		Watershed of the Rivers Khara and	grassland desert Sagebrush-																		
			Grass-forb steppe																		Μ
	abitats	Floodplain terrace of River Khara	Grass-forb steppe with Amygdalus nana						М												
	Zonal há	Yorthern slope of Ulagan Mountain	steppe Grassland desert Sagebrush-																		
		River Bol'shaya Smorogda	steppe Srassland desert Sagebrush-																		
		Left bank of	steppe Sagebrush desert						Μ												Μ
		HABITATS	SPECIES	Tachys (s.str.) scutellaris (Stephens, 1829)	Paratachys bistriatus (Duftschmid, 1812)	Paratachys centriustatus Reitter, 1894	Paratachys micros (Fischer von Waldheim, 1828)	Bembidion (Notaphus) varium (Olivier, 1795)	Bembidion (Philochtus) pallidiveste Carret, 1905	Bembidion (Emphanes) minimum (Fabricius, 1792)	Bembidion (Talanes) aspericolle (Germar, 1829)	Bembidion (Trepanes) octomaculatum (Goeze, 1777)	Bembidion (s. str.) qudrimaculatum (Linnaeus, 1761)	Cardiaderus chloroticus (Fischer von Waldheim, 1823)	Pogonus (Pogonoidius) cumanus Lutshnik, 1916	Pogonus (Pogonoidius) meridionalis Dejean, 1828	Pogonus (Pogonoidius) punctulatus Dejean, 1828	Pogonus (s. str.) iridipennis Nicolai, 1822	Pogonus (s. str.) luridipennis (Germar, 1823)	Pogonus (s. str.) orientalis Dejean, 1828	Pogonus (s. str.) transfuga Chaudoir, 1871
	/			33.	34.	35.	36.	37.	38.	39.	40.	<i>41</i> .	42.	43.	44.	45.	46.	47.	48.	49.	50.

s	habitats	Lakeside near the mouth of River Khara	Salt-marsh	Я	Я	R	Μ				Μ	М		S			S			М	
habitat	azonal	Floodplain terrace of River Khara	salina		М	Я	М	Μ			Я									Я	Σ
onal	Intr	Bank of River Khara	Reedbeds			Ч	М	М	Μ	s	ч	Μ	Μ		Μ			S	М	К	Σ
Az	Exclave habitat	eniveA "lesigoloid"	Boow anitaviA				Μ						Μ		Μ			S	R	R	М
		Watershed of the Rivers Khara and Lantsug	stebbe Brassland desert Sagebrush-				Μ		R											R	
			Grass-forb steppe					R	R											К	
	lbitats	Floodplain terrace of River Khara	Grass-forb steppe with Amygdalus nana				Μ	R	R	S					Μ	S			R	R	Μ
	Zonal ha	Northern slope of Ulagan Mountain	steppe grassland desert Sagebrush-												М					R	
		River Bol'shaya Smorogda	steppe Grassland desert Sagebrush-						М		Μ									R	
		Left bank of	steppe Sagebrush desert						R		Μ									R	
		HABITATS	SPECIES	Pogonistes (s. str.) angustus (Gebler, 1829)	Pogonistes (s. str.) comexicoltis Chaudoir, 1871	Pogonistes (s. str.) rufoaeneus (Dejean, 1828)	Poecilus (s. str.) cupreus cupreus (Linnacus, 1758)	Poecilus (s. str.) punctulatus (Schaller, 1783)	Poecilus (s. stt.) sericeus sericeus (Fischer von Waldheim, 1823)	Poecilus (Ancholeus) laevicollis Chaudoir, 1842	Poecilus (Ancholeus) mitens mitens Chaudoir, 1850	Poecilus (Ancholeus) puncticollis (Dejean, 1828)	Pterostichus (Platysma) niger niger (Schaller, 1783)	Pterostichus (Argutor) leonisi Apfelbek, 1904	Pterostichus (Adelosia) macer macer (Marsham, 1802)	Prevostichus (Pseudomaseus) piceolus (Chaudoir, 1850)	Pterostichus (Phonias) taksonyis Csiki, 1930	Pterostichus (Morphnosoma) melanarius melanarius (Illiger, 1798)	Calathus (s. str.) distinguendus Chaudoir, 1846	Calathus (Neocalathus) ambiguus ambiguus (Paykull, 1790)	Calathus (Neocalathus) melanocephalus melanocephalus (Linnaeus, 1758)
\bigvee				51.	52.	53.	54.	55.	56.	57.	58.	59.	60.	61.	62.	63.	64.	65.	66.	67.	68.

								Az	onall	abitats	
/				Zonal ha	bitats			Exclave habitat	Intra	zonal h	abitats
	HABITATS	Left bank of	River Bol'shaya Smorogda	Vorthern slope of Ulagan Mountain	Floodplain terrace of River Khara	Watershed of the	Lantsug Lantsug	snives" Ravine	Bank of River Khara	гіоодріялі тегтасе от Віует Кћага	Lakeside near the mouth of River Khara
	SPECIES	Sagebrush desert	stebbe Brassland desert Sagebrush-	stebbe Brassland desert Sagebrush-	oresserforb steppe with Amygdalus nana	Grass-forb steppe	Srassand desert	boow ənirəviA	Reedbeds	Salina	Salt-marsh
69.	Dolichus halensis (Schaller, 1783)					A	4	М	Σ	М	Μ
70.	Pseudotaphoxenus rufitarsis major Tschitscherine, 1895	R	R	R	Я	R	~	М	М	М	Μ
71.	Taphoxenus (s. str.) gigas (Fischer von Waldheim, 1823)	R	М	R	R	R	~	М	Σ		Μ
72.	Agonum (s. str.) gracilipes (Duftschmid, 1812)				М			М	R	М	
73.	Agonum (Agonothorax) lugens (Duftschmid, 1812)				S				S		
74.	Agonum (Agonothorax) sexpunctatum (Linnaeus, 1758)								S		
75.	Agonum (Europhilus) thoreyi thoreyi (Dejean, 1828)								S		
76.	Platynus (s. str.) longiventre Mannerheim, 1825							S			
77.	Anchomenus (s. str.) dorsalis (Pontoppidan, 1763)							S			
78.	Amara (Zezea) chaudoiri chaudoiri Putzeys, 1858					_	_		S		
79.	Amara (s. str.) aenea (De Geer, 1774)		Μ		М	M		М	Μ	Μ	М
80.	Amara (s. str.) eurynota (Panzer, 1796)				М			М	Μ	Μ	
81.	Amara (s. str.) littorea C.G. Thomson, 1857				Μ			Μ	Я	М	М
82.	Amara (s. str.) littoralis Mannerheim, 1843					S					
83.	Amara (s. str.) similata (Gyllenhal, 1810)				М			М	Μ	М	М
84.	Amara (s. str.) tibialis (Paykull, 1798)		Μ		М			М			
85.	Amara (Celia) bifrons (Gyllenhal, 1810)				М			М	Μ	Μ	
86.	Amara (Celia) municipalis municipalis Duftschmid, 1812							S			

	abitats	таксзіде пеят гле талі Кічег Кілага Кічег Кілага	Salt-marsh		Μ	М	Μ	М	М		Μ								М	М	Μ
habitats	azonal h	Floodplain terrace of River Khara	snils2		Μ	М	Μ	М			R	R					R		М		М
conal	Intr	Bank of River Khara	Reedbeds		Σ	Σ		Σ			Σ			Σ		Σ	Я		Μ	Σ	Ч
Az	Exclave habitat	Biological" Ravine	Biverine wood		Μ	Μ	Μ	Μ	М					Μ	Μ		Μ		М		
	1	Watershed of the Rivers Khara and Lantsug	stebbe Brassland desert Sagebrush-		М	М	Μ								Я						
			Grass-forb steppe		Σ	Σ	Σ								Я				Μ		
	bitats	Floodplain terrace of River Khara	Grass-forb steppe with Amygdalus nana	Μ	Μ	М	Μ						Μ		R				М		
	Zonal ha	Vorthern slope of Ulagan Mountain	steppe grassland desert Sagebrush-		Μ	R	Μ			S			R		R			S			
		River Bol'shaya Smorogda	steppe grassland desert Sagebrush-			Μ	Μ		Μ						R						
		Left bank of	steppe Sagebrush desert	М		М	Μ								К						
		HABITATS	SPECIES	Amara (Celia) saginata (Menétries, 1849)	Amara (Xenocelia) ingenua (Duftschmid, 1812)	Amara (Xenocelia) ambulans C. Zimmermann, 1832	Amara (Paracelia) saxicola C. Zimmermann, 1832	Amara (Bradytus) apricaria (Paykull, 1790)	Amara (Bradytus) consularis (Duftschmid, 1812)	Amara (Percosia) pastica Dejean, 1831	Amara (Amathitis) abdominalis (Motschulsky, 1844)	Amara (Amathitis) parvicollis Gebler, 1833	Amara (Ammoxena) diaphana Tschitschérine, 1894	Curtonotus (s. stt.) aulicus (Panzer, 1796)	Curtonotus (s. str.) desertus Krynicki, 1832	Curtonotus (s. str.) convexiusculus (Marsham, 1802)	Curtonotus (s. str.) propinquus (Menétries, 1832)	Curtonotus (Ammoleirus) megacephalus (Gebler, 1829)	Anisodactylus (Pseudanisodactylus) signatus (Panzer, 1796)	Anisodactylus (s. str.) binotatus (Fabricius, 1787)	Anisodactylus (Hexatrichus) poeciloides pseudoaeneus Dejean, 1829
\bigvee	/			87.	88.	89.	90.	91.	92.	93.	94.	95.	96.	97.	98.	99.	100.	101.	102.	103.	104.

ts	habitats	Lakeside near the mouth of River Khara	Salt-marsh			Μ			М			М	М	R	М		М	М			М
hahita	razonal	Floodplain terrace of River Khara	snils2			К							Μ	R	Μ	Μ	Μ	Μ			Σ
ona	Int	Вапк оf River Khara	Reedbeds	s		Я	Ч	S	R	R			R	Σ	Μ	Μ	Μ	М			Σ
Aa	Exclave habitat	sniveA "Issigoloid"	boow ənirəviA						М			М			Μ	М	М	Μ			Μ
		Watershed of the Rivers Khara and Lantsug	steppe Grassland desert Sagebrush-														М			М	
			Grass-forb steppe		s												Μ	М	Μ	R	Σ
	ıbitats	Floodplain terrace of River Khara	Grass-forb steppe with Amygdalus nana												Μ		Μ	Μ		R	М
	Zonal ha	Northern slope of Ulagan Mountain	steppe grassland desert Sagebrush-			Μ						М		М			М	М	М		Μ
		River Bol'shaya Smorogda	steppe grassland desert Sagebrush-														М			R	
		Left bank of	steppe Sagebrush desert								s		Μ				Μ	Μ			
		HABITATS	SPECIES	Diachromus germanus (Linnaeus, 1758)	Bradycellus (s. str.) caucasicus (Chaudoir, 1846)	Dicheirotrichus (s. str.) ustulatus (Dejean, 1829)	Dicheirotrichus (Trichocellus) discicollis (Dejean, 1829)	Dicheirotrichus (Trichocellus) stenothorux (Kabak & Kataev, 1993)	Stenolophus (s. str.) mixtus (Herbst, 1784)	Acupalpus (s. str.) elegans (Dejean, 1829)	Acupalpus (s. str.) exiguus Dejean, 1829	Acupatpus (s. str.) meridianus (Linnaeus, 1761)	Acupalpus (s. str.) parvulus (Sturm, 1825)	Daptus vittatus Fischer von Waldheim, 1823	Harpalus (Cephalophonus) cephalotes Fairmaire & Laboulbene, 1854	Harpalus (Pseudophonus) griseus (Panzer, 1796)	Harpalus (Pseudophonus) rufipes (De Geer, 1774)	Harpalus (Pseudophonus) calceatus (Duftschmid, 1812)	Harpalus (Semiophonus) signaticornis (Duftschmid, 1812)	Harpalus (s. str.) cyclogonius cyclogonius Chaudoir, 1844	Harpalus (s. str.) rubripes (Duftschmid, 1812)
\bigvee	/			105.	106.	107.	108.	109.	110.	111.	112.	113.	114.	115.	116.	II7.	118.	119.	120.	121.	122.

s	habitats	Lakeside near the Mouth of River Khara	Salt-marsh					М					М					М			R
habitat	azonal	Floodplain terrace of River Khara	salina		М			М		Μ			М		М	Μ		Μ			К
zonal	Intr	Bank of River Khara	Reedbeds		Σ			Μ					Μ			Μ		Σ			Σ
A	Exclave habitat	eniveA "lesigoloid"	boow ənirəviA				Μ			М			М		М	М					
		Watershed of the Rivers Khara and Lantsug	steppe grassland desert Sagebrush-		Я	s		М	М	М			М		Μ				S	R	
			Grass-forb steppe	s	Ч		Я	Μ	R	R			R		Σ	Μ		Σ		R	
	lbitats	Floodplain terrace of River Khara	Grass-forb steppe with Amygdalus nana		М		Μ		R	R	S		М	Μ	М	Μ	S	Μ			
	Zonal ha	Northern slope of Ulagan Mountain	steppe grassland desert Sagebrush-		R					М		S			Μ			Μ	S		Μ
		River Bol'shaya Smorogda	steppe grassland desert Sagebrush-				Μ		R	М					Μ	М		М		М	
		Left bank of	Sagebrush desert							М					М	М				М	
		HABITATS	SPECIES	i. Harpalus (s. str.) politus politus Dejean, 1829	(. Harpalus (s. str.) serripes serripes (Quensel, 1806)	Harpalus (s. str.) pumilus Sturm, 1818	 Harpalus (s. str.) picipennis Duftschmid, 1812 	. Harpalus (s. str.) amplicollis Menétries, 1848	. Harpalus (s. str.) anxius (Duftschmid, 1812)	 Harpalus (s. str.) calathoides Motschulsky, 1844). Harpalus (s. str.) froelichi Sturm, 1818	. Harpalus (s. str.) hirtipes (Panzer, 1796)	. Harpalus (s. str.) zabroides Dejean, 1829	t. Harpalus (s. str.) tardus (Panzer, 1796)	(. Harpalus (s. str.) oblitus oblitus Dejean, 1829	. Harpalus (s. str.) fuscipalpis Sturm, 1818	 Harpalus (s. str.) inexpectatus Kataev, 1989 	. Harpalus (s. str.) smanagdinus (Duftschmid, 1812)	 Harpalus (s. str.) autumnalis (Duftschmid, 1812) 	0. Harpalus (s. str.) foveiger Tschitschérine, 1895). Harpalus (s. str.) dispar splendens (Gebler, 1829)
\bigvee				123.	124.	125.	126.	127.	128.	129.	130.	131.	132.	133.	134.	135.	136.	137.	138.	139.	140.

ts	habitats	Lakeside near the mouth of River Khara	Salt-marsh	Μ			Μ									R				Μ	S
l habitat	azonal	Floodplain terrace of River Khara	snils2		S		Μ									Μ		S		М	s
conal	Int	Bank of River Khara	Reedbeds	Σ			М	Μ			Μ					R	S		s	К	
A	Exclave habitat	"Biological" Ravine	Riverine wood				М			S	М	М				М					
		Watershed of the Rivers Khara and Lantsug	steppe Grassland desert Sagebrush-				Μ	М	s			R	S								
			Grass-forb steppe		s		М				R	R	S								
	lbitats	Floodplain terrace of River Khara	Grass-forb steppe with Amygdalus nana	Μ		Μ	Μ				Μ	М			S	Μ					
	Zonal ha	Northern slope of Ulagan Mountain	steppe Grassland desert Sagebrush-	М		Μ	Μ	М	S					S							
		River Bol'shaya Smorogda	steppe Grassland desert Sagebrush-				Μ	М				М			S						
		Left bank of	steppe Sagebrush desert				М	М				R									
		HABITATS	SPECIES	Harpalus (s. str.) circumpunctatus Chaudoir, 1846	Harpalus (s. str.) steveni Dejean, 1829	Harpalus (s. str.) terrestris (Motschulsky, 1844)	Harpalus (s. str.) distinguendus distinguendus (Duftschmid, 1812)	Microderes (s. stt.) brachypus (Steven, 1809)	Acinopus (Haplacinopus) striolatus Zoubkoff, 1833	Ophonus (Metophonus) laticollis Mannerheim, 1825	Ophonus (Hesperophonus) azureus (Fabricius, 1775)	Ophonus (Hesperophonus) minimus Motschulsky, 1845	Ophonus (Hesperophonus) convexicallis Menétries, 1832	Dixus eremita (Dejean, 1825)	Dinodes decipiens (L. Dufour, 1820)	Chlaenius (Chlaenites) spoliatus spoliatus (P. Rossi, 1792)	Chlaenius (Chlaeniellus) nigricornis (Fabricius, 1787)	Chlaenius (Chlaeniellus) terminalis Dejean, 1826	Chlaenius (Chlaeniellus) tibialis Dejean, 1826	Chlaenius (Chlaeniellus) tristis tristis Schaller, 1783	Oodes (Lachnocrepis) prolixus (H. Bates, 1873)
1	/																				-

s	habitats	Lakeside near the mouth of River Khara	Salt-marsh							Μ			М								73
habitat	azonal	Floodplain terrace of River Khara	snils2		s			М	Μ				Μ				М		К		85
conal	Intr	Bank of River Khara	Reedbeds					Σ	Μ			s	Μ				Σ		Ч	S	97
Az	Exclave habitat	Biological" Ravine,	Boow aniraviA	s		s		Μ	Μ	М	S	S	Μ				М		Μ	S	69
		Watershed of the Rivers Khara and Lantsug	stebbe Brassland desert Sagebrush-			s							Μ			S					33
			Grass-forb steppe			s				Σ		s	Μ	s					Σ		46
	ıbitats	Floodplain terrace of River Khara	Grass-forb steppe with Amygdalus nana			s	s		Μ	R		s	R	S	S		Μ	S			69
	Zonal ha	Northern slope of Ulagan Mountain	steppe grassland desert Sagebrush-				S						R	S			R				39
		River Bol'shaya Smorogda	steppe grassland desert Sagebrush-										R				Μ				29
		Left bank of	Sagebrush desert										R								28
		HABITATS	SPECIES	Syntomus pallipes (Dejean, 1825)	Microlestes badulini Komarov, 1989	Microlestes fissuralis (Reitter, 1901)	Microlestes maurus maurus (Sturm, 1827)	Cymindis (s. str.) decora Fischer von Waldheim, 1829	<i>Cymindis</i> (s. str.) <i>picta picta</i> (Pallas, 1771)	Cymindis (s. str.) lineata (Quensel, 1806)	Cymindis (s. stt.) scapularis scapularis Schaum, 1857	Cymindis (Menas) miliaris (Fabricius, 1801)	Cymindis (Tarsostinus) lateralis Fischer von Waldheim, 1820	Polystichus connexus (Fourcroy, 1785)	Zuphium (s. str.) olens olens (P. Rossi, 1790)	Zuphium (s. str.) testaceum Klug, 1832	Brachinus (Brachinidius) costatulus Quensel, 1806	Brachinus (Cnecostolus) bipustulatus Quensel, 1806	Brachinus (Cnecostolus) hamatus Fischer von Waldheim, 1828	Mastax thermarum thermarum (Steven, 1806)	L SPECIES
\bigvee	/			159.	160.	161.	162.	163.	164.	165.	166.	167.	1 <i>6</i> 8.	169.	170.	171.	172.	173.	174.	175.	TOT

RESEARCH ARTICLE



When to sample in an inaccessible landscape: a case study with carabids from the Allgäu (northern Alps) (Coleoptera, Carabidae)

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Abstract

While pitfall trapping is generally accepted as the standard method for sampling carabid beetles, this method has rarely been used in mountain ecosystems, mainly due to the high labour intensity it involves. As part of a research project in the German Alps, we investigated the phenologic appearance of adult carabid beetles in mountain ecosystems along with the consequences of possible reductions in sampling periods. Our results show that an early activity peak among carabids is predominant in mountain ecosystems. However, there are differences among species: the main group of species showed the highest activity directly after snow melt, a second group showed a delayed activity peak and a small third group had no clear peak at all. Based on this study, we recommend two fortnightly sampling periods as a minimum for a sampling programme: one immediately after snow melt, and a second sampling period after a pause of two weeks.

Keywords

Carabidae, mountain ecosystems, phenology, sampling effort, pitfall traps

Introduction

Since harsh abiotic conditions along with high spatial heterogeneity dominate mountain ecosystems, in stark contrast to the surrounding landscapes, alpine sites are interesting for ecological and biogeographical research (Lomolino 2001). This is especially true for questions related to environmental changes (e.g. climate change or change of land use) with mountains serving as suitable model ecosystems (Haslett 1997).

Carabidae is a group often used as indicator and/or model taxon (Dufrene and Legendre 1997; Rainio and Niemela 2003; Szyszko et al. 2000). They have also been used to help understand fundamental ecological processes in mountain landscapes (e.g. Franz 1970; Holdhaus 1954).

Nevertheless, very few investigations have been carried out using pitfall traps in high elevation mountain areas (cf. Brandmayr et al. 2003a; Gesellschaft für Angewandte Carabidologie 2009), although this method is otherwise very widely used. The most cited reason given for the limited use of this method is that of labour intensity due to the difficulty in accessing these often remote study areas. To reduce the time invested, depending on the research issue, it might be possible to shorten the sampling period. A likely side effect will be a lower number of specimens captured, leading most probably to a reduction in the number of recorded species. An understanding of the relationship between reduced sampling effort and number of recorded species is needed as a basis for decisions regarding timing and frequency of sampling, especially in the context of long-term monitoring.

Annual rhythms of activity and reproduction have been a major issue in carabidology, dating back to Larsson's pioneering work in this field (Larsson 1939). His classification of carabids' annual rhythms was elaborated upon and modified by other carabidologists (Lindroth 1949; Thiele 1977), and the importance of reproductive behaviour as a life history trait in carabids was emphasized by den Boer and van Dijk (1998) and Paarmann (1979). Many studies have dealt with the relationship between activity patterns and habitat preference, and these studies have lead to a better understanding of distribution trends and specific habitat adaptations of carabids (Lys and Nentwig 1991; Riddick and Mills 1995; den Boer and van Dijk 1996; Matalin 1997; Fadl and Purvis 1998; Traugott 1998; Hutchison 2007).

For mountain ecosystems, literature covering the reproductive seasonality of ground beetles is sparse. There are some works dealing with the phenology of carabids at high altitudes (Lang 1975; De Zordo 1979a, b; Janetschek et al. 1987; Gereben 1995; Ottesen 1996; Sota 1996; Hosoda 1999; Sharova and Khobrakova 2005). Many of these report a shortened activity period, but none of them examine possibilities and consequences of reduced sampling time.

A long-term research project in the "Allgäuer Hochalpen" in the German Alps was conducted in an area protected under the European Union "Habitats Directive". The project aimed at assessing effects of intensive long-term grazing of sheep and associated grazing regime changes after extensive cattle pasturing in 2000. In this project, intensive sampling of epigeic arthropods was performed over 6 years using pitfall traps. In this paper we focus on the seasonal activity of carabid beetles, primarily in the subalpine, but also in the alpine research area. We (1) describe the phenology of carabid beetles in the mountain ecosystems; and (2) investigate the consequences of reducing the number of sampling periods in order to present an optimized sampling scheme for recording the maximum number of species in subalpine and alpine altitudes of the northern Alps.

Methods

Study area

The mountain pasture "Alpe Einödsberg" (10,28°; 47,32°) is located in the German Alps (south-western Bavaria) and is part of the "Allgäuer Hochalpen", an area protected under the European Union "Habitats Directive". The study area ranges in altitude from 1400 to 2000 meters above sea level (m a. s. l). and encompasses a total area of about 2 km². Most of the predominantly west-facing slopes consist of meadows dominated by *Nardus stricta*. Woodland belts dominated by Norway spruce (*Picea abies*) and krummholz made up of *Alnus viridis*, occur throughout the pasture zone (Fig. 1). There is a 2 km ridge running north-south along the upper segment of the pasture. Additional information about the vegetation and geology is given in Höfer et al. (2008), Höfer et al. (in press) and SMNK 2009.

In 2005, sampling was conducted at 25 sites. Sampling was focused on *Nardus stricta*-dominated meadows on slopes and on ridge sites dominated by *Deschampsia cespitosa*. In addition, several forest sites and open sites at lower altitudes were sampled (Table 1).

Sampling

At each sampling site, 6 pitfall traps (with a diameter of 6 cm, filled with 10% acetic acid, 90% water) were installed at a distance of 6 m from each other. In order to protect the traps from heavy rain and from cattle-related damage, traps were placed in a metal tube with a transparent plastic cover (Lederbogen et al. 2004).

The pitfall traps were installed at the beginning of June, just after the first snowmelt at the ridge, and were removed at the end of September 2005 after a period of snow cover. Traps were emptied every fortnight. Altogether, there were 8 sampling periods, these were numbered chronologically (1: June 5th – 18th, 2: June 19th – July 2nd, 3: July 3rd – July 18th, 4: July 19th – August 1st, 5: August 2nd – August 15th, 6: August 16th – August 29th, 7: August 30th – September 12th, 8: September 13th – September 26th).

Carabids were identified to species level; the nomenclature of the species follows Müller-Motzfeld et al. (2004). Not all specimens of *Bembidion incognitum* and *B. deletum* could be identified to species level and they were thus treated as '*Bembidion incognitum/deletum*' in Table 2.



Figure 1. The study area "Alpe Einödsberg". Position of some sampling sites is indicated.

Data analysis

In order to compare species and sites with different numbers of individuals, percentage of total catches per sampling period were used. Total number of species per sampling period and mean number of species per site and sampling period were compared.

For comparison of phenology at different altitudes, the sites were divided into three altitude classes (<1600, 1600–1850, >1850 m a. s. l.) which contained similar numbers of sites. The weighted mean phenological appearance was calculated for each species per altitude class. Differences among classes were tested with a t-test, whereby we only used data for species which occurred at each sampling site and for which at least 10 individuals per class were found. Differences in phenological appearance in the traits: 'hindwing development' and 'body length' were also tested. For 'hindwing length' the groups 'brachypter', 'dimorphic' and 'macropterous' were tested using a t-test; for body size, species were grouped into 7 classes (mean body length < 3 mm, 3–6 mm, 6–9 mm, 9–12.5 mm, 12.5–20 mm, 20–27 mm, >27 mm) and a Spearman rank correlation was performed. Bonferroni corrections were conducted for each test family. For t-tests, data were checked for normality with Shapiro-tests.

site	type	altitude	inclination	exposition
V02	ridge	1875	12	180
V03	ridge	1880	21	210
V05	ridge	1885	29	275
V06	slope	1751	34	255
V08	slope	1776	35	260
V10	slope	1809	38	235
V11	slope	1703	27	250
V16	surface erosion	1790	35	230
V23	sucession Alnus viridis	1765	38	300
X01	ridge	1884	25	250
X03	slope	1896	33	270
X04	ridge	1980	32	280
X05	ridge	1993	9	250
X07	slope	1781	39	265
X08	slope	1786	35	260
X09	slope	1798	37	255
X10	ridge	1911	28	275
X11	slope	1751	34	300
X13	Alnus viridis krummholz	1750	38	320
X14	forest	1565	24	270
X15	forest	1550	34	285
X17	open, low altitude	1434	24	245
X18	open, low altitude	1476	31	270
X20	slope	1720	31	300
X21	ridge	1990	5	280

Table 1. Sample sites. Altitude is given in m a. s. l., incline and exposition in °.

Species accumulation curves (also called sample-based rarefaction curves) were used to compare sampling effort and species richness measures (Buddle et al. 2005; Duelli et al. 1999; Gotelli and Colwell 2001; Ugland et al. 2003). Rarefaction curves for the whole dataset and for each unique sampling period were calculated using Kobayashi's formula (Kobayashi 1974) in the R package 'vegan' (Oksanen et al. 2008; R Development Core Team 2008).

Several reduced datasets with data from two sampling periods were produced. Rarefaction curves and species number per site were compared across the whole dataset, single sampling periods and different combinations of sampling periods.

To understand how the assemblage of carabid beetle species could be represented in the case of a reduced sampling effort we computed a dissimilarity matrix based on Bray-Curtis distances. For this analysis, species numbers were standardised to percentage-data of total species numbers per site and square-root-transformed. Based on this matrix a hierarchical cluster procedure was conducted using Ward's minimum variance method.

teric) and body	
achypter, d: dimorphic, m: macro	ing period 1 to 8 are given.
s 'hindwing development' (b: bı	centage of individuals per sampl
ampling period and their trait	aught (sum) as well as the perc
abids trapped over the whole s	pecies the sum of individuals c
Table 2. List of car	size class. For each s _l

Species	wing	body	uths	1	2	3	4	2	9	7	8
4	type	size		5.6	19.6	4.7	19.7	2.8	16.8	30.8	13.9
	1			18.6.	3.7.	18.7.	1.8.	15.8.	29.8.	12.9.	26.9.
Pterostichus jurinei (Panzer, 1803)	q	4	4431	30.1	33.2	16.1	7.3	2.7	1.9	4.7	4.0
Pterostichus burmeisteri Heer, 1838	q	5	2094	25.2	13.4	12.1	9.5	4.5	5.5	17.7	12.0
Pterostichus unctulatus (Duftschmid, 1812)	q	3	1386	24.4	21.2	17.0	11.8	5.3	8.0	9.2	3.2
Pterostichus pumilio (Dejean, 1828)	q	2	1044	20.3	15.8	23.7	23.6	8.7	2.6	2.7	2.7
Pterostichus multipunctatus (Dejean, 1828)	q	4	699	37.1	35.1	4.5	5.8	4.3	3.9	6.1	3.1
Pterostichus melanarius (Illiger, 1798)	р	5	578	13.5	31.1	30.3	11.8	5.4	3.1	4.0	0.9
Abax parallelepipedus (Piller & Mitterpacher, 1783)	q	5	577	9.5	25.1	16.8	19.6	7.3	10.1	10.6	1.0
Trechus obtusus Erichson, 1837	р	2	509	14.3	14.5	20.8	27.3	9.4	5.7	3.9	3.9
Carabus auronitens Fabricius, 1792	р	6	432	19.9	29.9	24.5	16.4	4.4	3.7	1.2	
Carabus violaceus Linné, 1758	q	7	365	5.5	21.9	27.4	29.0	6.8	6.6	2.5	0.3
Amara erratica (Duftschmid, 1812)	ш	3	282	31.6	52.8	13.5	1.4	0.7			
Leistus nitidus (Duftschmid, 1812)	р	3	167	10.2	26.3	24.6	16.8	5.4	6.6	9.0	1.2
Oreonebria picea (Dejean, 1826)	q	4	159	32.7	30.8	16.4	15.1	2.5	1.9	0.6	
Calathus melanocephalus (Linné, 1758)	р	3	102	5.9	2.9	28.4	17.6	26.5	12.7	4.9	1.0
Pterostichus strenuus (Panzer, 1796)	р	3	97	52.6	23.7	11.3	6.2		2.1	1.0	3.1
Calathus micropterus (Duftschmid, 1812)	р	3	76	14.5	23.7	28.9	14.5	3.9		11.8	2.6
Harpalus latus (Linné, 1758)	ш	4	74	10.8	20.3	12.2	21.6	16.2	12.2	6.8	
Poecilus versicolor (Sturm, 1824)	ш	4	73	26.0	52.1	12.3	4.1	4.1		1.4	
Pterostichus diligens (Sturm, 1824)	р	2	73	57.5	20.5	11.0	4.1			2.7	4.1
Dyschirius globosus (Herbst, 1784)	q	1	51	54.9	7.8	15.7	13.7	3.9	2.0		2.0
Cicindela campestris Linné, 1758	ш	4	44	15.9	22.7	27.3	13.6	11.4	2.3	4.5	2.3
Carabus sylvestris Panzer, 1796	р	6	36		58.3	16.7	2.8	8.3	2.8	8.3	2.8
Amara aulica (Panzer, 1797)	ш	5	32		6.3	50.0	43.8				
Bembidion bipunctatum nivale Heer, 1837	ш	2	32	84.4	3.1	9.4				3.1	

Species	wing	body	sum	1	2	3	4	2	9	7	8
4	type	size		5.6	19.6	4.7	19.7	2.8	16.8	30.8	13.9
	I.			18.6.	3.7.	18.7.	1.8.	15.8.	29.8.	12.9.	26.9.
Tricbotichnus laevicollis (Duftschmid, 1812)	р	3	30	26.7	23.3	13.3	23.3	3.3	6.7	3.3	
Amara lunicollis Schiödte, 1837	Е	3	24	29.2	62.5	4.2	4.2				
Notiophilus biguttatus (Fabricius, 1779)	р	2	23	8.7	17.4	17.4	30.4	4.3	4.3	13.0	4.3
Bembidion incognitum/deletum	ш	2	19	52.6	21.1	15.8		10.5			
Cychrus attenuatus (Fabricius, 1792)	p	5	19	5.3	5.3	15.8	36.8		5.3	21.1	10.5
Amara nigricornis C.G. Thomson, 1857	ш	3	17	17.6	41.2	17.6	17.6			5.9	
Nebria rufescens (Stroem, 1768)	Ш	4	17	23.5	23.5	23.5	11.8	11.8		5.9	
Bembidion lampros (Herbst, 1784)	q	2	15	73.3	6.7	13.3					6.7
Cychrus caraboides (Linné, 1758)	þ	5	11	27.3	45.5	9.1		9.1	9.1		
Bembidion properans (Stephens, 1828)	q	2	7	14.3	57.1	28.6					
Loricera pilicornis (Fabricius, 1775)	ш	3	6	16.7	66.7	16.7					
Nebria brevicollis (Fabricius, 1792)	Ш	4	3	33.3		33.3	33.3				
Agonum sexpunctatum (Linné, 1758)	ш	3	2			100.0					
Acupalpus flavicollis (Sturm, 1825)	Ш	2	1		100.0						
Amara familiaris (Duftschmid, 1812)	ш	3	1			100.0					
Amara praetermissa (C.R. Sahlberg, 1827)	Ш	3	1					100.0			
Carabus glabratus Paykull, 1790	р	7	1			100.0					
Chlaenius nigricornis (Fabricius, 1787)	ш	4	1	100.0							
Cicindela sylvicola Dejean, 1822	ш	5	1			100.0					
Harpalus affinis (Schrank, 1781)	ш	4	1						100.0		
Pterostichus vernalis (Panzer, 1796)	q	3	1			100.0					
Synuchus vivalis (Illiger, 1798)	q	3	1					100.0			
Total			13585	24.9	25.8	17.2	12.1	4.8	4.1	7.0	4.2

When to sample in an inaccessible landscape

Results

In total, 13,585 specimens representing 47 species of carabid beetles were trapped over the sampling period (Table 2). The 10 most abundant species occurred throughout the whole altitudinal range of the study area.

General seasonal activity began with a maximum at the beginning of the study and showed a continuously decreasing tendency up until the end of September (Fig. 1). Focusing on individual numbers, the highest activity was in June, where >50% of individuals were caught. In July, activity declined slowly, and in the second half of the sampling timespan, August and September combined, only 20% of the total number of individuals were trapped.

The number of recorded species follows a similar trend: after a minute increase up to the first half of July, the number of species decreased. Mean species number per site was almost constant from June to the beginning of July, and then decreased up to the end of the study period (Fig. 2 a).

The extremes in beetle activity were greatest at sites above 1850 m a.s.l. relative to the other two altitude classes: the maximum in June was higher and the low activity from the second half of July until September was even more pronounced (Fig. 2 b). Differences between the activity phenology of low and mid-altitude classes were not significant (t=-0.322, p=0.753); however, mean activity of ground beetle species occurring at all elevations was earlier at higher altitudes than at the mid-altitude and lower sites (t=4.33, p=0.001).

All species of which at least 10 individuals were caught had their activity peak in June or July, approximately two thirds of the species in June, and one third in July (Table 2).

Species can be divided into three groups according to their phenology: (1) The first and largest group of species shows quite a distinct activity peak in June (Fig. 3 a) and often a strong decline already occurring in July (e.g. *P. multipunctatus, B. bipunctatum*). Some of these species are almost absent in the second half of the year (*A. erratica, B. bipunctatum*). The strength of the spring activity peak may also be less pronounced (e.g. *C. auronitens*). (2) A second group of species shows a delayed activity peak (Fig. 3 b). In most cases, the magnitude of the peak was weaker than seen in the early species. In species with a delayed activity peak, there are also cases with absence in the second half of the year (*A. aulica*). (3) The third group is comprised of species that show no clear activity peak (Fig. 3 c), i.e. which are active over the entire sampling timespan. Only a few species fit into this latter scheme. Most of these are characterized by a weak peak in June, followed by a slow decline in activity. Some of the species exhibit a relatively high activity in the autumn (*P. burmeisteri, A. paralellepipedus*).

We were unable to find any significant relationship between phenological appearance and hindwing development of the species. Similarly, for body size no significant difference was found, although there is a weak trend of larger species appearing later in the year (t=1.61, df=44, p=0.114).

The sample-based accumulation curves of the first three sampling periods are almost identical at the start, and considerably steeper than the curves of subsequent



Figure 2. Phenology of ground beetles. **a** Overview over all sites. Number of individuals is converted to percentage of total catch. **b** Seperated for the three site classes of altitude. On the horizontal axis the sampling interval is given. For exact sampling periods, see Table 2.

periods and the curve based on the entire dataset (Fig. 4). After 25 samples, the curves of the first three periods split: the third period curve attains higher values, and the first and second period curves follow a similar trend. Decreasing overall activity after the spring peak is also discernible in the rarefaction curves: the curves for sampling periods



Figure 3. Phenology of single species. **a** Species with an early activity peak, **b** Species with a delayed activity peak and **c** Species without a clear activity peak. On the horizontal axis the sampling interval is given. For exact sampling periods, see Table 2.



Figure 4. Sample-based rarefaction curves. Numbers refer to the different sampling periods.

4–8 are clearly below the curve for complete sampling (the curve for sampling period 4 is greater than the total sample curve at the start of the rarefaction process and then falls below it).

Table 3 illustrates the effects of a reduced sampling effort on observed species richness. While single sampling periods achieve a maximum of 65% of the total number of species over the entire sampling timespan, a combination of two early sampling periods can exceed 80% of the total amount of species (sampling periods 1 and 2 or 1 and 3). Best results are obtained when sampling effort is reduced to sampling periods 1 and 3. With the reduced datasets for sampling periods 1 and 3, 91.3% of all species were detected. Per site, the mean quota was 83%, and varied between 68.8 and 100%. The quota of species detected was seen to be independent of altitude or number of specimens caught.

Classification showed that a reduced dataset (periods 1 and 3 only) represents the assemblage structure in a similar way to the complete dataset: All sites are grouped together until the last splitting, where they are divided as a result of sampling intensity (Fig. 5).

Discussion

The strong activity peak observed in our study at the start of the plant growing season has already been observed in many carabids in mountain regions, especially in subalpine and alpine ecosystems (Lang 1975; De Zordo 1979a, b; Refseth 1984; Janetschek, Meyer, Schatz and Schatz-de Zordo 1987; Gereben 1995; Ottesen 1996; Brandmayr et al. 2003b; Löffler and Finch 2005; Sharova and Khobrakova 2005). Depending on altitude, exposition and longitude, the weeks immediately after snow-melt are characterised by an activity peak in many species. The shortened plant growing season and

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V02	64	59	73	41	23	23	32	14	86	86	82	73	22
V03	68	64	73	32	36	32	32	27	86	86	82	73	22
V05	76	76	57	57	19	14	19	10	90	86	90	81	21
V06	56	75	50	38	56	44	38	6	81	69	75	63	16
V08	77	54	69	62	62	62	31	15	77	92	77	77	13
V10	45	65	80	60	45	40	25	20	65	85	95	65	20
V11	63	69	69	50	44	13	31	25	81	88	81	75	16
V16	71	53	47	29	41	29	18	12	71	88	71	76	17
V23	53	100	60	67	47	27	33	7	100	73	100	80	15
X01	82	88	71	47	24	12	18	24	94	88	94	82	17
X03	64	57	71	43	50	36	36	29	86	86	86	64	14
X04	61	56	50	44	44	44	33	28	72	72	67	72	18
X05	73	68	77	64	45	36	36	32	95	100	82	91	22
X07	53	53	60	73	60	40	20	27	67	73	67	80	15
X08	73	60	60	60	47	47	47	27	87	87	73	80	15
X09	83	67	67	67	50	33	33	25	92	83	83	100	12
X10	46	92	77	38	46	38	23	15	92	85	100	54	13
X11	63	53	63	42	37	37	32	32	68	79	68	68	19
X13	65	59	65	47	18	18	53	35	71	88	82	76	17
X14	53	73	67	53	33	47	47	33	87	80	80	60	15
X15	71	57	71	93	50	43	57	29	79	86	71	93	14
X17	79	43	50	43	36	14	21	21	79	79	50	86	14
X18	53	37	58	32	21	11	26	11	63	79	63	63	19
X20	63	69	44	56	44	25	19	44	81	69	88	69	16
X21	68	73	68	50	27	18	27	14	82	86	86	73	22
all sites	76	78	89	65	59	50	57	43	83	91	91	80	46
mean/site	65.4	65.3	64.8	52	40.9	32	32.4	23.2	81.3	82.9	7.97	75	100

Cluster Dendrogram



Figure 5. Dendrogram of sites with data from complete sampling (comp) and sampling periods 1 and 3 (part). The dendrogram is based on Bray-Curtis distances and uses Ward's minimum variance method.

the time in which the larvae are able to develop are given as an explanation for this. A fast start to reproduction in cool ecosystems is advantageous, as larval development takes longer under such conditions (cf. Paarmann 1966; Ferenz 1975). Food availability is another possible explanation; many swarming or flying insects (especially Diptera and Hymenoptera) are attracted to the white snow fields. After landing on these fields the insects are immobilised by the low temperatures. In most cases, ground beetles can pick them up live overnight or, later, as carcasses on snow fields after snowmelt. In these cases, some authors use the term "snow edge species", i.e. species which are adapted to cold and humid conditions and disappear very rapidly after snowmelt (Holdhaus 1954; Franz 1970; Marggi 1992; Brandmayr et al. 2005).

However, snow edge species (Marggi 1992), such as *Bembidion bipunctatum ni-vale*, are not the only species most often trapped after snow melt. Species with broader habitat preferences show increased activity during that time. Prevailing conditions after snow melt (open structure of vegetation and low "Raumwiderstand" sensu Heydemann 1956, the resistance of vegetation structure to the locomotory movement of a given species, high temperatures during sunshine combined with a high soil humidity) might be advantageous for several species.

While most papers focus on the abundant species, our data show that an early activity peak can also be observed for less abundant species. Ottesen (1996) made the same observation for carabids in alpine sites in Norway. However, this was not true for other groups of epigeic arthropods, as he observed an autumn activity peak for some species of staphylinids.

Although high spring activity was seen for all species, we observed differences between species: we were able to divide our species into three groups according to their phenological appearance. While the first group (early and strong spring activity peak) is most frequently described in mountain ecosystems, delayed spring activity has already been shown for some species by other authors (De Zordo 1979b; Refseth 1984), and a species without a strong activity peak was presented (Sharova and Khobrakova 2005). Our data do not give a clear indication of the reasons for the observed phenological differences among species, at least there were no simple relationships between the traits we tested.

The observed activity densities of species, with some species having a strong and early peak and others with a delayed peak led us to the conclusion that the best results can be expected by reducing the sampling to two periods at the beginning of the season. In fact, sampling periods 1 and 3 showed the highest average coverage of the sites' species richness, and the quota of species trapped was better than that suggested by Duelli et al. (1999) for the so-called standard minimum programme for lower altitudes. This means that for high altitudes our suggestion to reduce the sampling effort results in a more robust data set than similar approaches for lower altitudes, as the beetles' activity seems to be more concentrated within a shorter period in mountain ecosystems. The phenological data of other analyses conducted in different habitats from the upper montane zone upwards supports an approach that focuses on an early first sampling period and a delayed second (Lang 1975; De Zordo 1979a, b; Refseth 1984; Janetschek, Meyer, Schatz and Schatz-de Zordo 1987; Gereben 1995; Ottesen 1996; Löffler and Finch 2005; Sharova and Khobrakova 2005). Results of the classification procedure showed that with our reduction in sampling effort, community structure is represented well. A reasonably reduced sampling effort improves the chances of including carabid beetles in monitoring programmes in mountain areas, e.g. to evaluate the conservation status of habitats in Natura 2000 areas. If a reduction in sampling effort is inevitable, we recommend that the minimum sampling effort for carabids in mountain ecosystems should be two fortnightly sampling periods, the first immediately after snow melt and a second after a break of two weeks.

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RESEARCH ARTICLE



A plea for using qualitative aspects in the interpretation of ecological field data as revealed by carabid beetle assemblages of a pristine salt marsh

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Abstract

The evaluation of ecological field data can be done by an increasing number of quantitative methods. The application of these methods often is often blind against two kinds of problems: (i) the data often do not meet the requirements of a method, e.g., as an ultra-metric structure of the data in the case of hierarchical cluster analysis. In such cases, the result will be misleading because the presentation of results is ultra-metric independent on the structure of the data. (ii) Most of the animals are able to move actively or may drift passively by wind, etc. Therefore, species occurring by accident like vagrants have to be eliminated from the assemblage of animals at a particular site before a quantitative method is applied. In addition, the result of a quantitative analysis has to be checked for its ecological plausibility. This is a qualitative step, which can only be done by taking into account the known data on biology and ecology of the species. Some pitfalls of an exclusive application of quantitative methods will be demonstrated in this paper using a data set of salt marsh Carabidae.

Keywords

Cluster analysis, indicator value, qualitative interpretation, ecological field data, Carabidae

Introduction

In the literature, the representation and evaluation of ecological field data is achieved by a broad spectrum of different methods ranging from vegetation tables to trees of similarity of sites. McGeoch (1998) recommended a nine-step procedure for the evaluation of ecological field data in a paper on terrestrial insects as bioindicators. She explicitly demands that ecologists use quantitative data and procedures including statistics. In general, quantitative data are indispensable, and the interpretation and representation of data by quantitative methods is a must. But two kinds of problems exist when a quantitative method is applied blindly. (i) The data often do not meet the requirements of a method, e.g., as an ultra-metric structure of the data in the case of hierarchical cluster analysis. In such cases, the result will be misleading because the presentation of results is ultra-metric independent on the structure of the data. (ii) Most of the animals are able to move actively or may drift passively by wind etc. Therefore, species occurring by accident like vagrants have to be eliminated from the assemblage of animals at a particular site before a quantitative method is applied. In addition, the result of a quantitative analysis has to be checked for its ecological plausibility. This is a qualitative step, which can only be done by taking into account the known data on biology and ecology of the species.

Dufrène and Legendre (1997) developed the 'Indicator Value' (IndVal) method, which combines data on both abundance and frequency in an optimal manner. McGeoch and Chown (1998) published an enthusiastic review of the IndVal method entitled "Scaling up the value of bioindicators". Subsequently, this method was applied in many studies. In the intervening period, this method has been extended by Clarke et al. (2006; zero-adjusted Bray–Curtis coefficient), Dai et al. (2006; Total Indicator Value Method), and Bakker (2008; improvement of permutation test, consistency of index and binary data).

We use mainly the IndVal method to call attention to some problems of the application of quantitative methods and to show that qualitative aspects have to be included for data interpretation. In this paper the following questions are addressed:

• Hierarchical cluster analyses were often used to generate trees to arrange sites by the similarity of their faunal assemblages. What are the objectionable effects of these methods?

• Is the IndVal index simple and based only on within-species abundance and occurrence comparisons, without any comparison among species?

- Is it wise to always use the maximum of IndVal?
- What is the impact of a qualitative approach?

Salt marshes are considered to be optimal for the purpose of this paper because they offer a structured elevation gradient and they are an extreme habitat for carabid beetles (Mossakowski 2007): a low number of stenotopic species occur in high abundances in particular in lower salt marsh zones.

Material and Methods

Material

The test data were collected in a project on salt marshes and climate impact (Dormann et al. 2000, Dormann et al. 2008) on the pristine salt marshes of the East Frisian island Mellum, Germany. Pitfall traps were exposed during the seasons of three years from April to October in different configurations. To avoid damage from the tide and waves, an air-bell trap (Dormann 2000) was constructed and exposed at the lower salt marsh sites, between 20 cm below Mean High Water Level (MHW) (-20), at MHW and up to 40 cm above MHW. Only 'year' catches of 1998 (April to October) were used and numbered by elevation (Table 1). At 100 cm above MHW, three sites were selected due to different soil conditions at this elevation and indicated by adding an integer to the last position of the site number (101, 102, 103). Five traps were exposed at each site. Each trap was numbered with site elevation and a digit (-20-5: trap five at site -20; 101-1: trap one at site one of elevation 100).

Quantitative methods

1. IndVal of Dufrène and Legendre

In our opinion, the Indicator Value (IndVal) method of Dufrène and Legendre (1997) comprises three steps: (i) the arrangement of catches/sites. The data are represented in a tree constructed preferably from the distances in the species-site matrix. Dufrène and Legendre (1997) use a non-hierarchical cluster analysis in their paper but in their original program a hierarchical one is required. (ii) The information of the resulting tree must be transformed by hand into a matrix, which reflects hierarchically the arrangement of sites in the tree. (iii) The appropriate IndVal search for characteristic species: The maximum IndVal is calculated using the fidelity and specificity of a species for groups of sites that are taken from the tree via the matrix of step ii.

Test calculations with our data were performed with the original IndVal program (IndVal 2.0; Dufréne & Legendre 1997) using Ward's method with Relative Euclidean distances as well as with UPGMA with Bray-Curtis (Sœrensen) distances (step i). The problems of hierarchical cluster analysis were demonstrated by a calculation with the full data set. A recalculation was done after deletion of two sites (102 and 103).

↓ Elevation above MHV (cm)							
-20 0 10 20 40	60	80	100	120			
Number of pitfall traps							
5 5 5 5 5	5	5	3×5	5			

Table 1. Elevation gradient and number of exposed pitfall traps in the salt marshes of Mellum.

The impact of the tree structure (generated in step ii) on the result (step iii) is shown by a comparison of a hierarchical tree with a freehand produced tree on the basis of the site specific data.

2. The IndVal procedure of PC-ORD (McCune and Mefford 2006) was applied with the same data and a series of free-hand produced trees.

3. Other quantitative methods are applied to the identical sets of data: Principal Coordinate Analysis (PCO)/MVSP; Discriminant Analysis/Brodgar; Multivariate Partitioning (mvpart) Brodgar/R.

Applied statistics for IndVal: Random permutation test (999). Significance level: 0.01.

Qualitative methods

A table of year-catches for species x traps is presented (Appendix III), which covers the original year-catch numbers in an arrangement like that in vegetation tables. These data were freehand interpreted under consideration of the specific conditions at the study sites and the biological and ecological demands of the species.

Results

Quantitative evaluation: IndVal original program

The first step of the IndVal procedure yielded similar results with different procedures. In order to demonstrate characteristic effects of cluster methods, the result of Ward's method with Relative Euclidean distances including all trap-sites is presented in Fig. 1. In the resulting tree, two sites of very different elevation levels clustered together: four out of five traps of site -20 and all traps of site 103. They were placed together with another cluster of 0, 10, 20, 40 and the fifth trap of -20 (-20-5). All remaining sites of higher elevation (60-120) clustered closely together.

The result obtained by UPGMA with Bray-Curtis distances also showed a basic split of -20 against the cluster of 0, 10, 20, 40 and -20-5. At the other end, 103 splits off at the basis of all the sites at higher elevation.

Elimination of site 102 and 103 resulted in more plausible trees. In the case of Ward's method with Relative Euclidean distances, the traps of elevation -20 and those of site 20 and 40 were put in the cluster next to that of 0 and 10, which included trap -20-5.

In the second step of the original IndVal procedure, the information of the tree was transformed into a hierarchical notification (Appendix I). In order to get a clearly arranged result, the tree of the first step was simplified, as was the matrix for the calcu-


Figure 1. Result of a cluster analysis using Relative Euclidean distances and Ward's method. Most traps of the site at the lowest elevation (-20 cm below MHW) cluster with those of 100 cm above MHW. Arrow: One trap of -20 behaves differently.



Figure 2. IndVals at different levels in the UPGMA tree.

Result for a single species, *Dicheirotrichus gustavii*, calculated by the original IndVal program. Eight values of the nine levels are significant. Data: abundance/frequency data. 7/4: a total of seven specimens were found in four of the five traps. Sites 102 and 103 are omitted.

lation of the IndVal values. Sites 103 and 102 were omitted and all five traps of equal elevation were assigned to the same group.

The third step was performed first by the original IndVal program. Fig. 2 demonstrates the distribution of successive IndVal's at different levels of this simplified tree showing the result of one calculation for a single species. As an example, *Dicheirotrichus gustavii* was chosen as a highly abundant and specific species in salt marshes. All values shown are significant.

A result for *Cillenus lateralis* is shown in Fig. 3 in order to show the dependence of the IndVals on the tree structure. In the lower section, the original (simplified) matrix was used. A maximum indicator value of 90% was found for this species (sites –20 to 20) by the original IndVal program. In a calculation using a free-hand self-constructed, alternative tree, higher values were found.



Figure 3. Results of the IndVal procedure depend on the tree used.

Data: abundance/frequency of *Cillenus lateralis* along the elevation gradient. 3/3: a total of three specimens was found in three of the five traps. Sites 102 and 103 are omitted.

Quantitative evaluation: IndVal by PC-ORD

The application of the same data to the IndVal procedure of PC-ORD was carried out by different arrangements of sites to groups. The obvious first step was to take the five traps per elevation as groups (first data line in Table 2). Each result consists of a table of IndVals in which scores for each species and the chosen arrangement of groups are listed. As an example of differing results from multiple calculations with changing arrangements, the scores for *Cillenus lateralis* are listed in Table 2. The notation results differ from those of the original IndVal program; scores were not listed hierarchically, they were listed parallel. Therefore, scores of other groups apart from the maximum can be evaluated.

MHV	-20		0	10	20	40	60	80	101	120
(1)	48									
(2)		100								
(3)	65		34							
(4)		98		1						
(5)		98		1						
(6)	85			7						

Table 2. Indicator Values as a result of multiple calculations performed by PC-ORD. Results for *Cillenus lateralis*. Each line represents a separate calculation with the groups indicated by vertical lines. Bold face numbers indicate significance. **MHW**: Mean High Water Level.

Quantitative methods: Principal Coordinate Analysis

The test data were also applied to methods that do not use distance-based algorithms. As an example, the result of Principal Coordinate Analysis (PCO) is shown in the Appendix II. Similar to the grouping by distance methods, the lower sites form one group while the higher sites form another. One trap at site –20 is also positioned close to those of higher elevation (site 0, 10 etc). The position of site 103 is remarkable because it is arranged near to the site with the lowest elevation – far from those at equal elevation (101 and 102). The results of Discriminant Analysis and Multivariate Partitioning (not shown here) display similar effects.

Qualitative methods

In order to apply qualitative aspects of interpretation, we present the full data set in the Appendix III in order to enable the reader to evaluate our statements. We focus on two species, characteristic in a different way, of flooded and salty habitats.

The occurrence of *Dicheirotrichus gustavii* along the elevation gradient is characterised by very high numbers at an elevation 10 cm above MHW (site 10 with a mean of 3606, range 1181 - 5844 specimens per year-trap) and at MHW (site 0 with a mean of 824, range 256 - 1355). This species was found only in one trap at lower elevation (-20-5) and in moderate numbers at higher sites.

Cillenus lateralis was collected in traps of elevation –20 and 0 in moderate numbers (–20: mean = 74, range: 6–309; 0: mean = 76, range 6–161). This species occurred with single specimens at elevations 10 and 20.

Habitat conditions at the lower part of the Mellum salt marshes differ markedly in soil and flood frequency: sites -20 and 0 contain about 70–80% sand, they flooded regularly, at least once per day (1 – 1.5 times per day). Above this level, 10 to 80 cm above MHW, the soil consists of a high amount of clay and a low sand content. Site 10 is flooded about 0.7 times, site 20 about 0.5 times, and site 40 lower than 0.2 times per day.

Effects of cluster methods

There are two unexpected results in Fig. 1: (i) the position of trap -20-5 and (ii) that of site 103. These effects do occur also in results of multivariate methods but shall be discussed using the example of cluster analysis.

In particular, the positioning effects mentioned afore can be interpreted by viewing the data in detail. (i) In trap –20-5, *Dicheirotrichus gustavii* was caught but is missing completely in the other traps at elevation –20. But the number of this species found in this deviant trap is very low in comparison with the very high abundance at higher elevations (see full data in Appendix III). We have to take into account that these specimens are migrants from higher sites. (ii) The position of all the traps of site 103 depends on quite a different assemblage of species, which is obviously different not only from those at comparable elevations but also from all sites. This depends on the differences in sand content and wetness between the three sites at 100 cm above MHW: site 103 is a very dry, sandy habitat, and consequently, the assemblage of species is quite different (Table 3).

Because the clustering process will put the tho step most similar sites together in a step-by-step approach, site 103 and most traps of -20 remain at the end of the clustering process.

In general, a basic problem of distance methods is that trees showing similarity of sites are the result of a cluster analysis. This is critical because the condition for use, the existence of metric or ultra-metric data (Appendix IV), is often not realized in ecological field data and neither tested nor discussed by many authors. In the example

Elevation	-20	0	10	20	40	60	80	101	102	103	120
Taxon											
Calathus erratus			2							89	1
Amara fulva										30	
Amara spreta										20	
Calathus ochropterus										19	
Harpalus affinis										2	
Trechoblemus micros										1	
Dicheirotrichus gustavii	136	4134	18687	334	163	7	12			7	
Bembidion minimum			2		761	4				2	
Bembidion guttula								1	1		
Badister bullatus								14	1		17
Badister sodalis							4	22			10
Pterostichus niger						13	280	264	168		130
Calathus fuscipes		3	2		2	37	59	216	164	1	368
Dyschirius globosus	1		1		6	562	1210	1030	267	2	923

Table 3. Selected carabid species to show differences at site 100 (100 cm above MHW). Only species with characteristic distribution (more or less exclusive or missing) are included. The catches of five traps per site are summarized.

demonstrated, this problem is easy to see. But the problem exists also in the case of data with a structure closer to an ultra-metric one. But it will not be as obvious as in our example. The distance matrix can be tested for ultra-metric conditions by checking each triplicate of values whether the strengthened triangle inequality is given (see Appendix IV). But the programs do not output the distance matrix.

Transformation from tree to matrix

282

In the original IndVal program, a hierarchical tree is specified. Arranging a matrix with the correct information requires some patience. This may be because it is done for the first time, or because trees are usually being used for phylogenies. As such, this procedure is not simple.

IndVal based only on within-species data

This statement is only correct when considering the last step of IndVal evaluation. However, as has already been stated by Dufrène and Legendre (1997), and shown in Fig. 3, the resulting IndVal of a species depends on the arrangement of sites to groups, the corresponding tree or matrix. Therefore, the data of the total assemblage have an indirect influence on the IndVal scores. This is true, not only when using a cluster analysis but also for other techniques.

Qualitative interpretation and IndVal maximum

As an example, the data and IndVals for *Dicheirotrichus gustavii* are shown in Fig. 2. The highest value for this species (96%) was found for a group of sites; 0, 10, and 20. However, sites 0 and 10 form a group with an index (94%) similar to the former. Both are significant. But what is the difference? How can it be tested? Compared to the data for sites 0 and 10, the relatively low numbers below and above this elevation may indicate a suboptimal habitat for this species. Otherwise, we have to take into account that these beetles are able to walk and to fly or they may drift during flooding, which occurs at least once per day at this elevation. Thus, we prefer to take this species as an indicator for sites at elevation 0 and 10 (see also Appendix III).

The same problem can be identified for *Cillenus lateralis* (Fig. 3). A purely quantitative view will find an IndVal of max. 98.8%. But if we consider qualitative data, our knowledge of the ecology and biology of the species, the lower value (96.7%; for sites 0 and -20) is the appropriate one. *Cillenus lateralis* inhabits more or less pure sandy soils (about 70–80% sand at site -20 and 0 on Mellum), which must be flooded regularly. These conditions are only realized at this elevation. Specimens occurring above this level have to be classified as vagrants.

Conclusions

- 1. The construction of a tree using distance data by hierarchical cluster analysis always results in an ultra-metric tree although the data are not ultra-metric. Therefore, such procedures should not be used. Also non-distance methods yielded problem-atic results with the data set under study.
- 2. Because the original IndVal program requires a hierarchical tree transformed into a matrix, which is also structured hierarchically, we recommend using the IndVal function in PC-ORD as a simple procedure (not free of charge). The Mac version of the original IndVal program does not run on IntelMac. See also Bakker (2008; appendix: program in R).
- 3. The IndVal method is not only based on the within-species data because the arrangement of sites to groups depends on the whole data set.
- 4. The examples of *Cillenus* and *Dicheirotrichus* demonstrate that a quantitative analysis may involve some pitfall traps, e.g. the maximum of IndVal. An additional qualitative interpretation is necessary which incorporates biological and ecological data known for the species. It has to be remembered that a particular study never represents more than a small sample of the complete diversity. Thus, external data should be incorporated in order to avoid a narrow focus on one's own limited set of data. Large and good data sets on species and sites are presented by our colleagues in the Netherlands (Alders et al. 1991, Turin 2000).
- 5. The necessity to incorporate qualitative aspects is also an argument against the use of only binary (presence/absence) data recently proposed by Bakker (2008).
- 6. The classic characterization of ecological field data along habitat preference classes should be revived. As a student, D.M. learned from Wolfgang Tischler (1949) that we have to eliminate non-indigenous species such as vagrants even if they occur in larger numbers.

Consequently, a more qualitative evaluation requires the publication of a detailed specification of methods and of species x site data as done or requested by Dufrène and Legendre (1997), Desender et al. (2007) and Bakker (2008).

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Appendix I

Arrangement of sites represented by a tree and a matrix. (doi: 10.3897/zookeys.100.1532. app1) File format: Adobe Arcobat PDF.

