

Effects of climate on diversity patterns in ground beetles – a doctoral thesis combining methods of macroecology, phylogeography and global change biology

Katharina HOMBURG^{1,2}

¹ Alfred Toepfer Academy for Nature Conservation, Hof Möhr, D-29640 Schneverdingen, Germany,

E-Mail: katharina.homburg@nna.niedersachsen.de

² Leuphana University Lüneburg, Animal Ecology, Universitätsallee1, D-21335 Lüneburg

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Abstract: In times of biodiversity loss due to climate change, the development of effective conservation strategies still requires extensive ecological research.

Macroecological studies aim at the detection of large-scale taxonomic, geographic and temporal patterns and their potential drivers. Phylogeographic studies address the genetic level of biodiversity and are commonly used to study species' histories and locate glacial refugia. Newly established methods such as species distribution models (SDMs) project both historical as well as future distribution ranges of species. In my doctoral thesis I used a combined approach to gain new insights into the effect of climate change on diversity patterns of ground beetles.

In further steps, I used macroecological regression models to detect spatial patterns in the distribution of mean carabid body size and the proportion of flightless species. Carabid body size showed a positive relationship with contemporary environmental productivity and stability, while patterns in hind wing development were most notably influenced by historical climate stability. In an online database (www.carabids.org) a large data set on Palaearctic carabid traits was made available for future studies.

Phylogeographic analyses (using mtDNA) were combined with SDMs to identify multiple and isolated glacial refugia of *Carabus irregularis*, a cold-adapted, flightless ground beetles species. Strong intraspecific genetic differentiation was found between two ancient clades, which pointed to the existence of two evolutionarily significant units (ESUs). SDMs projected immense range contractions for both ESUs in future and thus high vulnerability of *C. irregularis*.

Taken as a whole, this combination of methods is conducive to a better understanding of potential effects of historical, contemporary and future climate on diversity patterns of insects and on specialised species with low dispersal abilities.

Keywords: body size, hind wing development, dispersal ability, traits, mtDNA, ecological significant units, species distribution models, range contractions, carabids.org

1 Introduction

1.1 Background

Biodiversity is a vital factor for the functioning of ecosystems, which provide ecological, economic and cultural services essential for human health and well-being (LOREAU et al. 2001; HOOPER et al. 2005; MEA 2005). International conservation efforts (e.g. based on the Convention on Biological Diversity: UNEP 1992) concentrate on the protection of bio-

diversity, especially because ongoing climate change is expected to increase diversity loss (ARAÚJO & RAHBEK 2006; BELLARD et al. 2012; PEREIRA et al. 2012). Since effective conservation strategies still require substantial research, many recent studies from a wide range of ecological disciplines aim at understanding the complex relationships between biodiversity and climate on various taxonomic, geographic and temporal scales (WOLTERS et al. 2006; FIELD et al. 2009; HORTAL et al. 2011).

The investigation of large-scale geographic diversity patterns has a long tradition and biogeographic rules such as Bergmann's and Allen's rule (BERGMANN 1847; ALLEN 1877) have long assumed relationships between species characteristics (i.e. body size and the size of body appendages) and environmental conditions (e.g. temperature). The study of broad-scale patterns has undergone a revival over the last few decades. Recent macroecological research aims at the detection of statistical patterns in large ecological data sets and the potential mechanisms driving these patterns (BROWN & MAURER 1989; BLACKBURN & GASTON 1994). Species' traits are increasingly used to examine spatial and temporal phenomena of species diversity and distribution, ranging from community organisation to ecosystem functioning (HOOPER et al. 2005; MCGILL et al. 2006; DE BELLO et al. 2010). Body size still appears to be the best studied trait in animal species (e.g. MEIRI et al. 2004; OLALLA-TARRAGA et al. 2006; MCNAB 2010). In 1847, Bergmann's rule was originally formulated for endotherms, and the pattern of increasing body size towards high latitudes and cold environments still applies for birds and mammals (e.g. BLACKBURN & HAWKINS 2004; OLSON et al. 2009). Interestingly, the pattern has also been detected in some ectotherms (BLACKBURN et al. 1999; HUEY et al. 2000). However, in some invertebrates (e.g. spiders and ants), inconsistent relationships between body size and contemporary climate have been identified, even in the same geographic region (cf. CUSHMAN et al. 1993; ENTLING et al. 2010). Patterns were assumed to be shaped by different mechanisms linked to species' physiological abilities ranging from energy allocation (ATKINSON 1995; MOUSSEAU 1997), to starvation and desiccation resistance (REMMERT 1981; CUSHMAN et al. 1993; ENTLING et al. 2010), and to dispersal abilities (CUSHMAN et al. 1993).

