EFFECTS OF CLIMATE ON DIVERSITY PATTERNS IN GROUND BEETLES: CASE STUDIES IN MACROECOLOGY, PHYLOGEOGRAPHY AND GLOBAL CHANGE BIOLOGY

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CONTENTS

ZUSAMMENFASSUNG

Biodiversität ist eine wichtige Grundlage funktionierender Ökosysteme, die für den Menschen lebensnotwendige Ökosystemdienstleistungen erbringen. Rapide Klimaveränderungen haben bereits zum Verlust von Biodiversität geführt und internationale Schutzbemühungen haben sich den Erhalt der biologischen Vielfalt zum Ziel gesetzt. Die Entwicklung erfolgreicher Schutzmaßnahmen setzt jedoch Wissen um komplexe Zusammenhänge zwischen Klima und Biodiversität voraus. Zahlreiche Untersuchungen aus unterschiedlichen biologischen Disziplinen befassen sich deshalb mit der Biodiversitätsforschung und der Ermittlung möglicher Einflussfaktoren auf die Verteilung von Biodiversität.

Makroökologische Studien untersuchen großräumige geographische Muster der Verteilung von Diversität und betrachten meist große Organismengruppen. Neben der Verteilung der Artenvielfalt werden in aktuellen Studien auch Muster in der Verteilung von Arteigenschaften erforscht, um Aufschluss über mögliche Effekte des heutigen, früheren und zukünftigen Klimas auf Arten, Artgemeinschaften und Ökosysteme zu geben. Phylogeographische Analysen (z.B. mithilfe mitochondrialer DNA = mtDNA) betrachten die genetische Ebene der Biodiversität, um historische Verteilungsmuster und glaziale Refugien zu rekonstruieren. Während die südeuropäischen Halbinseln als klassische Refugialgebiete gelten, in denen Arten die Eiszeiten überdauern konnten, wurden in neueren Studien auch Beweise für weiter nördlich gelegene Refugien gefunden. Neu entwickelte Modellierungsmethoden wie z.B. Klimanischenmodelle werden zunehmend eingesetzt, um sowohl historische als auch zukünftige Verbreitungsgebiete von Arten zu berechnen. In Zeiten des Klimawandels können diese Methoden aus dem Forschungsbereich der ‚Global Change Biology‘ hilfreich sein, die Verschiebung bzw. den Rückgang von geeigneten Lebensräumen für bestimmte Arten zu prognostizieren. Derartige Prognosen können für die Entwicklung konkreter, effektiver Naturschutzmaßnahmen eingesetzt werden, indem sie das Auffinden von zukünftig geeigneten Lebensräumen ermöglichen.

Während meiner Promotionsarbeit habe ich Methoden aus den Forschungsfeldern der Makroökologie, der Phylogeographie und der Global Change Biology kombiniert, um Diversitätsmuster auf verschiedenen taxonomischen, geographischen und zeitlichen Ebenen zu untersuchen. Die äußerst diverse Artengruppe der Laufkäfer wurde dabei als Modell-Taxon genutzt und diente dazu, Einblicke in Klimaeinflüsse auf Diversitätsmuster von Invertebraten zu erlangen.

Makroökologische Regressionsmodelle dienten der Erforschung großräumiger Verteilungsmuster in der Körpergröße und der Hinterflügelausbildung westpaläarktischer

Laufkäfer. In den Modellen wurde der Einfluss von Umweltfaktoren (Parameter des heutigen sowie vergangenen Klimas) auf die geographische Verteilung dieser beiden Arteigenschaften untersucht. Die mittlere Körpergröße von Laufkäfern und der Anteil ungeflügelter Laufkäferarten zeigten in Südeuropa ihre höchsten Werte. Während sich die Produktivität und Stabilität von Lebensräumen positiv auf die mittlere Körpergröße von Laufkäfern auszuwirken scheint, sind für die Verteilung des Anteils ungeflügelter Arten wahrscheinlich langfristige Umweltstabilität sowie historische Ausbreitungsprozesse verantwortlich. Die für diese Studie zusammengetragene große Datenmenge wurde in einer Online-Datenbank (www.carabids.org) für andere Wissenschaftler und zukünftige Forschungsarbeiten verfügbar gemacht. Damit können diese Daten auch in Zukunft zur Erweiterung unseres Verständnisses von Diversitätsmustern genutzt werden.

Desweiteren wurde eine an kühl-feuchte Gebirgshabitate angepasste und ausbreitungsschwache Laufkäferart, *Carabus irregularis,* hinsichtlich ihrer Geschichte untersucht. Sowohl phylogeographische mtDNA-Analysen als auch Klimanischenmodelle deuten darauf hin, dass *C. irregularis* das letzte glaziale Maximum in mehreren voneinander isolierten Refugien überlebt hat. Die Art zeigt zwei sehr alte Linien: eine im westlichen Teil des Verbreitungsgebietes und eine in den Karpaten. Eine starke genetische Differenzierung weist darauf hin, dass es sich um zwei ‚evolutionarily significant units‘ (ESUs) handelt, welche sich getrennt voneinander evolutiv entwickelt haben. Diese ESUs könnten sich nicht nur genetisch unterscheiden, sondern auch unterschiedliche ökologische (bzw. klimatische) Nischen besetzen.

Deshalb wurden für diese ESUs in einer weiteren Studie separate Klimanischenmodelle entwickelt, um die zukünftige Verbreitung von *C. irregularis* zu prognostizieren. Bei den Modellen wurden zwei verschiedene Ausbreitungsszenarien, maximale und minimale Ausbreitung, berücksichtigt. Die ESUs zeigten deutliche Unterschiede in ihrer zukünftigen Verbreitung, beide jedoch einen starken Rückgang geeigneter Lebensräume. Das Szenario der minimalen Ausbreitung führte zu einer weiteren Einschränkung der potentiellen Verbreitungsgebiete. Somit scheint *C. irregularis* vom zukünftigen Klimawandel stark bedroht zu sein und das geringe Ausbreitungspotenzial der Art wird die Bedrohung voraussichtlich zusätzlich verschärfen. Die entwickelten Klimanischenmodelle zeigen jedoch verbleibende Gebiete auf, die für ein zukünftiges Vorkommen der Art potentiell geeignet sind, jedoch nicht von der Art eigenständig besiedelt werden können. Diese Gebiete bieten sich als Zielregionen für Schutzmaßnahmen wie der gezielten Ansiedelung der Art an. Somit können Klimanischenmodelle, sofern sie intraspezifische ökologische Unterschiede sowie

Ausbreitungspotenziale von Arten berücksichtigen, gut geeignete Werkzeuge für die Vorbereitung effektiver Naturschutzmaßnahmen sein.

Insgesamt liefert mein Promotionsprojekt wertvolle Hinweise darauf, welchen Einfluss heutige sowie frühere und zukünftige Klimabedingungen auf die Verteilung von Biodiversität auf ihren verschiedenen Ebenen haben können. Die Vielfalt und Kombination der genutzten Methoden trägt zum besseren Verständnis von Klimaeinflüssen auf artenreiche Gruppen sowie auf stenotope, ausbreitungsschwache Insektenarten bei.

SUMMARY

Biodiversity is of great importance for ecosystem functioning which provides ecological, economic and cultural services essential to human well-being. In times of biodiversity loss due to climate change, international conservation efforts aim at the protection of biodiversity. As the development of effective conservation strategies still requires extensive ecological research activities, many recent studies from various disciplines aim at the investigation of the complex relationships between biodiversity and climate. Recent macroecological studies focus on the detection of large scale taxonomic, geographic and temporal patterns and the potential mechanisms driving these patterns. Besides species richness patterns, patterns in species' traits are increasingly being examined to enlarge our knowledge on climate-related effects on spatial and temporal phenomena of species diversity and distribution. Phylogeographic studies address the genetic level of biodiversity (e.g. analysing sequences of mitochondrial DNA = mtDNA) and are commonly used to identify and locate glacial refugia which were important for species survival during past climatic events such as ice ages. The southern European peninsulas are considered as classic refugia and sources of post-glacial dispersal processes. Recently, however, also northern refugia have been discovered. Newly established methods such as species distribution models (SDMs) have been used for the projection of both historical as well as future distribution ranges of species. In the field of global change biology, SDMs are increasingly being used to detect species' range contractions or shifts as a response to climate change. In order to prepare conservation strategies, SDMs can help to locate regions that might be important for future survival of species.

In my thesis, I applied a modern approach combining methods from three fields of biological research – macroecology, phylogeography and global change biology – to analyse patterns on different levels of biodiversity and on different geographic and temporal scales. The highly diverse group of ground beetles was used as a very valuable model taxon to get new insights into the effect of climate on patterns in invertebrate diversity.

Using macroecological regression models I studied broad-scale geographic patterns in two traits of western Palaearctic ground beetles: body size and hind wing development. In order to detect potential drivers of these patterns, the impact of environmental parameters representing both contemporary conditions and historical processes was analysed. Body size and the proportion of flightless species increased from northern towards southern Europe and then decreased again towards North Africa. 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 and dispersal processes. Subsequently, the large data set on Palaearctic carabid traits which has been collected for the macroecological study was made available in an online database (www.carabids.org). This database contributes to the rapid expansion and analysis of readily available traits data on species-rich invertebrates, which will help to advance our understanding of diversity patterns across large spatial scales.

To investigate the history of a cold-adapted, flightless ground beetles species, *Carabus irregularis*, I combined phylogeographic analyses (using mtDNA) with SDMs (calculated in MAXENT). Both methods indicated multiple and isolated glacial refugia, classical as well as northern and Carpathian ones. Two ancient clades, one from the western part of the distribution range and one from the Carpathians, showed strong intraspecific genetic differentiation and point to the existence of two evolutionarily significant units (ESUs). These ESUs might not only differ genetically, but also ecologically from each other.

In a further case study using SDMs, I projected the future distribution of *C. irregularis* and its ESUs under maximal and minimal dispersal scenarios. SDMs for two ESUs from the western and the Carpathian part of the distribution range showed immense, and deviating future range contractions reflecting divergent ecological requirements. The low dispersal ability of *C. irregularis* tend to strengthen the already high vulnerability of the cold-adapted mountain species to global warming, since SDMs assuming minimal dispersal revealed a stronger decline of future ranges than the maximal dispersal models. Areas emerging from our future projections offering climatically well-suitable habitats for *C. irregularis* can be taken into consideration for species conservation activities (e.g. assisted migration). Consequently, SDMs considering both different dispersal scenarios and different ESUs can be useful tools to develop effective species conservation strategies.

In summary, this thesis gives valuable insights as to the effects of climate on biodiversity on different taxonomic, geographic and temporal scales. The wide range and combination of methods used provide important results for 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.

1 GENERAL INTRODUCTION AND CONCLUSIONS

1.1 Background: Biodiversity studies and climate change

Biological diversity (= biodiversity), defined as the richness and variety of life on its three levels – ecosystems, species and genes – is a major issue in ecology and sustainability. Biodiversity is an important basis for healthy and functioning ecosystems which provide ecological, economic and cultural services such as water and nutrient cycling, biomass and food production and spiritual and recreational experiences that are essential to human well-being (Loreau *et al.* 2001; Hooper *et al.* 2005; MEA 2005). Thus, international conservation efforts aim at the protection of biodiversity (e.g. basing on the Converntion on Biological Diversity: UNEP 1992).

In recent years, many researchers have investigated geographic distribution patterns of biodiversity and detected effects of historical and contemporary climate conditions on various taxonomic, geographic and temporal scales (Wolters *et al.* 2006; Field *et al.* 2009; Hortal *et al.* 2011). A multitude of studies have been published highlighting the link between human-induced processes such as future climate change and biodiversity loss (Araújo and Rahbek 2006; Bellard *et al.* 2012; Pereira *et al.* 2012). However, effective conservation of biodiversity and the prevention of further diversity decline still require extensive ecological research activities. Today, combined approaches of various modern biological disciplines such as macroecology, phylogeography and global change biology are making enormous contributions to our understanding of the complex relationships between biodiversity and climate.

1.1.1 Macroecology

The study of large-scale geographic patterns in species richness and in the diversity of species' traits has a long tradition. Since the 18th century, biologists have been interested in spatial patterns of taxonomic diversity (Ricklefs 2004). Biogeographic rules such as Bergmann's and Allen's rule (Bergmann 1847; Allen 1877) have early hypothethised relationships between species characteristics (i.e. body size and the size of body appendages) and environmental conditions such as temperature to explain geographic distribution patterns of species traits. During the last decades, the study of these patterns has undergone a revival and today, macroecological approaches focus on the detection of statistical patterns in large ecological data sets and the potential mechanisms driving these patterns (Brown and Maurer 1989; Blackburn and Gaston 1994). Macroecological research does not only cover broad spatial ranges, but also wide taxonomic scales and considers recent climate as well as the impact of past climate changes (Blackburn and Gaston 1994).

Although, numerous recent studies have extended our knowledge of global distribution of and climatic impact on species richness, our understanding of distribution patterns of species traits is still limited. However, species' traits are increasingly being 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; Bello *et al.* 2010).

Many researchers have reported large-scale patterns in species traits (e.g. García-Barros 2000; Blanck and Lamouroux 2007; Keil *et al.* 2008), with body size being best studied in animal species (e.g. Meiri *et al.* 2004; Olalla-Tarraga *et al.* 2006; McNab 2010). Bergmann's rule, originally formulated for closely related endotherm species in 1847, predicts increasing body size towards high latitudes and cold environments in order to enhance heat conservation. This pattern still applies for birds and mammals (e.g. Blackburn and Hawkins 2004; Olson *et al.* 2009) and interestingly, has also been detected in some ectotherms (Blackburn *et al.* 1999; Huey *et al.* 2000). Invertebrate taxa, however, showed conflicting relationships between body size and contemporary climate, even in the same geographic region: The body size of western Palaearctic spiders tends to decrease towards cool and moist environments in northern Europe (Entling *et al.* 2010), while European ants displayed increasing body size towards higher latitudes (Cushman *et al.* 1993). These patterns were found to reflect 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), to dispersal abilities (Cushman *et al.* 1993).

Since we are only starting to understand the complexity of species' trait patterns, more research is required to enhance our knowledge of the relevant drivers, such as climate-related mechanisms, which shape spatial patterns especially in species-rich invertebrates.

1.1.2 Phylogeography

Current patterns in biodiversity have not only been shaped by contemporary climate, but also by past climate events such as ice ages. In Europe, the glaciers and permafrost grounds of the Quaternary caused the retraction of many species' distribution ranges as well as the extinction of species (Holdhaus 1954). During glacial and interglacial periods, glacial refugia were essential for species' survival as they hosted many species which recently have a widespread distribution across Europe (Hewitt 2000). For temperate and warm-adapted species, classical refugia of the Last Glacial Maximum (LGM) are assumed to have been located on the southern European peninsulas (Taberlet *et al.* 1998; Hewitt 2000). Cold-adapted (i.e. alpine and arctic) species are supposed to have survived in the margins of southern European mountain chains (Stewart *et al.* 2010). However, recent publications from the fields of palaeontology, palynology, and phylogeography, document evidence for so-called cryptic refugia north of the southern European peninsulas and the Alps which until now have been unknown (Bhagwat and Willis 2008; Provan and Bennett 2008).

There are many phylogeographic analyses of spatial patterns in genetic variation of widespread European species (Hewitt 1999; Schmitt 2007; Knopp and Merilä 2009; Valtuena *et al.* 2012), while studies considering mountain species with restricted and disjunct ranges are still scarce (but see Schmitt 2009). Nevertheless, both high (Ronikier 2011; Kropf *et al.* 2012) and low levels of genetic differentiation (Muster and Berendonk 2006; Schmitt and Haubrich 2008) have been detected for species from the Alps and geographically related high and low mountain ranges.

In addition to traditional phylogeographic research methods, species distribution models (SDMs) have been used in association with palaeoclimatic data to identify and locate potential glacial refugia (Waltari *et al.* 2007; Elith and Leathwick 2009). Many studies using this newly established modelling approach have detected classical as well as cryptic refugia (Vega *et al.* 2010; Rebelo *et al.* 2012).

As there are still many uncertainties regarding population histories and glacial refugia, in particular of cold-adapted and low-dispersal mountain species, further phylogeographic research in conjunction with modern methods such as SDMs is needed to develop reasonable scenarios of species' range retractions and expansions during the last ice ages and to understand the possible impacts of future climate changes.

1.1.3 Global change biology

In addition to contemporary and historical climate, future climate change will influence geographic patterns of biodiversity. During the last century, Earth's climate has changed immensely, global temperature has risen and patterns of temperature and precipitation have changed (IPCC 2007). Besides extinctions, phenological shifts, and evolutionary responses, shifts in species' distribution ranges have been observed, all of which are considered to be reactions to climate change (Walther *et al.* 2002). An increasing number of studies have documented range shifts towards higher altitudes or latitudes (Parmesan and Yohe 2003; Hickling *et al.* 2006).

Due to the loss of moist and cool habitats, cold-adapted mountain species are considered to be particularly sensitive to global warming (Wilson *et al.* 2007; Settele *et al.* 2009; Dieker *et al.* 2011). The low dispersal abilities of many of these species can lead to the further limitation of future distribution ranges (Svenning and Skov 2004; Schloss *et al.* 2012).

SDMs are being used to assess future species' distribution ranges by relating current species occurrence with climatic variables from future climate scenarios in addition to their usage in predicting past and present distribution patterns (Guisan and Thuiller 2005; Elith and Leathwick 2009). Although SDMs have been criticised for taking only climate parameters into account, and for neglecting other ecological factors such as species interaction and species' dispersal abilities (Araújo and Guisan 2006; Heikkinen *et al.* 2006), modelling methods are constantly being improved and can be valuable tools to support the localisation of future climatically suitable habitats (Elith and Leathwick 2009; Schwartz 2012). Predictions for species with restricted distribution ranges due to their adaption to special environmental conditions and/or low dispersal abilities are still rare. Prospectively, modelling results can be an essential precondition for the development of conservation strategies suitable for these species.

1.2 Ground beetles as a study taxon

Ground beetles (Coleoptera: Carabidae) are a very species-rich group, with about 40,000 species worldwide, more than 10,000 in the Palaearctic and approximately 3,000 species in the western Palaearctic region. The taxonomy and species' distribution of this group are very well-documented for the Palaearctic region (Löbl and Smetana 2003), and the evolutionary biology and ecology, especially of European species has been well studied for a long time (e.g. Burmeister 1939; Lindroth 1945; Thiele 1977; Lövei and Sunderland 1996; Rainio and Niemelä 2003). These are all essential preconditions for the compilation of large and reliable data sets for macroecological studies on a wide geographic extent (Isaac *et al.* 2004; Lovell *et al.* 2007; Hortal 2008) allowing the consideration of large geographic scales which is important for the comprehension of diversity patterns (Wolters *et al.* 2006).

Ground beetles are not only rich in species numbers, but also diverse in species' characteristics. The group contains both restricted-range (endemic) and widespread species, specialists as well as generalists species, and can be found in a wide variety of habitats (Thiele 1977). In addition, ground beetle species differ in terms of their dispersal abilities, with winged species, which are mostly able to fly, as well as wingless and flightless species (Lindroth 1949; Aukema 1986; Aukema 1990). Use of this taxon enables the study of biodiversity patterns that may differ between widespread and endemic species (Orme *et al.*

2005; Rahbek *et al.* 2007; Schuldt and Assmann 2009) and between species with high and low dispersal abilities (Baselga *et al.* 2012). Moreover, ground beetle species diversity correlates endemism and species richness patterns of numerous invertebrates, vertebrates and plants on broad geographic scales (Schuldt and Assmann 2010). Most ground beetles are predators (occupying high trophic levels), which are assumed to be very sensitive to climate changes (cf. Voigt *et al.* 2007). The carabid family includes many species inhabiting disjunct distribution ranges, such as those inhabiting mountains (Thiele 1977; Turin *et al.* 2003a). These species are, on the one hand, likely to be genetically differentiated which enables phylogeographic reconstruction of species' history (Avise 2000; Schmidt *et al.* 2012) and some wingless species belong to the most differentiated species (Matern *et al.* 2009). On the other hand, mountainously distributed species are considered to be very vulnerable to future global warming due to shrinking habitats (Wilson *et al.* 2007; Settele *et al.* 2009). However, the effects of climatic conditions on ground beetles, and their distributions and characteristics have so far only been studied on smaller scales. Thiele (1977) for instance found an influence of climate on single species' habitat preferences and a positive relationship between habitat continuity as a surrogate for stable environmental conditions and hind wing reduction was documented for a few species in ancient habitats (e.g. Brandmayr 1983; Desender *et al.* 1999).

In summary, ground beetles are a very valuable model taxon to get insights into diversity patterns which are also relevant to less well-documented invertebrate taxa with similar traits. The following four chapters present case studies using modern approaches combining methods from different three fields of ecological research: macroecology, phylogeography and global change biology. This thesis contributes to the understanding of climatic effects on geographic diversity patterns in the Palaearctic region, especially in Europe. My analyses address different levels of biodiversity, as I worked on assemblage, on single species and on intraspecific genetic levels. In addition, I studied the relationships between climate and diversity on different temporal scales taking into account the effects of contemporary, historical and future climate conditions. Figure 1.1 gives an overview on the different taxonomic, geographic and temporal scales of the case studies of my thesis. In addition, links between the chapters are shown.

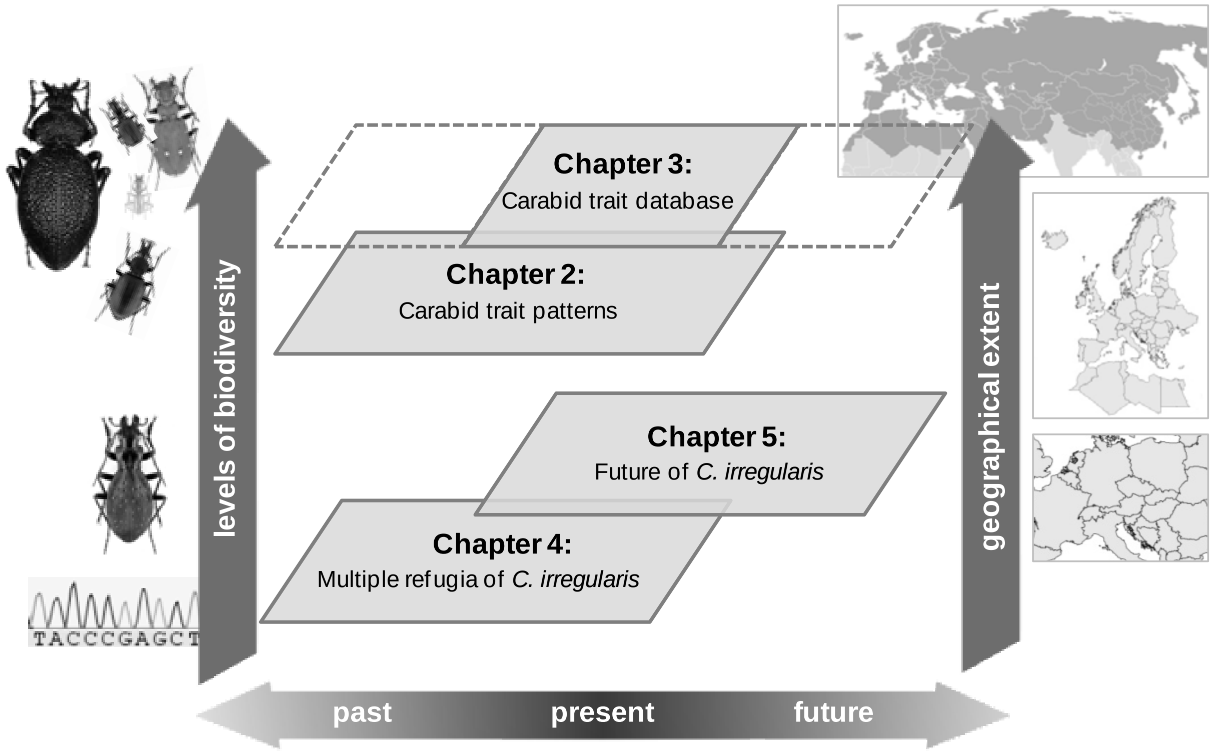

Figure 1.1. Overview as to the biodiversity levels, and the geographic and temporal scales addressed in this thesis, allocation of the chapters, as well as relationships between chapters. Dashed lines indicate that results of Chapter 3 can be readily used for further studies considering different temporal scales. (Photos of ground beetles by O. Bleich, www.eurocarabidae.de).