Explanation note: Sites are numbered by elevation (right column). The structure of the tree is displayed by a hierarchical notification of the matrix.

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Appendix II

Principal Coordinate Analysis of the whole data set. (doi: 10.3897/zookeys.100.1532. app2) File format: Adobe Arcobat PDF.

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Appendix III

Catches of carabid beetles on the island of Mellum. (doi: 10.3897/zookeys.100.1532. app3) File format: HTML.

Explanation note: Yellow colour indicates congruence between a pure quantitative and our qualitative interpretation. Blue colour indicates additional significant IndVal's due to pure quantitative results. Halobiontic and halophilic species are listed in the upper section (above first break). The first 30 species (above second break) are used for the calculations of IndVals. Sites were numbered by their elevation above MHW [cm]. 1,2...5: trap

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Appendix IV

Triangles and trees, the distance matrices of which fulfil metric or ultra-metric conditions respectively. (doi: 10.3897/zookeys.100.1532.app4) File format: Adobe Arcobat PDF.

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RESEARCH ARTICLE



Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions

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Abstract

Classic studies have successfully linked single-species abundances, life-history traits, assemblage structures and biomass of carabid beetles to past and present, human-caused environmental impacts and variation in 'natural' conditions. This evidence has led many to suggest carabids to function as 'indicators' - a term that bears multiple meanings. Here, a conservation-oriented definition for an indicator is used, carabid indicator potential from seven views is evaluated, and ways to proceed in indicator research are discussed. (1) Carabid species richness poorly indicates the richness and abundance of other taxa, which underlines the importance of using multiple taxa in environmental assessments. The ability of assemblage indices and specialist or functional-group abundances to reflect rare species and habitats should be examined in detail. (2) Experimental evidence suggests that carabids may potentially serve as keystone indicators. (3) Carabids are sensitive to human-altered abiotic conditions, such as pesticide use in agro-ecosystems and heavy metal contamination of soils. Carabids might thus reflect ecological sustainability and 'ecosystem health'. (4) Carabid assemblages host abundant species characteristic of particular habitat types or successional stages, which makes them promising dominance indicators. (5) Carabids reflect variation in 'natural' conditions, but vegetation and structural features are more commonly adopted as condition indicators. Carabids nevertheless provide yet another, equally accurate, view on the structure of the environment. (6) Carabids may function as early-warning signalers, as suggested by recent studies linking climate and carabid distributions. (7) Carabids reflect natural and human-caused disturbances and management, but the usefulness of these responses for conservation purposes requires further research. In summary, European carabids appear useful model organisms and possibly indicators because they are diverse, taxonomically and ecologically well-known, efficiently reflect biotic and abiotic conditions, are relevant at multiple spatial scales, and are easy to collect in sufficiently large numbers to allow statistical analyses. The assumption

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that carabid responses would reflect rare environmental conditions or the responses of rare and threatened species – crucial information for conservationists and managers – has not yet been critically evaluated. Even if it holds, the usefulness will be context dependent: species and their populations vary, conditions vary, questions put forward vary, and assessment goals vary.

Keywords

abiotic, assessment, bioindicator, biotic, change, conservation, disturbance, dominance, early warning, human impact, keystone, management, richness

Introduction

Indicators, in the most general sense, can refer to anything that have been shown to reflect something apart from their individualistic response. For example, different species reflect habitat types through their associations with particular biotic and abiotic conditions, and a common assumption is that the magnitude and direction of this reflection are not unique to the studied species. For conservationists and environmental managers, i.e., the potential end users of indicators, such general patterns will not suffice. For them, an indicator should permit conclusions regarding particular conditions or biodiversity, which could not otherwise be concluded either without using the indicator or through using easier, cheaper and/or quicker assessment tools. Indeed, Landres et al. (1988) described an indicator as being a taxon or a structure "...whose characteristics (e.g., presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest". Here I use the term 'indicator' following this strict definition unless stated otherwise.

In ecological impact studies carabid beetles are frequently cited as indicators in the vague sense described above, but according to the strict sense they should more often be cited as model or study organisms. A model organism is a (group of) species that is used to examine a particular study question (a hypothesis) under a research programme (sensu Underwood 1997; see also den Boer 2002). For example, the researcher's general question might be "Does fungicide spraying affect soil-dwelling animals?" which is then studied using carabids to model a biological response. If you type the words 'carab*' and 'indicator*' into Scopus you get 172 results, and similarly ISI Web of Science produces 186 results (26 May 2010). Many if not most of these studies have little to do with carabids indicating anything else but themselves, i.e., their individualistic response to treatments of interest, except perhaps trivial issues such as the sampled habitat type. Such 'watering down' of terms may lead to misunderstandings among scientists, practitioners and amateurs, including the media, and to an impoverishment of the scientific language.

Here I evaluate the indicator potential of carabid beetles for seven common applications of indicators (Lindenmayer et al. 2000): (1) indicating richness and abundance of taxa other than carabids; (2) functioning as keystone organisms; (3) indicating human-altered abiotic conditions, here pollution; (4) indicating particular environmental conditions through numerical or biomass dominance; (5) reflecting variation in 'natural' conditions; (6) acting as early-warning signalers; and (7) indicating disturbances and management. Generally speaking, the basic requirements for the use of indicators are fulfilled by most European carabids: good knowledge exists on (i) conditions to which these species are adapted to; (ii) distributions of the species in a given set of patches; (iii) the species' responses to environmental variation/alteration; and (iv) variation in the species' population dynamics (Andersen 1999; Lindenmayer et al. 2000; see "Carabids as model organisms" below).

In this review I ask three questions with a combined European and North American focus.

Which features characterize carabids as potential indicators? In "Carabids as model organisms" I briefly review the current state of ecological knowledge, information gaps, and methods used in carabid research.

What kinds of indicators might be found among carabids, considering the seven indicator categories above? In other words, what is the evidence for and against using carabids as indicators? In "Evaluation of carabids as indicators" my aim is to summarize key evidence for carabid indicator potential. This Section is intentionally critical, as the use of indicators in conservation should be on an exceptionally solid basis: threatened species or habitats are at stake.

Where, and how, should carabidologists proceed in their search for indicators? In "Identifying and using carabid indicators" I discuss (a) ways to incorporate carabids into routine environmental assessments, (b) issues about carrying out research searching for indicators, and (c) where to find new areas in the ongoing indicator hunt.

Carabids as model organisms

Prerequisites for being good model organisms and also potential indicators include vast knowledge on carabid taxonomy and ecology, as well as ease of collecting, but these hold mostly only for north-temperate regions (e.g., New 1998). Carabids are taxonomically well known, with relatively stable systematics, and their ecology has been widely studied (Lövei and Sunderland 1996). Variation in carabid morphology, life-history strategies and abiotic and biotic requirements are also extensively documented. We know, for example, many species that are specialized to certain moisture, temperature and shadiness conditions (Rainio and Niemelä 2003; Niemelä et al. 2007). Carabids are also widely distributed, from the arctic and alpine tundra to seashores, deserts and tropical rainforests, and they can be common in these environments (Lövei and Sunderland 1996). However, knowledge about basic life-history parameters appears limited to a few well-studied species. These parameters include birth and death rates, population age structure and growth rate, resource allocation between reproduction and growth, and the causes and magnitude of variation in

these. Such parameters are not only interesting but may appear crucial for indicator use (see "Identifying and using carabid indicators").

The reasons for particular distributions, local abundances or behavioral responses of carabids are generally well understood. Carabids are influenced by temperature, moisture and shade (Thiele 1977), food quality and abundance (Lenski 1984; Van Dijk 1994; Bilde and Toft 1998; Bilde et al. 2000; Bohan et al. 2001), habitat structure as reflected by the vegetation (Rykken et al. 1997; Siemann et al. 1998; Brose 2003; Koivula et al. 1999; 2003; Taboada et al. 2008), and substrate salts, sugars and acidity (Merivee et al. 2001, 2004, 2006; Milius et al. 2006). Moreover, seasonal and life-history fluctuations strongly affect observed abundances and distributions (Thiele 1977; Lindroth 1985, 1986; Lövei and Sunderland 1996). Of largely unknown – though often suggested – importance are intra- and interspecific interactions, of which competition has usually had minor effects (Loreau 1990; Niemelä and Spence 1991; Niemelä 1993a; Currie et al. 1996; Zetto Brandmayr et al. 2004).

In ecological research, both landscape and smaller scales appear relevant for carabids, although the former usually requires extensive sampling. Carabids are not always considered relevant at spatial scales larger than a few hectares (e.g., Pearce and Venier 2006). This view relies on the idea of local populations or 'home ranges' of carabids (e.g., den Boer 1990a; Gaston and Blackburn 1996; Charrier et al. 1997). However, carabids predictably respond to landscape- (here, areas larger than 50 ha) and even continent-level phenomena (e.g., Hengeveld 1987; Kotze and O'Hara 2003; Kotze et al. 2003). For example, carabids reflected isolation in southern Finnish farmlands (Kinnunen et al. 1996), and responded to patch size and matrix type in an urban landscape in Belgium (Gaublomme et al. 2008). The structural heterogeneity of landscapes had variable impacts on different trophic groups of carabids in Germany (Purtauf et al. 2005). Moreover, carabid assemblages gradually changed across a forest/farmland gradient in Scotland (Vanbergen et al. 2005), and in Canadian post-fire forests, logging variably affected carabids at the stand level but strongly and predictably at the landscape scale (Koivula and Spence 2006).

Most field studies on carabids have used pitfall traps, which is an easy and cheap method to collect sufficiently large samples to allow statistical analysis, by acknowledging that the catch indicates species-specific 'activity density' rather than true relative abundance (Greenslade 1964). The dominance of one method over others introduces a knowledge bias. New insights would be achieved by more often applying other collecting methods, such as capture-mark-recapture techniques, trapping and measuring live beetles, window trapping, tree-canopy pesticide spraying, hand collecting, and soil sampling to collect larvae (Sutherland 1996).

The carabid beetle literature reflects a wide spectrum of approaches to study ecological questions. Papers on single species, total abundance and species richness are common. If the numbers of collected individuals are small, or if generalizations are required, carabids are often divided into functional groups to test the hypotheses put forward. These groups include seasonal abundance peak, reproduction period, diurnal activity, body size, wing morphology (e.g., brachypterous/wing-dimorphic/long-winged/ flying), food preferences (e.g., predator/omnivore/plant-eater/specialist), associations with habitat openness (e.g., closed tree canopy or extensive vegetation cover/generalist/ open phase) and moisture preferences (e.g., dry/moist/wet). Clearly, species divisions into these groups involve subjectivity, because many categories were originally continuous variables, and may be poorly known even in regions with a long research tradition. Flight capability in carabids in Northern and Central Europe is a good example of such knowledge gaps (Niemelä et al. 2007). Morphospecies or higher-than-species level approaches are rarely applied by carabidologists, because different species within a genus are ecologically different and may consequently respond differently to the environment (Koivula et al. 2006; Langor and Spence 2006).

Various diversity indices have been used on the carabid catch. These include, for example, rarefaction (Sanders 1968) and the Shannon-Wiener and Simpson indices (Magurran 2003; Tóthmérész and Magura 2005a). However, diversity indices may perform inconsistently (O'Hara 2005) and therefore should not be used as a sole justification of indicator functioning. Another obstacle is that diversity measures based on pitfall-trap data are problematic because the samples are biased toward actively moving, large-sized species (e.g., Morrill et al. 1990; Lang 2000). As such, these samples may have little to do with true assemblage composition and structure. The relationship between trap samples and true assemblages is poorly understood due to the difficulty in reliably determining the latter.

Recent approaches to describe carabid assemblage structure include Mean Individual Biomass (Szyszko et al. 2000; see "Dominance indicators"), affinity indices (Allegro and Sciaky 2003; Tóthmérész and Magura 2005b) and indicator value calculations (IndVal; Dufrêne and Legendre 1997). Affinity indices aim at removing the effect of differences in species abundances among compared habitat types while simultaneously accounting for the species' habitat specificity (Magura et al. 2006a). The IndVal approach uses data collected from habitat types of interest, and identifies species characteristic of particular habitat types based on their abundances and presences/absences among all samples (Dufrêne and Legendre 1997).

Evaluation of carabids as indicators

Taxon indicators

The presence of a taxon indicator reflects the presence of a set of other species, and its absence indicates the absence of the entire set of species (Slobodkin et al. 1980; Lindenmayer et al. 2000). The underlying assumption thus is that the presence of a limited subset of all species would indicate the presence of the complete set. As everything cannot be measured this approach may sound appealing, but evidence of carabids as taxon indicators is poor. Weak richness correlations with carabids have been demonstrated for spiders (Rushton et al. 1989; Niemelä et al. 1996) and some other invertebrate taxa (Duelli and Obrist 1998; Niemelä and Baur 1998). Barbaro et al. (2005) found that the same structural features of forests predicted bird, spider and carabid richness in France. The utility of richness indicators becomes even more challenging at larger spatial scales, where richness correlations appear to be a biogeographic rule. Species richness of different taxa often correlate because of the general tendency of richness to increase toward the equator (Begon et al. 1996); for a national-scale invertebrate example, see Väisänen and Heliövaara (1994).

The taxon indicator potential of carabid beetles has not yet been subject to a severe test (sensu Mayo 1997), but such tests do exist for other taxa. Jonsson and Jonsell (1999) showed that stand structure and the richness of taxa bearing high conservation relevance (lichens, plants, wood-rotting fungi and bryophytes) appeared to be poor *a priori* indicators of each other in Swedish boreal forests. Likewise, Similä et al. (2006) found that structural characteristics and plant richness somewhat reflected the richness of some invertebrate groups, but beetles very poorly reflected the richness of other taxa in Finnish boreal forests. Moreover, Sætersdal et al. (2005) showed that the degree of overlap in richness among six ecological groups, consisting of polypores, bryophytes and lichens, varied considerably from site to site in Norwegian coniferous forests. While discouraging, these results highlight the importance of using multiple taxa in environmental assessments (cf. Taylor and Doran 2001; Duelli and Obrist 2003; Paillet et al. 2009) and the absurdity of the idea of the existence of a single 'biodiversity indicator'.

Conservationists and managers generally agree in that protecting species diversity is a priority at global and national scales. At smaller spatial scales, however, richness may appear a misleading conservation measure without considering species identities. For example, Koivula and Spence (2006) showed that, in recently burned Canadian forests, logging increased the total richness of carabids due to the colonization of generalist open-area associated species. But simultaneously most closed-forest species decreased in abundance, the most drastic case being the over tenfold decrease of *Calosoma frigidum*, a tree-canopy caterpillar hunter (Larochelle and Larivière 2003). So, at the operational scale of individual forest stands, should the forest manager adopt the message obtained from total richness or that from species requiring closed forests?

Keystone indicators

A keystone indicator is a species, a group of species, or a structure that affects its environment and therefore other species disproportionately strongly relative to its abundance (Mills et al. 1993). The lack of a keystone indicator would thus lead to major changes in some other species' occurrence, abundance and/or distribution. A classic example from forested environments is the woodpecker fauna (Virkkala 2006). These birds produce nesting sites for secondary cavity-nesters, are important vectors for wood-rotting fungi, and may even regulate bark beetle infestations, thus bearing economic importance (Fayt et al. 2004). Carabids have intrinsic biodiversity value and unknown future potential, and they can also be considered invaluable on an ethical basis, but can they serve as keystone indicators? Evidence on the importance of carabids comes from agro-ecosystems, greenhouses and laboratories. Under laboratory conditions carabids forage efficiently on slugs and eggs, pupae, larvae and adults of pest insects (Kromp 1999). In the field, carabids indeed prey on pest invertebrates, such as slugs, aphids and mites (e.g., Allen 1979; Edwards et al. 1979; Hengeveld 1980a, 1980b; Luff 1987; Sopp et al. 1992; Bohan et al. 2001). Menalled et al. (1999) manipulated onion fly (*Delia antiqua*) pupae using exclosures in corn fields and found a positive relationship between carabid abundance and pupal death rates. But can the rates of foraging in the field be ecologically and/or economically important?

Hance (1987) used 1 m² enclosures with sugar beet and natural densities of aphids feeding on these plants, and released 0–30 individuals of *Anchomenus dorsale* and *Asaphidion flavipes* into these enclosures. Such densities (up to 30 ind.m⁻²) are common in the field (Lövei and Sunderland 1996). In enclosures without carabids, the density of aphids increased exponentially. At intermediate carabid densities, the aphid increase was delayed, and at high carabid densities the aphids often did not increase at all. It is easy to argue that this is ecologically and economically important, contrary to some 'statistically significant' 20–30% abundance changes. While this experiment can be criticized for using unrealistic, closed miniature systems, it shows that carabids have the potential for being economically important.

Carabids thus have the potential, but lack field-based evidence, for truly functioning as keystone indicators. Are carabids necessary for ecosystem functioning, and even if they are, could other taxa replace them if they are removed from an ecosystem? Currently there are no answers to these questions, but in many ecosystems carabids are accompanied by other abundant generalist invertebrates, such as ants, staphylinid beetles and spiders (Turnbull 1973; Bohac 1999). Carabids are, on average, larger than these three, which suggests a higher trophic level and per capita effect on, for example, crop-pest invertebrates. On the other hand, carabids are often vastly outnumbered or even excluded by *Formica* wood ants in Fennoscandian boreal forests (e.g., Koivula et al. 1999).

Pollution indicators

Pollution indicators reflect human-altered abiotic conditions in the soil, water and the air (Spellerberg 1994). Urban ecological studies might be considered in this category, with the combined role of e.g. pollutants, soil compaction and the 'heat island' effect (Forman 2008; Marzluff et al. 2008). Pollution affects humans directly, and as such has been studied widely for several decades using several taxa, of which lichens may be the most famous (Lindenmayer et al. 2000). Other pollution indicators, too, have been proposed but not without problems. For example, the mollusc *Velesunio ambiguus* was long considered an excellent indicator of heavy metals in aquatic systems until it appeared that this species' uptake of metals did not reflect the extent of pollution (Lindenmayer et al. 2000).

Carabids have been commonly studied to evaluate the ecological effects of industry emissions and agriculture chemicals. The below examples demonstrate the potential for carabids to also act as indicators of ecologically sustainable farming, environmental recovery and 'ecosystem health'. The utility of carabids as indicators in these cases relies on the inadequately tested assumption that other, often more severely threatened, taxa similarly respond to these pollutants and chemicals. This issue concerns the other indicator categories as well.

Several case studies all suggest that heavy metals in the soil significantly and negatively affect carabids (e.g., Ermakov 2004; Gongalsky et al. 2004; Belskaya and Zinoviev 2007). Moreover, cadmium and zink affect the growth and body caloric value of *Poecilus cupreus* individuals (Maryański et al. 2002). Carabids have also been used to assess the recovery of ecosystems after pollution events (e.g., Schwerk et al. 2006; Cárdenas and Hidalgo 2007).

In agro-ecosystems, pesticide and fertilizer impacts on carabids have been studied (e.g., Dritschilo and Erwin 1982; Basedow 1990; Kromp 1990; Larsen et al. 1996; Bourassa et al. 2008). Carabids respond negatively to dimethoate (commonly-used pesticide) sprayings but their numbers may recover within a few weeks (Huusela-Veistola 1996). Fertilizer and herbicide impacts have often been minor, but may affect carabids indirectly through changes in the vegetation (Kromp 1999).

Also cumulative impacts may appear common. For example, the intensity of carabid response to pollutants and chemicals depends on additional stressors, such as food scarcity and chemicals. Stone et al. (2001) studied adults of *Pterostichus oblongopunctatus* at a chronically polluted mining area in Poland. They collected individuals at sites with different levels of soil metals and subjected these beetles to food shortages and an insecticide (dimethoate) in the laboratory. Carabid death rates, caused by these stressors, were higher the more severely the collecting site had been contaminated by metals. To determine whether these responses were genetically based or resulted directly from soil contamination, Lagisz and Laskowski (2007) collected additional individuals at Stone et al.'s (2001) sites, and reared a second generation in the laboratory. These laboratory specimens were subjected to food shortages and the same insecticide, and results showed that the collecting site of the parent individuals had no effect on death rates of the second generation. Thus, the interaction was not genetically based in this case.

Recent advances in agro-ecosystems concern gene-manipulated (GM) or transgenic plants that can be considered 'genetic pollutants', as evidenced by the hybridization of native and GM corn in Mexico (Quist and Chapela 2000). GM techniques have been rapidly adopted into agriculture to increase the crop plants' pest and disease tolerance, yield and/or nutritional value, but manipulating the genetic material of these plants is suspected to lead to unwanted consequences (e.g., Dunwell 1999). For example, the use of GM plants might directly or indirectly affect non-target organisms, including carabids. Non-target invertebrates were generally little affected by GM corn and cotton, as compared with non-transgenic versions of these plants, but were more affected by the use of pesticides (Marvier et al. 2007). Similarly, GM crops had a minor effect on adult carabids locally (Lopez et al. 2005; Szekeres et al. 2006; Floate et al. 2007). However, Waltz (2009) summarized the effects of GM crops on insects and reported drastic effects on, e.g., butterfly larval death rates. Hence, experiments on the larval development of seed-eating carabids in GM and conventional crop fields would significantly contribute to this area of research.

Dominance indicators

Dominance indicators make up much of the total biomass or the number of individuals in an area of interest (Lindenmayer et al. 2000) and predict particular ecosystems or assemblages. For example, certain tree species form much of the biomass and broadly reflect habitat type in forests. Similarly, carabid dominance indicators should reflect particular habitat types, degrees of disturbance and ecosystem recovery, hot-spots of rare species or particular habitat types of conservation interest. The use of carabids in this sense has faced certain difficulties that might be overcome.

Invertebrates are seldom used in environmental assessments because of the high expertise required (Andersen 1999; but see Andersen and Majer 2004). While strongly advocated here (see "Carabids as model organisms"), species-level approaches usually require considerable investments of expertise, time and money into education, sampling and analysis (Langor and Spence 2006). Hence, in rapid biodiversity assessments (e.g., Ward and Larivière 2004), numerical or biomass dominance might be alternative options.

Niemelä (1993b) showed that boreal-forest carabid assemblages consist of a few abundant (easily identifiable) and several scarce (often more difficult to identify) species. In these forests, early successional phases can be numerically dominated by *Pterostichus niger*, while closed phases are often dominated by *Calathus micropterus* (e.g., Koivula et al. 2002). However, as these species are generalists of forest succession (Niemelä et al. 2007) and occur in many forest types (Lindroth 1985, 1986), their presence may not indicate aspects useful for conservation or management.

Carabid body size has been linked to certain ecological processes, such as urbanization and succession (e.g., Magura et al. 2006b). The Mean Individual Biomass (MIB) approach requires only sampling, counting, weighing and using a simple equation developed by Szyszko et al. (2000). MIB is predicted to increase along gradual successional changes in vegetation that subsequently alters the carabid fauna, from smaller open-habitat (*Amara, Bembidion*, etc.) to larger closed-forest (*Carabus, Cychrus*, etc.) species (Szyszko et al. 2000). An increase in MIB should thus indicate conditions approaching late successional stages.

MIB is advocated as an easy tool for policy makers to assess the state of the environment. The method assumes a linear relationship between MIB and time since disturbance, which seems to hold through early successional phases, during which the carabid fauna changes rapidly (Szyszko et al. 2000; Koivula et al. 2002). However, at least in boreal spruce forests the carabid assemblage structure – and consequently MIB – changes little between 30 and 100 years following clear-cutting (Koivula et al. 2002; M. Koivula unpubl.), suggesting a plateau in the trend. For forests older than

100 years, MIB might even decrease, as these 'old growth' phases are characterized by disturbances that create new habitat for species associated with tree-canopy openness. In forests, these disturbances include falls and deaths of single or small groups of trees (Esseen et al. 1997; Bouget 2005; Skłodowski 2007). The 'behavior' of MIB warrants further research before applying it in conservation and management, but it may already have potential in landscape-level assessments.

Environmental indicators

An environmental indicator reliably reflects particular environmental conditions in soil quality, moisture, flooding regime, and so on (Klinka et al. 1989). Plants in particular have been widely used as indicators of e.g. soil quality, water levels, habitat types and, based on Christen C. Raunkiær's growth-form descriptions, biomes (Begon et al. 1996). Although carabids also have the potential to reflect soils, wetness and habitattype variation, they cannot currently compete with plants as environmental indicators for these factors.

Carabids efficiently reflect environmental variation, and bear indicator potential at various spatial scales. For example, variation in soil conditions within a few meters affected farmland carabid diversity in England (Sanderson et al. 1995). At larger scales, distinctive carabid assemblages are found at lake, river and sea shores, bogs and mires to very dry habitats (e.g., Lindroth 1961–1969, 1985, 1986; Larochelle and Larivière 2003), temporary wetland pools (e.g., Uetz et al. 1979; Brose 2003; Gerisch et al. 2006; Follner and Henle 2006) and in dry and sandy heathlands and grasslands (e.g., Vermeulen 1993; Magura and Ködöböcz 2006).

Carabids have occasionally been used as environmental indicators. Eyre and Luff (1990) attempted to classify European grassland habitats using carabids. They sampled 638 sites in Northern and Central Europe and distinguished 17 grassland types that were often shared among several countries. Likewise, Eyre et al. (1996) and Eyre and Luff (2002) classified riverside habitats using carabids. They distinguished several site groups, each with distinctive structural characteristics and associated carabid species. The value of carabids here is that they produced different but equally correct site classifications as compared with traditional, vegetation-based approaches.

The above examples concern relatively stable conditions, but carabids might be useful also in assessing *changes* in conditions (see "Early warning indicators") due to the ability of many species to disperse by flying. For example, the first colonizers appear within a few weeks or months following forest fires (e.g., Burakowski 1986; Koivula et al. 2006). Fragmentation provides a particularly promising framework in this sense. Due to fragmentation, similar-looking habitat patches vary in size and isolation, which might be reflected by the proportion of winged and wingless individuals. West European carabids have been classified based on their habitat affinity and ability to disperse, and these traits predict population extinctions and colonizations in fragmented heathland networks quite well (Turin and Heijerman 1988; Turin and den Boer 1988; Desender and Turin 1989; den Boer 1990b; de Vries et al. 1996).

Early warning indicators

Early-warning signalers are extremely sensitive to changing environmental conditions (Lindenmayer et al. 2000). Conditions of interest are often at large spatial scales, such as fire, climate, or the spread of urban areas. Species in this category are often referred to as true 'bio-indicators'. What is the evidence for carabid functioning as early warning indicators?

Many studies have documented changes in carabid assemblages due to drastic habitat alterations caused by forestry, wildfire, grazing, fertilization, fragmentation and so on (for reviews, see Luff 1987; Lövei and Sunderland 1996; Kromp 1999; Niemelä et al. 2007). For example, carabid responses to clear-cut harvesting are usually detectable within 1–3 years (e.g., Niemelä et al. 1993; Koivula 2002a). Of course, these responses may not always be clear and other taxa may more readily respond to changes in habitat quality (e.g., Matveinen-Huju et al. 2009), emphasizing context specificity of indicators. Another problem is that in many of these studies carabids did not truly indicate condition alterations before they became visually obvious, thus did not act as early warning indicators.

Climate change has dominated headlines for the past 10–15 years. High-impact journals have eagerly printed research on the climate responses of butterflies, frogs and birds (e.g., Parmesan et al. 1999; Pounds et al. 1999; Cotton 2003; Hüppop and Hüppop 2003). Carabids, too, reflect changes in climatic conditions but the rate of change in their distributions is largely unknown. Butterfield (1996) showed that carabid samples collected at 450 and >800 m a.s.l. were different, and Ashworth (1996) found fossil remains to indicate that the carabid fauna 10 000 years ago was different from the current fauna at the same sites. Preliminary results of two European studies suggest that carabids have moved tens of meters in altitude in the past 10–20 years (Assmann 2009; Pizzolotto 2009), coinciding with the general predictions of climate warming (Parry et al. 2007). Climate change possibly also interacts with other environmental factors, such as those associated with urbanization. For example, Bednarska and Laskowski (2009) showed that the death rate of larvae of *P. oblongopunctatus* was significantly affected by a combination of temperature and soil nickel content.

Disturbance and management indicators

Disturbance indicators reflect natural and human-caused disturbances (Milledge et al. 1991), whereas management indicators reflect human efforts in decreasing the biological impact of these disturbances (e.g., Günther and Assmann 2005). Again their usefulness relies on the assumption that what is detected by the indicator is similarly

affecting other, often threatened, taxa. In forestry, for example, several taxa respond to cutting of live trees in similar ways (see Barbaro et al. 2005): openness-associated species increase and closed-canopy specialists decrease, as have been shown for boreal ground-dwelling carabids (Niemelä et al. 1993; Koivula 2002a), plants (Jalonen and Vanha-Majamaa 2001) and birds (Koivula and Schmiegelow 2007). Although the indicator functioning clearly holds at this general level, whether these taxa function as indicators of each other in terms of spatial overlap (their predictive accuracy) is yet to be evaluated. Additional problems are many: for example, rare and threatened species may also respond to factors other than live-tree removal, such as the retention of snags or single live and dead trees (e.g., Kaila et al. 1997; Martikainen 2001). Results on epigaeic fauna sampled using pitfall traps may not necessarily apply to species associated with dead wood (but see Work et al. 2008) or canopy dwellers.

Structure-based disturbance (and environmental) indicators are commonly used for practical purposes. For example, in Fennoscandian and British forests, the quality and quantity of live and dead trees, certain biotopes, and signs of forestry are used together to indicate forests of high conservation priority, such as old-growth forests (Hallman et al. 1996; Angelstam 1997; Humphrey and Watts 2004; Hakalisto et al. 2008). These variables reflect rare habitat types, which are crucial for threatened forest species (e.g., Rassi et al. 2001; Gärdenfors 2005). Preliminary results on threatened polypores in Southern Finnish forests suggest that these structure-based indicators allow an efficient identification of stands of high conservation value (Juha Siitonen and Reijo Penttilä, Finnish Forest Research Institute, unpubl.). Could boreal forest carabids reflect variation relevant for conservationists and managers?

Carabid sensitivity to environmental variation suggests good potential here. The early phases of forest secondary succession are characterized by a different set of species than are the later phases with a closed tree canopy (e.g., Niemelä et al. 1993, 2007; Spence et al. 1996; Beaudry et al. 1997; Abildsnes and Tømmerås 2000). Carabids also respond differently to different logging regimes. Compared to unharvested stands, thinning (10-30% removal of trees) affects carabids only marginally, cutting small gaps (diameter 30-50 m) has variable impact, and clear-cutting causes open-area and succession-generalist species to increase and closed-forest carabids to decrease (e.g., Koivula 2002a, 2002b; Vance and Nol 2003; Work et al. 2004). Suggested closed-forest specialists are many but views may change with time: Halme and Niemelä (1993) proposed Carabus glabratus, C. violaceus and Cychrus caraboides to be such, but fifteen years later only the latter remained in this list (Niemelä et al. 2007). The reason is not rapid evolution but an accumulation of ecological knowledge. Finnish spruceforest carabid assemblages change remarkably during the first 20-30 years following clear-cutting, but not much after that, as samples from 60- and 100-year old forests are relatively similar (Koivula et al. 2002; M. Koivula, unpubl.). These carabids thus reflect canopy closure for sure, but the usefulness of this information in conservation and management is obviously low.

Perhaps particular boreal species would be useful indicators? *Platynus mannerheimii* is a suggested old-growth forest spruce-mire specialist (Lindroth 1986; Niemelä et al. 1987,

1993; Gärdenfors 2005; Paquin 2008). However, this species has also been found in 60year old regenerating stands (Koivula et al. 2002) and along roadsides (Koivula 2005), indicating more flexibility in habitat use and/or dispersal ability than previously thought. Even if this species reliably indicates mire patches worthy of special attention in forestry, such sites are easier identified using structural characteristics and vegetation (Hakalisto et al. 2008). At first glance Finnish forest carabids may not appear specialized enough for conservation and management purposes. This view may appear premature, however: attention could also be paid to the abundances/proportions of potential indicators rather than solely to their presence/absence (see "Identifying and using carabid indicators").

The message here is not that carabids would generally be useless management indicators, but rather that in the particular context of boreal managed forests, with the present state of knowledge, they are not useful. Indicator usefulness should be evaluated separately, depending on the context, for other habitat types, management questions or geographic areas and so on. In Western and Eastern Europe, the carabid fauna of ancient woodlands (forests covered by mature trees continuously at least since the end of the 18th century) differs from that of managed forests (Assmann 1999; Magura et al. 2002, 2003; Desender 2005; Skłodowski 2006; see also Davies and Margules 1998), and Carabus variolosus may indicate conditions characteristic for swamps and brooks of ancient woodlands (Matern et al. 2008). Geographic and/or habitat-type differences in carabid responses are common. For example, across grassland/closed-forest edges in Hungary, the grasslands, edges and forests hosted distinctive carabid assemblages (Magura et al. 2001; Lövei et al. 2006), but across clear-cut/closed-forest edges in Finland, edges differed from clear-cuts but were similar to the forest in this respect (Heliölä et al. 2001). A given species may also occur in different habitats in different regions (see discussion in Koivula et al. 2006).

Identifying and using carabid indicators

Sketching a road map for detecting useful indicators

Collecting data easily and cheaply, and then using these data to generalize about entities worth special attention, is an appealing idea. Indicators are more and more commonly applied in conservation and management through years of research (Meffe and Carroll 1997). Examples include the uses of habitat structure for identifying forests of high conservation value (Hakalisto et al. 2008), vegetation for identifying habitat types (Klinka et al. 1989) and ants for assessing effects of land management (Andersen and Majer 2004). Carabids have not yet been commonly incorporated into assessments of environmental change, biomonitoring programs, or protocols for identifying sites of high conservation value. Carabids are nevertheless promising candidates for these purposes. Instead of investing resources in finding completely new indicators, we should (1) identify a selection of easily-sampled and ecologically well-known taxa that cover multiple dimensions of biodiversity, and (2) critically evaluate their indicator functioning (Langor and Spence 2006).

Carabids have seldom, if ever, been used or even considered as indicators by conservationists and managers. This may result from (a) carabids being less appealing and charismatic than many hairy/feathered and large-eyed vertebrates; (b) carabids being inconspicuous and therefore easily overlooked by an untrained person; (c) the idea that protecting larger species with larger home ranges would simultaneously secure the well-being of smaller species (the umbrella species concept; see Simberloff 1998); and (d) carabids being uninteresting generalists that are laborious to collect and difficult to identify compared to, e.g., vegetation characteristics of a focal patch. This state of affairs can be changed, but it requires advertising campaigns (such as the Jakhalzen show about the XIV ECM on Dutch television on the 2nd of October 2009) and detecting a 'niche' for carabid use as indicators. For the latter goal it is important to increase knowledge about biodiversity covariation, to develop large-scale sampling networks, to develop and test easy-to-use approaches, and to initiate databases for life-history and indicator-concept information about carabids, including data on taxon overlap.

There is an urgent need for clarifying the abundance and response relationship between carabids and other taxa before using carabids in environmental assessments. Correlations between focal taxa are not enough for judging the adequacy of the proposed indicator – spatial and temporal overlapping, predictive power and error estimates must also be evaluated (see "Indicator hunt: common sense revisited").

Indicators need not be used to identify the obvious: for example, the conservationist does not need carabids to decide whether a clear-cut forest has experienced a considerable environmental change. More useful information in this example would be, e.g., how precisely species, functional groups and/or relative abundances of carabids reflect rare species. But conservationists and managers very often sample only at the focal site to decide whether the site is worth protecting. For such purposes, the assessment is difficult to do by using abundance and compositional data, because the composition is never stable due to factors of interest mixing with e.g. species-specific temporal variation. This difficulty might be overcome by defining limits for 'natural' variation in the indicator's abundance or proportion, which requires detailed information about population dynamics and thus long-term sampling in varying conditions (see "Carabids as model organisms").

The accumulation of knowledge may change how we see species, and thus relying on a single study may be a poor strategy. This is particularly important in selecting indicators, because the use of an inappropriate indicator may cause severe conservation and economic harm (Baker and Schonewald-Cox 1986). Species classifications based on only one or a few studies to derive habitat associations perpetuate a view that any species is a specialist (of 'open' or 'closed' canopy, for instance). As "Disturbance and management indicators" showed, this issue is not that straightforward. Carabids often occur across wide sections rather than at strictly delimited points of the multi-dimensional environmental space, and case studies seldom capture this pattern. Commonly-shared frameworks to keep track of the knowledge about habitat associations and other life-history variables, as ecological studies accumulate, are lacking but would be useful for indicator purposes.

An extensive use of assemblage composition as indicators may require reference sites. Concretely, this could mean a carabid equivalent of the Finnish National Forest Inventory (www.metla.fi/ohjelma/vmi/info-en.htm): a large-scale, long-term, reference sampling network. The first step towards a national protocol might be to establish smaller networks at areas with most critical conservation situation. The often remarkable variation in assemblage composition between adjacent, similar-looking sites, even within a given patch (Niemelä et al. 1992; den Boer 2002), suggests that such networks must be very dense and use high sampling effort. Volunteers could perhaps be used here to ease the work load of professionals. Moreover, the establishment and proper use of such networks involve high sampling-design and taxonomic expertise. Therefore, the development of simple, quick and cheap indicators (such as body-size based) should also be among the priorities. But how to concretely collect data relevant for conservationists looking for useful indicators?

Indicator hunt: common sense revisited

One of the basic issues is to clarify whether the researcher uses her/his favorite taxon as an indicator or simply as a model organism. To evaluate the indicator potential of carabid beetles, the following tips may be useful.

- 1. Define *a priori* what you would like (carabids) to indicate, i.e., state an assessment goal (Simberloff 1998; Caro and O'Doherty 1999).
- 2. Clearly define the aims, methods and appropriate spatial scale *a priori* (Underwood 1997; Duelli and Obrist 2003).
- 3. Experimentally test the functioning of the potential indicator (Mayo 1997; McGeoch 1998; Caro and O'Doherty 1999; Langor and Spence 2006).
- 4. Sample long enough, preferably for a number of years, to account for variation in temporal abundance and diversity (Lövei and Sunderland 1996).
- 5. At each study patch (replicate), sample extensively to cover multiple local populations (den Boer 2002) and within-patch variation.
- 6. Through analysis and critical interpretation of the data, explicitly state the specific entities and conditions the indicator reflects.
- 7. Identify and define sources of subjectivity (Landres et al. 1988; Caro and O'Doherty 1999).
- 8. The validity of the indicator should be evaluated independently.
- 9. Even if found successful, use the indicator only if other assessment options are unavailable (Landres et al. 1988; Lindenmayer et al. 2000).

Of course, the appropriateness of an indicator can be tested in many ways. There is room for descriptive studies in evaluations of spatial and temporal overlap between taxa, but otherwise experiments are crucial. Comparisons of replicated, unaltered controls with other treatments or collecting multiple samples along environmental continuums may prove useful. Replicate treatments not just samples (Hurlbert 1984). An example may clarify these issues. Assume you are interested in the impact of a fertilizer on meadow biodiversity, and you would like to study if carabids respond to the added fertilizer as an early warning indicator, i.e., before it can be detected by inventorying plants. You might have a reason for expecting some carabid species to be able to do so (see Merivee et al. 2006). You decide to explore slight differences in assemblage composition using pitfall traps.

The study can be done by sampling, for example, (i) several treated (fertilizer added) and untreated (no fertilizer added; control), randomly-assigned sub-plots within one or a few meadows. Such a protocol would be suitable for detecting small-scale phenomena, such as variation within meadows; (ii) several (say >10) meadows treated with different levels of the fertilizer. This protocol might be fine for assessing threshold conditions by using non-linear regression modeling to evaluate, e.g., if the threshold of abundance change occurs earlier for carabids than for plants; (iii) multiple meadow pairs of which one is treated and the other is not; or (iv) separate, treated and untreated meadows (see, e.g., Underwood 1997).

Assume that you end up using the last-mentioned option. A convincing demonstration of your case would require at least the following.

- a. Select meadows that are initially as similar as possible but still distinctive.
- b. Establish at least 3–4 treated and 3–4 untreated meadows to be able to calculate means and variances for both. The more meadows the better, as more natural variation will be covered and the more precise the estimate of mean. If possible, sample before and after the addition of the fertilizer to better account for initial variation (Underwood 1992). Concerning your study question, these meadows (not traps in them, irrespective of how they are placed) are your replicates: you are interested in a phenomenon that scales to variation between meadows.
- c. Spatially distribute your replicates evenly. They should not form treatment-specific clusters.
- d. The replicates should be separate, i.e., unlikely to affect each other ecologically. Sections of different habitat types between your study meadows help convince your colleagues that the meadows are indeed ecologically independent from each other.
- e. Synchronize the sampling, i.e., sample at every meadow over the same period.
- f. Collect multiple samples from each meadow (see point 5 above).
- g. Sample over a period long enough to representatively collect carabids, and also to see if the plant assemblage responds to the treatment. If the plants, or any other taxa other than carabids, do not respond to the treatment, you have failed to find an early warning indicator, whatever your result for carabids. The follow-up may easily take several years to produce useful information.

A lack of proper replication is surprisingly common in ecology, considering the amount of literature on this issue. In the above example, you might have selected only one treated and one untreated meadow and set 10 traps in each, perhaps 15–20 m apart for sample independence (Digweed et al. 1995). But you would then have no replication

for the factor of interest, viz. the addition of fertilizer, which operated at the meadow scale. As a solution you might treat each trap as a replicate in your analysis, but you would then introduce pseudo-replication because samples from a given meadow are inter-dependent through ecological interactions between the plots with traps (Hurlbert 1984). Likewise, in a laboratory experiment with two cages (control and treatment), you might consider each individual in a cage a replicate, but you would have difficulty to convince others that it was not some characteristic of the cage that produced the result. Another example is to use spatially clumped treatments: here, clusters of meadows with similar treatment. Now, underlying environmental gradients or local conditions could drive the result, not necessarily the fertilizer addition. Similarly, you should not compare moist Dutch meadows with dry Belgian meadows if your aim is to study the effect of moisture on carabids. The only exceptions for not properly replicating treatments concern studies on exceptionally rare (or dangerous) taxa, habitat types or phenomena.

Suggestions for further research

Carabidologists have much to contribute to indicator studies. First of all, the researcher must adopt the conservationists' view on what is an indicator. Second, the research must be properly carried out (see "Indicator hunt: common sense revisited"). Third, if the results suggest that carabids reliably reflect variation of high conservation relevance, the researcher should describe (i) the variables of the assemblage that best reflect this variation, (ii) the study conditions (context), (iii) the precision and accuracy of carabids in reflecting this variation based on, e.g., percent overlap, peak difference and confidence intervals, and (iv) the species or conditions that could not be easily observed without using carabids. Fourth, as the carabid ecological literature is vast (see "Carabids as model organisms"), and to increase the power of analyses, carabidologists should move on from two-tailed null hypothesis testing toward routinely formulating explicit, directional hypotheses – not just in indicator research but in modeling biological phenomena in general.

The various indicator categories ("Evaluation of carabids as indicators") provide potential for developing powerful management and conservation tools. Taxon, pollution, environmental and management indicators might be found by moving on from applying total richness toward using single-species abundances or their morphological/ genetic variation, groups of specialists, functional groups, or structural characteristics of assemblages (as reflected by, e.g., affinity indices; Magura et al. 2006a; Déri et al. 2010). A different way to approach the indicator issue might be to study if the presence of certain species would indicate the *lack* of conservation values at a given site ('negative indicators'). Keystone indicators, on the other hand, might be found through experiments with multiple trophic levels and manipulated abundances of potential competitors.

Early warning indicators are trendy because of their potential in assessing largescale environmental alterations, but the concept could also be examined through ecological interactions and at smaller spatial scales. For example, responses of carabids to changes in combinations of temperature, soil chemistry and/or expansion of urban areas may be fruitful (see Knowlton and Graham 2010). The micro scale appears equally promising: carabids are physiologically extremely sensitive to sugars, salts, amino acids, pH and temperature (Merivee et al. 2004, 2005, 2008; Must et al. 2006). Thus, physiological alterations due to changes in these factors might function as early warning signals of currently minor environmental variation, such that cannot be observed by visual inspection of the environment. Some of these aspects could also be explored using affinity indices.

Conclusions

No two species can precisely reflect each other, and one must be prepared for uncertainty and error when using an indicator. The competitive exclusion principle (Hardin 1960) postulates that members of a guild must be ecologically at least slightly different from one another to co-occur in terms of e.g. population dynamics, habitat and foraging requirements, aspects of reproduction and environmental grain size. Defining acceptable imprecision is a political question, but research can only determine confidence limits.

Indicators are assessment tools intended to be used in situations when habitats and species are lost, or conditions altered. Because humans will continue to utilizing the environment, some decrease in habitat area and, at some locations, quality is inevitable: biology competes with economics and social issues in policy. Detecting areas or sites of high conservation value assists in defining conservation priorities. Still, the conservationist may have to ask whether her/his statistically significant result is biologically or economically important, or whether a non-significant result is irrelevant. For example, if threatened or rare species are involved, the precautionary principle should apply (e.g., Haag and Kaupenjohann 2001): if a particular environmental impact is under evaluation, statistical non-significance should not be considered equal to no effect or zero difference (McGarvey 2007), and an indicator should be allowed to provide occasional 'false positives'. The latter is important in protecting metapopulations, with both occupied and presently unoccupied habitat patches being necessary for the long-term persistence of an organism (Hanski 1999). Likewise, within a given area, local populations of carabids may differ in their reproductive capacity and other qualities, and consequently fluctuate partly independently (e.g., den Boer 2002).

To be useful in conservation, an indicator must have high and consistent predictive power that relates to particular conditions and/or rare species. We still lack the first clear-cut case showing carabids to reliably predict entities of high conservation and management interest. To fill this gap, (a) knowledge on the relationship between carabids and other taxa must be greatly increased, and (b) strict tests must be applied to evaluate indicator functioning as outlined above. We should soon be able to define a 'niche' for carabids in environmental assessments. Cases of carabids fulfilling criteria to be useful indicators will possibly be documented in the near future, but the indicator functioning of particular taxa may always remain context specific.

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RESEARCH ARTICLE



Model of succession in degraded areas based on carabid beetles (Coleoptera, Carabidae)

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Abstract

Degraded areas constitute challenging tasks with respect to sustainable management of natural resources. Maintaining or even establishing certain successional stages seems to be particularly important. This paper presents a model of the succession in five different types of degraded areas in Poland based on changes in the carabid fauna. Mean Individual Biomass of Carabidae (MIB) was used as a numerical measure for the stage of succession. The run of succession differed clearly among the different types of degraded areas. Initial conditions (origin of soil and origin of vegetation) and landscape related aspects seem to be important with respect to these differences. As characteristic phases, a 'delay phase', an 'increase phase' and a 'stagnation phase' were identified. In general, the runs of succession could be described by four different parameters: (1) 'Initial degradation level', (2) 'delay', (3) 'increase rate' and (4) 'recovery level'. Applying the analytic solution of the logistic equation, characteristic values for the parameters were identified for each of the five area types. The model is of practical use, because it provides a possibility to compare the values of the parameters elaborated in different areas, to give hints for intervention and to provide prognoses about future succession in the areas. Furthermore, it is possible to transfer the model to other indicators of succession.

Keywords

Carabidae; degraded areas; logistic equation; Mean Individual Biomass (MIB); succession

Introduction

Nowadays, there is a rising awareness of our natural resources. Management of natural resources seems to be a key element of sustainable development. Among the many types of ecosystems and habitats, degraded areas have acquired special importance, particularly with respect to restoration measurements. A crucial aspect of many degraded areas seems to be a serious loss in biodiversity (Dobson et al. 1997). Consequently, the improvement of habitat conditions in degraded areas is often required to restore or maintain animal and plant communities. Careful management of successional stages is important with respect to the future development and faunal and floral post-disturbance recovery (e.g. Bradshaw 1984; Tilman 1987; Jochimsen 2001). This may imply the facilitation or inhibition of the successional process (e.g. Bradshaw 1983, 1984; Dobson et al. 1997). To carry out restoration efforts in an ecologically sound way, knowledge about processes of succession in degraded areas is obviously necessary.

Numerous publications focus on the mechanisms and phases of successional processes. Alternative pathways of succession are described in the models of Connell and Slatyer (1977) and Abrams et al. (1985). Drechsler et al. (2009) describe a disturbancesuccession model combined with a reserve selection algorithm as a tool for conservation planning. Complex mathematical models of succession are DRYADES (Mailly et al. 2000) and LANDIS (He et al. 2005; Scheller et al. 2007). However, for practical applications often more simple models are needed, which require relatively little effort in terms of data input.

The aim of this paper is to present a simple model established by Schwerk (2008), which allows for a description and comparison of the successional process on different types of degraded areas. The model will be constructed in two steps. Firstly, based on comprehensive field studies the basic parameters of succession in degraded areas will be extracted and a conceptual model will be described. Since carabid beetles are sensitive to alterations of environmental conditions (Rainio and Niemelä 2003), changes in carabid beetle fauna will be used as indicator of the succession process. In a second step these parameters will be specified mathematically. Thus, it will be possible to quantitatively express differences in succession between different types of degraded areas.

Methods

Elaboration of field data

Field data were collected at five different types of degraded areas in Poland, namely planted stands on forest soil, naturally regenerated stands on post-agricultural soil, planted stands on post-agricultural soil, planted stands on a heap of ashes produced by a power station and planted stands on a brown coal mining heap. All of these areas may be regarded as being degraded due to intense forestry or agriculture in the past or due to their anthropogenic origin. This results in decreasing timber, ineffective crop cultivation or difficulties with respect to restoration measures.

The differences in type of area (origin and soil properties) as well as origin of the vegetation constitute initial conditions for succession. The assumption was made that these differences will cause different succession trajectories. Thus, distinct phases of succession will occur, which are characterised by differences in the speed of succession for the different area types.

Study sites of different age were selected for each of the area types. On forest soil 14 study sites with an age ranging from 21 to 119 years were established. On postagricultural soil 13 study sites characterised by natural regeneration of pine with an age ranging from 0 to 64 years and 69 study sites on which pine was planted with an age ranging from 2 to 119 years were studied. On the ash heap 3 study sites with an age ranging from 8 to 14 years and on the mining heap 4 study sites with an age ranging from 3 to 23 years were established.

Beetles were collected from 2004–2006. Thus, for each study site three datasets of consecutive age were produced. In each year sampling was done during the whole vegetation period using pitfall traps (Barber 1931). Since the study sites differed significantly in size, different numbers of pitfall traps were installed. A detailed description of the study sites and the sampling design is provided by Schwerk (2008) (for a detailed description of the study sites see also Appendix I: Description of the study sites).

In the study sites on forest soil and post-agricultural soil, sampling took place from mid May to mid September, and for study sites on the ash and mining heaps, the sampling periods were mid April to mid October (2004) or the end of April to mid October (2005 and 2006), respectively.

Statistical analysis

Mean individual biomass (MIB) of Carabidae (Szyszko 1990; Szyszko et al. 2000) was applied to assess the stages of succession. MIB is calculated by dividing the biomass of all sampled carabids by the number of specimens caught. According to the observation that in habitats of advanced stages of succession carabid species with large individuals become dominant, MIB increases as succession progresses. An inverse relationship between body size of carabids and degradation of habitats has been demonstrated by several authors (e.g. Blake et al. 1994; Magura et al. 2006). MIB has already been applied successfully in different European countries (e.g. Szyszko et al. 1996; Serrano and Gallego 2004; Schwerk et al. 2006; Cárdenas and Hidalgo 2007).

MIB becomes inaccurate with decreasing numbers of individuals. Therefore, MIB values calculated from samples with less than 25 individuals are indicated in the figures.

Correlations between MIB values and age of the study sites were tested using the Spearman rank correlation coefficient (Sachs 1984).

Results

MIB values

Based on a total of 23,602 individuals of carabid beetles, MIB values were calculated for the various study sites. Fig. 1 shows the relationship between the MIB values and age of the study sites for the different types of degraded areas.

At stands on forest soil (Fig. 1A) MIB values range from about 50 mg to about 700 mg. Despite some variability, which may be due to the fact that most values were calculated from less than 25 individuals, values are generally high. Even if young study sites were not included in the study, there is a significant increase of MIB with age of the stands (Spearman rank correlation coefficient, p < 0.05). At an age of about 20–40 years, MIB values were at about 300 mg, but in very old stands, values were above 400 mg (mean).

The naturally regenerated stands on post-agricultural soil (Fig. 1B) show values from about 50 mg to about 400 mg. The significant increase of MIB values with age of stands (Spearman rank correlation coefficient, p < 0.001) was comparatively even. At very young age, MIB values were below 100 mg, at an age between 5 and 10 years they were about 100 mg, at an age of about 25 years they were about 200 mg, and at an age of about 250 mg.

Concerning planted stands on post-agricultural soil (Fig. 1C) MIB values range from about 50 mg to about 600 mg. There is only one exception (MIB >1,000 mg). Here, MIB values increase significantly with age of stands (Spearman rank correlation coefficient, p <0.001). Despite high variation within the data a rapid increase during the early phase is visible. At very young age, some MIB values exceed 100 mg and at an age of 10 years some values already exceed 200 mg. However, after about 20 years of forest age MIB values seem to stay at a constant level (a mean of about 250 mg).

On the ash heap (Fig. 1D) almost all MIB values are below 80 mg up to a forest age of almost 15 years, which indicates a delay in succession. The one exception, with a value of about 120 mg, was calculated based on less than 25 individuals. Here we observe no correlation between MIB values and age of stands (Spearman rank correlation coefficient, n.s.).

At the mining heap (Fig. 1E) values range from below 50 mg to about 250 mg. Up to about 15 years of forest age all values fall far below 100 mg, indicating a delay in succession. A significant increase of MIB values with age of stands can be observed (Spearman rank correlation coefficient, p < 0.001), mainly due to an increase at about 15 years.

Construction of a conceptual model

Despite remarkable variability for some of the types of study areas, characteristic differences between the area types can be observed. In advanced stages of succession MIB values were highest in planted stands on forest soil and lowest on the brown coal min-



Figure 1. Relationship between MIB values (mg) and age of stands in **A** planted stands on forest soil (r = 0.343, p < 0.05), **B** naturally regenerated stands on post-agricultural soil (r = 0.677, p < 0.001), **C** planted stands on post-agricultural soil (r = 0.238, p < 0.001), **D** stands on ash heap (r = 0.025, n.s.) and **E** stands on mining heap (r = 0.839, p < 0.001) (Open circles indicate that MIB was calculated from less than 25 individuals).

ing heap. Planted stands on post-agricultural soil show a much faster process of succession during the early phase compared to naturally regenerated stands on the same soil type. The post-industrial areas are characterized by an initial delay of succession. These differences suggest that the initial conditions (origin of the soil, origin of the vegetation) indeed seem to be important parameters determining the future trajectory of succession. However, the high variability, particularly in the post-agricultural areas, implies that other parameters are important, too. Especially landscape-related aspects, e.g. distance from resource habitats of colonizing species, may play a role. E.g., Koivula et al. (2002) showed that the degree of heterogeneity of forest landscapes affects the catches of forest carabids.

Based on these results the process of succession may be simplified to the following elements: An 'initial degradation level', a possible 'delay phase' in the beginning of succession, a more or less 'steep' phase of progress of succession ('increase phase') and a convergence to a kind of 'recovery level'.

Fig. 2 presents a model integrating the different factors and phases. The important factors are type of area (particularly soil characteristics) and origin of vegetation, but also landscape-related aspects (sources for settling species, etc.) may have a reasonable impact (Schwerk 2008). The 'initial degradation level' should depend on area type, type of treatment before degradation and type of degradation. At the 'initial degradation level' there might be a 'delay phase', depending on the type of area to a high degree, but also on the treatment (origin of vegetation) and surrounding landscape. An important characteristic of the 'delay phase' is its duration. The subsequent 'increase phase' is characterized by its speed, i.e. the steepness of the curve. It should be influenced by similar factors as the 'delay phase'. Finally, we may define a 'stagnation phase' in which the succession process runs towards the 'recovery level'. The 'recovery level' may be identical to the predisturbance level (Majer 1989). As important factors influencing the 'recovery level', soil types and surrounding landscape may be assumed.

Quantification of the model

A quantification of the model can be done using MIB to represent the state of succession. For the construction of a quantitative model it is necessary to comprise mathematically (1) the 'initial degradation level', (2) the possible 'delay' in succession, (3) the 'increase rate' (acceleration), and (4) the deceleration or 'recovery level'.

The logistic equation (Eq. (1)) has been frequently used to describe growth processes, for example growth of populations (e.g. Begon and Mortimer, 1986; for a review on logistic growth models see Tsoularis and Wallace, 2002).

$$dN/dt = rN(K-N)/K \tag{1}$$

Taking into account parameters 1, 3, and 4 mentioned above, the logistic equation may be useful to describe the process of succession observed in the study sites. *N* may



Figure 2. Schematic illustration of the model. Succession starts from an 'initial degradation level', followed by a facultative 'delay phase' (characterized by the time of 'delay'). The optional 'delay phase' is followed by an 'increase phase' (characterized by the 'increase rate'), and a 'stagnation phase' in which the succession process runs towards a 'recovery level'. The type of area, origin of vegetation, and landscape-related aspects are assumed to influence the trajectory of succession.

be regarded as the state of succession defined by the 'initial degradation level', r may be regarded as 'increase rate', and K as 'recovery level'. An additional parameter has to be included, however, which describes a possible 'delay' at the beginning of the successional process (parameter 2).

To receive exact results the analytical solution of Eq. (1) must be used, which is provided by Wissel (1989) as follows:

$$N = e^{rt}c/(1 + e^{rt}c/K) \tag{2}$$

with

$$c = N(t=0)/(1-N(t=0)/K)$$
(3)

To describe the 'delay', a 'starting time' $t_{start} = 0$ and a 'delay time' t_{delay} will be defined. Further we define:

$$t = t_{\text{start}} - t_{\text{delay}} \tag{4}$$

At t < 0 the value of N remains at the 'initial degradation level', whereas at t >= 0 the analytical solution (Eqs. (2) and (3)) is valid.

Applying Eqs. (2), (3) and (4), values for the respective parameters may be specified for the process of succession in the different area types. A graph visualising the run of succession can be easily drawn by selecting values for the four parameters. Fig. 3 shows the respective graphs together with the MIB values for the area types during the



Figure 3. Model graphs based on the parameters in Table 1 for the relationship between MIB values (mg) and age of stands for the first 60 years in **A** planted stands on forest soil, **B** naturally regenerated stands on post-agricultural soil, **C** planted stands on post-agricultural soil, **D** stands on ash heap, and **E** stands on mining heap (Open circles indicate that MIB was calculated from less than 25 individuals; broken lines indicate that the respective part of the graph cannot be verified due to a lack of data).

first 60 years of forest age, using the values provided in Table 1. These values, which have been chosen in approximation to the empirically elaborated MIB values, seem to result in a suitable description of the respective successions. Table 1 shows clear differences for most of the parameters, particularly the 'delay' and 'increase rate'.

Based on the MIB data an 'initial degradation level' of 40 mg (MIB) was chosen for all analysed area types. Due to a lack of data this value cannot be verified for stands on forest soil. For stands on forest soil as well as post-agricultural soil no 'delay phase' is given, a fact which is impossible to verify for the forest stands, too. A 'delay' exists on both post-industrial areas with a value of about 10 years on the mining heap. The 'increase rates' differ strongly. Due a to lack of young study sites it is difficult to specify this value for stands on forest soil. Therefore, the same value as for the naturally regenerated stand on post-agricultural soil was chosen (0.18). The rapid increase at planted stands on post-agricultural soil is represented by a value of 0.5. The increase is even faster on the mining heap (value 0.6). Due to a lack of data after 14 years this value cannot be specified for stands on the ash heap (the dashed line in Fig. 3D is based on a theoretical value of 0.28, see Table 1). The highest 'recovery level' is observed for stands on forest soil. Taking into account the first 60 years, a 'recovery level' of 290 mg (MIB) was chosen. Both naturally regenerated as well as planted stands on post-agricultural soil show a mean 'recovery level' of about 250 mg (MIB) after 60 years. The lowest value exists for the mining heap with 210 mg (MIB). Due to a lack of data this value cannot be determined for the ash heap.

Discussion and conclusion

The successional patterns in the present study are in line with runs of succession described in other publications. Schwerk (2008) compared the trajectory of succession on the ash heap and the mining heap with data obtained in a study on a colliery spoil heap in Germany and pointed out clear analogies. Majer (1989) reported a strikingly similar pattern with respect to data on thrip (Thrysanoptera) recolonisation of Illinois surface-mine spoils. Paquin (2008) identified four groups of species in the succession in black spruce forests of Eastern Canada after forest fire, which characterise differ-

Parameter	Planted stands on forest soil	Natural regenerated stands on post- agricultural soil	Planted stand on post- agricultural soil	Stands on ash heap	Stands on mining heap
Initial degr. Level, MIB (mg)	40?	40	40	40	40
Delay, time (Years)	0?	0	0	10?	10
Increase rate, (time ⁻¹)	0.18?	0.18	0.5	0.28?	0.6
Recovery level, MIB (mg)	290	250	250	210?	210

Table 1. Parameters used for the model graphs in Fig. 3 (Question marks indicate that the respective value cannot be verified due to a lack of data).

ent phases of succession. The first three of them seem to fit the successional phases described in the present study.

The mathematical description of the patterns of succession by help of the four parameters revealed similarities as well as differences among the different types of areas.

The same 'initial level' after degradation was chosen for the different area types. However, particularly on forest soil the 'initial level' might be elevated when compared to the other study sites. For example, Skłodowski (2007) showed less pronounced degradation of forest habitats after a windbreak, probably due to good condition of soil litter. Szyszko (1990) described different degrees of degradation after clear-cuts. Broen (1965) compared clear-cut areas on sandy soil with those on loamy soil. He showed differences in species composition between these two types, with a higher number of forest species in the latter.

A 'delay' at the beginning of succession seems to be characteristic for post-industrial areas, particularly those showing primary succession. In the study of Majer (1989) a rapid increase in the number of species took place between 10 to 20 years after the start of succession. Prach et al. (1993) demonstrated a very low initial rate of succession on spoil heaps resulting from brown coal mining. A delayed ecosystem development of the ecosystem on post-industrial areas has been reported also by Bradshaw (1984, 1987).