The genetic level of biodiversity has been addressed by phylogeographic studies (e.g. analysing sequences of mitochondrial DNA = mtDNA), which are commonly used to identify and locate glacial refugia. The southern European peninsulas are considered as classical refugia, which were important for species survival during past climatic events such as ice ages (TABERLET et al. 1998; HEWITT 2000). Cold-adapted (i.e. alpine and arctic) species are assumed to have survived in the margins of southern European mountain chains (STEWART et al. 2010). Recent publications, however, document evidence for additional refugia north of the southern European peninsulas

and the Alps (BHAGWAT & WILLIS 2008; PROVAN & BENNETT 2008).

Many phylogeographic analyses focus on the genetic variation of widespread species (HEWITT 1999; SCHMITT 2007; KNOPP & MERILÄ 2009; VALTUENA et al. 2012). Studies on mountain species with restricted and disjunct ranges are still scarce (but see SCHMITT 2009).

In order to identify and locate potential glacial refugia, many studies using newly established modelling methods such as species distribution models (SDMs) have been used in association with palaeoclimatic data (WALTARI et al. 2007; ELITH & LEATHWICK 2009). In addition to phylogeographic analyses, these modern approaches have also detected classical as well as cryptic refugia (VEGA et al. 2010; REBELO et al. 2012). However, there are still many uncertainties regarding glacial refugia, in particular for cold-adapted and low-dispersal mountain species. Consequently, further research is needed to develop reasonable scenarios of species' population histories including range retractions and expansions during the last ice ages.

SDMs have been used for the projection of both historical as well as future distribution ranges of species. Over the past century, Earth's climate has changed immensely (IPCC 2007). Besides extinctions, phenological shifts, and evolutionary responses, range shifts have been observed as potential reactions to climate change (WALTHER et al. 2002). SDMs are increasingly used in the field of global change biology to detect species' range shifts in times of climate change (GUISAN & THUILLER 2005; ELITH & LEATHWICK 2009). Numerous studies have documented range shifts towards higher altitudes or latitudes (PARMESAN & YOHE 2003; HICKLING et al. 2006). Cold-adapted mountain species are considered to be particularly sensitive to global warming, since it is assumed that cool and moist habitats decrease in future (WILSON et al. 2007; SETTELE ET AL. 2009; DIEKER et al. 2011). An additional factor limiting the future distribution ranges of many of these species might be their low dispersal ability (SVENNING & SKOV 2004; SCHLOSS et al. 2012). In conjunction with future climate scenarios, SDMs can help to develop conservation strategies for these vulnerable species, as they allow the location of regions that might be suitable for their future survival (ELITH & LEATHWICK 2009; SCHWARTZ 2012).

Especially for invertebrate species, much more research is still required to enhance our knowledge on

the complexity of diversity patterns and on relevant drivers.

1.2 Study taxon

Ground beetles (Coleoptera: Carabidae) are a highly diverse taxon comprising approximately 40,000 species worldwide, more than 10,000 in the Palaearctic and about 3,400 species in the western Palaearctic region. The taxonomy and species' distribution of the Palaearctic ground beetle species are very well-documented (LÖBL & SMETANA 2003), and the evolutionary biology and ecology of the European species in particular have been well studied for a long time (e.g. BURMEISTER 1939; LINDROTH 1945; THIELE 1977; LÖVEI & SUNDERLAND 1996; RAINIO & NIEMELÄ 2003). Thus, large and reliable data sets are available for a wide geographic range and allow the realisation of macroecological studies (ISAAC et al. 2004; LOVELL ET AL. 2007; HORTAL 2008).