1.3 Aims and hypotheses of this thesis

1.3.1 Large-scale patterns in carabid species' traits

Chapter 2 documents my analysis of macroecological patterns in two traits of the species-rich insect taxon of carabid beetles – body size and hind wing development, with the latter being linked with dispersal ability. Potential impacts of contemporary as well as historical climate were tested using regression models which included spatial, areal, topographic and climate-related variables for (1) *all*, (2) *widespread* and (3) *endemic* (restricted-range) species. Invertebrate body size has been assumed to increase with productivity as well as with metabolic rate in regions with high energy availability (cf. Mousseau 1997; Wilson *et al.* 2007; Entling *et al.* 2010; McNab 2010). It is also assumed to increase towards arid regions due to the higher desiccation resistance of larger bodies (Remmert 1981; Yom-Tov 1986; Yom-Tov and Geffen 2006). Since biodiversity pattern, especially in Europe, have also been shaped by past climate changes and events such as glacial periods (Holdhaus 1954; Schmitt 2007), historical climate stability and dispersal processes might also play an important role in explaining current geographic patterns of carabid species' traits.

In studies on smaller spatial scales, hind wing reduction has been found to increase with habitat stability (cf. Brandmayr 1983; Assmann 1999; Desender *et al.* 1999). This may be due to a trade off in energy allocation between dispersal ability and reproduction effort (oogenesis flight syndrome: Roff 1986b; Desender 2000).

In this macroecological chapter, I test the following main hypotheses:

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.

This macroecological study provides valuable insight into the potential mechanisms driving large-scale spatial patterns of two species traits of a highly diverse invertebrate taxon.

In **Chapter 3** I present the content and the structure of a database on carabid species traits which I developed (started with data collection for Chapter 2; Figure 1.1). This database is now available freely online (http://www.carabids.org) and contains species classification and distribution data for over 10,000 Palaearctic carabid species (obtained from Löbl & Smetana 2003). For almost all (over 3,400) western Palaearctic species, size and dispersal traits (body and eye size and hind wing development) are available. For most Central European (about 1,000) species, ecological and life-history traits are made available. Traits data can be easily downloaded by registered users.

Data expansion and analyses are meant to contribute to the investigation of a multitude of future research questions on community assembly and on functional diversity of species-rich invertebrate taxa across large spatial scales.

1.3.2 Glacial refugia of a cold-adapted, flightless ground beetle species

In **Chapter 4** I used a combined approach of species distribution modelling and phylogeographic analysis of two mitochondrial DNA loci to investigate the history of *Carabus irregularis*, a flightless ground beetle species, which occurs in a disjunct range across high- and low-altitude mountains in Central and eastern Europe.

Previous studies have used SDMs to locate classical refugia (in the Alps and on the southern European peninsulas) as well as northern glacial refugia of plant and animal species (e.g. Vega *et al.* 2010; Rebelo *et al.* 2012). Studies using more traditional tools for the reconstruction of species' population histories as phylogeographic analyses, are still more abundant for widespread species than for mountain species with restricted or disjunct ranges. Nevertheless, high genetic differentiation and ancient phylogenetic splits have been documented for some plant species inhabiting parts of the Alps and geographically associated mountain systems (e.g. the Central European mountain ranges, the Carpathians) (Ronikier 2011; Kropf *et al.* 2012). For arthropod species with relatively high dispersal abilities (e.g. spiders and butterflies: Muster and Berendonk 2006; Schmitt and Haubrich 2008), low levels of genetic differentiation indicate young and even post-glacial splits between populations from the Alps and from neighbouring high and low mountain ranges (Schmitt 2009). Since *C. irregularis* is a low-dispersal species with a scattered distribution, it is likely to show strong genetic differentiation. It is assumed to have survived the last glacial maximum in northern refugia, which have been repeatedly found for low-dispersal species (Bhagwat and Willis 2008; Provan and Bennett 2008). In addition, *C. irregularis* is comprised of three subspecies, two of which have geographically separated distributions (Turin *et al.* 2003a) and thus might represent divergent phylogenetic groups.

In this chapter I address the following main hypotheses using phylogeographic and 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*.

1.3.3 Future distribution and conservation of a flightless ground beetle species

In the framework of the evolutionarily significant unit (ESU) concept (Moritz 1994) addressed in **Chapter 5**, I projected the future distribution ranges of the two phylogenetic units discovered with the analyses described in Chapter 4 using SDMs for two different future climate scenarios (A2a and B2a, IPCC) and two different dispersal scenarios. The modelling results were used to suggest conservation strategies which might be applicable for the cold-adapted mountainously distributed ground beetle species *Carabus irregularis.*

SDMs have mostly been applied to predict range retractions and loss of suitable habitat conditions, however, for species conservation it can be even more useful to locate regions that will provide suitable climate conditions in the future (Schwartz 2012). *C. irregularis* is assumed to be very vulnerable to climate change due to its cold-adaptedness and low dispersal ability (see Chapters 1.1.3 and 1.2) and therefore developing sound conservation strategies for this species is of great importance.

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

i) The ESUs of *C. irregularis* show divergent current and future potential distribution ranges.

ii) The minimal dispersal scenario will lead to smaller future ranges than projected by the maximal dispersal model.

I used these results to identify potential consequences of climate change and suggest effective species conservation activities.

1.4 Main findings and prospects

This thesis brings together insights as to the effects of climate on biodiversity on different taxonomic, geographic and temporal scales. The highly diverse group of ground beetles turned out to be an appropriate model taxon to analyse diversity patterns and their potential determinants in invertebrates on the large scale. *Carabus irregularis* studied on both species level and intraspecific genetic level, can be considered as one representative of cold-adapted low-dispersal species. The variety and combination of methods used provide a better understanding of the effects of historical, of contemporary and of future climate on diversity patterns in insects. My main results are in accordance with my hypotheses formulated in the above section.

1.4.1 Insights from a species-rich taxon and future research perspectives

On large taxonomic and geographic scale, I detected spatial patterns in both carabid species' traits – body size and hind wing development. Resembling hump-shaped distribution patterns of carabid diversity in the same study area (cf. Schuldt and Assmann 2009), carabid body size and the proportion of flightless species increased from North Africa towards southern Europe and decreased towards northern Europe. According to mechanisms assumed for other taxa (cf. Blackburn and 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, however, might result in low values of carabid body size despite high energy values. Although in other arthropod taxa a shortage of water in arid regions such as North Africa is thought to lead to larger body sizes in order to heighted desiccation resistance (Remmert 1981; Entling et al. 2010), mechanisms in carabids seem to be different. Desiccation risk in arid regions may 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). Similar to previous studies on smaller scales, high proportions of flightless species were found in regions of current climatic stability represented by measures of balanced water-energy availability. The proportion of flightless individuals and of flightless species was found to increase towards habitats with low environmental variability (documented for permanent/stable habitats: Brandmayr 1983; 1991; Assmann 1999; Desender et al. 1999). Microevolutionary processes such as wing reduction due to energy allocation between dispersal and reproduction can increase fecundity and promote local recruitment (Roff 1986a; Desender 2000), enabling carabid beetles to adapt to specific habitats and/or changing environments (cf. Thiele 1977). These processes might also drive patterns at larger geographic scales. However, decreasing flightlessness from southern towards northern Europe might also result from historical dispersal processes, which are in Europe strongly affected by historical climate events such as glaciations (Holdhaus 1954; Schmitt 2007). Scenarios of the survival of species in southern European refugia and postglacial re-colonisation towards northern Europe have been supported by several molecular analyses (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. Winged species, currently occurring more widespread might have been able to colonise larger geographic ranges due to higher dispersal ability (cf. Gutiérrez and Menéndez 1997; Svenning and Skov 2007; Araújo *et al.* 2008). Flightless species, however, currently inhabit restricted ranges of southern Europe. Here it remains unclear whether low dispersal of flightless species caused their restricted range in regions of former glacial refugia or flightlessness evolved in restricted habitats of refugia. Refugia could have offered restricted but long-term suitable habitats supporting the reduction of wings (Brandmayr 1991).

In summary, carabid traits do not show simple latitudinal clines but distinct geographic patterns that tend to be influenced by both contemporary environmental conditions and by historical processes. Thus, my results contribute to the understanding of diversity patterns in insects. Although insects represent large parts of the global biodiversity and are often assumed to provide key functions in ecosystems (Samways 2005), data on insect species traits is still not readily available on large taxonomic and geographic scales. As trait-based approaches are increasingly being used to analyse and understand a multitude of spatial and temporal patterns of species distribution and abundances (McGill *et al.* 2006; Bello *et al.* 2010), I intended to enhance my large data set on carabid traits and make it available for other scientists. The online database www.carabids.org is meant to be a collaborative and interactive project offering a variety of future research opportunities in different ecological fields.

1.4.2 Insights from a specialised species and future research perspectives

On the diversity level of species distribution ranges, I have found several independent mountainous regions across Central and southern Europe which could have acted as glacial refugia during the LGM due to their highly suitable climate conditions for *C. irregularis* during this period. While some of these coincide with classical refugia on the southern European peninsulas (Hewitt 1996; 1999; 2000), other potential refugia of *C. irregularis*, for instance those at the margins of the Alps and in neighbouring mountain ranges, have only recently been recognised (Schönswetter *et al.* 2005; Pauls *et al.* 2006; Schmitt *et al.* 2006). Additionally, potential refugia far north of the southern European peninsulas and the Alps have been assumed for an increasing number of species (Stewart and Lister 2001; Provan and Bennett 2008) and were also detected for the studied ground beetle. Thus, *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). As mountain species are assumed to have survived in several spatially restricted refugia rather than in extensive and consistent ones (Holderegger and Thiel-Egenter 2009; Schoville *et al.* 2012), multiple refugia appear feasible for the cold-adapted mountain species, *C. irregularis.*

The assumption of the existence of multiple-refugia during the LGM was supported by phylogenetic analyses on the genetic, intraspecific level of diversity. My analyses revealed two well-supported and spatially congruent major clades: one Central European with three subclades and one Carpathian clade with two subclades. The ages of all major phylogenetic splits predating the last ice age and high genetic intraspecific differentiation in *C. irregularis* imply that the ancestors of the (sub)clades remained isolated from each other for a long period of time. The locations of potential refugia found in phylogeographic study partially coincide with the potential refugia found using SDMs. Two refugia located close to the Alps or on the Balkan Peninsula and one northern refugium were found using both methods. However, phylogenetic analyses indicated the existence of independent Carpathian refugia, which were hardly evident from the western European distribution model for LGM conditions. Northern and Carpathian refugia are not considered as classical ones and phylogeographic studies including the Carpathian region are still rare. However, the investigation of the Carpathians appears to be very interesting, as this mountain range has faced a different glacial history than the well-studied Alps (Ronikier *et al.* 2008; Ronikier 2011). However, there are some botanical studies that showed similar patterns to those I detected: Alpine plants showed distinct and strongly differentiated genetic groups within the Carpathians, also pointing to long-term isolation and restricted gene flow between several areas within the mountain system (Mráz *et al.* 2007; Ronikier *et al.* 2008; Ronikier 2011). While Ronikier et al. (2008) discovered the strongest differentiation between western and eastern Carpathian samples, my results for *C. irregularis* resemble findings of Mráz et al. (2007), who detected high differentiation between southern and eastern Carpathian populations. *C. irregularis* is the first animal species showing this phylogeographic ancient differentiation pattern with basal splits between the Carpathians and the western part of the distribution range.

In part, the phylogenetic results of my study resembled subspecies systematics: One monophyletic clade represented the Carpathian subspecies *C. i. montandoni*, the other clade was paraphyletic and contained two subspecies (*C. i. irregularis* and *C. i. bucephalus*). Thus, in the case of *C. irregularis* conventional taxonomy must be questioned. Altogether my results indicate that *C. irregularis* has a very interesting history resulting in two geographically and genetically independent groups which might have varying ecological niches. These two groups can be considered to be two evolutionarily significant units (ESUs, *sensu* Moritz 1994, (Moritz 1994) which should be investigated in more detail by further phylogeographic analyses – also in the framework of the whole *Platycarabus* group.

In my further study, the two ESUs of *C. irregularis* indicated differing environmental or climate niches as SDMs handling the ESUs separately showed clear differences between the current and future potential distribution ranges of the two groups. Other studies revealed strong differences of habitat requirements and habitat association also within other beetle species (e.g. Vogler *et al.* 1993b; Vogler and DeSalle 1994), and especially ancient lineages, tend to show strong intraspecific ecological differentiation due to evolutionary processes (Rasplus *et al.* 2001). As habitat preference is assumed to be a heritable attribute in ground beetles (Thiele 1977), and different intraspecific variability in habitat requirements can result in different distribution patterns, ecological divergences between subgroups need to be considered in SDMs for a proper estimation of future species distributions.

My SDMs projecting the future distribution of the two ESUs of *C. irregularis* showed only very small remaining areas of suitable climate conditions in relation to the species' recent distribution range. This finding is in accordance with the assumption 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). The realised distribution of the flightless ground beetle, *C. irregularis*, tends to be further restricted by dispersal limitations and cannot be equatable with the distribution of suitable climate conditions (Engler and Guisan 2009; Kharouba *et al.* 2012; Schlaepfer *et al.* 2012). Consequently, it appears more useful to apply SDMs for the identification of future suitable habitats than for the estimation of potential habitat loss (cf. Schwartz 2012). Future suitable regions may then be involved in the development of effective species conservation strategies such as assisted migration. Assisted colonisation of suitable habitats which could not be reached self-initiatedly due to low dispersal has been successfully implemented for other ground beetle species *(*e.g. *Carabus olympiae*: Malausa and Drescher 1991). Thus, assisted migration using enclosures and providing thus comparable and controllable settings *(e.g. already applied for Carabus, Poecilus* and *Olistopus species*: De Vries 1996; Schwöppe *et al.* 1998) seems to be a useful strategy for *C. irregularis*.

In summary, *C. irregularis* was studied across its entire distribution range and its population history was analysed on a large temporal scale, ranging from the last glacial maximum to forecasts under global change conditions. SDMs projecting past and the future species distribution ranges proved to be useful tools for the reconstruction of species' histories and for the preparation of species conservation strategies, and the modelling approach should be applied for further studies on species that are sensitive to climate change. Especially, the combination of SDMs with phylogeographic results in order to take account of potential ecologically divergent subgroups within species appears reasonable.

1.5 Appendix: Authors' contributions to manuscripts

This thesis is a cumulative dissertation with four manuscripts that have been either published, submitted for publication or are close to submission for the publication in international peer-reviewed journals. The manuscripts are the work of multiple authors, whose contributions are shown below. Table 1.1. gives an overview of the manuscripts in this thesis with declaration of the portion of my personal contribution to each study, publication status of each manuscript and information on the chosen publication media.

Katharina Homburg[1] is the lead author of all manuscripts. She carried out the majority of the research, and personally wrote and edited all manuscripts. She developed the main ideas of all the manuscripts, collected all data for the studies, and performed all analyses. In addition, she created all of the figures, tables and supplementary materials for the manuscripts. Furthermore, she was responsible for the correspondence with editors and reviewers of the international scientific journals.

Table 1.1. Overview of the manuscripts in this thesis with declaration of the portion of my personal contribution to each study, publication status of each manuscript and information on the chosen publication medium. In addition, titles, places and dates of presentations of related results at academic conferences are given (including www-links of the calls for these conferences). WF = Weighting Factor according to §§9 and 12 "Richtlinie zur kumulativen Dissertation – Dr. rer. nat. der Fakultät Nachhaltigkeit, 24.02.2012"; IF = 2011 Impact Factor according to the ISI Web of Knowledge

Chapter	My portion of contribution to (WF)	Publication status of the manuscript	Publication medium (IF)	Presentation of results at conferences
2	predominant portion (1.0)	published: DOI: 10.1111/ j.1600-0587. 2012.07488.x	international peer-reviewed journal (4.19)	**Schäfer *et al. (2010)*:** Do carabids follow Bergmann's rule? – A macroecological study on ground beetles in the western Palaearctic (Coleoptera: Carabidae). The GfÖ 40th Anniversary Meeting. Aug 30 - Sept 3, 2010, Gießen, Germany. Poster. http://www.gfoe-giessen-2010.de/
3	predominant portion (1.0)	published: DOI:10.1111/ icad.12045	international peer-reviewed journal (1.71)	*Planned*
4	predominant portion (1.0)	published: DOI:10.1111/ j.1365-294X. 2005.02506.x	international peer-reviewed open access journal (4.09)	**Homburg *et al. (2012)*:** Linking phylogeography and global change biology: history and future of the cold-adapted ground beetle *Carabus irregularis*. 42th annual Meeting of the GfÖ. Sept 10 - Sept 14, 2012. Lüneburg, Germany. Talk. http://www.gfoe-2012.de/
5	predominant portion (1.0)	submitted	international peer-reviewed journal	

Thorsten Assmann[1] was the main supervisor of this thesis. He gave input as to the main ideas and the development of the applied analyses methods. He also commented on earlier versions of all manuscripts.

Claudia Drees[1,2,3] was involved in the development and optimisation of laboratory procedures as well as in the discussion of (especially phylogeographic) data analyses and result presentation. She commented on earlier drafts of three manuscripts.

Andreas Schuldt[1] was involved in the discussion of statistical analyses of macroecological data and commented on early versions of two manuscripts.

Nils Homburg[4] developed the www.carabids.org web site and was involved in data migration. **Florian Schäfer**[5] developed computer programmes which were used for data migration from a printed catalogue to a digital database.

Patric Brandt[1,6] provided assistance with species distribution modelling and was involved in the development and analyses of complex models. He commented on the first drafts of one manuscript.

Martin M. Gossner[7], **László Rakosy**[8] and **Al Vrezec**[9] provided help with data and sample collection from Germany, Romania and Slovenia for modelling and/or phylogenetic analyses. They commented on early versions of one manuscript.

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VERSICHERUNG

Ich versichere, dass alle in diesem Anhang gemachten Angaben jeweils einzeln und insgesamt vollständig der Wahrheit entsprechen.

Lüneburg, 20.12.2013

2 BROAD-SCALE GEOGRAPHIC PATTERNS IN BODY SIZE AND HIND WING DEVELOPMENT OF WESTERN PALAEARCTIC CARABID BEETLES (COLEOPTERA: CARABIDAE)

Published Article

Katharina Homburg, Andreas Schuldt, Claudia Drees and Thorsten Assmann, Ecography 36 (2013): 166-177. DOI: 10.1111/j.1600-0587.2012.07488.x

Abstract

Research into large-scale ecological rules has a long tradition but has received increasing attention over the last two decades. Whereas environmental, especially climatic, influences on the geographic distribution of species traits such as body size are well understood in mammals and birds, our knowledge of the determinants and mechanisms which shape spatial patterns in invertebrate traits is still limited. This study analyzes macroecological patterns in two traits of the highly diverse invertebrate taxon of carabid beetles: body size and hind wing development, the latter being directly linked to species' dispersal abilities. We tested for potential impacts of environmental variables (spatial, areal, topographic and climate-related) representing both contemporary conditions and historical processes on large-scale patterns in the two traits. Regression models revealed hump-shaped relationships with latitude for both traits in the categories (1) all species, (2) widespread and (3) endemic (restricted-range) species: Body size and the proportion of flightless species increased from northern towards southern Europe and then decreased towards North Africa. The shared and independent influence of environmental factors was analyzed by variation partitioning. While contemporary environmental productivity and stability (represented by measures of ambient energy and water-energy balance) had strong positive relationships with carabid body size, patterns in hind wing development were most notably influenced by topography (elevation range). Regions with high elevation range and low historical climate variability (since the last ice age), which likely offer long-term stable habitats (i.e. glacial refugia), coincide with regions with high proportions of flightless species. Thus geographic patterns in carabid traits tend to be formed not only by recent climate but also by dispersal and historical climate and processes (i.e. glaciations and postglacial colonization).

2.1 Introduction

Whilst broad-scale ecological rules have been known for a long time (e.g. Bergmann 1847), macroecological approaches providing new insights to this field of research have gained increasing interest during the last two decades. Numerous recent studies have reported large-scale geographic patterns in species characteristics (e.g. García-Barros 2000; Blanck and Lamouroux 2007; Keil *et al.* 2008), with body size being one of the best-studied traits in animal species (e.g. Olalla-Tarraga *et al.* 2006; McNab 2010). The prediction of increasing body size towards high latitudes and cold environments (Bergmann's rule) was originally formulated for closely related endotherm species, and the associated heat conservation hypothesis still applies for birds and mammals (e.g. Blackburn and Hawkins 2004; Olson *et al.* 2009). Interestingly, some studies on ectotherms also show geographic patterns in body size variation (Blackburn *et al.* 1999; Huey *et al.* 2000). However, even in the same study region, invertebrate taxa show converse patterns: e.g. decreasing body size of western Palaearctic spiders (Entling *et al.* 2010) and increasing body size of European ants towards northern Europe (Cushman *et al.* 1993). Thus, driving mechanisms appear to be complex and not yet well understood – especially since studies on species-rich invertebrates are still scarce.

Here, we study geographic patterns in body size for a hyperdiverse (about 3,400 species in the study region) invertebrate taxon, carabid beetles (Coleoptera: Carabidae), in the western Palaearctic. In addition, we investigate patterns in hind wing development, a trait directly linked to dispersal ability and important for carabids, as they comprise both flightless species as well as winged species, which are mostly able to fly. In contrast to other invertebrate taxa, carabids are well-examined in terms of ecology and physiology (e.g. Thiele 1977; Lövei and Sunderland 1996), bioindication potential (e.g. Rainio and Niemelä 2003) and distribution of the individual species (e.g Löbl and Smetana 2003; Turin *et al.* 2003a). Furthermore, species richness and endemism also show strong positive cross-taxon correlations with diversity patterns of other invertebrates and vascular plants (Schuldt *et al.* 2009; Schuldt and Assmann 2010). Thus, carabids are well-suited to further our understanding of distribution patterns in the traits of species-rich ectothermic invertebrates. Richness patterns of widespread carabid species tend to be affected by contemporary climate more strongly than patterns in range-restricted species (Schuldt and Assmann 2009). This finding has also been reported for other groups of organisms (Jansson 2003; Jetz *et al.* 2004; Orme *et al.* 2005) and reflects a persisting impact of historical processes such as postglacial re-colonization on diversity patterns in endemics (Hewitt 1999; Drees *et al.* 2010; Habel *et al.* 2010b). Therefore, our study on carabid traits differentiates between widespread and endemic to take into account potential effects of current climate but also of historical processes.

We analyzed the relationships between spatial distribution patterns of two traits – carabid body size and hind wing development – and environmental factors (climate, area, topography and historical climate variability) to test biogeographical hypotheses. Climatic measures represent contemporary environmental productivity and stability (e.g. water and energy availability and water-energy balance). Historical climate variability (climatic changes since last glaciations) is reflected by the degree of glaciation at the end of the last ice age (cf. Hewitt 1999), where low degrees of glaciation indicate low climate variability and long-term stable climatic/environmental conditions. Additionally, regions with high elevation ranges can represent low values of historical climate variability, as glacial refugia were located in mountainous regions (Hewitt 1999, Drees *et al.* 2010).