According to Horn (1980) succession proceeds rapidly when every species can replace every other species more or less stochastically. Succession proceeds slowly when species of its early stages first have to change environmental conditions for colonization of subsequent species. Since many degraded areas are characterised by poor environmental conditions, the facilitation model described by Connell and Slatyer (1977) seems to be of special importance on these types of areas. A limiting factor seems to be nutrients, particularly a lack of nitrogen (Bradshaw 1984). Depending on previous agricultural practices nutrient contents may vary strongly among post-agricultural areas. This may explain the comparatively high variability in MIB values observed in this type of areas. The higher 'increase rate' in planted stands on post-agricultural soil compared to naturally regenerated ones may be explained by a facilitation of succession due to the artificial introduction of pine. However, rates of early forest succession may also differ between different regions as was shown by Yang et al. (2005).

The highest 'recovery level' on forest soil indicates most advanced regeneration at these study sites. In accordance with these results, several studies (Szujecki et al. 1983; Szyzsko 1990; Skłodowski 1999) have shown that pine stands on forest soil are more developed than stands on post-agricultural land. On the contrary, study sites on the mining heap showed the lowest 'recovery level'. Schwerk (2008) discovered even lower MIB values on a colliery spoil heap in Germany after about 40 years. Nagler and Wedeck (1998) reported that forest areas on a brown coal mining heap in western Germany were not in a natural forest state after 20–30 years. In addition, Majer (1989) shows that the number of thrip species on surface mine spoils does not reach the level of control areas after 32 years. The presented model is of practical value because the four parameters facilitate comparisons of successional processes in different areas. A deviation from desired trajectories of succession, e.g. those in undisturbed reference areas, may point to the need for intervention. Based on some years of monitoring MIB values in a given study site, prognoses may become possible, supported by data from comparable areas. For example, the succession on the ash heap will possibly proceed similar to the succession on the colliery spoil heap in Germany (Schwerk 2008). Furthermore, it is possible to transfer the model to other indicators, which provide numerical values to represent the state of succession. Thus, the model can be used in the context of studies that lack data on carabid beetles (either because carabids were not studied or because of habitats where carabids do not occur, e.g. aquatic habitats).

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Appendix I

Description of the study sites (doi: 10.3897/zookeys.100.1534.app) File format: Microsoft Excel Spreadsheet (xls).

Explanation note: The additional file contains a table with the main characteristics of the study sites (enumeration according to Schwerk 2008, data on age relate to the year 2004, age values of "0" and "1" relate to an active management of the respective study sites).

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Poleward range expansion without a southern contraction in the ground beetle Agonum viridicupreum (Coleoptera, Carabidae)

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Abstract

We investigated the extent of poleward shifts in the distribution range of *Agonum viridicupreum* due to climate change in the western Palaearctic. Species' records were obtained from extensive literature sources as well as from collections, and consistent amateur entomologists' recordings. Within the general geographic range of the species, we analyzed in detail two parts of both, the northern and southern distribution range boundaries: (1 and 2) north-western Germany (leading or high-latitude edge), (3) Israel and (4) southern Italy (rear or low-latitude edge). Temporal changes in the occurrence data of the species indicated a northward shift of the leading edge of a minimum of 100 km within the last 50 to 100 years. In contrast, according to the data gathered, the rear edge has not changed during the last decades. Further studies are

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needed in order to fully understand the underlying mechanisms of the different behaviour of leading and rear range edges of *A. viridicupreum* in the current context of global change. Despite our incomplete understanding, chronosequences of the occurrence of the given species have the potential to optimize climate niche modelling to predict trends in the distribution range in the future.

Keywords

chronosequence, climate change, distribution area, global change, wetlands, power of dispersal, migration, range shift

Introduction

For about 250 years, man has released radiatively active gases and particles in substantial amounts into the atmosphere. As one of the consequences, the global mean near surface temperature has increased, a phenomenon commonly referred to as 'global warming' or 'climate change'. Deduced mainly from instrumental observations initiated around 1860, the observed climate change can be attributed to a large extent to human activities, which influence not only global temperature, but also pH-values of the oceans, precipitation and the general hydrological cycles on Earth (IPCC 2007; Quante 2010).

For many animal and plant species, theoretical analyses on the climate determination of the species' occurrence have predicted a general poleward shift and (in mountain areas) an uphill shift of the given distribution areas and populations, respectively, as a response to climate change. In agreement with theory, numerous range shifts have been documented in the last years. Examples are known from vascular plants, birds, and many insects such as butterflies, dragonflies and damselflies (Hickling et al. 2006; Parmesan 2006; Pauli et al. 2007). Carabid beetles and other epigean soil invertebrates are well known as highly dynamic colonizers of glacier forelands in the last two centuries, and uphill shifts of several hundred metres altitude have been described in the Austrian and Italian Alps and for Scandinavian mountains (Gobbi et al. 2006; Gobbi et al. 2007).

Poleward shifts of distribution areas are very likely also for widely distributed carabid species (in contrast to species with restricted distribution areas, i.e. endemics), as their patterns of geographic distribution are strongly determined by climatic factors (as shown by a large-scale analysis of West Palaearctic ground beetle diversity, Schuldt and Assmann 2009). Indeed, northward shifts of ground beetle species have been documented several times in the literature. Already Lindroth (1972), certainly the most important carabid biogeographer, demonstrated that several species, especially those with flight activity, have expanded their distribution areas northwards in Fennoscandia since the middle of the last century. Some of these species went on spreading polewards, e.g. *Stenolophus mixtus* in Scandinavia (Kvamme 1978; Palm 1982) or in Great Britain (Blake 2001).

Moreover, ground beetles with their northern distribution limit in Britain have moved about 50 km northwards within a period of about two decades (Hickling et al.

2006). Further examples of poleward shifts in the geographic distribution of carabids can be obtained from the faunistic literature throughout Europe, e.g. *Demetrias imperialis* in countries around the Baltic Sea (Silfverberg 2005), and *Tachyta nana, Diachromus germanus*, and *Acupalpus luteatus* in north-western German lowlands (Ziegler 2004). Besides, expansions of carabid species' distribution areas are conspicuous and numerous amateur entomologists consistently notify new records.

However, previous studies on poleward range margin shifts of ground beetles have mainly focused on the leading (i.e. current high altitudinal and latitudinal) edges of their distribution areas (literature cited above). Changes occurring at the leading edge are interesting, especially in the framework of dispersal biology, and they enable us to understand many population biological processes (Hengeveld 1985; 1989). In contrast, despite the fact that leading edges seem to be more relevant than rear (i.e. current low altitudinal and latitudinal) edges, the latter may be of greater importance for the long-term survival of species (Hampe and Petit 2005). This is related to the different histories of leading and rear edges. In general, at the poleward limits of distributions newly founded populations are recent and, therefore, only short-term adaptations have been possible. In contrast, many of the rear edge populations are close to their glacial refuges, i.e. the specimens are genetically more variable and, thus, allow greater power of adaptability and preadaptation (Hampe and Petit 2005).

Nevertheless, up to now, there is no available study comparing the reaction of a ground beetle species at both margins of its distribution range. Thus, in this study we aimed at investigating the extent of poleward range shifts at both the leading and rear edges of the distribution area of a carabid species due to recent climate changes. We selected *Agonum viridicupreum* as our study object because it fulfils many preconditions of a suitable model species to assess potential margin shifts: The specimens can be easily found in the field, they are fully winged and fly actively, and the species' habitat preferences are well-known. Furthermore, the species, and, therefore, allowing suitable faunistic data from large parts of its distribution area. Moreover, the species is not restricted to habitats that are influenced or even destroyed by other drivers of global change, nor have been altered simultaneously by the temperature increase in the last decades (e.g. oligotrophic peat bogs affected by increased atmospheric nitrogen depositions due to pollution, Bobbink et al. 1998).

Material and methods

The study species

Agonum viridicupreum (Goeze, 1777) is a macropterous and thermophilous species restricted to open, wet habitats such as meadows, fens and rain ponds. The day-active beetle prefers sun-exposed muddy sites where it can be easily detected by its green-bronze-coloured surface. Due to its occurrence in floodplain areas (with high prob-

ability of diversion), the dispersal of individuals is not only determined by the species' ability to fly. Specimens can be transported downstream by flooding events into areas where the species might not be able to establish autochthonous populations (Bonn 2000; Turin 2000; personal observations).

In the Levant (Middle East, see below), the beetle lives in wet habitats, mostly close to winter or rain ponds (personal observations). In southern Italy (Calabria) the species lives in river bank habitats around *Typha* swamps or in other wet vegetation types and crops, and on lake shores, until about 1400 m above sea level.

Distribution area and temporal changes

We reviewed the available faunistic literature for the western Palaearctic (Europe, the Mediterranean area) to determine the general distribution area of the study species (Horion 1941; Jeannel 1941f; Antoine 1955f; Kocher 1963; Magistretti 1965; Bonadona 1971; Burakowski et al. 1973f; Alfieri 1976; Bangsholt 1983; Lindroth 1985; Jeanne and Zaballos 1986; Hieke and Wrase 1988; Marggi 1992; Zaballos and Jeanne 1994; Guérguiev and Guérguiev 1995; Kryzhanovskij et al. 1995; Hur-ka 1996; Machard 1997; Köhler and Klausnitzer 1998; Casale and Vigna-Taglianti 1999; Drovenik and Peks 1999; Neculiseanu and Matalin 2000; Turin 2000; Marggi and Luka 2001; Bousquet 2003; Serrano 2003; Müller-Motzfeld 2004; Brandmayr et al. 2005; Curcic et al. 2007; Luff 2007; Austin et al. 2008; Desender et al. 2008) and of *Agonum fulgidicolle* Erichson, 1841, an allopatric sibling taxon of *A. viridicupreum* (ranked by some authors as a subspecies, e.g. Puel 1938), which occurs in north-western Africa.

The situation of faunistic recordings is sufficient for one region at the northern distribution edge (north-western Germany) and for two regions at the southern distribution edge (Levant in the Middle East, mainly Israel, and Calabria in southern Italy).

- North-western Germany has been studied by numerous amateur entomologists who have greatly contributed to our knowledge on the geographic distribution of carabid beetles. We therefore analyzed the changes in the species' distribution separately for (a) West Lower Saxony (west of river Weser) and for (b) East Lower Saxony (east of river Weser), Hamburg, and Schleswig Holstein. For these regions records from three periods (before 1950, between 1951 and 1980, after 1980) were summed up to document tendencies in the numbers of catches.
- For Israel, the first records date from the 1920s (the beginning of modern zoological exploration of the given region by local scientists, in former times only explorers from abroad collected beetles there). We therefore distinguished only two periods of collecting: before 1980 and after 1980.
- For southern Italy (Calabria) there are scarce historical records (before 1980). However, after 1980, intensive ecological surveys were carried out on populations in several sites of the Crati river valley (Mazzei et al. 2010).

Consequently, within the global distribution area of the study species, we analyzed the northern and southern range boundaries by studying in detail the three above mentioned concrete margin regions, where the coverage of the faunistic recordings is amply and sufficient: (1 and 2) a part of the leading edge (north-western Germany: Lower Saxony, Hamburg and Schleswig-Holstein, divided into regions west and east of the river Weser), and (3 and 4) the only continental areas at the rear edge that are not limited by the sea or by the presence of A. fulgidicalle (the Levant in the Middle East: mainly Israel, and Calabria, (southern Italy)). For these areas we compiled numerous faunistic records mostly published in local journals (Westhoff 1881, 1882; Bodenheimer 1937; Barner 1954; Lohse 1954; Gersdorf and Kuntze 1957; Assmann and Ehrnsberger 1990; Assmann and Ehrnsberger 1990; Angelini 1991; Assmann 1991; Mossakowski 1991; Gürlich et al. 1995; Handke 1995; Handke and Kundel 1996; Bonn et al. 1997; Fuellhaas 1997; Nitzu 1997; Ziegler 1997; Fischer et al. 1998; Bonn 2000; Hannig and Schwerk 2000; Hannig 2001; Bonn et al. 2002; Assmann et al. 2003; Hannig 2004; Günther and Assmann 2005; Hannig 2005, 2008; Wrase 2009; Mazzei et al. 2010). At the leading edge, Assmann and Ehrnsberger (1990) as well as Irmler and Gürlich (2004) have previously observed an enlargement of the distribution range in northern Germany. Moreover, we also incorporated in our data base the species' records obtained from museums and private collections (collections of several authors and David Wrase, Berlin (CWB), the Collection Assmann Bleckede (CAB), The National Collection of Natural History of the Tel Aviv University (TAU)) and data bases available on the internet (mainly www.entomologie.de/hamburg/ karten/%0bfhl_02/_agovir1.htm and www.eurocarabidae.de). Generally, several specimens from identical dates and locality are regarded only as one record.

Climate changes in the regions of interest

We surveyed climatological literature and compiled information about recent climate changes in the three regions north-western Germany, Israel and southern Italy (Calabria). We focussed only on changes in temperature and precipitation, the main factors influencing the ground beetles' biology and distribution.

Results

Climate changes

North-West Germany – warmer springs with wetter winters and drier summers

Over the last 150 years a considerable increase of the global mean **temperature** by about 0.8°C has been observed. Also for western Europe the measurements show a warming trend. For Germany during the 20th century a mean temperature rise of about 1.0°C

was reported by Schönwiese and Janoschitz (2008). This warming is not homogenous; there are noticeable seasonal and regional differences. In the western part of northern Germany a linear trend value for the temperature between 0.6°C and 0.8°C appears to be typical. For the period from 1951 to 2000 this linear trend value is slightly higher and comes close a 1°C with a tendency of marginally higher values towards the southeast. The increase in winter temperatures was higher than that for the summer. For the last decades the strongest warming was found to appear in spring. An evaluation of station data for different states in northern Germany using a different averaging method came to the conclusion that during the 20th century the mean temperature in Lower Saxony rose by 1°C, in Schleswig Holstein by 0.8°C and in the metropolitan region of Hamburg by 1.1°C (I. Meinke, GKSS pers. comm.). For the Hamburg area Schlünzen et al. (2010) report an increase in the decadal warming rate, which underlines that the temperature trend was significantly larger in the last three decades. The corresponding rates from a piecewise linear trend evaluation are 0.07 K/decade for 1891-2007, 0.19 K/decade for 1948-2007 and 0.60 K/decade for 1978-2007. Recently the strongest warming appeared in the winter months. A comparison of mean temperatures for the first and last decade of the 20th century suggests that the region in Lower Saxony west of the river Weser faced a slightly higher warming than the eastern part. This result is in conflict with the pattern shown by Schönwiese and Janoschitz (2008) and probably due to the method of comparing only two decades.

Linear 20th century **precipitation** trends for Germany have been reported to be about 8.5% (an increase from 750 mm to 800 mm, Schönwiese and Janoschitz 2008). However, because of a strong interannual variability this trend is not statistically significant. Over this period especially the winter precipitation increased, while for the summer months a decrease was observed. This increase in winter precipitation and decrease in summer precipitation was also reported for the western part of northern Germany. An evaluation of station data for different states in northern Germany using a different averaging method came to the conclusion that during the 20th century precipitation in Lower Saxony increased by about 10%, in Schleswig Holstein by about 12.5% and in the metropolitan region of Hamburg by about 12% (I. Meinke, GKSS pers. comm.). For the Hamburg area Schlünzen et al. (2010) report a significant increase in precipitation rate. The corresponding rates from a piecewise linear trend evaluation are ~0.8 mm/year for 1891-2007 and 1.3 mm/year for 1948-2007. The increase again is most pronounced for the winter months. For the months April and July in the period between 1978 and 2007 a significant decrease in precipitation in the Hamburg area has been found.

Levant (Israel): warmer and drier in the north, wetter in the south

An analysis for the period 1964 to 1994 of **temperature** measurements at 40 stations evenly distributed over Israel came to the conclusion that there appears to be a general warming trend, with some local exceptions, i.e. in the south, which could be related to enhanced aerosol emission (Ben-Gai et al. 1999). This general trend has been confirmed by a more recent reanalysis study (Saaroni et al. 2003); this study also notes that for the last decades July replaces August as the warmest month of the year. The overall analysis reveals a complex change pattern. First, the summers have become warmer, while the winters became colder; second, there exists a significant decreasing trend of the daily maximum and minimum temperature during the cool season and an increasing trend during the warm season (Ben-Gai et al. 1999).

Concerning climatological **precipitation** trends the Levant has to be divided into a southern and northern part. An analysis of winter half-year precipitation over the entire Mediterranean region reveals predominating rainfall decreases during the last 50 years. The areas deviating from this general trend includes southern Israel (Jacobeit et al. 2007). Several studies report opposing trends of annual rainfall for the eastern Mediterranean (e.g. Steinberger and Gazit-Yaari 1996; Jacobeit et al. 2007; Khatib et al. 2007), a decrease of rainfall amounts in the northern part of Israel and increase for southern regions during recent decades. There are indications that the observed trend differences are the outcome of changes in synoptic conditions in the eastern Mediterranean region (Steinberger and Gazit-Yaari 1996). In the overall series of wettest winters (see above, analysis by Luterbacher et al. 2006) the southern part of the Levant was slightly drier than the climatological mean and in the overall driest winter series this region was wetter than the 1961 to 1990 average (Luterbacher et al. 2006). For the northern part of the Levant the trends seem to be *vice versa*; consistently different trend behaviour in the southern part compared to the northern part of Levant has been observed.

Calabria: Warmer and drier

From the maps of linear trends in annual mean **temperature** for Europe compiled by Schönwiese and Janoschitz (2008) for Calabria a warming trend of about 1°C for the entire last century can by extracted, the value is consistent with the analysis by Gerstengarbe and Werner (2007), who compared the first and last decades of the 20th century. The respective value for the period from 1951 to 2000 is slightly larger than 0.6°C. This annual mean temperature trend does not reflect seasonality; warming was driven mainly by the summer months while for the winter months even a slight cooling trend was observed.

Overall it can be said that the most southern part of Italy and especially Calabria has become drier over the last decades. While the linear trend in annual **precipitation** for the entire 20th century for the Calabria region is almost zero, a pronounced trend exists for the period from 1951 to 2000 with a decrease in precipitation by about 20% in the annual mean with a decrease in summer precipitation of about 40% (Schönwiese and Janoschitz 2008). A comparison of the first three decades with the last three decades of the 20th century reveals a slightly drier Calabria at the end of the century (Gerstengarbe and Werner 2007). Luterbacher et al. (2006) analyzed winter precipitation anomalies for the last centuries in the Mediterranean region. The wettest decade

was 1961 to 1970 and the driest was 1986 to 1995. The wettest (driest) multidecadal periods (30 winters in a row) were from 1951 to 1980 (1973 to 2002) with 5 mm (-15 mm) departures from the climatological average (1960 to 1990). Interestingly, in the overall wettest winters Calabria was drier than the climatological mean (10 to 20 mm) and in the overall driest winter series Calabria was about 10 to 20 mm wetter than the 61 to 90 average.

Geographic and altitudinal distribution area of A. viridicupreum

The distribution area of the species within the western part of the Palaearctic is given in Fig. 1. *A. viridicupreum* occurs around the Mediterranean Sea (with a distribution gap in north-eastern Africa). The northern edge of the distribution area runs from the Netherlands through northern Germany and Poland (see also Fig. 2). In the south-east the species occurs in Turkey, Lebanon, and Israel.

In the southern Iberian Peninsula and Morocco, the beetle prefers mountainous areas (Zaballos and Jeanne 1994), but in the central and northern parts of Spain it also thrives well in lowland habitats (down to sea level, e.g. close to Oviedo, in the mountains up to about 2000 m a.s.l., CAB). In south-eastern Europe, the species occurs in mountains as well as lowlands (e.g. Peloponnese, CAB).

The south-eastern distribution edge in the Levant virtually coincides with the border of the Mediterranean climate (Fig. 3). In this study, we report the first record for Egypt ([(T)El Arish, Sinai, leg. L. Fishelsohn, 12.03.1956], record in TAU, Fig. 3). However, the single specimen collected is not a proof of the existence of an autochthonous population here. The same is true for records obtained from the desert regions (e.g. Dead Sea Region, where no suitable habitats for the species occur, cf. Fig. 3).

Faunistic analyses of the distribution margins

West Lower Saxony (west of the river Weser): Although *A. viridicupreum* has been known from the Netherlands since the 19th century, no specimens were recorded from West Lower Saxony until the 1980s (Table 1). Indeed, in the 1950s the northern distribution limit of the species' range was located southwards of Lower Saxony, in the Westphalian Lowlands (Horion 1941; Barner 1954; Westhoff 1881). However, after 1981 numerous records from the whole Lower Saxonian (and Westphalian) Lowlands, northwards to the North Sea, were reported (Assmann and Ehrnsberger 1990; Mossakowski 1991; Handke and Kundel 1996; Fuellhaas 1998; Günther and Assmann 2005; Hannig and Schwerk 2000; Hannig 2001, 2005, 2008, numerous records in collections, e.g. CAB), thus, expanding the former northern distribution margin (Fig. 2). The distance between the known northern limit of the 19th century (central Westphalian Lowlands) and the present records close to the North Sea coast is more than 100 km (Fig. 2).



Figure 1. Distribution of *Agonum viridicupreum* (shaded in grey) and its sister taxon *A. fulgidicolle* in the western Palaearctic. Map modified after Turin et al. (2003) using information from Brandmayr et al. (2005) and personal observations. Frames indicate regions selected for more detailed analyses of records, see Figs 2 and 3.

East Lower Saxony (east of river Weser): Horion (1941) and Gersdorf and Kuntze (1957) listed records of the species from the hilly countryside close to Hannover. The latter authors questioned the occurrence of the species in the lowlands of eastern Lower Saxony. Along the river Elbe, one old record (19th century) is known from one site south-east of Hamburg ("?" in Fig. 2, Table 1). Lohse (1954) interpreted the presence of these specimens as vagrants transported downstream by flooding events from south-eastern Germany. However, these specimens could have originated also from temporal populations.

Between 1951 and 1980, only one record from another site in the Lower Saxonian floodplain area of the river Elbe is known (Table 1). Records from sites outside the given floodplain are exclusively known since 1981, when the number of records greatly increased.

Today, the species is found northwards, up to central Schleswig-Holstein (www. entomologie.de/hamburg/karten/fhl_02/_agovir1.htm), and reaches also the northwestern parts of the considered area. Interpreting the old records from the floodplain area of the river Elbe as autochthonous populations leads us to think that the species' geographic range has experienced a northward shift of about 100 km during the last century. Even if these records were not seen as autochthonous populations, the shift would have spanned over about 200 km (Fig. 2).



Figure 2. Distribution of *A. viridicupreum* (shaded in grey) in North-West Germany with eastern parts of the Netherlands. Arrows indicate minimum range expansion in the last three decades (for explanation and records see text). Range expansion in the Netherlands indicated after Turin, pers. comm.

Levant: Bodenheimer (1937) listed *A. viridicupreum* from Israel for the first time, and the former documented records were taken in the 1920s (TAU). In this region, the beetle is abundant at many rain or winter ponds (up to ca. 20 individuals per hour can be collected by hand picking; personal observations). So, it is very likely that the late discovery of the species at its south-eastern distribution edge would be a consequence of the poor carabidological exploration of the country. Since Bodenheimer's time, numerous new records of the species have been reported, also during the last years (Fig. 3). *A. viridicupreum* reaches the south-eastern limit of the Mediterranean climate in Israel. There is no evidence for a northward shift of its distribution range, as the known southern Israeli populations are close to the semi-arid climate region from where the species is virtually unknown; only singletons – not indicating autochthonous populations – have been found (see above and Fig. 3).

Calabria: For southern Italy (Calabria) there are scarce historical records (before 1980; Magistretti 1965; Angelini 1991). After 1980, a total of 37 specimens were recorded (Mazzei et al. 2010).



Figure 3. Distribution of *A. viridicupreum* in Israel. The striped area indicates Mediterranean climate zone (according to Yom-Tov and Tchernov 1988). Species' records are taken from collections TAU, CAB and CWB.

Study region	Number of records			
	before 1950	1950-1980	after 1980	
Leading edge:				
North-West Germany – West Lower Saxony	0	0	26	
North-West Germany – East Lower Saxony	1^{1}	12	24	
and Schleswig Holstein				
Rear edge:				
Israel	1	2	14	

Table 1. Number of records of *A. viridicupreum* in the different periods of time in north-western Germany (leading edge) and Israel (rear edge).

¹ Close to Geesthacht (leg. Kolze, 1890 [river Elbe, east of Hamburg], because of lacking records from the surrounding seen as diversion by Lohse, 1954)

² Pevestorf [river Elbe, south-east of Lüneburg]

Discussion

Poleward shift of the leading edge

The compilation of the faunistic data showed that the distribution range of *A. vir-idicupreum* had significantly shifted northwards within the last 50 to 100 years. Up to 1950, in the analyzed region, the northern edge of the species' distribution had stretched from the Netherlands (Nijmegen, Enschede; Turin 2000) southwards to the Westphalian Lowlands (south-western Lower Saxony), and again northwards to Hannover and Braunschweig (Fig. 1). The historical lack of the species studied in the region around Osnabrück (south-western Lower Saxony) does not need to be the result of undersampling, as also other thermophilous insects colonized this region later than the neighbouring western or eastern regions (e.g. several grasshopper species; Hochkirch 2001; Hochkirch and Damerau 2009).

Today, in the western part of Lower Saxony, *A. viridicupreum* can be found up to the North Sea, confirming a northwards range expansion of about 100 km. Similarly, in the neighbouring Netherlands the beetle has expanded its distribution range northwards and can nowadays be recorded close to the city of Groningen (Turin, pers. comm.). Also in the eastern part of Lower Saxony the species has spread northwards a minimum distance of 100 km and it reaches the centre of Schleswig-Holstein today. These results allow the assumption that a further temperature rise will make the species' occurrence in Denmark highly probable in the near future.

Stable rear edge

Unlike the northern distribution edge, the southern range margin (rear edge) of *A. viridicupreum* has not changed within the last decades. Indeed, there are still populations with numerous individuals south of Tel Aviv, which is close to the southern limit of the

Mediterranean climate. Consequently, in Israel we expect the beetle to occur in most of the regions characterized by Mediterranean climate. In southern Italy (Calabria) *A. viridicupreum* shows a stable rear edge north of the 39th parallel, with permanent populations in the Crati Valley in the Cosenza province, in areas marked by Submediterranean or Mediterranean climate.

Different behaviour of leading and rear edges

In accordance with numerous other authors (e.g. Hengeveld 1985; Hickling et al. 2006), we interpret the poleward shift of the leading edge of this species as a consequence of increasing temperature. It seems to be more difficult to describe the differences between leading and rear edge. In general, they could be explained by either intrinsic or extrinsic factors, or even a combination of both. The influence of *intrinsic* factors would imply that distinct genetic make-ups of the populations from the opposite edges of the distribution range are likely (Hampe and Petit 2005). However, so far there are no available investigations to corroborate this hypothesis for A. viridicupreum or other ground beetle species with the tendency of invasions in the Levant. Consequently, additional investigations are necessary. For non-migratory butterflies, it has been demonstrated that population size fluctuations are more pronounced at the leading edge than at the rear one (Parmesan et al. 1999) – a possible indication of less well-adapted populations at the leading edge. As our data do not give information about the population sizes of A. viridicupreum at the various sites, on the one hand, we cannot investigate this assumption. On the other hand, the high catching rates (which are comparable to catches from sites in northern Italy and Germany) do not support the assumption of the species declining in the Levant.

On the contrary, *extrinsic* factors may be acting differently at the leading and rear edge of the distribution range of *A. viridicupreum*. Our compilation of recent climate trends, however, reveals generally rising temperatures in all regions under study. In contrast, less consistent changes in precipitation can be observed. The populations in both, Calabria and the Levant will have to deal with a reduction in mean annual precipitation. In the face of the virtual exclusive occurrence of the species close to rain ponds in the southern edge of its distribution, it seems likely that the southern populations are limited by the given ground water tables which predominantly result from the annual amount of precipitation (mainly in the winter months).

In the Levant, larval development takes place during winter and early spring, as revealed by numerous tenerals, even at higher altitudes, e.g. 900 m a.s.l., in the Golan Heights, in April and May (personal observation). In contrast, the northern populations in Central Europe are unlikely to be limited by the amount of precipitation, but rather by temperatures during the species' activity period. In fact, in this region, larval development takes place during summer and tenerals occur in late summer and autumn (August to October; Turin 2000; personal observations; during this season tenerals has never been found in the Levant). Finally, the role of other factors such as interactions with other organisms cannot be excluded when interpreting the distribution changes at the species' range margins. Nonetheless it is possible that the northern and southern limits of *Agonum viridicupreum* are determined by different climatic factors: increasing summer temperature in the north and increasing precipitation during the winter in the south can explain the poleward shift of the leading and the stable rear edge of the given species' distribution.

Potential of A. viridicupreum for further ecological research on global change

This study is the first one that investigates simultaneously the possible shifts of the northern and southern margins of a carabid species' distribution due to climate change. Undoubtedly, at present we are not able to fully understand the underlying mechanisms of the different behaviours of the leading and rear boundaries of the geographic range of A. viridicupreum in the actual context of global change. However, our analysis suggests that the reaction of the study species to climate change may be more intricate than expected at first. For this reason, we think that the more complex situation in A. viridicupreum has important potential for further carabidological investigations at the interface of global change ecology and conservation biology. For instance, predictions based on climate envelope modelling, which has become both commonplace for many other animal species and the object of an intensive (and critical) scientific discourse (Settele et al. 2009; Rödder and Dambach 2010), can be optimized (and evaluated) by using the chronosequences of distribution data. To our knowledge, this approach has not yet been applied for ground beetles, although they appear to be an excellent object to validate climate envelope models, thanks to the outstanding faunistic work with numerous records from many regions and time periods (e.g. Luff 1998; Turin 2000; Desender et al. 2008; Trautner, in prep.).

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RESEARCH ARTICLE



Habitat disturbance and hydrological parameters determine the body size and reproductive strategy of alluvial ground beetles

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Abstract

Environmental variability is the main driver for the variation of biological characteristics (life-history traits) of species. Therefore, life-history traits are particularly suited to identify mechanistic linkages between environmental variability and species occurrence and can help in explaining ecological patterns. For ground beetles, few studies directly related species traits to environmental variables. This study aims to analyse how life-history traits of alluvial ground beetles are controlled by environmental factors. I expected that the occurrence of species and the occurrence of specific traits are closely related to hydrological and disturbance parameters. Furthermore I expected most of the trait-variation to be explained by a combination of environmental variables, rather than by their isolated effects. Ground beetles were sampled in the year 2005 in floodplain grassland along the Elbe River in Germany. I used redundancy analysis to quantify the effects of hydrological, sediment, and disturbance related parameters on both species occurrence and species traits. I applied variation partitioning to analyse which environmental compartments explain most of the trait variation. Species occurrence and trait variation were both mainly controlled by hydrological and flood disturbance parameters. I could clearly identify reproductive traits and body size as key traits for floodplain ground beetles to cope with the environmental variability. Furthermore, combinations of hydrological, habitat disturbance, habitat type, and species diversity parameters, rather than their isolated effects, explained large parts of ground beetle trait variation. Thus, a main conclusion of this study is that ground beetle occurrence is mainly determined by complex, multi-scale interactions between environmental variability and their life-history traits.

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Keywords

life-history traits, environmental variability, species sorting, trait shifts, floodplain, ecosystem processes

Introduction

Observing the occurrence of species and evaluating the response of biodiversity to changing environmental conditions is a major task of ecologists. With increasing ecological knowledge, however, the scientific focus shifted from purely observational to rather explanatory and predictive approaches. Recent attempts try to understand the observed occurrence patterns by focusing on the relationships between environmental variability and the life-history traits of organisms (Naeem and Wright 2003). Life history traits are biological characteristics of species allowing them to survive in their environments, including morphological, behavioural, and physiological characteristics. Current theory, like the habitat templet theory (Townsend et al. 1997), predicts that species traits are mainly constrained by the environmental variability of their habitats and that abiotic factors act like filters, sorting organisms with unique trait combinations appropriate for specific habitat conditions (Statzner et al. 2004). In the past years, several studies successfully applied this theory to determine or predict biodiversity effects of altering environmental conditions and showed the suitability of life-history traits for ecological research. For example, Dalgleish et al. (2010) highlighted the usefulness of trait-based approaches to predict species vulnerability to climate change. Snyder (2008) noted that life-history traits can reveal how species can coexist and several studies described the effects of environmental variables on species traits (e.g. Lehsten et al. 2009; Pausas et al. 2004; Ilg and Castella 2006). The main conclusion of these studies is that functional traits of organisms can explain the ecological response of species (Lavorel et al. 1997). Thus, functional approaches can be seen as an extension of traditional ecological research, as they can reveal general assembly rules to explain ecosystem processes, and to give sound ecological interpretations.

Previously, such analyses were mainly applied to plants, but an increasing number of studies directly related environmental variables also to ground beetle life-history traits. Gobbi and Fontaneto (2008) noted that proportions of short winged, large and predatory species were negatively related to habitat disturbance. Similar results were found by Pizzolotto (2009) and Ribera et al. (2001), stressing that management intensity can influence trait dispersion and morphological characteristics of ground beetles, such as body size or wing morphology. For agricultural landscapes Hendrickx et al. (2009) found that especially ground beetles with low dispersal ability are threatened by habitat fragmentation and Lambeets et al. (2008) demonstrated multiple trait shifts of ground beetles along gradients of flood disturbance. The main conclusion of all these studies is that life-history traits of ground beetles are strongly affected by a variety of different environmental variability in a large range of different habitats.

Analysing trait-environment relationships is especially suitable in naturally dynamic landscapes, because this allows for observing biological patterns without elaborately manipulate environmental conditions (Henle et al. 2006). Floodplains provide excep-

tional opportunities for such kind of research, since the episodic alternation of floods and droughts causes high spatio-temporal habitat heterogeneity (Tockner and Stanford 2002), being one of the most important drivers for species assemblages and the high species richness of these ecosystems (Adis and Junk 2002). Floodplain faunal species are therefore expected to display a large range of adaptations and strategies to cope with varying environmental conditions (Robinson et al. 2002). However, given this high biotic and abiotic variety of floodplains, mechanistic linkages between environmental variability and life-history traits of organisms are difficult to reveal and thus still insufficiently understood. This is to some degree also true for ground beetles, although they are one of the best studied, most species rich and abundant macroinvertebrate taxon in terrestrial and semi-terrestrial habitats and particularly suitable for the investigation of species-environment relationships (Lövei and Sunderland 1996; Rainio and Niemelä 2003). Recently, some considerable progress has been made to identify the life-history traits of ground beetles to understand their response to floodplain dynamics. Most of the species are good flyers, which enables them to actively evade rising floodwaters and to quickly recolonise the habitats after flooding (Desender 1989). Additionally, a huge amount of alluvial ground beetles are habitat generalists (Weigmann and Wohlgemuth-von-Reiche 1999), which may increase the chance of finding surrogate habitats and to quickly recolonise habitats after flooding. The adults of several alluvial species can stay submerged for a considerable time period and are thus able to outlast flood events for a certain time in the floodplain (Siepe 1989; Rothenbuecher and Schaefer 2006). In contrast, ground beetle larvae are rather intolerant to hydrological stress (den Boer and den Boer-Daanje 1990) and therefore many alluvial species develop in less flood exposed habitats (Rothenbuecher and Schaefer 2006). Spring reproduction is another crucial strategy to ensure reproductive success in these highly dynamic floodplain habitats. Early reproduction enables the larvae to develop during summer, which is usually a period of low hydrological disturbance, and thus can decrease larval mortality and increase reproductive success (Thiele 1977).

Despite the general knowledge of ground beetle survival strategies in floodplains, it is yet not clear how environmental variability controls the distribution of particular traits within species assemblages. Lambeets et al. (2008) and Bates et al. (2006) gave some first insight, as they directly related floodplain variables to specific life-history traits of the species. They stressed the importance of flood disturbance and soil conditions on the variation of species traits. However, these studies were conducted on river banks, being characterised by an extremely high disturbance regime with rapidly altering environmental conditions. For other habitats, like less disturbed floodplain grasslands, other parameters might be of greater importance for the species. The primary aim of this study is to explain the occurrence of ground beetles by linking species lifehistory traits with environmental variability and species occurrence patterns in floodplain grassland. I expect that the occurrence of ground beetle species and the variation of their traits are strongly affected by hydrological and disturbance related parameters. Due to the environmental complexity of floodplain habitats I further hypothesise that most of the trait variation will be explained by a combination of different environmental variables, rather than by their isolated effects.

Methods

Study area

The study was conducted at the UNESCO Biosphere Reserve "Elbe River Landscape" in Central Germany at the Elbe River. With a length of about 1,100 km and a catchment area of about 150,000 km² the Elbe River is the third largest stream in Germany and ranks among the largest streams in Europe. The mean annual discharge of the Elbe River ranges from 336m³/s upstream to 730m³/s downstream. The water level is mainly dominated by snow-melt in spring and erratic precipitation over the year, inducing high discharge in winter and spring, and low discharge in summer. In general, flood regime and floodplain habitats of the Elbe River in Central Germany can be considered close to the natural state (Scholten et al. 2005).

The survey was carried out in the year 2005 on 36 plots located in seasonally flooded grasslands. The study site is located near the village of Steckby, close to Dessau town in the state of Saxony-Anhalt. The plots were located following a stratified, randomised design. For this, the study site was subdivided into three habitat types regarding vegetation and soil morphology: floodchannels, humid grasslands and mesophilous grasslands. The sampling plots were then randomly located within each of the three habitats (see Henle et al. 2006 for a detailed description of the study design). The study site is characterised by a mosaic of higher and lower areas, which are differently exposed to floods (Fig. 1), whereas the more elevated and dryer areas were cut twice a year and the lower ones (e.g., floodchannels) were spared from utilisation. On each plot five pitfall traps were installed and filled with a 7% solution of acetic acid and a detergent to reduce surface tension. The traps were exposed from May to June and from September to October with a trap exposure time of 28 days per period. All adults were determined to species level and stored in a solution of two-thirds ethanol (70%) and one-third acetic acid (30%).

Life-history traits

Information on the life-history traits of ground beetles were queried from a selfcompiled database. The included trait data came from standard references on Central European ground beetles, mostly determination keys and ground beetle compendia. Altogether 18 traits with 60 trait categories, ranging from biological and morphological to ecological characteristics, were included in the database. For this study I used 8 traits and 25 trait categories to describe the effects of environmental variables on the variation of the traits. See Appendix II for an overview of the traits included in the database and the ones used in this study including the references used to compile the database. To obtain a rectangle traits-by-site matrix that can be analysed by multivariate statistics, the number of individuals possessing a particular trait



Figure 1. Grassland habitats displaying different hydrological conditions in the study site Steckby. Copyright Mathias Scholz (UFZ, Leipzig).

category (e.g. spring breeders) was allocated to each plot, similarly to an ordinary species-by-site matrix (i.e. species were replaced by trait categories). If individuals shared more than one trait category, e.g. dimorphic species, they received an entry for each category.

Environmental variables

In the years 1998 and 1999, dipwell and crest gauges were installed on each sampling plot to measure maximum groundwater depth (in m), mean groundwater depth (in m), duration of inundation (in weeks), and inundation height (in m). Follner and Henle (2006) correlated these plot-measurements with data from official Elbe gauges near the study site Steckby, which are daily collected by the German Waterways and Shipping Administration. By additionally accounting for evapotranspiration, a hydrological model was set up to calculate the selected hydrological variables (see Table 1) even for the year 2005, although hydrological field measurements did not continue after 1999. The reliability, the temporal and statistical robustness, as well as the application of this hydrological model was recently tested and approved in the framework of developing a bioindicator system for ecological changes in floodplains (Follner et al. 2009). Soil substrate data came also from the survey in 1999, but as the substrate type of the sampling plots did not change during the 6-year time span, I used this data for the analyses as well.

Trait	Trait categories	comments
Body size	1 – diminutive	< 3.0 mm
	2 – very small	3.1 – 6.0 mm
	3 – small	6.1 – 10.0 mm
	4 – medium	10.1 – 19 mm
Wing morphology	1 – macropterous	
	2 – brachypterous	
Season of reproduction	1 – spring	From February to June
	2 - autumn	From July to Oktober
Hatching season	1 – spring	
	2 – atumnn	
Overwintering type	1 – as imago	
	2 – as larvae	
Daily activity	1 – diurnal	
	2 – nocturnal	
Body pubescence	1 – head	
	2 – pronotum	
	3 – elytra	
	4 – hairless	
Food strategy	1 – opportunistic carnivores	
	2 – specialized carnivores	
	3 – phytophagous	
	4 – polyphagous	

Table 1. Life-history traits of ground beetles used in this study.

Data analysis

Ecological studies are often biased by spatial autocorrelation, i.e. closely located samples are not independent because they can share attributes of their neighbouring samples (Dormann et al. 2007). However, independence of data points is a crucial assumption for most statistical methods. To identify spatial autocorrelation of ground beetle species richness, relative abundances and Simpson's diversity I used Moran's I, which is a weighted correlation coefficient that detects spatial randomness or spatial clustering of variables. Values being larger than zero show positive, and values less than zero indicate negative spatial dependence of the variables. I used the knearneigh-function of the R-package spdep (Bivand 2009) using 6 plots as nearest neighbours to calculate the spatial weights matrix. Statistical significance of the autocorrelation was tested with saddlepoint approximation tests.

Principal Component Analysis (PCA) was conducted i) to identify the most important environmental variables and ii) to exclude highly correlated variables prior to further analyses. Since the environmental variables were measured on different scale units (see Table 1), I standardised them to a zero mean and unit variance to equally weight the variables. Data for substrate, management intensity, and habitat type were categorical. Therefore, these variables were transformed into dummy coded binary data before included into the analysis. I aimed to assess the influence of environmental variables on both species assemblages and on particular species traits. A preliminary Detrended Correspondence Analysis revealed very short gradient lengths of the species and the trait datasets, suggesting low turnover rates of species and traits among the axis-gradient and thus a linear response. Therefore, I performed Redundancy Analysis (RDA) on the species (which is referred to as "species-RDA" in the following) and the traits dataset ("trait-RDA"), being much better suited for linear response patterns than unimodal models like Canonical Correspondence Analysis (Leps and Smilauer 2003). I compared the RDA models (i.e. ordination constrained by environmental variables) with unconstrained PCA models to identify the relative influence of environmental factors on the ordination models.

To determine the degree to which the occurrence of species and the occurrence of particular species traits are correlated, I performed a Procrustes rotation analysis on the species and the trait dataset. Procrustes rotation aims to find maximal congruency, i.e. similarity of data points, between two ordination models by rotating, expanding and rescaling an ordination model towards a target ordination (Legendre and Legendre 1998). To estimate if environmental variables affect the correlation I performed two Procrustes rotations: i) without environmental variables, i.e. rotation of a species-PCA model against a trait-PCA model, and ii) constrained by environmental variables, i.e. a rotation of a species-RDA model and a trait-RDA model. Statistical significance of the Procrustes rotation models were tested with a randomization test with 9,999 permutation iterations.

Variation partitioning was then used to separate the effects of different environmental compartments (predictor variables) on the variation of ground beetle life-history traits (response variable). Variation partitioning is based on RDA and tries to identify how successful a set of different predictor variables is at explaining the response variable (Legendre 2008). Hereby, the total percentage of variation explained by an RDA-model is partitioned into unique and common contributions of the predictor variables. I assumed variables related to hydrology and disturbance to explain most of the trait variation. Therefore, I divided the environmental dataset into a "hydrology" and a "disturbance" compartment (see Table 2). I additionally created a "habitat" compartment to account for the effects of environmental variables that were not measured, but being reflected in the habitat type, such as soil moisture, pH value, nutrient content etc. I assumed that species rich ground beetle assemblages should explain large parts of the trait-variation, because they should contain a large proportion of species with different biological characteristics. To account for these effects, I set up a "species diversity" compartment, containing species richness and Simpson's diversity. Since preliminary analyses showed that soil substrate did not explain any variation in the trait-data, I excluded the soil compartment from variation partitioning.

Relative abundances of the individuals were log-transformed to reduce the skew in the data. All statistical analyses were performed with the packages vegan (version 1.15–4; Oksanen et al. 2009), spdep (version 0.4–54; Bivand 2009), and ade4 (version 1.4–14; Dray and Dufour 2007) in the R environment (version 2.10.0; R Development Core Team, 2009).

Results

Overall, 26,557 individuals from 107 species were sampled. *Agonum emarginatum* (Gyllenhal 1827; 27.7%), and *Poecilus versicolor* (Sturm 1824; 12.4%) made out 40% of the overall individual density. 38 species were recorded with less than 5 individuals, including some stenotopic alluvial species like *Agonum dolens* (Sahlberg 1827), *Bembidion argenteolum* (Ahrens 1812) and *Omophron limbatum* (Fabricius 1776). See Appendix I for a full species list. I found only minimal spatial autocorrelation of Simpson's diversity, as seen by the relatively low Moran's I value (M), which was only slightly greater than zero (M=0.178, p=0.015) (Table 3). Spatial dependency of both species richness (M=0.292, p=0.001) and species abundances (M=0.394, p<0.001) was little higher, nevertheless indicating a minor role of spatial autocorrelation in this study.

To reduce the complexity of the subsequent models by excluding highly correlated data, I conducted a PCA on the full environmental dataset. The full PCA model explained 68.4 % (F1: 49.4, F2: 19.3) of the total variance in the environmental data, but due to collinearity I excluded 10 environmental variables from this model (abbreviations see Table 2): gw.level.max, flood.height.max, flood.duration, gw.level.varcoef, substrate.silt, substrate.sand2, management.unused, habitat.floodchannel, habitat. meadow.medium, habitat.meadow.humid. The reduced model consisted of 5 variables and explained 79.7 % of the variation of the remaining environmental data (F1: 44.1%, F2: 35.6%). The sampling plots were ordinated along gradients of hydrological, habitat disturbance, and soil parameters (Fig. 2). Plots on the first PCA axis were mainly influenced by habitat management as well as flood and groundwater related variables, whereas soil type was the most important factor on the second axis. There are three groups of plots with similar environmental conditions, which clearly refer to the habitat types defined prior to the analyses. Habitats located in floodchannels were strongly influenced by the mean groundwater depth, whereas humid grassland habitats were more affected by the numbers of floods. The driest plots have also the highest amount of sand and are mown once or twice a year, compared to the unused floodchannels.

To evaluate how environmental variables affected the composition of species and traits I performed a Redundancy Analysis (RDA) with the reduced environmental dataset on the species and the trait dataset. The first two axes of the species-RDA explained 58.54% of the variance in the species dataset (F1: 54.00%, F2: 5.84%, Fig. 3A). It is obvious that mainly management and hydrological variables, such as the mean groundwater depth, are the main drivers affecting species occurrence. Mainly hygrophilous alluvial species, such as *Agonum* or *Bembidion* species, but also *Oodes helopioides* (Fabricius 1792) and *Pterostichus anthracinus* (Illiger 1798) are related with these environmental conditions. Therefore, plots possessing a high proportion of alluvial species, like *Pterostichus melanarius* (Illiger 1798), *Poecilus versicolor* (Sturm 1824) and *Nebria brevicollis* (Fabricius 1792), as well as xerophilous species like *Amara equestris* (Duftschmid 1812) were rather correlated with increasing human management and higher groundwater levels and thus ordinated to the right side of the diagram. Because



Figure 2. PCA of the reduced environmental dataset. Points represent the sampling plots and the colours the different habitat types: Black = floodchannels, grey = mesophilous grassland, white = humid grassland.

of the low explanatory power of the second RDA axis, soil type has only little impact on species occurrence patterns.

The first two axes of the trait-RDA explained 64.35% of the total trait variance in the dataset (F1: 59.90%, F2: 4.45%, Fig. 3B). The results indicate that especially reproductive traits and body size are strongly affected by the disturbance regime and by the hydrology of the habitats. On the left side of the ordination diagram, plots are located with a high amount of individuals reproducing in spring and hatching in summer. Most of them are additionally small sized species. On the contrary, summer/autumn breeding species and larger species are plotted more on the right side of the diagram.

Procrustes rotation analysis showed a significant correlation between species ordination and trait ordination, relatively independent from the presence of environmental constraints in the ordination (Table 4). This shows that sampling plots with a unique species composition also possess organisms with specific life-history traits. The PCA models (ordination of species and traits is not constrained by environmental variables) showed a higher congruency between each other, whereas the rotation of the RDA models tended to be less precise and showed a large part of unexplained variance, evident from the RSS values four times higher than those from the PCA model rotation.

The environmental compartments hydrology, disturbance, habitat type, and species diversity explained 72% of the overall variation of the ground beetles life-history traits (Fig. 4). However, partitioning the effects of the predictor variables on ground beetle trait variation revealed only little explanatory power of each environmental compartment separately. Hydrology alone explained the largest part and diversity and distur-



Figure 3. Relationship between environmental variables and species occurrence **A** and occurrence of species traits **B** by means of Redundancy Analysis. Points represent the sampling plots. Species scores omitted due to clarity. The colours indicate the habitat type of the sampling plots: black=floodchannels, grey=mesophilous grassland, white=humid grassland. Traits and species that accounted most for the explained variance along the first RDA axis are plotted in italics.

bance explained the smallest part of the overall variation. The unique contribution of all compartments to the overall trait variation was 22%, whereas the common contribution (i.e. the combination of all compartments) was about 50%. In other words, the different environmental compartments explained to large degrees similar parts of the trait variation, indicating a certain amount of explanatory redundancy in the predictor variables.

V. : 11		D 1	C
Variable	Description	Data scale	Compartment
Flood.height.max	Maximum flood height	Continous (cm)	Disturbance
Flood.nr/year	Number of floods per year	Continous (no.)	Disturbance
Flood.duration	Flood duration	Continous (weeks)	Disturbance
Gw.level.max	Maximum ground water depth	Continous (cm)	Hydrology
Gw.level.mean	Mean groundwater depth	Continous (cm)	Hydrology
Gw.level.varcoef Variation coefficient of groundwater		Continous (no	Hydrology
	depth	dimension)	_
Substrate.loam	Loamy substrate	Binary (0=no, 1=yes)	-
Substrate.sand1	Sandy substrate (<90% sand amount)	Binary (0=no, 1=yes)	-
Substrate.sand2	Sand (>90% sand amount)	Binary (0=no, 1=yes)	-
Substrate.silt	Silty substrate	Binary (0=no, 1=yes)	-
Management.mown	Plot mown	Binary (0=no, 1=yes)	Disturbance
Management.unused	No management	Binary (0=no, 1=yes)	Disturbance
Habitat.floodchannel	Habitat type "floodchannel"	Binary (0=no, 1=yes)	Habitat
Habitat.meadow.medium	Habitat type "mesophilous grassland"	Binary (0=no, 1=yes)	Habitat
Habitat.meadow.humid	Habitat type "humid grassland"	Binary (0=no, 1=yes)	Habitat

Table 2. Environmental variables used in the study

Discussion

This study tackles the problem of identifying mechanistic linkages between environmental variability, biotic characteristics of organisms and the occurrence of species in dynamic landscapes. Here I show that both species occurrence and the variation of ground beetle life-history traits are controlled by similar environmental variables. Reproductive traits and body size were found to be key traits of floodplain ground beetles enabling them to cope with management intensity and groundwater depth. Furthermore, combinations of hydrological, habitat disturbance, habitat type, and species diversity parameters, rather than their isolated effects, explained large parts of ground beetle trait variation. A main conclusion of this study is therefore that ground beetle occurrence in floodplain grasslands is mainly determined by complex interactions between environmental variability and specific life-history traits.

Environmental variability and species occurrence

Management intensity, groundwater depth, and to a lesser degree soil substrate were the most important environmental variables driving the occurrence of species and the variation of ground beetle traits. Previous work on ground beetles in floodplains highlighted the importance of environmental variables for species occurrence in these dynamic habitats. For riverbanks, being considered as the most disturbed habitats in floodplains, Eyre et al. (2001), Kleinwaechter and Rickfelder (2007), and Framenau et al. (2002) noted that sediment type and flood disturbance are the most important factors affecting the occurrence of ground beetles. In this study I revealed that sediment



Figure 4. Partitioning the effects of four environmental compartments hydrology, disturbance, habitat type, and species diversity on the variation of ground beetle life-history traits. See Table 2 for a description of the variables included in each compartment. Values < 0.03 are not shown.

type had only little influence on species occurrence and trait variation. This was not surprising, as soil dynamics, e.g. sediment erosion or deposition, are relatively low in floodplain grasslands and might therefore not be of primary importance for grassland arthropods. Rather than soil variables I found that habitat disturbance and hydrological parameters are the main factors that drive the occurrence of ground beetles in the study site. This is coincident with Antvogel and Bonn (2001), Gerisch et al. (2006) and Eyre (2006) stating that flood duration, groundwater depth and habitat management are the main factors influencing the occurrence of ground beetles in floodplains.

However, species occurrence patterns are often distance related, i.e. the values of variables (species, individuals) sampled at nearby locations are not independent from each other and lead to spatial autocorrelation (Legendre and Legendre 1998; Dormann et al. 2007). The relatively low Moran's I values in this analysis indicate that ground beetles were rather dispersed than clustered within certain habitat types. This means that the differences in species diversity are not primarily due to spatial proximity of the sampling plots, but mainly caused by environmental variability and habitat configuration. Nevertheless, there is obviously a relationship between species assemblages located close together.

Environmental effects on species traits

The results indicate that species assemblages of certain habitat types share unique combinations of traits, which clearly confirms the habitat templet theory. The im-

Metric	Moran's I	р
Species richness	0.292	0.001
Species abundances	0.394	< 0.001
Simpson's diversity	0.178	0.015

Table 3. Moran's I values

portance of hydrological and disturbance parameters for wetland ground beetle traits is well documented in the literature. Thiele (1977) stressed the importance of floodplain species to reproduce in spring to avoid flood disturbance. Eyre et al. (2001) suggested that small body size and high mobility enable floodplain ground beetles to quickly respond to increasing disturbance. Bates et al (2006) and Lambeets et al. (2009) confirmed these assumptions, showing that several life-history traits of riverbank spiders and ground beetles are strongly affected by flood disturbance parameters. According to Ribera et al. (2001), Lambeets et al. (2009) and Sadler et al. (2006), disturbance mainly affects the dispersal capacity and the body size of ground beetles. Hence, a small body size and fully developed wings enable species to quickly evade the disturbance or quickly recolonise the disturbed plots. Overall, it is not surprising that both, the occurrence of species and their particular traits, are affected by similar environmental variables. It is suggested that only certain traits enable organisms to cope with environmental variability or extreme environmental conditions (Townsend 1997). Obviously, the set of suitable traits for coping with environmental stress is limited by nature. Therefore, "successful" strategies can be shared by several species simultaneously. The rising question of species coexistence can be best explained with functional redundancy (Petchey et al. 2007; Flynn et al. 2009) and flexible niche partitioning (Finke and Snyder 2008). Thereafter, species possessing similar life-history traits (i.e. being functionally redundant) are still able to coexist in the same habitat, because species resource use behaviour is expected to be plastic to minimise competition. Unfortunately, there are no ground beetle studies addressing functional redundancy issues, which is why an increased research on those topics is crucial to verify these assumptions.

Combined environmental effects on species traits

Partitioning the effects of environmental variables clearly showed that a combination of all four compartments hydrology, habitat disturbance, habitat type, and species diversity explained the largest part of the overall trait variation. However, this does not automatically mean that each compartment separately is unimportant for ground beetles. In fact, each environmental compartment explained unique parts of the ground beetle trait variation, although to a comparable little amount. For example, flood disturbance is closely connected to hydrological parameters, i.e. frequently flooded plots are often the ones with the lowest groundwater depth. However, hydrological factors

	Unconstrained	Constrained by environmental		
	(PCA)	dataset (RDA)		
Correlation coefficient	0.69	0.61		
Residual Sum of squares	20.37	82.73		
Root mean squared error	0.12	0.13		
p-value	< 0.001	< 0.001		

Table 4. Procrustes rotation analysis of species and the trait dataset

might not necessarily have similar impacts on the trait variation than habitat disturbance parameters. Habitat disturbance primarily affect morphological characteristics of the species, like wing morphology or body size (Ribera et al. 2001; Lambeets et al. 2009). In contrast, the alternation of hydrological parameters might more relate to reproductive traits, as shown in this study. This is also supported by Cardenas and Hidalgo (2007) noting that although most ground beetles in floodplains are spring breeders, also autumn breeding can take place at the more elevated plots. They also state that reproduction in spring might be a useful strategy for floodplain ground beetles to avoid hydrological stress for their larvae, as soil humidity in floodplains mainly the variation of reproductive traits, while habitat disturbance parameters explain large parts of dispersal related traits of floodplain ground beetles. Nevertheless, the relatively high explanatory redundancy of the predictor variables suggests that there are other important variables affecting the variation of ground beetle life-history traits.

Conclusions

This study confirms current knowledge about (pre-)adaptations of alluvial ground beetles to floodplain dynamics. As is evident from previous work, traits related to dispersal and reproduction are the most affected ones by flooding and are shown to change strongly with increasing inundation. This trait variation is best explained by a combination of different abiotic variables, indicating that ground beetle life-history traits are affected by multiple environmental stressors. Consequently, future ecological work and floodplain conservation measures should both focus on different facets to maintain the high trait diversity of alluvial ground beetles and the ecological functions they have in ecosystems.

Based on this work I can conclude that life-history traits can be used to predict the occurrence of organisms with certain biological characteristics to altering floodplain dynamics and to better understand ecological patterns (i.e. species occurrences). Therefore, combining traditional taxonomic approaches with current trait-based approaches is a great chance to reveal ecosystem processes and identify "rules" describing how organisms interact with their dynamic environments. Due to the high variety of different traits and strategies to cope with habitat dynamics, I appeal to intensify the application of trait-analyses also for ground beetles to increase our knowledge on processes affecting carabid-environment relationships.

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Appendix I

List of sampled individuals (doi: 10.3897/zookeys.100.1427.app1). File format: Microsoft Excel Spreadsheet (xls).

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Appendix II

Overview of the traits included in the database and the ones used in this study (doi: 10.3897/zookeys.100.1427.app2). File format: Microsoft Word Document (doc).

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RESEARCH ARTICLE



Ground beetle (Coleoptera, Carabidae) assemblages inhabiting Scots pine stands of Puszcza Piska Forest: six-year responses to a tornado impact

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Abstract

Ground beetle assemblages were studied during 2003-08 in the Pisz Forest by comparing stands disturbed by a tornado to undisturbed control stands. The following exploratory questions were put forward. (1) How do the carabid assemblages change during six years following the tornado impact? (2) Does the carabid assemblage recovery begin during the six first post-tornado years? To assess the state of carabid assemblages we used two indices: the MIB (Mean Individual Biomass) and the SPC (Sum of Progressive Characteristics). Carabid assemblages in the disturbed and in the control stands, as expressed by these two indices, were compared using the length of a regression distance (sample distance in a MIB:SPC coordinate system). A cluster analysis revealed that the assemblages of the disturbed and the control stands were different. The tornado-impacted stands produced lower carabid catch rates, but species richness was significantly higher there than in the control stands. They hosted lower proportions of individuals of European species, of large zoophages, and of forest and brachypterous species, than the control stands. The observed reduction in SPC and MIB, and an increase in the regression distances may indicate that the carabid assemblages had not started to recover from the tornado-caused disturbance. Carabid assemblages apparently responded to the tornado in two steps. Firstly, the first three years were characterized by moderate decreases of index values. Secondly, from the fourth to the sixth year after the tornado, many observed changes became magnified. We did not observe clear signals of the recovery of forest carabid assemblages during the six follow-up years.

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Keywords

carabid beetle, disturbance, assemblage structure, Mean Individual Biomass, Sum of Progressive Characteristics, forest fauna

Introduction

Natural disturbances of ecosystems are often short term but characterized by high amplitude. Disturbances are influential for the dynamics of both structure and functioning of ecosystems, and are their integral part. They vary from large scale (e.g., wildfire or hurricane) to local ones that may concern only single or small groups of trees (Pickett and White 1985; Faliński 1986; Pontailler et al. 1997; Bengtsson et al. 2000; Szwagrzyk 2000; Chapin et al. 2002; Wolf et al. 2004).

Following a disturbance, such as a tornado impact, forest stands (here, stand is a patch with a cluster of dominant trees of the same origin, e.g., initiated by a clear-cutting event, and that is surrounded by patches of other types of habitat or trees of different origin) consist of a mosaic of patches impacted to varying degrees, from completely destroyed trees to remnants of untouched forest. The heterogeneity and diversity of microhabitats rapidly increase. In these stands, patches of barren soil, directly exposed to the drying effect of the sun and wind, may be abundant. Under such conditions, the structure and composition of forest-floor vegetation are obviously altered: the soil becomes drier, and the ground surface may be covered by fallen trees and other organic material subject to slow decomposition (Ulanova 2000; Bouget and Duelli 2004; Bouget 2005a, 2005b; Skłodowski 2007a). Such dramatic changes in the environmental conditions in turn alter invertebrate assemblages, including carabid beetles (Bouget 2005c). However, the speed and duration of these alterations are poorly understood.

In the short term, a tornado-caused disturbance changes the functioning and structure of the forest ecosystem. The lack of canopy shelter triggers a regression process (here, a decrease in the number of species associated with closed forests and a simultaneous increase of open-area species), but the emergence of tree saplings starts at the onset of the regeneration succession. The regeneration of a disturbed ecosystem may be faster due to the mosaic-type spatial pattern. For example, under mosaic-like spatial conditions, the emergence and subsequent growth of Scots pine (*Pinus sylvestris*) saplings takes place through the seed pool accumulated in the soil before the disturbance and also through the seed fall from the survived trees. Similarly, stands not impacted by the disturbance may act as sources of organisms recolonizing the disturbed stands.

Carabid beetles have been extensively studied in various, disturbed forest ecosystems (e.g., Ings and Hartley 1999; Bouget 2005c; for a review, see Niemelä et al. 2007). Most studies on carabids in disturbed stands usually cover only the first 2-3 years after the disturbance and – most likely because of this short-term nature – have not revealed information on how quickly carabid assemblages might recover after the disturbance (Bouget 2005c). Follow-up studies lasting more than a couple of years would identify the onset of carabid assemblage recovery.