Ground beetles comprise both restricted-range (endemic) and widespread species, specialist as well as generalist species, and can be found in a wide variety of terrestrial habitats (THIELE 1977). The species differ in terms of their dispersal abilities, with wingless and winged species, the latter being mostly able to fly (LINDROTH 1949; AUKEMA 1986; AUKEMA 1990). Since biodiversity patterns may differ between widespread and endemic species (ORME ET AL. 2005; RAHBEK et al. 2007; SCHULDT & ASSMANN 2009) and between species with high and low dispersal abilities (BASELGA et al. 2012), ground beetles are well suitable for this kind of studies. Most ground beetles are predators (occupying high trophic levels), which are assumed to be highly sensitive to climate changes (cf. VOIGT et al. 2007). Moreover, many ground beetle species (e.g. mountain species such as *Carabus irregularis*) inhabit disjunct distribution ranges (THIELE 1977; TURIN et al. 2003). These species are likely to be genetically differentiated (AVISE 2000; SCHMIDT et al. 2012), and assumed to be highly vulnerable to future global warming due to shrinking cool and moist habitats (WILSON et al. 2007; SETTELE et al. 2009). Thus, ground beetles serve as a very valuable model taxon for the study of climatic effects on biodiversity.

2 Parts of the cumulative thesis

My PhD thesis contributes to a better understanding of climatic effects on invertebrate diversity patterns

in the Palaearctic region, especially in Europe. In my approach I applied methods from three fields of biological research – macroecology, phylogeography and global change biology – in order to gain new insights into the effect of climate on patterns in invertebrate diversity. Geographic diversity patterns were analysed on different geographic and temporal scales. Furthermore, different levels of biodiversity were addressed, since I worked on assemblage, on single species and on intra-specific genetic levels. This highly diverse group of ground beetles served as a very valuable model taxon for my cumulative dissertation, which comprise four studies published in international peer-reviewed journals. Figure 1 gives an overview of the different taxonomic, geographic and temporal scales of the four case studies of my thesis. The manuscripts are the work of multiple authors.

2.1 Large-scale patterns in carabid species' traits

HOMBURG et al. (2013a) document the analysis of macroecological patterns in two traits of carabid beetles – body size and hind wing development, with the latter being linked with dispersal ability. We tested potential impacts of contemporary as well as historical climate using regression models for (1) *all*, (2) *widespread* and (3) *endemic* (restricted-range) species. The models included spatial, areal, topographic and climate-related variables. The body size of invertebrates has been hypothesised to increase towards regions with high energy availability due to high productivity and metabolic rates (cf. MOUSSEAU 1997; WILSON et al. 2007; ENTLING et al. 2010; MCNAB 2010). Invertebrate body size is also assumed to be greater in arid regions due to the better desiccation resistance of larger bodies (REMMERT 1981; YOM-TOV 1986; YOM-TOV & GEFFEN 2006). In Europe, patterns in biodiversity have also been affected by past climate events such as glacial periods (HOLDHAUS 1954; SCHMITT 2007). Thus, current geographic patterns of carabid species' traits might also be shaped by historical climate and dispersal processes. On smaller spatial scales, a positive relationship between habitat stability and hind wing reduction has been found (cf. BRANDMAYR 1983; ASSMANN 1999; DESENDER et al. 1999, LINDROTH 1949).

In order to gain insight into large-scale spatial patterns and potential mechanisms driving geographic patterns in two species traits, we addressed the following main hypotheses in the first macroecological