First, we test the hypothesis (H1) that carabid body size increases towards both (a) lower latitudes (increasing body size with productivity and metabolic rate in regions with high energy availability; cf. Mousseau 1997; Entling *et al.* 2010; McNab 2010), and (b) arid regions (increasing desiccation resistance of larger bodies; cf. Remmert 1981; Yom-Tov 1986; Yom-Tov and Geffen 2006).

Second, with regard to hind wing development we hypothesize (H2) increasing flightlessness towards (long-term) stable environments and regions of low historical climate variability (e.g.in lower latitudes or higher altitudes and in glacial refugia; Holdhaus 1954; Brandmayr 1983; 1991). A positive relationship between wing reduction and environmental stability (due to energy allocation between dispersal and reproduction in stable environments; cf. Assmann 1999; Desender *et al.* 1999) has repeatedly been postulated (e.g. for ancient habitats), but has as yet only been studied at small scales (e.g. Brandmayr 1983, Desender *et al.* 1999).

We also studied the geographic patterns of both traits within the subfamilies of Carabidae, in order to estimate whether interspecific patterns on a family level tend to be the result of an uneven distribution of phylogenetic subunits with different traits (cf. Entling *et al.* 2010). In sum, our study provides insight into the potential mechanisms driving spatial patterns in two species traits, which have rarely been tested for such a species-rich invertebrate taxon at a large scale.

2.2 Material and methods

2.2.1 Study area

The study area comprised 39 European and North African countries with a well-sampled carabid fauna (see also Schuldt and Assmann 2009). Small countries (e.g. Andorra and Liechtenstein), islands (e.g. Cyprus and Iceland) and Russia were excluded due to incomplete data (for a complete list, see Supplementary material, Table S2.1). Species accumulation curves by Schuldt and Assmann (2009) document data completeness and reliability for the chosen western Palaearctic countries. Species richness in countries of the study region reached a clear asymptote during the 20th century (for accumulation curves exemplary of small as well as larger countries, see Supplementary material, Figure S2.1). Countries with anomalous values of species richness and also of body size and hind wing development (i.e. particularly the North African countries) were reviewed before our analyses to identify and exclude outliers. Libya was excluded to ensure an unbiased analysis of western Palaearctic patterns, since measures of carabid body size were extraordinarily high in comparison to all other countries in the study area – potentially an artifact of low species numbers.

2.2.2 Species data

A database of 3,136 carabid species was compiled for the western Palaearctic countries included in the study. Species nomenclature, classification and data on distributions were extracted from the Catalogue of Palaearctic Coleoptera (Löbl and Smetana 2003). Investigations into the species distribution of invertebrates are commonly based on country-level data, since it is difficult to investigate most of these taxa at more detailed scales across a large geographic area (Baselga 2008; Hortal 2008; Ulrich and Fiera 2009). Data from Löbl and Smetana (2003) were complemented by additional information on body size and hind wing development taken from the relevant literature (769 original species descriptions, monographs and other treatises; see entire bibliography in Supplementary material Appendix 2). In some cases, not even the original species descriptions contained information on the traits analyzed in the present study. However, a maximum of 3% of size data and 10% of wing data were missing for individual countries in the study region (with the exception of Egypt with 12% and 10% missing data on size and wings, respectively). The low frequency of missing data was unlikely to affect the results of this study.

In carabids, there is a strong relationship between body mass and body length described by a power function (Booij *et al.* 1994). Consequently, body mass, the crucial trait for macroecological issues related to body size, can be approximated well by body length. As body size is usually documented as body length instead of body mass, we used this measure rather than converting to mass.

For each species, minimum and maximum values of body length were collected and the arithmetic mean body size of the species was calculated from these values, followed by a log-transformation to normalize distributions. Then we calculated geometric means of carabid body size for each country of the study region (Quinn and Keough 2002).

The hind wing development of carabid species results in two phenotypes: brachypterous (hind wings shorter than elytra or missing) and macropterous (hind wings fully developed) individuals (cf. Lindroth 1970; Aukema 1986; Aukema 1990). In the database we classified species into three categories of hind wing development: (i) ‘brachypterous’, (ii) ‘macropterous’, and (iii) ‘dimorphic’ (species containing individuals with reduced as well as fully developed hind wings). For further analyses of the geographic distribution of different hind wing morphs and a potential relationship with the dispersal power of the species, brachypterous species were considered as ‘flightless’, macropterous and dimorphic species were pooled and rated as ‘winged’ and potentially flying. In the following, the terms ‘winged’ and ‘flightless’ are used for the two groups of hind wing development and/or dispersal power.

For each country, we calculated the proportion of flightless species in the total number of all, widespread and endemic species. Species were classified as 'endemic' (range sizes < 6 x 10^5 km²) or 'widespread' (range sizes > 6 x 10^5 km²; classes defined by Lumaret and Lobo 1996) based on the combined area of the countries in which they have been recorded, refined by expert knowledge on distributions of the individual species (i.e., occurrence of species only in parts of larger countries, e.g. species restricted to the Alps). Occurrences outside the study regions were also taken into account to avoid border effects.

2.2.3 Environmental data

In order to test hypotheses regarding geographic patterns in body size and hind wing development, we included data on space, area, current climate, topography and historical climate variability (15 variables in the form of country-level averages; Supplementary material, Table S2.2) in our analyses. Variable selection for the analyses in our study was predominantly based on our hypotheses on productivity (H1), environmental stability as well as historical climate variability (H2) and included temperature and precipitation data, topographic data and spatial variables, which are commonly used in comparable studies (e.g. Ulrich and Fiera 2009; Entling *et al.* 2010). In order to account for a possible effect of patterns in species diversity on patterns in species traits, species richness (number of species occurring in each country) and species density within each country (number of species per km²) were also considered in our analyses.

The selected variables represent environmental productivity and resource availability (water and energy availability: measures of precipitation and temperature; cf. Hawkins *et al.* 2003, McNab 2010) and current environmental stability (measure of seasonality in water and energy availability and water-energy balance – actual evapotranspiration; Hawkins and Porter 2003). In addition, topographic variability (elevation range) reflects habitat heterogeneity (cf. Willig *et al.* 2003; Jetz *et al.* 2004) and especially for the western Palaearctic, it might be indicative of regions providing long-term possibilities for survival and speciation in glacial refugia in mountainous regions (cf. Hewitt 1999). Historical climate variability (*variability*) was additionally tested as a trinomial explanatory variable accounting for the degree of glaciation at the end of the last ice age. Countries were rated as (1) non-glaciated, (2) permafrost and (3) glaciated areas (cf. Hewitt 1999) depending on to which category more than 50% of the country area belong. Historical climate variability was tested independently from current climate, since some variables of historical and current climate tend to be highly correlated (cf. Araújo *et al.* 2008) and their effects on patterns in species' traits may not be easy to separate.

We included latitudinal (*lat*) and longitudinal (*long*) coordinates (decimal degrees) of the central point of each country for a general characterization of spatial patterns in species traits. Latitude and longitude, as well as country size (in km^2 = *area*) and data on topographic variability (represented by elevation range in m = *elev*) were extracted from CIA (2008). *Area* was included to account for differences in country size and potentially associated effects of sampling effort (assuming that the probability of finding very large and very small species increases with country size; cf. Ulrich and Fiera 2010). However, as mentioned above, all countries considered for the analyses are well-sampled and show high values of data completeness. Climatic variables comprised temperature variables (°C: mean annual temperature = *temp*; temperature of the coldest = *cold* and warmest month = *warm*; temperature seasonality = *seast*) and precipitation variables (mm: mean annual precipitation = *prec*; mean precipitation from March to November = *prec_mn*; precipitation seasonality = *seasp*) as well as data on frost frequency (number of days with temperatures below 0°C = *frost*). These data were extracted from Mitchell *et al.* (2002). Mean values for actual (*AET*) and potential evapotranspiration (*PET*; mm yr^{-1}) were calculated using Thornthwaite's method (Thornthwaite and Mather 1963; Thornthwaite and Mather 1964).

2.2.4 Statistical analyses

To analyze environmental predictors for patterns in body size (mean logarithmic body size) we computed ordinary linear regression models. Patterns in hind wing development (proportion of flightless species) were analyzed with generalized linear models (GLMs) with quasi-binomial errors (due to overdispersion of the data). For each trait, we developed three models for (1) *all* carabid species together and for (2) *widespread* species and (3) *endemic* species separately. Non-linear relationships between the traits and environmental variables were checked prior to model selection (cf. Quinn and Keough 2002). The values of environmental variables were centered prior to calculating polynomials to reduce co-linearity between linear and quadratic terms (Legendre and Legendre 1998). *Area* was $\log_{10}$-transformed to normalize distributions. We calculated multiple-term regression models and GLMs for four different sets of predictors (spatial, areal, topographic and climatic) to assess independent as well as collective statistical effects of space, area, topography and climate (Lobo *et al.* 2002; Hortal *et al.* 2008). Model selection was performed using Akaike's information criterion (AICc) in the case of linear regression models and by stepwise backward elimination of non-significant variables from GLMs. Variation partitioning (partial regression analysis) was used to calculate independent and shared statistical effects of the models for space, area, topography and climate on the geographic distribution of the studied traits (Legendre and Legendre 1998, Hortal *et al.* 2008). Some climatic variables were highly correlated and multicollinearity can influence regression analysis. Thus, we ran a collinearity diagnosis to exclude variables with very low tolerance values (<0.1) due to high covariation (r > 0.7) with other model variables of the same set (Quinn and Keough 2002). Since spatial autocorrelation in macroecological data often produces statistical errors, we checked the residuals of each non-spatial GLM (considering area, topography and/or climate) for spatial autocorrelation (Moran's *I*). In linear regression models, we accounted for autocorrelation by calculating Spatial Autoregressive Models using Simultaneous Autoregression (SAR) (Diniz-Filho *et al.* 2003; Bini *et al.* 2009; Zuur *et al.* 2010). To account for potential species richness effects on patterns of mean body size (increasing body size with increasing species richness), the number of species occurring in each country was $\log_{10}$-transformed and tested as a covariate (*richness*; cf. Ulrich and Fiera 2010). For the same reason, species density (logarithmic number of species per logarithmic country area) was also tested as a covariate (density; cf. Baselga 2008). In addition, we performed variation partitioning for a supplementary set of models to calculate independent and shared statistical effects of the models for space, area, topography and historical climate variability (instead of current climate) on the two studied traits.

We also examined relationships between the two traits, carabid body size and hind wing development, to compare the proportion of flightless species for the groups of *all*, *widespread* and *endemic* species (chi-square test) and to determine whether flightless or winged species were significantly larger in size (one-way ANOVA test for *all*, *widespread* and *endemic*species). The significance level was corrected for multiple testing following Benjamini *et al.* (2001). As we found significant relationships between body size and hind wing development, hind wing development was tested as a covariate in regression models of body size.

In addition, we analyzed latitudinal patterns in mean body size for three species-rich subfamilies – Trechinae, Harpalinae and Carabinae – and the relationship between body size and the proportion of flightless species within these subfamilies, to check for a phylogenetic signal on interspecific spatial patterns in carabid body size.

All statistical analyses were run in R 2.10.1 (Team 2009) and SAM 4.0 (Spatial Analysis in Macroecology; Rangel *et al.* 2010).

2.3 Results

2.3.1 Body size

Carabid body size displayed a hump-shaped relationship with latitude in the three observed data sets (Figure 2.1), but the pattern was most pronounced in *endemic* species (Figure 2.1c).

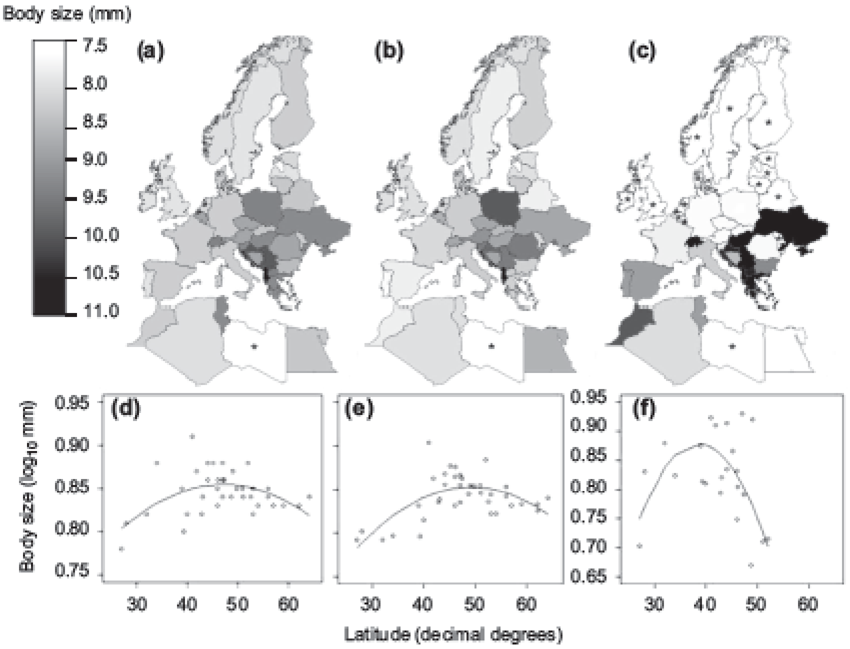


Figure 2.1. Mean **body size** (mm) of (a) *all*, (b) *widespread* and (c) *endemic* species occurring in the countries of the study region, and latitudinal relationships of body size ($\log_{10}$mm) of (d) *all*, (e) *widespread* and (f) *endemic* species in the western Palaearctic. Countries labeled '*' were not included due to the absence of restricted-range species or because they were identified as outliers; ordinate scale in the scatter plots for *endemic* species differs from scales used for *all* and *widespread* species.

Hence, carabid mean body size is highest in southern Europe (latitudes about 47°N, Figure 2.1d,e,f) and decreases towards North Africa and northern Europe. The spatial regression models of *all* and *widespread* species also included longitude, representing an increase in carabid body size from western towards eastern Central Europe (about 15°E; Figure 2.1a,b; Table 2.1) and then a decrease towards Asia. Spatial models (including both latitude and longitude) accounted for 50% and 66% of geographic body size variation in *all* and *widespread* species, respectively (Table 2.1). In *endemic* species, a purely latitudinal model explained 26% of data variation. Longitude and also topographic, areal and climate related variables did not show significant relationships with body size of *endemic* species.

Table 2.1. Results (Coefficients of determination, F-values, degrees of freedom and probabilities) of regression models for geographic distribution of mean **body size** of *all*, *widespread* and *endemic* species in the western Palaearctic study region. The functions consist of single and/or polynomial terms (e.g., '*factor–factor*^{2}' or '*factor+factor*^{2}'). '+' indicates positive linear, '–' negative linear relationships, 'n.s.' non-significant cases. See Supplementary material, Table S2.2 for abbreviations of the variables.

Model type	Model (function)	R^2_{adj}	F	DF	p
All					
Space	lat−lat^2 + long−long^2	0.50	17.35	4; 33	<0.001
Area	−area	0.22	10.11	1; 36	0.003
Climate	cold−cold^2 + seast + prec + AET	0.64	14.94	5; 32	<0.001
Complete	lat−lat^2 + long−long^2−area + cold−cold^2 + seast + prec + AET	0.68	6.64	10; 27	<0.001
Widespread					
Trait (hind wings)	+ flightless_wide	0.11	4.26	1; 36	0.05
Space	lat−lat^2 + long−long^2	0.66	16.35	4; 33	<0.001
Climate	−cold + AET−frost	0.59	16.59	3; 34	<0.001
Complete	flightless_wide + lat−lat^2 + long−long^2 −cold + AET−frost	0.79	13.60	10; 27	<0.001
Endemic					
Space	lat−lat^2	0.26	4.57	2; 22	0.02

p-values corrected for spatial autocorrelation.

Topography and historical climate variability did not show any significant relationships with carabid body size. We found a negative linear effect of *area* for body size of *all* species ($R^2 = 0.22$): carabid body size increased towards smaller countries. We did not detect any effect of species richness, and no effect of species density on body size of *all* an *endemic* species. Only *widespread* species showed a positive relationship between body size and species density (Supplementary material, Table S2.3).

Climate models combining significant and non-collinear variables of contemporary climate included measures of temperature (*cold*) as well as precipitation (*prec*) and measures representing seasonality (*seast*), water-energy balance (*AET*) and harshness of climate (*frost*). High levels of precipitation and water-energy balance tended to have a positive effect, mean temperatures of coldest month and long frost periods showed negative relationships with carabid body size. Climate models had high explanatory value in *all* species ($R^2 = 0.64$) and in *widespread* species ($R^2 = 0,59$; Table 2.1) and provide support for H1 in regard to (a) productivity but not (b) aridity.

Together, the examined factors (space, climate and area and/or the other trait, i.e. hind wing development) explained 68% of data variability in *all* species and 79% in *widespread* species. Variation partitioning indicated the strongest independent effect on body size for *all* species and for *widespread* species to be climate (R^2 0.16 and 0.06, respectively; Figure 2.2a,b). In both data sets (*all* and *widespread* species) the highest shared explanatory power (R^2 0.27 and 0.60, respectively) was observed in spatially structured climatic conditions (shared variation between space and climate, Figure 2.2a,b). Since we found no further predictor (no spatial, but also no climatic, areal or topographic), variation partitioning was not performed for distribution patterns in *endemic* body size.

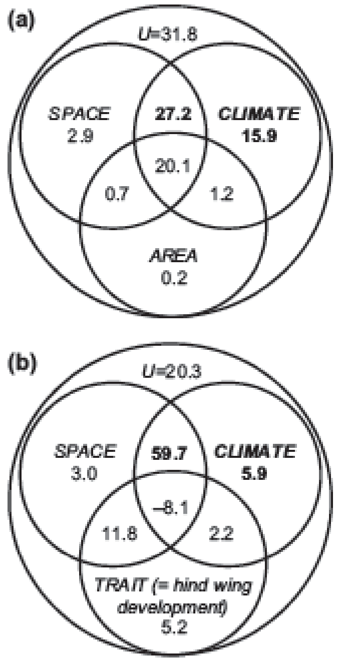


Figure 2.2. Variation partitioning for **body size** of (a) *all* species and (b) *widespread* species between independent and shared effects of regression models including variables of space, climate and area or the other trait studied, i.e. hind wing development. ‘U’ indicates the proportion unexplained by our models. Variation partitioning was not performed for body size of *endemic* species, since only a spatial effect was detected.

Within the three studied subfamilies (Trechinae, Harpalinae and Carabinae) latitudinal patterns in mean body size in part resembled patterns found on family level. The mean body size of the subfamily Carabinae was an exception to this, showing a negative linear (and not a quadratic/ hump-shaped) relationship with latitude (Supplementary material, Table S2.4).

2.3.2 Hind wing development

The proportion of flightless species showed a hump-shaped relationship with latitude in the data sets of *all* and *widespread* species (Figure 2.3d,e), and a positive linear relationship for *endemic* carabid species (Figure 2.3f; for detailed data on model selection, see Supplementary material, Table S2.5). Spatial models (purely latitudinal models) explained 63% of data variance in *all* species and 46% and even 79% of the distribution patterns in *widespread* and *endemic* species, respectively (Table 2.2). Topography had a high explanatory power for *all* and *widespread* species (71% and 43% of explained variance, Table 2.2). For *endemic* species, no relationship was shown between topography and hind wing development; however, the proportion of flightless *endemic* species decreased with increasing country size.

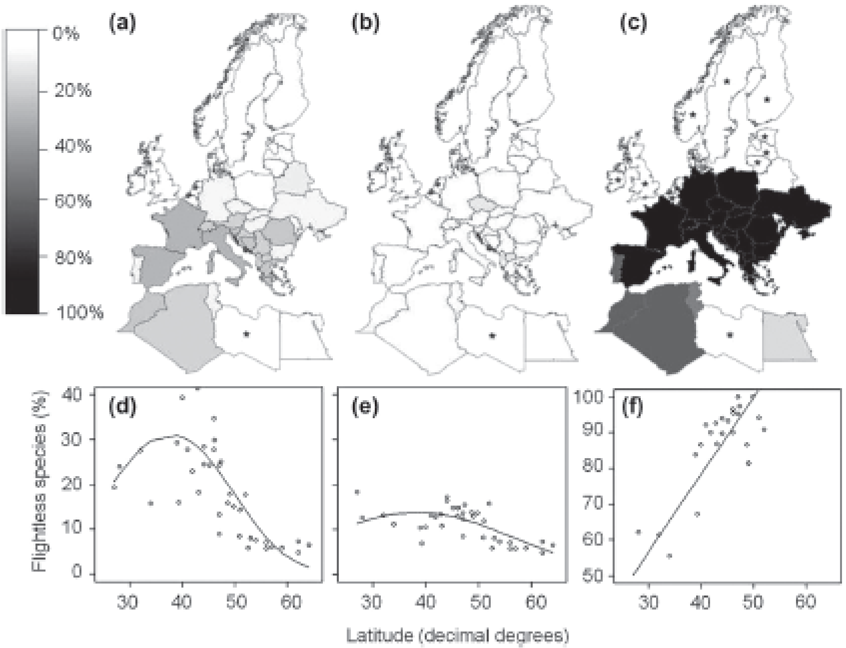


Figure 2.3. Proportion of **flightless species** (%) in (a) *all*, (b) *widespread* and (c) *endemic* species occurring in the countries of the study region, and latitudinal relationships of proportion of flightless species (%) of (d) *all*, (e) *widespread* and (f) *endemic* species in the western Palaearctic. Countries labeled '*' were not included due to the absence of restricted-range species or because they were identified as outliers; ordinate scale in the scatter plots for *endemic* species

Whilst climatic regression models for *widespread* species included measures of water availability (measures of precipitation) and temperature seasonality (stability in energy availability), models for *endemic* species contained measures of energy availability (temperature). Models for *all* species comprised both measures of water and energy availability and seasonality measures. The proportion of flightless species tended to be highest in regions of balanced temperature (mean temperature and mean temperature of warmest month) with high precipitation levels. Low temperatures of the coldest month and high seasonality in precipitation seem to have a negative effect on the proportion of flightless carabids in *widespread* and *endemic* species. These results are consistent withH2. The effect of climate on the proportion of flightless species ranged from 37% (in *widespread* species) to 61% (in *all* species) and 84% (in *endemic* species, Table 2.2). Topography had the strongest independent impact on hind wing development in *all* and *endemic* species (23.5% and 18.0% of explained variance, Figure 2.4a,b) and climate (including temperature seasonality) was the strongest predictor for hind wing development of *endemic* species (38.1%, Figure 2.4c). In all species sets, the largest share of variation was explained by a complete model, i.e. by spatially structured components of climatic and topographic factors (Figure 2.4a,b,c).

Historical climate variability had a negative linear effect on the proportion of flightless species and explained 53.1% of data variation in *all* and 35.3% in *widespread* species (Supplementary material, Table S2.6). High proportions of flightless species in regions of high elevation range and low historical climate variability support H2. Variation partitioning for space, historical climate variability and topography showed strong effects of spatially structured climate variability, but low independent effects of historical climate variability (2.0% and 6.2% of explained variance for *all* and for *widespread* species, respectively; Supplementary material, Figure S2.2a,b). Similar to variation partitioning with current climate instead of historical climate variability, topography holds the strongest independent effects (28.0% for patterns in *all* species and 14.0% for *widespread* species). For *endemic* species, we did not detect any relationships between hind wing development and historical climate variability (i.e. no additional variation partitioning for this group).