A unique opportunity to follow disturbance-initiated changes in forest-carabid assemblages over a long time period appeared in July 2002, when a tornado destroyed 33,000 hectares of Scots pine forest in north-eastern Poland. The majority of the damaged stands were soon cleared and planted with pine saplings. However, an untouched area of about 445 ha ("Szast Protective Forest") was left unmanaged. A research project on the tornado impact started in 2003 (Skłodowski and Zdzioch 2005; Skłodowski 2007b, 2007c; Skłodowski and Garbalińska 2007a, 2007b) and continues to date. In the present paper, the following exploratory questions were put forward, using data on the first six post-tornado years: (1) How do carabid assemblages change during the first six years after the tornado-caused disturbance? In particular, we predicted that (a) large forest species with low dispersal power would be less abundant in the disturbed stands, compared to undisturbed control stands, and that (b) non-forest species with good dispersal potential would show the opposite. (2) Does the carabid assemblage recovery begin during the first six years after the disturbance? Earlier Niemelä et al. (1993) showed that carabid assemblages had partially recovered from clear-cut harvesting after a 25-30 years time span in Canada.

Study area and methods

The present study was done in Scots pine forests growing on podzol soils in the Pisz Forest District area, in post-tornado (disturbed stands; Szast Protective Forest) and in intact stands (control; Maskulińskie Forest District). The two study areas were located 20 km apart in order to exclude any influence of tornados in the control stands. The two study areas both hosted three replicate stands (study plots) for each of the following five age classes: 20-40 years old (class I), 40-50 (class II), 50-60 (class III), 60-80 (class IV) and >80 years old (class V). We thus had a total of 15 stands in the disturbed area ('disturbed stands') and 15 in the control area ('control stands'), making up altogether 30 stands (plots).

Five pitfall traps (0.5 l glass jar with a plastic funnel, 12 cm in diameter, containing 100 ml 70% ethylene glycol, and covered by a 20 cm x 20 cm roof a few cm above soil surface to protect the samples against rain and litter) were arranged 15 m apart along a transect in each study stand. The traps were continuously operating between early May and the end of October, and serviced every six weeks. For each carabid individual caught, body length was measured with a microscope and with accuracy of 0.5 mm (from the top of mandibles to the tip of elytra) in order to calculate their biomass following Szujecki et al. (1983).

All specimens captured were identified to species level. The collected data were pooled separately for each stand. A standardized catch rate (individuals/day*trap) was calculated to account for occasional trap losses. The following measures were subjected to analysis: standardized catch rates for each species and individuals, species richness, and the proportion of individuals belonging to various functional groups. For the latter purpose, species were grouped according to geographic distribution (inhabiting European or Palearctic and Holartic regions), habitat association (forest and non forest species), food preference (large zoophages, small zoophages and hemizoophages) and wing morphology (brachypterous species and macropterous species). Species richness was standardized to the lowest number of specimens in the samples using rarefaction (Krebs 1999).

Moreover, two indices were calculated for the total catch: Mean Individual Biomass (MIB; e.g., Szyszko 1990, 1997) and the Sum of Progressive Characteristics (SPC; Skłodowski 1995, 1997, 2009). Both indices are positively correlated with stand age: for MIB, see Szyszko (1983, 1997) and Skłodowski (1995, 2002, 2006a, b), and for SPC, see Skłodowski (1997, 2006a, b, 2009). The latter is calculated as follows:

SPC = 74.9 + 102 * LOG (stand age) (1)

The two values in the formula (1) are model coefficients: 74.9 for the intercept and 102 for the regression slope. SPC is the sum of proportions of species associated with successional "old-growth" stands over all sampled stands. These species are, in particular, large, zoophagous, European forest carabids with autumn development (Skłodowski 1995, 1997, 2002, 2006a, 2009). In assessing the state of carabid assemblages these indices are complementary because they have different characteristics (dynamics) with the age of the forest: MIB increases more rapidly in stands older than 20 years, while SPC increases rapidly somewhat later, 40 years after the initiation of secondary succession.

The MIB and SPC indices can be presented in an X-Y coordinate system to produce an SPC/MIB model that efficiently summarizes the successional development status of species assemblages (Skłodowski 1997, 2009). Carabid assemblages inhabiting old-growth stands scatter in the upper right-hand corner of such a graph, while assemblages of clear cut areas (recent, severe disturbance) tend to be located down and to the left. In this coordinate system, the distance between the old-growth stands and newly-planted forest cultures reflects the so-called "regression distance" that may be calculated using the cosine rule (Skłodowski 1995, 1997, 2009). As a regression of carabid assemblages we assume transformation of functional structure of assemblages characterized by high level of ecological successive development (ex. inhabiting old growth stands) into assemblages characterized by low level of successive development (ex. inhabiting clear cut areas or young coppices). This means an increase of species number due to colonization of open habitat species and a decline of forest species. Also the participation of individuals belonging to big zoophageous species decreases while the participation of small hemizoophageous, non forest species with high dispersal powers, increases in the assemblages. The angle at which a vector connecting extreme points is directed reflects the trend of the change, being either regressive or regenerating (Skłodowski 1995, 1997, 2009). By calculating the square root of the product MIB×SPC, one obtains an average value for MIB:SPC coordinate pairs, thus producing a value that reflects the developmental phase of carabid assemblages, which can be tested statistically. The difference between the roots of the product MIBxSPC in assemblages of the disturbed and control stands gives a regression distance between the two stand types. In other words, the regression distance shows a difference between two phases of succession that can be expressed as a distance between two compared assemblages plotted on a graph.

Prior to the statistical analyses, data were tested for the normality of distributions and variance homogeneity using Shapiro-Wilks and Levene's statistics (Statistica; Stat-Soft Inc. 2008). For data with equal variances and normal distribution, ANOVA with repeated measures was applied to assess the similarity between disturbed and control stands for most comparisons. However, Mann-Whitney U test was used to examine the proportion of individuals of forest species due to a lack of data normality.

The dependence of carabid recovery in time since the tornado was tested using ANOVA with repeated measures (if normality and variance homogeneity assumptions were fulfilled) or Mann-Whitney U test (Statistica; StatSoft Inc. 2008). We verified the impact of the tornado on the proportion of individuals of European species, on MIB and SPC, as well as on the regression distances. We thus compared two stand types: disturbed versus control, both with nested plots of five age classes (I–V), each class being replicated three times for both stand types. The six years (2003-2008) defined the repeated measures. Subsequent pair-wise comparisons for significant differences were done using the least significant difference (LSD) *post hoc* test. Mann-Whitney U test was used to verify the impact of the tornado on the total catch rate, number of species, proportion of individuals of forest and eurytopic species, large and small zoophages, hemizoophages, and brachypterous and macropterous species. We examined compositional similarities among stands of different age and habitat type (disturbed vs control) using Ward cluster analysis based on Euclidean distances (Statistica; StatSoft Inc. 2008).

Results

During the first six years following the tornado impact, the disturbed stands produced a total of 18,022 individuals belonging to 82 species, while the control stands produced 19,550 individuals representing 53 species. Altogether these made up 37,572 specimens representing 90 species. The catch rate over all years was 0.18 individuals/ trap*day in the disturbed and 0.26 individuals/trap*day in the control stands (Z = 5.29; p < 0.001). This difference was statistically significant for the years 2003-2006. During 2007-2008 the catch rate of carabids in the disturbed stands was marginally higher than in the control (Table 1).

The mean number of carabid species was greater in the disturbed than in control stands throughout the study: 11.13 vs. 8.33 (Z = 4.60, p < 0.001). During 2004-2005, the number of species was similar in the disturbed and control stands (Table 1) but during 2006-2008), the number of species was higher in the former, the difference being most pronounced in 2007. These observations reflect the ongoing process of species turnover in the disturbed stands: forest species decline and non-forest species and/ or species absent from control stands increase, such as *Amara aenea, A. communis, A. equestris, Harpalus flavescens, H. solitaris* and *Microlestes minutulus*.

Table I. Mann-Whitney U test for the total carabid catch rate (number of individuals/trap*day), rarefaction standardized species richness, and the proportion of individuals of different ecological, trophic and dispersal groups of carabids. Disturbed (D) and control (C) stands were compared during 2003-2008; test statistics (U), statistical significance (asterisks), and mean and SD values for D and C are shown. Significance levels: *** – p < 0.001; ** – p < 0.01; * – p < 0.05; n.s. – p > 0.05.

	2003	2004	2005	2006	2007	2008			
Catch rate									
U	1.929 *	4.646 ***	3.380 ***	3.733***	n.s.	n.s.			
D	0.11±0.06	0.06±0.02	0.14±0.07	0.15±0.06	0.36±0.23	0.28±0.12			
С	0.20±0.10	0.25±0.06	0.24±0.09	0.29±0.09	0.34±0.14	0.22±0.06			
Spec	ies number								
U	4.314 *	3.380 ***	n.s.	3.443 ***	4.646 ***	3.899 ***			
D	9.05±1.79	6.93±1.56	8.65±1.66	11.79±2.45	16.43±3.89	13.92±3.86			
С	6.31±0.87	8.81±1.15	8.72±1.15	8.61±0.78	8.51±0.92	9.01±1.32			
Fore	st species								
U	4.148***	3.795***	4.500***	4.646***	4.646***	4.646***			
D	87.7±11.11	87.0±11.10	86.7±8.4	65.8±17.11	57.9±15.31	46,3±15.43			
С	98.6±2.08	98.7±1.61	97.8±1.56	98.5±0.91	99,2±1.12	96,5±4.15			
Eury	rtopic species								
U	2.966**	2.903**	4.653***	4.646***	4.646***	4.646***			
D	7.1±8.17	5.9±5.33	8.2±5.95	23.4±15.78	34.5±13.23	47.7±15.94			
С	1.2±1.55	1.1±1.58	0.5±0.71	0.5±0.64	0.6±0.87	2.5±3.95			
Larg	e zoophages								
U	1.494*	n.s.	n.s.	2.737***	2.115**	4.272***			
D	60.3±17.11	63.4±16.49	72.7±12.4	43.0±21.21	45.7±17.67	33.2±11.46			
С	71.8±10.89	67.2±8.88	66.2±11.74	63.0±10.33	59.8±13.51	63.7±12.84			
Sma	ll zoophages								
U	n.s.	n.s.	3.526***	n.s.	3.650***	2.862**			
D	31.3±14.58	26.6±12.55	17.4±7.18	30.2±11.88	19.6±10.49	21.4±11.11			
С	28.1±11.04	32.7±8.82	33.6±11.76	36.6±10.19	39.6±13.27	34.3±11.75			
Hen	nizoophages								
U	4.604***	3.899***	4.521***	4.646***	4.646***	4.646***			
D	8.5±10.08	10.0±9.18	9.8±7.88	26.8±16.34	34.6±16.17	45.4±16.50			
С	0.1±0.31	0.1±0.19	0.3±0.41	0.4±0.71	0.6±1.21	2.0±3.64			
Brachypterous species									
U	n.s.	n.s.	n.s.	3.816***	4.134***	4.646***			
D	72.5±15.78	65.3±17.07	78.4±11.02	58.4±16.75	54.3±15.71	42.1±12.72			
С	75.2±9.52	68.9±8.56	80.9±7.38	83.2±5.00	85.6±5.18	79.6±7.62			
Mac	Macropterous species								
U	n.s.	n.s.	n.s.	3.028**	3.892***	4.438***			
D	21.5±13.53	31.1±16.37	20.3±11.25	33.2±17.20	37.5±16.00	50.0±15.88			
С	23.5±8.60	29.8±8.78	18.6±7.43	16.3±5.00	14.0±5.06	19.1±7.13			

During the six study years, the proportion of individuals of species with European distribution gradually decreased in the disturbed stands; as a consequence, the shares of Palaearctic and Holarctic species increased there (Fig. 1). Considering the entire six-years period, the average share of species with European distribution was 35.2% in the disturbed and 58.8% in the control stands (LSD test, p < 0.001). The difference in the proportion of individuals of European species between disturbed and control stands increased from 5.0% (55.8% vs. 50.8%) in 2003 to 45.3% (70.9% vs. 25.6%) in 2007 (Fig. 1).

The dominance structure of carabids changed from 2003 to 2008. In the disturbed stands in 2003, the Palaearctic *C. arvensis* (28.2%) was nearly equally abundant as the European *C. violaceus* (24.8%). However, in 2007, the Palaearctic *C. arvensis* and *A. lunicollis* dominated, altogether making up 62.1% of the total catch in the disturbed stands, and 15.1% in the control stands.

During the six years of study, the proportion of individuals of forest carabids was on average 26.3% lower in disturbed than in control stands (71.9% *vs.* 98.2; Z =10.74; p < 0.001). Until 2005, individuals of forest species were 87.7%-86.7% in the disturbed stands and 97.8%-98.7% in the control stands. Since 2006, the proportion of individuals of forest carabids in the disturbed stands decreased, reaching an alltime low of 46.3% in 2008. In the control stands for the same period, the proportion consistently remained around 96.5% (Table 1). These differences can be seen at the species level too. In the disturbed stands, the dominant species during 2003-2008 was the forest dweller *C. arvensis* (up to 43.9 ± 15.1% of the total catch in the disturbed and 26.1 ± 11.50 in the control stands). Simultaneously, the proportion of many other forest species gradually decreased: *C. hortensis*, *C. violaceus* and *P. oblongopunctatus* (Appendix A).

In the disturbed stands, forest species decreased and eurytopic species increased during the six study years. Eurytopic carabid individuals made up on average 21.1% of the catch in the disturbed and 1.1 % in the control stands (Z = 10.08; p < 0.001). During the first three years following the tornado, the proportion of individuals of eurytopic species in the disturbed stands varied between 5.9% and 8.2%; however, since the fourth year (2006), the proportion increased to, on average, 47.7% in 2008 (Table 1). The increase of eurytopic carabid individuals in successive years was significant (from 2005 to 2008; Z = 2.16 to 3.23, p = 0.028 to 0.001). Eurytopic species that dominated in the disturbed stands included *Amara lunicollis* (6.6%-36.7%), *Calathus erratus* (2.8%-4.8%) and *Harpalus rufipalpis* (3.3%-5.0%; Appendix B). Open-area species could also be found in the disturbed stands at a rather constant proportion of 5.1%-10.8%.

Considering the entire period of study, the proportion of individuals belonging to large zoophages in the disturbed stands was, on average, 12.2% lower than that in control stands (53.1% vs. 65.3%; Z = 3.93; p < 0.001). However, in 2004 and 2005 (second and third year after the tornado), the difference was not significant (Table 1). In the control stands in 2003-2005, large species dominated: *C. arvensis* (20.0%-24.9%), *P. niger* (20.3%-24.7%), *C. violaceus* (10.6%-16.8%) and *C. coriace*-



Figure 1. The proportion of individuals of European carabid species living in tornado-impacted and in control stands during 2003-2008.

us (5.4%-8.3%). In the disturbed stands, on the other hand, *C. arvensis* was the most numerous species (24.4-43.9% of the total catch), *C. violaceus* contributed 19.6%-25.4%, and *P. niger* made up 6.4%-7.7% there. During 2006-2008, the proportion of large zoophages was 14.0%-30.4% lower in disturbed than in control stands. During the six years of study, also the proportion of individuals of small zoophages decreased in the disturbed stands from 31.3% to 21.4% but increased in the control stands from 28.1% to 34.3% (Table 1).

The decreasing proportion of individuals of either large or small zoophages in the disturbed stands was accompanied by an increase of the hemizoophages; their proportion was on average higher in disturbed than in control stands (22.5% *vs.* 0.6%; Z = 10.84, p < 0.001). The disturbed stands had apparently been subject to colonization by hemizoophages since the first year after the tornado (2003), but the proportion of their individuals started to significantly increase in the fourth year after the tornado (2006). In the year 2008, individuals of hemizoophages contributed > 45% of all individuals in the disturbed stands (Table 1). The most frequent hemizoophage caught in disturbed stands was *A. lunicollis* that dominated the catch in 2008 (36.7%), replacing *C. arvensis* (17.2%) as the most abundant species there (Appendix B).

During 2003-2008, the average proportion of individuals of the brachypterous species in the control stands was 78.9%, while in the disturbed stands it was 61.8% (Z = 6.14, p < 0.001). During the first three years of study (2003-2005), the difference in proportion of individuals of wingless carabids between disturbed and control stands was non-significant (Table 1). Since 2006, the proportion of individuals of brachypterous species decreased in the disturbed stands from 58.5% to 42.1%, and

the difference between disturbed and control stands was 37.5% in 2008 (42.1% vs. 79.6%; Table 1). Wingless species decreased and macropterous species increases in the disturbed stands. Over the whole study period, the individuals of macropterous species made up 32.3% in the disturbed and 20.2% in the control stands (Z = 4.56, p < 0.001). The increase in the proportion of macropterous species in the disturbed stands apparently started in 2006, when the macropterous A. *lunicollis* started to become abundant (Appendix B). Individuals of wing-dimorphic species became slightly more abundant in the disturbed stands, but never reached 10% during the study years (averages 5.9% for disturbed and 0.9% for control stands; Z = 7.10, p < 0.001).

A cluster analysis (Fig. 2) for the carabid data similarity indicated faunal differences between disturbed and control stands, indicated by two stand clusters already in the first year after the tornado (2003). The analysis also lumped the oldest disturbed stand into the cluster of control stands. In the subsequent years, the carabid assemblages of the disturbed and control stands were distinctive, with decreasing similarity. Fig. 2 shows similarity diagrams for 2003 and 2008. These observations were somewhat supported by the indices: the Renkonen index for the similarity between disturbed and control stands was 64.4% in 2003 and 45.8% in 2008 (Table 3).

The response of carabid assemblages to the tornado disturbance could also be demonstrated using MIB and SPC indices and the regression distances retrieved from a SPC/ MIB model (see Material and methods). The mean MIB during the six years of study was 214.3 mg for the disturbed and 303.0 mg for the control stands (LSD test; p < 0.001; Table 2).

During the first three years after the tornado (2003-2005), a relatively small decrease of about 20.2 mg in MIB was observed in the disturbed stands (from 306.7 mg to 286.5 mg) and about 55.1 mg in the control stands (from 388.0 mg to 332.9 mg; Fig. 3). In 2006, MIB was 134.0 mg lower in disturbed than in control stands (149.4 mg *vs.* 283.4 mg; LSD test, p < 0.001). The largest difference in MIB between disturbed and control stands was in 2008 (121.1 mg *vs.* 260.8 mg; LSD test, p < 0.001; Fig. 3).

Considering the entire study period, the SPC values were on average 200.0 in the disturbed and 280.0 in the control stands (LSD test, p < 0.001; Table 2). In 2006, the difference in SPC between disturbed and control stands was 111.1 units (180.5 *vs.* 291.5; LSD test, p < 0.001). The highest difference was 128.8 units in 2008 (268.8 *vs.* 144.0; LSD test, p < 0.001). Both ANOVA and LSD test confirmed the reduction of MIB and SPC in the disturbed stands, compared with the control stands (Table 2).

In the first year after the tornado (2003), the mean regression distance of carabid assemblages between disturbed and control stands was 79.0 ± 47.9 (Fig. 4). In 2004 and in 2005, the regression distances were 61.8 ± 44.0 and 66.2 ± 35.4 , respectively. The regression distance peaked in 2006, being 174.8 ± 28.1 (LSD test, p < 0.001), and remained high until 2008 (188.1 ± 29.4).



Figure 2. Dendrograms of species similarity of carabid beetle assemblages inhabiting tornado-impacted (D) and control stands (C) in age classes I–V (see text) in the first (2003) and last (2008) years of observation. The analysis was performed with the Ward method and Euclidean distance as the measure of similarity.

Discussion

The environment under study had been subject to a major disturbance that severely affected carabid assemblages in the impacted stands: a tornado. During the first few years after the disturbance, soil weight humidity was 1.6% lower in the disturbed than in the control stands; moreover, soil nitrogen concentration was higher, and the lack of tree crowns that usually acidify the rain water may have led to an increase in the soil pH (Skłodowski 2007a). The soil of the disturbed stands, compared to the control stands, was characterized by a lower rate of soil CO₂ diffusion and lower decomposition rate of

Table 2. Repeated-measures ANOVA for the proportion of individuals of European species, for MIB and SPC indices, and for the regression distances describing the carabid assemblage of stands disturbed by the 2002 tornado, and in intact control stands. Factors: Stand (disturbed vs control stands), Age (stand age class I-V), and Time (2003–2008). LSD post hoc test explanation: 1-3 (2003-2004), 4-6 (2005-2006), D (disturbed stands), C (control stands), I-V (age class). Significance levels: *** – p < 0.001; ** – p < 0.01; * – p < 0.05; n.s. – p > 0.05).

Effect	SS	df	MS	F	Р	Post-hoc test		
European sp.						-		
Time	3422.2	5	684.4	7.82	< 0.001	1-3 > 4-6**		
Time*Stand	8879.0	5	1775.8	20.28	< 0.001	D < C***		
Time*Age	1576.4	20	78.8	0.90	n.s.			
Time*Stand*Age	1634.2	20	81.7	0.93	n.s.			
Error	8754.9	100	87.5					
MIB								
Time	694244.8	5	138849.0	48.03	< 0.001	1-3 > 4-6***		
Time*Stand	65289.1	5	13057.8	4.52	< 0.001	D < C***		
Time*Age	105863.3	20	5293.2	1.83	0.0269	I-III < IV-V**		
Time*Stand*Age	56179.9	20	2809.0	0.97	n.s.			
Error	289092.1	100	2890.9					
SPC	SPC							
Time	69415.4	2	13883.1	20.60	< 0.001	1-3 > 4-6***		
Time*Stand	92119.1	2	18423.8	27.33	< 0.001	D < C***		
Time*Age	10586.2	20	529.3	0.79	n.s.			
Time*Stand*Age	11353.2	20	567.7	0.84	n.s.			
Error	67402.1	100	674.0	0.84				
Regressive distance								
Time	200832	5	40166	14.24	< 0.001	1-3 < 4-6***		
Time*Age	45559	20	2278	0.81	n.s.			
Error	141080	50	2822					

organic matter (Skłodowski 2007a). In the disturbed stands, mosses and dwarf shrubs may consequently have suffered: *Pleurozium schreberi*, *Dicranum* spp. and *Vaccinium myrtillus*. However, the percent covers of *V. vitis-idaea* and *Deschampsia flexuosa* – species favored by an increased amount of light and soil nitrogen supply (Skłodowski and Buszyniewicz 2007; Sławski 2007) – had increased. The above characteristics suggest drastic changes in environmental conditions of the disturbed stands. These changes were in turn accompanied by alterations in the carabid assemblage structure.

During the entire six-years period following the tornado impact, carabid richness was 33% higher in disturbed than in control stands (Table 1). This finding is in agreement with several studies done in tornado-impacted stands (Otte 1989a, 1989b; Bouget and Duelli 2004; Bouget 2005c; Gandhi et al. 2008). Despite this higher carabid species richness, carabids were generally less abundant in the disturbed stands for the second and third post-tornado summers. Similarly, Bouget (2005c) and Gandhi et al. (2008) observed up to two times lower catch rates in tornado-impacted than in adjacent intact forests 2-4 years after the tornado. As late as post-tornado years 5 and

Index	2003	2004	2005	2006	2007	2008
Sørensen	58.46	55.17	68.97	67.44	65.91	65.17
Renkonen	64.43	68.00	55.37	45.78	36.19	45.80

Table 3. Sørensen index for compositional similarity and Renkonen index for dominance structure for carabid assemblages inhabiting tornado-disturbed and intact control stands during 2003–2008 (% units).

6, species richness became higher in the disturbed than in the control stands (Table 1), which suggests a delayed response for a tree-fall caused increase in openness and micro-climatic changes. During the first three years after the tornado (2003-2005), some forest species declined (e.g., *C. violaceus*) while non-forest species had not yet started to colonize the tornado-impacted forests. Many non-forest species appeared in the fourth post-tornado year, such as *A. aenea, A. communis, A. equestris, A. lunicollis, H. flavescens, H. solitaris* and *M. minutulus*.

Generally, carabid species richness is positively influenced by disturbances in forest ecosystems, such as wildfire (e.g., Szyszko 1990; Skłodowski 1995; Fernández Fernández and Saldago Costas 2004; Buddle et al. 2006; Koivula and Spence 2006; Paquin 2008) and clear-cutting (e.g., Szujecki et al. 1983; Szyszko 1983, 1990; Niemelä et al. 1993; Haila et al. 1994; Skłodowski 1995, 1997, 2006a, 2006b, 2008, 2009; Koivula 2002a, 2002b; Koivula et al. 2002; du Bus de Warnaffe and Lebrun 2004; Huber and Baumgarten 2005; Martikainen et al. 2006). An increase in carabid species richness in disturbed forest ecosystems is one consequence of the transformation of an earlier structurally homogenous forest stand (only one or a few tree species with even age structure of dominant trees) into a mosaic of smaller sub-patches that have been impacted by the disturbance to varying degrees (Otte 1989a, 1989b; Niemelä et al. 1996, 2007; Koivula et al. 2002; Bouget and Duelli 2004; Bouget 2005c; Koivula and Spence 2006; Pearce and Venier 2006; Ulyshen et al. 2006; Gandhi et al. 2008; Paquin 2008). Open gaps become rapidly colonized by open-area and eurytopic species (Koivula 2002a, 2002b); besides, also most forest species may survive (Buddle et al. 2006; Koivula and Spence 2006). Because the rate of immigration by species not associated with closed canopy is higher than the rate of decline of canopy-closure specialists, the total number of species increases, at least in the short term (Niemelä et al. 1988, 1993, 2007; Koivula 2002a, 2002b; Bouget 2005c; Huber and Baumgarten 2005).

The decrease in epigeic carabid catch rates can be related with the development of forest floor vegetation (Skłodowski 2002, Poole et al. 2003, Sroka and Finch 2006, Taboada et al. 2006).

Another explanation could be the fact that the decline of forest species in the disturbed stands was not accompanied by the appearance of non-forest species during the first three years after the tornado. The disturbed stands started to be colonized by eurytopic and open-area species (particularly by *A. lunicollis*) as late as in 2006, which resulted in an increase in the total catch rate. Yet another explanation might be obtained from weather conditions. Many indices peaked in 2006. Over the entire period of study, that year was characterized by cold winter air temperature (-32,2°C near the ground) and high summer temperature (maximum air temperature +32,6°C) accom-



Figure 3. The MIB/SPC model of carabid assemblages living in tornado-impacted (D) and control stands (C) during 2003-2008.

panied by the lack of precipitation (data from the Hydrologic-Meteorological Station of Olsztyn; Biuletyn Państwowej Służby Hydrologiczno-Meteorologicznej IMiGW).

During 2007-2008, carabids with an European range, including western Siberia, decreased (Fig. 1). Similar changes have previously been associated with other disturbances, such as clear-cutting and wildfire (Szyszko 1983, 1990; Skłodowski 1995, 1997). In the disturbed stands, a decrease of forest species (including specialists and succession generalists) was observed. In the last study year these species contributed to about 46% of all carabids in disturbed stands in comparision to 96% in the control (Table 1), which is in line with Otte (1989a, 1989b), Bouget and Duelli (2004), Bouget (2005c) and Gandhi et al. (2008). Eurytopic species, characterized by high tolerance against changing environmental conditions, slowly appeared in the posttornado stands. Niemelä et al. (1993) and Koivula et al. (2002) found that clearcutting may not significantly influence the frequency of eurytopic species during 2-3 years after the disturbance. However, in the tornado-disturbed stands, studied here, the proportion of euryptopic species increased significantly. This increase was associated with a comparable decline of forest carabids and contributed to the elevated catch rate of eurytopic carabids and consequently total species richness in 2006-2008 (see also Niemelä et al. 1993, 1996, 2007; Skłodowski 1995, 1997, 2002; Bouget 2005c; for clear-cut areas, see Szujecki et al. 1983; Szyszko 1983, 1990; Koivula et al. 2002; Elek et al. 2005; Huber and Baumgarten 2005; for post-fire forests, see Fernández Fernández and Saldago Costas 2004; Pearce and Venier 2006; Ulyshen et al. 2006).

The delayed tornado response of three years by carabids was most clearly seen in the decreasing catches of both large and small zoophages and an accompanying, up to



Figure 4. Regression distances between carabid assemblages inhabiting post-tornado (disturbed) and control stands during 2003-2008.

45.5%, increase in the share of hemizoophages (Table 1). At the beginning of the present study, large zoophages dominated the carabid assemblages in both the tornado-impacted and the control stands, but since 2006 the impacted stands became dominated by hemizoophages, particularly *A. lunicollis*. Otte (1989a) and Gandhi et al. (2008) recorded an appearance of hemizoophagous *Amara* and *Harpalus* species two years after the tornado. Similarly, Bouget (2005c) found that carabid species characteristic for post-tornado stands are hemizoophages, such as *Amara plebeja* and *Amara similata*. The increase of hemizoophages and the decrease of large zoophages are general patterns following a disturbance, such as clear-cutting and wildfire (Szujecki et al. 1983; Szyszko 1983, 1990; Skłodowski 1995, 1997, 2006a, 2006b). The colonization of *Deschampsia flexuosa* in the tornado-impacted stands (Skłodowski and Buszyniewicz 2007; Sławski 2007) may favor seed-eating hemizoophages, such as *A. lunicollis, H. rufipalpis* and *H. rufipes*.

In the tornado-impacted stands, brachypterous species declined while macropterous species associated with arid, sunny, grassy habitats increased (Burakowski et al. 1973, 1974; Niemelä et al. 1993; Koivula 2002a; Koivula et al. 2002; Koivula and Niemelä 2003; Huber and Baumgarten 2005). This tendency became particularly clear in 2006 (Table 1) and is in line with Otte (1989a), Du Bus de Warnaffe and Lebrun (2004), Bouget (2005c) and Gandhi et al. (2008). Similar observations have been made in post-fire areas (Fernández Fernández and Saldago Costas 2004; Skłodowski 1995), in clear-cuts (Szujecki et al. 1983; Szyszko 1983, 1990; Skłodowski 1995, 1997, 2006a, 2006b; Butterfield 1997; du Bus de Warnaffe and Lebrun 2004; Elek et al. 2005), and in clear-cuts with prescribed fire (Martikainen et al. 2006).

The species composition of tornado-impacted stands was different in impacted and in control stands. Similar decreases in species similarity in carabid assemblages between
post-tornado and control stands have been reported by Otte (1989a) and Gandhi et al. (2008). The similarity of carabid assemblages between disturbed and control stands decreased with time: the lowest similarity was recorded in 2007. In the subsequent years the faunistic differences became more pronounced due to the species-exchange process and to the changing dominance structure of the assemblages inhabiting the disturbed ecosystem. On the other hand, the observed increase in the compositional similarity along with an increase in the structural dominance in 2008 suggests a slowing-down of the tornado-caused changes in the carabid assemblages.

The effect of the tornado on forest carabids was best illustrated by the MIB and SPC indices (Fig. 3). The decrease in MIB in the control stands throughout the study may have resulted from an increasing proportion of the small zoophage C. micropterus and proportional decreases of the larger C. arvensis and C. violaceus. The pattern was different in the disturbed stands where both indices used for the construction of the SPC/MIB model had been continuously decreasing, visualized by their gradual movement towards the bottom-and-left-hand corner in Fig. 3. Such a pattern suggests an enhanced regression (changes in structure and functioning of assemblages from higher to lower levels of succession development) of carabid assemblages and their habitat after disturbance (Skłodowski 1995, 1997, 2009). The unequal rate of change of indices between disturbed and control stands is worth noting. During 2003-2005, MIB and SPC marginally decreased in the tornado-impacted stands, and the regression changes, as expressed in the length of the regression distance, seemed not to grow (Fig. 4). A shorter regression distance means smaller differences in the structure and functioning of carabid assemblages between disturbed and control stands. Based on the SPC index alone, one may come to the conclusion that the carabid assemblages inhabiting post-tornado stands in 2005 may be considered typical for 30-70-years old stands (as predicted in a calibrated SPC/MIB model; see Skłodowski 1995, 1997, 2009). In 2006 the loss of carabids associated with mature, undisturbed stands is also worth noting: the decline of species with an autumn development, European, and big forest zoophages species also influenced the decrease of SPC and the regression distance more than doubled, suggesting increasingly pronounced changes in the structure and functioning of carabid assemblages (Fig. 3). Until 2008, no significant changes in the direction of succession in the tornado-damaged stands were observed; as a matter of fact, during 2006-2008 the rate of faunal change slowed down, indicated by only slight changes in MIB, SPC and the regression distances. A decrease in SPC, observed especially in the sixth year after the tornado, was equivalent with a change of carabid fauna to a phase typical for 3-10-years old Scots pine stands (the calibrated SPC/MIB model; Skłodowski 1995, 1997).

The most important change in the carabid assemblages of tornado-disturbed stands was the change toward a species composition typical for early-successional, regenerating forests: carabids associated with late-successional forests were partly replaced by eurytopic and pioneer species characteristic of early successional phases. The chronology of the observed successional changes is particularly interesting. The most drastic change in the carabid fauna takes place during the first three years following a disturbance (Szyszko 1990, Koivula et al. 2002). In the present study, however, changes in

the post-tornado stands really accelerated 4-6 years after the tornado impact, which suggests that the most drastic alterations in carabid assemblage, caused by the tornado, are delayed by 4-6 years. Besides, based on the present results it is reasonable to assume that faunal changes will continue and possibly become more pronounced more than six years after the disturbance event, even though the rate of change may be slower. It has to be emphasized that no signs of recovery of the impacted carabid assemblages were observed during this study.

This six-year study demonstrated a long-lasting down-turn of the forest carabid assemblage, suggesting a substantial change in this environment. Field data collected in the seventh year after the tornado impact, that is 2009, are subject to analyses. Even though these data have been only preliminarily elaborated so far, it seems that the carabid communities have eventually started to recover. Among other signals of recovery, forest species seem to increase in abundance, and the values of MIB and SPC are also increasing, and the regression distance between disturbed and control stands has decreased. Following the emergence of new, naturally regenerated seedling trees (apart from 2-3 years old pine and birch) one can expect that the subsequent years will be characteristic of both the recovery of forest-carabid fauna, and the recovery of the entire ecosystem. It is noteworthy that in the Pisz Forest the trees that survived are not threatened by under-the-bark pests, due to the fact that the hurricane disturbance of the forest had taken place in the month of July, thus disrupting the main season of these pests' flight and the period of egg lying, a yearly spring event. Moreover, in the subsequent years, the injured trees became dry and did not attract dead-wood dependent insects any more. Therefore, a reasonable suggestion is to retain some fallen trees in the tornado-impacted stands and wait for the spontaneous natural regeneration of the forest ecosystem.

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Appendix A

The most abundant carabid species and their participation in communities inhabiting disturbed stands and controls stands during observations performed in years: 2003-2008.

Control		Disturbed				
2003						
Carabus arvensis	24.4 ± 15.1%	Pterostichus niger	24.7 ± 12.4%			
Carabus violaceus	25.4 ± 15.2%	Carabus arvensis	$20.0 \pm 11.6\%$			
Pterostichus oblongopunctatus	12.4 ± 9.5%	Pterostichus oblongopunctatus	23.3 ± 8.8%			
Calathus micropterus	11.9 ± 8.8 %	Carabus violaceus	16.8 ± 10.1%			
Pterostichus niger	7.7 ± 5.5%	Carabus coriaceus	7.1 ± 5.2%			
2004						
Carabus arvensis	31.7 ± 15.8%	Pterostichus oblongopunctatus	29.6 ± 8.7%			
Pterostichus oblongopunctatus	19.6 ± 12.3%	Carabus arvensis	24.9 ± 12.8%			
Carabus violaceus	19.5 ± 12.4%	Pterostichus niger	20.3 ± 8.5%			
Pterostichus niger	6.8 ± 5.1%	Carabus violaceus	12.2 ± 6.5%			
C		Carabus coriaceus	5.4 ± 3.3%			
2005						
Carabus arvensis	43.9 ± 15.1%	Carabus arvensis	22.3 ± 9.0%			
Carabus violaceus	20.5 ± 11.1%	Pterostichus niger	21.8 ± 7.9%			
Pterostichus niger	6.4 ± 4.6%	Calathus micropterus	14.5 ± 13.0%			
Pterostichus oblongopunctatus	7.6 ± 5.4%	Pterostichus oblongopunctatus	16.8 ± 7.0%			
Amara lunicollis	6.6 ± 5.8%	Carabus violaceus	10.6 ± 5.4%			
Calathus micropterus	5.7 ± 3.9%	Carabus coriaceus	$8.3 \pm 4.2\%$			
2006						
Carabus arvensis	31.7 ± 23.9%	Pterostichus niger	27.3 ± 9.4%			
Calathus micropterus	15.2 ± 11.6%	Calathus micropterus	$22.2 \pm 10.1\%$			
Amara lunicollis	12.7 ± 12.2%	Carabus arvensis	17.4 ± 6.5 %			
Carabus violaceus	7.1 ± 5.0%	Pterostichus oblongopunctatus	$14.4 \pm 4.3\%$			
		Carabus violaceus	8.6 ± 3.0%			
2007						
Carabus arvensis	31.4 ± 22.2%	Pterostichus niger	30.5 ± 12.4%			
Amara lunicollis	22.9 ± 14.3%	Calathus micropterus	25.5 ± 12.1%			
Calathus micropterus	8.4 ± 3.7%	Carabus arvensis	15.1 ± 6.7%			
Pterostichus niger	9.1 ± 7.4%	Pterostichus oblongopunctatus	$13.2 \pm 4.8\%$			
Harpalus rufipalpis	5.0 ± 3.3%	Carabus violaceus	7.8 ± 4.1%			
2008						
Amara lunicollis	36.7 ± 18.7%	Carabus arvensis	26.1 ± 11.5%			
Carabus arvensis	$17.2 \pm 11.0\%$	Pterostichus niger	$20.2 \pm 10.0\%$			
Calathus micropterus	8.7 ± 5.7%	Pterostichus oblongopunctatus	16.4 ± 6.4%			
Pterostichus niger	$10.4 \pm 8.1\%$	Calathus micropterus	15.0 ± 9.3%			
Carabus violaceus	5.1 ± 3.8%	Carabus violaceus	11.8 ± 3.4%			

Appendix B

The changes of dominance indices of some of the most abundant carabid species inhabiting disturbed stands D and controls stands C.

Species	Stand type	2003	2004	2005	2006	2007	2008
Amara lunicollis	D	1.15	2.57	6.63	12.66	22.92	36.69
(Schiodte 1837)	С	0	0.04	0.06	0.19	0.28	1.2
Calathus erratus	D	3.07	1.09	0.31	3.29	3.79	5.1
(C.R. Sahlberg 1827)	С	0.29	0.2	0.18	0.09	0.06	0.52
Calathus micropterus	D	11.95	2.96	5.8	15.21	8.38	8.79
(Duftschmid 1812)	С	2.89	2.28	14.52	22.28	25.49	15.01
Carabus arvensis	D	24.36	31.68	43.89	31.68	31.44	17.15
Herbst 1784	С	19.99	24.94	22.32	17.39	15.11	26.14
Carabus coriaceus	D	0	0	0	0	0	0.01
(Linnaeus 1758)	С	7.13	5.39	8.38	4.93	2.88	2.74
Carabus hortensis	D	1.09	1.54	0.81	0.17	0.26	0.14
Linnaeus 1758	С	0.73	1.12	0.86	0.85	0.81	0.51
Carabus violaceus	D	25.37	19.56	20.48	7.06	4.45	5.14
Linnaeus 1758	С	16.79	12.2	10.66	8.6	7.89	11.75
Harpalus rufipalpis	D	0.31	0.33	0.41	3.44	4.96	3.22
Sturm 1818	С	0	0	0	0.02	0.02	0
Pseudoophonus rufipes	D	0.85	0.6	1.34	3.81	3.92	1.74
(Degeer 1774)	С	0	0	0	0.01	0.02	0.02
Pterostichus niger	D	7.71	6.84	6.41	3.64	9.11	10.38
(Schaller 1783)	С	24.67	20.32	21.8	27.31	30.53	20.2
Pterostichus oblongopunctatus	D	12.41	19.61	7.63	4.28	1.69	1.89
(Fabricius 1787)	С	23.34	29.65	16.84	14.38	13.25	16.39

RESEARCH ARTICLE



Carabid beetle diversity and mean individual biomass in beech forests of various ages

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Abstract

Carabid beetle diversity and mean individual biomass (MIB) were analysed in three different successional stages of beech tree stands (60, 80 and 150 years old). Carabid beetles were captured using pitfall traps placed at nine sites (three per age class) in the Papuk Mountain of East Croatia during 2008. A cluster analysis identified three groupings that corresponded to the beech age classes. MIB values increased with stand age, ranging from 255 in 60-year-old stand to 537 in the oldest forests. The 80-year-old stand showed the highest species richness and diversity values. With respect to species composition, large species such as *Carabus scheidleri* and *Carabus coriaceus* were dominant only in the oldest forests. Furthermore, species that overwinter in the larval stage were more abundant in the oldest forests (45% of the total number of individuals from the 150-year-old stand) than in the younger ones (20% of individuals from 60-year-old, and 22% of individuals from 80-year-old stands). Our results showed that the analyses of species composition and life history traits are valuable for estimating the conservation values of older forests. Although the investigated sites form part of a continuous forested area and are only a couple of kilometres apart, MIB values detect significant differences associated with forest age and can be a useful tool in evaluating the degree to which a forest reflects a natural state.

Keywords

carabid beetles, MIB, over-wintering stages, beech forests succession, Papuk Nature Park

Introduction

In forest management, sustainability is an internationally accepted goal. One technique by which sustainability is assessed is through the monitoring of indicator species (Pearce and Venier 2006). Due to the large number of studies, particularly in the Northern Hemisphere, carabid beetles are one of the most frequently used biological indicators of boreal forest quality (Desender et al. 1994, Niemelä 2001, Niemelä et al. 2007). Several methods have been developed to quantify carabid beetle responses to environmental change and forestry practices (Dufrene and Legendre 1997, Koivula and Niemelä 2003, Rainio and Niemelä 2003).

Generally, it is assumed that older forests have less species richness than younger stages, but analysing species richness alone without considering species composition (e.g., forest specialists, saproxilic species) would underestimate the conservation value of older forests (Paquin 2008, Taboada et al. 2008). Succession is the change in community structure through time, where species characteristic of young stages are replaced with species characteristic of older stages (Schwerk and Szyszko 2007, Gotelli 2008). The end point of this process may be a climax community of insects that is invasion-resistant and cannot be replaced by other groups of insects until another disturbance event occurs (Gotelli 2008). For carabid beetles, such patterns have been observed during reforestation (after clear cutting or in plantations), where smaller carabids with better powers of dispersal were present in relatively greater abundance in younger forests than in older forests, which were dominated by larger, non-flying, and forest specialist species (Šustek 1981, Niemelä et al. 1993, Spence et al. 1996, Szyszko et al. 2000, Koivula 2002, Magura et al. 2002, Elek et al. 2005). In contrast to the wealth of studies on changes in carabid beetle diversity with boreal forest succession, little is known about this process in southern forests of Europe.

According to changes in species body sizes as well as their community composition, the Mean Individual Biomass (MIB) index of carabid beetles has been proposed as a good indicator of succession (Szyszko et al. 2000). Thus far, this index has been used to monitor succession in forest habitats (Serrano and Gallego 2004, Schwerk and Szyszko 2007) and post-industrial areas (Schwerk and Szyszko 2008) and to assess recovery after a mining accident (Cárdenas and Hidalgo 2007).

The aim of this study is to compare carabid beetle assemblages (species composition and richness) and MIB index values in mesophyllous beech forest stands of various successional ages (60-, 80- and 150-year-old forests). Our hypotheses are that the Mean Individual Biomass index will increase with forest age and species with overwintering larvae will be more abundant in the older forests. Similar trends were evident from previous studies (Butterfield 1997, Magura et al. 2002) assessing carabid community succession in conifer plantations.

Materials and methods

Study area

The study was performed in the Papuk Nature Park in continental Croatia (Fig. 1). The area was proclaimed protected in 1999 and represents a hilly and forested wildlife area within a lowland, agricultural region. The highest peak is 954 m above sea level (a.s.l.). The total area of Papuk Nature Park is 336 km² and is mostly (96%) covered by forest, and the rest of the habitat consists of settlements and small agricultural areas. Sessile oak (*Quercus petraea* (Mattuschka) Liebl.) forests dominate areas up to 350 m a.s.l. Beech trees (*Fagus sylvatica* L.), depending upon geological substrate and microclimatic conditions, grow in several different forest associations and cover more than 50% of the forested area, whereas mixed beech-fir forests grow in areas higher than 700 m a.s.l. Forests are of natural origin but are influenced by forestry. Deciduous forests are managed as even-age stands. Beech-fir forests are managed following the selection cutting system. Logged areas are mainly under natural regeneration. Most forests in the Park are 60 to 80 years old. Jankovac forest (660 ha), which has been left unmanaged, is the only large beech-forest stand that is more than 150 years old. The carabid fauna was



Figure 1. Position of investigated sites labelled according to the age of the forest ("60y 1–3" denote sites 1 to 3 in the 60-year-old forest, "80y 1–3" denote sites 1 to 3 in the 80-year-old forest and "150y 1–3" denote sites 1 to 3 in the 150-year-old forest). Insert: location of Papuk Nature Park in Croatia.

compared among three different beech forest stand ages: younger (60-year-old forest), middle-aged (80-year-old forest) and old beech forest (150 years old). For this study, we selected nine sampling sites (three per age class) (Fig. 1).

Beetle sampling and data analyses

Carabid beetles were collected from mid May to mid September in 2008. We used plastic pitfall traps (0.5 L volume, 10 cm diameter) filled with a mixture of 96% ethanol, 9% acetic acid and water in equal proportions and covered with roofs for protection against rain and evaporation. At each sampling site, three individual traps were placed 10 m apart to form a triangle. Traps were emptied on the same day approximately every three weeks (a total of six visits).

Carabid beetles were collected using 27 traps from 162 trapping events altogether (3 traps x 9 sampling sites x 6 visits). Samples were pooled per site across all visits, resulting in 9 sampling sites (three per age class) for analyses.

The species collected were identified using keys (Hůrka 1996, Freude et al. 2004) and the Croatian Natural and History Museum collections in Zagreb. The total body length (from tip of abdomen to tip of mandibles) of each individual was measured (mm), and the mean body length of each species was calculated for all sampling sites. Species were also categorised according to their over-wintering strategy as adults or larvae (Thiele 1977, Hůrka 1996), and their frequency per sampling site was calculated.

To compare carabid diversity, we calculated Margalef species richness (number of species per standardised number of individuals), Shannon diversity index and Pielou's evenness. For similarity between sites, Bray-Curtis indices using presence/absence data, and the number of individuals were calculated and used in cluster analyses with the complete linkage method for constructing dendrograms (Krebs 1989). Carabid beetle Mean Individual Biomass (MIB) was calculated to assess the stage of succession of the sites (Schwerk and Szyszko 2007, after Szyszko 1983). We used the following formula:

 $\ln y = -8.92804283 + 2.5554921 \ln x,$

where x is the body length of a specimen and y is the live estimated body weight of the individual. The estimated biomass of a species was calculated by multiplying the estimated body weight of the individual times its abundance for all sampled individuals per sampling site.

Differences in MIB values and diversity parameters among the three forest age classes were tested using analyses of covariance (ANCOVA), where mean individual biomass, species richness, evenness and Shannon diversity index were used as dependant variables, forest ages as categorical predictors and proportion of species with respect to overwintering strategy as the covariate, followed by the Scheffé post-hoc test. Pearson product-moment correlation coefficient was used for analyses. Statistical tests were performed using Primer 6 (PRIMER E Inc 2002) and Statistica 8 (Statsoft Inc 2008).

Results

A total of 1244 carabid beetles belonging to 31 species were collected (Table 1). Between 9 and 18 species were collected per sampling site. Similar species richness levels have been recorded in other beech forests in nearby countries as well as in similar forest communities in Croatia (Elek et al. 2005, Magura et al. 2006, Šerić Jelaska and Durbešić 2009).

Table 1. List of species, their mean body sizes (authors' measurements), over-wintering stage (a-adults, l-larvae), estimated body weight values and number of individuals in 60-, 80- and 150-year-old forests. Body weight values were calculated according to Szyszko (1983).

	Mean	Over-	Body	Nu	ımber	of
Species	body size /	wintering	weight /	inc	lividu	als
	mm	stage	mg	60 y	80y	150y
Abax carinatus (Duftschmid 1812)	16	a	158.4	139	228	133
Abax parallelepipedus (Piller & Mitterpacher 1783)	20	a	280.1	1	32	62
Abax parallelus (Duftschmid 1812)	17	a	184.9	0	26	15
Aptinus bombarda (Illiger 1800)	12	a	75.9	1	36	3
Calosoma inquisitor (Linné 1758)	21	1	317.3	2	1	1
Carabus arcensis Herbst 1784	20	a	280.1	36	38	1
Carabus convexus Fabricius 1775	17	а	184.9	1	0	1
Carabus coriaceus Linné 1758	39	1	1543.7	0	0	29
Carabus intricatus Linné 1761	30	а	789.5	3	0	1
Carabus irregularis Fabricius 1792	25	а	495.5	1	0	0
Carabus nemoralis O.F.Müller 1764	25	а	495.5	4	0	5
Carabus scheidleri Panzer 1799	30	1	789.5	0	16	119
Carabus ullrichii Germar 1824	25	а	495.5	3	53	20
Carabus violaceus Linné 1758	32	1	931.1	42	75	46
Cychrus attenuatus (Fabricius 1792)	17	1	184.9	0	6	1
Cychrus semigranosus Palliardi 1825	20	1	280.1	0	9	4
Harpalus affinis (Schrank 1781)	12	1	75.9	0	1	1
Leistus piceus Frölich 1799	8	а	26.9	0	1	1
Licinus hoffmannseggii (Panzer. 1797)	13	1	93.2	0	4	0
Limodromus assimilis (Paykull 1790)	11	а	60.8	0	1	0
Molops elatus (Fabricius 1801)	19	а	245.7	0	0	1
Molops piceus (Panzer 1793)	11	а	60.8	3	5	4
Myas chalybeus (Palliardi 1825)	16		158.4	4	1	0
Notiophilus rufipes Curtis 1829	6	а	12.9	0	0	1
Platyderus rufus (Duftschmid 1812)	7	1	19.2	1	0	0
Platynus scrobiculatus (Fabricius 1801)	11	1	60.8	0	1	0
Pseudoophonus rufipes (DeGeer 1774)	16	1	158.4	2	1	1
Pterostichus aethiops (Panzer 1796)	14		112.6	0	0	1
Pterostichus niger Schaller 1783	23	1	400.4	0	4	0
Pterostichus oblongopunctatus (Fabricius 1787)	12	а	75.9	0	8	0
Pterostichus transversalis (Duftschmid 1812)	16		158.4	0	3	0
N (species)				15	22	22
N (individuals)				243	550	451

The 80- and 150-year-old forests yielded 22 species each, whereas 15 species were collected from the 60-year-old forest sites. Nine species (29%) were present in all three forest age classes; one species was recorded only from the 60-year-old stand, six species only from the 80-year-old stand, and three only from the oldest forests.

The greatest number of individuals (44%) was recorded from the 80-year-old forest sites, 36% from the 150-year-old forest sites, and 20% from the 60-year-old forest sites (Table 1). Two species, *Abax carinatus* and *Carabus violaceus*, were collected from all nine sites with the greatest number of individuals, accounting for 40.2 and 13.1% of the total catch, respectively. Although *A. carinatus* and *C. violaceus* were numerous at all three forest ages, two large species, *C. scheidleri* and *C. coriaceus*, were mainly collected from the 150-year-old sites. *C. scheidleri* and *C. coriaceus* accounted for 33% of the 451 individuals in the oldest forest and 12% of the total catch.

The 80-year-old sites showed the highest average Shannon-Wiener index value, whereas the lowest value was recorded from the youngest sites. The variability of data in the whole sample could be explained by the second order polynomial with $R^2 = 0.54$. The same trend was observed for the average standardised species richness (Margalef's index) (Table 2). MIB values increased with forest age. Beech forests that are 150 years old have the highest mean individual biomass values for carabids (Table 2, Fig. 2). Similar trends were recorded for proportion of species that hibernate as larvae. There were more carabid beetles that hibernate as larvae (45% of individuals collected) in the oldest forest than in the younger forest stages; in the 60- and 80-year-old forests, 80 and 78% of specimens hibernate as adults, respectively (Fig. 3). MIB was highly correlated with the proportion of carabids that hibernate as larvae (r = 0.84, p < 0.05).

MIB values, Shannon–Wiener indices, Margalef's indices and Pielou's evenness did not differ significantly among forests of various age groups (ANCOVA, p<0.05), (Table 3). The covariate, hibernation strategy as larvae, was significantly related to the Mean Individual Biomass and Shannon–Wiener indices values (ANCOVA, p<0.05), (Table 3). Although they differed among forest age-groups at significance level slightly higher than p=0.05, performed post hoc comparison confirmed significant differences in MIB values of carabids between 150 year old forests and younger sites (60 and 80 year old forests) and for Shannon–Wiener indices between the 80-year-old sites from the youngest and the oldest sites (Scheffé test, p<0.05, Table 3).

Based on presence/absence data, a cluster analysis identified three groups: one with all 60-year-old forest sites, one with all 80-year-old sites as well as one 150-year-old site, and a third group with two 150-year-old forest sites (Fig. 4). A cluster analysis based on the number of individuals, grouped 60-year-old sites with two 80-year-old sites and all 150-year-old sites with one 80-year-old site (figure not shown).

Discussion

MIB values increased with forest age, confirming MIB as a useful indicator in evaluating later succession stages. An increase in MIB values was accompanied by changes in

Plots	Total species	Total number of individuals	Margalef species richness	Pielou's evenness	Shannon- Wiener index	MIB (mg)
60y1	9	43	2.13	0.72	1.59	458
60y2	9	118	1.68	0.48	1.06	255
60y3	10	82	2.04 0.63		1.45	367
80y1	15	80	3.19 0.8		2.18	343
80y2	11	342	1.71	0.62	1.49	260
80y3	17	128	3.30	0.74	2.11	496
150y1	9	110	1.70	0.81	1.77	515
150y2	11	175	1.94	0.76	1.82	537
150y3	18	166	3.33	0.66	1.90	532
		Average va	lues per age			
60y	9.33	81.00	1.95	0.61	1.37	360
80y	14.33	183.33	2.74	0.72	1.92	366
150y	12.67	150.33	2.32	0.74	1.83	528

Table 2. Number of species and individuals, diversity indices and MIB (mg) values from the nine sites in Papuk Nature Park, Croatia.



Figure 2. MIB values (mg) compared to the age of the forests stands (years).

community structure, i.e., a decreasing portion of smaller carabids and an increasing proportion of the largest species, as well as their abundance, with forest age. A similar trend has been reported in Szyszko et al. (2000), Cárdenas and Hidalgo (2007), and Schwerk and Szyszko (2007, 2008).

Although evenness slightly increased with forest age, other diversity parameters showed nonlinear patterns, with the highest average values for forests of mid-age. Cluster analyses of carabid composition in this study clearly divided the youngest and the oldest forests, whereas middle-aged forests occupied an intermediate position.



Figure 3. Proportion of species according to their hibernation strategies (larvae – black columns, adults – white columns) in relation to forest age (years).

Differences within 80-year-old forest sites were more pronounced than between sites from other age classes that show a more diverse data set. Similar results were found by Paquin (2008) who observed the highest variability in mid-aged classes during the natural regeneration cycle of burned forests.

Forest age could affect the carabids assemblages due to changes in habitat structure, where early and later forest successional stages differ in vegetation structure, and in the accumulation of dead and decaying wood (Tyrrell and Crow 1994, Ings and Hartley 1999). As older forests increase in resources and heterogeneity, they seem to support more large-sized carabid beetles. Due to habitat quality, mid-aged forests can be inhabited by species from younger and older forests, but because habitat resources might not be developed well enough to support the dominance of large species, overall carabid beetle biomass stay low despite showing greatest abundance. There are numerous studies focusing on carabid beetle body sizes among different habitats (Šustek 1987; Blake et al. 1994; Szyszko et al. 2000; Ribera et al. 2001; Braun et al. 2004; Weller and Ganzhorn 2004; Šerić Jelaska et al. 2007; Gaublomme et al. 2008; Šerić Jelaska and Durbešić 2009; Gómez 2010), with most of these confirming an increase in size with succession and habitat stability. Smaller carabid species develop faster with shorter generation times (Peters 1983, Blake et al. 1994), whereas larger carabid species have longer developmental periods (Blake et al. 1994) that can be supported in stable habitats with sufficient resources (Peters 1983, Lomolino 2005). As was shown here, younger beech forests were not characterised by large carabids, unlike the older forests. Carabid species that over-winter as larvae usually have larger adults as a result of a longer developmental period (Blake et al. 1994), which is supported by our results showing that the 150-yearold forests had a higher proportion of species that hibernate as larvae in comparison to the 80- and 60-year-old forests. Habitat conditions in the oldest forests without forest

Table 3. ANCOVA results for the effects of forest age on mean individual biomass, the Shannon-Weiner diversity index, Pielou's evenness and Margalef's richness of carabid beetles, followed by the Scheffé posthoc test.

Variables	SS	DF	MS	F	Р	Scheffé test						
Dependant variable: MIB (g)												
Corrected Model	0.100	3	0.033	39.883	0.001							
Intercept	0.079	1	0.079	95.071	0.000							
Species that hibernate as larvae	0.045	1	0.045	54.156	0.001	150>80=60						
Forest age (years)	0.010	2	0.005	5.712	0.051							
Error	0.004	5	0.001									
$R^2 = 0.960$ (Adjusted $R^2 = 0.963$)												
Dependant variable : Shannon-Wiener index												
Corrected Model	0.796	3	0.265	7.268	0.028							
Intercept	2.184	1	2.184	59.831	0.001							
Species that hibernate as larvae	0.265	1	0.265	7.251	0.043	80>150=60						
Forest age (years)	0.338	2	0.169	4.634	0.073							
Error	0.183	5	0.037									
$R^2 = 0.813$ (Adjusted $R^2 = 0.702$)												
Dependant variable: Pielou's evenness												
Corrected Model	0.055	3	0.018	2.786	0.149							
Intercept	0.414	1	0.414	63.233	0.001							
Species that hibernate as larvae	0.026	1	0.026	3.948	0.104							
Forest age (years)	0.011	2	0.005	0.804	0.498							
Error	0.033	5	0.007									
$R^2 = 0.626$ (Adjusted $R^2 = 0.401$)												
Dependant variable: Margalef richness												
Corrected Model	1.651	3	0.550	1.099	0.431							
Intercept	3.558	1	3.558	7.106	0.045							
Species that hibernate as larvae	0.722	1	0.722	1.442	0.284							
Forest age (years)	0.919	2	0.459	0.918	0.458							
Error	2.504	5	0.501									
$R^2 = 0.397$ (Adjusted $R^2 = 0.036$)												

management practices are quite likely stable enough to support the dominance of large species and species with longer developmental periods. As such, these older forests are of considerable conservation value. The conservation value of these older forests is also supported by the study of bird communities. Mature forest specialists like the White-backed woodpecker (*Dendrocopus leucopterus*), which had previously been considered extinct in this part of Croatia, and the Red-breasted flycatcher, (*Muscicapa parva*) breeds only in the oldest forests in Papuk Nature Park (Dumbović 2007).

To summarise, MIB values showed significant differences associated with forest age and can be a useful tool in evaluating whether a forest reflects a natural succession. Furthermore, our study indicates that for preserving stable communities and overall carabid diversity, it is important to have part of the forest unmanaged or at least leave



Figure 4. Dendrogram of cluster analyses among forest sites using presence/absence carabid beetle data. Two distinct clusters are formed at roughly 30% similarity. Marks 60y 1–3, 80y 1–3 and 150y. 1–3 denote investigated sites placed in the 60-, 80- and 150-year-old forests.

some stands to reach the decomposition phase, taking into account the spatial connectivity of stands enabling the migration of species.

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RESEARCH ARTICLE



Changes in salt-marsh carabid assemblages after an invasion by the native grass Elymus athericus (Link) Kerguélen

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Abstract

As a result of an invasion by the native grass *Elymus athericus* (Link) Kerguélen (Poaceae) in the last 10 years, a major change in vegetation cover has occurred in salt marshes of the Mont Saint-Michel bay, Western France. The impact of such an invasion on carabid assemblages, a dominant group of terrestrial arthropods in these habitats and containing several stenotopic species, is investigated here. In our study site, carabid data are available from 1983 and 1984, allowing a comparison of species distribution ranges in salt marshes before (1983–1984) and after (2002) the *E. athericus* invasion. A total of 16,867 adults belonging to 40 species were caught. By considering the presence-absence of species shared between studies, we show that the invasion by *E. athericus* promoted the progression of non-coastal species (mainly *Pterostichus* s.l. spp.). This did however not interfere with resident species distributions, finally resulting in higher carabid species richness in the entire area. The species composition and abundances of carabid assemblages were also compared between natural and invaded stations in 2002. The main result is that abundances of some halophilic species decreased in one invaded plot (in case of *Pogonus chalceus* (Marsham 1802)) whereas the opposite pattern was observed for other species (e.g., *Bembidion minimum* (Fabricius 1792)). Invaded habitats were characterized by lower percentages of halophilic species and higher total species richness.

Keywords

Coleoptera, Carabidae, native invasive species, salt marsh, ecological indicators

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Introduction

Intertidal salt marshes are ecosystems located between land and sea, undergoing periodical flooding during tides, occurring around twice a month in West-Europe. This creates some special habitat conditions, and marsh plants and animals often have special adaptations to cope with these. Salt-marsh arthropods are able to withstand floods and salinity by physiological, behavioural or morphological adaptations (e.g., Foster & Treherne 1976, Irmler et al. 2002, Pétillon et al. 2009). Salt marshes are among the rarest habitats in the world, covering less than 0.01% of the Earth's surface (Desender & Maelfait 1999, Lefeuvre et al. 2003). In Europe, their surface strongly declined during the last decades, reinforcing the conservation interest in their original flora and fauna (Bakker et al. 2002). There is thus an urgent need to study human impacts that can either threaten (by e.g., over-grazing or habitat destruction), or enhance (by appropriate management) halophilic species in salt marshes (Goeldner-Gianella 1999, Adam 2002).