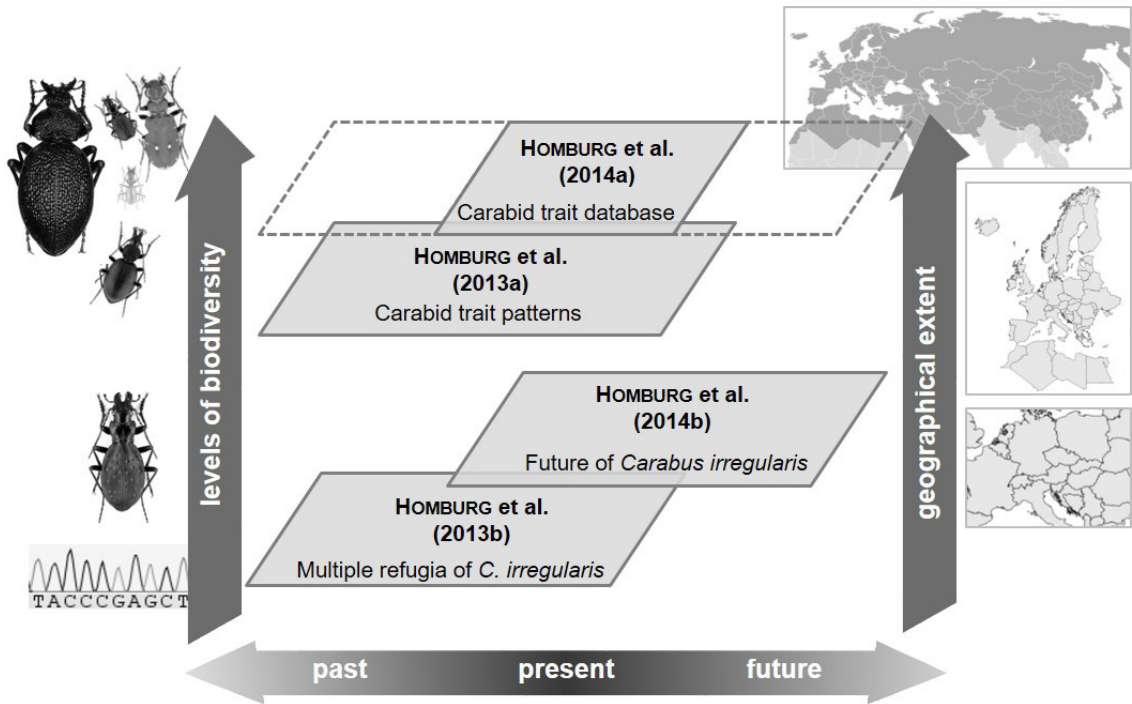


Fig. 1: Overview of the biodiversity levels, and the geographic and temporal scales addressed in my doctoral thesis, of the allocation of the independent studies, as well as relationships between the studies. Results of HOMBURG et al. (2014a) can be used for further studies considering different temporal scales (indicated by dashed lines). Photos of ground beetles by O. Bleich, www.eurocarabidae.de.

article:

- i) Carabid body size increases towards both (a) lower latitudes representing more productive environments and (b) arid regions.
- ii) The proportion of flightless species increases towards environments with long-term stability as well as regions of low historical climate variability.

HOMBURG et al. (2014a) present the content and structure of a database on carabid species traits which was developed as part of my PhD thesis. The database is available online (<http://www.carabids.org>) and contains species classification and distribution data for over 10,000 Palearctic carabid species (obtained from LÖBL & SMETANA 2003). Data on size and dispersal traits (body and eye size and hind wing development) are available for almost all (over 3,400) western Palearctic species. Ecological and life-history traits have been compiled for most Central European (about 1,000) species. The collected traits data can be easily downloaded by registered users. These users who are also invited to add new and edit the existing entries. The database contributes to future research

on community assembly and on functional diversity of species-rich invertebrates, which will help to advance our understanding of diversity patterns across large spatial scales.

2.2 Glacial refugia of *Carabus irregularis*

HOMBURG ET AL. (2013b) document a combined approach of species distribution modelling and phylogeographic analysis of two mitochondrial DNA loci. The study investigates the history of *Carabus irregularis*, a flightless ground beetle species. The species occurs in low- and high-altitude mountains of Central and eastern Europe and has a disjunct distribution range.

SDMs have been used previously to locate classical glacial refugia (in the Alps and on the southern European peninsulas) as well as northern refugia of plant and animal species (e.g. VEGA et al. 2010; REBELO et al. 2012). There are numerous phylogeographic analyses on widespread species that endeavour to reconstruct species' population histories. Nevertheless,