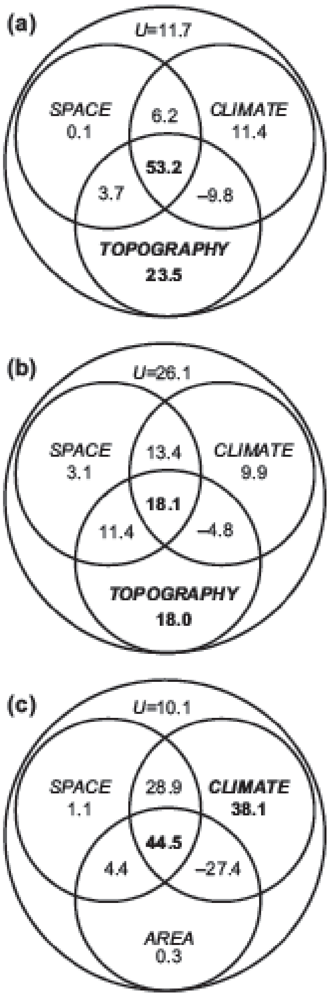
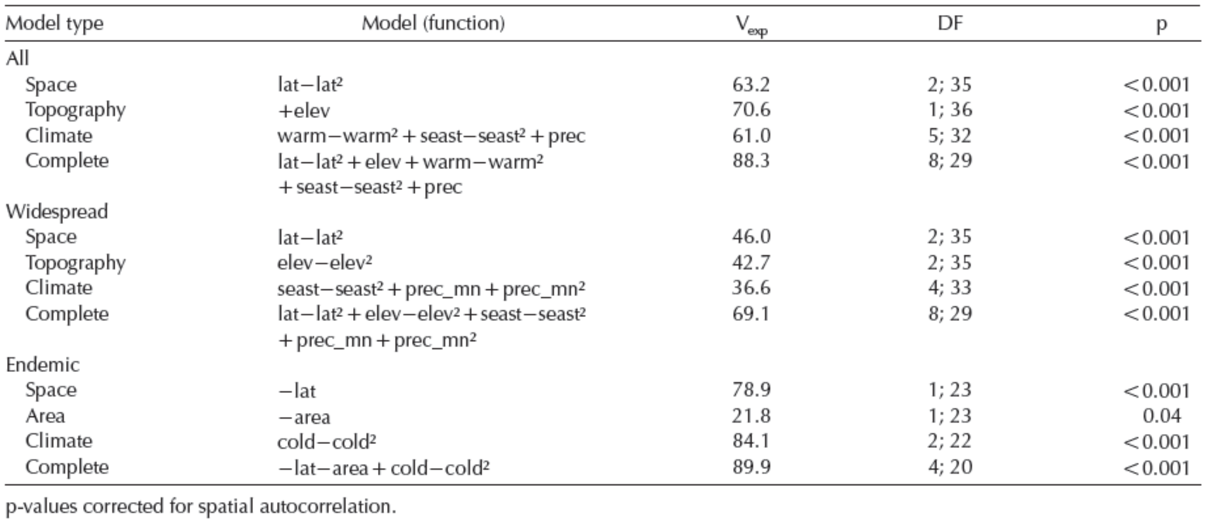


Figure 2.4. Variation partitioning for **hind wing development** (proportion of flightless species) of (a) *all* species, (b) *widespread* and (c) *endemic* species between independent and shared effects of regression models including variables of space, climate and topography. 'U' indicates the proportion unexplained by our models.

The occurrence of constantly brachypterous, constantly macropterous as well as dimorphic species in all species-rich subfamilies of carabid beetles indicates that hind wing polymorphism has appeared repeatedly in the phylogeny of Carabidae and is not phylogenetically conserved (Supplementary material, Figure S2.3). Thus, our analyses of geographic distribution of hind wing development are not influenced by phylogenetic patterns within the family of carabid beetles.

Table 2.2. Results (percentage of explained variability, degrees of freedom and probabilities) of regression models for geographic distribution patterns of **hind wing development** (proportion of flightless species) for *all*,*widespread* and *endemic* species in the western Palaearctic study region. See Table 2.1 for function notation and Supplementary material, Table S2.2 for abbreviations of the variables.



Model type	Model (function)	V_{exp}	DF	p
All				
Space	lat−lat^2	63.2	2; 35	<0.001
Topography	+elev	70.6	1; 36	<0.001
Climate	warm−warm^2 + seast−seast^2 + prec	61.0	5; 32	<0.001
Complete	lat−lat^2 + elev + warm−warm^2 + seast−seast^2 + prec	88.3	8; 29	<0.001
Widespread				
Space	lat−lat^2	46.0	2; 35	<0.001
Topography	elev−elev^2	42.7	2; 35	<0.001
Climate	seast−seast^2 + prec_mn + prec_mn^2	36.6	4; 33	<0.001
Complete	lat−lat^2 + elev−elev^2 + seast−seast^2 + prec_mn + prec_mn^2	69.1	8; 29	<0.001
Endemic				
Space	−lat	78.9	1; 23	<0.001
Area	−area	21.8	1; 23	0.04
Climate	cold−cold^2	84.1	2; 22	<0.001
Complete	−lat−area + cold−cold^2	89.9	4; 20	<0.001

p-values corrected for spatial autocorrelation.

2.3.3 Relationships between body size and hind wing development

In the study region, spatial distribution of body size of *widespread* species was significantly related to hind wing development ($R^2 = 0.11$; Table 2.1): The proportion of flightless *widespread* species increased with increasing mean body size. Thus, hind wing development was considered for the variation partitioning for the body size of *widespread* species (Figure 2.2b). For *all* and *endemic* species, however, there was no relationship between the two observed traits.

In general, our data revealed a significantly higher proportion ($p < 0.001$) of flightless species for the group of *endemic* species (85% of species are flightless), whereas most species are winged in the category of *widespread* species (only 20% of species are flightless). One-way ANOVA tests also confirmed that flightless species tended to be larger than winged species in the three studied data sets for *all* ($F = 44.062$, df = 1; 3,135, $p = 0.017$), *widespread* ($F = 269.22$; df = 1,259; $p = 0.033$) and *endemic* species ($F = 4.296$; df = 1; 1,876; $p = 0.05$; corrected for multiple tests). Within the subfamilies we found different relationships between the two observed traits. Harpalinae showed a similar trend to that on the family level: the frequency of flightlessness increased with mean body size of carabids ($F = 257.31$, df: 1;

1,396, $p < 0.001$). In Carabinae and Trechinae no relationship was detected between the two traits.

2.4 Discussion

Studies on broad-scale geographic body size patterns in ectothermic taxa are still scarce but have increased rapidly in number over the last two decades (García-Barros 2000; Angilletta *et al.* 2004; Olalla-Tarraga *et al.* 2006; Pincheira-Donoso *et al.* 2008). We studied body size of western Palaearctic carabids as one characteristic of the species, but also hind wing development as a second trait which is directly linked with species' dispersal ability and makes it possible to draw conclusions with respect to (historical) dispersal processes. For our study, we collected data on body size and hind wing development for altogether 86% of the carabid species recorded in the whole study region (and up to 97% of traits data per country) – a relatively high level of data completeness compared to other studies on hyperdiverse invertebrate taxa (cf. Entling *et al.* 2010).

Our results revealed hump-shaped relationships with latitude for both studied traits: Body size and proportion of flightless species increased from North Africa towards southern Europe and decreased towards northern Europe. Hence, these patterns resemble distribution patterns of carabid diversity in the same study area (cf. Schuldt and Assmann 2009). However, we could not detect a direct richness effect on body size as found in other invertebrates (e.g. springtails; Ulrich and Fiera 2010).

2.4.1 Contemporary climate

Our study shows significant relationships between body size and measures of contemporary climate related to both available energy and water-energy balance. Models with measures of ambient energy show unimodal trends with increasing body size along with increasing energy values, followed by a decline in mean carabid body size towards extremely high values. A positive linear relationship with AET, a measure of joint availability of energy and water, indicates the importance of a water-energy balance. As assumed in H1a, these patterns in carabids are in accordance with predictions of high values of body mass in regions of high resource availability and productivity (cf. Blackburn and Gaston 1994; Mousseau 1997; McNab 2010). Despite very high values of available ambient energy, there is a decrease in carabid body size towards North Africa, which might result from a shortage of water in this region (quantified in our models by precipitation measures; opposed to H1b). Several studies demonstrate that various species groups (even of endothermic taxa) do not simply follow Bergmann's rule but show decreasing body size towards arid regions (Yom-Tov 1986; Yom-Tov and Geffen 2006). In contrast, in some arthropod taxa larger bodied species tend to have a higher desiccation resistance (Remmert 1981; Entling *et al.* 2010). Taking data for Europe alone, spiders and carabids – both are macrofaunal predators occurring in subterranean to arboreal habitats across a broad elevation range – show similar latitudinal patterns in mean body size. Nevertheless, mean body size of spiders increases from the cool moist habitats of northern Europe towards warm and dry habitats (Entling *et al.* 2010), while patterns in carabids indicate a particular demand for energy, water and also a balance between water and energy availability (represented by a strong impact of AET and of high temperature and precipitation measures in climate models). Thus, physiological mechanisms of desiccation resistance tend to be different in carabids. Our results indicate that desiccation resistance of carabids might not directly increase with increasing body size, but aridity may change the reproduction cycle resulting in smaller body sizes. In North Africa, most carabids develop winter larvae to shift the sensitive life stage of their reproduction towards less arid periods (Paarmann 1979; Kotze *et al.* 2011). This tends to decrease the desiccation risk of larvae, but lower productivity levels during the larval stage may also result in smaller imagines.

Similarly to body size, hind wing development of *all*, *widespread* and *endemic* species also showed hump-shaped latitudinal distribution patterns and (spatially structured) climate – measures and seasonality of temperature and precipitation – tended to have a strong influence on large-scale patterns. Again, not only energy availability but also a certain degree of water availability seems crucial, which reflects current environmental stability and provides support for H2. Their high dispersal ability allows winged carabid beetles (Lindroth 1946; Thiele 1977; Turin 2000) to escape from and re-colonize temporal habitats and is an important factor for survival in dynamic habitats (den Boer 1970; Thiele 1977; den Boer 1980; Ås 1984; Desender 1989b). In contrast, the proportion of flightless individuals and species increases towards habitats with low environmental variability (documented for permanent/stable habitats: Brandmayr 1983; 1991; Assmann 1999; Desender *et al.* 1999), since wing reduction can originate from a balance of energy allocation (trade-off between dispersal and reproduction). These microevolutionary processes increase fecundity and promote local recruitment (Roff 1986a; Desender 2000), enabling carabid beetles to adapt to specific habitats and/or changing environments (cf. Thiele 1977). As our results show, these processes might also drive patterns at larger geographic scales. In the mountains of the study area, microevoloutionary processes appear to be particularly active, as shown in our models by the impact of topography on the hind wing development of *all* species – an indication of the importance of the evolutionary pathway of carabids into the mountains.

2.4.2 Dispersal and historical climate

Decreasing flightlessness from southern towards northern Europe has earlier been documented for carabids on the interspecific level and at smaller spatial scales. This pattern is assumed to result from dispersal processes and wing reduction in stable environments. Wing-dimorphic carabids distributed across Central and northern Europe showed a higher proportion of fully winged populations in the north due to higher dispersal power of winged individuals (Lindroth 1949; 1970). Other works document high proportions of winged species in Scandinavian mountains (Nilsson *et al.* 1993), whereas in southern Europe the proportion of flightless species is much higher (Brandmayr 1983), and concentrates on solid bedrock substrates from the lower hills to the mountaintops (Brandmayr 1991). Our study demonstrates a congruent pattern even at a large spatial scale: In *widespread* as well as in *endemic* species the proportion of flightless species is highest in southern Europe and decreases towards northern Europe (and for *widespread* also towards North Africa). Regression models show high explanatory power of topography, spatially structured topography and climate variability for this pattern and thus add support for H2.

In Europe, broad-scale dispersal processes are strongly affected by historical climate changes such as glaciations (Holdhaus 1954; Schmitt 2007). Consequently, not only present-day climatic conditions but also historical events might have an important impact on broad-scale spatial distribution of species traits in carabids – as they have on geographic patterns in carabid species richness and endemism (Schuldt and Assmann 2009). Historical climate variability revealed a negative effect on the proportion of flightless species in *all* and *widespread* species, but not in *endemics* – most likely because almost all *endemic* species are flightless. Since explanatory values of models for historical climate variability (Supplementary material, Table S2.6) resemble those of current climate models (Table 2.2), the influence of historical climate tends to be equally effective as current climate measures to account for contemporary patterns in species traits (cf. Araújo *et al.* 2008). The independent contribution of historical climate variability is lower than the one of current climate, and the low resolution of the trinomial variable does not enable us to reveal more detailed assertions on the effect of past climate. Separating the complex interactions of past and recent climates and processes would require more detailed analyses (e.g. performed for diversity pattens of European dung beetles by Hortal *et al.* 2011). However, also topography is assumed to hold a historical signal, since regions with high elevation ranges allowed species to survive past climate changes (such as glaciations) by climbing or descending to elevations offering suitable conditions (Hewitt 1999). Mountainous regions such as the “Massifs de refuge” are described as glacial refugia in the Pyrenees, the Alps, the Carpathians and the mountains of the Balkan Peninsula, and as hotspots of speciation and endemism (Holdhaus 1954; Habel *et al.* 2010). Postglacial re-colonization scenarios from southern refugia towards northern Europe are supported also by several molecular analyses (e.g. Taberlet *et al.* 1998; Habel *et al.* 2005; Drees *et al.* 2010). Currently widespread species might have been able to colonize larger geographic ranges due to higher dispersal ability (Gutiérrez and Menéndez 1997; Svenning and Skov 2007; Araújo *et al.* 2008). In carabids, most widespread species tend to be winged, whereas large proportions of endemic carabids are flightless and restricted to southern Europe. Thus, low dispersal of flightless species may have caused their restricted range in regions of former glacial refugia.

However, flightlessness might also have evolved in restricted habitats of refugia. Mountainous regions could have offered restricted but long-term suitable habitats supporting the reduction of wings (Brandmayr 1991; Desender *et al.* 1999). Thus, patterns in flightlessness and endemism in carabids tend to be strongly influenced by historical climate variability and postglacial re-colonization of Europe. In North Africa, low proportions of flightless species might be a result not only of postglacial colonization processes but also of historical climatic conditions. Climatic changes took place rapidly from former moist landscapes (during the early and middle Holocene) to the arid and even desert areas of today (cf. deMenocal 2008; Feakins and deMenocal 2008). Hence, North Africa did not offer long-term stable habitats which are needed to support wing reduction in carabids (Brandmayr 1983).

2.4.3 Phylogeny

Some studies showed an uneven distribution of small- and large-bodied taxa within a higher taxon across Europe and argue that large-scale patterns might be influenced by phylogenetic relationships (such as family sorting; Hawkins and Lawton 1995; Entling *et al.* 2010).

In carabids, body size is a phylogenetically conservative trait (Ulrich 2007), whereas hind wing development and other ecological traits such as fecundity, habitat preference or reproduction rhythm can develop within short periods to adapt to changing environmental conditions (Thiele 1977; Desender 1987). Mean carabid body size differs clearly between the subfamilies (Supplementary material, Table S2.2), a phenomenon also observed in other taxa

(Diniz-Filho *et al.* 2007; Entling *et al.* 2010). Nevertheless, we were unable to confirm a phylogenetic influence on spatial patterns in body size of carabids, since latitudinal patterns within the subfamilies resembled those across subfamilies. Only the subfamily of Carabinae showed a linear and no hump-shaped relationship with latitude: Body size decreased from North Africa towards northern Europe. This might be explained by relatively few Carabinae species occurring in North Africa, which are mostly large, and relatively high numbers and smaller sizes of Carabinae in Europe. However, the relationship between body size and latitude within the carabid family is not attributable to a disproportionately high ratio of subfamilies with larger species in southern Europe, or conversely to a predominance of subfamilies with smaller species in North Africa and northern Europe.

Although the overall probability of larger species being flightless is higher, the species-rich subfamilies with the largest representatives of carabid beetles in the western Palaearctic (e.g. Carabinae) as well as those including the smallest species (e.g. Trechinae), show hind wing polymorphism (Supplementary material, Figure S2.3). Thus, also for the detected large-scale patterns in hind wing development a strong phylogenetic influence is unlikely. Accordingly, the detected interspecific patterns in the geographic distribution of both carabid traits tend to have a common ecological, but not a phylogenetic origin (cf. Blackburn *et al.* 1999; Brehm and Fiedler 2004; Meiri and Thomas 2007).

2.4.4 Country size

Whereas body size of other invertebrates tends to increase with country/island area (e.g. springtails; Ulrich and Fiera 2010) mean body size of *all* carabids (and also the proportion of flightless *endemics*) showed the converse relationship. Species richness had no significant influence on species' traits, whereas species density (which might be higher in small countries) had a positive effect on *widespread* species' body size. Nevertheless, as we could not find any generic effect of species richness or density on body size data and as carabid species richness is also not correlated with area (Schuldt and Assmann 2009), this pattern cannot be explained by increasing carabid species richness with country size. When we assume that the probability of finding very small species to an equal extent as large species increases with sampling completeness, small countries appear to be less well-sampled than larger ones. However, species accumulation curves for small as well as large countries were used to check species records in each country for completeness before analyses and did not confirm this assumption (Supplementary material, Figure S2.1).

2.5 Conclusions

Carabid traits do not show simple latitudinal clines but distinct geographic patterns (latitudinal and longitudinal relationships). These patterns tend to be influenced by contemporary environmental conditions and by historical (dispersal) processes but not by phylogeny. Our results support our hypotheses H1a and H2 predicting an increase of carabid body size and of the proportion of flightless species with resource availability/productivity, (long-term) environmental stability and thus towards former glacial refugia. *Widespread* and *endemic* species differ in terms of the mechanisms which might have formed spatial patterns in species traits: there is a strong influence of recent climatic conditions and spatially structured climate in *widespread* species, while *endemic* species are more strongly affected by history and dispersal processes (as indicated by distinct patterns in hind wing development which represent dispersal ability).

2.6 Acknowledgements

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2.7 Supplementary Material

Table S2.1. Countries of the western Palaearctic study region with latitude and longitude (decimal degrees).

code	country	area (km²)	latitude (dec)	longitude (dec)
Europe				
AL	Albania	27,398	41.00	20.00
AU	Austria	82,444	47.34	13.34
BE	Belgium	30,278	50.84	4.00
BH	Bosnia and Herzegovina	51,129	44.00	18.00
BU	Bulgaria	110,550	43.00	25.00
BY	Belarus	207,600	53.00	28.00
CR	Croatia	56,414	45.17	15.50
CZ	Czech Republic	77,276	49.75	15.84
DE	Denmark	42,394	56.00	10.00
EN	Estonia	43,211	59.00	26.00
FI	Finland	304,473	64.00	26.00
FR	France (incl. Corsica, Monaco)	545,630	46.00	2.00
GB	Great Britain (incl. Channel Islands)	241,590	54.00	-2.00
GE	Germany	349,223	51.00	9.00
GR	Greece (incl. Crete)	130,800	39.00	22.00
HU	Hungary	92,340	47.00	20.00
IR	Ireland	68,890	53.00	-8.00
IT	Italy (incl. Sardinia, Sicily, San Marino)	294,020	42.84	12.84
LA	Latvia	63,589	57.00	25.00
LT	Lithuania	65,200	56.00	24.00
MC	Macedonia	24,856	41.84	22.00
MD	Moldova	33,371	47.00	29.00
NL	The Netherlands	33,883	52.50	5.75
NR	Norway	307,442	62.00	10.00
PL	Poland	304,465	52.00	20.00
PT	Portugal	91,951	39.30	-8.00
RO	Romania	230,340	46.00	25.00
SK	Slovakia	48,800	48.67	19.50
SL	Slovenia	20,151	46.12	14.83
SP	Spain (incl. Gibraltar)	499,542	40.00	-4.00
SV	Sweden	410,934	62.00	15.00
SZ	Switzerland	39,770	47.00	8.00
UK	Ukraine	603,700	49.00	32.00
YU	Jugoslavia (Serbia, Montenegro)	102,148	44.00	21.00
North Africa				
AG	Algeria	2,381,740	28.00	3.00
EG	Egypt	995,450	27.00	30.00
MO	Marocco (incl. Western Sahara)	446,300	32.00	-5.00
TU	Tunesia	155,360	34.00	9.00
LB	Libya	1,759,540	25.00	17.00

Table S2.2. Summary statistics (mean, median, minimum and maximum values, standard deviation) of mean body size and the proportion of flightless species within the different species groups and environmental variables used in regression analyses.

Variable	Code	Mean	Median	Min	Max	SD
Mean body size (mm): *all* species	*size_all*	8.15	8.17	0.70	51.5	5.75
Mean body size (mm): *widespread* species	*size_wide*	8.40	13.23	0.80	50.0	5.62
Mean body size (mm): *endemic* species	*size_end*	7.98	7.35	0.70	51.5	5.93
Mean body size (mm): flightless species	*size_flightless*	8.81	6.65	0.70	51.5	6.60
Mean body size (mm): winged species	*size_winged*	7.20	6.25	0.80	33.5	4.05
Mean body size (mm): Trechinae	*size_trech*	4.37	4.25	0.75	11.5	1.17
Mean body size (mm): Harpalinae	*size_harp*	9.87	9.00	1.33	28.5	4.75
Mean body size (mm): Carabinae	*size_carab*	23.80	23.00	12.0	33.5	6.19
Proportion of flightless in *all* species	*flightless_all*	0.18	0.17	0.05	0.41	0.10
Proportion of flightless in *widespread* species	*flightless_wide*	0.14	0.12	0.05	0.18	0.04
Proportion of flightless in *endemic* species	*flightless_end*	0.64	0.90	0.27	1.00	0.40
Number of *all* species	*richness_all*	462.6	395.5	201.0	1195.0	218.9
Number of *widespread* species	*richness_wide*	398.9	366.0	164.0	770.0	136.7
Number of *endemic* species	*richness_end*	96.5	62.0	5.0	425.0	110.8
Density of *all* species (number/km^2)	*density_all*	5.53	4.50	0.17	23.47	4.93
Density of *widespread* species (number/km^2)	*density_wide*	4.97	3.74	0.14	19.06	4.34
Density of *endemic* species (number/km^2)	*density_end*	0.84	0.57	0.03	4.42	0.99
Latitude (decimal degrees)	*Lat*	46.5	47.0	25.0	64.0	9.5
Longitude (decimal degrees)	*long*	15.0	15.67	-8.0	33.0	11.3
Area (10^3 km^2)	*area*	290.6	100.25	9.2	2381.7	473.3
Elevation range (m)	*elev*	2170.8	2386.0	180.0	4809.0	1307.6
Mean annual temperature (°C)	*temp*	10.3	9.2	1.5	22.5	5.3
Mean temperature coldest month (°C)	*cold*	0.6	-1.3	-11.3	12.9	6.4
Mean temperature warmest month (°C)	*warm*	19.6	18.4	11.7	32.4	4.8
Temperature seasonality (°C)	*seast*	19.0	19.7	9.8	26.6	3.8
Mean annual precipitation (mm)	*prec*	712.0	677.0	51.0	1537.0	313.7
Mean precipitation March-November (mm)	*prec_mn*	514.7	584.7	30.2	713.9	182.3
Seasonality precipitation (mm)	*seasp*	342.6	351.6	22.7	559.6	123.5
Potential evapotranspiration (mm/yr)	*PET*	709.1	640.5	461.6	1192.5	187.5
Actual evapotranspiration (mm/yr)	*AET*	504.3	551.8	56.4	683.7	151.6
Frost frequency (days)	*frost*	98.0	103.5	14.1	203.5	54.1
Historical climate variability (degree of glaciations 18,000BP)	*variability*	1=non-glaciated, 2=permafrost, 3=glaciated				

Table S2.3. Results (percentage of explained variability, degrees of freedom and probabilities) for regression models testing species richness (number of species occurring in a country) and species density (number of species per country area) as predictors for **body size**. See Table S2.2 for abbreviations.