More recently, salt marshes have been invaded in many West-European sites by the nitrophilous grass *Elymus athericus* (Poaceae) (Valéry et al. 2004), probably due to increases in soil nitrogen (via the accumulation of nitrogenous compounds in the plant: Leport et al. 2006) and/or to the abandonment of agricultural practises (e.g., Esselink et al. 2000). Although *Elymus athericus* is a native species in Europe (Bockelmann & Neuhaus 1999) – usually growing in the upper parts of salt marshes – it can form dense, mono-specific stands, which corresponds to an invasion. This is likely to modify biodiversity and consequently ecosystem proprieties and functions as well as the conservation value of invaded areas (Valéry et al. 2009). Invaded areas mainly differ from natural habitats (usually dominated by *Atriplex portulacoides*, Chenopodiaceae, in ungrazed middle marshes) by their enhanced litter layer and by their higher plant cover.

According to McGeoch (1998), a taxonomic group is an ecological indicator if it responds to environmental changes, stressful or not. In this study, we focussed on ground beetles (Coleoptera, Carabidae) as they are known to react quickly and strongly to changes in micro-habitat conditions. This group is thus frequently used as an indicator of human disturbances or management practices (e.g., Luff et al. 1992, Georges 1994, Sunderland & Lövei 1996, Rainio & Niemelä 2003). The assessment of human impact was conducted by comparing two conservation criteria, i.e., abundance of halophilic species and species richness, between natural and invaded stations. Species richness is widely used as a conservation target (e.g., Noss 1990, Bonn & Gaston 2005). The use of stenotopic species is also recommended in studying the impact of human activities on arthropod communities (Samways 1993, New 1995, Dufrêne & Legendre 1997). In this study, the target species were halophilic species, defined by their preference or exclusive presence in salt-marsh habitats (Kamer et al. 2008), which can be assessed using distribution maps (in our study, relevant atlases are Luff 1998 and Turin 2000). Two approaches were used for assessing changes in natural salt marshes compared to invaded ones: (i) a diachronic (before vs. after the invasion) comparison

of species distribution along a land-sea gradient and (ii) a synchronic comparison of species assemblages between invaded and natural habitats.

Methods

Study site and sampling design

The Mont Saint-Michel bay (NW France) is an extensive littoral zone (500 km²) located between the regions Brittany and Normandy (48°40'N, 1°40'W). Two sites have been studied in salt marshes: "la Ferme Foucault", on the western part of the Mont St.-Michel (coded F; 48°37'N, 1°32'W) and "la Rive" on the eastern part of the Mont St.-Michel (coded R; 48°37'N, 1°29'W) (Fig. 1).

For the diachronic approach, ground beetle populations were compared at seven stations (A to G) located along the same land-sea transect at the "Ferme Foucault" site between 1983–1984 and 2002. During the study of 1983–1984, *Elymus athericus* was restricted in this salt marsh to the dyke (station A) and to the upper marsh (station B), but absent from stations C-G. Invasion by *Elymus athericus* modified the plant cover of the sampling stations between 1984 and 2002. The middle marsh and lower marsh stations (station C till F), dominated in 1984 by *Atriplex portulacoides* (Chenopodiaceae), were dominated by *E. athericus* in 2002.

Secondly, natural (dominated by Atriplex portulacoides), and invaded (dominated by Elymus athericus) stations were studied at different marsh levels in the synchronic approach. Comparisons of paired stations (natural and invaded - coded N and I, respectively) were spatially replicated three times for avoiding pseudo-replication (Hulbert 1984). Paired stations were located at the same distance from the dyke because of the existence of a salinity gradient influencing both species richness and abundance (Pétillon et al. 2004): stations 1 (350m), stations 2 (800-900m; both couples of stations at the "Ferme Foucault" site) and stations 3 (1000 meters from the dyke; "La Rive" site). Because of the clonal progression of the invasive species, all *Elymus* populations (stations I1, I2 and I3) formed a uniform and continuous plant cover. The natural areas sampled were either patch-like formations (in case of stations N1 and N2) or strip-like formations (station N3). Mean salinities did not significantly differ between invaded and natural stations at each salt marsh level (Pétillon et al. 2005) and elevations were similar between compared stations (J.C. Castel & J. Huet, 1999, unpublished data). More details on the sampling stations can be found in Fouillet (1986) and Pétillon (2005).

Sampling techniques and species identification

For both the synchronic and diachronic approaches, ground beetles were sampled with pitfall traps, consisting of polypropylene cups (10 cm diameter, 17 cm deep) with



Figure 1. Location of the study sites (Mont St-Michel Bay, France). Codes: F 'Ferme Foucault' R 'la Rive'.

ethylene-glycol as preservative. Traps were covered with a raised wooden roof to keep out rain. They were emptied weekly when tides permitted (i.e., about three weeks per month). Pitfall traps were grouped by four and spaced 10 m apart, this being considered to be the minimum distance for avoiding interference between traps (Topping & Sunderland 1992). Before the *Elymus* invasion, Fouillet (1986) sampled the transect with one trap per station from May to September in 1983 and 1984, for a total of 16 five-day samples. In 2002, four traps were installed at each station in both study sites, from April to November 2002. Sampling time was comparable between both periods (90 days in 1983–1984 and 96 days in 2002). Because of the differences in sampling efforts, we only compared the two studies on the basis of species presence / absence (i.e., distribution range along the land-sea transect).

Ground beetles were preserved in 70% ethanol and identified using Jeannel (1942) and Trautner & Geigenmüller (1987). Nomenclature follows Lindroth (1992) as far as possible, and Fauna Europaea otherwise (http://www.faunaeur.org/).

Data analyses

Statistics on the abundances of halophilic species were performed only for species represented by at least 10 individuals in couples of stations. Catches in pitfall traps were related to trapping duration and pitfall trap perimeter, which calculates an "activity trappability density" (number of individuals per day and per meter – Sunderland et al. 1995). Mean species richness and mean abundances were compared using a two-way mixed model (habitat × station) with habitat type as fixed factor, station (1, 2 and 3) and interaction habitat*station as random factors. In case of non-significant interaction between habitat type and station, the interaction was removed from the model and a new model was performed for detecting significant effects of habitat type and/or station. In case of significant interaction between habitat type and station (one-way ANOVA). Statistical analyses were performed using the Statistica-7 software.

Results

Diachronic approach

A total of 24 species (represented by 7,774 individuals) and 35 species (represented by 8,588 individuals) were caught in 1983–1984 and in 2002, respectively. Five species were exclusive to the first sampling period and 16 to the second one. All the species that were only recorded in 1983–1984 were caught in very low numbers (max. 2 individuals), four species on the dyke (*Clivina colaris, Dromius linearis, Harpalus rufibarbis* and *H. rufipes*) and only one in the salt marsh (*Dyschirius chalceus*). As the sampling effort was quite different between 1983–1984 and 2002 (see Material and Methods), it cannot be concluded that the 'appearance' of species between the two studies can be related to the invasion by *Elymus athericus*. The comparison in distribution was thus restricted to the 19 shared species (Table 1).

In terms of distribution ranges, two groups of carabids were distinguished: species with constant distribution range in the salt marsh or on the dyke and species with an increased distribution range between 1983–1984 and 2002. Eight species were caught on the dyke in 1983–1984 and in 2002, and seemed not to have progressed with *Elymus athericus* in the salt marsh (*Amara equestris, Anisodactylus binotatus, Bembidion tetracolum, Harpalus anxius, Leistus fulvibarbis, Nebria brevicollis, Pterostichus melanarius* and *P. niger*: Table 1). Eight other species had a similar habitat range in the salt marsh, extending from the upper to lower marsh or from the dyke to the lower marsh (halophilic species: bold in Table 1), plus two high-marsh living species (*Badister bipustulatus* and *Pterostichus vernalis*), one low-marsh living species (*Dyschirius salinus*) and one species with a discontinuous range along the land-sea transect (*Loricera pilicornis*). Only three species showed an extension of their distribution in the salt marsh, both to the upper and lower marsh (*Bembidion iricolor, B. lampros* and *Pterostichus cupreus*).

The *Elymus athericus* invasion led to a decrease in the percentage of halophilic species in invaded salt marshes (Fig. 2).

Table 1. Comparison of total catches (number of individuals) between 1983–1984 and 2002 along a land-sea transect (Foucault site; bold: halophilic species). The letters **A–G** indicate different sampling stations. In 1983–1984, only stations **A–B** had a dominant *Elymus athericus* cover; in 2002 at all stations *Elymus athericus* was present (dominant cover for stations **A** to **F**).

	Period	Α	B	С	D	E	F	G	Total
SHARED SPECIES									
Amara equestris	1983–84	1							1
(Duftschmid 1812)	2002	1							1
Anisodactylus binotatus	1983-84	3							3
(Fabricius 1787)	2002	6							6
Badister bipustulatus	1983-84		1						1
(Fabricius 1792)	2002	2	2						4
Bembidion iricolor Bedel	1983-84	2		2	2				6
1879	2002	5	98	89	21	1	4		218
Bembidion lampros	1983-84	1		2					3
(Herbst 1784)	2002	1	12	18	3	5	4	1	44
Bembidion minimum	1983-84	4	1	40	52	10	2		109
(Fabricius 1792)	2002	1	31	13	5	80	96	3	229
Bembidion normanum	1983-84	1		24	39	244	149	53	510
Dejean 1831	2002	2	6	8	13	212	131	24	396
Bembidion tetracolum (Say	1983-84	1							1
1823)	2002	1							1
Dicheirotrichus gustavii	1983-84	2		11	83	2121	2622	393	5232
Crotch 1871	2002	2	8	2	3	136	237	156	544
Dyschirius salinus	1983-84						1	1	2
Schaum 1843	2002							5	5
Harpalus anxius	1983-84	2							2
(Duftschmid 1812)	2002	1							1
<i>Leistus fulvibarbis</i> Dejean	1983-84	3							3
1826	2002	1							1
Loricera pilicornis	1983-84				1				1
(Fabricius 1775)	2002					1		1	2
Nebria brevicollis	1983-84	3							3
(Fabricius 1792)	2002	1							1
Pogonus chalceus	1983-84	8	4	65	42	678	617	436	1850
(Marsham 1802)	2002	13	100	193	126	1628	1290	2243	5593
Pterostichus cupreus	1983-84	3		5					8
(Linnaeus 1758)	2002	7	41	9			2		59
Pterostichus niger (Schaller	1983–84	24							24
1783)	2002	1							1
Pterostichus vernalis	1983-84	4							4
(Panzer 1795)	2002	2	1						3

	Period	Α	B	С	D	E	F	G	Total
Pterostichus melanarius	1983–84	4							4
(Illiger 1798)	2002	12							12
SPECIES NOT RECOLL	ECTED IN	N 2002	2						
<i>Clivina collaris</i> (Herbst	1983–84	2							2
1786)	2002								0
Dromius linearis (Olivier	1983–84	1							1
1795)	2002								0
Dyschirius chalceus	1983–84							1	1
Erichson 1837	2002								0
Harpalus rufibarbis	1983–84	2							2
(Fabricius 1792)	2002								0
Harpalus rufipes (Degeer	1983–84	1							1
1774)	2002								0
NEW SPECIES FOUND	IN 2002								
Anchomenus dorsalis	1983–84								0
(Pontoppidan 1763)	2002	1							1
Agonum muelleri (Herbst	1983–84								0
1784)	2002			5	1				6
Amara lunicollis Schiödte	1983–84								0
1837	2002	3							3
<i>Amara plebeja</i> (Gyllenhal	1983–84								0
1810)	2002		2					1	3
Amara tibialis (Paykull	1983–84								0
1798)	2002	2							2
Anisodactylus poeciloides	1983–84								0
(Stephens 1828)	2002			2					2
Bembidion obtusum	1983–84								0
Serville 1821	2002	10	16	1					27
Calathus mollis (Marsham	1983–84								0
1802)	2002		1						1
Clivina fossor (Linnaeus	1983–84								0
1758)	2002							1	1
Dicheirotrichus	1983–84								0
<i>obsoletus</i> (Dejean 1829)	2002		2	12	5	478	572	301	1370
Harpalus distinguendus	1983–84								0
(Duftschmid 1812)	2002	1		2					3
Harpalus melancholichus	1983-84								0
Dejean 1829	2002	1							1
Microlestes minutulus	1983–84								0
(Goeze 1777)	2002	2							2

	Period	Α	B	С	D	Ε	F	G	Total
Pogonus littoralis	1983-84								0
(Duftschmid 1812)	2002	1	13		1				15
Pterostichus versicolor	1983-84								0
(Sturm 1824)	2002	4	14	2					20
Tachys scutellaris	1983-84								0
Stephens 1828	2002		10						10
Total		156	363	505	397	5594	5727	3620	16362

Synchronic approach

A total of 505 individuals belonging to 17 species were sampled in the three pairs of natural and invaded stations. The synchronous comparison of natural and invaded habitats revealed the existence of eight shared species. Two species were exclusive to natural habitats (Pogonus littoralis and P. luridipennis) and six to invaded habitats (Anisodactylus poeciloides, Bembidion obtusum, Harpalus anxius, H. distinguendus, Pterostichus cupreus and *P. versicolor*). Total species richness was higher in invaded habitats than in the natural ones (Table 2). Significant interactions between habitat type and station were found for species richness and two species Pogonus chalceus and Dicheirotrichus gustavii. Mean species richness was significantly higher in an invaded station compared to its adjacent natural one (one-way Anova, F-ratio=22.04, p=0.003, d.f.=7). More P. chalceus were caught at a natural station than at the paired invaded one (one-way Anova, F-ratio=14.68, p=0.009, d.f.=7). D. gustavii was significantly higher in an invaded station compared to the natural one (one-way Anova, F-ratio=6.89, p=0.039, d.f.=7) and the opposite pattern was found in another couple of stations (one-way Anova, F-ratio=11.94, p=0.014, d.f.=7). Bembidion minimum was significantly higher in invaded habitats compared to natural ones (Factorial Anova, F-ratio=5.91, p=0.025, d.f.=20). No difference between habitat types was found for *Dicheirotrichus obsoletus* and *Bembidion normanum* (Table 2).

Discussion

By comparing data from 1983–1984 to 2002, we could show that only three species have extended their distribution range with the *Elymus* invasion, despite the existence of several dyke-inhabiting species (eight continental species with constant distribution). This result is opposite to those obtained for spiders in the same study site, with many range-expanding species (Pétillon et al. 2005). This pattern can also be related to the high percentage of halophilic carabid species found in salt marshes, much higher than for spiders (Pétillon et al. 2008). Assemblages of ground beetles in salt marshes proportionally contain more specific, halophilic species, and continental species are conversely unlikely to colonize this habitat. Meijer (1980) also noted that spiders were less sensitive to variations in soil salinity than ground beetles. Higher percentages of



Figure 2. Changes in the percentage of halophilic species in the salt marsh after the invasion by *Elymus athericus*.

stenotopic species in ground beetle assemblages than in spider assemblages have been recorded in other flooded habitats, such as river floodplains (Rothenbücher & Schaefer 2006) and riverbanks (Bonn & Kleinwächter 1999).

Although the sampling effort was quite different between 1983–1984 and 2002, we assume that around 11 records of the 16 new species during the second sampling period can also be due to the invasion by *Elymus*. In fact, several continental species were discovered after the invasion in relatively high numbers (i.e., more than five individuals), both on the dyke and in the salt marsh. Among them, most species are linked to high contents of organic matter and a more pronounced litter layer (e.g., Agonum muelleri, Bembidion obtusum and the polyphagous Pterostichus versicolor) or are even partly phytophagous (Amara spp. and Harpalus spp.: Dajoz 1988, Ikeda et al. in press). Conversely, halophilic species discovered in 2002 are hardly related to the invasion. Pogonus littoralis and Dicheirotrichus obsoletus could have been misidentified earlier, as these species are very similar to *P. chalceus* and *D. gustavii*, respectively (Forel & Leplat 2005, Dhuyvetter et al. 2007). D. obsoletus could also have been missed in 1983-1984 (the sampling stopped in September) as more than 89% of individuals were caught in October-November during 2002. Tachys scutellaris appears as a new species in 2002, but was present in 1983–1984, but at another station located below the mean sea level (slikke habitat: Fouillet 1986). The 'appearance' of several species, sampled in low numbers in 2002, can be due to differences in sampling effort and/or to random catches.

The synchronic study revealed that almost half of the species (8/19), both continental and halophilic ones, were shared between natural and invaded habitats. Three species, all halophilic, were exclusive to natural habitats. Conversely, six species were

Table 2. Comparison of total species richness (total S), mean species richness (mean S) and means abundances (as expressed in number of individuals per day and per meter) of *Pogonus chalceus*, *Dicheirotrichus obsoletus, Bembidion normanum, Dicheirotrichus gustavii* and *Bembidion minimum* between natural (**N**) and invaded (**I**) habitats. Means in bold are significantly different (p<0.05) between habitat types (mean \pm s.e., see text for details in statistics).

	Ν	Ι	N1	I1	N2	I2	N3	I3
Total S	11	14						
Mean S	6.17	6.92	5.50	8.75	6.25	6.50	6.75	5.50
	±0.35	±0.51	±0.50	±0.48	±0.63	±0.65	±0.63	±0.65
P. chalceus	7.66	4.75	1.11	1.68	13.50	10.76	8.37	1.80
	±1.90	±1.91	±0.32	±0.24	±3.35	±4.63	±1.55	±0.74
D. obsoletus	1.38	1.68						
	±0.60	±0.72						
B. normanum	0.78	0.98						
	±0.35	±0.40						
D. gustavii	0.45	0.68	0.03	0.02	1.14	1.99	0.19	0.05
	±0.15	±0.29	±0.02	±0.01	±0.15	±0.29	±0.04	±0.02
B. minimum	0.29	0.52						
	±0.11	±0.10						

exclusive to invaded habitats, among them some of the species that colonized the marsh after the invasion by *Elymus athericus* (e.g., *Bembidion lampros* or *Pterostichus cupreus*). New conditions created by the grass *Elymus* – mainly an enhanced litter layer and higher plant cover – thus lead to the establishment of several continental species directly or indirectly linked to organic matter or to the litter (as shown by Pétillon et al. 2008).

Although few deleterious impacts of invasion by *Elymus athericus* on carabids were found, management could be necessary to reduce the effects of invasion and decrease the rate of spread of the invasive plant. Sheep grazing – despite being a good potential method for biological control of invaders (Shea & Chesson 2002) – is at the moment carried out too intensively in the Mont Saint-Michel bay, leading to a decrease in carabid species richness (Pétillon et al. 2007). A low stocking rate (i.e., between 0.5 and 1.5 sheep ha⁻¹) can therefore be recommended, assuming greatest positive effects at intermediate disturbance intensities (for arthropods: e.g., Dennis et al. 2001, Suominen et al. 2003).

Long-term monitoring of population dynamics is thus recommended for halophilic species in invaded, natural and managed habitats. Special attention could be paid to less dominant species, as their small populations could be reduced faster than other, dominant, salt-marsh carabids. This study confirms the high value of carabids as bioindicators (as they present a high percentage of specialist species) and shows the possibility of using long-term surveys for ecological studies, if carefully interpreted.

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RESEARCH ARTICLE



Effects of ecological flooding on the temporal and spatial dynamics of carabid beetles (Coleoptera, Carabidae) and springtails (Collembola) in a polder habitat

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Abstract

Within the scope of the Integrated Rhine Program an ecological flood gate and channel was inserted into the polder "Ingelheim" to enhance animal and plant diversity. In 2008, carabid beetles and springtails were collected, using pitfall traps, to measure the effects of ecological flooding and a strong precipitation event at a flood-disturbed and a dry location in this area. At both localities, xerophilic and mesophilic carabid beetle species were dominant throughout the study period. The total number of individuals of hygrophilic species was comparatively constant, while species number increased, partly due to the changed moisture conditions caused by ecological flooding and strong precipitation. Carabid beetle diversity and evenness decreased marginally when ecological flooding was absent. Springtails represent a less mobile arthropod order, and as such the impact of ecological flooding was stronger. An increase in both numbers of species and individuals of hygrophilic and hygrotolerant species occurred in the flood-disturbed location after ecological flooding. After the sites at both locations had dried, the number of individuals belonging to these species declined rapidly. In contrast to carabid species, the strong precipitation event showed no influence on hygrophilic springtail species. Thus, collembolan diversity and evenness decreased markedly in the absence of flooding. We showed that ecological flooding has an influence on the spatial and temporal dynamics of different arthropod groups that inhabit the polder "Ingelheim". These findings demonstrate the importance of using different arthropod groups as bioindicators in determining the ecological value of a particular polder design.

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Keywords

bioindication, community dynamics, drought, flooding, Integrated Rhine Program (IRP)

Introduction

During the last three decades flood protection has become one of the most important goals of countries along the entire course of the river Rhine. Therefore, in 1982 the Integrated Rhine Program (IRP) was established to reduce the economic and ecological impacts of a 200-year flood (an extraordinary flood event, which hypothetically occurs only once in 200 years). The program includes the specific use of hydroelectric power plants, the construction of several polder sites (floodwater retention basins) and the relocation of dikes to enlarge the flooding area of the river Rhine. An essential aim of the IRP is to combine economic (flood protection) and ecological protective measures (Strähle 1992). While it is relatively easy to measure the economic value of such a flood protection area, it is more difficult to evaluate the benefits to plants and animals. The polder "Ingelheim" is an example of a new generation flood prevention site along the Northern Upper Rhine region. It was constructed bearing ecological aspects in mind and completed in September 2006. For the protection of rare plant species found in the ruderal (former seepage) areas (Isoeto-Nanojuncete), a smaller gate was inserted (Fig. 1B) in addition to the main flood gate, which is only opened in the case of very high Rhine water levels (water gauge Mainz: > 7.00 m). Only when the main flood gate is opened, the whole polder area (160 ha) is completely flooded. The smaller gate is open most of the time and is only closed after a so-called "ecological flooding" of the smaller ruderal area (20 ha) caused yet by higher Rhine water levels (water gauge Mainz: > 5.00 m). Therefore, ecological flooding of the ruderal area occurs periodically (ca. every eight months) induced not only by higher Rhine water levels but also by the amount of precipitation. In addition to the preservation of the hygrophilic plant community, the aim of ecological flooding is to enhance the diversity and density of animal species and accelerate recovery after flood events. Studies in the polder "Altenheim" showed decreased densities of animal populations after flooding but fast recolonisation after this habitat had dried again (Siepe 1989; 2006).

For this reason the mobile carabid beetles (Coleoptera; Carabidae) and the less mobile springtails (Collembola) were chosen to detect the effects of ecological flooding on these arthropod groups. The ecology and taxonomy of most Middle European species belonging to these two groups have been well researched, making them particularly suitable for such a study. As they can be sampled easily and cost-efficiently, they are also potentially suitable bioindicators (Hopkin 1997; Rainio and Niemela 2003). Carabid beetles are also considered valuable indicators of hydrological conditions in floodplains or other dynamic landscapes (Bonn and Kleinwächter 1999; Ellis et al. 2001; Bonn et al. 2002; Gerisch et al. 2006). In this study the mobile carabid beetles are expected to react relatively quickly to changing moisture conditions, which include abundance and species number shifts between hygrophilic and xerophilic spe-



Figure 1. Location of the polder "Ingelheim" in Germany and location of the different areas and pitfall trap localities (L1–L6) within this polder (**A**). Abbreviations: LA 0: ruderal area; HB 0: fallow area; LA 0 + HB 0: transition area between LA 0 and HB 0; HA 0: agricultural fields; L1–6: locations of the six pitfall trap groups (three pitfall traps per locality). The pictures show the main flood gate (left) and the ecological flood gate (right), and an ecological flooding in March 2007 (**B**) and the fast drying event in the ruderal area after ecological flooding in April 2007 (**C**).

cies. Large populations of the less mobile springtails inhabit the soil and are important members of the soil food web (Hopkin 1997). According to Russell et al. (2002) this group is also believed to show very flexible responses to changed habitat conditions and the way they react in flood disturbed habitats is more an adjustment of dominance than the appearance or disappearance of species (Deharveng and Lek 1995; Sterzyńska and Ehrnsberger 1999). Russell et al. (2004) and Russell and Griegel (2006) classified collembolan species of different floodplain habitats into isovalent species groups based on moisture preference. Marx et al. (2009) described several strategies of springtails to survive flooding under both hypoxic and anoxic conditions.

The main aims of this investigation were to determine the effects of ecological flooding on ground beetles and springtails, and to determine their bioindication value. Therefore, results of the 2008 vegetation period are presented, during which both an ecological flood event caused by high Rhine water levels and a flood caused by a strong precipitation event occurred. Between these two flooding events a short but severe drought period occurred at the study site. This vegetation period was of particular importance in answering the main questions posed here because of the fast sequence of the different flood and drought events.

Material and methods

The Polder "Ingelheim" (49°59'N; 8°03'E, 81–82m a.s.l.) is located in a nature protection area called "Sandlache" near Mainz in the Northern Upper Rhine region. The feed stream of the polder flows through a natural backwater of the river Rhine, the "Alte Sandlache" (Fig. 1A). The central part of the study site was formerly characterised as a ruderal seepage area (now ruderal area) because of seepage water. Ecological flooding, through the ecological flood gate, should prevent the succession of this area from ruderal to fallow. The remainder of the study site is an active agricultural area. After the polder had been built between the agricultural land (HA 0) and the ruderal area (LA 0), an unused fallow area (HB 0) with a dense shrub layer developed (Fig. 1A). This area is dominated by Limosella aquatica (L.), Gnaphalium uliginosum (L.), Juncus bufonius (L.), Cyperus fuscus (L.), Potentilla supina (L.) and Lythrum hyssopifolia (L.) and serves as the riverbank during the ecological flooding of the ruderal area. The ruderal area mainly consists of Cirsium arvense (L.), Conyza canadensis (L.), Lactuca serricola (L.) and Sinapis arvensis (L.) and is usually completely flooded during an ecological flood event caused by high Rhine river water levels. During the vegetation period of 2008 the fallow area had a flood disturbance of less than 5% and the ruderal area of more than 30% (flood disturbance was calculated as the percentage of days that sampling could not be performed due to flooding). The soil of the polder is secondary loess with a high sand and loam content, typical of the region. Because of these soil conditions, strong precipitation events are sufficient to flood the ruderal area in particular.

For the study a total of 18 pitfall traps at six locations (three traps per location, distance between the traps: 5m) were used. Two locations were in the ruderal area

(L5, L6) and the remaining four locations were situated in the fallow area (L1–L4, Fig. 1A). The pitfall traps had a diameter of 10 cm at ground level and were protected from direct rainwater infiltration by a transparent cover (10×10 cm; plexiglas). The traps were filled with a saturated NaCl-solution and detergent as killing agent (Teichmann 1994; Muster 2002). The traps were replaced once every second week and the contents brought to the laboratory, where laboratory ethanol (70%) was used to preserve the catch. The sampling period presented here was from 28 February to 22 October 2008. The ruderal area was flooded from February to May, thus sampling took place for 168 days, while the dry fallow area was sampled for 237 days due to the small number of flood disturbances. The ruderal area dried up very quickly after a flooding event (Fig. 1C). This area was partly flooded again on 25 June 2008 for ca. 20 days as a result of a strong precipitation event (which equated to almost two-thirds of the long-term average of total monthly precipitation). July of 2008 was relatively dry compared to the long-term average of total monthly precipitation (-37.5%). Results are only presented for two localities (L1= fallow area and L6= ruderal area), as it was not possible to determine the collembolan communities in the other four localities (L2–L5) due to the fact that the springtail project ended in May 2008. These two localities are close to each other (< 25 m) but represent different areas and flood disturbances.

Because a number of pitfall traps failed, mainly in the ruderal area (due to flood disturbance), the total number of individuals collected was transformed to the mean number of individuals per trap and day (± Standard error; SE). Diversity (Shannon and Weaver 1949; Wiener 1949) and evenness (Pielou 1975) were first calculated using data from the whole sampling period in order to show the impact of ecological flooding on the different arthropod communities. To determine the influence of the strong precipitation event only, we removed data corresponding to the period of ecological flooding (28 February to 21 May 2008 for the fallow area; 28 February to 18 June for the ruderal area). These indices were calculated to show differences in the community structure between the dry and flood periods. For the comparison of the similarity of carabid beetle and springtail communities of the fallow and ruderal area, the speciesbased Jaccard and the dominance-based Renkonen indices were used. Furthermore the combined species- and dominance-based Wainstein-index was also calculated to compare the arthropod communities of both locations. This is calculated by the sum of the Jaccard and Renkonen similarities. For carabid beetles, the ecological classification followed Freude et al. (2004) and GAC (2009), and for springtails the classification into isovalent species groups followed Weigmann (1997), Russell et al. (2004) and Russell and Griegel (2006). Dominance classification for both groups followed Engelmann (1978). A PCA was run to show differences in species composition and dominance structure of the two areas. Because of the non-normal distribution of the arthropods in the pitfall traps and the small sample size a non parametric Mann Whitney U-test was calculated to measure significant differences between mean individual numbers caught during the flood and drought events. For statistical analyses Statistica 6.1 (StatSoft company) was used.

Results

Carabid beetles

In the fallow area, 46 carabid species of 1490 individuals were collected, while 33 species of 514 individuals were collected in the ruderal area. In the fallow area, 26 xerophilic and two mesophilic species dominated, representing more than 64% of all individuals collected, while five eurytopic species comprised more than 28% of the catch. The 12 hygrophilic species only made up 8% of the catch (see Appendix 1). Harpalus luteicornis (Duftschmid, 1812) was the only species that could not be clearly classified using the literature and is thus marked uc (unclassified) in Table 1 and in Appendices 1 and 2. In the ruderal area, 12 hygrophilic species dominated the catch (20% of all individuals collected), while 12 xerophilic and one mesophilic species comprised nearly 30% of all individuals. This area was dominated by six eurytopic species, representing almost 50% of the catch, while Bembidion species are predominantly limited to the ruderal area (Fig. 2). There were only two species without clear classification (see Appendices 1 and 2). Table 1 shows the classification of the species and individuals with and without the impact of ecological flooding. When the ecological flooding period (and data) was excluded, only a small decrease in abundance and a disappearance of four species were detected in both localities. In the fallow area, the hygrophilic species Bembidion biguttatum (Fabricius, 1779), Ocys harpaloides (Audinet-Serville, 1821) and Stenolophus mixtus (Herbst, 1784) as well as the xerophilic species Microlestes maurus (Sturm, 1827) disappeared (Appendix 2). In the ruderal area, in addition to Demetrias atricapillus (L.), the hygrophilic species Anisodactylus binotatus (Fabricius, 1787), Bembidion biguttatum and Stomis pumicatus (Panzer, 1796) disappeared (Appendix 2). However, all species that disappeared comprised only small numbers of individuals. This is also confirmed by the comparison of diversity and evenness values with and without the ecological flood data. In both locations without the ecological flood data, Shannon-diversity showed only a small decrease, whereas evenness values remained almost unchanged (Table 1). Furthermore, both areas showed a constant dominance of xerophilic and mesophilic species in terms of species number and abundance over hygrophilic species throughout the vegetation period (Fig. 3). Especially Pterostichus melanarius (Illiger, 1798), Poecilus cupreus (L.), Harpalus rufipes (De Geer, 1774) and Harpalus affinis (Schrank, 1781) occurred as dominant and subdominant species (Appendix 2). Thus, ecological flooding appeared not to cause species or dominance shifts. This is also confirmed by the dominance of hygrophilic and xerophilic/mesophilic species during the different moisture periods (Fig. 4). In the fallow area the drought period showed significantly higher abundances of hygrophilic (Fig. 4A: U-test: $p \le 0.01$) as well as xerophilic/mesophilic species (Fig. 4C; U-test: $p \le 0.01$). Higher abundances after the strong precipitation event in the fallow area were only detected for xerophilic/ mesophilic species (Fig. 4C; U-test: p = 0.044). In contrast to the fallow area, there

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Figure 2. PCA of carabid beetle communities in the fallow area (location 1) and the ruderal area (location 6) during ecological flooding, the flood caused by a strong precipitation event and drought conditions. Only species with more than 1% dominance value in at least one area are included. Abbreviations of the species: **A.mar**=*Agonum marginatum*; **A.bif**=*Amara bifrons*; **A.sim**=*Amara similata*; **B.lam**=*Bembidion lampros*; **B.pro**=*Bembidion properans*; **B.qua**=*Bembidion quadrimaculatum*; **C.pur**=*Carabus purpurascens*; **H.aff**=*Harpalus affinis*; **H.ruf**=*Harpalus rufipes*; **H.sma**=*Harpalus smaragdinus*; **N.bre**=*Nebria brevicollis*; **O.ard**=*Ophonus ardosiacus*; **P.cup**=*Poecilus cupreus*; **P.ant**=*Pterostichus anthracinus*; **P.mel**=*Pterostichus melanarius*; **P.nig**=*Pterostichus nigrita*. Percentage variation explained by the two PCA axes is included.

were no clear differences between the mean carabid beetle abundances during the flooding and drought periods at the ruderal area (Location 6; Fig. 4B and 4D).

The different species- (Jaccard) and dominance- (Renkonen) based similarity indices confirmed this stable community structure (Table 2). However, during the entire vegetation period some hygrophilic species with similar numbers of individuals occurred in both areas, although the dominance of the most dominant hygrophilic

Table 2. Comparison of the carabid beetle and springtail communities of the fallow area (location 1) and the ruderal area (location 6) using different species based and dominance based similarity indices (Jaccard, Renkonen and Wainstein) with and without data from the ecological flooding period. The percentages show the degree of similarity of the carabid beetle and springtail communities between the fallow and ruderal area. Values higher than 50% represent higher similarity of the communities between the two areas.

Comparison location 1 with location 6	C	arabid beet	es		Springtails	
	Jaccard	Renkonen	Wainstein	Jaccard	Renkonen	Wainstein
With data of	46.3	52.5	24.3	60.0	53.1	31.7
ecological flooding						
Without data of	51.1	51.5	26.3	60.0	95.7	57.4
ecological flooding						

species varied markedly. In the fallow area, *Pterostichus anthracinus* (Illiger, 1798) and *Pterostichus nigrita* were the most dominant hygrophilic species, whereas in the ruderal area *Nebria brevicollis* and *Agonum marginatum* dominated (Appendix 2). Species with a dominant or subdominant occurrence in only one location were *Carabus purpurascens* Fabricius, 1787, *Pterostichus nigrita* (Paykull, 1790) and *Amara bifrons* (Gyllenhal, 1810) in the fallow area and *Bembidion quadrimaculatum* (L. 1761), *Bembidion lampros* (Herbst, 1784), *Nebria brevicollis* (Fabricius, 1792) and *Agonum marginatum* (L.) in the ruderal area (Appendix 2). As such, the species- and dominance-based Wainstein-similarity index values were only about 25%, which is very low given the proximity of the two locations.

Springtails

In the fallow area, 15 collembolan species and 7001 individuals were caught. With the ecological flooding data included, seven xerotolerant and mesophilic species dominated the catch (90% of all individuals collected), while the three hygrophilic and hygrotolerant species comprised less than 10% of all individuals collected (Table 1). Mainly xerotolerant and mesophilic species were detected when data from the ecological flood period were excluded. In the ruderal area, nine collembolan species with 5405 individuals were captured. Here, however, the ecological flooding data showed that three hygrophilic and hygrotolerant species made up 56% of the catch, while four xerotolerant and mesophilic species made up almost 44% of all individuals collected (Fig. 5). Without the ecological flooding data, hygrophilic and hygrotolerant individuals were almost absent, which resulted in a dominance value of almost 100% for xerotolerant and mesophilic species. This result was also reflected in the lower diversity and evenness values (Table 1). In the ruderal area in particular, these indices decreased markedly. During and shortly after ecological flooding caused by a higher Rhine water level, three hygrophilic and hygrotolerant species *Podura aquatica* (L.), *Isotomurus palustris* (Mül-



Carabid beetles (Fallow area, L1)

Figure 3. Mean number of individuals per trap and day (\pm SE) and total carabid beetle species number at location 1 (fallow area) and location 6 (ruderal area) (n=3) during the vegetation period of 2008. Hygrophilic species (black bars) and xerophilic as well as mesophilic species (grey bars) are shown. Abbreviations: ef = ecological flooding; spe = strong precipitation event.

ler, 1776) and Sminthurides aquaticus (Bourlet, 1842) were highly abundant compared to all other species in both locations (Figs. 5 and 6, Appendix 3). The mean number of individuals of these species caught in the pitfall traps during the ecological flood was significantly higher than the mean number of individuals caught during the flood caused by the strong precipitation event (Fig. 7A and 7B; U-test: fallow area (L1): p \leq 0.01; ruderal area (L6): p = 0.025). After the ecological flood event, these species completely disappeared from both areas. Furthermore, compared to the dry period, the strong precipitation event at the end of June had no effect on hygrophilic and hygrotolerant species (U-test: fallow area (L1): p = 0.89; ruderal area (L6): p = 0.36). Compared to the ecological flood event, mean numbers of individuals belonging to the mesophilic species Isotoma viridis Bourlet, 1839 and the xerotolerant species Orchesella villosa (Geoffroy, 1762) increased significantly during the flood caused by the strong precipitation event and under drought conditions (Fig. 7C and 7D; U-test: fallow area (L1): $p \le 0.01$; ruderal area (L6): p = 0.022). During the sampling period, many collembolan species show a spring and autumn peak with very high individual numbers. In the polder this autumn maximum was also dominated by these two species (Isotoma viridis and Orchesella villosa). The species-based Jaccard similarity index showed a value of 60% for both areas with and without the impact of ecological flooding, which indicates stable collembolan communities (Table 2). However, differences were obvious concerning the dominance-based Renkonen index and the combined Wainstein index. Without the ecological flooding data, the values of these indices were remarkably high at almost 96% (Renkonen) and 58% (Wainstein), due to the eudominance of Orchesella villosa and the dominance of Isotoma viridis in both locations (Table 2). However, with the inclusion of the ecological flooding data, these values were lower, mainly because of the influence of the eudominant species Isotomurus palustris in the ruderal area. As such, without data from the ecological flooding event, the collembolan communities of both locations were highly similar, while ecological flooding increased

Discussion

The carabid beetle community structure showed clear differences between the two locations. The fallow area is characterized by more vegetation with higher structural diversity and plant heterogeneity, while the ruderal area is characterized by a high level of flood disturbance and less vegetation. The largest number of carabid beetles was collected from the fallow area. The dominance of xerophilic species such as *Harpalus rufipes* or *Harpalus affinis* was expected. A comparatively high number of hygrophilic species were also collected from this area, but with only a small number of individuals. Interestingly, *Agonum marginatum* was found in the fallow area even though this species prefers riverbanks with less vegetation (GAC 2009). This may be an escape strategy of this species to survive extreme flood events (Siepe 1994, Decleer 2003). It was only collected from the fallow area when the ruderal area was flooded.

the heterogeneity of the collembolan communities of both locations.

The high dominance of *Pterostichus melanarius* and *Poecilus cupreus* underlines the character of the fallow area. *Carabus purpurascens* is described as a mesophile wood-land species and it is possible that this large species prefers habitat in the fallow area where it finds more food and encounters fewer natural enemies (Hildebrandt 1997; Hildebrandt and Handke 1997).

Because of the prolonged flood disturbance from March to May and the strong precipitation event at the end of June 2008 fewer carabid beetles were collected from the ruderal area. Flood events in this area could favour the higher dispersal capacity of pioneer species (Wohlgemuth von Reiche et al. 1999). The appearance of species such



Fallow area (location 1)

Ruderal area (location 6)

Figure 4. Mean number of individuals of hygrophilic (A/B) and xerophilic/mesophilic (C/D) carabid beetle species at the fallow (A/C) and ruderal area (B/D) during different moisture conditions. Abbreviations: **ef** = ecological flooding (higher Rhine water levels); **spe** = flood caused by a strong precipitation event; **dc** = drought conditions; ° outliers. Different letters represent statistically significant differences (Mann-Whitney U-test).



Springtails (Fallow area, L1)

Figure 5. Mean individual numbers per trap and day (\pm SE) and total species numbers of springtails of the pitfall traps of location 1 and location 6 (n=3) over the vegetation period 2008. Hygrophilic and hygrotolerant species (black bars) and xerotolerant as well as mesophilic species (grey bars) are shown. Abbreviations: **ef** = ecological flooding; **spe** = strong precipitation event.



Figure 6. PCA of springtail communities in the fallow area (location 1) and the ruderal area (location 6) during ecological flooding, the flood caused by a strong precipitation event and drought conditions. Only species with more than 1% dominance value in at least one area are included. Abbreviations of the species: **I.pal**=*Isotomurus palustris*; **I.vir**=*Isotoma viridis*; **L.cya**=*Lepidocyrtus cyaneus*; **O.vil**=*Orchesella villosa*; **P.aqu**=*Podura aquatica*; **S.aqu**=*Sminthurides aquaticus*. Percentage variation explained by the two PCA axes are included.

as *Amara bifrons* or some *Harpalus* species in the ruderal area after flooding confirm the findings of Wohlgemuth von Reiche et al. (1999). Flooding influenced plant species richness as well as carabid species richness. Changing environmental conditions also have a major impact on the presence of carabid beetle species (Brose 2003). Gerisch et al. (2006) underlined the strong relationship between both flood duration and groundwater depth and the occurrence of carabid beetles. The main activity period of carabid beetles is between May and October and the ecological flood event lasted until the end of May. Our result showed that disturbance to the carabid beetle community



Figure 7. Mean number of individuals of hygrophilic/hygrotolerant (A/B) and xerotolerant/mesophilic (C/D) collembolan species at the fallow (A/C) and ruderal area (B/D) during different moisture conditions. Abbreviations: **ef** = ecological flooding (higher Rhine water levels); **spe** = flood caused by a strong precipitation event; **dc** = drought conditions; ° outliers. Different letters represent statistically significant differences (Mann-Whitney U-test).

caused by this flood was very low. The disappearance of only four species, albeit with very low numbers of individuals, confirmed this in particular, because ecological flooding occurred before the onset of the main activity period of many carabid species. After the ruderal area had dried up in July 2008, a migration of eurytopic and xerophilic species, possibly from the fallow area, was observed (*Bembidion lampros, Bembidion quadrimaculatum* and *Pterostichus melanarius*). Similar observations were made in a marshland habitat (Decleer 2003).

Furthermore, the dominance of small carabid beetles such as *Bembidion quadri*maculatum or *Bembidion lampros* can be explained by the work of Schwerk and Szyszko (2007a, b), who found that habitats at an early successional stage are characterised by smaller species compared to habitats of later successional stages. This conclusion was also supported by our results as the less disturbed fallow area included larger carabid beetles (*Carabus purpurascens*). Our conclusion is, thus, that the effect of the 2008 ecological flooding on the carabid beetle fauna was quite minimal.

In contrast to the mobile carabid beetles, ecological flooding had a considerable impact on the collembolan community at both areas. Hygrophilic and hygrotolerant species occurred only during and shortly after this flood event. The adaptation of these species to coping with floods is passive drifting (Coulson et al. 2002; Moore 2002; Hawes et al. 2008). The cuticle of most springtail species is hydrophobic due to its typical structure; it is composed of hexagonal subunits with microtubercles, which varies between different species (Lawrence and Massoud 1973; Eisenbeis and Wichard 1985). Furthermore, the existence of an epicuticular hydrophobic lipid layer was demonstrated by Ghiradella and Radigan (1974). The unwettable properties of the springtail cuticle produces a small air layer (plastron structure), which prevents the species from submersion and enables them to drift passively on the water surface. The feed stream of the polder flows through a natural backwater of the river Rhine, which is colonized mainly by epineustic species such as Podura aquatica and Sminthurides aquaticus as well as the typical riverbank species Isotomurus palustris. This explains both the dominance of these species during and shortly after ecological flooding in both areas and the fact that they quickly disappeared during the short drying period. The fallow area was constantly dominated by xerotolerant and mesophilic species, while the disappearance of hygrophilic and hygrotolerant species caused only a small decrease in diversity and evenness. Hydrological parameters are key factors in determining vegetation structure, carabid beetle and collembolan communities, as well as for other invertebrate taxa (Uetz et al. 1979; Zulka 1993; Russell and Griegel 2006; Siepe 2006; Ilg et al. 2008; Marx 2008). The community structure of the ruderal area showed a higher dominance of hygrophilic and hygrotolerant species; this resulted in a strong decrease of diversity and evenness values when the ecological flood data were excluded. This demonstrates the heterogeneity of the collembolan communities of these two areas, which are probably caused by ecological flooding. The dominance-based similarity indices, in particular, clarify this result. Without the ecological flood data, only the two xerotolerant and mesophilic species Orchesella villosa and Isotoma viridis dominated both areas. This demonstrates the importance of protecting such rare ruderal areas of this polder with the help of ecological flooding.

Conclusion

This investigation showed that, in addition to ecological flooding, other flooding events, such as strong precipitation or seepage water, are important factors for the spatial and temporal dynamics of different arthropod groups in such ruderal and seepage areas. These findings emphasize the value of using different taxa in the designing of future polder constructions. If only one arthropod group had been studied this might have led to the erroneous conclusion that ecological flooding has no effect or that it only affects this one bioindicator group. The data collected from several arthropod groups, however, provide more reliable and comprehensive information on the real ecological value of the polder structures.

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Appendix I.

Dominance [%] of hygrophilic (**h**), xerophilic/mesophilic (**x/m**), eurytopic (**e**) and unclassified (**uc**) carabid beetle species and individuals at location 1 (fallow area) and location 6 (ruderal area):





Appendix 2.

Total number of carabid beetle individuals (Carabidae), number of flood-undisturbed pitfall traps and trapping days of location 1 (fallow area) and location 6 (ruderal area). Abbreviations: ec=ecological classification, h=hygrophilic, x=xerophilic, m=mesophilic, uc=unclassified, e=eurytopic.

Location 1 (fallow area)	ec	13.03	01.04	23.04	07.05	21.05	04.06	18.06	02.07	16.07	30.07	13.08	27.08	10.09	24.09	09.10	22.10	
no. of pitfall traps		3	3	2	1	2	3	3	3	3	3	3	3	3	3	3	3	total
trapping days		14	19	22	14	14	14	14	14	14	14	14	14	14	14	15	13	
Acupalpus meridianus	x					2		1										3
Agonum marginatum	Ч	3				1	1	1	1									7
Agonum muelleri	Ч					1		2				1						4
Agonum sexpunctatum	Ч										1							1
Amara aenea	×						4											4
Amara apricaria	×													1			1	2
Amara aulica	×								1		1			-				2
Amara bifrons	×						7	16	4		5	2	2	3	3	9	3	51
Amara consularis	×																1	1
Amara similata	x						1	2	1	11	8	2	1		1			27
Anchonemus dorsalis	x							2										2
Badister unipustulatus	Ч						1	2			1		1					2
Bembidion biguttatum	Ч		1															1
Bembidion lampros	e								1		1		1					3
Bembidion obtusum	x	2	6				1											12
Bembidion properans	e	2			2	2					3							6
Bembidion quadrimaculatum	e	3				2	3			1	3	1	1			1		15
Brachinus explodens	×						1											1
Bradycellus harpalinus	×								1									1
Calathus ambiguus	x										1	1	1	3	1			7
Calathus fuscines	x										_	_	4	-				7

		000) o	,) C) C				000	000		00		0		
Location 1 (fallow area)	ပ္ပ	15.03	01.04	25.04	CU./U	21.05	04.06	18.06	0.70	16.07	30.0/	15.08	27.08	10.09	24.09	01.00	22.10	
no. of pitfall traps		3	3	2	1	2	3	3	3	3	3	3	3	3	3	3	3	total
trapping days		14	19	22	14	14	14	14	14	14	14	14	14	14	14	15	13	
Calathus melanocephalus	×												-	2	2	2		2
Carabus purpurascens	E						1	7	6	9	25	64	87	98	18	4		319
Chlaenius nigricornis	ч											1					-	4
Harpalus affinis	×					12	9	8	9	5	7	8	2			2	2	58
Harpalus distinguendes	×		2			-	3					-						8
Harpalus latus	e										-		9					8
Harpalus luteicornis	uc						2					1	1					4
Harpalus rubripes	×				1		2	-			2							7
Harpalus rufipes	×						1	3	4	10	13	30	16	13	1	1		92
Harpalus smaragdinus	×					1	3	2	1	2	1	2	2					14
Leistus ferrugineus	×															1		1
Microlestes maurus	×		3															3
Microlestes minutulus	×		1				1											2
Nebria brevicollis	Ч					1	2								1			4
Notiophilus palustris	Ч											1				-		2
Ocys harpaloides	Ч	1																1
Ophonus ardosiacus	х					1		1	1	2	10	2			1			18
Ophonus azureus	x					1	1	1			1	1						5
Ophonus laticollis	х											2	1	1				4
Poecilus cupreus	x		3			39	16	57	21	19	32	33	32	17	4	10	8	291
Pterostichus anthracinus	Ч								2		4	2	3	6	1	3		21
Pterostichus melanarius	e						6	28	16	7	27	74	94	98	10	17	3	383
Pterostichus nigrita	h							4	2	2	9	11	6	19	4	5		62
Pterostichus oblongopunctatus	Ξ													3				3
Stenolophus mixtus	Ч					-												1

01.04 23.04 07.05 21.05 04.06 18.06 02.07 16
1 2 1
14 14
2 8
2
1
1
5
5
2
2

Location 6 (ruderal area)	ec	13.03	01.04	23.04	07.05	21.05	04.06	18.06	02.07	16.07	30.07	13.08	27.08	10.09	24.09	09.10	22.10	
no. of pitfall traps		2	۱	ı	ı	ı	1	2	1	2	2	ŝ	ŝ	ŝ	ŝ	ŝ	ŝ	total
trapping days		14	١	۱	ı	ı	14	14	14	14	14	14	14	14	14	15	13	
Ophonus azureus	х									1								1
Poecilus cupreus	х					ю	1	ю	13	1	4	3	8		4			40
Pterostichus anthracinus	h												2					2
Pterostichus melanarius	e									4	18	14	48	7				94
Pterostichus nigrita	h									1	5	3	5					14
Stomis pumicatus	h					1												1
Trechus quadristriatus	х															1		1

Appendix 3

Total number of springtail individuals (Collembola), number of flood-undisturbed pitfall traps and trapping days of location 1 (fallow area) and location 6 (ruderal area). Abbreviations: ec=ecological classification, h=hygrophilic/hygrotolerant, x=xerotolerant, m=mesophilic, uc=unclassified.

Location 1	ec	13.03	01.04	23.04	07.05	21.05	04.06	18.06	02.07	16.07	30.07	13.08	27.08	10.09	24.09	06.10	22.10	
no. of pitfall traps		3	3	7	1	7	æ	3	3	3	3	ŝ	3	3	ŝ	ŝ	ŝ	total
trapping days		14	19	22	14	14	14	14	14	14	14	14	14	14	14	15	13	
Ceratophysella bengtssoni	nc	3	4					1	-									10
Ceratophysella denticulata	nc		1															-
Neanura muscorum	Ш		1															1
Podura aquatica	ч	13	50			12												75
Isotomurus palustris	h	437	106	10	4	15	2											574
Isotoma viridis	E	34	24			-	59	101	56	56	47	32	8	2	8	125	753	1308
Entomobrya lanuginosa	ш	2	41			2	5	1										51
Lepidocyrtus cyaneus	х	3	4			2	27	32	42	33	23	9	1		~	39	77	296
Lepidocyrtus paradoxus	nc		1															1
Orchesella villosa	х	6	5	2		15	162	411	377	638	543	429	106	192	412	453	876	4630
Bourletiella hortensis	nc							2										2
Sminthurus viridis	х		11			3	2	10	1								1	28
Sminthurus nigromaculatus	Е	2			1			9	7	2	1							19
Sminthurides aquaticus	q	3																3
Deuterosminthurus pallipes	uc				1		1											2

Location 6 (ruderal area)	ec	13.03	01.04	23.04	07.05	21.05	04.06	18.06	02.07	16.07	30.07	13.08	27.08	10.09	24.09	09.10	22.10	
no. of pitfall traps		2	۱	ı	١	١	1	2	1	2	2	3	3	3	3	3	3	total
trapping days		14	١	١	١	١	14	14	14	14	14	14	14	14	14	15	13	
Ceratophysella bengtssoni	uc	1																1
Podura aquatica	h						192	65	67									324
Isotomurus palustris	h	7					1318	823	388	3								2539
Isotoma viridis	ш	3					1	5	4	66	19	6			98	188	177	567
Lepidocyrtus cyaneus	х							2	1	6	1	3			2	1		19
Orchesella villosa	х							34	41	308	178	90	15	7	79	349	675	1776
Sminthurus viridis	x									1								1
Sminthurides aquaticus	h	6					75	76	17									177
Deuterosminthurus pallipes	uc												1					1

RESEARCH ARTICLE



Assemblages of carabid beetles (Coleoptera, Carabidae) in humid forest habitats of different stages of succession in the Puszcza Knyszyńska Forest (northeastern Poland)

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Abstract

During a period of three years (2006–2008) the carabid fauna in wet and humid forest habitats of different stages of succession was studied at the Puszcza Knyszynska (north-east part of Poland). The aim of this study was to determine how the assemblages of the carabid fauna change in relation to the ongoing process of succession. Using pitfall traps, 24 plots were sampled. The plots were located in stands of different age, from two year old plantations to more than 100 year old forests. Additionally, the stands were ordered in three moisture classes (wet, humid and very humid) and two classes of soil richness. As indicators for change in the carabid fauna in relation to age of the stands Mean Individual Biomass (MIB), species diversity and share of forest species were used. By applying multivariate statistics the relation of the different habitat characteristics to changes in the carabid fauna was examined. During the study 8903 individuals belonging to 57 species were collected. Pterostichus niger represented 28% of the total catches and therefore the most common species. Another common species, Pterostichus melanarius, contributed to 13% of the total catch. This species was caught at every plot, even in the old forests. In contrast to the results obtained by Szyszko (1990) for fresh and dry pine stands, in this study the relation of MIB with the age of forest was not significant. Although the number of species was rather constant, the number of individuals belonging to the group of forest species significantly increased with the ageing of the forest. The multivariate analysis showed a relationship with ageing of the stands and soil richness rather than with moisture and size of the forest. According to the present paper, clear cuttings in wet and humid habitats do not cause a strong degradation of the carabid fauna.

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Keywords

Carabidae, Puszcza Knyszyńska, process of succession, wet and humid, forest habitats, Mean Individual Biomass

Introduction

Carabid beetles represent one of the largest groups of animals, occurring in almost every type of terrestrial habitat. In Poland over 500 species of these insects are recorded (Burakowski et al. 1973, 1974). The reaction of these animals to environmental changes is fast and pronounced. Habitat changes may be natural due to succession, or anthropogenic due to human management. Therefore, AT each stage of succession, carabid beetles are characterised specific assemblages. Consequently, this group of animals can be used as an indicator of environmental changes (Rainio and Niemelä 2003, Pearce and Venier 2006).

Szyszko (1990) used the Mean Individual Biomass (MIB) of carabid beetles as an indicator of successional changes in pine forests growing in dry and fresh habitats. However, data concerning wet and humid forest habitats are lacking. Therefore, a study on carabid fauna in this type of habitat was carried out over a period of three years (2006 - 2008) in the Puszcza Knyszyńska forest. This forest is located in the north-eastern part of Poland and it is characterized by many small forest rivers. In the valleys of the forest rivers and streams, wet and humid forests on organic and very rich soil have developed. In the past, forests growing in this type of habitat were exploited using clear cuts. In the last few years single clear cuts were restricted to an area of 2-3 ha. Therefore, the study sites, where the research was carried out, usually are no larger than 3 ha. Nowadays, the forest service tries to avoid using clear cuts, because this type of forest management is thought to have negative impact on the environment (Dyrektor Generalny Lasów Państwowych 1999). On the other hand, a clear cut can be, to a certain degree, compared to a natural catastrophe (e.g. wind break, fire), which arrests the process of succession. After a clear cut, secondary succession starts from a comparably young stage. With increasing age of the forest stand, advanced stages of succession develop at various speeds (Szyszko 1990). Studies on carabid beetles (see Rainio and Niemelä 2003) show that these animals react quickly after disturbance of their environment. After a clear cut, species characteristic of forests disappear, whereas species typical for open habitats rapidly colonise the area. However, with ongoing succession, typical forest species reappear and their share consequently increases (Szyszko 1990, Koivula and Niemelä 2002, Paquin 2006).

The aim of the study was to analyse how the assemblages of carabid beetles occurring in wet and humid forest habitats change with an ongoing process of succession (age of the forest stands). These changes were expected to be analogous to those observed in other forest types as pine forests (Szyszko 1990) and boreal mixed-wood forests (Jacobs et al. 2008). Therefore, the main hypothesis is that with preceding succession the characteristics of the carabid fauna change from those typical for open land to those typical for forest habitats. Accordingly, MIB values as well as the share of forest species, autumn breeders and large zoophages, which are supposed to predominate in mature forests (Skłodowski 2006), should significantly increase, but the number of species should decrease.

However, besides age of the forest stands, other factors like environmental conditions or habitat fragmentation (e.g. Desender 2005) may have an influence on the development of the carabid assemblages. Therefore, a second aim was to analyze the impacts of age of size of the forest stand, as well as its moisture and soil richness on the carabid assemblages.

Methods

The study was carried out in 24 sampling plots (Fig. 1), in the Puszcza Knyszyńska forest, located in the forest district Czarna Białostocka (north-eastern Poland). The sampling plots were located in independently treated units of the forest of different age and size, at least 50 m apart. The age of the units ranges from a 2 year old plantation after clear cut to over 100 year old forests and size ranges from about 1 ha to almost 11 ha. Additionally, the units were classified with respect to moisture conditions and soil richness (Table 1) accordingly to the periodical inventories of forest habitats and forest resources done for the forest district Czarna Białostocka (Biuro Urządzania Lasu i Geodezji Leśnej Białystok 2006). Based on these data, moisture of the sampling plots was assessed on a scale of three grades: 1 – humid plots, 2 – wet plots, 3 – marshy plots. Soil richness was assigned to two levels: 1 – rich soil (mixed deciduous forest), 2 – very rich soil (deciduous forest).

Carabid beetles were collected using pitfall traps (Barber 1931), with modifications according to Szyszko (1981). Jar glasses were used as traps. A funnel with an upper diameter of about 10 cm and a lower diameter of about 1.6 cm was placed above them flush with the soil surface. A roof was installed a few centimeters above the funnel and ethylene glycol was used as trapping fluid.

At each sampling plot three pitfall traps were situated 5 m apart. Collection of carabids was carried out from 2006-2008, from mid-May to the end of September and traps were emptied three times during this period. Carabid beetles were identified using the keys of Hurka (1996) and Müller-Motzfeld (2004). The nomenclature follows Hurka (1996).

For each sampling plot the following parameters of the carabid fauna were calculated: number of collected species, share of individuals of typical forest species, share of individuals of big zoophages, share of individuals of autumn breeding species (Lindroth 1945; Burakowski et al. 1973, 1974; Hurka 1996; Müller-Motzfeld 2004) and MIB value. MIB values were calculated by dividing the biomass of all sampled carabids by the number of specimens caught. Biomass values were fixed for the recorded species using values from Szyszko (1990) or, with respect to species not included in his paper, using the formula by Szyszko (1983) that describes the relationship between the body length of a single carabid individual (x) and its biomass (y):

 $\ln y = -8.92804283 + 2.55549621 \text{ '} \ln x \qquad (\text{eq. 1})$



Figure 1. Location of the sampling plots in the Puszcza Knyszyńska forest. For specifications, see Table 1.

Correlations between these parameters and the age of the forest sites were tested using the Spearman rank correlation coefficient (Sachs 1984).

To analyse the impact of the factors size, age, soil richness and moisture of the sampling plots, a multivariate analysis (RDA) was carried out using the CANOCO for Windows software package, v. 4.5 (ter Braak 1987; ter Braak and Šmilauer 2002). Detrended Canonical Correspondence Analysis (DCCA) was carried out in advance to select the appropriate response model (ter Braak and Prentice 1988). Redundancy Analysis (RDA) was performed using inter-species correlations and dividing by standard deviation. Data were not transformed. Centering was done only by species. No forward selection was carried out. A triplot was created with species fit range adjusted from 25 to 100 % (passed by 15 species).

Results

During the three years of investigation 8903 individuals, belonging to 57 species of carabid beetles, were collected (Table 2). Seven of these protected by law in Poland (Ministerstwo Środowiska 2004). Being the most common species, *Pterostichus niger* contributed 27.8% to the catches. Another very common species, with a percentage share of 13.7%, was *Pterostichus melanarius*. Irrespective of the age of the stands, this species was recorded from each plot,.

With increasing age of the forest stands the share of forest species increased significantly from below 50% in the young stands to almost 90 % in the older stands

Number of sampling plot	Size (ha)	Age (years)	Moisture	Soil richness
1	2.09	68	1	1
2	7.16	73	2	1
3	1.87	91	1	1
4	1.59	4	1	2
5	1.11	13	1	2
6	2.82	7	3	2
7	1.91	127	3	2
8	2.39	3	3	2
9	4.35	46	1	2
10	2.02	93	3	2
11	3.35	28	3	2
12	1.64	29	1	2
13	7.46	81	1	2
14	1.05	22	2	1
15	2.09	8	2	1
16	2.35	3	1	1
17	10.72	83	2	1
18	2.9	26	3	2
19	1.86	46	1	1
20	2.2	3	2	1
21	1.06	103	2	1
22	2.07	93	2	1
23	1.72	78	3	2
24	6.51	101	1	1

Table 1. Characterisation of the studied forest units with respect to size, age, moisture and soil richness. See text for explanations.