there are also a few studies on range-restricted mountain plants displaying high genetic differentiation and ancient phylogenetic splits between occurrences in the Alps and geographically associated mountain systems (RONIKIER 2011; KROPF et al. 2012). For arthropod species with relatively high dispersal abilities (e.g. spiders and butterflies: MUSTER & BERENDONK 2006; SCHMITT & HAUBRICH 2008), low levels of genetic differentiation indicate more recent and even post-glacial splits between populations from the Alps and from neighbouring high and low mountain ranges (SCHMITT 2009). Our study species, *C. irregularis*, is likely to show strong genetic differentiation, since this low-dispersal species has a disjunct distribution. It is assumed to have survived the last ice age in northern refugia, which have been repeatedly found for low-dispersal species (BHAGWAT & WILLIS 2008; PROVAN & BENNETT 2008). *Carabus irregularis* is comprised of three subspecies which may represent not only geographically separated distributions but also divergent phylogenetic groups (TURIN et al. 2003).

Our study addressed the following main hypotheses using traditional methods from the field of phylogeny and modern modelling methods:

- i) *C. irregularis* survived the last glacial maximum in classical refugia for cold-adapted species, such as the margins of the Alps, as well as in northern refugia (close to the northern edge of its current distribution).
- ii) High genetic differentiation of *C. irregularis* will provide molecular evidence for low dispersal and for multiple refugia.
- iii) Taxonomic subspecies delineation is congruent with the phylogeny of *C. irregularis*.

2.3 Future distribution and conservation of *Carabus irregularis*

The fourth study (HOMBURG et al. 2014b) addresses the evolutionarily significant unit (ESU) concept (MORITZ 1994). The future distribution ranges of the two phylogenetic units (discovered by HOMBURG et al. 2013b) are projected using SDMs for two different future climate scenarios (A2a and B2a, IPCC) and two different dispersal scenarios. The modelling results were intended to support the development of conservation strategies which might be applicable for the cold-adapted mountain species *C. irregularis*.

SDMs have most often been applied to project range retractions and loss of suitable habitat conditions. However, they may also support species con-

servation, as they can be used to locate regions that will provide suitable climate conditions in the future (SCHWARTZ 2012). Due to its cold-adaptedness and low dispersal ability, *C. irregularis* is assumed to be vulnerable to climate change. Therefore, the development of sound conservation strategies for this species is urgently needed.

This study addresses the following main hypotheses from the field of global change biology:

- i) The ESUs of *C. irregularis* show divergent potential distribution ranges.
- ii) The minimal dispersal scenario will lead to smaller future ranges than projected by the maximal dispersal model.

3 Results and prospects

My doctoral thesis brings together findings on the effects of climate on biodiversity on different taxonomic, geographic and temporal scales. My main results are in accordance with my hypotheses presented above.

The highly diverse group of ground beetles served as a valuable model taxon to investigate diversity patterns and their potential determinants on community level and on large geographic scale. Phylogeographic and modelling methods from the studies on *Carabus irregularis* provide results on species level and on intra-specific genetic level that are important for understanding the population histories and potential future distribution patterns of cold-adapted low-dispersal species. The combination of traditional and modern methods gives valuable insights on the impacts of historical, contemporary and future climate on diversity patterns in insects.

3.1 Insights from a species-rich taxon

Spatial patterns on large taxonomic and geographic scale were detected for carabid body size and hind wing development in the western Palaearctic. Carabid body size and the proportion of flightless species increased from North Africa towards southern Europe and decreased again towards northern Europe. This pattern resembles the hump-shaped distribution of carabid diversity in the same study area (cf. SCHULDT & ASSMANN 2009). According to mechanisms assumed for other taxa (cf. BLACKBURN & GASTON 1994; MOUSSEAU 1997; MCNAB 2010), high resource availability and productivity tend to have a positive