Modeltype	Model (function)	V_{exp}	df	p
All				
Species richness	*n.s.*			*n.s.*
Species density	*n.s.*			*n.s.*
Widespread				
Species richness	*n.s.*			*n.s.*
Species density	*+density_wide*	29.8	1; 36	0.04
Endemic				
Species richness	*n.s.*			*n.s.*
Species density	*n.s.*			*n.s.*

p-values corrected for spatial autocorrelation

Table A2.4. Determinants for regression models of **body size** of three species-rich subfamilies of Carabidae against the proportion of flightless species in the respective group. The functions consist of single and/or polynomial terms that significantly accounted for the distribution (e.g., ‘$factor–factor^2$’ or ’$factor+factor^2$’). ‘+’ indicates a significant positive linear relationships, ‘n.s.’ non-significant cases. See Table S2.2 for abbreviations.

Subfamily	**Trechinae**		**Harpalinae**		**Carabinae**	
Variable	Function	R^2_{adj}	Function	R^2_{adj}	Function	R^2_{adj}
Proportion of flightless species	n.s.		*+flightless_harp*	0.12*	*–flightless_carab*	0.15*
Latitude (decimal degree)	$lat–lat^2$	0.60**	$lat–lat^2$	0.42*	*–lat*	0.45**

***p<0.001, **p<0.01, *p<0.05

Table S2.5. Determinants for latitudinal GLMs of **hind wing development** including the linear term only or the linear and the quadratic term, respectively, and results of the ANOVA for model comparison.

		Estimate	Std. Error	t value	p
All					
Model_all1	(Intercept)	-1.365	0.094	-14.52	< 0.001
	lat (centered)	-0.054	0.012	-4.41	< 0.001
Model_all2	(Intercept)	-1.196	0.084	-14.31	< 0.001
	lat (centered)	-0.087	0.015	-5.92	< 0.001
	lat^2 (centered)	-0.005	0.001	-4.24	< 0.001
ANOVA(Model_all1,Model_all2), Deviance=338.47, F=22.41, p<0.001					
Widespread					
Model_wide1	(Intercept)	-2.048	0.049	-41.64	< 0.001
	lat (centered)	-0.023	0.006	-3.64	< 0.001
Model_wide2	(Intercept)	-1.960	0.050	-38.96	< 0.001
	lat (centered)	-0.029	0.006	-4.51	< 0.001
	lat^2 (centered)	-0.001	0.001	-3.20	0.003
ANOVA(Model_wide1,Model_wide2), Deviance=32.05, F=11.14, p=0.002					
Endemic					
Model_end1	(Intercept)	2.752	0.173	15.89	< 0.001
	lat (centered)	0.150	0.018	8.35	< 0.001
Model_end2	(Intercept)	2.621	0.215	12.20	< 0.001
	lat (centered)	0.100	0.057	1.77	*n.s.*
	lat^2 (centered)	-0.003	0.003	-0.91	*n.s.*

Table S2.6. Results (percentage of explained variability, degrees of freedom and probabilities) of regression models for geographic distribution patterns of **hind wing development** (proportion of flightless species) for *all*, *widespread* and *endemic* species in the western Palaearctic study region. See Table 2.1 for function notation and Supplementary material, Table S2.2 for abbreviations of the variables.

Modeltype	Model (function)	V_{exp}	df	p
All				
Space	*lat–lat*^{2}	63.2	2; 35	< 0.001
Topography	*+elev*	70.6	1; 36	< 0.001
Historical climate variability	*–variability*	53.1	1; 36	< 0.001
Complete	*lat–lat*^{2}*+elev–variability*	87.7	4; 33	< 0.001
Widespread				
Space	*lat–lat*^{2}	46.0	2; 35	< 0.001
Topography	*elev–elev*^{2}	42.7	2; 35	< 0.001
Historical climate variability	*–variability*	35.3	1; 36	0.006
Complete	*lat–lat*^{2}*+elev-elev*^{2}*–variability*	65.4	5; 32	< 0.001
Endemic				
Space	*+lat*	78.9	2; 22	< 0.001
Area	*–area*	21.8	1; 23	0.04
Historical climate variability	*n.s.*			*n.s.*

p-values corrected for spatial autocorrelation

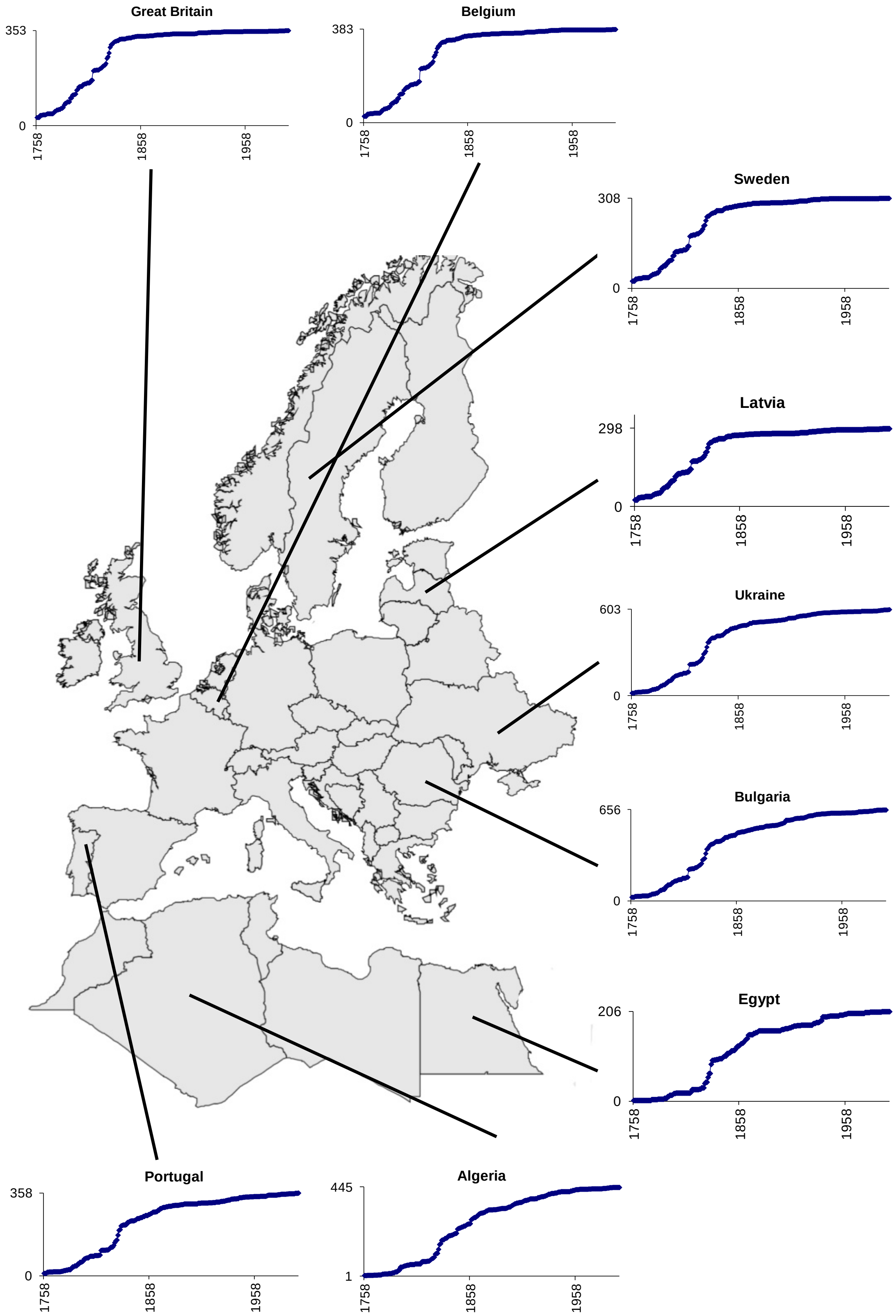


Figure S2.1. Species accumulation curves showing accumulative species numbers versus the year of description for a selection of small and large countries all over the study region.

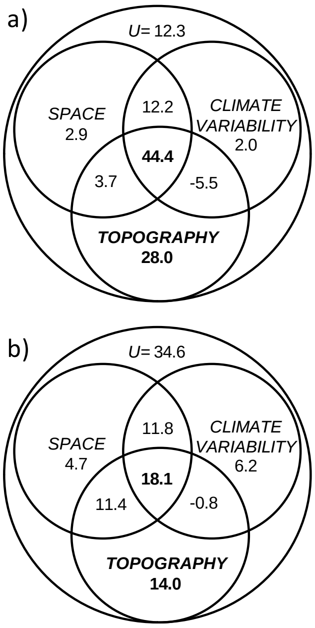
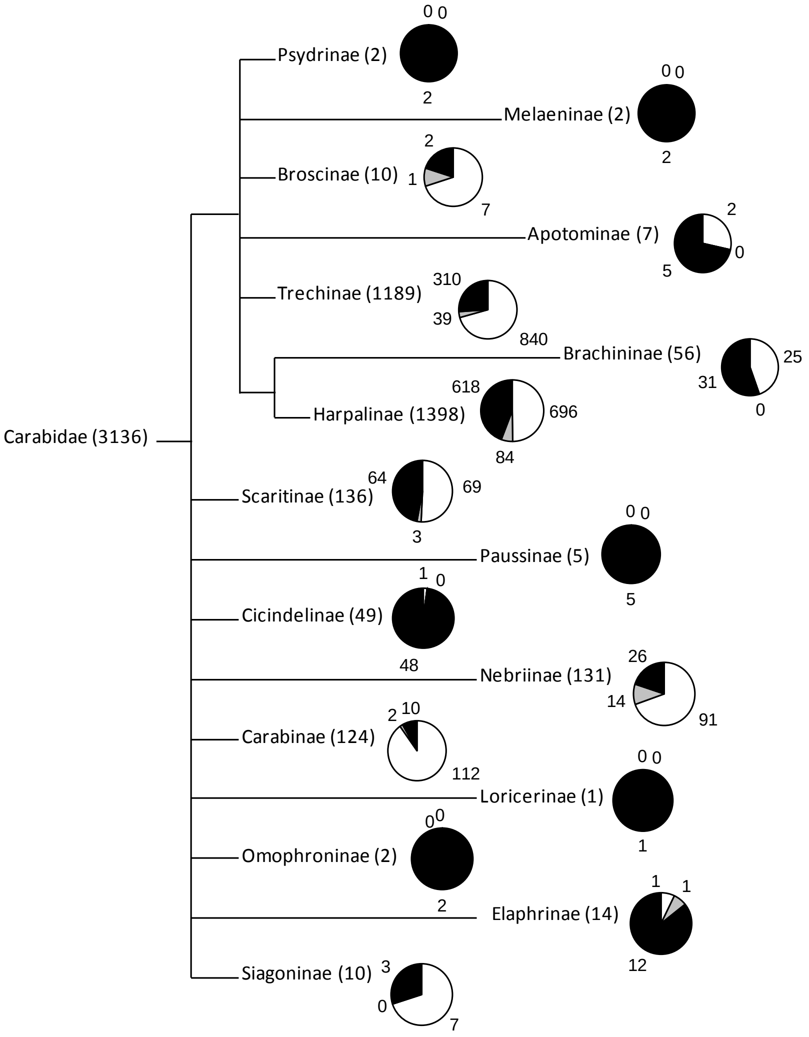


Figure S2.2. Variation partitioning for **hind wing development** (proportion of flightless species) of (a) *all* and (b) *widespread* species between independent and shared effects of regression models including variables of space, historical climate variability (here: climate variability) and topography. 'U' indicates the proportion unexplained by our models. For *endemic* species no effect of climate variability was detected (for variation partitioning for space, topography and current climate see Figure 2.4c).

Figure S2.3. Total species numbers within subfamilies in the western Palaearctic (in brackets) and species numbers within fractions of macropterous (black), brachypterous (white), and dimorphic (grey) species. Phylogenetic relationships of the 16 subfamilies of Carabidae are modified from Maddison (2006) and are well supported by molecular genetic analyses (e.g. Ober and Maddison 2008; Ober and Heider 2010).



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Appendix 2

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3 CARABIDS.ORG – A DYNAMIC ONLINE DATABASE OF GROUND BEETLE SPECIES TRAITS (COLEOPTERA, CARABIDAE)

Published Article

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3.1 Abstract

Carabids are a species-rich group (more than 10,000 species in the Palaearctic region) and are intensively studied, inter alia due to their roles as bioindicators and mediators of nutrient flows in ecosystems. Numerous aspects of species' systematics, distribution, evolutionary biology (and phylogeny) and their ecology are well documented for the western Palaearctic and large data sets have already been compiled for macroecological studies. The online database carabids.org holds species classification and country level data on species distribution range for over 10,000 Palaearctic carabid species. Size and dispersal traits (body and eye size and hind wing development) are available for almost all (over 3,400) western Palaearctic carabid species and ecological and life-history traits (regarding food and habitat preferences as well as time of reproduction and activity) can be offered for most Central European (about 1,000) species. Carabids.org is meant to be a collaborative and interactive project offering a variety of research opportunities. Our project contributes to the rapid expansion and analysis of freely available traits data on species-rich invertebrates, which will help to advance our understanding of community assembly and functional diversity effects of such taxa across large spatial scales. We would very much appreciate data contributions from carabidologists, other scientists and interested parties.

3.2 Introduction

Species traits are increasingly being used to analyse and understand a multitude of spatial and/or temporal phenomena of species distribution and abundances ranging from community organisation to patterns in the distribution of biodiversity as well as ecosystem functioning (Hooper *et al.* 2005; McGill *et al.* 2006; Bello *et al.* 2010). Trait-based approaches – particularly studies combining various traits with phylogenetic aspects and biogeographic data (e.g. range sizes) – provide new perspectives to understand ecological, evolutionary biological and biogeographic phenomena (e.g Schuldt *et al.* 2012). Consistent and easily accessible trait data is the basis for valuable research into species characteristics, and open-access online databases can be used as a suitable instrument for data provision. Nevertheless, to date, freely accessible databases are only available for very few organism groups and geographical areas. Plant traits appear to be best-organized for a variety of biomes and geographic areas: There are several databases holding trait data of European (e.g. LEDA: Kleyer *et al.* 2008; BROT: Paula *et al.* 2009) and North American plants, mosses and lichens. Projects such as TRY (Kattge *et al.* 2011), GLOPNET (Wright *et al.* 2004) and TraitNET (http://traitnet.ecoinformatics.org/) even aim at coordinating a global set of plant trait data.

Databases holding animal trait information, however, are still scarce and rare examples cover lotic invertebrates (Vieira *et al.* 2006) and freshwater fishes (e.g. Coker *et al.* 2001; Frimpong and Angermeier 2009) only.

Although insects represent large parts of the global biodiversity and they often assume key functions in ecosystems (Samways 2005), databases on insect species traits are still underrepresented. Up to now no freely accessible trait databases for insects are known, with the exception of a database on traits of Northern European saproxylic organisms (including Coleoptera, Diptera and Hymenoptera species; Stokland and Meyke 2008). Carabids are a species-rich group (more than 3,000 species in the western Palaearctic) and are intensively studied, *inter alia* due to their roles as bioindicators (Rainio and Niemelä 2003; Kotze *et al.* 2011) and mediators of nutrient flows in ecosystems (Loreau 1995). Numerous aspects of species' systematics, distribution, evolutionary biology (and phylogeny) and their ecology are well documented for the western Palaearctic (e.g. Lindroth 1945; Lindroth 1949; Thiele 1977) and large data sets have already been compiled for macroecological studies (Schuldt and Assmann 2009; Schuldt *et al.* 2009; Schuldt and Assmann 2011). These are all essential preconditions for the compilation of a trait database for this taxon. First macroecological analyses on species traits have also been realised (Homburg *et al.* 2013a). Here, we introduce a database on carabid species traits which is now freely available online (www.carabids.org). Until now the carabids.org database holds species classification and country level data on species distribution range for over 10,000 Palaearctic carabid species (obtained from Löbl & Smetana 2003). Size and dispersal traits (body and eye size and hind wing development) are available for almost all (over 3,400) western Palaearctic carabid species and ecological and life-history traits (regarding food and habitat preferences as well as time of reproduction and activity) can be offered for most Central European (about 1,000) species. Here we present the content and structure of the open access database, carabids.org. Traits data can be readily downloaded after a simple user registration and can then be used for a wide range of research questions considering community level or even macroecological scales. In addition, we appreciate data contributions and describe the possibility of data submission from registered users. An example of application shows how our database can be used to test hypotheses on species traits.

3.3 Content of carabids.org

3.3.1 Taxonomic and systematic affiliation

Species classification and systematic affiliation of carabids (Carabidae) were taken from the first volume of the Catalogue of Palaearctic Coleoptera (Löbl and Smetana 2003). The catalogue information was scanned and transformed into a Comma Separated Value (CSV) file. This transformation was done by a simple computer program, which was developed in the Java scripting language Groovy. The script used a pattern matching algorithm to extract only the relevant information from the input file and transformed data into the CSV format required by the used database software (FileMaker, Inc., Santa Clara, CA, USA).

For the whole Palaearctic region (including Europe, Africa north of the Sahara and Asia north of the Himalaya foothills) the database holds 10,509 species, thereof 3,409 western Palaearctic species (comprising Europe and North Africa) and therefrom 936 Central European species (including Germany, Poland, Czech Republic, Slovakia, Switzerland, Austria, Hungary and Slovenia; see Figure 3.1 and Supporting Information, Tables S3.1 and S3.2).

3.3.2 Distributional range

Our database contains data on several characteristics of the species' distribution range. First the catalogue of Löbl & Smetana (2003) provided a list of countries in which the species occur. Then species were categorized in Central European, western Palaearctic and Palaearctic species according to their main ranges. In order to find an estimate of species range sizes, the area of all countries with species occurrence was added up. Species were then classified as '*endemic*' (range sizes $< 6 \times 10^5$ km²) or '*widespread'* (range sizes $> 6 \times 10^5$ km²; classes defined by Lumaret and Lobo 1996) based on the combined area of the countries in which they have been recorded, refined by expert knowledge on distributions of the individual species (i.e., occurrence of species only in parts of larger countries, e.g. species restricted to the Alps). In addition, for each species the centre of its occurrence was defined by computing mean values of latitudes and longitudes of all countries in which the given species occurs.

Figure 3.1. Map of the Palaearctic study region (light grey) including the western Palaearctic (medium grey) and Central Europe (dark grey). For country abbreviations see Supporting Information, Tables S3.1 and S3.2.

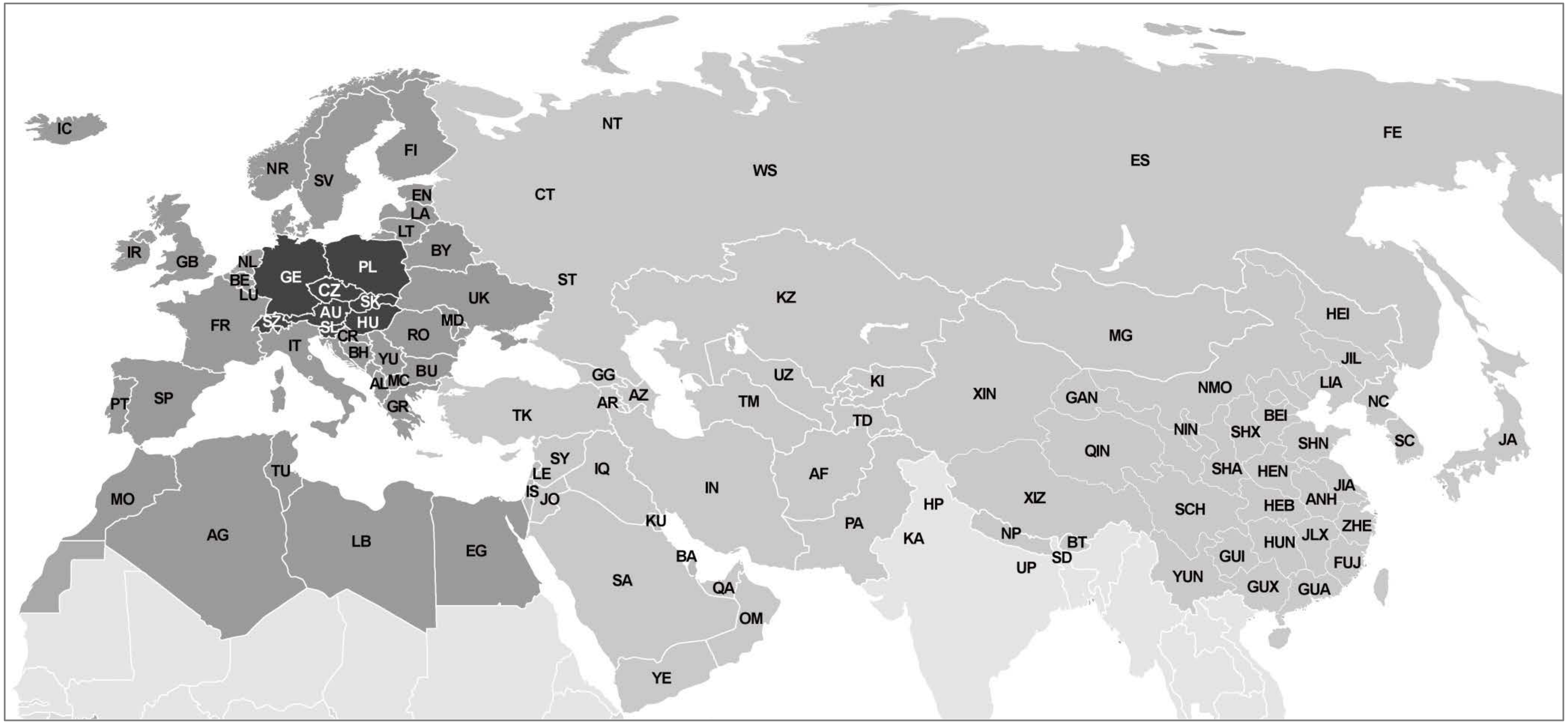

Table 3.1. Overview of terms used and traits included in the database, trait units or categories of measurement and the recent number of species with respective trait information available.

Tab in database	Trait	Available for: Main region	Available for: Number of species	Category/code	Description and unit of measurement
Classification					
	Taxonomic group	Palaearctic	10,509		
				Subfamily	Classification according to Löbl and Smetana (2003)
				Tribe	
				Subtribe	
				Genus	
				Subgenus	
				Species	
				Author	First describing author
				Year	Year of description
Distribution					
	Distribution range		10,509		
	Region	Palaearctic		Palaearctic	
				Western Palaearctic	
				Central Europe	
	Range	Palaearctic		restricted-range	
				widespread	
	Countries	Palaearctic		see entire list of countries and abbreviations in Supporting Information, Tables S3.1 and S3.2	
	Number of countries	Palaearctic			Total number of countries with species occurrence
	Area	Palaearctic			Total area of all countries with species occurrence; 1,000 km²
	Center of occurrence (latitudinal)	Palaearctic			Mean latitude of all countries with species occurrence; decimal degree
	Center of occurrence (longitudinal)	Palaearctic			Mean longitude of all countries with species occurrence; decimal degree

Table 3.1. Continued.