(Fig. 2; Spearman rank correlation coefficient $r_s=0.696$, p<0.001). The share of large zoophages also increased significantly (Fig. 3; Spearman rank correlation coefficient $r_s=0.485$, p<0.05), whereas the share of autumn breeders did not show a significant increase with the age of the stands (Spearman rank correlation coefficient $r_s=0.371$, n.s.). Species numbers remained rather constant with increasing age of the forest stands (Spearman rank correlation between MIB values and the age of the stands was observed (Spearman rank correlation coefficient $r_s=0.111$, n.s.).

The first two axes of the RDA explain 36.2% of the variance in the species data and 91.5% of the variance in the fitted species data. The diagram (Fig. 4) indicates a stronger impact of age of the stands and soil richness, whereas the impact of moisture and size of the forest stands is less strong. The latter has the lowest impact on the structure of the carabid assemblages among the four studies factors. Age of the forest stand and soil richness are not correlated. Accordingly, the sampling plots are located along **Table 2.** List of collected species and their ecological characteristics concerning habitat preference, breeding type and feeding type. Species are sorted by total abundance and dominance (%) (nomenclature according to Hurka 1996).

<u> </u>	Habitat	Breeding	Feeding	Total	Dominance
Species	preference	type	type	abundance	(%)
Pterostichus niger	F	A	В	2472	27.78
Pterostichus melanarius	0	А	В	1219	13.70
Pterostichus oblongopunctatus	F	S	S	599	6.73
Oxypselaphus obscurus	F	S	S	589	6.62
Patrobus atrorufus	F	А	S	486	5.46
Carabus granulatus *	E	S	В	414	4.65
Carabus hortensis *	F	A	В	389	4.37
Epaphius secalis	E	А	S	308	3.46
Pterostichus aethiops	F	S	S	285	3.20
Carabus coriaceus *	F	А	В	269	3.02
Cychrus caraboides	F	A	В	246	2.76
Europhilus fuliginosus	F	S	S	198	2.22
Pterostichus strenuus	F	S	S	164	1.84
Carabus glabratus *	F	А	В	159	1.79
Agonum afrum	F	S	S	142	1.60
Platynus assimilis	F	S	S	92	1.03
Calathus micropterus	F	A	S	86	0.97
Carabus nemoralis *	F	S	В	80	0.90
Carabus arvensis *	F	S	В	67	0.75
Pterostichus anthracinus	0	S	S	60	0.67
Poecilus versicolor	0	S	S	54	0.61
Pterostichus nigrita/rhaeticus	E	S	S	51	0.57
Badister lacertosus	F	S	Н	44	0.49
Bembidion mannerheimi	0	S	S	44	0.49
Notiophilus palustris	F	S	S	37	0.42
Harpalus latus	E	A	Н	35	0.39
Pterostichus vernalis	Е	S	S	31	0.35
Stomis pumicatus	E	А	S	31	0.35
Clivina fossor	0	S	S	29	0.33
Loricera pilicornis	E	S	S	29	0.33
Agonum sexpunctatum	E	S	S	24	0.27
Harpalus quadripunctatus	F	S	Н	24	0.27
Carabus cancellatus *	0	S	В	22	0.25
Pterostichus minor	E	S	S	17	0.19
Badister sodalis	0	S	Н	16	0.18
Bembidion lampros	0	S	S	14	0.16
Leistus terminatus	F	A	S	12	0.13
Amara familiaris	E	S	Н	9	0.10
Pseudoophonus rufipes	0	A	Н	9	0.10

	Habitat	Breeding	Feeding	Total	Dominance
Species	preference	type	type	abundance	(%)
Synuchus vivalis	Е	А	S	8	0.09
Amara lunicollis	Е	S	Н	5	0.06
Leistus piceus	F	A	S	5	0.06
Amara communis	0	S	Н	3	0.03
Amara plebeja	Е	S	Н	3	0.03
Pterostichus diligens	F	S	S	3	0.03
Dyschirius globosus	Е	S	S	3	0.03
Amara curta	0	S	Н	2	0.02
Harpalus luteicornis	Е	S	Н	2	0.02
Nebria brevicollis	F	А	S	2	0.02
Notiophilus biguttatus	F	S	S	2	0.02
Amara similata	0	S	Н	2	0.02
Agonum viduum	Е	S	S	2	0.02
Amara brunnea	F	А	Н	1	0.01
Harpalus anxius	0	S	Н	1	0.01
Anisodactylus binotatus	Е	S	Н	1	0.01
Amara nitida	0	S	Н	1	0.01
Platynus krynickii	F	S	S	1	0.01

* - species protected by law in Poland

Habitat: F - typical forest species. E - eurytopic species. O - open habitat species

Breed: S - spring breeder. A - autumn breeder

Food: **B** – large zoophage. **S** – small zoophage. **H** – hemizoophage

the first and second ordination axes concerning their soil richness and age. Sampling plots with very rich soil are located to the left of the diagram, whereas sampling plots of less rich soil are located to the right of the diagram. Younger sampling plots are located in the lower part and the older sampling plots are located on the upper part of the diagram.

Discussion and conclusion

The main hypothesis of the study was only partly confirmed. The contribution of forest species and large zoophages to the carabid fauna increased significantly with age of the forest stands, but that of autumn breeders, number of species and MIB values did not. Age of the forest stands and soil richness were more important regarding the structure of carabid assemblages, whereas moisture and size of the forest stands appeared to be of less importance.

This increase of the contribution of forest species and large zoophages was expected, since it was observed in other studies as well, for example pine forests and boreal mixed-wood forests (Szyszko 1990, Schwerk 2008, Jacobs et al. 2008). After



Figure 2. Relationship between the contribution of forest species and the age of sampled forest stands (Spearman rank correlation coefficient $r_{=}0.696$; p=0.001)

disturbance of a forest environment, which arrests succession, the number forest specialists rapidly decreases (Szyszko 1990, Koivula and Niemela 2002, Paquin 2006). The observed increase in share of typical forest species and large zoophages shows that with ongoing succession the carabid fauna is changing from species typical for open areas to a typical forest fauna.

However, the contribution of autumn breeders and species numbers did not change significantly, the latter contradicts the results found for the succession in pine forests (Szyszko 1990). Also the increase of MIB values with the age of stands was not significant. Szyszko (1990, 1991) presented MIB as simple and good indicator that describes the stages of succession in pine forests growing on dry and fresh soil. In humid and wet forests this indicator seems to be less useful, the process of succession is slower or the impact of clear cuttings is less sever in humid and wet habitats.

The results of the study indicate that the degree of degradation and the process of regeneration of the carabid fauna in wet and humid forest habitats on organic soil is somewhat different compared to habitats of dry pine stands. This might be due to the fact that the forests of the present study grow on very rich, organic soil. After a clear cut in this type of forests, the method of soil preparation before planting young trees is different from forests on dry and mineral soil. The soil of the forests studied in the presented paper was never ploughed. However, ploughing destroys the litter layer of the habitat, which is necessary for the occurrence of many species characteristic of for-



Figure 3. Relationship between the contribution of large zoophages and age of the sampled forest stands (Spearman rank correlation coefficient r=0.485; p<0.05)

ests (Skłodowski 2006, Pihlaja et al. 2006). In the present study almost all MIB values for young sampling plots exceed 100 mg, which indicates that the degradation of the habitat by clear cutting and soil preparation was comparatively low. MIB values for young stages of succession in fresh pine forests often amount to about 40 mg (Schwerk 2008). The assumption of a low degradation of the studied forest sites is also supported by the fact that soil richness and age of the sampling plots are not correlated in the RDA analysis.

In the Puszcza Knyszyńska forest, clear cuts in wet habitats are usually no larger than 3 ha. Even if the size of the forest seems to have a comparatively low impact on the structure of the carabid assemblages in the present study, the size and shape of clear cut areas may be important factors. In order to support species diversity, it seems to be necessary to avoid creating large-sized open areas by clear cutting in large forest complexes. In this context the dispersal power of the respective species is important. For example, according to Spence et al. (1996) beetles characteristic of old forests may be not be able to recolonize patches of uncut forests if the distance between suitable patches becomes too large. On the other hand, clear cuts create suitable conditions for species with preferences for open areas (Skłodowski 2002, Koivula and Niemelä 2002). As many of these species are able to fly, these areas can be colonized rapidly even when located inside large forest complexes, for which also forest-roads can be used (Koivula and Niemelä 2002). In the present study twelve species of open areas were recorded only in young plantations of an age of 2–5 years.



Figure 4. Multivariate analysis (RDA) carried out with the dataset (number of the sampling plots as in Table 1). See text for explanations.

Despite some areas of clear cuts, the Puszcza Knyszyńska forest as a whole can be regarded as an ancient woodland. However, these clear cuts may contribute to fragmentation of the ancient forest, thus being a threat for forest species diversity. Assmann (1999) and Desender (2005) showed that for forest species with a low dispersal power the size of ancient forests is most important. Therefore, excessive fragmentation of ancient forests may lead to the extinction of local populations of species specialized on forests (Desender 2005). In the present study *Carabus glabratus*, which according to Assmann (1999) is a characteristic species of ancient woodlands, was recorded from 15 of the 24 sampling plots. This suggests that the applied practice of small sized, narrow clear cuts seems not to affect species diversity in the Puszcza Knyszyńska forests much.
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RESEARCH ARTICLE



Belowground carabid beetle diversity in the western Palaearctic – effects of history and climate on range-restricted taxa (Coleoptera, Carabidae)

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Abstract

Broad-scale patterns of subterranean diversity are a fascinating but neglected part of biodiversity research. Carabid beetles adapted to belowground habitats form a particularly species-rich part of the subterranean fauna. We studied large-scale diversity patterns of these belowground carabids across the western Palaearctic and evaluated potential impacts of historical and contemporary environmental conditions on the distribution of these taxa, using available species richness and environmental data at country level. Regression modelling and variation partitioning showed a strong relationship between species richness and range in elevation. Potential effects of climatic variables, mainly those related to ambient energy input, were much weaker. We discuss the implications of this combination of effects, which suggests, concordant with the absence of subterranean carabids in northern and highest richness in southern Europe, a strong prevailing influence of historical processes on current richness distributions of these taxa. Previous studies did not provide clear indications for such an influence. In contrast to more mobile and widespread carabid beetles, dispersal limitation due to high adaptation of belowground carabids to subterranean habitats has probably hindered their re-colonization of former permafrost and glaciated regions. Hotspots of highest belowground diversity are located in regions with an assumed long-term stability of environmental conditions, correlating with patterns of other dispersal-limited taxa such as many endemic plants. Our study provides important new information in the discussion of potential determinants of the distinct geographic patterns of belowground diversity. Moreover, it contributes to a better understanding of range size related differences previously found in the distribution of diversity and environmental dependencies of widespread and range-restricted species within the highly diverse carabid beetles.

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Keywords

Cave fauna, endogeic, glaciations, geographic range, insects, latitudinal gradient, macroecology, permafrost, subterranean

Introduction

Studies on the spatial patterning of biodiversity and its potential determinants have gained much attention over the last decades, especially in light of global change and its assumed effects on the distribution and survival of many species (Kerr et al. 2007). In this regard, the diversity of belowground habitats has been studied only poorly, even though it comprises many rarely recorded and highly adapted species (Culver et al. 2006). These habitats are characterized by much lower temporal variability of the physical environment than aboveground habitats (Wilkens et al. 2000; Assmann et al. 2010). Still, dependencies on environmental factors that have been identified as potential drivers of the distribution of diversity of many aboveground organism groups are being assumed also for subterranean diversity (Culver et al. 2006; Zagmajster et al. 2008). Especially productivity of the aboveground habitats, which again is determined by an interplay of energy input and water availability (Hawkins et al. 2003), has repeatedly been suggested as a possible factor influencing diversity in these subterranean habitats, which are often considered (and this particularly applies to caves) to be to a large part dependent on allochtonous input of resources (Gers 1998; Culver et al. 2006). Such a dependency on environmental factors could have far-reaching consequences for the strongly dispersal-limited Belowground taxa regarding future shifts in environmental conditions due to climate change (Sharratt et al. 2000).

However, reduced dispersal abilities due to their strong habitat specialization also suggest that especially processes and environmental conditions over historical times have played important roles in the survival and present distribution of these species. Regions with high numbers of subterranean species have probably been subject to lower variability in environmental conditions over long time periods and a higher persistence of ecosystems than other western Palaearctic regions (Casazza et al. 2008; Assmann et al. 2010).

About 50% of the terrestrial fauna in subterranean habitats are beetles (Zagmajster et al. 2008). With more than 1,000 troglobiont and endogeic species described so far, carabid beetles make up a large part of this subterranean fauna in the western Palaearctic, which harbours one of the hotspots of highest diversity of terrestrial troglobites in the northern hemisphere (Casale et al. 1998; Culver and Sket 2000; Culver et al. 2006; Assmann et al. 2010). Carabids are thus also well suited to provide important insights into aspects of faunal diversity of subterranean habitats. Moreover, results from the study of the highly diverse subterranean carabid fauna also have implications for the understanding of general patterns in the distribution of biodiversity over large geographic extents. Schuldt & Assmann (2009) found differences in the potential impact of current climate and historical processes on overall diversity and that of widespread

and endemic species of carabid beetles in the western Palaearctic, probably due to differences in the dispersal abilities of these taxa. Comparison of these patterns to those of the strongly range-restricted carabids living in belowground habitats can help to extend our understanding of the distribution of diversity and the possible mechanisms behind such range-size dependent diversity patterns.

The aim of our study was to analyse spatial patterns in the species richness of belowground carabids and their potential environmental determinants on a large scale across Europe and North Africa. Distinguishing between the carabid fauna of deeper soil horizons, beetles of the so-called superficial underground compartment ("milieu souterrain superficiel", MSS; Juberthie 1979) as a macroporal system in rocky material, and obligate cave-dwellers is not possible for all regions of the western Palaearctic, as species known as specialized cave dwellers have also been recorded in the MSS (e.g., *Aphaenopidius kamnikensis* DROVENIK 1987, a carabid until recently known to occur only in caves; Drovenik et al. 2007). Thus, in our analysis we combine all species from these systems with an obligate subterranean way of living and use the term "belowground fauna" for these taxa from hereon. Species with the ability to fly and also occurring in aboveground habitats (e.g., species of *Limnastis*) were not treated as part of the belowground fauna.

Analysing country-level species and environmental data, we hypothesize weak links between belowground diversity and current climatic conditions and a strong signal of history contained in broad-scale distribution patterns of belowground carabids. This would support and help to explain the previous findings concerning range size dependent differences between total, widespread and endemic richness of carabids in the response to large-scale environmental conditions (Schuldt and Assmann 2009).

Methods

Species and environmental data

Species numbers of carabid beetles were extracted from Löbl and Smetana (2003) for 39 countries of the western Palaearctic. The distribution of diversity for most invertebrates is not well documented at smaller scales over such large geographic extents, which hinders analysis on a more detailed scale or assigning reliable data to equal-area grids (Baselga 2008; Hortal 2008). In contrast, country-level data for carabid beetles in the western Palaearctic is quite comprehensive and allows accurate analysis of macro-ecological patterns for such a highly diverse insect taxon (Schuldt and Assmann 2009; Schuldt et al. 2009). In our analyses, we excluded Iceland due to its strong insularity as well as Andorra, Liechtenstein and Luxembourg because of their small country size. All species with a strict subterranean or cave-dwelling lifecycle, as documented in the literature and indicated by reduced and missing eyes, were classified as belowground species (see Table S1 in Supplementary Material for a list of the genera included). While total species richness is well documented for most western Palaearctic countries (Schuldt and Assmann 2009), new species are still being recorded from subterranean

habitats in the most species-rich southern European countries. However, this does not affect the overall spatial pattern of species richness, neither for total nor for belowground carabid richness. We used patterns of total species richness of all carabids and the richness of widespread and endemic carabids (all extracted from Löbl and Smetana 2003) for comparison with distribution patterns of belowground beetles. Widespread (range sizes >6 x 10⁵ km²) and endemic carabids (range sizes <6 x 10⁵ km²) were classified following the definition of Lumaret and Lobo (1996). As we were also interested in the relationship with species richness of vascular plants, we compiled data for this taxon from Walter and Gillett (1998), Groombridge and Jenkins (2002) and CBD National Reports (www.cbd.in/countries).

For our analyses we used a set of environmental variables related to recently intensively discussed hypotheses (Willig et al. 2003) on the influence of climatic and topographic factors on the spatial distribution of species richness (see Table 1 for a complete list of variables used). Climate data were obtained as country-level averages of highresolution data from Mitchell (2002) and comprised mean annual temperature, mean temperature of the coldest and the warmest month, temperature seasonality (difference between warmest and coldest month), mean annual precipitation, mean precipitation from March to November, seasonality in precipitation (difference between wettest and driest month) and the number of days with frost. Additionally, mean annual potential and actual evapotranspiration (PET and AET) were calculated using Thornthwaite's method (Thornthwaite and Mather 1963; 1964; Black 2007). AET is often considered a surrogate measure for productivity (Hawkins et al. 2003). Finally, range in elevation (i.e. the difference between the highest and lowest elevation within each sampling unit) was compiled from CIA (2008) as a measure of both habitat heterogeneity as well as prevailing signals of evolutionary and historical processes (Schuldt and Assmann 2009). From the same source, we extracted midpoint latitude and longitude of the countries to quantify the spatial dimension of richness distributions.

Statistical analyses

Environmental correlates of species richness of belowground carabids were first analysed in regressions with single environmental variables. Second- or third-order polynomials were added to the centred predictor variables in case of significant non-linear relationships. Species richness and country area were log₁₀-transformed to normalize distributions.

We then used regression modelling to assess the separate and combined impact of three different sets of predictor variables (spatial, topographic and climatic) on the richness pattern of belowground carabids. Spatial, topographic and climatic factors might explain similar proportions of the variability in the observed richness patterns. Our approach allows us to handle the non-independence of predictor variables, which might show the same autocorrelated pattern but relate to different conceptual frameworks in the explanation of diversity patterns, and thus to identify the isolated influence of different sets of explanatory variables (Baselga 2008; Hortal et al. 2008). For each set, we com-

	Model (function)	R ² _{adi}	F	DF	р	
a) single regressions						
Latitude (decimal degrees)	lat-lat ² +lat ³	0.51	12.6	3, 35	0.012	
Longitude (decimal degrees)	n.s.					
Area (km ²) (log ₁₀)	n.s.					
Elevation range (m)	elev (+)	0.52	38.7	1, 37	< 0.001	
Mean annual temperature (°C)	mean_temp-mean_temp ²	0.26	6.4	2, 36	0.042	
Mean temperature coldest month (°C)	n.s.					
Mean temperature warmest month (°C)	mean_warm-mean_warm ²	0.24	5.8	2, 36	0.052	
Temperature seasonality (°C)	n.s.					
Mean annual precipitation (mm)	n.s.					
Mean precipitation March-November (mm)	n.s.					
Seasonality precipitation (mm)	n.s.					
Potential evapotranspiration (mm/yr)	PET-PET ²	0.38	11.1	2, 36	0.020	
Actual evapotranspiration (mm/yr)	n.s.					
Frost frequency (days)	frost (-)	0.14	5.0	1, 37	0.048	
b) regression modelling						
Spatial (S)	$lat-lat^2+lat^3$	0.51	12.6	3, 35	0.012	
Topographic (T)	elev	0.52	38.7	1, 37	< 0.001	
Climatic (C)	PET-PET ²	0.38	11.1	2, 36	0.020	
Combined (T+C)	elev; PET-PET ²	0.69	26.5	3, 35	< 0.001	
Total (S+T+C)	lat-lat ² +lat ³ ; elev; PET-PET ²	0.68	13.5	6, 32	< 0.001	

Table 1. Results (coefficients of determination, F-values, degrees of freedom and spatially corrected probabilities) of **a** regressions of belowground carabid species richness against single environmental variables and **b** regression modelling of species richness of belowground carabid beetles in the western Palaearctic.

Appendix 1, Figure S1 and Table S1.pdf - Spatial correlogram and list of Belowground genera.

puted stepwise regression models with backward elimination, excluding variables that caused low tolerance (<0.1) due to high multicollinearity (r >0.9) with other variables in the predictor sets (Quinn and Keough 2002). Variation partitioning was used to assess the independent (i.e., purely spatial, topographic and climatic) and shared (spatially structured and co-varying) effects of the three predictor sets on Belowground carabid richness in a combined model (Legendre and Legendre 1998; Hortal et al. 2008). We included area as a co-variable into the analyses to account for differences in country size.

Spatial autocorrelation can inflate statistical errors in analyses of geographic diversity patterns (Diniz-Filho et al. 2003). To account for this, we recalculated significance of regressions using spatially corrected degrees of freedom by correlating observed and predicted values of regressions (Qian et al. 2007) according to the modified t-test by Dutilleul (1993). Additionally, we checked the adequacy of our non-spatial regression on climate and topography to explain the spatial structure in the belowground carabid data by generating a correlogram with Moran's I coefficients, which show the reduction in spatial autocorrelation after fitting the regression model (Diniz-Filho et al. 2003). Moran's I values of zero indicate absence of spatial autocorrelation, whereas larger or smaller coefficients (usually ranging between +1 and -1) show the degree of positive or negative autocorrelation between neighbouring sampling units. Non-significant values of Moran's I coefficients after fitting the explanatory variables indicate that the variables selected well account for the spatial pattern in the richness data (Diniz-Filho et al. 2003).

All statistical analyses were performed with SPSS 15.0 for Windows (SPSS, Chicago) and SAM 2.0 (Rangel et al. 2006).

Results

The distribution of species richness of carabids adapted to belowground habitats showed a clear and significant latitudinal gradient across the western Palaearctic (Table 1). Richness was highest in southern European regions (Fig. 1). This especially applies to Italy, which featured highest species numbers. Larger countries such as France and Spain had lower numbers and even for the Balkan Peninsula, species numbers were lower even when an area of comparable size and latitudinal extent was considered (i.e., Albania, Bosnia-Herzegovina, Greece, Macedonia and Serbia-Montenegro, which as a whole is slightly larger than Italy but harbours only 146 species as compared to 195 species for Italy). Even with Romania, Bulgaria and Croatia added to this latter region, which increases the area to more than twice the size of Italy, this region harbours only 36 more species than Italy.

Species numbers decreased towards northern Europe and North Africa (Fig. 2a) and most countries completely lacked belowground carabids, especially in the northern part of Europe (Fig. 1). In contrast to latitude, subterranean carabids did not show a significant relationship with longitude. Species numbers were also not significantly related to the size of the countries analysed (Table 1a). Several environmental variables were correlated with species richness of belowground carabids. Richness showed a linear increase with and was most strongly (R^2 =0.52; p<0.001) related to range in elevation (Table 1a, Fig. 2b). Variables related to ambient energy input (PET, mean annual and mean temperature of the warmest month) showed a hump-shaped relationship with species richness (R^2 between 0.24 and 0.38; p<0.052), which increased up to a certain level with increasing available energy and decreased again at highest levels of energy input (Table 1, Fig. 2c). Frost frequency was negatively related to species richness, whereas precipitation measures and AET were not significantly related to belowground carabid diversity (Table 1).

Regression modelling identified a polynomial term of latitude, the linear measure of elevation range and a quadratic term of PET as the best predictors of spatial, topographic and climatic models for species richness of belowground carabids (Table 1b). A combined model of elevation range and PET explained 69% of the variability in the carabid data. It removed all significant spatial autocorrelation from the carabid data. Moran's I coefficients in a spatial correlogram over ten distance classes were all close to zero and non-significant after fitting the model (see Appendix 1, Figure S1: Spatial correlogram). This shows that these variables quite well account for the spatial structure in the distribution of subterranean carabid diversity and that modelling results are not affected by spatial autocorrelation (Diniz-Filho et al. 2003). The total model, adding a spatial component to these variables, did not increase the goodness of fit and explained



Figure 1. Distribution of species richness of belowground carabid beetles across the western Palaearctic, based on Löbl and Smetana (2003). Shadings and symbols indicate the number of species recorded for each country. Countries with 11–20 subterranean species are marked by a filled circle, countries with 1–10 species by an open circle. Countries for which no subterranean species have been recorded are white and without a symbol.

68% of the data variability (Table 1b). Variation partitioning showed that range in elevation had by far the strongest independent effect on species richness of belowground carabids, accounting for 19% of the explained variance. Together with the spatially structured effect of elevation range, this factor explained 30.1% of the carabid data variability (Fig. 3). In comparison, independent spatial and climatic as well as spatially structured climatic effects were weak. The shared variation for all three components together, i.e. spatially structured climatic and topographic effects, was 23.4% (Fig. 3).

Richness of Belowground carabids was strongly correlated with total species richness of carabid beetles (Pearson' r=0.76; p<0.001, corrected for spatial autocorrelation), less strongly with richness of widespread species (r=0.63; p=0.001) and most strongly



Figure 2. Relationship between species richness of belowground carabid beetles (\log_{10} -transformed) and **a** latitude ($R^2_{adj.}$ =0.51; p=0.012), **b** range in elevation (i.e., topograohic variability; $R^2_{adj.}$ =0.52; p<0.001) and **c** annual potential evapotranspiration ($R^2_{adj.}$ =0.38; p=0.020) in the western Palaearctic.



Figure 3. Partitioning of variation from regression modelling for species richness of belowground carabids. Values give the % of the total variation independent and shared effects of spatial (**S**), topographic (**T**) and climate (**C**) models account for in the explanation of richness patterns. **U** is the unexplained variation.

with richness of endemic carabids (r=0.87; p<0.001). It was also highly correlated with species richness of vascular plants (r=0.86; p<0.001) across the western Palaearctic.

Discussion

The spatial analysis of belowground carabids clearly identifies southern Europe, and especially Italy, as the region with highest species richness in the western Palaearctic. Generally, this region has been classified as one of the hotspots of overall terrestrial troglobiont diversity based on the comparison of local species numbers from single caves (Vigna Taglianti 1982; Culver and Sket 2000) and from the small-scale study of selected regions across Europe (Culver et al. 2006). Our study extends this knowledge to the regional scale for one of the most species-rich terrestrial belowground taxa using a spatially and temporally comprehensive dataset. So far, the diversity of separate subterranean groups has scarcely been studied in detail (Zagmajster et al. 2008). Moreover, in contrast to most previous studies focusing on obligate cave-dwellers, our study comprises a broader range of subterranean species, including those living in the superficial underground compartment (MSS; Juberthie 1979), and thus provides a more general picture of belowground diversity patterns.

Species richness of carabid beetles adapted to belowground habitats significantly and most strongly co-varied with range in elevation. To a certain extent, this might reflect ef-

fects of habitat heterogeneity and availability (Kerr and Packer 1997; Rahbek and Graves 2001), as mountainous regions are likely to feature extensive cave and karst systems. However, large karst areas also occur in regions which harbour only few or no belowground carabids at all (e.g., Belgium, England, Switzerland; see also Culver et al. 2006). Rather, our findings indicate a strong effect of historical processes on the present distribution patterns of belowground beetles. Regions with high altitudinal ranges can promote diversification processes through isolation and segregation along altitudinal gradients in environmental conditions (Jetz et al. 2004; Rahbek et al. 2007; see also Casale 2009). Moreover, topographically highly variable regions allow species to effectively compensate climatic shifts (Hewitt 1999) and not surprisingly, the highest belowground diversity of carabids was found in mountainous regions where probably the southern refugia of many taxa during the last ice age were located (Hewitt 1999; Casazza et al. 2008; Drees et al. 2010). The latitudinal pattern with a steep decrease in richness towards northern Europe, combined with relatively low effects of climate variables, yields further information regarding historical impacts. Due to their very specific habitat requirements and morphological adaptations, carabid beetles of belowground environments are strongly limited in their dispersal (Lamoreux 2004; Assmann et al. 2010). The lack of belowground species in central and northern Europe, despite suitable habitats, might be attributed to extinctions during Pleistocene glaciations and the inability of range-restricted taxa to re-colonize these regions (see also Schuldt and Assmann 2009). For many range-restricted and even for widespread vascular plants, effects of dispersal limitation on the current distribution across Europe have been suggested (Svenning and Skov 2007; Svenning et al. 2008). A strong correlation between richness patterns of belowground carabids and vascular plants might indicate a similar historical signal prevailing in the distribution patterns of both taxa (cf. Hewitt 1999).

Concerning the distribution of hotspots of overall troglobiont diversity in Europe, Culver et al. (2006) found weak support for an influence of Pleistocene glaciations. Similarly, belowground carabids are also missing south of the former boundary of the Pleistocene ice sheet. However, the coarse-scale distribution of belowground carabid beetle diversity seems to largely conform to patterns postulated by Holdhaus (1954), who hypothesized that the occurrence of terrestrial cave fauna in Europe has been influenced by the spatial extent of permafrost soil, stretching much farther south than the ice sheet. According to his studies, the northern limit of these taxa runs along a line (the "Holdhausline") from the southern part of the Alps eastwards to the Carpathians (Holdhaus 1954; Drees et al. 2010). Concordance between the distribution of several groups of blind carabids and the theory of Holdhaus has also been found by Drees et al. (2010). Further reexamination on a more detailed scale will be needed to accurately evaluate these findings in light of the numerous new records of subterranean taxa from the last decades. While some species are considered to have survived in isolated refuges north of the Holdhausline (Holdhaus 1954), further deviations from the general pattern might be explained by postglacial range expansions (Drees et al. 2010). In contrast, an Anillus species recorded in park locations of Belgium (Desender 1986) and Germany (Malzacher 2000) was probably introduced with soil from the root system of trees imported from southern Europe. The survival of this species shows that suitable habitats also exist now in northern regions

of Europe and can be seen as further evidence for strong effects of dispersal limitation on re-colonization processes in the western Palaearctic (Drees et al. 2010).

As mentioned above, the influence of dispersal limitation might also become evident from the fact that current climate accounted for much smaller amounts of explained variation than elevation range in both single regressions as well as in regression modelling. Species with well-developed dispersal abilities are assumed to have tracked post-Pleistocene climate changes to a certain degree, and high co-variation between species richness of many taxa and climatic variables support this view (reviewed by Hawkins et al. 2003). Within the highly diverse carabid beetles, the same is true for the richness of more mobile, widespread species, which is strongly related to climatic variables and much less to elevation range (Schuldt and Assmann 2009). In contrast, more range-restricted endemic species show the opposite pattern, with a strong impact of topographic variability and low influence of current climate pointing to prevailing effects of historical processes on distribution patterns (Schuldt and Assmann 2009). Our results for belowground beetles as part of the range-restricted carabids strongly support these findings and thus provide further insight into potential mechanisms underlying spatial distributions of diversity. They show that the significance of historical processes in explaining contemporary richness distributions might increase as dispersal abilities of the species decrease. In this respect, belowground carabids have a strong impact on overall patterns of rangerestricted (endemic) species. A larger influence of climate on these overall patterns of endemics (Schuldt and Assmann 2009) compared to belowground diversity, even though still secondary to effects of elevation range, indicates that postglacial range expansions are easier in above- than in the often spatially isolated belowground habitats (Porter 2007).

At least at the coarse scale of our analysis, we did not find evidence for the assumptions of Culver et al. (2006) that centres of highest belowground diversity might be located in regions of long-term high aboveground productivity. Current and past climate are correlated (Araújo et al. 2008) and AET as a measure of productivity (Hawkins et al. 2003) was not related to richness patterns of belowground carabids in our study. Rather, an influence of variables representing ambient energy input (temperature, PET) and the potential effects related to topographical variability suggest that in the western Palaearctic highest richness of these taxa is determined by historical/evolutionary processes and a general long-term stability of environmental conditions (temperature) which supported survival and, especially regarding the strong signal of history, promoted diversification processes in belowground habitats (e.g., through isolation from other similar habitat patches or other phenomena relevant for evolutionary processes; Casale and Vigna Taglianti 2005).

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Appendix I

Spatial correlogram and list of Belowground genera. (doi: 10.3897/zookeys.100.1540. app) File format: Adobe PDF (.pdf).

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RESEARCH ARTICLE



Recent records of steppe species in Belarus, first indications of a steppe species invasion?

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Abstract

Belarus is situated at a crossroad of natural borders of species distributions: the NE part is situated in a taiga zone, whereas the other part of terrain is in the European forest zone. The distance of Belarus to the steppe zone is about 330 kilometers. This geographical position and the extensive knowledge of its fauna can be used to monitor changes in the distribution of different species. An intensive study of open habitat ground beetles was carried out from 1975–2008 in Belarus, using pitfall traps, quadrate-sampling methods, hand collecting, netting and light traps. In total, more than 130 000 specimens of ground beetles belonging to 169 species were collected from 62 fields and 11 meadows of different types. 217 specimens of *Calosoma investigator* (Illiger 1798), 2 specimens of *C. denticolle* (Gebler 1833), and one specimen of *Harpalus subcylindricus* (Dejean, 1829), *H. honestus* (Duftschmid 1812) and *Zabrus tenebrioides* (Goeze 1777) were present in this material. All specimens were macropterous and exclusively caught at fields and waste grounds on sandy soil. Nowadays Belarus is the northernmost location for these species in Eastern Europe. Steppe species most probably migrated to SE Belarus from NE Ukraine, using Dnieper and its river valleys. The shift in the geographic distribution of steppe species during the last thirty years in Belarus have been attributed to a higher frequency of warmer and wetter summers in the last few decades.

Keywords

Carabidae, Belarus, steppe species, geographic ranges

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Introduction

Every aspect of an insect's life cycle depends on temperature. As such, these organisms respond quickly to climatic changes by shifting their geographical distribution. This quick response allows them to take advantage of new climatic environments. A wide variety of vertebrate and invertebrate species have moved northwards and uphill in response to global warming. These changes have already been documented in Europe (Ohlemuller et al. 2006).

Similar shifts in geographic distribution were also documented among well-studied insect groups in Belarus (Eastern Europe). In the last decade, xerophilous steppe species from different insect orders were recorded from SE Belarus, for example: *Scolia hirta* (Schrank 1781) and *Megascolia maculata* (Drury 1773) (Prischepchik 2008), *Mantis religiosa* (Linnaeus 1758) (Dictyoptera, Mantidae) (Kulak 2009), and *Zerynthia polyxena* (Denis et Schiffermuller 1775) (Lepidoptera, Papilionidae) (Krasnaya Kniga Respubliki Belarus).

Belarus is situated at a crossroad of natural borders of species distributions: according to the biogeographical regionalization of Europe (Biogeographical provinces) the northeastern part is situated in the taiga zone, whereas the rest of the terrain is within the European forest zone (Fig. 1). The distance from Belarus to the steppe zone is about 330 kilometers.

This geographic position makes Belarus ideal for monitoring changes in the geographic distribution of the fauna. Fortunately, the fauna of South East Belarus has been studied extensively, which is well documented in publications and collection material.

At the end of the 19th century the beetles of South East Belarus were one of the most intensively studied groups within the Russian Empire. The first checklist of Mogilev province (including the Mogilev and Gomel regions of Belarus) was compiled by Arnold (1901). In 1992 a check was made of the list of carabid beetles as found by Arnold. This list includes 120 species is housed in the Museum of the Zoological Institute of the Academy of Science of Russia in St. Petersburg (Aleksandrowicz 1992).

The faunistic inventory of carabids was continued in the second half of 20th century (Gorbunova 1956; Aleksandrowicz 1979, 1991). In the last 20 years an intensive study in South East Belarus was executed to analysis of the distribution, abundance and occurrence of carabid beetles. The aim of this study is to determine whether changes occurred in the carabid fauna of Belarus.

Location, methods and material

Belarus is situated in eastern Europe, on the eastern of Poland (53°00'N, 28°00'E). The total territory of Belarus is 207.6 thousand km² (Fig. 1. Landscape and climate).

Climate in Belarus is moderately continental: a transitional form of maritime to continental climate with mild and humid winters, warm summers and damp autumns.



Figure 1. Biogeographic regions and the geographic location of Belarus.

The terrain is generally flat and contains much marshland, especially in the southern part near the Ukraine border, which is named Polesie (Fig 1. Wetlands). The Polesie lowlands lie mainly along the Pripyat river and occupy 80 000 km². The Polesie area presents a plain with rare and irregularly distributed hills with flat tops and gentle slopes. Sand is common in places of higher elevation on which pine trees are typical. Wide and swampy river valleys are a characteristic feature of the landscape. The Polesie lowlands are only 100–150 m a.s.l., with the western part slightly higher than the eastern parn. During the last 20 years, intensive drainage of the Polesie swamps has occurred. The aim of this activity is to turn the swamps into hay-fields. Many swamps have disappeared, and many canals have been cut through the region (Belarusian Lowlands).

Intensive inventories of open habitat carabids in 1975–1976 were carried out in Belarus Polesie, using pitfall traps and quadrate sampling method (0.25 m^2). These studies have been repeated in the area of Luninetz, in the Brest district of Belarus ($52^{\circ}14'26''N$, $26^{\circ}37''E$) in 1982–1983.

The entire terrain of Belarus was studied in 1980–1985 during 12 expeditions of the Belarus Institute of Plant Protection. The purpose of these expeditions was to reveal grain crop pests. Hand collecting and netting were used to collect the insects.

Studies were performed by collecting material from light traps in crop fields and orchards of the Gomel Regional Crop Protection Service in 1980–1990.

Later studies (1990-2005) evaluated the effects of insecticide and herbicide spraying on carabid communities in wheat and barley fields in the Minsk and Mogilev districts, using pitfall traps (Central and East Belarus).

In 2005–2008, faunistic inventories were continued in the east of Polesie: in the vicinity of Gomel and Polesie Radio-Ecological Reserve, using pitfall traps, netting and hand collection. The main focus was arable fields and the terrain of the Prypiatski National Park (Aleksandrowicz et al. 1996, 1997; Aleksandrowicz and Kapcjugh 2002). Also, wing development of all specimens was determined.

The level of faunistic knowledge in Belarus allows us to monitor the appearance or disappearance of carabid species. In all likelihood, steppe species will have colonised Belarus during decent decades. A steppe species is defined as a species of euroasiatic subboreal geographic ranges. These species only colonise on open (mainly arable) habitats with mostly continental climate. This definition is similar to Tischler's (1965) definition of steppe species.

Results

In total, during the period 1975–2008, more than 130 000 specimens of ground beetles belonging to 169 species were collected, mainly by pitfall traps from 62 fields and 11 meadows of different types.

Among this material, 217 specimens of *Calosoma investigator* (Illiger 1798) and 2 specimens of *Calosoma denticolle* (Gebler 1833) were found. *Harpalus subcylindricus* (Dejean, 1829), *H. honestus* (Duftschmid 1812) and *Zabrus tenebrioides* (Goeze 1777) were represented by only one specimen.

Calosoma investigator is widespread in the steppe zone of Eurasia, from South-East Europe to Baikal (Catalogue of Palearctic Coleoptera 2003). Its distribution in Middle Europe is not clear. According to Lindroth (1945) it is absent from Sweden. Only one old (from the 19th century) specimen of *C. investigator* is known from museum material ("Oland, Mortonson, Mus. Goteborg") without an exact locality.

The distribution of *C. investigator* in North-East Poland (Ost Preussen) is unclear. Bercio and Folwaczny (1979) concluded that *C. investigator* was absent from Ost Preussen and data collected by Lesniak (1964) for northeast Poland are based on misidentifications.

In SE Europe *C. investigator* is known from the Ukraine, Moldova, Romania, Bulgaria and European Turkey (Catalogue of Palearctic Coleoptera 2003). The first records in Rumania are from 1991 (Nitu 1991).

In Belarus *C. investigator* was collected for the first time in 1975 near Luninetz (52°14'21"N, 26°37'46"E) in barley field. Nowadays it can be found up to Slutsk (52°57'40"N, 27°37'27"E) and Bobruysk (52°12'27"N, 29°02'25"E) (Fig. 2).

At the moment, *Calosoma investigator* occupies almost the entire southeastern part of Belarus. It inhabits arable lands on sandy soils and are sometimes locally abundant. All of the 217 collected specimens were macropterous. Their expansion rate is estimated at about 50–60 km in 10 years.

The geographic distribution of *Calosoma denticolle is* limited by the steppe zone of Eurasia, from southeast Europe to northeast China (Catalogue of Palearctic Coleoptera 2003).

In northern Europe only one specimen is known from southern Finland in an atypical locality. It was collected from the Baltic shore after a strong gale in 1935 (Lindroth 1945).



Figure 2. Actual distribution of *Calosoma investigator* in Belarus.

In Belarus it was caught for the first time in 1988 near Turov (52°3'33.29"N, 27°44'36.15"E) in an arable field. A second specimen was captured in 2007 near the village Arevithcy in a wasteland (51°36'52.72"N, 29°50'49.50E) (Fig. 3).

Harpalus subcylindricus is widespread from southern Europe and southern part of Middle Europe to the Caucasus to West Asia (Catalogue of Palearctic Coleoptera 2003). It is not know from Poland, the Baltic States or northwestern Russia. Recently it has also been recorded from the southern parts of Poland (pers. comm. M. Stachow-iak). In southeast Belarus one macropterous specimen was collected near Homel in a barley field in 1998 (52°22'50.85"N, 30°50'9.33"E) (Fig. 4).

Harpalus (s.str.) *honestus* is distributed from southern Europe and southern part of Middle Europe to the Caucasus to West Asia (Catalogue of Palearctic Coleoptera 2003). It is absent from the North of Poland, the Baltic States and northwestern Russia. In Belarus, one macropterous specimen was collected near the village Liaskovitchy on a sandy beach of the Pripyat river in 1997 (52° 7'3.68"N 28°10'57.60"E) (Fig. 5).

Zabrus tenebrioides is widespread from southern Europe and southern part of Middle Europe and the Caucasus to Turkey. Distribution of Z. tenebrioides in the former USSR (South-West Russia, Caucasus and Ukraine) has been studied well because of its eco-



Figure 3. Actual catch of *Calosoma denticolle* in Belarus ($\Box - 1988$; $\blacksquare - 2007$) and its known distribution in eastern Europe (chequered area).

nomic damage to grain crops (Interactive Agricultural Ecological Atlas). In Fennoscandia it is known from the south of Sweden and Denmark only. Old data from Latvia and Estonia are erroneous (Silfverberg 2004). So far it has never been registered from Belarus, Lithuania, northwest and north of European Russia (Kryzhanovsky et al. 1995; Aleksandrovich et al. 1996; Silfverberg 2004). As such, data from the Catalogue of Palearctic Coleoptera (2003) and the distribution map on the site Fauna Europea (Distribution of *Zabrus*) *tenebrioides*) are erroneous and should be corrected.

For the first time, one macropterous specimen was collected in southeastern Belarus near the village Khvashchouka, in a dry meadow in 2007 (51°38'49.18"N, 29°47'3.09"E) (Fig. 6).

Discussion and conclusions

The data presented most likely show the northern most locations for these steppe species in eastern Europe.

The different types of forests, meadows and marshes (Gorburova 1956, Kipenvarlits 1961; Khotko et al. 1980; Aleksandrowicz 1991; Aleksandrowicz et al. 1997;



Figure 4. Actual catch of *Harpalus subcylindricus* in Belarus ($\circ - 1988$) and its known distribution in eastern Europe (chequered area).



Figure 5. Actual catch of *Harpalus honestus* in Belarus (■ – 1997) and its known distribution in eastern Europe (chequered area).

Khotko 1993; Chumakou 1994), as well as anthropogenic landscapes: cities (Molodova 1990) and fields (Aleksandrowicz 1979; Molodova 1980) have been investigated by different entomologists for the last 50 years.

All steppe species found in these studies were exclusively caught in fields and waste grounds on sandy soils. This seems to confirm the theory of Elton (1958) that migrants invade arable fields or waste grounds first, where competition is lower and migrants can dispersed successfully. Of all the steppe species, only macropterous specimens have been found. Except for *C. investigator* and *C. denticolle* the other three steppe species were caught only as single specimens.

The new species probably migrated to the north and to the northwestern part of Belarus from the southeast (connected to the northeast part of the Ukraine). The Polesie lowland, in the south west of Belarus, harbours an extensive complex of marshes and lakes that might act as a natural barrier for migrations from northern Ukraine.

Migrations from the Ukraine probably occurred along the Dnieper river valleys and its affluent: Pripyat, Sozh and Berezina (Fig. 1). The actual distribution of steppe species in Belarus is in the valleys of these rivers (Figs 3–6). Only *C. investigator* migrated beyond the river valleys and nowadays can be found on arable lands north from this river system (Fig. 2).



Figure 6. Actual catch of *Zabrus tenebrioides* in Belarus (■ – 2007) and its known distribution in eastern Europe (chequered area).

The changing of geographic ranges can have an economic impact on the local agricultural society. *Calosoma* species will probably be beneficial in this case as general predators. But *Zabrus tenebrioides* is known as a serious pest of winter wheat in eastern Europe and a local pest in central Europe (Kromp 1999; Mrówczyński et al. 2007).

Global or local climatic changes is frequently mentioned as one of the reasons for shifts in geographic ranges. Over a long period of observation (1881–2001) Loginov et al. (2003) estimated an average annual temperature increased of 1 °C. Average winter and spring temperatures increased even more. During this period the most significant increase in temperature took place at the end of the last and the beginning of the current century, with an average temperature increase of 3-4 °C.

This change in temperature makes it plausible that shifts in the geographic distribution of some insect species during the last thirty years in the Belarus have been the result of a higher frequency of warmer and wetter summers. To complete its life cycle, steppe species need high summer temperatures, which makes it possible for them to move further north. As in the steppe of the Ukraine and Russia, winters are colder than in Belarus (www.agroatlas.ru), and an increase of winter temperature probably does not have any impact on their distribution. However, in the Polesie region in Belarus, intensification of agriculture and changes in land use (e.g., first of all Polesie's peat-bog drainage) also took place. This kind of management might also cause shifts in geographic changes. These hypotheses indicate the general problem of separating climatic effects from human effects in interpreting biological patterns.

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RESEARCH ARTICLE



How unique is the tiger beetle fauna (Coleoptera, Cicindelidae) of the Balkan Peninsula?

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Abstract

The tiger beetle fauna of the Balkan Peninsula is one of the richest in Europe and includes 19 species or 41% of the European tiger beetle fauna. Assembled by their biogeographical origins, the Balkan tiger beetle species fall into 14 different groups that include, Mediterranean, Middle Oriental, Central Asiatic, Euro-Siberian, South and East European, Pannonian-Sarmatian, West Palaearctic, Turano-European and Afrotropico Indo-Mediterranean species. The Mediterranean Sclerophyl and the Pontian Steppe are the Balkan biogeographical provinces with the highest species richness, while the Balkan Highlands has the lowest Cicindelidae diversity. Most species are restricted to single habitat types in lowland areas of the Balkan Peninsula and only *Calomera aulica aulica* and *Calomera littoralis nemoralis* occur in respectively 3 and 4 different types of habitat. About 60% of all Balkan Cicindelidae species are found in habitats potentially endangered by human activity.

Keywords

Balkan Peninsula, biodiversity, distribution, Europe, zoogeography

Introduction

Tiger beetles occur world-wide, with the exception of the polar regions and some oceanic islands (Cassola and Pearson 2000, Pearson and Vogler 2001). Detailed studies from different regions show that many species have narrow habitat specialization and occur only in one or at most in few very similar types of habitat. As a result, tiger beetles have become a significant global flagship group for beetle conservation used as biological indicators for determining global and regional patterns of biodiversity (Knisley and Hill 1992; Pearson and Cassola 1992, 2007; Carroll and Pearson 1998a, b; Andriamampianina et al 2000; Pearson and Vogler 2001; Arndt et al. 2005). In most species, adult beetles are diurnal and highly mobile, while larvae are sedentary and live in burrows constructed in the substrate where the eggs are oviposited (Pearson 1988). Both imagines and larvae are predators that prey on small invertebrates, a characteristic that makes them potentially natural biological controls of pests with an economic value (Rodriguez et al. 1998).

The Balkan Peninsula is part of the Mediterranean basin. It is one of the 25 most important world hotspot areas of biodiversity (Myers et al. 2000). Together with two other South European peninsulas, the Iberian and the Italian, the Balkans were the most important terrestrial Pleistocene glacial refugia in Europe. Phylogeographical studies on many different groups of animals and plants show that these areas are regions from which the re-colonisation of northern Europe started after the last glaciation period (Hewitt 1996, 1999; Blonden and Aronson 1999; Thompson 2005). Weiss and Ferrand (2007) suggest that high biodiversity of the South European Peninsulas, including the Balkan Peninsula, can be explained by relatively high climatic stabilization of this region as well as heterogeneous landscapes occurring in this area. Moreover, the Balkans have served as an important natural bridge for historical dispersal between Asia Minor and northern, western and central Europe (Crnobrnja-Isailovic 2007).

The first data on the tiger beetle fauna of the Balkan Peninsula were published at the end of the 19th and beginning of the 20th century (Reitter 1881; Horn and Roeschke 1891; Apfelbeck 1904–1907). Since then, more than 40 papers have been published on this topic, many of which however only describe information on a single species or present incomplete faunistic and taxonomic data. Recently more complete information on the fauna of some regions have been summarized for Bulgaria (Guéorguiev and Guéorguiev 1995), Montenegro (Jaskuła et al. 2005), Albania (Guéorguiev 2007; Jaskuła 2007a), Romania (Cassola and Jaskuła 2004; Jaskuła 2007b), Greece (Franzen 2005; Jaskuła et al. – in preparation) and the European part of Turkey (Cassola 1999; Avgin and Özdikmen 2007).

The aim of this paper is to summarize knowledge on the diversity of tiger beetles in the Balkan Peninsula with particular emphasis on total group diversity, zoogeographical composition, distribution, and ecological preferences of the species.

Study area

We can define the Balkan Peninsula as a part of southeastern Europe with its northern boundary at the Danube, Sava and Kupa rivers. The rest of its margins are made up of the Black Sea in the east, the Adriatic Sea in the west, and the Mediterranean Sea (including the Aegean and Ionian seas) in the south (Fig. 1). The region has a combined



Figure 1. Geographical and administrative divisions of the Balkan Peninsula: I Dinaric region II Pindus region III Tracian-Macedonian region IV Balkanid region V Danubian plain region VI North-Dobroudzha region AL Albania BG Bulgaria BH Bosnia and Herzegovina CR Croatia GR Greece KO Kosovo MA Macedonia FYR, MO Montenegro RO Romania SB Serbia SL Slovenia TR Turkey.

area of ca. 550,000 km², which is nearly 5% of the entire European continent. The peninsula includes twelve countries, seven of which are completely confined to the Balkan Peninsula (Albania, Bulgaria, Greece, Macedonia FYR, Montenegro, Kosovo, and Bosnia-Herzegovina), and five (Romania, Serbia, Croatia, Slovenia, and Turkey) have only a part of their territories on the peninsula.

The largest surface of the Balkan Peninsula is mountainous. Lowlands extend along the lower reaches of rivers that are grouped into three catchments draining into the Adriatic, Aegean, and Black Sea (Reed et al. 2004). Geographically this area is divided into the following main regions: Dinaric, Pindus, Tracian-Macedonic, Balkanic, Danubian plain, and North-Dobroudzha (Fig. 1). According to Udvardy (1975) the Balkan Peninsula belongs to three main biogeographical provinces (Fig. 2): Mediterranean Sclerophyl – which includes European parts of Turkey, the Adriatic coast of Albania, Montenegro, Bosnia-Herzegovina, Croatia and Slovenia, and the sea coast of continental Greece; Balkan Highlands – with mountain areas of Bulgaria, Albania, Montenegro, Kosovo, Bosnia-Herzegovina, Serbia (except Voivodina), and partly also the mountains of Greece, Croatia and Slovenia, as well as the southern part of the Bulgarian Black Sea Coast; Pontian Steppe – the smallest area of the Balkans with only a small part of the northeastern Bulgarian Black Sea Coast and southeastern Romania, with its northern border at the Danube Delta.

Material and methods

The basis for this analysis of Balkan tiger beetles comes from published literature data; such as museum collections of the Museum and the Institute of Zoology, Polish Academy of Sciences (Warsaw, Poland), Royal Belgian Institute of Natural Sciences (Brussels, Belgium), Zoological Museum (Copenhagen, Denmark), Finnish Museum of Natural History (Helsinki, Finland), University of Montenegro (Podgorica, Montenegro); and original collections made by the author in the years 2005–2009 during five scientific expeditions covering almost all Balkan countries ("I-III Amphi-Balkan expeditions").

Tiger beetle species richness and distribution of taxa were analysed based on squares of 1° latitude and longitude. In each square the number of all species recorded was summarized. Similarities among tiger beetle fauna between geographical units were measured using the Bray-Curtis index for presence/absence data (Primer v.2.0). Jaccard's (1902) index was used to present the degree of dissimilarity between zoogeographic regions distinguished by Udvardy (1975):

R= 100c/a+b-c

where: a = number of species in the richest fauna; b = number of species in the poorest fauna, c = number of species comon to both faunas.

Chorotypes follow Vigna Taglianti et al. (1999).

Results

Diversity of tiger beetles in the Balkan Peninsula

According to Putchkov and Matalin (2003), López et al. (2006) and Fauna Europea Web Service (2004) 49 tiger beetle species occur in Europe. Of these, 19 species have been found in the area of the Balkan Peninsula (Table 1), or 39% of all European tiger

beetle species. This number increases to 41% if three species known only from Mediterranean islands of Europe are excluded (*Cephalota tibialis* – Cyprus, *Calomera lunulata* – Sicily, *Habrodera nilotica* – Canary Islands). The Balkan species belong to five genera (55.5% of European fauna) including: *Myriochila* (1 species, 50% of European species), *Cephalota* (4 species, 33%), *Calomera* (4 species, 57%), *Cylindera* (4 species, 57%), and *Cicindela* (7 species, 41%). Only four European genera – *Megacephala*, *Lophyra*, *Cassolaia* and *Habrodera* do not occur in this area. Two taxa (*Cicindela campestris oliviera* and *C. monticola albanica*) are endemic to this area. Additionally, for eleven species the Balkan Peninsula is the only place in Europe where they occur (having also distributions outside Europe).



Figure 2. Tiger beetle faunas in the biogeographical provinces of the Balkan Peninsula (division after Udvardy 1975): light grey – Mediterranean Sclerophyl, dark grey – Pontian Steppe, black – Balkan Highlands. Numbers in the circles indicate the number of cicindelid taxa for the separate regions and the squares give the number of taxa common to the provinces shared.

Region	Area (km ²)	Number of species	Species density (species number/1000 km ²)
Balkan Peninsula	550 000	19	0.034
Iberian Peninsula	580 000	19	0.033
Italian Peninsula	150 000	13	0.086
Scandinavian Peninsula	800 000	5	0.006
France (mainland)	675 000	14	0.021
Ukraine	603 700	19	0.031
Russia (European part)	4 268 850	23	0.005

Table 1. Comparison of area and tiger beetle species richness of some European regions [based on Putchkov and Matalin (2003) and Fauna Europea Web Service (2005)].

The number of Balkan tiger beetle species is high compared with the number noted from other European regions with similar sized areas, especially north of the Balkan Peninsula (Table 1). Moreover, the diversity of the tiger beetle fauna in the studied area is similar to the fauna known from the entire territory of the European part of Russia. Among European regions with a similar area, only the Iberian Peninsula and the Ukraine exhibit similar numbers of tiger beetle species.

Balkan Cicindelidae belong to 14 different groups according to their geographical origin (Vigna Taglianti et al. 1999, Table 2). Except Balkan endemics and Mediterranean species, representatives of Middle Oriental, Central Asiatic, Euro-Siberian, South and East European, Pannonian-Sarmatian, West Palaearctic, Turano-European, or even Afrotropico Indo-Mediterranean taxa can be found in this area.

Balkan endemics	Cicindela campestris oliviera, C. monticola albanica
Mediterranean	Calomera littoralis nemoralis, Cephalota circumdata circumdata,
	Calomera aulica aulica
East Mediterranean	Calomera concolor concolor
West Mediterranean	Cylindera trisignata trisignata
Middle Oriental	Calomera fischeri fischeri
Central Asiatic	Cephalota chiloleuca, Cylindera contorta contorta
Northeast Mediterranean (Aegean)	Cephalota turcica, Cylindera trisignata hellenica
East European	Cephalota elegans stigmatohora
West Palaearctic	Cicindela campestris campestris, Cylindera germanica germanica,
	Cicindela hybrida
Turano-European	Cicindela monticola rumelica
South European	Cicindela sylvicola, Cylindera germanica muelleri
Pannonian-Sarmatian	Cicindela soluta pannonica
Euro-Siberian	Cicindela sylvatica, Cylindera arenaria viennensis
Afrotropico Indo-Mediterranean	Myriochila melancholica melancholica

Table 2. Chorotypes of Balkan tiger beetles (after Vigna Taglianti et al. 1999).
Distribution of tiger beetles in the Balkans

Within the Balkan Peninsula, species richness of particular regions differs both in number of taxa and species composition. Records from the literature and my own observations within single squares of 1° latitude and longitude show that the highest numbers of tiger beetle species are along sea coasts (Fig. 3). Moreover, within biogeographic provinces as definied by Udvardy (1975) the greatest tiger beetle species richness in the Balkan Peninsula is found in the Mediterranean Sclerophyl region (13 species, 68% of the Balkan fauna), and somewhat lower in the Pontian Steppe (10 species, 52%), and the Balkan Highlands (12 species, 63%). This, despite the fact that the Balkan Highlands cover a part of the peninsula that is larger than both previous biogeographical provinces combined. Moreover, the Balkan part of the Pontian Steppe



Figure 3. Species richness of tiger beetles within the Balkan Peninsula. The colour gradient indicates an enhanced diversity from one species (white square) to eight (black square).



Figure 4. Similarities among tiger beetle faunas inhabiting regions of the Balkan Peninsula (Bray-Curtis similarity index for presence/absence data).

is almost 17 times smaller than the Balkan Highlands and about ten times smaller than the Mediterranean Sclerophyl (Fig. 2).

Bray-Curtis analysis of similarities among tiger beetle faunas from different Balkan geographical regions shows the presence of three main clades (Fig. 4). The Dinaric, Tracio-Macedonian and Balkanic regions group mainly mountain areas, with lowlands only as very small parts, and covers a great part of Udvardy's (1975) Balkan Highlands. The Danubian plain and North-Dobroudzha regions compose the second group, mentioned in biogeographic studies as the Pontian Steppe and north-eastern part of the Balkan Highlands. Clearly different is the Pindus area, which covers a large area of the Mediterranean Sclerophyl province. The Jaccard's similarity index for Mediterranean Sclerophyl – Pontian Steppe was 53%, for Mediterranean Sclerophyl – Balkan Highland was 47%, and for Pontian Steppe – Balkan Highland was 38% (Fig. 4).

Ecotypes of Balkan Cicindelidae

The most eurytopic species are *Calomera littoralis nemoralis* and *Calomera aulica aulica* (Table 3), occupying four and three habitats respectively. Ten species have been found occurring in only one type of habitat, including three *Cephalota* species in saltmarshes,

No.	Species	1	2	3	4	5	6	7
1	Calomera aulica aulica	+	+					+
2	Calomera concolor concolor		+					
3	Calomera fischeri fischeri			+				
4	Calomera littoralis nemoralis	+	+	+	+			
5	Cephalota (Cephalota) turcica	+						
6	Cephalota (Taenidia) chiloleuca	+						
7	Cephalota (Taenidia) circumdata circumdata	+						
8	Cephalota (Taenidia) elegans stigmatophora	+		+				
9	Cicindela (Cicindela) campestris					+	+	
10	Cicindela (Cicindela) hybrida			+			+	
11	Cicindela (Cicindela) monticola albanica			+				
12	Cicindela (Cicindela) soluta pannonica			+				
13	Cicindela (Cicindela) sylvatica					+		
14	Cicindela (Cicindela) sylvicola					+	+	
15	Cylindera (Cylindera) germanica	+					+	
16	Cylindera (Eugrapha) arenaria viennensis			+				
17	Cylindera (Eugrapha) contorta contorta		+					
18	Cylindera (Eugrapha) trisignata	+	+					
19	Myriochila (Myriochila) melancholica melancholica	+		+				
	Total	9	5	8	1	3	4	1

Table 3. Tiger beetles of the Balkan Peninsula and their ecological distribution: I salt marshes **2** sandy sea beaches **3** banks of rivers **4** banks of lakes **5** forest roads **6** mountain and highland pastures **7** flat coastal rocks (based on literature data and personal observations).

three species restricted to sandy sea coasts (*Calomera concolor*, *Cylindera contorta*, *C. trisignata*), four to river banks (*Calomera fischeri*, *Cicindela sahlbergii albanica*, *C. soluta pannonica*, *Cylindera arenaria viennensis*), and one – *Cicindela sylvatica*, to forested sandy areas. Another five species were noted as occurring only in two types of habitat. Among all these tiger beetles, fifteen species (79% of the fauna) can be classified as coastal and riverine taxa, occurring in habitats adjacent to water, such as sea coasts, salt marshes (including lagoons and estuaries), and banks of rivers and freshwater lakes.

Discussion and conclusions

Diversity and distribution of tiger beetles in the Balkan Peninsula

Compared to the area size of other regions of Europe, the diversity of tiger beetles of the Balkan Peninsula is high and constitutes about 41% of all European tiger beetle species. This result confirms an important role of the Balkans as a biodiversity hot-spot noted earlier for many other groups of organisms (Blonden and Aronson 1999, Kryštufek and Reed 2004, Thompson 2005). The high diversity of tiger beetles in the Balkans can be explained by two characteristics. The first is the topographic position



Plate I. Balkan tiger beetle species: **A** *Calomera littoralis nemoralis* **B** *C. f. fischeri* **C** *Cephalota chiloleuca* **D** *C. c. circumdata* **E** *Cicindela sylvicola* **F** *C. campestris oliviera* **G** *Cylindera trisignata hellenica* **H** *Myriochila m. melancholica.*

of this area within the European continent – the Peninsula was (and still is) a natural dispersal bridge for faunas from the Middle East and West, North and East Europe. The second is the high diversity of open habitats prefered by these beetles, including salt marshes, salty lagoons, sandy beaches, river banks, steppes, or mountain areas.