influence on carabid body size. A shortage of water in arid regions such as North Africa is thought to lead to larger body sizes in order to increase desiccation resistance in other arthropod taxa (REMMERT 1981; ENTLING et al. 2010). In ground beetles, however, a shortage of water in North Africa seems to result in low body sizes values. Desiccation risk in arid regions might be reduced by shifts of sensitive larval stages to less productive, but less dry periods, resulting in smaller adult size (cf. PAARMANN 1979; KOTZE et al. 2011). High proportions of flightless species were found in regions of current climatic stability represented by measures of balanced water-energy availability. This pattern resembles relationships documented in previous studies on smaller spatial scales (i.e. stable/permanent habitats). Several authors (BRANDMAYR 1983; BRANDMAYR 1991; ASSMANN 1999; DESENDER et al. 1999) found that the proportion of flightless individuals and of flightless species increased towards habitats with low environmental variability. Wing reduction due to energy allocation between dispersal and reproduction can increase fecundity and promote local recruitment (ROFF 1986; DESENDER 2000), enabling carabid beetles to adapt to specific habitats and/or changing environments (cf. THIELE 1977). This kind of microevolutionary processes might influence distribution patterns of flightless ground beetles not only on habitat level but also on larger geographic scales. The decreasing proportion of flightless species from southern towards northern Europe might also result from historical dispersal processes, which in Europe are strongly affected by historical climate events such as glaciations (HOLDHAUS 1954; SCHMITT 2007). Molecular analyses corroborated scenarios of species' survival in southern European glacial refugia and postglacial re-colonisation towards northern Europe (e.g. TABERLET et al. 1998; HABEL et al. 2005; DREES et al. 2010). In my analyses, historical climate variability revealed a negative effect on the proportion of flightless species. Many winged species currently occur widespread, and they might have been able to colonise larger geographic ranges due to higher dispersal ability (cf. GUTIÉRREZ & MENÉNDEZ 1997; SVENNING & SKOV 2007; ARAÚJO et al. 2008). Flightless species, however, currently inhabit restricted ranges in former glacial refugial areas of southern Europe. Here it remains unclear the low dispersal of flightless species caused their restricted range in southern Europe or winglessness evolved in restricted habitats of former

southern European refugia. Restricted regions of the refugia are assumed to have offered stable environmental conditions over long periods of time, which might have been conducive to the reduction of wings (BRANDMAYR 1991).

In summary, carabid traits show distinct geographic patterns that tend to be influenced by both contemporary environmental conditions and by historical processes. In this way, my findings contribute to a greater understanding of diversity patterns in insects. Although insects are often assumed to provide key functions in ecosystems and represent large parts of the global biodiversity (SAMWAYS 2005), insect trait data is still not easily available on large taxonomic and geographic scales. However, trait-based approaches are increasingly used to study spatial and temporal patterns of species distribution and abundance (MCGILL et al. 2006; DE BELLO et al. 2010). My aim is thus to support future research by making available the data collected for the study of carabid traits on an online database (www.carabids.org). This collaborative interactive project offers a multitude of future research opportunities in different ecological fields.

3.2 Insights from a specialised species

Modelling results indicate that several mountainous regions across Central and southern Europe might have offered suitable conditions for the survival of *C. irregularis* during the last glacial maximum (=LGM). While some of these regions coincide with classical refugia on the southern European peninsulas (HEWITT 1996; HEWITT 1999; HEWITT 2000), other potential refugia of *C. irregularis* have only recently been recognised for other species (e.g. at the margins of the Alps and in neighbouring mountain ranges: cf. SCHÖNSWETTER et al. 2005; PAULS et al. 2006; SCHMITT et al. 2006). Potential refugia far north of the Alps were also detected for the studied ground beetle species and have also been assumed for numerous animal and plant species (STEWART & LISTER 2001; PROVAN & BENNETT 2008). *C. irregularis* seems to have survived in refugia typical for both low-altitude (TABERLET et al. 1998; PETIT et al. 2003) and mountain species (SCHÖNSWETTER et al. 2005; SCHMITT et al. 2008). Since mountain species are assumed to have survived in several spatially restricted refugia rather than in extensive, consistent regions (HOLDEREGGER & THIEL-EGENTER 2009;

SCHOVILLE et al. 2012), *C. irregularis*, the cold-adapted mountain species, is assumed to have survived in multiple refugia.