Tab in database	Trait	Available for: Main region	Available for: Number of species	Category/code	Description and unit of measurement
Size and dispersal					
	Body size	western Palaearctic	3,558		
	Minimal size (mm)				Minimal body length; mm
	Maximal size (mm)				Maximal body length; mm
	Hind wing development	western Palaearctic	3,447		
				short-winged/wingless	Hind wings always shorter than elytra or missing
				winged	Hind wings always fully developed
				dimorphic	Species including individuals with reduced and fully developed hind wings
	Eye-head proportion	Central Europe	1,135		Proportion eyes to head (%)
Food and habitat					
	Trophic level	Central Europe	1,123		
				Predator	Mainly carnivorous, preying on organisms
				Herbivore	Mainly herbivorous, feeding on plants and seeds
	Hunting abilities	Central Europe	589		
				Visual hunter	Predator, detecting their prey visually
				Snail hunter	Predator, mainly feeding on snails
				Collembola hunter	Predator, mainly feeding on Collembola
				Isopod/diplopod hunter	Predator, mainly feeding on isopods and/or diplopods
	Habitat preferences	Germany	496	1	Coastal habitats and inland saline habitats
				2	Mountain habitats
				3	River banks and scarcely vegetated shores
				4	Riparian habitats, swamps, bogs, moist and swamp heathlands
				5	Moist and wet woodlands
				6	Forests, pioneer forests
				7	Dry grasslands and dwarf-shrub heathlands
				8	Skeletal soils, caves and clefts
				9	Open grassland, arable land and pastures

Table 3.1. Continued.

Tab in database	**Trait**	**Available for:** **Main region**	**Number of species**	**Category/code**	**Description and unit of measurement**
Reproduction					
	Hibernation	Central Europe	668		
				larvae	Hibernation takes place in the larval stage
				imago	Hibernation takes place as imago
				larvae/imago	Hibernation as larvae and/or imago
	Activity	Central Europe	72		
	start (month)			Jan-Dec	Month of activity start
	end (month)			Jan-Dec	Month of activity end
	Reproduction time	Central Europe	190		
				spring	Reproduction takes place in spring
				summer	Reproduction takes place in summer
				autumn	Reproduction takes place in autumn
				winter	Reproduction takes place in winter

3.3.3 Trait data

Species classification and distribution from Löbl & Smetana (2003) was supplemented with data on species traits from relevant literature (original species descriptions, monographs and other treatises; see entire bibliography on www.carabids.org). We chose traits that were (1) available and comparable for a large number of species and (2) representing ecological key functions for the species such as physiological, dispersal and reproduction abilities and trophic level. The extent of additional data varies for partitions of the Palaearctic, increasing from eastern Palaearctic towards Central European species. For eastern Palaearctic species elementary data on species taxonomy and distribution is available. For most western Palaearctic species, additional data on two main traits relevant according to persistence and dispersal (body size and hind wing development) are available. Since species of Central European countries are very well-studied, data on nearly all considered species traits (Table 3.1) could be compiled for most of the approximately 1,000 species occurring in this region. Table 3.1 shows an overview of terms used and traits included in the database, their units or categories of measurement and the current number of species with respective trait information available.

3.3.4 Body size and dispersal

Invertebrate body size has been considered in an increasing number of macroecological studies on large geographic scales and reflects physiological abilities such as starvation and desiccation resistance (Remmert 1981; Cushman *et al.* 1993; Entling *et al.* 2010) and energy allocation (Atkinson 1995; Mousseau 1997) as well as dispersal abilities (Cushman *et al.* 1993). Broad-scale patterns in body size distribution of western Palaearctic carabids showed increasing body size towards regions with (long-term) stable climate conditions and high energy and water availability (Homburg *et al.* 2013a).

Crossing experiments on some ground beetle species revealed that hind wing development of carabids is inherited in a diallelic Mendelian fashion (Aukema 1986; Desender 1989a), resulting in brachypterous (hind wings reduced; flightless) and macropterous (hind wings fully developed; winged) individuals. Hind wing development appears to be linked with the fitness of individuals within a species, since brachypterous specimens tend to have higher fecundity (Aukema 1987; Desender 2000). In addition, hind wing development is directly linked to dispersal ability and relevant for carabids, since they include constantly brachypterous and constantly macropterous species as well as dimorphic species holding flightless and winged individuals. Macropterous individuals are mostly able to fly and as flying allows escaping and re-colonizing temporal habitats it is an important factor for survival in dynamic habitats (Lindroth 1946; den Boer 1970; Thiele 1977; den Boer 1980; Ås 1984; Gerisch *et al.* 2012). Since wing (and wing muscle) reduction can originate from a balance of energy allocation (trade-off between dispersal and reproduction), wingless species have been mainly documented in permanent and stable habitats (Brandmayr 1983; 1991; Assmann 1999; Desender *et al.* 1999). These microevolutionary processes enable carabid beetles to adapt to specific habitats (cf. Thiele 1977) and might even drive patterns at smaller and larger geographic scales, which have been documented (Šerić Jelaska and Durbešić 2009; Homburg *et al.* 2013a).

3.3.5 Food and habitat preferences

Food and hunting preferences are well-documented for many carabid species and partly studied on small spatial and/or taxonomic scales (Hengeveld 1980a; Melber 1983; Mundy *et al.* 2000; Barton *et al.* 2011). For most Central European species, carabids.org includes the eye size (eye to head proportion), which can be an indicator for a species' habitat (belowground beetles tend to be anophthalmous; cf. Schuldt and Assmann 2011) and its visual hunting abilities (as it is implied by large and efficient eyes). While broad-scale geographic patterns in subterranean carabid diversity in the western Palaearctic showed relationships with climate and topography reflecting historical (dispersal) processes (Schuldt and Assmann 2011), a relationship between eye size and other species traits, preferences or abilities has not yet been analysed in a rigorous way. For many Central European species, trophic levels and hunting preferences are now also available from the recent version of carabids.org, differentiating between (mainly) herbivores and predators and listing the preferred prey where appropriate (snails, Collembola and/or isopods/diplopods). When food preferences were not explicitly documented (e.g. by Brandmayr and Zetto Brandmayr 1980; Bauer 1981; Lindroth 1985; 1986; Brandmayr *et al.* 1994), they were assumed from mandible shapes and other morphological characteristics of the species (cf. Bauer 1974; Brandmayr and Zetto Brandmayr 1986; Bauer and Kredler 1988; Bauer, pers. communication). This is especially relevant for numerous species which are able to feed on both plants and animals (Hengeveld 1980a; 1980c; 1980b). Species of the genera *Carabus* and *Pterostichus*, for example, are classified as predominantly predatory (cf. extraintestinal digestion; Metzenauer 1981; Metzenauer and Kloft 1981) despite the fact that they sometimes also feed on plants (e.g. attracted by the smell of overripe fruits). Studies on the gut contents of carabid species showed that species with broad mandibles more regularly feed on seeds and/or plant material, and some species even store seeds for their brood (Melber 1983; Saska 2008; Saska *et al.* 2008). For carabids.org, those species were classified as predominantly herbivorous.

Food preferences might be linked with other characteristics such as body size or habitat preferences, as species with large eyes seem to prefer diurnal activity and open habitats with suitable light conditions (Schiller and Weber 1975; Bauer 1977; Thiele 1977). These assumptions result from small-scale studies, but a rigorous statistical analysis for a large set of species across larger spatial extents is still missing. Habitat preferences are well-documented for some species but are not easy to categorise. Up to now, carabids.org includes main habitats of carabid species occurring in Germany compiled by a large group of experts (GAC 2009).

3.3.6 Activity and reproduction

Timing of daily and annual activity is well-documented for some European carabid species (e.g. diurnal and nocturnal activity: Weber 1965; 1966b; Thiele and Weber 1968). In addition, several authors recorded the reproduction rhythms of carabid species (Larsson 1939; Schjøtz-Christensen 1957; den Boer and den Boer-Daanje 1990) and the life history stage (larva or imago), in which hibernation takes place (Lindroth 1985; 1986). We have to keep in mind that these traits can show intraspecific variability between different habitats of the species: The same species can be predominantly nocturnal in one habitat and diurnal in another (Schiller and Weber 1975). Moreover feeding and seasonality can have a strong impact on the locomotory activity of a species (Meyer-Peters 1993a; 1993b). Although timing of reproduction tends to be genetically controlled, populations from different altitudes showed different reproduction and hibernation rhythms after assisted migration into identical environmental conditions: *Carabus auronitens*, for example, produces winter larvae in high altitudes, while it brings out summer larvae in lowland habitats (Schwöppe *et al.* 1998). However, carabids.org holds information on the variation of these traits for some species and can easily be extended by stronger differentiated data where appropriate.

3.4 Structure and application of carabids.org

3.4.1 Technical structure

Carabids.org is a web application allowing users to execute complex search queries, view and edit detailed data sheets, export large bulks of data and upload new data using an intuitive and dynamic web interface. The application uses HTML, JavaScript and CSS on the front end (client side), while the interface to the MySQL data base relies on PHP, SQL and JSON (server side). Thus, carabids.org runs on any up-to-date release of a common web browser. Detailed trait data is presented in a clearly arranged tab view offering immediate data editing, which facilitates enrichment of trait data by users.

3.4.2 User registration

To ensure scientific use and prevent misuse of the compiled data, we ask scientists interested in using carabids.org to register first. The registration form requests the user's contact data such as an e-mail address, the affiliation to an institution and the intended use of carabid data. The user data will not be provided to third parties nor will be used for any other purposes. The registration enables users to view, edit, export or upload data.

3.4.3 Data search and export

An easily usable search form enables registered users to search for data by species, genus or other taxonomic groups. The user can also search for species occurring in one or more countries or in a certain range (Palaearctic, western Palaearctic or Cenral Europe). In addition, the search form allows the selection of species by range (restricted-range and widespread species) and by traits (dispersal ability, trophic level, hunting abilities). Carabid trait data can be exported based on search queries or on CSV file uploads containing a list of carabid species (species name has to be the identifier based on the nomenclature of Löbl and Smetana 2003). Exported CSV data can be easily processed within Microsoft Excel or other spreadsheet software.

3.4.4 Data contributions

Registered users can not only use already entered data but also add new and edit the existing entries. New species entries can be added into a blank form (Add Data) and existing species data can be extended or modified directly in the species data sheet (tab view). Edited data will be reviewed by the authors of carabids.org before online activation and publishing to ensure high data quality – this may take up to two workdays.

3.4.5 Relationship between body size and taxon description

With an example, we demonstrate the applicability of carabids.org in regard to testing hypotheses on species traits. Studying the beetle fauna of Australian lowland rainforest, Storck *et al.* (2008) showed that small species are more likely to be undescribed than larger species (see also Baselga *et al.* 2006; Jiménez-Valverde and Ortuño 2007). This might also be true for the western Palaearctic carabid fauna: We hypothesised that smaller species have been overlooked with higher probabilities than larger species. Data that was needed to test this hypothesis could be easily downloaded from carabids.org: year of description and mean body size of the species that occur in the study region. Data for all western Palaearctic species was searched online with the "Search Database" function at carabids.org by selecting the Region "Western Palaearctic" under the "Basic Information" section. The list of results shows western Palaearctic species which also include Central European species. Then the search result was exported as a CSV file including the species names, the classification, the year of description and species' traits which contain the mean body size of most Palaearctic species. CSV data could be easily processed within Microsoft Excel: columns with extraneous data were deleted. To visualise the temporal trend of species discovery in carabids of different body sizes, we generated accumulation curves (Figure 3.2) for three groups, each comprising approximately 1,000 carabid species: small (≤ 4.9 mm), medium (5.0 – 9.9 mm) and large (≥10.0 mm) species.

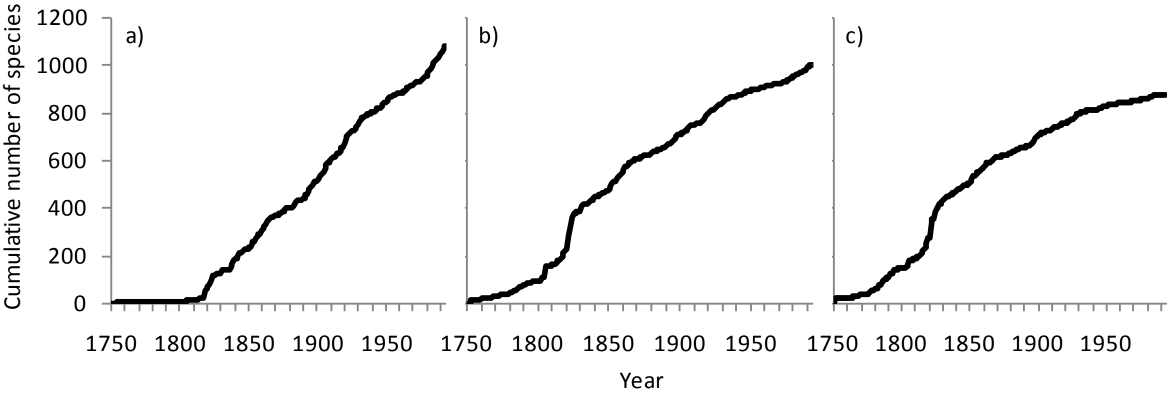

Figure 3.2. Cumulative number of (a) small, (b) medium and (c) large carabid species described from 1758 to 2000.

While species accumulation curves of medium and large species tended to reach an asymptote during the 20th century, the curve of small species showed a continuous rise. In addition, the description of small species appeared to have started later than the discovery of medium and large species. A non-parametric one-way analysis of variance (Kruskal-Wallis test) attested significant differences in the temporal pattern of species discovery between the three size groups ($\chi^2 = 274.71$, df = 2, $P < 0.001$) and pairwise Wilcoxon tests confirmed that the mean year of description significantly increased from large to small species ($P < 0.001$ in all cases). Thus, we can verify our hypothesis that smaller species have been described on average later than larger species.

3.5 Prospects

3.5.1 Extension of the database

We intend to continue data collection to enhance data on habitat preference and life-history traits firstly for the western and then for the whole Palaearctic species. However, data availability depends on the study intensity of regions of the Palaearctic and the resulting completeness of species records. Since data search, gathering and entry can be very time consuming, we would very much appreciate data contributions from carabidologists, other scientists and interested parties. Finally, carabids.org is meant to be a collaborative and interactive project offering a variety of research opportunities.

Further conceivable is an addition of data from book series such as Erwin's treatise series (Erwin 2007; 2008; 2011) and an integration of information from large carabid collections such as Basilewski's special collection located in the Royal Museum for Central Africa in Tervuren, Belgium. In addition, a long-term goal might be to link carabids.org with an interactive species identification tools basing on free access software such as Xper^2 (Ung *et al.* 2010; http://lis-upmc.snv.jussieu.fr/lis/?q=en/resources/software/xper2).

We hope that carabids.org contributes to the rapid expansion and analysis of freely available traits data on species-rich invertebrates, which will help to advance our understanding of community assembly and functional diversity effects of such taxa across large spatial scales.

3.6 Acknowledgements

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3.7 Supplementary Material

Table S3.1. Abbreviations and denotations of European and North African countries and further ecozones considered in the carabids.org database (according to Löbl & Smetana 2003).

E	Europe	N	North Africa
AL	Albania	AG	Algeria
AN	Andorra	CI	Canary Islands
AU	Austria	EG	Egypt
AZ	Azores	LB	Libya
BE	Belgium	MO	Morocco (incl. Western Sahara)
BH	Bosnia and Herzegovina	MR	Madeira Archipelago
BU	Bulgaria	TU	Tunisia
BY	Belarus	Further ecozones	
CR	Croatia	AFR	Afrotropical Region
CT	Russia: Central European Territory	AUR	Australian Region
CZ	Czech Republic	NAR	Nearctic Region
DE	Denmark	NTR	Neotropical Region
EN	Estonia	ORR	Oriental Region
FA	Faeroe Islands		
FI	Finland		
FR	France (incl. Corsica, Monaco)		
GB	Great Britain (incl. Channel Islands)		
GE	Germany		
GR	Greece (incl. Crete)		
HU	Hungary		
IC	Iceland		
IR	Ireland		
IT	Italy (incl. Sardinia, Sicily, San Marino)		
LA	Latvia		
LS	Liechtenstein		
LT	Lithuania		
LU	Luxembourg		
MA	Malta		
MC	Macedonia		
MD	Moldova		
NL	The Netherlands		
NR	Norway		
NT	Russia: North European Territory		
PL	Poland		
PT	Portugal		
RO	Romania		
SK	Slovakia		
SL	Slovenia		
SP	Spain (incl. Gibraltar)		
SR	Svalbard (Spitzbergen)		
ST	Russia: South European Territory		
SV	Sweden		
SZ	Switzerland		
TR	Turkey		
UK	Ukraine		
YU	Jugoslavia (Serbia, Montenegro)		

Table S3.2. Abbreviations and denotations of Asian countries and Chinese provinces considered in the carabids.org database (according to Löbl & Smetana 2003).

A	Asia	Chinese provinces	
AE	Arab Emirates	AHN	Anhui (Anhwei)
AF	Afghanistan	BEI	Beijing (Peking or Peiping)
AR	Armenia	FUJ	Fujian (Fukien)
AB	Azerbaijan	GAN	Gansu (Kansu)
AP	Arunachal Pradesh	GUA	Guandong (Kwantung)
BA	Bahrain	GUI	Guizhou (Kweichow)
BT	Bhutan	GUX	Guanxi (Kwangsi)
CE	China: Central Territory	HAI	Hainan
CH	China	HEB	Hubei (Hopeh)
CY	Cyprus	HEI	Heilongjiang (Heilungkiang)
GG	Georgia	HEN	Henan (Honana)
ES	Russia: East Siberia	HKG	Hongkong
FE	Russia: Far East	HUB	Hubei (Hupeh)
HP	Himachal Pradesh	HUN	Hunan
IN	Iran	JIA	Jiangsu (Kiangsu)
IQ	Iraq	JIL	Jilin (Kirin)
IS	Israel	JLX	Jiangxi (Kiangsi)
JA	Japan	LIA	Liaoning
JO	Jordan	MAC	Macao
KA	Kashmir (India)	NIN	Ningxia (Ningsia)
KI	Kyrgyzstan	NMO	Nei Mongol (Inner Mongolia)
KU	Kuwait	QIN	Qinghai (Tsinghai)
KZ	Kazakhstan	SCH	Sichuan (Szechwan)
LE	Lebanon	SHA	Shaanxi (Shensi)
MG	Mongolia	SHG	Shanghai
NP	Nepal	SHN	Shandong (Shantung)
NE	China: Northeast Territory	SHX	Shanxi (Shansi)
NC	North Korea	TAI	Taiwan (Formosa)
NO	China: Northern Territory	TIA	Tianjin (Tsiensin)
NW	China: Northwest Territory	XIN	Xinjiang (Sinkiang)
OM	Oman	XIZ	Xizang (Tibet)
PA	Pakistan	YUN	Yunnan
QA	Qatar (incl. United Arab Emirates)	ZHE	Zhejiang (Chekiang)
RU	Russia		
SA	Saudi Arabia		
SC	South Korea		
SD	Sikkim, Darjeeling (India)		
SE	China: Southeast Territory (incl. Macao, Hongkong)		
SI	Egypt: Sinai		
SW	China: Southwestern Territory		
SY	Syria		
TD	Tadzhikistan		
TM	Turkmenistan		
UP	Uttar Pradesh (India)		
UZ	Uzbekistan		
WP	China: Western Plateau		
WS	Russia: West Siberia		
YE	Yemen (incl. Socotra)		

4 MULTIPLE GLACIAL REFUGIA OF THE LOW-DISPERSAL GROUND BEETLE *CARABUS IRREGULARIS*: MOLECULAR DATA SUPPORT PREDICTIONS OF SPECIES DISTRIBUTION MODELS

Published Article

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4.1 Abstract

Classical glacial refugia such as the southern European peninsulas were important for species survival during glacial periods and acted as sources of post-glacial colonisation processes. Only recently, some studies have provided evidence for glacial refugia north of the southern European peninsulas. In the present study, we combined species distribution models (SDMs) with phylogeographic analyses (using mitochondrial DNA = mtDNA) to investigate if the cold-adapted, stenotopic and flightless ground beetle species, *Carabus irregularis,* survived the Last Glacial Maximum (LGM) in classical and/or other refugia. SDMs (for both a western European and for a Carpathian subgroup) were calculated with MAXENT on the basis of 645 species records to predict current and past distribution patterns. Two mtDNA loci (CO1 and ND5, concatenated sequence length: 1785bp) were analyzed from 91 *C. irregularis* specimens to reconstruct the phylogeography of Central and eastern European populations and to estimate divergence times of the given lineages. Strong intraspecific genetic differentiation (inter-clade Φ_{ST} values ranged from 0.92 to 0.99) implied long-term isolation of major clades and subsclades. The high divergence between the nominate subspecies and the Carpathian subspecies *C. i. montandoni* points to two independent species rather than subspecies (K-2P distance 0.042 ± 0.004; supposed divergence of the maternal lineages dated back 1.6 to 2.5 million years BP) differing not only morphologically but also genetically and ecologically from each other. The SDMs also inferred classical as well as other refugia for *C. irregularis*, especially north of the Alps, in southeastern Europe and in the Carpathians. The coincidences between the results of both methods confirm the assumption of multiple glacial refugia for the studied species and the usefulness of combining methodological approaches for the understanding of the history of low-dispersal insect species.

4.2 Introduction

The glaciers and permafrost grounds of the Quaternary ice ages shaped distribution patterns in biodiversity, as they caused species extinctions as well as the retraction of species' distribution ranges. Glacial refugia were important for species survival in glacial and interglacial periods and hosted many species which had recently been widespread across Europe (Hewitt 2000). Temperate and warm-adapted species in particular are assumed to have colonised central and northern parts of Europe after the Last Glacial Maximum (LGM), originating from classical refugia such as the southern European peninsulas (Iberian, Apennine and Balkan: Taberlet *et al.* 1998; Hewitt 2000). Cold-adapted species which had recently inhabited alpine and arctic habitats are assumed to have survived in the margins of southern European mountain chains (Stewart *et al.* 2010). In recent decades, palaeontological, palynological and phylogeographic studies have provided evidence for glacial refugia far north of the southern European peninsulas and the Alps (so-called cryptic refugia: Bhagwat and Willis 2008; Provan and Bennett 2008). In contrast to the species which were widespread across Europe (Knopp and Merilä 2009; Valtuena *et al.* 2012), species with restricted and disjunct ranges in the European low and high mountain chains are poorly studied with regard to spatial patterns in genetic variation. However, some mountain plant species inhabiting the Alps and geographically relatively close mountain systems (e.g. the Central European mountain ranges, the Carpathians) show high genetic differentiation (Ronikier 2011; Kropf *et al.* 2012). Zoological studies have covered arthropod species with high dispersal abilities (e.g. due to flight activity or ballooning): Butterflies (Schmitt and Haubrich 2008) and spiders (Muster and Berendonk 2006) show low level differentiations and indicate young and even post-glacial splits between populations from the Alps and adjoining high and low mountain ranges (Schmitt 2009). In contrast, low-dispersal species are likely to show stronger genetic differentiation patterns due to the absence of gene flow (e.g. flightless carabids: Matern *et al.* 2010; Schmidt *et al.* 2012); however, the population histories of these species have been studied only insufficiently to date.

New study methods such as species distribution models (SDMs) have become useful tools to predict potential habitat distribution of species under current climate conditions and – when analysed in conjunction with palaeoclimatic data – to project species' past distributions (Elith and Leathwick 2009). Many studies detected classical as well as cryptic refugia using past predictive models (e.g. Vega *et al.* 2010; Rebelo *et al.* 2012). Unaffected by incomplete sampling, the extinction of genetic variants and large-scale range shifts of species, past predictive models can contribute to the localization and sizing of species' glacial refugia (Waltari *et al.* 2007). Consequently, past predictive models and phylogeographic analyses can be used complementarily to develop reasonable scenarios of species' range retractions during glaciations and of range expansions during interglacial stages.