The Balkan Peninsula is inhabited by a mixed tiger beetle fauna with representatives of 19 species belonging to 14 different groups according to their geographical origin (Table 2). Such a mosaic of faunal elements clearly suggests an important role of the Balkan Peninsula as a natural geographic "bridge" between Europe and Asia Minor for this group in the past. Similar patterns have been noted also among other groups of insects (Kenyeres et al. 2009), spiders (Deltshev 1999, 2000, 2004), amphibians and reptiles (Crnobrnja-Isailovic 2007; Džukić and Kalezić 2004), mammals (Kryštufek 2004) and plants (Thompson 2005).

A high level of landscape heterogeneity also helps in explaining the general distribution pattern of tiger beetle species within the Balkan Peninsula and their higher species richness in the lowlands. Sandy habitats preferred both by larvae and adult are more diverse at sea coasts than those found in mountain areas. This patterns for Balkan tiger beetles is similar to that reported from other regions of the Mediterranean area (Cassola 1970, 1973, Lisa 2002, Jaskuła – unpublished). Moreover, a higher diversity of tiger beetles along sea coasts over that found in mountain areas has been found on the Indian subcontinent and in western and northern Australia (Pearson and Cassola 1992). It is most likely attributed to high habitat diversity occurring in lower altitudes (sandy beaches, salt marshes, lagoons, dunes, ect).

Ecological preferences in Balkan Cicindelidae

The narrow specialization to habitat type recorded for most of the Balkan tiger beetle species is similar to that in tiger beetles occurring in other regions of the world, both for adults and larvae. For example, of the 151 species noted on the Indian subcontinent by Acciavatti and Pearson (1989) only one - Calochroa flavomaculata Hope - was recorded from several different habitat types. In Australia among 29 species only two - Myriochila mastersi Castelnau and M. semicincta Brulle - occur found as occurring in several habitat types (Freitag 1979). In the Tambopata Reserve Zone (Madre de Dios, Peru) only one of 29 species - Odontocheila annulicornis Brulle - occurred in more than one forest habitat type (Pearson 1984), and of the 20 species noted in the Sulphur Springs Valley (Arizona, USA) only Cicindelidia nigrocoerulea Leconte was recorded as inhabiting more than one habitat type (Knisley and Pearson 1984). Moreover, the specialization can be so narrow that species occurrence can be restricted to only a small part of a particular habitat. Schultz and Hadley (1987) showed during their studies of two riparian species in the USA that Cicindela oregona Leconte occurred mainly at stream edges while Cicindela tranquebarica (Herbst) preferred dry areas. Also Ganeshaiah and Belavadi (1986) noted that four tiger beetle species segregated distinctly along river beds into separate microhabitats in India. In the Balkans, I observed similarly narrow microhabitat specialization in the Evros river delta (eastern Greece) for *Calomera littoralis nemoralis* (wet sand), *Cephalota circumdata circumdata, Cylindera trisignata hellenica* (dry parts of river bed), and in the Danube river delta (eastern Romania) for *Cephalota chiloleuca* (drier salt marsh substrate), and *Calomera littoralis nemoralis* (edge of reservoirs).

Such narrow specialization to habitat/microhabitat types among tiger beetle species is explained by physiological (Schultz and Hadley 1987, Hadley et al. 1990), morphological (Pearson and Mury 1979, Schultz and Hadley 1987), and behavioural (Knisley and Pearson 1981, Pearson and Lederhouse 1987) adaptations of adults and larvae.

Most Balkan tiger beetles occupy sandy habitats localized in lowlands, mainly on the sea coasts and in river deltas (Table 3). More than 90% of south-east European salt marshes are found in the Balkan Peninsula (Dijkema 1984). As a result of human activity some of these areas have been significantly altered (Saveljić 2008, Davy et al. 2009) and are threatened. Therefore, this habitat is included among important biodiversity sites in the European Union's Habitats Directive and Water Framework Directive (Directive 1992, 2000). Given the ecological distribution of Balkan tiger beetles (Table 3), at least 42% of the recorded species occur in these threatened environments. Moreover, studies of *Calomera* species show that some tiger beetles characteristic of coastal sandy beaches are negatively influenced by tourist activity and rapid development of tourist infrastructure (Arndt et al. 2005). If valid for the Balkan Peninsula, this adds an additional two or three species to the list of potentially threatened tiger beetles, and a total of almost 60% of all Balkan tiger beetle fauna. What more, the Balkan Peninsula is a biogeographical melting pot, and a transition zone where faunal elements of various origins meet. Thus, such a biogeographical structure, unique both at a scale of the southeastern Mediterranean region and the entire European continent, is particularly vulnerable to deterioration.

Hopefully the plight of these tiger beetles will help focus the attention of biologists, ecologists, and nature conservationists on the Balkan Peninsula as an important European hotspot area for conserving biodiversity of the European fauna.

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RESEARCH ARTICLE



Ground beetles of the Ukraine (Coleoptera, Carabidae)

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Abstract

A review of the ground beetles of the Ukrainian fauna is given. Almost 750 species from 117 genera of Carabidae are known to occur in the Ukraine. Approximately 450 species of ground beetles are registered in the Carpathian region. No less than 300 species of ground beetles are found in the forest zone. Approximately 400 species of Carabidae present in the forest-steppe zone are relatively similar in species composition to those in the forest territories. Some 450 species of Carabidae are inhabitants of the steppe zone. Representatives of many other regions of heterogeneous biotopes such as forest, semi desert, intrazonal, etc. can be found in the steppe areas. The fauna of Carabidae (ca. 100 species) of the lowlands of southern Ukraine (sandy biotopes), situated mostly in the Kherson region, is very peculiar. The fauna of the Crimean mountains contains about 300 species. Conservation measures for the Carabidae are discussed.

Keywords

Coleoptera, Carabidae, distribution, geographic region, Ukraine

Introduction

The first published observations of ground beetles in the Ukraine appeared at the end of 18th / beginning of the 19th century (Pallas 1776; Steven 1806; Zawadski 1825; Fischer-Waldhaim 1820–1822). Since then the number of publications steadily increased, especially from the second half of the 19th century (Motschulsky 1845, 1850; Chaudoir 1850, 1863; Nowicki 1865, 1873; Hochguth 1871, Łomnicki 1884, 1913;

Pliginsky 1911 and others). All these data have been compiled in the fundamental monograph by GG Jacobson (1905–1916). Many further studies on the diversity, ecology and practical importance of Carabidae of the Ukraine had been conducted starting in the early 20th century (Roubal 1924, 1930; Znojko 1927; Lutschnik 1934; Averin 1938; Medvedev 1950, 1954; Arnoldi LV 1953; Arnoldi KV 1958; Kryshtal 1956; Ponomarchuk 1956, 1958, 1963, 1969; Medvedev and Shapiro 1957; Petrusenko AA and Petrusenko SV 1970, 1971, 1973, 1975; Kulyanda 1978; Rizun 1986, 1990, 1994, 1998, 1999, 2003; Eidelberg et al. 1988; Petrusenko et al. 1999; Putchkov 1998, 2008 and many others).

At present, there are more than 1000 literature sources that concern the general biology, systematic and ecology of ground beetle species, recorded from the territory of present-day Ukraine. The checklist of Carabidae of Russia and adjacent territories (Kryzhanovskij et al. 1995) is the largest summary on the species diversity of ground beetles in the Ukraine. In this book, data on the East Carpathian, Crimea and other regions of the Ukraine are presented. Furthermore, a more recent survey in the first volume of the Catalogue of Palearctic Coleoptera (2003) lists nearly 720 species of Carabidae that are indicated for the whole territory of the Ukraine. However, in spite of the fact that these publications span different geographical zones of the Ukraine, the distribution of ground beetles within the country remains poorly studied. Besides, there are nearly thirty species of Carabidae registered in the Ukraine that are not included in the Catalogue of Palearctic Coleoptera, 2003 (marked in this article by*).

The aim of the present paper is to summarise all available data from literature sources and collections and to provide an overview of the present-day species composition and distribution of ground beetles in the Ukraine.

Material and methods

The complete list of Carabidae of the Ukraine (Appendix 1) was compiled on the basis of a critical literature review and collections in several biological institutions in Kiev, Moscow, St.-Petersburg, Budapest, Vienna and Prague, including my own large collection. The tiger beetles (Coleoptera, Cicindelidae), as a separate family (Putchkov, Cassola, 2005) is not included in this article. The classification of Carabidae follows Kryzhanovskij et al. (1995) with some additional revision (Catalogue of Palearctic Coleoptera, 2003). The analysis of the distribution of Carabidae in the Ukraine is given on the basis of the whole territory of the country; however special attention was paid to 13 separate specific regions, districts and provinces (Fig. 1).

Results and discussion

Ground beetles (Carabidae) are one of the largest beetle families in the territory of the Ukraine. There are nearly 750 species from 117 genera present. Such rich biodiversity



Figure 1. A map of certain geographic regions of the Ukraine: **TL** – Transcarpathian lowland (H < 200 m.); **CM** – Carpathian mountains (H>200 m); **RF**– Right-Dnieper-bank (westwards) of forest zone; **LF** – Left- Dnieper-bank (eastwards) of forest zone; **WRS** – Western part of right- Dnieper-bank (west-west-wards) of forest-steppe zone; **ERS** – Eastern part of right- Dnieper-bank (west-eastwards) of forest-steppe zone; **ELS** – Left- Dnieper-bank (eastwards) of forest-steppe zone; **ELS** – Left- Dnieper-bank (eastwards) of steppe; **NLS** – Northern subzone of left- Dnieper-bank (eastwards) of steppe; **SRS** – Southern subzone of right- Dnieper-bank (westwards) of steppe; **SRS** – Southern subzone of right- Dnieper-bank (eastwards) of steppe; **SC** – Steppe of Crimean peninsula; **MC** – Crimean Mountains (with south-eastern coastal beach). A list of carabid species recorded from the Ukraine is provided in Appedix 1.

is due to the large area of the country on one hand, and the heterogeneity of natural conditions of the separate geographical regions on the other hand.

The ground beetle fauna of TL and CM are most diverse in the Ukraine (ca 330 and 400 species from 75 genera were found here, respectively) (Table 1). Eight endemic taxa are registered in the East Carpathians: *Leistus baenningeri* Roubal, 1926, *L. ucrainicus* Lazorko, 1954, *Nebria heegeri* Dejean, 1826, *Duvalius transcarpathicus* Shilenkov et Rizun, 1989, *D. ruthenus ruthenus* Reitter, 1878, *D. corpulentus* Weise, 1825, *Trechus pseudomontanellus* Rizun, 1994, *Carabus zawadskyi serriatissimus* Reiter, 1896, *C. fabricii ucrainicus* Lazorko, 1951. More than 20 taxa are subendemic for this region (mostly from the genera *Carabus, Nebria, Trechus* and *Pterostichus*). In addition, more than 80 species that are known from the East Carpathians are absent from other geographic regions of the Ukraine. For approximately 50 taxa the Carpathians appear to be the eastern border of their ranges. These are some species belonging to the genera *Nebria, Carabus, Pterostichus, Tachyura, Trechus*, and separate species of *Bembidion*.

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and; C	eper-ba	right-]	
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Tribes					Certain	geograp	hic regio	ns of the	Ukraine	(numbe	r genera	(species)				
	ΤΓ	CM	F	orest zor	Je		Forest-ste	sppe zone	a		, ,	Stepp	e zone			MC
			T	RF	LF	н	WRS	ERS	ELS	T	NRS	NLS	SRS	SIS	SC	
1. Omophronini	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
2. Nebriini	2/6	2/16	2/6	2/6	2/6	2/8	2/8	2/5	2/5	2/4	2/4	2/2	1/3	1/1	1/1	2/4
3. Notiophilini	1/5	1/7	1/6	1/6	1/4	1/7	1/6	1/6	1/7	1/6	1/5	1/6	1/6	1/4	1/2	1/5
4. Carabini	2/22	2/30	2/20	2/14	2/18	2/32	2/30	2/21	2/23	2/26	2/22	2/19	2/17	2/16	2/11	2/14
5. Cychrini	1/1	1/2	1/1	1/1	1/1	1/2	1/2	1/2	1/1	1/1	1/1	1	1	1	1	1
6. Elaphrini	2/5	2/5	2/5	2/5	2/3	2/6	2/5	2/4	2/6	1/2	1/2	1/1	1/1	1/1	1/2	1/2
7. Loricerini	1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1		1	1	1	I	1
8. Scaritini	1	1	1	1	1	1	1			1/2	1/1	1/1	1/2	1/2	1/2	1/1
9. Clivinini	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/3	1/2	1/2	1/3	1/3	1/3	1/2
10. Dyschiriini	1/9	1/13	1/10	1/10	1/10	1/17	1/16	1/12	1/15	1/22	1/14	1/16	1/25	1/20	1/22	1/6
11. Broscini	1/1	1/1	1/2	1/2	1/1	1/1	1/1	1/1	1/1	1/2	1/1	1/2	1/2	1/2	1/2	1/2
12. Apotomini	I	I	1	I	I	I	I	I	1/1	1/1	I	1/1	1/1	1/1	1/1	I
13. Trechini	5/5	8/23	6/7	6/7	6/6	6/9	6/9	6/6	4/4	3/3	3/3	3/3	2/2	2/2	2/2	6/8
14. Tachyiini	2/3	2/3	2/2	2/2	2/2	2/4	2/4	2/2	2/2	2/5	2/2	1/2	2/4	2/5	2/6	2/3
15. Bembidiini	2/52	2/70	2/40	2/38	2/31	2/59	2/57	2/36	2/33	2/34	2/28	2/28	2/30	2/31	35	2/33
16. Pogonini	I	I	I	I	I	I	1	1/1	1/2	3/14	1/2	1/8	3/11	3/14	3/13	I
17. Patrobini	1/2	1/3	1/1	1/1	1/1	1/1	1/1	1/1	1/1	I	I	I	I	-	I	I
18. Deltomerini	I	1/1	I	I	I	I	I	I	I	I	I	I	I	I	I	I
19. Pterostichini	6/25	6/35	5/26	5/24	5/23	6/31	6/30	5/22	4/21	4/22	4/18	4/21	3/19	3/19	3/18	3/14
20. Sphodrini	2/5	3/8	3/7	3/7	2/7	3/8	3/8	2/6	2/6	3/11	3/5	3/5	3/8	3/10	3/10	3/14
21. Platinini	8/24	9/28	8/30	8/28	7/26	8/28	8/28	7/21	7/21	5/15	5/14	5/12	5/15	4/13	3/12	6/15
22. Zabrini	3/31	3/35	3/33	3/33	3/33	3/38	3/36	3/31	3/33	3/36	3/28	3/25	3/28	3/33	3/35	3/30

Tribes					Certain	geograph	nic region	ns of the	Ukraine	(numbe)	r genera/	species)				
	ΤΓ	CM	Ä	orest zon	e		orest-ste	ppe zone				Steppe	e zone			MC
			T	RF	LF	Т	WRS	ERS	ELS	Т	NRS	NLS	SRS	STS	SC	
23. Harpalini	10/57	10/55	10/50	9/49	8/46	10/64	10/64	8/50	8/68	17/ca	11/72	10/75	14/ca	14/ca	16/ca	11/
-										130			100	110	120	ca70
24. Perigonini	I	I	I	I	Ι	I	1	1	1	1	1	I	I	-	1/1	I
25 Panageini	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/1	1/1
26 Callistini	3/9	2/8	2/7	2/7	2/6	3/9	2/9	3/9	3/9	4/15	3/10	3/10	3/14	4/15	4/14	3/11
27 Oodini	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2	1/2
28 Licinini	2/6	2/6	2/10	2/7	2/10	2/10	2/9	2/8	2/10	2/9	2/9	2/9	2/9	2/8	2/7	2/7
29 Masoreini	I	I	1/1	1/1	1/1	1/1	1/1	1/1	I	1/1	I	I	I	1/1	I	1/1
30.Corsyrini	I	I	I	I	I	I	1	I	I	1/1	1	1/1	1/1	I		
31 Odacanthini	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1
32 Lebiini	9/22	9/20	8/19	8/19	8/18	8/20	9/25	8/15	8/20	8/ca 40	8/18	8/17	8/26	8/30	8/35	9/25
33 Dryptini	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	1/1	2/2	1/1	1/1	2/2	2/2	2/2	2/2
34 Zuphiini	1/1	I	1/1	I	1/1	I			1/1	2/3	1/1	1/2	2/3	2/3	2/2	2/3
35 Brachinini	1/1	1/3	1/2	1/2	1/1	2/4	2/3	2/4	1/3	2/16	2/4	2/5	2/10	2/11	2/15	2/11
Totals	71/327	75/390	70/300	70/280	69/265	75/390	73/365	69/275	65/310	76/ca	64/273	63/275	68/ca	70/ca	70/ca	68/ca
										450			340	360	370	280

Most of these species inhabit subalpine and alpine biotopes. Some typical Middle-European species occur in the different types of mountain forests, where they comprise one of the major components of carabid diversity in the Carpathians. At the same time, the fauna of ground beetles in the Carpathians includes also many widespread species that inhabit other forest and forest-steppe areas of the Ukraine.

The fauna of forest areas of the Ukraine is represented by no less than 300 species from 70 genera and is characterized by considerable similarity in species composition in all separate regions and zones (Table 1). It appears also similar to those from other northern areas of eastern Europe. Endemics are absent from forest area of the Ukraine, although about 10 species are present only in forest areas of the country. There are some boreal taxa of carabids that are registered only in the north-western part of the Ukraine (some species of *Carabus, Miscodera*, Agonum, Trechus, Pterostichus*). The territory of RF is slightly richest in terms of species diversity of Carabidae then LF of the forest zone (Table 1).

Ground beetles of the present-day forest-steppe zone are represented by nearly 400 species from 75 genera (Table 1). The fauna of this zone is not typically transitional from forest to steppe. Obviously, the species composition of ground beetles in the forest-steppe can be characterized as quite distinct, although with some similarities to the forest zone. The variety and number of typical forest species (especially hygrophilous and mesophilous ones) exceeds the number of steppe-specific inhabitants. The territory of WRS is the richest (365 species from 73 genera) in terms of species diversity of Carabidae as compared to that of ERS (310 species from 65 genera) (Table 1). Forest species are more common in the western region between the Dniester and South Bug rivers. Four species - Carabus sibiricus rybinskii Reitter, 1896, Laemostenus tichyi Kult, 1946 (both are endemics of the Ukraine), Poecilus szepligetii Csiki, 1908 and Aptinus bombarda Illiger, 1800 occur only in the western area. Moreover, some ground beetles (Carabus excellens Fabricius, 1798, C. marginalis Fabricius, 1794, C. scabriusculus Olivier, 1795, some Calathus) are more abundant in the forest-steppe zone than in northern or southern regions. However there are many forest species of Carabidae that occur in WRS that are absent from the ERS. The composition Carabidae in the ELS is characterized by an increasing number of mesoxerophilous species, which are more common in the steppes than in the forest-steppe (Harpalus, Cymindis) (Table 1).

The ground beetle fauna of the steppe area of the Ukraine is the richest in species diversity and is characterized by the presence of approximately 450 species from 76 genera (Table 1). The taxonomic structure of ground beetles of the steppe is very diverse due to the heterogenous origin of steppe Carabidae fauna. The occurrence of many extrazonal (forest or semi-desert) and intrazonal (littoral, halophilous) species in the steppe region zone makes it difficult to characterize the general composition of the carabid fauna. As a whole, about 100 taxa of ground beetles in the fauna of the Ukraine occur exclusively in the steppe area (especially the genera *Scarites, Apotomus, Zuphium*, many Harpalini, Zabrini and some species of *Poecilus, Chlaenius* and *Brachinus*). However, the majority of ground beetles in this area is formed by typical steppe or Mediterranean taxa (mostly from the tribes Harpalini, Zabrini, Lebiini). Some forest and forest-steppe species (tribes Nebriini, Carabini, Platinini) are more common in the northern subzone (NRS and NLS) of the steppe zone. In addition, anthropogenic factors have supported predominance of some widespread mesophilous species in this subzone.

The ground beetle fauna of the steppe area of NLS is similar as a whole to that of the NRS; however it is characterized at the same time by the predominance of typical steppe taxa. Only the district of the Donetskyi heights (ridge) is characterized by more mesophilous elements including polytopic and forest species (some *Carabus, Pterostichus* and *Agonum*). At the same time, the occurrence of typical steppe taxa, including separate inhabitants of Caucasian and Kazakhstanian steppes (*Poecilus anodon* Chaudoir, 1868, *P. lyroderes* Chaudoir, 1846, *Curtonotus propinquus* Menetries, 1832, and some *Cymindis* species) could be observed in this region. Possibly, earlier, the Donetskyi ridge was characterised by a ground beetle fauna transitional between forest-steppe and steppe zones. Present-day diversity of Carabidae of this region is relatively closer to that of typical steppe fauna.

The southern steppe subzone (SRS and SLS) is characterized by the prevalence of xerophilous and mesoxerophilous species from the tribes Harpalini and Lebiini, while relatively mesophilous taxa occur more exceptionally in river valleys, ravines or in agricultural biotopes. The occurrence of some mesohygrophilous species in the steppe is usually related to irrigation.

The majority of littoral and halophilous species (tribes Clivinini, Bembidiini, Tachyini, Pogonini and Stenolophina) occur in river valleys, coastal beaches of gulfs, lakes, estuaries and other water basins. The ground beetle fauna of seashores and estuaries is characterized by the prevailence of many species that are absent from other regions of the Ukraine (some *Dyschirius, Tachys, Bembidion, Acupalpus, Trichocellus* etc.).

Quite specific, although poor in species number (no more than 100), is the carabid fauna of sandy habitats in the lowlands of Dnieper River (Kherson region, Oleshie). It is represented by both typical steppe species and psammophilous and some semi-desert elements (*Cymindis medvedevi* Kryzhanovskij et Emetz, 1973, *Corsyra fusula* Fischer von Waldheim, 1820*, *Polystichus connexus* Fourcroy, 1785*, *Parazuphium chevrolatii* Castelnau, 1833*). Many halophilous and littoral species from the tribes Pogonini, Scaritini, Bembidiini and Harpalini also occur here. In addition, some typical forest inhabitants were also recorded from this region (*Carabus, Pterostichus, Agonum* occurring in groves).

The ground beetle fauna of the Crimean Peninsula is one of the most specific in the Ukraine (about 390 species from 74 genera). There are some typical inhabitants of steppe and halophitic biotopes of the plains of Crimea (near 370 species): *Calosoma Carabus, Poecilus, Amara,* many Harpalini and Cymindina (Table 1). On the Kerch Peninsula some relatively forest mesophilous species occur: *Carabus cancellatus* Illiger, 1798, *Leistus ferrugineus* Linnaeus, 1758, *Pterostichus niger* Schaller, 1783 and *Pt. an-thracinus* Illiger, 1798. This confirms the presence of arboreal areas in the ancient past.

The fauna of MC (no less than 280 species from 68 genera) has quite a different composition from that of the plain regions of the Crimea (Table 1). It is characterized

by some Crimean endemics (about 15 taxa, e.g. some cave species from the genera *Pseudophaenops* and *Taurocimmerites*, as well as *Carabus gyllenhali* Fischer von Waldheim, 1827, *C. hungaricus gastridulus* Fischer von Waldheim, 1823, *C. perrini planus* Gehin, 1885, *C. sabrosus tauricus* Bonelli, 1811, *Trechus lioplerus jailensis* Winkler, 1911, *Bembidion iphigenia* Netolitzky, 1931, *Laemostenus jailensis* Breit, 1911, *Cymindis vagemaculata* Breit, 1914). Some taxa are subendemic to MC and are recorded from the Caucasus as well (*Leistus caucasicus* Chaudoir, 1876, *Carabus sibiricus bosphoranus* Fischer von Waldheim, 1823, *Bembidion lederi* Reitter, 1888, *Laemostenis sericeus tauricus* Dejean, 1828) or in other southern European countries (*Laemostenus cimmerius* Fischer von Waldheim, 1823*, *L. venustus* Clairville, 1828*, *Cymindis ornata* Fischer von Waldheim, 1824, *C. scapularis* Schaum, 1857*). However, the bulk of the ground beetle fauna of the Crimea Mountain consists of taxa that are widespread in the Mediterranean region and/or in forest-steppe areas of the Ukraine.

Special attention should be paid to the fauna of anthropogenic landscapes of the Ukraine. In agricultural habitats, the species composition of ground beetles is relatively uniform throughout the different geographical regions. Agrocenoses are generally poor in species richness consisting of some 70–100 widely distributed common species, but the abundance of some of these is much higher than in natural biotopes. The core faunal composition consists of approximately 20 widespread (mainly polytopic) species from the genera *Amara*, *Bembidion*, *Harpalus*, *Poecilus* and *Pterostichus*. The fauna of urban territories (for example cities) is rather impoverished as a rule and consists of some 10–15 polytopic species.

Currently ten species of ground beetles (*Calosoma sycophanta* Linnaeus, 1758 *Carabus bessarabicus* Fischer von Waldheim, 1823, *C. estreicheri* Fischer von Waldheim, 1822,, *C. hungaricus* Fabricius, 1792, *C. scabrosus tauricus* Bonelli, 1811, *C. stscheglowi* Mannerheim, 1827, *Pseudophaenops jacobsoni* Pliginsky, 1913, *Taurocimmerites dublanskii* Belousov, 1998, *Carterus dama* Rossi, 1792 and *Parazuphium chevrolatii* Castelnau, 1833*) are protected and enlisted in the "Red Book of Ukraine, 2009". Most of these species are rare or vulnerable in the Ukraine; moreover the last two are cave endemics of the Crimea. Additionally, three species that occur in the Ukraine (*Carabus hampei* Kuster., 1846, *C. zawadskyi* Kraatz, 1854, *C. variolosus* Fabricius, 1794) are included in the European Data Red List as vulnerable. In general, approximately 40 species of Carabidae in total need to be protected in the Ukraine (Table 2).

Conclusions

I conclude that the overall species composition of the ground beetle fauna of the Ukraine is well studied. Therefore, finding new taxa in any part of the Ukraine is not likely to happen in the near future. Regions where new taxa for the Ukraine could be found are mainly boundary regions of the country (the Carpathians, Crimea, north and east regions), as well as in errors of some findings in the past (for example, misidentifications of some taxa or species with wrong labels).

Ν	Species	Region, biotope	Ν	Species	Region, biotope
1	Leistus caucasicus	Crimea Mnts, beech	20	Poecilus anodon	south-east, steppe
	Chaudoir, 1876	forest		Chaudoir, 1868	
2	L. baenningeri	Carpathian, subalpine	21	Laemostenus jailensis	Crimea Mnts,
	Roubal,1926	zone		Breit, 1914	subalpine zone
3	Nebria heegeri	Carpathian, subalpine	22	Taphoxenus gigas	south steppe
	Dejean, 1826	zone		Fischer von	
	,			Waldheim, 1823	
4	Carabus menetriesi	forest zone, swampy	23	Bradycellus caucasicus	forest zone
	Faldermann, 1827			Chaudoir, 1846	
5	C. intricatus	west Ukraine, forest	24	Parophonus planicollis	south steppe
	Linnaeus, 1761			Dejean, 1829*	
6	C. ullrichi Germar,	west -south part,	25	Carterus angustipennis	East Crimea, steppe
	1824	Carpathian, forest		lutschniki	
		zone		Zamotailov, 1988	
7	C. nitens Linnaeus,	north of Ukraine,	26	Ditomus calydonius	south steppe
	1758	forest		oriens Rossi, 1790	
8	C. fabricii ucrainicus	Carpathian, alpine	27	Eucarterus sparsutus	south steppe
	Lazorko, 1951	zone		Reitter, 1898	
9	Elaphrus uliginosus	Forest and east of	28	Epomis	south-east, littoral
	Fabricius, 1792*	forest steppe zones,		circumscriptus	
		Crimea		Duftschmidt, 1812	
10	Scarites laevigatus	south steppe	29	Chlaenius alutaceus	forest zone, swampy
	Fabricius, 1792			Gebler,1829	
11	Apotomus testaceus	south steppe	30	Ch. costatulus	forest zone, swampy
	Dejean, 1825			Motschulsky, 1859*	
12	Duvalius	Carpathian, subalpine	31	Masoreus wetterhali	forest and forest-
	transcarpathicus	zone		Gyllenhal, 1813	steppe zones
	Shilenkov et Rizun,				
	1989				
13	Pseudaphaenops	caves of Crimea	32	Cymindis	Crimea mnts, beech's
	tauricus Winkler,	Mnts		<i>vagemaculata</i> Breit,	forest
	1912			1914	
14	Trechus fontinalis	Carpathian, subalpine	33	C. medvedevi	sand of south steppe
	Rybinsky, 1900	zone		Kryzhanovskij et	(Kherson reg.)
				Emetz, 1973	
15	<i>Tr. plicatulus</i> Miller,	Carpathian, subalpine	34	Zuphium olens Rossi,	south steppe
	1868	zone		1790*	
16	Bembidion lederi	Crimea Mnts, near	35	Brachinus	south steppe, Crimea
	Reitter, 1888	streams		<i>bipustulatus</i> Quensel,	
				1806	
17	B. iphigenia	Crimea Mnts, near	36	Br. hamatus Fischer	south steppe, Crimea
	Netolitzky, 1931	streams		von Waldheim,	
				1828*	
18	Pogonus cumanus	south-east, halobiont	37	Mastax thermarum	south-west, forest
	Lutschnik, 1916			Steven, 1806*	zone
19	Pedius longicollis	south-east, steppe	38	Aptinus bombarda	south-west region
	Duftschmidt, 1812			Illiger, 1800	

Table 2. Rare and little-known species of Carabidae of the Ukrainian fauna.

Poorly answered questions that remain include the origins of carabid fauna of the Ukraine. Moreover it is necessary to study the preimaginal stages of ground beetles. For example the larvae of only 360 species from 86 genera are described, representing only 45% of carabid species from the Ukraine. Further studies on the bionomics of single species require urgent attention. This applies in particular to ecologically related, non-competitive species occurring in common biotopes, e.g. many littoral species of *Bembidion, Dyschirius, Acupalpus* or some steppe species of the Harpalini tribe.

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Appendix I

Checklist of ground beetle species recorded from the Ukraine. (doi: 10.3897/zook-eys.100.1545.app) File format: Microsoft Word (doc).

Explanation note: The additional file contains a list of all ground beetle species recorded from the Ukraine.

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RESEARCH ARTICLE



What do we know about winter active ground beetles (Coleoptera, Carabidae) in Central and Northern Europe?

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Abstract

This paper summarizes the current knowledge on winter active Carabidae in Central and Northern Europe. In total 73 winter active species are listed, based on literature and own observations. Ground beetles are among the three most numerous Coleoptera families active during the autumn to spring period. The winter community of Carabidae is composed both of larvae (mainly autumn breeding species) and adults, as well as of epigeic species and those inhabiting tree trunks. Supranivean fauna is characterized by lower species diversity than the subnivean fauna. The activity of ground beetles decreases in late autumn, is lowest during mid-winter and increases in early spring. Carabidae are noted as an important food source in the diet of insectivorous mammals. They are also predators, hunting small winter active invertebrates.

Keywords

Coleoptera, Carabidae, Central Europe, winter activity, subnivean fauna

Introduction

During winter, invertebrates are mostly inactive in diapause as eggs, larvae or pupae, but less often as adult stages (Leather et al. 1993). Body fluids may freeze in low temperatures, so to avoid death, insects employ two main strategies: avoiding freezing or tolerating freezing. The adaptation to avoid freezing is the ability of supercooling by synthesizing antifreezing agents (e.g., glycerol) (Moore & Lee 1991). Some poikilothermic organisms may stay active in winter. These organisms use favourable atmos-

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pheric condition – mild winter days with low air pressure – for migration and copulation (Soszyńska 2004). Their activity in low temperatures is usually related to the presence of snow and to their thermal properties. Snow cover has a high insulation capacity and low thermal conductivity due to its high air content. Low density and a greater thickness of snow (depending on geographical area) provide better insulation. The soil and litter can remain warm even if air temperature is very low (Aitchison 1974, 2001).

Snow cover provides winter active animals with three different microhabitats. The insulating properties of snow make the space under the snow a favourable habitat for invertebrates (subnivean microenvironment). The subnivean microhabitat is relatively warm, humid, thermally stable and protects organisms from wind and lethal temperatures in contrast to the snow surface (supranivean environment), which is highly variable and completely dependent on atmospheric factors. Within the snow, the so-called intranivean habitat, temperatures are lower but organisms are still protected from the external environment (Aitchison 2001). Animals that are active in snow can be divided into two main groups, depending on their period of activity. The first group consists of "true winter" organisms that are active during the winter months (end of November until the beginning of April) both under and on the snow cover. The second is a nival fauna that are active on the snow cover outside the winter months. Examples of these fauna are permanent residents of high-altitude regions and glaciers. These invertebrates are adapted to permanent snow, glacier surfaces, etc. Their food source is the aeolian fauna, which consists of invertebrates passively deposited on snow fields (Mani 1962, Aitchison 2001).

The snow fauna is an ecological group, which consists of permanent snow active invertebrate species. The first observations regarding invertebrate activity on the snow was made in Poland in the middle of 18th century (Fedorowicz 1968). Since then, snow active insects have been the main subject of investigation in only a few elaborate studies. Snow activity was observed in many insect orders: Collembola, Trichoptera, Plecoptera, Blattodea, Hemiptera, Mecoptera, Coleoptera, Diptera, and Hymenoptera (Frey 1913, Tahvonen 1942, Szulczewski 1947, Ulfstrand 1968, Brummer-Korvenkontio & Brummer-Korvenkontio 1980, Leinaas 1981, 1983, Hågvar 1995, 2000, Aitchison 2001, Soszyńska and Durska 2002, Soszyńska 2004, Hågvar and Greve 2003).

The first information about subnivean fauna appeared almost two centuries later than that of the fauna living on the snow. The subnivean microenvironment is inhabited by more numerous groups of invertebrates, such as oligochaetes, molluscs, crustaceans, arachnids and insects. Among these, insects and spiders clearly predominate, being the major representatives of the snow active fauna. The subnivean fauna was studied more often than the snow active fauna. Main studies came from Canada (Aitchison 1978, 1979ad, 1984, 2001), the USA (Schmidt and Lockwood 1992, Addington and Seastedt 1999), as well as from central and northern Europe (Renken 1956, Ackefors 1964, Näsmark 1964, Merriam et al. 1983, Itämies and Lindgren 1989, Łęgowski and Łoziński 1995). The most common orders in terms of species diversity as well as percentage contribution to this ecological group are Collembola, Coleoptera, Diptera, but also Hymenoptera, and Hemiptera (Tahvonen 1942, Ackefors 1964, Aitchison 1979 a-d, 1984, 2001). During the last decades, global climate change has become an important scientific topic. However its influence on poikilothermic organisms has been poorly investigated. It seems that the occurrence of snow cover during the winter period plays an important role in the biology of many different invertebrate groups.

The aim of this paper is to summarize knowledge regarding winter active Carabidae fauna from Central and Northern Europe. In the present paper we discuss only the "true winter active" ground beetles, and not members of the nival fauna occurring in high-altitude regions or glaciers.

Methods

Winter season is defined here as the period between the end of November and the beginning of April. All available literature data on winter active Carabidae recorded from Central and Northern Europe were used in this study. In total, data from five countries and published in 17 papers were analyzed (see Table 1). Data of mountain Carabidae active on the snow and glaciers as well as species found overwintering in diapause were not included. In addition, our unpublished records of winter active Carabidae from Central Poland were included. This material was collected occasionally during different field studies using pitfall traps (subnivean species) and active searching on the snow cover. The list of species analyzed in this study is given in Table 1.

All recorded ground beetle species were divided into three groups, according to the microenvironment in which they were noted: epigeic (subnivean), active on the snow cover (supranivean), and actively walking on tree trunks. Data on activity of both the adults and the larvae are also shown in Table 1.

The ecological response towards snow active ground beetle species was done according to Fudakowski (1959) and Pruitt (1978). These authors distinguished the following species groups according to their ecological reaction towards snow: chionobionts – stenothermic species with adaptations to survive on snow and to reproduce in winter, chionophiles – eurythermic permanent snow active group, but its members occur also in other seasons, chionoxenes – species accidentally found in winter; chionophobes – group that avoids snow.

For the nomenclature of Carabidae species, the Fauna Europea Web Service (2004) was followed, while the zoogeographical analysis of ground beetles was based on the study by Leśniak (1988).

Results and discussion

Winter active Carabidae – a short history of faunistic studies

Most studies performed on winter active ground beetles are rather recent (Table 1). The first faunistic data on winter active Carabidae came from the beginning of 20th century, when five species belonging to the genera *Leistus*, *Bradycellus*, *Dromius*, *Ocydromus* and *Pterostichus*

			Snow	Epigeic	Tree	
No.	Species		cover	(subnivean)	trunks	Source
1	<i>Abax parallelepipedus</i> (Piller et Mitterpacher, 1783)	A		XI-XII, III-IV		Greenslade 1965, Murdoch 1967
2	Abax sp./Pterostichus sp.	L		XI-XII		Evans 1969
3	<i>Acupalpus dubius</i> Schilsky, 1888	A		XII		Murdoch 1967
4	<i>Agonum gracile</i> Sturm, 1824	A		IV		this paper
5	<i>Agonum muelleri</i> (Herbst, 1784)	A	Ι			Szulczewski 1947
6	<i>Agonum viduum</i> (Panzer, 1796)	A		XI		Murdoch 1967
7	<i>Amara aulica</i> (Panzer, 1796)	L		XI-I		Traugott 1998
8	<i>Amara brunnea</i> (Gyllenhal, 1810)	А		XI-XII		this paper
9	<i>Amara communis</i> (Panzer, 1797)	А		XI-XII		Flatz & Thaler 1980, this paper
10	<i>Amara infima</i> (Duftschmid, 1812)	A		XI-I (?)		Kaczmarek 1958
11	<i>Amara familiaris</i> (Duftschmid, 1812)	A			III-IV	Hannig et al. 2006
12	<i>Amara lunicollis</i> Schiødte, 1837	А		III-IV		Greenslade 1965
13	Amara sp.	Α		XI-IV		Kennedy 1994
14	Anchomenus dorsalis (Pontoppidan, 1763)	А		XI-IV		Renken 1956, Greenslade 1965, Weber 1965, Flatz & Thaler 1980
15	<i>Anisodactylus binotatus</i> (Fabricius, 1787)	A		IV		this paper
16	<i>Asaphidion flavipes</i> (Linné, 1761)	A		XI-IV		Weber 1965, Murdoch 1967
17	<i>Asaphidion pallipes</i> (Schrank, 1781)	A		IV		this paper
18	<i>Badister sodalis</i> (Duftschmid, 1812)	A		III-IV		Murdoch 1967
19	<i>Bradycellus caucasicus</i> (Chaudoir, 1846)	А	Ι	XI-I		Frey 1913, Kaczmarek 1958
20	<i>Bradycelus harpalinus</i> (Audinet-Serville, 1821)	A		XI-XII		this paper
21	<i>Bradycellus verbasci</i> (Duftschmid, 1812)	A		XI-XII, II-III		Evans 1969, this paper
22	<i>Calathus erratus</i> (C.R. Sahlberg, 1827)	A		XI		Renken 1956, Kaczmarek 1958

Table 1. List of winter active ground beetles (**A** – adults, **L** – larvae). Roman letters indicate the month(s) of observation(s). Nomenclature after Fauna Europaea Web Service (2004).

			Snow	Epigeic	Tree	
No.	Species		cover	(subnivean)	trunks	Source
23	<i>Calathus fuscipes</i> Goeze, 1777	A		XI-IV		Greenslade 1965, Flatz & Thaler 1980, Kennedy 1994, this paper
		L		XI-IV		Traugott 1998
24	Calathus melanocephalus	Α		XI-IV		Greenslade 1965, Kennedy 1994
	(Linné, 1758)	L		XII-I		Traugott 1998
25	<i>Calathus micropterus</i> (Duftschmid, 1812)	А	XI	XI-I (?)		Kaczmarek 1958, this paper
26	<i>Calathus rotundicollis</i> Dejean, 1828	А		XI-XII		Greenslade 1965
27	<i>Calodromius bifasciatus</i> (Dejean, 1825)	А			XI-III	Hannig et al. 2006
28	<i>Calodromius spilotus</i> (Illiger, 1798)	А			XI-III	Hannig et al. 2006
29	<i>Carabus convexus</i> Fabricius, 1775	А		XI-III		this paper
30	<i>Carabus coriaceus</i> Linné, 1758	L		XII-I		Traugott 1998
31	<i>Carabus hortensis</i> Linné, 1758	L		XII		Traugott 1998
32	<i>Carabus nemoralis</i> O. F. Müller, 1764	А	Ι	XI-IV		Greenslade 1965, Weber 1965, Evans 1969, Kennedy 1994, this paper
33	<i>Carabus problematicus</i> Herbst, 1786	А		XI		Greenslade 1965, Evans 1969, Betz 1992
34	<i>Carabus</i> sp.	L		XI-III		Evans 1969
35	<i>Cychrus caraboides</i> (Linné, 1758)	L		XI-XII, III		Evans 1969
36	<i>Demetrias atricapillus</i> (Linné, 1758)	А		+		Renken 1956
37	<i>Dicheirotrichus cognatus</i> (Gyllenhal, 1827)	А		+		Renken 1956
38	<i>Dicheirotrichus placidus</i> (Gyllenhal, 1827)	А		XII		Murdoch 1967
39	<i>Dromius angustus</i> Brullé, 1834	А			XII	Hannig et al. 2006
40	Dromius quadrimaculatus (Linné, 1758)	А			XI-III	Hannig et al. 2006
41	<i>Dromius schneideri</i> Crotch, 1871	А	Ι			Frey 1913
42	<i>Dyschiriodes globosus</i> (Herbst, 1784)	A		XI-IV		Weber 1965
43	<i>Elaphrus cupreus</i> Duftschmid, 1812	А		III		Murdoch 1967
44	<i>Epaphius secalis</i> (Paykull, 1790)	А		XI-I (?)		Kaczmarek 1958

No.	Species		Snow cover	Epigeic (subnivean)	Tree trunks	Source
45	<i>Leistus rufomarginatus</i> (Duftschmid, 1812)	A		XI, I-II		Jaskuła & Grabowski 2003, this paper
46	Leistus ferrugineus	Α		XI-I (?)		Kaczmarek 1958
	(Linné, 1758)	L	Ι	XI-XII,		Levander 1913, Näsmark 1964,
				III-IV		Greenslade 1965
47	<i>Leistus fulvibarbis</i> Dejean, 1826	A		XI-XII		Murdoch 1967
48	Leistus terminatus	Α		XI-II		Murdoch 1967
	(Panzer, 1793)	L		XI-IV		Murdoch 1967
49	Leistus sp.	L	XII	II-III		Evans 1969, this paper
50	<i>Loricera pilicornis</i> (Fabricius, 1775)	A		XI-IV		Greenslade 1965, Murdoch 1967, Kennedy 1994, this paper
51	<i>Metallina lampros</i> (Herbst, 1784)	A		XI-IV		Greenslade 1965, Kennedy 1994, this paper
52	<i>Nebria brevicollis</i> (Fabricius, 1792)	A		XI-IV		Renken 1956, Greenslade 1965, Murdoch 1967, Evans 1969, Flatz & Thaler 1980, this paper
		L		XI-IV		Murdoch 1967, Evans 1969, Traugott 1998
53	<i>Notiophilus biguttatus</i> (Fabricius, 1779)	A	XII-I	XI-IV		Greenslade 1965, Evans 1969, Kennedy 1994, this paper
54	<i>Notiophilus rufipes</i> Curtis, 1829	A		XI, I-II		Greenslade 1965
55	<i>Notiophilus substriatus</i> C.R. Waterhouse, 1833	A		XI, I-II		Greenslade 1965
56	Ocydromus tetracolus (Say, 1823)	A	XII	XI-IV		Frey 1913, Murdoch 1967, Weber 1965, Kennedy 1994
57	<i>Panagaeus bipustulatus</i> (Fabricius, 1775)	A		IV		this paper
58	<i>Paradromius linearis</i> (Olivier, 1795)	A	XII	XII		Murdoch 1967, this paper
59	<i>Paranchus albipes</i> (Fabricius, 1796)	A		XI, II-IV		Murdoch 1967
60	<i>Philochthus aeneus</i> (Germar, 1824)	A		XI-IV		Kennedy 1994
61	<i>Philochthus biguttatus</i> (Fabricius, 1779)	A		XI-IV		Murdoch 1967
62	<i>Philochthus guttula</i> (Fabricius, 1792)	A		XI, I-IV		Murdoch 1967
63	Philorhizus melanocephalus (Dejean, 1825)	A		+	XII	Renken 1956, Hannig et al. 2006
64	<i>Phyla obtusa</i> (Audinet-Serville, 1821)	A		XI-IV		Weber 1965, Kennedy 1994
65	Poecilus versicolor (Sturm, 1824)	A		XI, I,II		Greenslade 1965, Flatz & Thaler 1980

			Snow	Epigeic	Tree	
No.	Species		cover	(subnivean)	trunks	Source
66	Pseudoofonus rufipes (De	Α		XI-IV		Greenslade 1965, Weber 1965
	Geer, 1774)	L		XI-III		Traugott 1998
67	Pterostichus diligens (STURM, 1824)	A	XII	IV		Frey 1913, this paper
68	<i>Pterostichus madidus</i> (Fabricius, 1775)	А		XI-IV		Greenslade 1965, Murdoch 1967
69	<i>Pterostichus melanarius</i> (Illiger, 1798)	A		XI-IV		Weber 1965, Flatz & Thaler 1980, Kennedy 1994
		L		XI-I		Traugott 1998
70	Pterostichus niger (Schaller, 1783)	A		IV		this paper
71	<i>Pterostichus nigrita</i> (Paykull, 1790)	A	XII	XI-XII, II-IV		Murdoch 1967, this paper
72	Pterostichus oblongopunctatus (Fabricius, 1787)	A		XII, III-IV		this paper
73	Pterostichus quadrifoveolatus Letzner, 1852	A		XI-XII		Kaczmarek 1958
74	Pterostichus strenuous (Panzer, 1796)	A		XI-IV		Murdoch 1967, Evans 1969
75	Pterostichus sp.	L		XI-IV		Weber 1965
76	Stomis pumicatus (Panzer, 1796)	A		III		Murdoch 1967
77	<i>Trechus obtusus</i> Erichson, 1837	А		XI-XII, III		Murdoch 1967
78	<i>Trechus quadristriatus</i> (Schrank, 1781)	A		XI-IV		Renken 1956, Weber 1965, Kennedy 1994
79	Larvae gen. sp.	L		XI-IV		Renken 1956, Kaczmarek 1958, this paper
TOT	AL		11	66	6	

were noted in Finland as active on the snow surface by Frey (1913) and Levander (1913). After more than three decades, one additional species from the genus *Agonum* was found on the snow surface by Polish entomologist Szulczewski (1947) in the Wielkopolski National Park (western Poland). More recently, one additional species – *Nebria brevicollis* – was reported by Jaskuła et al. (2005) from central Poland. All these papers presented only single, accidental observations. Our work summarizes up-to-date knowledge about this ecological group and gives a list of 11 species belonging to 10 genera, including first data on activity of the genera *Calathus, Carabus, Notiophilus*, and *Paradromius* from the snow surface.

Compared to supranivean species (which are easier to observe because of the contrast between the white colour of the snow and the dark coloured insects), the carabids active under the snow surface (subnivean fauna) were discovered rather late. First data on subnivean ground beetles became available after using Barber's traps as a collecting method, and in Central and Northern Europe were given from Germany by Renken (1956). He provided information on seven species of Carabidae from the following genera: *An-chomenus, Demetrias, Dicheirotrichus, Calathus, Nebria, Philorhizus* and *Trechus*. All these species were imagines. However Evans (1969), using the same method of study, recorded also larvae of *Cychrus caraboides, Nebria brevicollis, Abax* sp., *Pterostichus* sp., *Leistus* sp., and *Carabus* sp. as being active under the snow surface. Additional records of Carabidae larvae were added by Kaczmarek (1958), Näsmark (1964), Greenslade (1965), and here.

More adult beetles were later collected by Kaczmarek (1958 – 6 species from 6 genera), (Näsmark (1964 – 1 species), Greenslade (1965 –18 species from 12 genera), Murdoch (1967 – 17 species from 12 genera), Flatz and Thaler (1980 – 6 species from 6 genera), Betz (1992 – 1 species), Kennedy (1994 – 11 species from 8 genera), Traugott (1998 – 7 species from 5 genera), and Jaskuła and Grabowski (2003 – 1 species). Finally, in the present paper a list of 66 Carabidae species is given, including one genus (*Anisodactylus*) recorded for the first time as a supranivean taxon.

Comparing the two above-mentioned "ecological groups", it becomes clear that in the studied area, diversity of the subnivean carabid fauna is more than five times higher than that of the supranivean species (Fig. 1). A similar tendency was observed in Collembola, but was opposite when compared to some other insect groups like Diptera or Mecoptera (Soszyńska-Maj 2005).

Tree trunks are the third type of microhabitat where winter active Carabidae occur. The only paper on this topic known to us comes from Hannig et al. (2006) who noted six species in Germany: *Amara familiaris, Calodromius bifasciatus, C. spilotus, Philorhizus melanocephalus, Dromius angustus,* and *D. quadrimaculatus.* Among them, *D. quadrimaculatus* predominated and the genus *Calodromius* was noted as winter active for the first time (see Felix and Van Wielink 2011).

Winter active carabid communities

524

The most common groups among winter active invertebrates are spiders and insects. Among hexapods, springtails (Collembola), beetles (Coleoptera), flies (Diptera) and scorpionflies (Mecoptera) predominate. Beetle activity under snow cover is well documented. Investigations on winter active fauna in central Poland show that the supranivean and subnivean insect winter assemblages differ in terms of percentage contribution of orders, as well as in species composition. Beetles have only a share of 13% in snow active insect communities, and 25% in material collected under the snow (Soszyńska-Maj 2005). Among subnivean Coleoptera, three families clearly predominate: Staphylinidae, Carabidae and Cantharidae (larvae), while carabids are only found accidentally on the snow. These three beetle groups are known as winter dominants, both in terms of species diversity and abundance (Wolska 1957, Strübing 1958, Renken 1956, Näsmark 1964, Weber 1965, Aitchison 1979b, 1984, 2001, Merriam et al. 1983, Itämies and Lindgren 1989, Łęgowski and Łoziński 1995, Traugott 2002). A total of 16 Coleoptera families have thus far been recorded as winter active (Hannig et al. 2006, Soszyńska-Maj and Jaskuła unpublished data).



□epigeic/subnivean space ■ snow cover ■ tree trunks

Figure 1. Comparision of subnivean, supranivean and tree trunk fauna of Carabidae from Central and Northern Europe during the winter season (based on different sources).

In general, the winter activity of Carabidae varies seasonally. Its peak – both according to the number of species and individuals – is observed in late autumn and early spring. The lowest activity is observed in mid-winter (Fig. 1). Current analysis suggests that the diversity of ground beetles that are active under the snow cover is even several times higher than in supranivean fauna. The number of subnivean species active during the winter can be similar for months, whereas supranivean carabids occur more accidentally. As can be seen from Table 1, only a few species are regularly observed as being active during the whole winter and from many regions. For most species described as winter active only one observation of a single individual is recorded. A good example comes from a study by Kennedy (1994) who recorded, between 22 November and 4 April, at least 12 Carabidae species (genus Amara was provided with no details about species number) in winter-wheat fields in Ireland. Among these percentages, only the proportion of Phyla obtusa was higher than all other recorded species - more than 70% of the caught individuals. Only three other species (Metallina lampros, Philochthus aeneus and Trechus quadristriatus) had a share higher than 5%. Similar results came from Murdoch (1967) who recorded 17 species. In this case only Nebria brevicollis and Leistus terminatus were caught in 'high' proportions: respectively 68,9% and 9,1%. Nebria brevicollis also clearly predominated among 18 ground beetle species found in winter by Greenslade (1965). Dominance of only single species was noted by Flatz & Thaler (1980; Poecilus versicolor) and Hanning et al. (2006; Dromius quadrimaculatus). All these results suggest that also among the epigeic ground beetle fauna some species are found occasionally, while at least several others can be classified as permanently winter active.

According to literature data, winter active carabid species are known both from forests and open habitats as well as from species living on tree trunks (Table 1). Moreover, Kennedy (1994) showed that at least some carabid species can be active during the winter period both during night and day. From these investigations it became clear that *Phyla obtusa* was a day active species from 2nd to 24th of January; unfortunately no data about temperature or other environmental factors were given.

In general, Carabidae can be divided into two main breeding groups: autumn breeders (eggs are laid during the last weeks of summer and first weeks of autumn) and spring breeders (eggs are laid from March to May). As a result of this division, winter and summer carabid larvae can be distinguished (Luff 1993). Usually winter larvae hatch from from September to November, and can be found (instars 1–3) throughout the winter and in the following spring period. Although the total number of Carabidae species that breed in the autumn period is much higher, at the moment larvae of 12 different species have been distinguished as winter active (Levander 1913, Näsmark 1954, Renken 1956, Kaczmarek 1958, Greenslade 1965, Weber 1965, Murdoch 1967, Evans 1969, Luff 1993, Traugott 1998, this paper; Table 1). Among these, the occurrence of larvae of *Amara aulica, Calathus melanocephalus, Carabus coriaceus, C. problematicus, Nebria brevicollis, Pseudoophonus rufipes, Pterostichus melanarius*, and *Leistus* species can be explained as a result of autumn breeding (Betz 1992, Luff 1993, Traugott 1998). Weber (1965) and Evans (1969) did not provide any details on the identity of the *Carabus* and *Pterostichus* larvae found during the winter period. However, these genera do have species that belong to autumnal breeders too (Luff 1993).

Luff (1993) suggested that winter larvae of ground beetles must survive not only low temperatures and food shortages, but also a long period of exposure to natural enemies, and possible flooding. He also noted that, especially at lower temperatures, some winter carabid larvae can survive without food for up to 30 days.

A zoogeographical analysis shows that the Central and northern European winter active Carabidae most frequently belong to the Palaearctic fauna (54%). Interesting is that Euro-Siberian and Euro-Arctic species (groups that should be adapted evolutionary to low temperatures) made up only 14% of the recorded ground beetle species, while 12% of the species belong the Euro-Mediterranean fauna (Fig. 2).

Role of carabids in the winter food chain

High densities per square meter and high percentages of Carabidae in winter active insect communities make this group an important source of food for insectivorous vertebrates, particularly shrews. Due to their very high metabolic rate these mammals must feed almost constantly to stay alive. They are active all year round, without a hibernation period in winter and their food requirement is 43% higher in winter than in summer (Randolph 1973). As indicated in the literature, shrews do not feed on hibernating invertebrates, but rather on winter-active species, including Carabidae (Ackefors 1964, Pernetta 1977, Aitchison 1984, Itämies and Lindgren 1989). Ground beetles can be an attractive type of food for these mammals as they are present in relatively high densities - up to 23 individuals per square meter (Kennedy 1994). Rudge (1968) found that the percentage frequency of beetles in the diet of *Sorex araneus* varies from 66–72% in the autumn and spring. This increases up to 84% in the winter months. In this study only plants had a higher share during the autumn-spring period (percentage frequency 96–100%) and other small vertebrates in autumnal months (100%).



Figure 2. The relative zoogeographical structure of winter active Carabidae (based on Leśniak 1988).

From the winter active Central and North European group of Carabidae, 79% of the species appear to be predators (Table 1). Among them there are both large zoophagous species hunting for various types of prey (e.g., *Carabus* species) and specialists collecting small but very abundant prey items, i.e., springtails and aphids (e.g., Aitchison 1978, 1979, Leinaas 1981, 1983, Hågvar 2000). Springtails are known as one of the most abundant subnivean invertebrate groups (e.g., Näsmark 1964, Aitchison 1984). They were regarded as an important food source in the winter active *Phyla obtusa* with a percentage frequency from 4 to 20% (Kennedy 1994). In the latter study *Ph. obtusa* was also noted as a predator of mites (8–30%) and aphids (4–33%) during January-March. Among winter active carabids, species belonging to the genera *Loricera, Notiophilus, Leistus*, and some small species of *Pterostichus* are also well known as predator of springtails. Most probably the winter activity of species belonging to *Dromius* s.l. (e.g., Hannig et al. 2006) group can be related to the activity of their usual type of prey, i.e., aphids. On the other hand, winter activity of omnivorous (5%) and phytophagous (16%) carabids can be explained by a relatively easy access to their food, i.e., dry or decaying wood, fungi, leaves and seeds.

Many Carabidae species can change their diet according to the availability of food in the environment. Some predatory beetles (e.g., some *Carabus* species, *Pterostichus melanarius*, *Calathus fuscipes*, *Nebria brevicollis*) occasionally eat plant material. Also some typically phytophagous species (*Amara* spp., *Harpalus* spp., *Bradycellus* spp.) are able to change their diet to eggs and pupae of flies (Tischler 1971). When temperatures become too low, some species can stop feeding even if they are still active (Aitchison 2001). In extreme situations some beetles (including larvaal stages) can survive up to one month without food while remaining active (Luff 1993).

An important adaptation that protects winter active arthropods from freezing is nonfeeding behaviour during lower temperatures (Aitchison 1987). The presence of food in the gut significantly increases the possibility of spontaneous freezing as ice nucleators are present in the food (Salt 1968). As a special adaptation to prevent freezing during eating at cold temperatures, external digestion can be seen in some Carabidae species, including members of *Carabus, Cychrus, Pterostichus*, and ground beetle larvae (Hengeveld 1980a-b, Evans and Forsythe 1985). As was shown by Aitchison (1987), who studied spiders, a group that feeds by means of external digestion, such behaviour allows the avoidance of consuming dust particles on which spontaneous ice formation can occur. One of the most common and abundant groups of winter active arthropods is Collembola, which is also a popular type of prey for some Carabidae species. The study of Aitchison (1978) showed that springtails contain some cryoptotectans in their haemolymph allowing survival in cold temperatures. Feeding mechanisms observed in spiders and carabids suggest that these chemical compounds can possibly be transferred from a prey to a predator body during eating. As a result cryoprotectans of the prey may allow its predator to survive low temperatures.

Weather conditions and winter activity of ground beetles

Based on literature data we can assume that the activity of Carabidae species decreases in late autumn. Activity will be lowest during the winter period, and increases in the early spring (e.g., Evans 1969, Table 1, Fig. 1). The subnivean environment is characterized by a much higher number of carabid species compared to the supranivean one (Fig. 1). This is observed in many other insect groups and is usually explained by the role of thermally isolated snow cover that protects the environment from wind and lethal temperatures (Aitchison 2001). Literature data and our own results show that Carabidae are active on the snow surface only from November to January, while subnivean activity occurred during the entire winter season. In general, ground beetles are only accidentally found on the snow cover and because of this, they should be classified as chionoxenes.

In the literature there are almost no data on the effects of weather factors on winter active Carabidae. A study by Weber (1965) suggests that air temperature rising from -2° C to $+6^{\circ}$ C increased activity of *Phyla obtusa* almost eight times. Similar observations were made by the same author for *Trechus quadristriatus*.

Interesting observations were made by Haning et al. (2006), who noted *Calodromius bifasciatus* to be active on tree trunks at -3°C and from -1 to +10°C, with males preferring lower temperatures than females (see also Felix and Van Wielink 2011). For supranivean active carabids, temperature data are known for only four species: *Dromius schneideri* was found at -1°C, *Pterostichus diligens* at +1°C (Frey 1913), *Agonum muelleri* at +2°C (Szulczewski 1947) and *Calathus micropterus* at -2°C (Soszyńska-Maj & Jaskuła unpublished).

Conclusions

Present knowledge on winter active Carabidae from Central and Northern Europe is rather poor. Literature data are mostly from a few old papers, and usually were fragmentary.
In total, 73 species have been recorded as active in winter, including 11 species belonging to 10 genera found on the snow surface, and 66 species from 33 genera being subnivean. Four species were recorded for the first time as snow active and one as a subnivean carabid.

Ground beetles are one of the dominating Coleoptera groups in winter insect assemblage. The community of winter active Carabidae is composed of larvae and adult beetles, and consists of both epigeic species and species active on tree trunks. In general, winter active larvae are representatives of autumn breeders. A comparison of the supranivean and subnivean carabid fauna shows significant differences in species diversity. In the first group the number of species are five times lower than in the latter. It suggests that snow active species appear in supranivean microhabitats only accidentally, but they are known to be winter active in litter or soil environments. They should probably be classified as chionoxenes.

Winter activity of ground beetles decreases in late autumn, is lowest during midwinter and increases in early spring. This might be correlated with weather conditions, especially air temperature. The present state of knowledge suggests that further studies are needed to confirm this hypothesis.

The high proportion of Carabidae in winter communities make this group an important food source in the diet of insectivorous mammals, especially shrews. On the other hand these carabids are predators, hunting springtails and other small winter active invertebrates.

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RESEARCH ARTICLE



Calodromius bifasciatus and other Carabidae on 26 oaktrunks in a nature reserve in the Netherlands

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Abstract

The discovery of *Calodromius bifasciatus* in the nature reserve 'De Kaaistoep', the Netherlands, initiated research on this and related carabid beetles between 2000 and 2006. During this period we investigated the trunks of 26 Pedunculate oaks, mainly during nightly observations, to learn more about arboricolous carabid species. We observed more than 3000 specimens of 24 carabid species. The majority of these species were *Dromius s.l.*, however *C. bifasciatus* dominated the dataset. Our data on phenology clearly show that *C. bifasciatus* is mainly active in winter; it even copulates just above freezing point. Other interesting observations were made as well; for instance the presence of a small sphere at the end of the abdomen and their hiding behaviour at low temperatures. Subsequently, we obtained similar information about other tree dwelling carabid species. In this article we present an overview of all species observed on the trunks, after which we shall focus on the observations made on *Calodromius bifasciatus*.

Keywords

arboricolous, Dromius s.l., Laemostenus terricola, phenology, spheres

Introduction

A decade ago, the discovery of *Calodromius bifasciatus* (Dejean) on the trunk of a small Pedunculate oak (*Quercus robur*) near Tilburg (the Netherlands) was the start of a long term survey of tree trunks in that area. Until its discovery in the Netherlands, *C. bifasciatus* was considered a Western Mediterranean species (Felix & Van Wielink

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2000). Because *C. bifasciatus* turned out not to be uncommon in the area of discovery, research into the biology and ecology of the species was initiated.