Phylogenetic analyses supported the assumption of multiple refugia during the LGM. My analyses on the intra-specific genetic level of diversity revealed two well-supported and spatially congruent major clades: a Central European clade with three subclades, and a Carpathian clade with two subclades. All major phylogenetic splits predate the last ice age and high genetic intra-specific differentiation in *C. irregularis* reinforces the possibility that the ancestors of the clades remained isolated from each other for a long period of time. The locations of potential refugia found in phylogeographic studies partially coincide with the potential refugia found using SDMs. Nevertheless, phylogenetic analyses indicate the existence of independent Carpathian refugia, which were hardly evident from the modelling results. Phylogeographic studies including the Carpathian region are still rare and Carpathian refugia are not considered as classical ones. However, as this mountain range has a different history than the well-studied Alps (RONIKIER et al. 2008; RONIKIER 2011), the future investigation of the Carpathians appears to be very promising. There are some studies documenting alpine plants with distinct and strongly differentiated genetic groups within the Carpathians, suggesting long-term isolation and restricted gene flow between areas within this mountain system (MRÁZ et al. 2007; RONIKIER et al. 2008; RONIKIER 2011). While RONIKIER et al. (2008) detected the strongest differentiation between western and eastern Carpathian populations, my results for *C. irregularis* are similar to results of MRÁZ et al. (2007), who found high differentiation between southern and eastern Carpathian samples. *C. irregularis* is the first animal species showing this ancient differentiation pattern with basal splits between the Carpathians and the western part of the distribution range.

The phylogenetic results partly resembled subspecies systematics: One monophyletic clade represented the Carpathian subspecies *C. i. montandoni*, the other (monophyletic) clade contained paraphyletic lineages of two other subspecies (*C. i. irregularis* and *C. i. bucephalus*). Thus, conventional taxonomy must be questioned in the case of *C. irregularis*. *C. irregularis* appears to have a very interesting history resulting in two geographically and genetically independent groups. These two groups might have varying ecologi-

cal niches and can be considered to be two evolutionarily significant units (ESUs, sensu MORITZ 1994). Especially in the framework of the other *Platycarabus* species, the two ESUs of *C. irregularis* should be investigated in more detail by further phylogeographic analyses.

SDMs handling the ESUs separately showed clear differences between the current and future potential distribution ranges of the two groups, indicating differing climate niches of them. Within other beetle species, differing of habitat requirements and habitat association have already been documented (e.g. VOGLER et al. 1993; VOGLER & DESALLE 1994). Especially ancient lineages tend to show strong intra-specific ecological differentiation due to evolutionary processes (RASPLUS et al. 2001). For an accurate prognosis of future species distributions using SDMs, ecological differences of subgroups need to be taken into consideration, as divergent habitat requirements can result in different distribution patterns. Here, the consideration of ESUs seems to be reasonable, since habitat preference is assumed to be a heritable attribute in ground beetles (THIELE 1977).

SDMs projecting the future of the two ESUs of *C. irregularis* showed only very small remaining areas with suitable climate conditions in relation to the species' recent distribution range. This finding is in line with the postulation that mountain-inhabiting species are particularly vulnerable to global warming due to shrinking cool and moist habitats (WILSON et al. 2007; SETTELE et al. 2009; DIEKER et al. 2011). Dispersal limitations tend to restrict the realised distribution of the flightless ground beetle, *C. irregularis*, even further. Thus, as documented by other studies the future distribution cannot be equated with the distribution of suitable conditions (ENGLER & GUIBAN 2009; KHAROUBA et al. 2012; SCHLAEPFER et al. 2012). The application of SDMs therefore appears more appropriate for the identification of future suitable habitats than for the estimation of potential habitat loss (cf. SCHWARTZ 2012). Regions with potentially suitable climate conditions may then be involved in the development of effective species conservation strategies. For other ground beetle species (e.g. *Carabus olympiae*: MALAUSA & DRESCHER 1991), the assisted colonisation of suitable habitats has already been implemented. Thus, assisted migration (e.g. already applied for *Carabus*, *Poecilus* and *Olistopus* species: DE VRIES 1996; SCHWÖPPE et al. 1998) to regions with future climatically suitable hab-

itats might be a useful strategy for the conservation of *C. irregularis* and its genetically distinct lineages.

To summarize, *C. irregularis* has been studied on a large geographic and temporal scale, ranging from the last glacial maximum to predictions under global change. SDMs proved to be useful tools for the reconstruction of species' histories and for the preparation of species conservation strategies. For future studies on other species with an intraspecific variability of habitat requirements, it seems reasonable to combine SDMs with phylogeographic results in order to take account of potential ecologically divergent subgroups.

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