In this study we applied a combined approach using modelling and of phylogeographic analysis of two mitochondrial DNA loci (CO1 and ND5) to investigate the history of the flightless ground beetle species, which occurs in a disjunct range across high- and low-altitude mountains of Central and eastern Europe: *Carabus irregularis.* We aimed to test (i) whether the cold-adapted species survived the LGM in classical and/or cryptic refugia and (ii) whether the low-dispersal species shows old phylogenetic groups and high intraspecific variation. Since the CO1 locus has been successfully used in barcoding (Hebert *et al.* 2003), we also checked (iii) whether the phylogeny of *Carabus irregularis* is consistent with the intraspecific taxonomy of the species.

We addressed the following specific study questions: (1) Where did *C. irregularis* find suitable climate conditions (refugia) to survive the LGM? (2) Does the species' genetic differentiation pattern provide molecular evidence for low dispersal and for the detected potential glacial refugia? (3) Is the phylogeny of *C. irregularis* congruent with its taxonomic subspecies delineation?

4.3 Material and methods

4.3.1 Study species

Carabus (Platycarabus) irregularis Fabricius, 1792 occurs in cold and mesic habitats in montane to subalpine altitudes (e.g. beech forests and high mountain meadows). Suitable habitats are predominantly on limestone and are rich in snails, the preferred food of *C. irregularis*. The disjunct distribution of *C. irregularis* ranges from the Teutoburg Forest in the north to the Dinaric Mountains in the south and from the Carpathians in the east to the Jura Mountains in the west (Figure 4.1; Turin *et al.* 2003a). In the taxonomic literature, three subspecies are well-accepted even though different names are sometimes used (Bousquet *et al.* 2003). In this study we follow Casale and Kryzhanovskij (2003) and use the following binomials: *C. i. irregularis* s.str. in Central Europe including the northern Alps, *C. i. bucephalus* Kraatz, 1879 in the southeastern Alps and the northern Balkan Peninsula, and *C. i. montandoni* Buysson, 1882 in the Carpathians (Figure 4.1). While the distribution ranges of *C. i. irregularis* and *C. i. bucephalus* pass into each other in the southeastern Alps, *C. montandoni* is geographically separated from the other two subspecies (see subspecies affiliation in the Supplementary material, Table S4.1). The species is declining in some regions (Assmann *et al.* 2003; Lorenz 2003) and already extinct in some parts of its former distribution range (e.g. in Belgium: Desender *et al.* 2008).

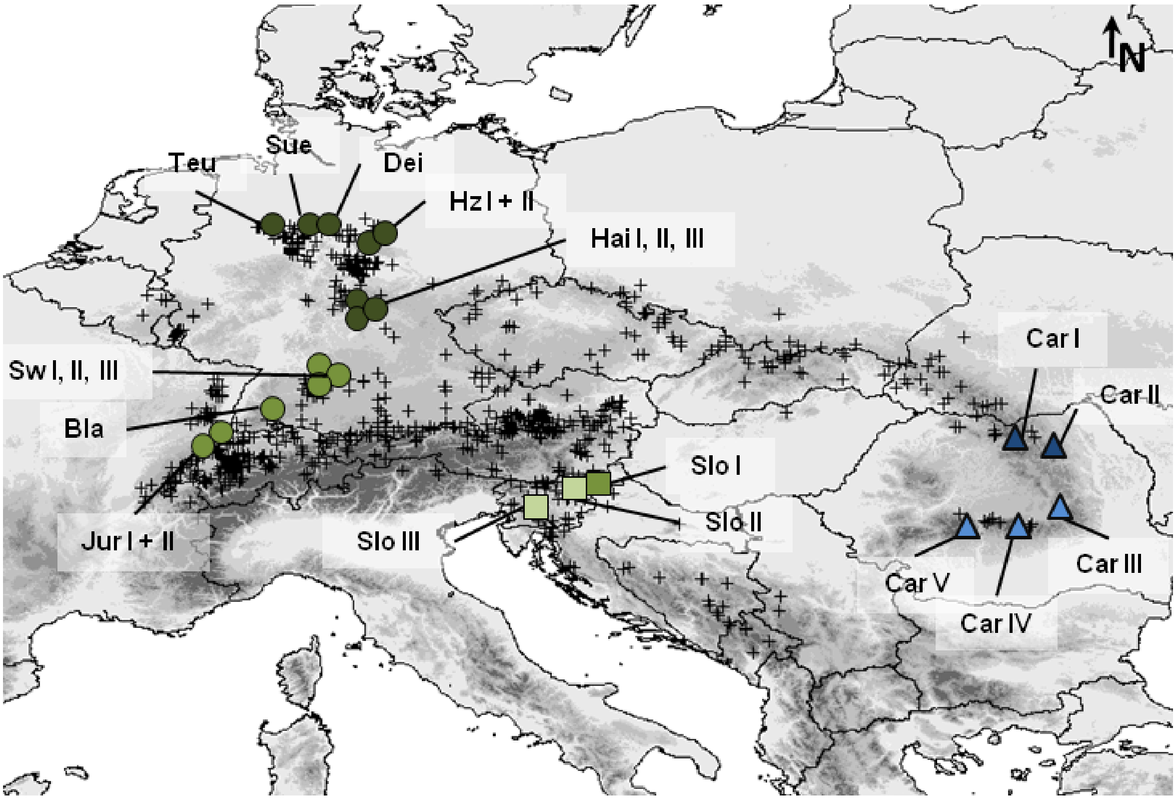

Figure 4.1. Species records of *Carabus irregularis* used for species distribution modelling and populations sampled for genetic analyses. SDMs included species records displayed as small crosses. Genetic analyses included populations of the three subspecies – *C. i. irregularis* (circles), *C. i. bucephalus* (squares) and *C. i. montandoni* (triangles). Genetic analyses resulted in two major clades: a Carpathian clade (Clade A = blue colours) and a European clade (Clade B = green colours). The clades split into five subclades: an eastern Carpathian (Ae = dark blue), a southern Carpathian (As = light blue), a northern European (Bn = dark green), a southern European (Bs = olive green) and a purely Slovenian clade (Bsl = light green).

4.3.2 Species distribution modelling

In order to predict the potential habitat distribution of the study species under current and past climate conditions, we compiled 1,005 data points of observed occurrences of *C. irregularis* from the literature and databases (e.g. Sokolár 1909; Weber 1966a; Franzen 1995; Hartmann 1998; Flechtner 2000; Gebert 2006; Köhler and Flechtner 2007; Hejda 2011), from museum and private entomological collections as well as our own field surveys (see complete list of records in the Supplementary material, Table S4.1). Since spatial clumping of species records due to different sampling intensities may bias SDMs, redundant localities were excluded by the model software, and the final locality input included 645 records. In addition to the geographic separation, there are also differences in the altitudinal distribution pattern of the two western European subspecies (*C. i. irregularis* and *C. i. bucephalus*) and the Carpathian subspecies (*C. i. montandoni*).

Table 4.1. Populations of *Carabus irregularis* sampled for genetic analyses and occurrence data used for species distribution models.

Code	Population	Altitude (m a.s.l.)	Geographical coordinates	(Sub-) species	Sample size	Year
Teu	Teutoburg Forest: Wehdeberg (D)	261	52°08.5'N, 08°11.0'E	*irregularis*	5	2010
Sue	Weser Hills: Süntel (D)	231	52°12.2'N, 09°16.3'E	*irregularis*	6	2009
Dei	Weser Hills: Deister (D)	227	52°13.2'N, 09°32.0'E	*irregularis*	1	2010
Hz I	Harz: Schreckenberg (D)	227	51°58.6'N, 10°13.4'E	*irregularis*	6	2010
Hz II	Harz: Fürstenhagen (D)	334	51°49.3'N, 10°09.9'E	*irregularis*	5	2010
Hai I	Hainich: Küllstedt (D)	456	51°16.1'N, 10°14.4'E	*irregularis*	6	2010
Hai II	Hainich: Dingelstädt (D)	455	51°20.2'N, 10°21.9'E	*irregularis*	5	2010
Hai III	Hainich: Mühlhausen (D)	379	51°12.6'N, 10°22.2'E	*irregularis*	4	2011
Sw I	Swabian Mountains: Gomadingen (D)	790	48°23.8'N, 09°27.2'E	*irregularis*	5	2011
Sw II	Swabian Mountains: Münsingen (D)	791	48°23.4'N, 09°30.1'E	*irregularis*	5	2011
Sw III	Swabian Mountains: Engstingen (D)	763	48°22.5'N, 09°20.3'E	*irregularis*	4	2011
Bla	Black Forest: Wutachschlucht (D)	696	47°50.6'N, 08°20.2'E	*irregularis*	6	2010
Jur I	Jura: NO Jougne (F)	1190	46°47.5'N, 06°25.9'E	*irregularis*	1	2010
Jur II	Jura: NW Jougne (F)	1100	46°47.0'N, 06°22.7'E	*irregularis*	5	2010
Slo I	Poljčane: Boč, Formila (SLO)	633	46°17.3'N, 15°37.3'E	*bucephalus*	4	2011
Slo II	Konjiška gora: Stolpnik (SLO)	790	46°20.0'N, 15°22.9'E	*bucephalus*	5	2011
Slo III	S Ljubljana: Krim (SLO)	950	45°54.6'N, 14°27.6'E	*bucephalus*	4	2011
Car I	Carpathians: Rodnei (RO)	1560	47°36.5'N, 24°38.8'E	*montandoni*	2	2009
Car II	Carpathians: Rarău (RO)	1529	47°27.0'N, 25°33.8'E	*montandoni*	5	2009
Car III	Carpathians: Bucegi (RO)	1128	45°29.9'N, 25°30.7'E	*montandoni*	4	2009
Car IV	Carpathians: Făgăraş (RO)	1327	45°38.0'N, 24°36.5'E	*montandoni*	1	2009
Car V	Carpathians: Parang (RO)	1950	45°22.1'N, 23°35.9'E	*montandoni*	2	2009
creutzeri 1	Julian Alps, Mangart (SLO)	1905	46°26.1'N, 13°38.5'E	*C. creutzeri*	1	2011
creutzeri 2 + 3	Triglav, Pokljuka (SLO)	1316	46°19.9'N, 13°54.5'E	*C. creutzeri*	2	2011
depressus 1 + 2	Adamello, Val di Daone (I)	2028	45°05.1'N, 10°34.1'E	*C. depressus*	2	2011
depressus 3	Valais Alps, Gran San Bernhardo (I)	2223	45°51.8'N, 07°09.5'E	*C. depressus*	1	2011

D: Germany, F: France, RO: Romania, SLO: Slovenia, I: Italy; m a.s.l.: metres above sea level.

According to the compiled species records, *C. i. irregularis* and *C. i. bucephalus* occur in high as well as low altitudes in the western part of its distribution range and on average in lower altitudes (altitudes as low as 250m a.s.l.; mean altitude of western records = 765m a.s.l.). From the eastern part of the range (the Carpathian mountain system), however, the species was scarcely recorded from altitudes below 600m a.s.l. (mean altitude of Carpathian records = 867m a.s.l.; see Supplementary material, Figure S4.1). Due to geographically separated and different altitudinal distribution ranges of the subspecies, we could not exclude different habitat preferences of the Carpathian subspecies. Thus, species records were split into two sets before modelling: one included occurrences of the Carpathian subspecies, the other comprised occurrences of the two other subspecies from the western part of the distribution range (Central Europe and Balkan). Climate data (monthly temperature and rainfall values) was generated according to Hijmans et al. (2005) to 19 bioclimatic variables (BIO1-BIO19; Supplementary material, Table S4.2) which representing factors of climate which are particularly significant in determining species' distributions (Waltari *et al.* 2007). For carabids, temperature and humidity variables have been demonstrated to be the most important environmental factors influencing habitat selection (Thiele 1977).

Current climate data (i.e. period 1950-2000) was downloaded with a spatial resolution of 30 arc s (~ 1 x 1 km) from the WorldClim database (www.worldclim.org/). Past (Last Glacial Maximum = LGM; 21,000 BP) climate data downscaled from the MIROC general circulation models to the required spatial resolution (2.5 arc min) was provided by the Paleoclimate Modelling Intercomparison Project Phase II (http://pmip2.lsce.ipsl.fr/). Since our SDMs were to include only predictors with high explanatory power and ecological relevance (Araújo and Guisan 2006; Rödder and Dambach 2010), we included only the variables which are most likely to influence the occurrence of *C. irregularis*. Therefore, we extracted all 19 bioclimatic variables at coordinates of species records and performed a principal component analysis (PCA). To reduce multicollinearity, we compiled a correlation matrix and excluded all strongly correlated variables (Pearson's $r^2 > 0.75$: Guisan and Thuiller 2005). Final models included five uncorrelated predictor variables: 'Isothermality' (BIO3), 'temperature seasonality' (BIO4), 'minimum temperature of coldest month' (BIO6), 'precipitation of wettest month' (BIO13) and 'precipitation of driest month' (BIO14) – climatic measures reflecting habitat conditions which are likely to affect the occurrence of *C. irregularis* (Weber 1966a; Hartmann 1998). The bioclimatic layers were cut to cover the recently documented distribution range of the species sufficiently but not too generous, since large layer extents could have a negative effect on SDM results (Anderson and Raza 2010). The layers used ranged from 0 to 30 decimal degrees North and from 30 to 60 decimal degrees East.

We used the maximum entropy approach (Phillips *et al.* 2006), which repeatedly performed better than other methods using species presence data in comparative studies (Elith *et al.* 2006; Heikkinen *et al.* 2006). Three sets of SDMs – one with the western record set (hereafter western distribution model), one with only Carpathian records (hereafter Carpathian distribution model) and one model including all records together (hereafter entire distribution model) were generated with MAXENT 3.3.3 (www.cs.princeton.edu/~schapire/maxent), with automatically sampled random background points and species records split into 75% model training and 25% model evaluation data. Model quality was evaluated by a bootstrap validation and the Area Under Curve method (AUC > 0.7: Fielding and Bell 1997). The logistic output of 100 model replicates was transformed to species maps showing the potential distribution of *C. irregularis* under current climate conditions and under LGM conditions. Species maps were processed in DIVA-GIS v7.1.7 (www.diva-gis.org). We compared the Maxent outputs of the three model sets using the software ENMtools (Warren *et al.* 2010). Niche overlap was quantified by two metrics of niche similarity introduced by Warren et al. (2008): *D* (Schoener's statistic for niche overlap: Schoener 1968) and *I* (derived from Hellinger distance). Both measures range from 0 (no niche overlap) to 1 (identical niches). In addition, a niche identity test was run to evaluate niche similarity between the western and the Carpathian distribution model (Warren *et al.* 2010).

4.3.3 Sample collection and molecular methods

In total 91 specimens of the study species were collected from 23 localities across its entire distribution range (Table 4.1, Figure 4.1). In spite of conscientious efforts and communications with numerous coleopterologists, no fresh beetles were available from certain parts of the distribution range (possibly due to the recent decline mentioned above). Adult beetles were collected from hibernation in autumn or caught by pitfall trapping during the activity periods. The specimens were preserved at –80 °C or in pure ethanol at –20 °C until DNA extraction.

Mitochondrial genomes within the genus *Carabus* can be influenced by horizontal gene flow (secondary contact after speciation: Sota and Vogler 2001; Brouat *et al.* 2006; Deuve *et al.* 2012). In natural habitats, *C. irregularis* seems to produce hybrids with related species (members of the same subgenus *Platycarabus*: *C. creutzeri* and *C. depressus*: Breuning 1937). Therefore, we used six individuals of the latter species from three different sites as outgroups for rooting phylogenetic trees and for checking the reliability of mitochondrial DNA (mtDNA) as a phylogenetic marker. In comparative studies, the two different mitochondrial genes studied, CO1 and ND5, have outperformed nuclear markers in terms of giving a reliable estimates in timing of splits and phylogenetic reconstruction because of their maternal heritability (Andujar *et al.* 2012). Moreover, CO1 is a valuable barcoding marker in animals (Hebert *et al.* 2003) which makes it possible to study the performance of such a marker system on an infraspecific level.

Genomic DNA was extracted from one femur of each specimen by CTAB (Cetyldimethylethyl-Ammoniumbromid) lysis (Doyle and Doyle 1987), where we reached a

DNA concentration of min. 200 ng/µl. Two regions of mtDNA, Cytochrome c Oxidase I (CO1) and NADH Dehydrogenase 5 (ND5), were amplified and sequenced using the primers Jerry (C1-J-2183) 5’-CAA CAT TTA TTT TGA TTT TTT G-3’ and Pat (L2-N-3014) 5’-TCC AAT GCA CTA ATC TGC CAT ATT A-3’ (Simon *et al.* 1994) for CO1 and ND5-His (V1.06-1) 5’-CCT GTT TCT GCT TTA GTT CA-3’ and ND5-Phe (V1.04-4) 5’-GTC ATA CTC TAA ATA TAA GCT A-3’ (Su *et al.* 1998) for ND5. Polymerase chain reactions (PCRs) were carried out on a Thermal Cycler TGradient (Biometra GmbH, Göttingen, Germany). The PCR mix of 20 µl contained 1µl of extracted DNA, 2.5µl of 10X DreamTaq Green Buffer and 0.4 µl dNTP mixture (10mM each; both Fermentas GmbH, St. Leon-Rot, Germany), 0.1 µl of each primer (50 pmol/µl; Biomers GmbH, Ulm, Germany), 0.2µl DreamTaq Polymerase (5U/µl; Fermentas GmbH, St. Leon-Rot, Germany) and 16.2 µl of DNA-free water. Cycling conditions for CO1 started with an initial denaturation for 5 min at 94 °C, followed by 35 cycles of denaturation for 45 at 94 °C s, annealing for 45 s at 50 °C and extension for 1 min at 72 °C. Final elongation was performed for 8 min at 72 °C. For ND5 the following PCR program was used: initial denaturation at 94 °C for 5 min, 35 cycles (1 min at 94°, 1 min. at 50°C, 2 min at 70°C), then final elongation for 7 min at 70°C.

PCR products were visualised on 2% agarose gels, dyed with Roti-Safe Gelstain (Carl Roth GmbH, Karlsruhe, Germany) and then purified with the GeneJET PCR Purification Kit (Fermentas GmbH, St. Leon-Rot, Germany). The manufacturer’s protocol was slightly modified: only 50µl elution buffer were used for final elution to ensure a minimum DNA concentration of 100 ng/µl. Purified PCR products were again checked on agarose gels. Sequencing (both forward and reverse strands) of PCR products was carried out at the laboratory of LGC Genomics (Berlin, Germany) using an Automatic Sequencer 3730xl (Applied Biosystems, Foster City, USA).

4.3.4 Sequence alignment and phylogenetic analysis

Forward and reverse sequences were assembled and manually corrected using the software Geneious v4.8.5 (Drummond *et al.* 2009). Sequences were aligned and checked for reading frame errors in MEGA5 (Tamura *et al.* 2011). Prior to phylogenetic analysis, MrModeltest v2.3 (Nylander 2004) was used to identify the best nucleotide substitution model for each mtDNA fragment (CO1 and ND5) ranked by Akaike Information Criterion (AIC). For each gene, we performed an independent run of 60 x 10^6 generations, sampling one tree every 1,000 generations. Based on the selected evolutionary models, we investigated phylogenetic relationships within the species *C. irregularis* (including two outgroups) using Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP). The BI tree was calculated by MrBayes v3.2.1 (Huelsenbeck and Ronquist 2001) running 2 x 10^6 generations, while reaching an average standard deviation of split frequencies <0.01. The ML method was conducted in RAxML v7.3.0 (Stamatakis 2006) performing 10,000 thorough bootstrap replicates. MP analysis was carried out in MEGA5 (Tamura *et al.* 2011) using 5,000 bootstrap replicates. Divergence times were estimated by using strict molecular clocks in BEAST v1.7.1 (Drummond *et al.* in press) considering gene-specific mtDNA substitution rates for the two studied loci (1.45% My^{-1} for CO1, and 1.59% My^{-1} for ND5) based on rates determined for other carabid beetle species (Osawa *et al.* 2004; Andujar *et al.* 2012). Population size through time was applied by a Yule speciation model, and Markov-Chain-Monte-Carlo (MCMC) chain length was set to 200 x 10^6, whereas other parameters remained in default settings.

4.3.5 *Intraspecific divergence and genetic diversity*

Measures of DNA sequence variation within different hierarchical levels (populations, subclades and clades) and in all sequences together (total) were computed for concatenated sequences and for CO1 and ND5 separately using DnaSP v5.10.01 (Librado and Rozas 2009). Variation measures included the number of polymorphic/segregating sites (S), number of haplotypes (H), haplotype diversity (h) and nucleotide diversity (π). In addition, we performed an analysis of molecular variance (AMOVA) using ARLEQUIN v3.5 (Excoffier *et al.* 1992) to estimate the level of genetic differentiation (Φ_{ST}) among populations, subclades and clades. We used the median-joining approach (Bandelt *et al.* 1999) implemented in the NETWORK Software v4.6.1.0 (www.fluxus-engineering.com) to illustrate phylogenetic and geographic patterns in haplotype diversity. Intraspecific genetic divergence in CO1 – both within and between major clades – and interspecific genetic divergence in the studied outgroup species of the subgenus *Platycarabus* were calculated by pairwise comparisons (4,005 intraspecific pairs and 554 interspecific pairs) using Kimura's two parameter (K-2P) model in MEGA.

4.4 Results

4.4.1 *Current and past predicted distribution*

High average training AUC values over all replicate runs for all models – the entire (AUC = 0.92 ± 0.001), the western (AUC = 0.92 ± 0.001) and the Carpathian distribution model (AUC = 0.98 ± 0.002), reflected the high accuracy of our models. Niche overlap was high between the entire distribution model and the western distribution model (*D* = 0.85; *I* = 0.98) and low between the entire and the Carpathian distribution model was low (*D* = 0.39; *I* = 0.71). Lowest niche overlap was found between the western and the Carpathian distribution model (*D* = 0.29; *I* = 0.58). The potential (a) current and (b) past (LGM) distribution of *C. irregularis* computed with the entire distribution model is documented in the Supplementary material (Figure S4.2). Figure 4.2 shows maps of the potential (a and b) current and (c and d) past (LGM) distribution of *C. irregularis* calculated with the western and the Carpathian record set, respectively. The SDMs for the western European and the Carpathian populations differed markedly from each other.