A literature survey revealed that occurrence data from Northern France, Italy, Switzerland, Germany and Eastern Europe were based on very old records and could not be checked. Its presence and/or arrival in the Netherlands therefore seems difficult to relate to its currently known occurance. A source area for this species remains unknown. Although *C. bifasciatus* is macropterous, flight observations are unknown. To obtain more insight into its dispersal behaviour, we placed flight interception traps (window traps) near and under trees where this carabid occurs, pitfall traps in the ground near the base of the trunk (but not beyond the outer range of the crown) but we never caught *C. bifasciatus*. This was also the case with a frequently used light trap and a malaise trap in the vicinity.

Subsequently, we concentrated on the trunks themselves to learn more about the behaviour and life cycle of *C. bifasciatus*. During this study we observed many more beetles and other tree-dwelling species (Van Wielink and Felix 2009a,b). Very little is known about the ecology of *C. bifasciatus*, several publications only mention that the species has been found under the bark of dead trees. According to other publications it is a corticolous species (inhabiting bark), with a tendency to lapidicol (living under stones) (Aguiar and Serrano 1995, Ortuño and Torribio 1996). In Algeria it was found in the galleries of *Scolytes* species in branches of cedars and oaks (Mehenni and Bosmans 1994).

In this paper we present information on the biology and ecology of *C. bifasciatus*, as could be gathered by observing and collecting the species from 26 Pendunculate oak trees. Additionally, we provide some results on other observed carabid species of the same tree trunks.

Site description, material and methods

De Kaaistoep

The nature restoration area 'De Kaaistoep' lies immediately west of Tilburg in the south of the Netherlands. It is a former agricultural area, belonging to a waterworks company. The actual research site consists of open arable grasslands on poor sandy soil. This open area is bordered by woodland in the west, north and east. In the area itself there are three large and two small artificial pools, a brook and some patches or rows of deciduous trees and shrubs. Almost in the middle of these grasslands there are two rows of Pedunculate oaks, the trunks of which were investigated. One short row (A) runs from north-north-west to south-south-east and numbers seven oaks. Another, longer, row (B) runs from south-west to north-east and numbers 19 oaks. Some of the trees in row B stand alone, this means that their crowns do not touch other trees. Most of the oaks in row B are bigger and have lower branches than the oaks in row A. The ground around row B is covered with shoots of European elder (*Sambucus nigra*) and American black cherry (*Prunus serotina*), grasses and dead twigs and branches of the trees. Many rabbit holes surround row B. The trunks of row A are more exposed to

the sun and wind than those of row B. In row A the ground around the trunks is only sparsely vegetated with short grasses, a few mosses and only few tree branches lie on the ground. All trunks are covered by lichens and algae and at the base of the trunks mosses are present. The oaks in row A are much more densely covered by lichens than those of row B. All oaks are healthy and undamaged. They stand at various distances from each other, are 15–22 m tall, bear a crown of 10–20 m in diameter and have a trunk girth of 90–230 cm. More details on 'De Kaaistoep' can be found in Felix and Van Wielink (2008).

Sampling the tree trunks

We used a non-standard method to collect carabid beetles from the tree trunks: 'wrapped paper bands' (Fig. 1). The bands consisted of packing paper, longitudinally rumpled and wrapped around the trunk. They were put on two oak trees (on A5, i.e., the fifth tree from the north in row A; and on B6, i.e., the sixth oak from the west of row B). The bands were placed at about 1.6 m above ground level and were operational for four years. Later we installed additional bands around branches of tree A5 at various heights (4, 6 and 7 m high and close to the trunk, and one at 6 m height but at 4 m distance from the trunk). These additional bands were operational for three years. Every 6–8 weeks the bands were inspected by shedding the paper bit by bit over a white plastic tray. While removing the paper bands the bark underneath was carefully inspected and carabid beetles were identified and afterwards often released on the trunk they originated from.

Monitoring the tree trunks at night

During more than six years, we monitored all 26 oaks from the base up to about 3 m height, 144 times at night. For more than two years within that period, the inspections were carried out nearly every week always on the same day (104 times). We started 1 to 6 hours after sunset; early in summer and in relatively late winter. Each visit took 35 to 90 minutes, depending on the number of beetles found. The trunks were illuminated by torch and we counted and noted the carabid beetles and their behaviour. For Dromius s.l. species (which includes Dromius, Calodromius, Paradromius and Philorhizus species), we noted the height and direction on the trunk, observations on their mating and other behaviour, as well as the presence of spheres on the tip of their abdomen (apex). Weather conditions (temperature, direction and strength of the wind, humidity, presence of fog, etc.) were noted as well. The light of the torches used was too bright and disturbed the beetles. They immediately tried to seek a hiding place or even dropped to the ground, so we switched to using LED lights. Again, almost all carabid beetles were released after identification. The circumference of each tree was measured at 1.60 m height, as well as the depth of the clefts in the bark at that height. A more detailed description of these methods can be found in Felix and Van Wielink (2008).



Figure 1. Paper bands at several heights. Photo: Paul van Wielink

Results

Carabid beetles on tree trunks

In total, we observed 3069 specimens of 24 carabids beetle species (Table 1). Of all carabid beetles found in the bands, 87% were *Dromius s.l.* and 17% *C. bifasciatus* (Fig. 2). Of all carabid species noted during nightly observations, 92% were *Dromius s.l.* and 64% *C. bifasciatus* (Fig. 2).

We observed six species of *Dromius s.l.* in and underneath the bands and during the nightly observations: 1718 *Calodromius bifasciatus* specimens (1654 at night and 64 in the bands), 542 *Dromius quadrimaculatus* (377 at night and 165 in the bands),

464 *Calodromius spilotus* (378 at night and 86 in the bands), 43 *Dromius agilis* (41 at night and 2 in the bands), 42 *Paradromius linearis* (38 at night and 4 in the bands) and 14 *Philorhizus melanocephalus* (10 at night and 4 in the bands). It must be noted that these numbers give no reliable indication of population size. Because we seldom collected specimens, many specimens were probably counted several times.

On some trees we always saw more *C. bifasciatus* than on other trees. We counted the number of specimens we saw on every tree. We computed the amount of square meters of a trunk up to 2.5 m of the tree and the average number of specimens per square meter of that part of the trunk, and there was no relation between the circumference of the tree and the number of specimens. We also counted every *Calodromius spilotus* and *Dromius quadrimaculatus* observed. There was no correlation between the numbers of the three carabid species on the separate trees. For results concerning these observations we refer to a previous publication (Felix & Van Wielink 2008). On some trees we saw many of ants (Formicidae) or isopods (Isopoda), and some trees carried more algae, lichens or mosses than others. We never quantified these phenomena, but we have gained the impression that there is also no relation between the abundance of the mentioned species and *C. bifasciatus*.

The four most abundant species *Dromius s.l., C. bifasciatus, C. spilotus* and *D. quadri-maculatus* were also present in the band on a branch at 6 m height and at 4 m from the main trunk but in far lower quantities than in the other bands. All specimens of *D. agilis* were found in row B. Perhaps the sheltered position of the trunks in this row explains this observation.

Phenology of C. bifasciatus and Dromius s.l. species

Calodromius bifasciatus was active on the bark at an air temperature between -3.5 and 17°C, and mostly in the range 4–8°C. The maximum number of specimens we observed on one single evening was 85 on the 20th November and the 27th of December 2003. The temperatures were 8°C and 6°C respectively, the wind was southwest, strength 4 and 3. During both evenings the atmosphere was humid without rain or wet trunks. Hannig et al. (2006) found similar weather preferences for *C. bifasciatus*. The number of *C. bifasciatus* specimens per tree varied considerably: the total number of specimens varied from 20 to 169, with three trees with more than 120 observed specimens. Although the exact numbers are different when taking the area of inspection into consideration (i.e., individuals/m² trunk varied between 4.7 and 34.5), the same trees had the highest numbers. We observed one tree several times during one night; even the presence on one oak in one night at several times in time varied substantially. Also the position on the bark varies substantially (for details see Felix & Van Wielink 2008).

Based on weekly observations at night on the lower 3 m of the trunks during two years we can present the phenology of *C. bifasciatus* (Fig. 3). Its main activity takes place in winter: observation periods November 2003 to January 2004 and December 2004 to February 2005. In summer, this species was almost absent. *Dromius quadrimaculatus* and *C. spilotus* have their optimum from September to March (Fig. 4). *Dromius agilis* was seen in far lower numbers, and practically only from April to September (Fig. 4).



Figure 2. Relative abundance of Carabidae during weekly observations at night (a) and in the bands (b).
(a) Of the 1903 Carabidae observed weekly at night, *Dromius s.l.* (the *Dromius, Calodromius, Paradromius* and *Philorhizus* species mentioned in the graph) accounts for 92% and *Calodromius bifasciatus alone* for 64%.
(b) Of the 373 Carabidae observed in the bands, *Dromius s.l.* accounts for 87% and *C. bifasciatus* for 17%.

Observations on behaviour and biology of C. bifasciatus

During the 144 nightly observations, we noted 63 copula in 1654 *C. bifasciatus* of which there were 46 copula amongst 1219 specimens during the 104 weekly observations. Copula were seen during the whole activity period from October to April, and at temperature ranges of -1 to 17°C. During the evening, eight copula were seen; 21%



Figure 3. Phenology of *Calodromius bifasciatus*: relative presence in 29 consecutive months. Relative presence: the number of beetles per month divided by the number of nightly observations during that month (the number of nightly observations varied between 2 and 4 per month).

of the observed specimens. The temperature that evening was 8°C and humidity was high. Also *C. spilotus* was seen copulating in winter.

We never found larvae, neither on the trunks at night, nor in the bands. However we found two freshly emerged specimens of *C. bifasciatus* on a trunk on the 24th August 2001, indicating recent pupation at this time and location.

Observing C. bifasciatus, we noticed 'spheres' on the abdomen of females (Fig. 5). These spheres were different in size, from about 0.3 to 1.0 mm. Their outside is granulated with lichens or algae and the inner side is very smooth. These spheres are probably egg-cases (see discussion). We collected a few females with spheres and almost always they dropped these structures rapidly. We noted 69 females with a smaller or greater sphere during the 144 nightly observations. In the 104 weekly observations there were 60 of them, about 5% of the observed specimens. The spheres were almost exclusively seen from November to May. A few times we even saw matings while the female was bearing a sphere. The spheres were seen during nights when the temperature was between 3 and 15°C, so within the normal range of activity and copula. We also noted behaviour that indicated how C. bifasciatus makes these spheres. We found C. bifasciatus specimens biting algae or lichens, then stepping forward and rubbing the tip of the abdomen over the spot where they had just bitten. While biting, the abdomen was directed upwards and the hind legs were stretched. While rubbing their abdomen against the lichens, the posture was reverse. Sometimes the specimens had a sphere on their abdomen, sometimes they did not. When we saw this behaviour, the temperatures ranged from 3 to 13°C and air humidity was usually high.



Figure 4. Phenology of *Calodromius spilotus*, *Dromius quadrimaculatus* and *D. agilis*: relative average presence per month. Relative presence: see Fig. 3. Blue: *C. spilotus*, Red: *D. quadrimaculatus*, Yellow: *D. agilis*.

Discussion and conclusions

Carabid beetles on tree trunks

Dromius s.l. species were by far the most abundant Carabidae on the trunks. In addition, 23 other species of Carabidae were observed, most of them in very low numbers (Table 1). Some genera were often found on the trunk, whether in sight at night, or in/underneath the paper bands: Carabus s.l. (especially Carabus problematicus) Leistus s.str. (especially Leistus spinibarbis), Nebria s.str. and Laemostenus terricola. With some of these species, it was previously unknown that they climbed trees. For example, Paradromius linearis and Philorhizus melanocephalus were known as 'strictly ground dwelling' (Turin 2000). One of the most abundant other Carabidae seen on the trunks (and almost exclusively on those of row B) was Laemostenus terricola. In the Netherlands this species is known especially from sandy, hilly, warm regions. In the northern parts of its distribution area it is often found in cellars, but also in rabbit holes and underneath stones, in woods and heathlands. It is not clear what the relation is between its presence in woods and heaths and the presence of mammal holes. Several times we saw specimens walking from the deep of a rabbit hole, close to the trunk of an oak, towards the entrance. As soon as they were illuminated, they ran back, as in panic, into the darkness of the rabbit hole. We saw 77 specimens at night, especially in summer, sometimes high up on a tree trunk. We also noticed individuals on the ground between



Figure 5. Abdomen with sternites of *Calodromius bifasciatus* with a sphere. Note the granulate outside of the sphere. Photo: Ron Felix.

tree trunks and nearby rabbit holes. The times we saw them were 1.5–2.5 hours after sunset at temperatures between 10 and 18°C. We assume that this species rests in rabbit holes and forages in the trees.

Biology of C. bifasciatus and other Dromius s.l. species

Dromius s.l. species are flat (but relatively broad) and are built to hide in very narrow places. It probably moves all over the trees when it is dark and during daytime it stays in the lower parts, where hiding is easier. Trunks with (at least partially) a structure of many fine and narrow clefts (in the lower parts) would be more appreciated by *C. bi-fasciatus* and other tree-living *Dromius s.l.* species than trunks with deep, but open and wide clefts. Scheffler (1997) found that *C. spilotus* prefers places in which it experiences pressure: aggregation experiments showed that more specimens crawl underneath flat filter paper on the bottom of Petri dishes, than under folded paper. This also explains why we found more specimens underneath than within the paperbands.

Calodromius bifasciatus seems to avoid contact with the ground. We hardly ever found them in pitfall traps that were placed in the close surroundings of the investigated trees and we did not find them in the soil after digging at the foot of the tree either. Once we observed an agglomeration at the base of a tree. This agglomeration was observed during a very cold, freezing night, and was located about 1 cm below the soil surface, but it was still on the bark. On the other hand, Van Malderen (2007) mentions that *C. bifasciatus* can be found by sifting leaves and dead wood underneath oaks and poplars.

Species	Nightly inspection	In/behind bands		
Carabus problematicus Herbst, 1786	18	2		
Carabus nemoralis Müller, 1764	5	-		
Leistus rufomarginatus (Duftschmid, 1812)	4	-		
<i>Leistus spinibarbis</i> (Fabricius, 1775)	44	1		
Leistus ferrugineus (Linnaeus, 1758)	8	1		
Nebria brevicollis (Fabricius, 1792)	2	3		
Nebria salina Fairmaire & Laboulbene, 1854	-	9		
Nebria brevicollis/salina	13	-		
Notiophilus rufipes Curtis, 1829 (larf)	1	-		
Trechus obtusus Erichson, 1837	1	-		
Bembidion tetracolum Say, 1823	1	-		
Pterostichus niger (Schaller, 1783)	1	2		
Calathus melanocephalus (Linnaeus, 1758)	-	1		
Calathus rotundicollis Dejean, 1828	1	-		
Laemostenus terricola (Herbst, 1784)	77	27		
Limodromus assimilis (Paykull, 1790)	1	-		
Agonum thoreyi Dejean, 1828	1	-		
Bradycellus harpalinus (Serville, 1821)	9	-		
Bradycellus verbasci (Duftschmid, 1812)	1	-		
Dromius agilis (Fabricius, 1787)	41	2		
Dromius quadrimaculatus (Linnaeus, 1758)	377	165		
Paradromius linearis (Olivier, 1795)	38	4		
Calodromius bifasciatus (Dejean, 1825)	1654	64		
Calodromius spilotus (Illiger, 1798)	378	86		
Philorhizus melanocephalus (Dejean, 1825)	10	4		
larvae undet	8	4		
Total number	2694	375		

Table 1. Survey of species and numbers of Carabidae observed at nightly inspections and in or behind bands on oak trees.

The common opinion seems to be that *Dromius s.l.* species are not seen on the lower parts of the tree in summer, because they are high up in the crown (Scheffer 1997, Irmler 1998, Simon 2001, Hannig et al. 2006). Temperatures should be lower there and humidity higher and there should be a greater availability of food in summer. Irmler (1998) installed window traps in forests at different heights and found *D. agilis* and *D. quadrimaculatus* more often in higher window traps than in lower ones in spring, summer and autumn. However, this only means that these species fly at these heights, but this does not mean that they stay high up in the trees in summer. Maybe these species need a specific height to fly away. In contrast to these studies, we did find *Dromius s.l.* species also in summer, in lower parts of trees. Our impression is that in summer clefts in the trunks, especially on shaded

sides or on the north side at the bottom 2-3 m, are humid and cool too. Therefore the availability of food should be sufficient on the lower parts of the trunks as well. We suggest that the niche of *C. bifasciatus* is determined by the presence of suitable clefts. In the crown and thinner branches clefts are hardly to be found. When threatened or disturbed by light, *C. bifasciatus* immediately seeks shelter in the clefts of the trunk. These shelter opportunities seem harder to find high up in the trees where trunk and branches have no clefts. Furthermore, our bands around the trunks and branches provided no indication for migration upward to the tree crown in summer. There is no direct evidence for the actual presence of *C. bifasciatus* or other *Dromius s.l.* species high up in the tree crown in summer. The absence of *C. bifasciatus* could simply mean that only a few survive the warmer part of the year, if any. We assume that most adults of *C. bifasciatus* die before summer.

C. bifasciatus reproduction

The behaviour of biting algae and sphere building has not been recorded before in Europe. Will (1998) extensively describes exactly the same behaviour prior to oviposition of *Dromius piceus* (Dejean) in Ithaca, New York, USA. Casale et al. (1996) also mention 'egg-cases' for *Dromius meridionalis* and *D. quadrimaculatus*. We did not find eggs in the spheres of *Dromius s.l.* species; all were empty. Perhaps the egg(s) is inserted into the sphere just before it is dropped. In this respect the spheres should probably be named 'pre-ootheca'. We noticed spheres in almost every month, but predominantly in winter. Depending on the developmental time of the embryo and possible dormancy of the young larva, larvae could be active from early winter and adults may subsequently appear from August to late summer. This is in line with the discovery of two freshly emerged adults in August. Although we never found larvae, we assume that they live on the trunks as well and not on or in the ground. This assumption is also based on the observations of Casale et al. (1996) of *D. meridionalis* larvae on broad-leaved lime trees (*Tilia platyphyllos*) in a busy street where the ground surface was paved up to the trunk.

During the nightly observations many copula of *C. bifasciatus* were seen during the whole activity period from October to April, during nights with temperatures ranging between -1 to 17 °C. Nightly observations on tree trunks, especially in autumn, winter and spring, can thus be very rewarding in observing ecological phenomena of corticolous Carabidae.

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Historical ecology meets conservation and evolutionary genetics: a secondary contact zone between *Carabus violaceus* (Coleoptera, Carabidae) populations inhabiting ancient and recent woodlands in north-western Germany

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Abstract

Only very few cases have documented that an increase in connectivity after a period of fragmentation in ecological time has had an effect on the distribution, genetic structure and morphology of stenotopic species. In this study we present an example of clinal variability in a woodland ground beetle as a result of changes in the connectivity of a landscape during the last two centuries. The study area hosts both the nominate form *C. violaceus* s. str. and the subspecies *C. v. purpurascens*, which is ranked as a distinct species by some authors. We studied 12 *Carabus violaceus* populations from a 30 km transect of ancient and recent forests in north-western Germany. We analyzed three polymorphic enzyme loci, classified the elytron sculpture and measured the shape of the aedeagus tip of the specimens. *C. violaceus* showed secondary gradients both in allozyme markers and morphometric characters in our study area. A genetic differentiation of 16% between the populations is high but lies within the range of intraspecific variability in habitat specialists of the genus *Carabus*. Populations had no significant deficit of heterozygotes. We found many hybrid populations in terms of morphological properties. This study highlights the conservation value of

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ancient woodland and the consequences of landscape connectivity and defragmentation on the genetic setting of a ground beetle. Moreover, it shows that differences in the external shape of male genitalia do not prevent gene flow within the genus *Carabus*. Thus, the establishment of species status should not exclusively be based on this property.

Keywords

fragmentation, afforestation, allozymes, morphometrics, *Carabus violaceus purpurascens*, hybridization, hybrid zone

Introduction

The history of a landscape has a tremendous effect on both the species composition of communities and assemblages on the one hand and the genetic variability of species on the other. This is especially true for woodlands, which have become highly fragmented since the Middle Ages in large areas of north-western Europe including Britain, southern Scandinavia, Belgium, the Netherlands and the lowlands of northern Germany (Desender 2005). Against this background, ancient woodlands, i.e. primary and ancient secondary woods (semi-natural stands and plantations), originating before a threshold date linked to the availability of sufficiently good maps, have a special ecological and historical significance compared to recent woodlands (e.g. Peterken 1993; Rackham 2003). While 1600 AD is used to define ancient woodland in England (Peterken 1977), the first maps available for north-western Germany are from the end of the 17th/beginning of the 18th century (e.g. LeCoq 1805), so that woodlands existing since that time are considered ancient in the sense of Rackham (2003). For northwestern Europe, several studies have demonstrated that ancient woodlands host species that do not occur in recent woodlands (for plants: e.g. Peterken 1974; Hermy et al. 1999; Wulf 2004; for animals: e.g. survey in Peterken 1993; Assmann 1999; Desender et al. 1999).

At the genetic level some studies have shown a strong differentiation between remnants of stenotopic woodland species in ancient woodlands that were at least in former times isolated from one another (e.g. Assmann and Günther 2000; Desender et al. 2002; Desender et al. 2005; Drees et al. 2008). Only very few cases are known that have documented that an increase in connectivity after a period of fragmentation in ecological time has had an effect on the distribution, genetic structure and morphology of stenotopic woodland species (Hale et al. 2001; Hale and Lurz 2003; Drees et al. 2008).

In this study we present an example of clinal variability as the result of an increase in the connectivity of a landscape during the last two centuries. We selected a network of woodlands in north-western Germany that stretches between the only two ancient woodland remnants in the region, and studied the genetic variability and differentiation of the woodland specialist *Carabus violaceus* Linné 1758. Due to its flightlessness, this ground beetle has a low power of dispersal. We used two sets of markers for the analysis, morphometric characters and allozymes, in order to determine typical features of the source populations and their geographic distribution within the contact zone. The results are of increased significance, as the study area hosts not only the nominate form but also *C. violaceus purpurascens* Fabricius, 1787, which is ranked as a distinct species by some authors (cf. Jeannel 1941; see also Turin et al. 2003). The existence of these two taxa, however, is assumed to go back at least to range changes and isolation during glacial periods (Assmann and Schnauder 1998), like in many European organisms with hybrid zones in Central Europe (e.g. Hewitt 1999). Thus, the amount of genetic differences between both taxa, which is not the main focus of our study, is likely to be the result of a time span of much more than 200 years.

Material and Methods

Study area

The study area is located northwest of Osnabrück in the morainic hill country between the convent of Börstel and Bramsche (Fig. 1). About 200 years ago the region had only two remnants of woodlands according to the geodesic survey of north-western Germany (LeCoq 1805). These are henceforth called "Börsteler Wald" (north) and "Gehn" (south). The historical situation of the study region is well documented. Excessive heathlands covered the area between the two remnants of (now ancient) woodlands about 200 years ago (Hesmer and Schroeder 1963; Pott and Hüppe 1991). Changes in the socio-economic situation in north-western Germany resulted mainly in the afforestation of heathland and other nutrient poor habitats since ca. 1800 (Hesmer and Schroeder 1963; von Oheimb et al. 2008), thus creating a network of recent woodlands that have connected the ancient woodlands Börsteler Wald and Gehn. This is in contrast to many other European countries with temperate climate where the area of woodlands has steadily decreased (Desender 2005). In addition, the forests are connected by a number of hedgerows established over the last two centuries. A comparison of the old and recent situation is exemplified by sections of the original maps in Assmann and Kratochwil (1995: 290 and 291). We studied 466 specimens from 12 populations that were sampled with baited pitfall traps between July and September 1999.

Study species

Carabus violaceus is a flightless woodland species which, in north-western Germany, is more frequently recorded from ancient than from recent woodlands and which is sometimes found in open habitats adjacent to woodlands (Blumenthal 1961; 1965; Dülge 1992; Assmann and Schnauder 1998; Assmann 1999; Falke et al. 2000; Eggers et al. 2010). In the Netherlands, approximately 4 km of open peaty grassland



Figure 1. *C. violaceus* populations studied and proportion of specimens with different elytron sculptures (pie charts). White sections indicate the frequencies of smooth elytra, black sections indicate the frequencies of more than three striae per elytron, and grey sections indicate the frequencies of intermediate phenotypes, i.e. class "1". Numbers next to the pie charts indicate population number followed by sample size in brackets. The location of the study area is indicated as a white square on the map of Germany. Woodlands in the study region northwest of the town of Bramsche according to TK 50 3512 Bramsche (Landesvermessungsamt Niedersachsen 1998) are presented as striped patches. Size and position of ancient woodlands (black patches) are taken from the map by LeCoq (1805). In this study, these are called "Börsteler Wald" (in the north) and "Gehn" (in the south). White patches within woodlands indicate openings. Hedges are not shown.

were found to prevent *C. violaceus* (subspecies *purpurascens*) from colonizing neighbouring forests, so that the beetle is regarded as highly sensitive to fragmentation of forests (cf. Blumenthal 1981). In our study area, *C. violaceus* occurs in both ancient and recent woodlands.

C. violaceus is an extensive, manifold Euro-Siberian species complex with numerous forms that display slight morphological differences, for example with regards to elytral sculpture, colour and body proportions, and some of which are of doubtful status. Turin et al. (2003) gave an extensive overview regarding current knowledge and discussions on the various forms and their geographic distributions. Two major groups, *C. violaceus* s. str. and *C. v. pupruascens*, are distinguished whose morphological divergence is particularly distinct. The distribution of *C. v. purpurascens* extends from Germany, Austria and Switzerland westwards to north-western Spain. *C. violaceus* s. str. reaches its southwestern distribution in Germany and in parts of the northern Alps and has a Central European to Northern European range up to the British Isles, Scandinavia, the Russian plain close to Moscow, Romania, Bulgaria and Hungary. Combined distribution maps including chorological and taxonomical discussions can be found in Blumenthal et al. (1977) and Assmann and Schnauder (1998). Contact zones exist at least in Germany, Austria and Switzerland.

C. v. purpurascens and the nominate form of *C. violaceus* exhibit hybrid populations in north-western Germany (Assmann and Schnauder 1998) and Switzerland (Marggi 1992) that have so far been determined on the basis of the taxonomically relevant differences in elytral sculpture and aedeagus tips. While *C. violaceus* s. str. has a broad aedeagus tip and smooth elytra, *C. v. purpurascens* has a slender aedeagus tip and elytra with distinct ridges (e.g. Henseler 1940; Blumenthal 1976). Isolated populations of *C. violaceus* s. str. can be found at least in the Eifel and in the Black Forest (Assmann and Schnauder 1998).

Allozyme analysis

The abdomina of *C. violaceus* (without guts and pygidial glands) were homogenized in 600µl 0.15M Tris-Citrate buffer (pH 7.8, 30% Sucrose, 1% Triton-X-100). After centrifugation, the homogenates were applied to vertical polyacrylamide slab gels and electrophoresis was run at 3°C. Both the mixture of the polyacrylamide slab gels and the staining was performed according to Murphy et al. (1990) with slight modifications (see Appendix 1). From seven enzyme loci screened (AAT, EST-X, GPI, IDH, MPI, PGM, 6-PGD) three were polymorphic and showed interpretable patterns: glucose-6-phosphate isomerase (GPI, Enzyme Commission number 5.3.1.9), mannose phosphate isomerase (MPI, EC 5.3.1.8) and tissue esterase (EST-X, EC 3.1.1.1). Allozymes were numbered in order of increasing anodal migration, and samples were run side by side for comparison (Ayala et al. 1972).

Allele frequencies, observed heterozygosity (H_o) and mean gene diversity (H_E) (Nei 1978) were estimated for each locus in each sample using POP100GENE (Piry and Bouget 1999). Tests for Hardy-Weinberg equilibrium were performed with GE-NEPOP 4.0 (Raymond and Rousset 1995). Data were tested with a probability test (exact HW test) using the Markov chain method. Multiple-testing was corrected for

false discovery rate (BL procedure, Benjamini et al. 2001). Tests for genotypic linkage disequilibrium were carried out using FSTAT, V 2.9.3 (Goudet 1995). FSTAT also yielded F_{ST} estimates (theta, Weir and Cockerham 1984) and pairwise F_{ST} estimates.

Data were investigated for the occurrence of clinal variation by spatial autocorrelation analysis implemented in SGS ver. 1.0 d (Spatial Genetics Software, Degen et al. 2001). This approach tests whether the observed population genetic measure (such as allele frequency) at one sampling site is dependent on the respective measure from samples at neighbouring localities (Barbujani 2000; Manel et al. 2003). A set of genetic distance values increasing from significantly negative to significantly positive scores describes a cline, while values increasing from significantly negative at short distances to insignificant at large distances indicate a pattern of isolation by distance (Chikhi et al. 1998; Barbujani 2000). 6 km-intervals were used as distance classes (distance intervals similar to those chosen for *Poecilus lepidus* by Drees et al. 2010), so that we had five distance classes with between six and 20 data pairs. Confidence intervals were calculated in SGS by running 1000 permutations.

Morphometric analysis

After material had been taken for allozyme analysis, the animals were placed in Scheerpeltz solution (70% ethanol, 5–10% acetic acid, 15–20% aqua dest.). Male genitalia were prepared and mounted on cards. The remains of the exoskeletons were pinned to dry and deposited in the entomological collection of Thorsten Assmann, Bleckede (to be donated to the Zoological State Collection, Munich).

Two morphological properties that are relevant for taxonomic distinction between both forms of *C. violaceus* were analyzed. Since measurements of the aedeagus tips provide suitable characteristics to distinguish *C. violaceus* s. str. and *C. v. purpurascens* (Assmann and Schnauder 1998), we measured the maximum width (AedMax) and minimum width (AedMin) of the aedeagus tip (Fig. 2). Measurements were taken using a stereomicroscope with 25 times 4.0 (ocular times lens) magnification. To keep measurement error at a minimum, parameters for each specimen were measured twice and the termini of the measured lengths were in the same focal plane. Descriptive statistics were performed with STATISTICA Ver. 7.1. We conducted a Kruskal-Wallis-Anova to test for equality of population medians among the groups. Moreover, all populations were tested against each other using the Mann-Whitney-U-test to evaluate differences in aedeagus shape. Multiple testing was corrected for false discovery rate (BL procedure, Benjamini et al. 2001).

As a second morphological character, we used elytron sculpture to classify individuals into the following categories: Class "0" for animals with typically smooth elytra as in the nominate form of *C. violaceus*; class "1" for individuals with three striae per elytron; and class "2" for individuals with more than three striae per elytron – as in typical specimens of *C. v. purpurascens*.



Figure 2. Aedeagus tip of *C. violaceus*. | Maximum aedeagus width (AedMax), 2 minimum aedeagus width (AedMin), and 3 preputial field.

Results

Allozyme analysis

A total of 21 alleles were scored at three loci across the 12 populations studied. The number of alleles detected at each locus ranged from five (MPI) to nine (GPI). Allele frequencies, expected and observed heterozygosities and F_{IS} values are shown in Table 1. No significant deviations from Hardy-Weinberg equilibrium were observed for any of the populations or loci after correcting for multiple tests (nominal level of p = 0.05). There seems to be a tendency of populations to display a positive F_{IS} , i.e. a deficit of heterozygotes. However, after correction for multiple testing by Fstat (nominal level of p = 0.05, 720 randomizations), no significant deficit or excess of heterozygotes were found. No significant linkage disequilibrium was found, thus the studied loci can be interpreted as independent markers.

The overall F_{ST} value was 0.160 and ranged from 0.127 (GPI) to 0.201 (EST-X). Pairwise population differentiation in F_{ST} between the 78 pairs in our study ranged between 0.011 and 0.501, with a significant differentiation for 54 population pairs after standard Bonferroni corrections (Table 2).

Spatial genetic structure analysis revealed gradients in allele frequencies in the EST-X locus, in the MPI locus, and in the whole sample (Fig. 3, Table 3).

Morphometric analysis of the elytron sculpture

The vast majority of beetles in the northernmost populations 1 to 4 and population 9 showed the typical smooth elytra of the nominate form, while more than half of the beetles in each of the three southernmost populations (10 - 12) showed the elytron sculpture typical of *C. v. purpurascens* (Fig. 1). No specimens of *C. v. purpurascens* were found in the very north and no specimens of *C. v. violaceus* in the very south. The northernmost indi-

Alleles	Populations											
	1	2	3	4	5	6	7	8	9	10	11	12
EST-X												
Ν	70	64	68	46	54	92	22	38	58	48	52	6
1	0	0	0.015	0.022	0.259	0.413	0.091	0.211	0.052	0.042	0.173	0
2	0.714	0.875	0.824	0.783	0.574	0.337	0.182	0.342	0.707	0.146	0.154	0.333
3	0.229	0	0.015	0.043	0.074	0	0	0	0	0	0	0
4	0.057	0.125	0.147	0.087	0.056	0.207	0.682	0.395	0.103	0.354	0.308	0.5
5	0	0	0	0	0	0.011	0	0	0.086	0.25	0	0
6	0	0	0	0.065	0.037	0.033	0.045	0.053	0.052	0.208	0.327	0.167
7	0	0	0	0	0	0	0	0	0	0	0.038	0
Ho	0.257	0.25	0.265	0.348	0.37	0.609	0.545	0.684	0.448	0.5	0.462	0.333
H _E	0.441	0.222	0.304	0.382	0.604	0.679	0.515	0.698	0.485	0.762	0.758	0.733
F _{IS}	0.420	-0.127	0.132	0.090	0.392	0.105	-0.062	0.021	0.077	0.348	0.396	0.600
GPI												
Ν	76	96	86	80	72	114	28	48	56	70	84	100
1	0	0	0	0	0	0.009	0	0	0	0	0.024	0
2	0	0	0.012	0	0.028	0.018	0	0.083	0	0.043	0.06	0.07
3	0	0	0	0	0	0	0	0	0	0.071	0	0
4	0.263	0.135	0.093	0.225	0.347	0.377	0.536	0.208	0.304	0.257	0.417	0.42
5	0	0	0.058	0.05	0.097	0.096	0	0.063	0.071	0	0.012	0.04
6	0	0	0	0	0	0	0	0	0	0	0	0.01
7	0.697	0.813	0.767	0.65	0.25	0.254	0.179	0.25	0.196	0.414	0.286	0.21
8	0.013	0.01	0.047	0.075	0.278	0.246	0.286	0.396	0.357	0.214	0.202	0.25
9	0.026	0.042	0.023	0	0	0	0	0	0.071	0	0	0
Ho	0.421	0.375	0.372	0.375	0.611	0.649	0.5	0.667	0.607	0.714	0.786	0.78
H _F	0.449	0.323	0.401	0.525	0.74	0.729	0.622	0.742	0.745	0.72	0.708	0.718
F	0.064	-0.163	0.072	0.289	0.176	0.111	0.202	0.104	0.188	0.008	-0.111	-0.088
MDH												
Ν	76	84	84	80	64	108	28	44	56	68	70	66
1	0	0	0	0	0.016	0	0	0	0.161	0.088	0	0.045
2	0	0	0	0	0.047	0.019	0.036	0.182	0.054	0	0.029	0.03
3	1	1	1	0.988	0.906	0.981	0.964	0.818	0.75	0.868	0.714	0.682
4	0	0	0	0	0	0	0	0	0.018	0.044	0.257	0.242
5	0	0	0	0.013	0.031	0	0	0	0.018	0	0	0
Ho	0	0	0	0.025	0.188	0.037	0.071	0.364	0.429	0.206	0.371	0.576
H _F	0	0	0	0.025	0.178	0.037	0.071	0.304	0.416	0.241	0.429	0.481
F _{IS}	NA	NA	NA	0.000	-0.054	-0.010	0.000	-0.200	-0.032	0.148	0.136	-0.202
All loci												
Mean H _o	0.226	0.208	0.212	0.249	0.39	0.432	0.372	0.572	0.495	0.473	0.54	0.563
H _o SD	0.212	0.191	0.192	0.195	0.212	0.342	0.262	0.18	0.098	0.255	0.218	0.224
Mean H _r	0.297	0.182	0.235	0.311	0.507	0.482	0.403	0.582	0.549	0.574	0.632	0.644
H _F SD	0.257	0.165	0.209	0.258	0.293	0.386	0.292	0.241	0.174	0.289	0.177	0.142
F _{IS}	0.241	-0.148	0.098	0.200	0.235	0.105	0.078	0.018	0.100	0.178	0.148	0.168

Table 1. Diversity of allelic variation. \mathbf{N} = gene number investigated per sample and per locus; \mathbf{H}_{o} = observed heterozygosity; \mathbf{H}_{E} = expected heterozygosity; \mathbf{F}_{IS} = inbreeding coefficient according to Weir and Cockerham (1984); \mathbf{NA} = no estimate owing to monomorphic sample.

Table 2. Significant genetic differentiation (\mathbf{F}_{sT}) between population pairs after standard Bonferroni correction. * indicates a nominal level of p < 0.05; n.s., not significant.

	Pop2	Pop3	Pop4	Pop5	Pop6	Pop7	Pop8	Pop9	Pop10	Pop11	Pop12
Pop1	n.s.	*	n.s.	*	*	*	*	*	*	*	*
Pop2		n.s.	*	*	*	*	*	*	*	*	*
Pop3			n.s.	*	*	*	*	*	*	*	*
Pop4				*	*	*	*	*	*	*	*
Pop5					n.s.	*	n.s.	*	*	*	*
Pop6						n.s.	n.s.	*	*	*	*
Pop7							n.s.	*	*	*	n.s.
Pop8								*	*	*	*
Pop9									*	*	*
Pop10										*	n.s.
Pop11											n.s.





Figure 3. Correlogram showing the result of spatial autocorrelation analysis at three allozyme loci. Genetic distances D (Nei 1972) are indicated for the population pairs of the respective distance classes (squares). Dashed lines show the 95% confidence interval (1000 permutations) under the null hypothesis of spatially random differentiation. Significant deviations from the mean are indicated by filled squares (p < 0.05).

vidual classified as *C. v. pupurascens* according to elytron sculpture is one specimen found in population 4, while the southernmost individual classified as *C. v. violaceus* is one specimen from population 10. All populations contained varying amounts of intermediate individuals of class "1" and, with the exception of population 9, changes in the proportions of different elytron classes are more or less gradual between the ancient woodlands.

Table 3. Spatial autocorrelation analysis of genetic variation at three allozyme loci (multi- and singlelocus analysis) in the *Carabus violaceus* populations studied. D values indicate the mean genetic distance observed of samples within each distance class. –, D significantly lower; +, D significantly greater than the mean genetic distance over all distance classes. ***p < 0.001; **p < 0.01; *p < 0.05; n.s., not significant.

Locus	Distance class [km]								
	0–6	6–12	12–18	18–24	24-30				
Pairs of data	16	20	14	11	7				
all loci	0.086 (- ***)	0.171 (n.s.)	0.196 (n.s.)	0.206 (n.s.)	0.326 (+ **)				
EST-X	0.236 (- *)	0.411 (n.s.)	0.536 (n.s.)	0.657 (n.s.)	0.982 (+ **)				
GPI	0.094 (- **)	0.307 (n.s.)	0.346 (n.s.)	0.285 (n.s.)	0.384 (n.s.)				
MPI	0.014 (-*)	0.015 (n.s.)	0.030 (n.s.)	0.033 (n.s.)	0.062 (+ **)				

Morphometric analysis of the aedeagus tip

Both the maximum width and the ratio of maximum width to minimum width show significant differences among population medians (AedMax: H(11, N = 220) = 71.157 p < 0.001; AedMax/AedMin: H(11, N = 219) = 22.737 p = 0.019). The pattern of AedMax is very similar to that of the elytron properties. The maximum width of the genital tip is generally highest in populations adjacent to the northern ancient woodland Börsteler Wald, which is characteristic of C. v. violaceus, and smallest in one of the populations close to the southern ancient woodland Gehn, which is characteristic of C. v. purpurascens. Several population comparisons between these two groups display significant differences (Fig. 4). However, the highest and lowest medians of AedMax are not found in the populations directly next to the ancient woodlands, but in populations 4 and 10, respectively, each of which had one specimen with elytron sculpture belonging to the respective other form. Again, we find intermediate values in the forests between the northernmost and southernmost ancient forests, but the overlap of ranges and medians with either populations to the north and to the south is quite high. While the median of AedMax in population 9 is strikingly similar to the medians in the northernmost populations, the median of AedMax/AedMin of population 9 is significantly different from otherwise very similar population 1 (p < 0.05) as AedMin is wider in this population. No other significant difference between populations was found concerning AedMax/AedMin.

Discussion

The contact zone

Carabus violaceus shows clear gradients both in allozyme markers and morphometric characters in our study area. Clinal variability can be caused by adaptation to geographically changing environmental conditions and by secondary contacts. In the first case, selection is the driving force to create specific patterns of genetic differentiation (e.g. Sezgin et al. 2004; Case et al. 2006). Secondary gradients are the result of



Figure 4. Maximum width of the aedeagus tip **A** and the quotient of maximum and minimum width of the aedeagus tip **B** are plotted for each population. Boxes display 25–75%- quartiles and bars indicate medians. Whiskers show the total range of values without outliers. Outliers are indicated as circles and extreme outliers as diamonds. Numbers of measured individuals per population are shown in brackets. Pie charts show frequencies of elytral sculpture classes "**0**" (white), "**1**" (grey), and "**2**" (black) in each population. Significant differences between populations are indicated by the lines marked with asterisks.

evolutionarily neutral processes and describe the situation of a contact zone, which developed after populations had differentiated in disjunct areas. This kind of gradient is a consequence of both range expansion and gene flow (Endler 1977; Hewitt 1988; Kontula and Vainola 2004).

The gradients found in C. violaceus stretch across an area of recent woodlands, which developed during the last two centuries. Only the outer woodlands are ancient and had the potential to host the woodland restricted beetle during the Middle Ages and early modern times. It is likely that C. violaceus survived the period of woodland devastation in the ancient woodlands Börsteler Wald and Gehn. Final confirmation that both these areas hosted the source populations for the northern and southern set of characters is still needed. The nearest other potential refuges (ancient woodlands) that are inhabited by C. violaceus are located several kilometres south and southeast of Bramsche (e.g. Wiehengebirge, Gries et al. 1973; Alt Barenau, Assmann 1999). To the north, there used to be a large peat bog surrounding the Börsteler Wald and there is a gap of at least 20 km in the distribution of C. violaceus (Gersdorf and Kuntze 1957; Assmann and Schnauder 1998; Assmann 1999). The existence of a different source population at a greater geographic distance cannot totally be ruled out. However, since the area between Börsteler Wald and Gehn was not forested about 200 years ago, the gradients must therefore be secondary. Thus, our study (1) highlights the conservation value of ancient woodland and the consequences of landscape connectivity and defragmentation (sensu Hale et al. 2001) on the genetic setting of a ground beetle and (2) yields insights into the evolutionary biology of external male genitalia, gene flow and species delineation.

A stenotopic woodland ground beetle benefits from habitat defragmentation

Numerous studies have dealt with habitat fragmentation at different levels from populations to whole communities. In general, habitat fragmentation has led to genetic differentiation and extinction processes at the population level and is discussed as one of the driving forces for the loss of species worldwide (Noss et al. 2006; Allendorf and Luikart 2007). Corridors have been discussed as a concept to overcome the problems of habitat fragmentation for some decades (Chetkiewicz et al. 2006), but only a few studies have been able to demonstrate positive outcomes in terms of recovering lost distribution areas or range expansion or recolonizations (Hale et al. 2001; Davies and Pullin 2007).

Our study provides a case of colonization as a result of increased connectivity by means of hedges and afforestation – even though this may not have been the major aim of anthropogenic landscape changes. This is an encouraging example for nature conservation, which generally aims to purposefully reconnect fragmented landscapes. The gradients detected for *C. violaceus* cover a distance of approximately 30 kilometres, which is similar to the geographic distances between the postulated source populations of *Carabus auronitens* in the Westphalian Lowlands, NW-Germany, as revealed by both

allozymes and microsatellites (Drees et al. 2008). In this species, secondary clines have also developed in a comparable time frame after recolonization of a formerly devastated area. In case of *C. auronitens* there is ample evidence that gene flow still exists today (Drees et al. in prep.). Such evidence is strongly dependent on landscape connectivity and history (Desender 2005). In landscapes with more fragmented habitats, where corridors such as hedgerows or small woodlands which can function as stepping stones are lacking, the same species shows strongly differentiated populations without any evidence of recent gene flow (e.g. *C. violaceus* in Switzerland: Keller and Largiadèr 2003; Keller et al. 2004; *C. auronitens* in Belgium: Desender et al. 2002).

Excessive gene flow despite differences in aedeagus shape

Elytral sculpture, aedeagus tips and allozymes show that strongly differentiated populations of *C. violaceus* survived forest destruction in ancient woodlands within (or close to) the northern and southern edge of the study range. Our results suggest that *C. violaceus* s. str. survived in the north, while *C. v. purpurascens* survived in the south of the study area. These refuges correspond to the overall geographic distribution of the two subspecies (Assmann and Schnauder 1998; Turin et al. 2003).

Elytral sculpture is especially well suited for an unambiguous distinction between both forms, whereas the width of the aedeagus shows significantly differentiated groups, but is a more or less continuously or clinally varying property in the populations. We found many hybrid populations with regards to both properties. Also Assmann and Schnauder (1998) found hybrid populations where numerous individuals showed intermediate characters concerning elytral sculpture and aedeagus shape (two populations were from our study region).

Identifying typical or exclusive alleles for either *C. violaceus* form is difficult, as the studied loci generally show clinal variation and as many alleles can be found in populations 1 to 4 as in populations 10 to 12. However, it is likely that the northern refuge population was monomorphic for MDH allele "3", while the Est-X allele "6" probably originated from a southern population (Table 1). The overall F_{ST} value of 0.160 is considerable and shows a fairly high genetic differentiation between the populations in comparison to other organisms studied earlier in this respect, especially with regards to the small geographic scale of the study area (Ward et al. 1992). However, this value lies within the range of "normal" intraspecific variability in habitat specialists of the genus *Carabus* (cf. Matern et al. 2009).

The shape of the aedeagus tip is not only used for taxonomic distinction between different carabids, but also for a justification of species rank (Assmann et al. 2008). Some forms of the *C. violaceus* complex already have species status, especially because of sympatry without hybridization (e.g. *C. violaceus* and *C. germari*, Casale and Kryzhanovskij 2003; Turin et al. 2003). For other forms, such as the populations within our study area, there is a discussion on the subspecies or species status. Our study reveals the existence of populations with mixed genomes. Both (1) the lack of a sig-

nificant deficit of heterozygotes (allozyme markers) within the hybrid zone and at the same time a strong differentiation of the postulated source populations and (2) the concordance of different clines concerning different markers and including numerous individuals with intermediate characters, indicate that the populations are real hybrid populations and not co-occurring species which hybridize occasionally or up to the level of some percentages such as *C. auronitens* and *C. splendens* in the eastern Pyrenees and *C. glabratus* and *C. hortensis* in north-western Germany (Assmann 2003). At least occasionally, other *Carabus* species can show higher hybridization rates, e.g. *C. lineatus* and *C. splendens* in the Val d'Hayra (northern Spain) where, in some years, the proportion of hybrids exceeds 40% (Mossakowski et al. 1986; 1990). However, the difference between these beetles and the hybrid zone of the two *C. violaceus* forms is obvious, because the former are co-occurring species which do not show a tendency to "melt down their differentiation" in a hybridization process (own observations two decades after the cited studies).

The existence of a hybrid zone without strong selection pressure (since we found no deviations from Hardy-Weinberg equilibrium after correcting for multiple tests) despite strong differences in the shape of the aedeagus of both forms has consequences for taxonomy within the genus *Carabus*: differences in the male genitalia (especially those of the external shape of the aedeagus tip) do not prevent excessive gene flow and should thus not be used as a character to establish species' status of forms (cf. Assmann et al. 2008). Moreover, the *a priori* assumption of species-specificity of the genitalia (especially of the external shape of the aedeagus) prevents the detection of species with genitalia differentiated at the subspecies or population levels (Huber 2003). Therefore the establishment of species within the genus *Carabus* should not exclusively be based on differences in the external shape of male genitalia but include other characters such as DNA sequences.

The strong differentiation of the endophallus in some species of the subgenus *Ohomopterus* demonstrates that (1) copulatory pieces can reduce cross-breeding and (2) the fitness costs of interspecific matings are high in the given species (e.g. Sota and Kubota 1998). In these cases the shape of the endophallus and its appendages, not the external shape of the aedeagus, are an excellent character to delineate species within the genus *Carabus*. Moreover, morphological characters to differentiate *Carabus* species should be clear without ambiguity as is the longitudinal striation in *C. v. purpurascens* in comparison to the smooth elytra of the nominate form.

Numerous questions that are important for a better understanding of the investigated hybrid zone are still unanswered, e.g. if the contribution to gene flow into the hybrid zone is the same for both sexes or if the diffusion rate of markers differs. These and others can only be studied when further molecular, both mitochondrial and nuclear markers are analysed. mtDNA analysis, which is presently being conducted at our institute, may enable us to further estimate evolutionary divergence time between the two investigated subspecies with the help of phylogenetic analysis. The results of the present study reveal that *Carabus violaceus* has the potential to be an important model species in the fields of conservation genetics and evolutionary biology at the interface to systematics.

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Appendix I

Gel and staining recipes and electrophoresis conditions used in this study. (doi: 10.3897/zookeys.100.1546.app) File format: Adobe Acrobat (pdf).

Explanation note: The additional file contains gel, staining recipes and protocols for GPI, MPI and EST-X.

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REVIEW ARTICLE



Animals as an indicator of carbon sequestration and valuable landscapes

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Abstract

Possibilities of the assessment of a landscape with the use of succession development stages, monitored with the value of the Mean Individual Biomass (MIB) of carabid beetles and the occurrence of bird species are discussed on the basis of an example from Poland. Higher variability of the MIB value in space signifies a greater biodiversity. Apart from the variability of MIB, it is suggested to adopt the occurrence of the following animals as indicators, (in the order of importance), representing underlying valuable landscapes: black stork, lesser spotted eagle, white-tailed eagle, wolf, crane and white stork. The higher number of these species and their greater density indicate a higher value of the landscape for biodiversity and ecosystem services, especially carbon sequestration. All these indicators may be useful to assess measures for sustainable land use.

Keywords

Carabidae, indicators, landscape evaluation, Mean Individual Biomass (MIB)

Animals, carbon sequestration and landscapes

As part of the ongoing discussion on the sustainable use of landscapes and ecosystem services we give here an overview on the relationship between biodiversity and carbon sequestration in forests as revealed by a long-term study in north-western Poland with particular reference to carabid beetle diversity. From the very beginning of life, environmental resources on Earth have been shaped by natural succession processes, influenced by climate, and by various disturbances such as orogenic movements, windfall, floods and fires. Depending on latitude and the geological base, these disturbance factors vary among various places on the globe. The lack of catastrophes entails the buildup of organic substances, which can be measured simply with the content of carbon. The content of carbon in a single hectare of natural forest of the moderate climatic zone shaped by succession processes for thousands of years, exceeds 350 tons/ha with upper limits estimated between 500 and 700 tons/ha (Luyssaert et al. 2008). Half of this resource is stored in living organisms (plants, animals, fungi) while the other half is stored in the soil (litter and humus compounds in the mineral soil) (e.g. Oak Ridge National Laboratory 2010).

In such old forests (old ecosystems created by nature), ecosystems have a specific composition of plant, animal and fungal species. Species that are linked to old trees, old decaying wood, and well developed soil, occur here (Fig. 1). In such forests in the European geographic zone the full range of carabid species with a narrow geographic arrangement, low dispersal power and large body size occurs. The Mean Individual Biomass (MIB) of the carabids beetles might exceed 350 mg in such forests (Szyszko 1990, 2002). Forests of old successional stage are poor in butterflies (Szyszko K. 2003), the majority of bumblebees (Skrok 2003) and open-area birds (Kruszewicz 2007). With no humans present, their occurrence could only be possible due to ecological catastrophes mentioned above. Fires, floods or windfalls decelerated developmental succession processes (buildup of organic substance) and thereby impoverish these systems by releasing carbon in the form of carbon dioxide to the atmosphere (Magnani et al. 2007). Such disturbances create opportunities for species characteristic for early stages of succession, e.g., carabids species of open and low vegetation or the above mentioned butterflies, bumblebees and birds characteristic of open areas. Historically, nature itself provided advantageous conditions for the full range of biodiversity of the native fauna and flora thanks to events we call "ecological catastrophes". These catastrophes destroy old stages of succession containing much carbon and create room for species characteristic of early successional stages (Fig. 2). It is here that species such as the nightjar (Caprimulgus europaeus), skylark (Alauda arvensis), northern dune tiger beetle (Cicindela hybrida) and, with the appearing pine wilding, the sticky bun (Suillus luteus) can strive (Fig. 2). The created open areas are also an excellent place for "landscape species", i.e., species that need different succession stages in a wider landscape for establishment of their populations (Szyszko K. 2002, Skrok 2003). Such species breed for example in places of advanced stages of succession (natural forests with high carbon content) and hunt in open areas (early successional stages with low carbon content). The common buzzard and the majority of falconids are typical examples of such species. They nest in old trees in forests and hunt where visibility is good, i.e. in open areas or environmental systems of early successional stages, with low carbon content. Ecological catastrophes also create opportunities for many species associated with different stages of natural succession by setting back the climax situation and thereby reducing the carbon content in the environmental systems (Fig. 3).



Figure 1. A natural forest with a carbon content within the limit of 350 tons per ha and a mean individual biomass (MIB) for carabid beetles exceeding 350 mg and with species characteristic for that environmental system. *Lucanus cervus* – a species linked to old decaying oak wood (top right), *Cerambyx cerdo* – a species linked to living old oaks (top left), *Boletus erythropus* – a mycorrhizal species occurring in soils with a historically well developed soil profile (bottom right), *Carabus intricatus* – a species occurring in old forest environmental systems with an easily decomposing duff (bottom left).



Figure 2. Succession of carbon content (left y-axis and black line) and species diversity (right y-axis and striped line) in a stand after the destruction of the trees by fire. After the fire, the carbon content is low with *Cicindela hybrida* and the sticky bun (*Suillus luteus*) as characteristic species (left photographs). In 100 years old stands the carbon content is high with *Carabus intricatus* and the dotted stem bolete *Boletus erythropus* as characteristic species (right photographs) (from Szyszko 2007).



Figure 3. a Relationship between the age of a forest stand and thickness of the litter layer **b** relationship between the thickness of the litter layer and the weight of carbon per 1 sq. m (from Szyszko et al. 2003).

Humans play a similar role in shaping ecosystems and landscapes. Ecological catastrophes can destroy the effects of our economic activities and constitute a danger our its safety. This is why humans manage the environment by trying to reduce floods, fires and windfalls. However, to preserve the full range of biodiversity, humans replace the forces of nature and mimic its destructive role by active management. This can clearly be illustrated for forests in Poland. If it was not for the interference with natural succession and the reduction of the carbon content of up to a few dozen tons per ha (Fig. 4a) due to clearcuts, no pine cultivations could have emerged in forest areas. Consequently, bird species such as the nightjar (Camprimulgus europaeus) and woodlark (Lullula arborea) would have had no place to nest and the majority of birds of prey nesting in old trees would not have been able to hunt. Carabid beetles like Carabus nitens, Bembidion nigricorne, Pterostichus lepidus, Calathus erratus, Masoreus wetterhallii and Harpalus rufitarsis (resulting in a MIB value of about 50 mg) would not have occurred in this region (Szyszko 1990). Additionally, the mass appearance of fungal species such as sticky buns (Suillus luteus), sulfur tufts (Hypholoma fasciculare) or, slightly later, chanterelles (Cantharellus cibarius) and porcinis (Boletus edulis) would not have been possible (Fig. 4a). The destruction of forest habitats due to the felling of trees provides opportunities for the natural succession to start again, entailing a change in species composition with time. With an increase in the carbon content of a stand an increase in the MIB value of epigeic carabid beetles takes place, indicating regeneration of the environmental resources. In a ca. sixty year old pine stand (Fig. 4b), carbon content and the MIB value



Figure 4. The occurrence of characteristic birds, carabid beetles and fungi as well as the structure of the carbon content in tons per ha in a forest stand, litter and mineral soil up to 10 cm in depth in a: **a** 10 year old pine stand with a MIB value of about 50 mg, created after the clear-cut of a timber pine stand (more than 100 years old) **b** ca. 60 year old pine stand with a MIB value about 250 mg. **c** ca. 80 year old beech stand created from the undergrowth after the clear-cut of a pine stand with a MIB value of about 350 mg. In all graphs the annual accumulation of carbon in that stand, the value of such accumulation and the value of the entire carbon content (forest stand + litter + mineral soil) are expressed in carbon dioxide at the prices of the European Emission Trade System on 15.08.2008 (all graphs from Szyszko 2007).

(about 250 mg) is higher compared to a young pine plantation (Fig. 4a). The species composition of birds, carabids and fungi differs clearly. Birds characteristic for the old pine stand include the chaffinch (Fringilla coelebes), great tit (Parus major) and coal tit (Parus ater). Carabids characteristic for this stage of succession include Carabus arcensis, C. nemoralis and Pterostichus niger and the most frequent and numerous fungi include the sickener (Russula emetica), brown roll-rim (Paxillus involutus), false morel (Gyromitra esculenta) and the cauliflower mushroom (Sparassis crispa). The planting of beech as undergrowth in ca. sixty year old pine stands followed by the removal of the pines ten years later results in the creation of beech stands, several of which in Poland are about eighty years old (Rylke and Szyszko 2002, Fig. 4c). When compared with a sixty year old pine stand, those old beech stands have higher carbon content and the MIB value of the carabid beetles exceeds 350 mg. Logically, characteristic species of birds, carabids and fungi are also different for the forest types (successional stages) presented above. Characteristic birds in the old beech stands are the black woodpecker (Drycopus martius), stock pigeon (Columba oenas) and chaffinch (Fringilla coelebes). Characteristic carabids include Carabus coriaceus, C. hortensis and C. intricatus. Characteristic fungi are the dotted stem bolete (Boletus erythropus), fleecy milk-cap (Lactarius vellereus) and the death cap (Amanita phalloides).

Data on different forests presented above suggest that a greater spatial differentiation of the carbon content in environmental systems, or in other words a greater differentiation of successional stages as measured using the MIB value of carabid coenoses, entails greater biodiversity (Fig. 5, Szyszko 2002). Hence, variability in space of the MIB value is a good measure for the value of the landscape (Fig. 5, see also Rylke and Szyszko 2001). However, the value of a landscape can be even more completely assessed if we also take into account the occurrence of species that use various successional stages, so called landscape species (Szyszko 2002). Typical examples of such species among birds are the black stork (*Ciconia nigra*) and the lesser spotted eagle (*Aquila pomarina*) (Fig. 6). These birds nest in old trees in vast forests, similar to natural ones, while they hunt in nearby meadows, floodplains and marshes. If these species are present, we can be sure that the said habitats occur in a given environmental complex and, what is more, they are not far apart. Species with similar requirements are the white-tailed eagle (Haliaetus albicilla) and the wolf (Canis lupus) (Szyszko 2002). The existence of both species seems to be linked to vast areas covered by both old and young successional stages. The former seem to play a significant role as localities for reproduction while the latter serves as a food acquisition area. Among these generally known and easily recognizable species, two others are worth mentioning: the crane (Grus grus) and white stork (Ciconia ciconia) (Szyszko 2002). Cranes choose old peatbogs and marshes surrounded by forests as a nesting site and gather food in meadows and fields, while the white stork nests mainly in villages surrounded by extensively used arable lands and feeds in meadows, marshes, fields and pastures. If we adopt Andrzejewski's (1992) definition of the landscape as a "set of ecosystems linked by mutual dependencies creating an ecological system of a higher order", we can assume that, as the occurrence of species characteristic for individual stages of succession is a measure of the advancement of these processes in biocoenoses, the oc-



Figure 5. Examples of several habitats with different carbon contents and different characteristic carabid species, building a heterogenous landscape. Top left – a natural forest with a carbon content of 350 ton per ha with *Carabus coriaceus*, top right – arable land with a carbon content 20 tons per ha with *Cicindela campestris*, in the middle – a peatbog with a very high content of carbon per ha with *Panagaeus bipustula-tus*, bottom left – a clear-cut with a carbon content of ca. 90 tons per ha with *Harpalus rufitarsis*, Bottom right – a timber stand with the carbon content 124 tons with *Carabus nemoralis* (from Szyszko 2007).

Heterogenous landscape



Figure 6. Landscape species in a heterogenous landscape. The lesser spotted eagle (*Aquila pomarina*) nests in old trees in natural and cultivated forests, and hunts in wastelands. The crane (*Grus grus*) nests in peat bogs and hunts in wastelands. The kestrel (*Falco tinnunculus*) nests in old trees in natural and cultivated forests and hunts in clear-cut areas. The black stork (*Ciconia nigra*) nests in old trees in natural and cultivated forests and hunts in peat bogs (from Szyszko 2007).

currence of species using varied successional stages can be a measure of the quality and value of a landscape and an indicator of its functionality in space (Szyszko 2002). In light of these results, the suggestion to adopt the mentioned 'landscape species' as landscape value indicators has to be taken into account, with order of importance as follows: black stork, lesser spotted eagle, white tailed eagle, wolf, crane and white stork. The higher the number of these species and the greater their density, the higher the value of a landscape, in terms of environmental quality and biodiversity (Szyszko 2002).

Landscape quality includes biodiversity (highest in mosaic landscapes) and carbon storage (highest in peat bogs and old forests) and sequestration (highest in regenerating forests), as well as other ecosystem services. Sustainable land use is essential in maintaining or creating landscapes with high natural qualities. There is a need to assess measures of sustainable land use, and various animals mentioned in this paper, including carabid beetles and their MIB values, may serve as important indicators for this.

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