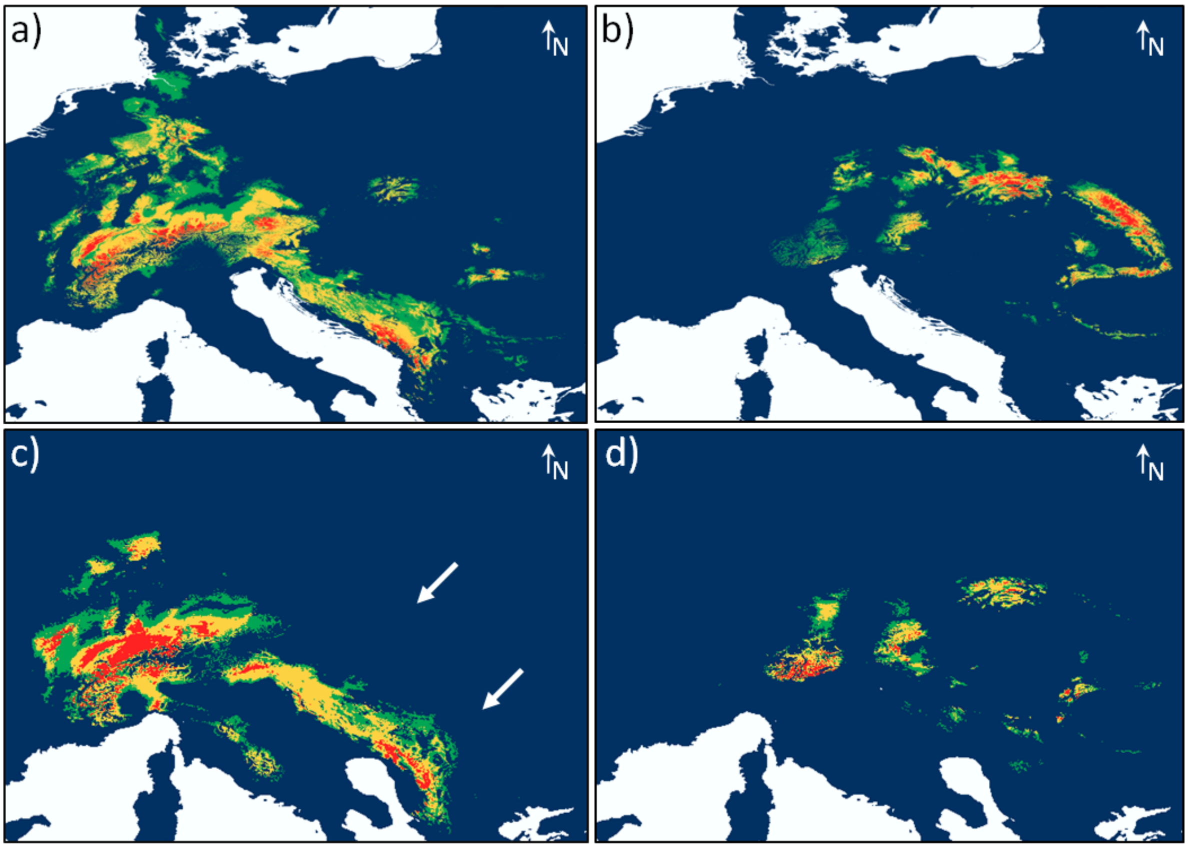

Figure 4.2. Western European distribution model for (a) current and (c) past climate conditions and Carpathian distribution model for (b) current and (d) past climate conditions. Past distribution is shown for the Last Glacial Maximum (LGM, 21,000 BP). Warmer colors show areas with better predicted conditions (green: $p > 0.3$, yellow: $p > 0.5$, red: $p > 0.7$).

The western distribution model for current climate showed the most suitable conditions ($p > 0.7$) in the Jura and Vosges Mountains in eastern France, parts of the Alps (in Switzerland, Germany, Austria and Slovenia), the Southern Carpathians (Transylvanian Alps) and the Apuseni Mountains in Romania as well as in the western Balkan (Dinaric Alps). Moderate suitability ($0.5 < p < 0.7$) was found in the lower mountain regions of southern Germany (e.g.

Black Forest, Bavarian Forest) and in the low mountain range of northwestern and Central Germany (i.e. Teutoburg Forest, Weser Mountains and Harz) and also in the northern Carpathians (Tatra Mountains). Low suitability ($0.3 < p < 0.5$) was attributed to the eastern Carpathians (Romania, Ukraine), the Ardennes (France, Belgium, Luxembourg), large parts of Germany and also up to Denmark. Areas with high suitability rates were always surrounded by areas with lower rates, resulting in a disjunct distribution of suitable habitats. Thus, the model was widely consistent with the documented actual distribution of *C. irregularis*. However, the study species is not known from the regions with low suitability rates, with the exception of the Romanian and Ukrainian Carpathians.

The Carpathian distribution model for current climate conditions (Figure 4.2b) displayed the most suitable conditions in parts of the Alps and several high-altitude regions in the Carpathian mountain system.

The past predictive model of *C. irregularis* using the western European data set showed the most suitable conditions ($p > 0.7$) during the LGM along the edges of the large Alpine glacier: in the southwestern Alps, the Vosges and Jura and in the Ligurian part of the Apennines. Well suited climatic conditions were also shown in a large area on the Balkan Peninsula (large parts of the Dinaric Alps) and in a small part of the northwestern German low mountain range. Moderately suitable regions were found in the central Apennines, in the eastern parts of the Alps and in the western Balkan. In the Carpathians, models for LGM conditions showed only small regions with low suitability rates (see arrows in Figure 4.2c).

The past distribution model for the Carpathian data set (Figure 4.2d) illustrated large areas with highly suitable climate conditions in the southern parts of the Eastern Alps and also high suitability rates for the Tatra Mountains and for some parts of the Southern and the Serbian Carpathians.

4.4.2 Sequence characteristics

For 96 individuals (including outgroups), the concatenated mtDNA sequence matrix included 1785bp: partitioned into 786bp at the CO1 and 999bp at the ND5 locus. From these mtDNA sequences, we detected 31 haplotypes in *C. irregularis* and 5 in the outgroups (2 *C. depressus*, 3 *C. creutzeri*). In total, 144 sites were variable (67 in CO1, 77 in ND5) and 127 sites were parsimony-informative (CO1: 56, ND5: 71), with no significant difference between the two studied loci (Supplementary material, Table S4.3). Both mitochondrial loci were heavily biased toward high A+T-contents of 71.8% (CO1) and 80.6% (ND5).

4.4.3 Phylogenetic analyses and divergence time estimation

For both loci, the best evolutionary model identified by the AIC was the general time reversible model with Gamma distributed rate variation across sites and a proportion of invariable sites (GTR+G+I; Rodríguez *et al.* 1990). Since there has been concern about estimation problems in this model type due to interactions between the proportion of invariable sites and the Gamma distribution (Stamatakis 2006), we also checked the model without +I and chose this simpler model for the ML analysis in RAxML.

BI, MP and ML yielded highly congruent phylogenetic trees with the same major nodes and branching order. The majority-rule consensus tree (Figure 4.3) displays the Bayesian posterior probability (BPP), parsimony bootstrap percentages (PB) and maximum likelihood bootstrap percentages (MLB), where BBP ≥ 0.5 and bootstrap values (PB and MLB) ≥ 50% represent well-supported nodes (Hillis and Bull 1993). In addition, nodal ages and 95% confidence intervals are represented for each node.

In the phylogenetic tree, all basal nodes had very high support (BPP ≥ 0.98; PB ≥ 93; MLB ≥ 65) and branches represent two major clades with the following groups of populations: (A) an eastern clade including two Carpathian subclades and (B) a western clade. The eastern clade covers (Ae) an eastern Carpathian subclade (populations Car I and Car II) and (As) a Southern Carpathian subclade (Car III, Car IV and Car V). The western clade comprises (Bn) a northern/central German subclade (Teu, Sue, Dei, Hz I, Hz II, Hai I, Hai II and Hai III), (Bs) a subclade including populations from Southern Germany (Bla, Sw I, Sw II, Sw III), the French Jura mountains (Jur I, Jur II) and Slovenia (Slo II, Slo III) and (Bs1) a purely Slovenian subclade (Slo I; Figure 4.3). Assumed divergence times spanning the last 2 million years (Figure 4.3) indicated that major clades and subclades within *C. irregularis* were formed long before the last glacial period. The separation of *C. irregularis* from other species of the subgenus *Platycarabus* was found to have taken place earlier than the separation of the species used as outgroups (*C. creutzeri and C. depressus*). Additionally, the split into the two major lineages within *C. irregularis* appears to be older than the split of the two species *C. creutzeri and C. depressus.* Only one of the three subspecies was monophyletic (*C. i. montandoni*), while *C. i. irregularis* and *C. i. bucephalus* are paraphyletic.

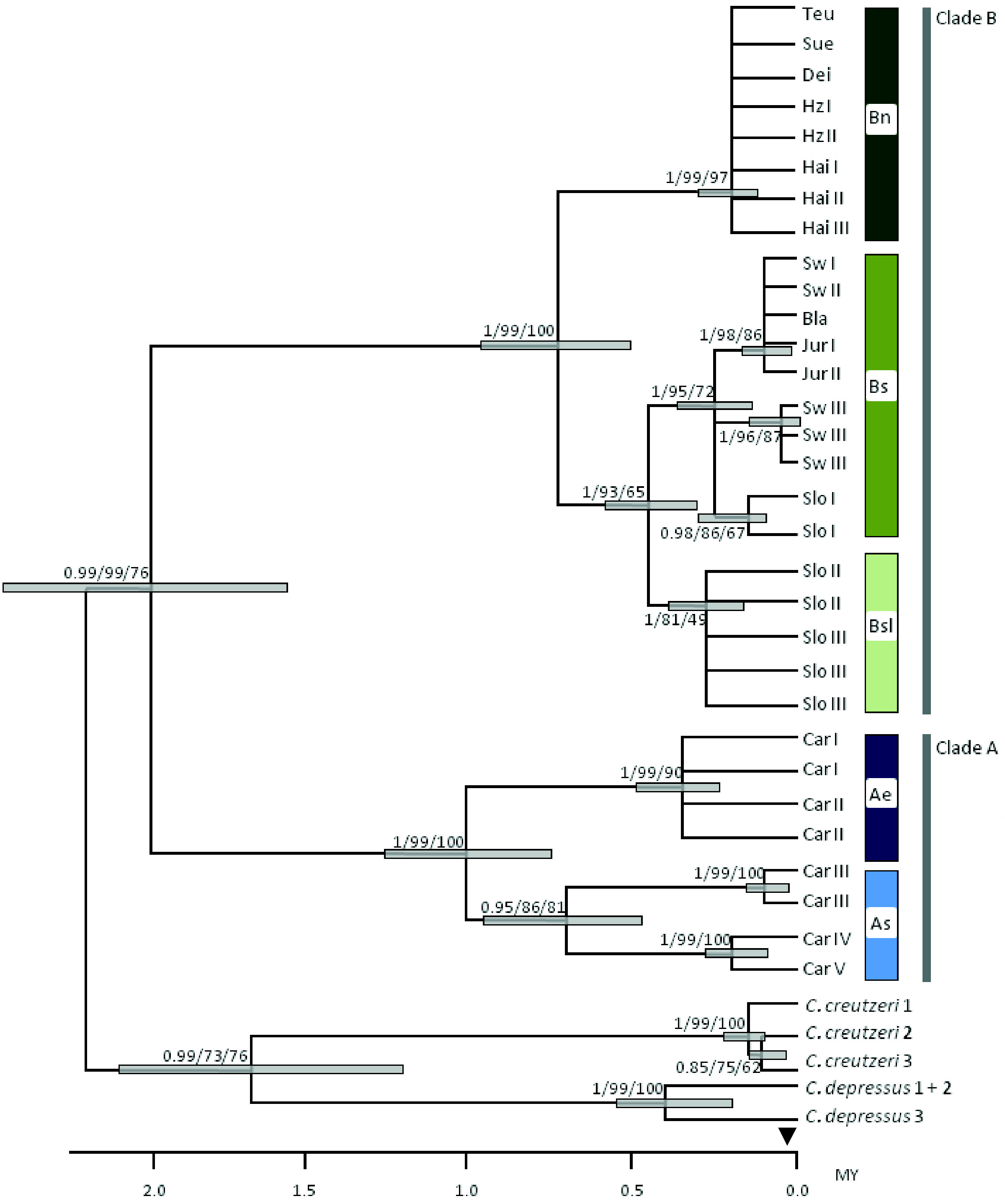

Figure 4.3. Majority-rule consensus tree for *Carabus irregularis***.** The tree shows results for the Bayesian posterior probability (BPP) / the parsimony bootstrap percentages (PB) / the maximum likelihood bootstrap percentages (MLB) for well-supported nodes. Divergence times are displayed with median values and 95% confidence intervals for nodal ages (bars) in million years BP (MY; scale at the bottom). See Table 4.1 for population abbreviations and Figure 4.1 for clade abbreviations and colour codes.

4.4.4 Intraspecific diversity and geographic distribution of genetic diversity

The overall haplotype diversity (h = 0.882 ± 0.0006) and nucleotide diversity (π = 0.017 ± 0.002) were high, with clade A showing higher haplotype and nucleotide diversity (h = 0.901; π = 0.016) than clade B (h = 0.838; π = 0.009; Table 4.2). In general, haplotype and nucleotide diversity tended to be higher in populations from the southern part of the distribution range (Supplementary material, Figure S4.3). Within clades, subclade As showed higher diversity than Ae and the subclades Bsl and Bs are more diverse than subclade Bn (see Table 4.3 for a summary of computed diversity measures of different hierarchical levels). The mean intraspecific variation in CO1 (K-2P; d = 0.027 ± 0.004) was also very high. The inter-clade K-2P divergence was 0.042 ± 0.004 and the frequency distribution of intraspecific genetic divergence in CO1 within and between major clades showed a clear pattern (Figure 4.4). On the population level, K-2P distance values ranged from 0.0 to 0.016 between populations within clade B to 0.022 between populations within clade A. Between populations of clade A and B, genetic distance ranged from 0.040 to 0.044 (Supplementary material, Table S4.4).

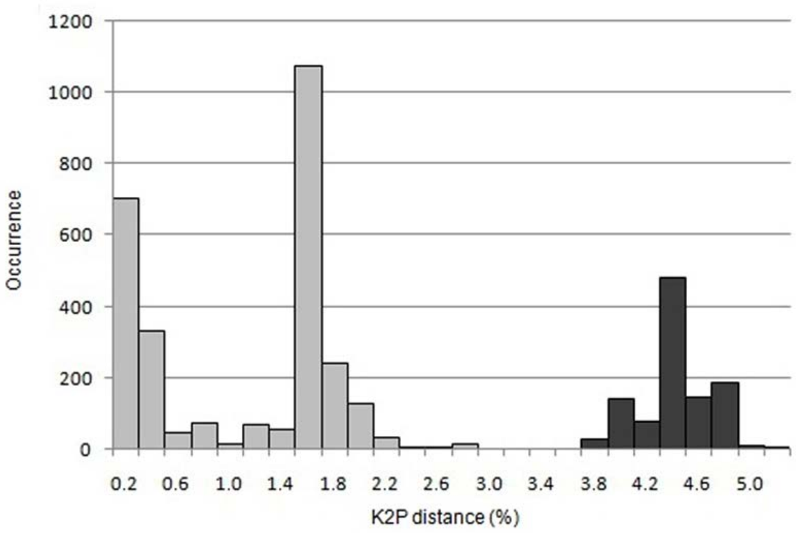

Figure 4.4. Frequency distribution of intraspecific genetic divergence in CO1 – within (light grey) and between major clades (dark grey). Pairwise distances (4005 intraspecific comparisons within *C. irregularis*) were calculated using Kimura's two parameter (K-2P) model.

Table 4.2. Diversity statistics based on concatinated CO1+ND5 sequences (1785 bp) of *C. irregularis* populations (sampled with more than one specimen) and in subclades and clades (as determined by the phylogenetic tree).

Group	Sample size	Polymorphic sites	Number of haplotypes	Haplotype diversity	Nucleotide diversity
Total	90	144	30	0.882	0.017
Clade A	14	73	8	0.901	0.016
Subclade Ae	7	23	4	0.714	0.005
Car I	2	17	2	1.000	0.010
Car II	5	11	2	0.400	0.002
Subclade As	7	39	4	0.857	0.011
Car III	4	2	2	0.667	0.001
Car V	2	0	1	-	-
Clade B	76	61	22	0.838	0.009
Subclade Bn	38	10	8	0.559	0.001
Sue	6	1	2	0.333	-
Hz I	6	0	1	-	-
Hz II	5	3	2	0.400	0.001
Hai1	6	2	2	0.333	-
Hai2	5	4	4	0.900	0.001
Hai3	4	2	2	0.667	0.001
Subclade Bs	30	17	9	0.667	0.002
Sw I	5	0	1	-	-
Sw II	5	1	2	0.400	0.000
Sw III	4	2	3	0.833	0.001
Bla	6	6	2	0.533	0.002
Ju I	5	1	2	0.400	-
Slo I	4	4	2	0.500	0.001
Subclade Bsl	8	25	7	0.964	0.006
Slo II	4	20	4	1.000	0.007
Slo III	4	11	3	0.833	0.003

In addition, we detected a significant differentiation structure among all populations (Φ_{ST} = 0.935, $p < 0.001$) and no shared haplotypes between the clades, subclades and subspecies but between populations within clades and subclades. Additionally, AMOVAs for different hierarchical groups (subclades, clades, subspecies) revealed significant genetic variance among these hierarchical groups, among populations and also within populations of the hierarchical groups. Most of the diversity was observed among subclades (88.1%), among clades (72.3%) and among subspecies (63.7%), while low percentage of variance was detected within populations (3.1 to 4.8%; Table 4.3).

Table 4.3. Results of Analysis of Molecular Variance (AMOVA) for different hierarchical levels: subclades, clades and subspecies.

Source of variation	d.f.	Sum of squares	Variation components	Variation (%)	Fixation indices	p value
Among subclades	4	1176.326	18.473	88.100	CT: 0.88100	0.000
Among populations/ within subclades	17	151.648	1.944	9.050	SC: 0.65091	0.000
Within populations	68	70.900	1.043	4.860	ST: 0.95144	0.000
Among clades	1	602.756	24.131	72.250	CT: 0.72247	0.000
Among populations/ within clades	20	691.222	8.227	24.630	SC: 0.88752	0.000
Within populations	68	70.900	1.043	3.120	ST: 0.96878	0.000
Among subspecies	2	683.794	15.251	63.730	CT: 0.63730	0.000
Among populations/ within subspecies	19	610.184	7.637	31.910	SC: 0.87988	0.000
Within populations	68	70.900	1.043	4.360	ST: 0.95643	0.000

Differentiation between the single populations of clade B ranged from lower values in geographically closer populations (Φ_{ST} = 0.10) to higher values in geographically distant populations (Φ_{ST} = 0.99). Populations of clade A also showed very high Φ_{ST} values (> 0.9; Supplementary material, Table S4.4), even though the sampled populations were geographically closer than those from clade B. Inter-clade Φ_{ST} values comparing populations of clade A and clade B ranged from 0.92 to 0.99. The haplotype network (Figure 4.5) supports these findings and illustrates a similar pattern: high genetic distance between the two geographically distant (~1,500km) major clades, but also large genetic distance and a high number of substitutions between the geographically closer (~300km) Carphathian subclades (Ae and As). In contrast, populations within subclade Bs showed very low genetic distance, although geographic distance is quite large (between Bla/Sw I-III/Jur I-II and SloI ~900km).

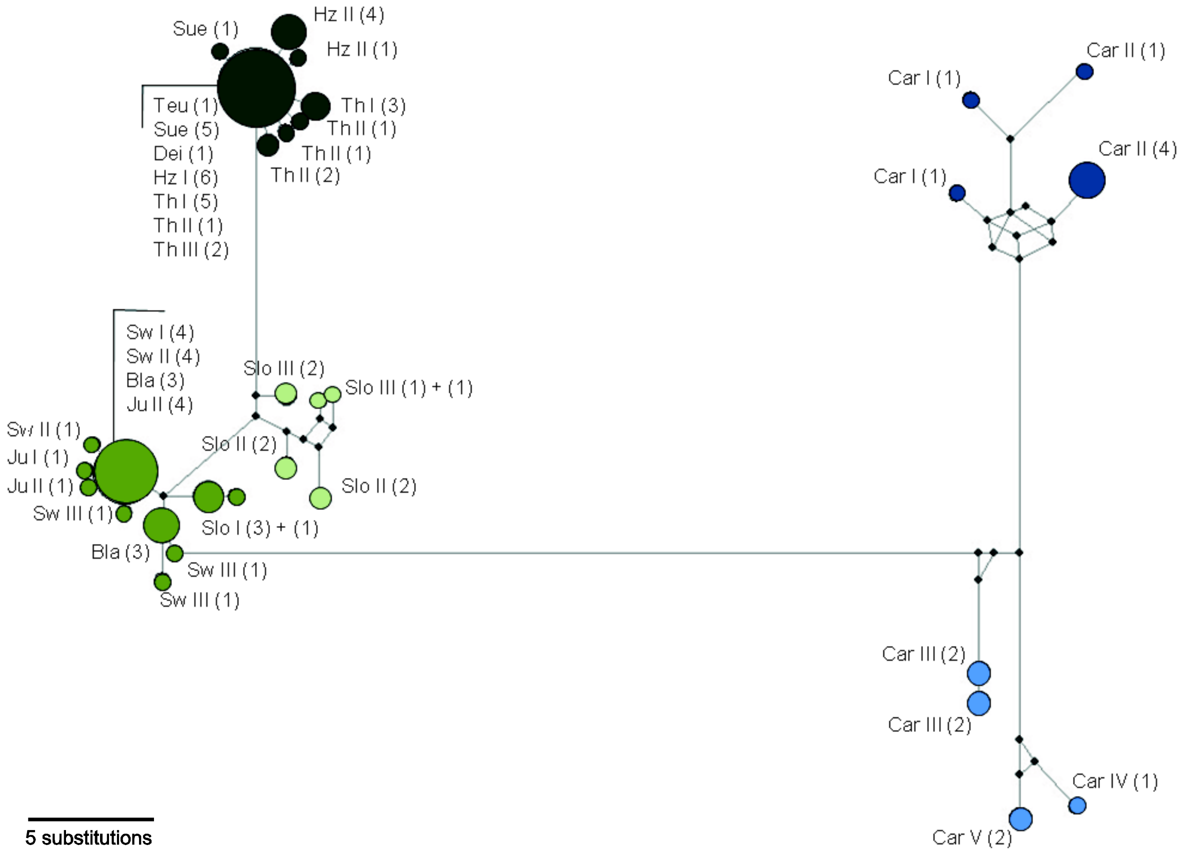

Figure 4.5. Median-joining network of mtDNA haplotypes based on concatenated CO1+ND5 sequences. Circles represent haplotypes; circle size and numbers in brackets indicate the haplotype frequency within our samples. Small black circles/nodes indicate intermediate haplotypes between observed haplotypes. Haplotype circles are filled corresponding to the colour code for the subclades also used in Figures 4.1 and 4.3.

4.5 Discussion

4.5.1 Potential glacial refugia

Our past predictive models showed several independent mountainous regions across Central and southern Europe with highly suitable climate conditions for *C. irregularis* which could have acted as glacial refugia during the LGM. Some of these potential refugia (e.g. in the Dinaric Alps) conformed to classical refugia on the southern European peninsulas (Hewitt 1996; 1999; 2000) and other refugia at the margins of the Alps and in neighbouring mountain ranges (e.g. the Jura, the Black Forest), some of which have quite recently been recognised as refugia (Schönswetter *et al.* 2005; Pauls *et al.* 2006; Schmitt *et al.* 2006). In addition, our model pointed to refugial areas far north of the southern European peninsulas and the Alps. So-called cryptic refugia have been assumed for a growing group of other species (plants as well as animals) (Stewart and Lister 2001; Provan and Bennett 2008).

While the southern European peninsulas are typical glacial refugia of current lowland plant and animal species (Taberlet *et al.* 1998; Petit *et al.* 2003), mountain species potentially persisted in refugia along the border of the Alps when higher altitudes were covered with ice sheets (Schönswetter *et al.* 2005; Schmitt *et al.* 2008). According to our results, *C. irregularis* seems to have survived in refugia of both low- and high-altitude species. Our models projected relatively large and consistent areas of suitable and moderately suitable conditions during the Last Glacial Maximum (comprising the maximum extension of the continental glaciers), suggesting that *C. irregularis* was relatively widespread during glaciations. In general, numerous mountain species (even though mostly defined as species with their main distribution above the timber line) are assumed to have survived in several spatially restricted and isolated refugia rather than in single extensive and consistent refuge areas (Holderegger and Thiel-Egenter 2009 and references therein; Schoville *et al.* 2012). Consequently, *C. irregularis*, a cold-adapted montane to subalpine species, can be expected to have survived the last ice age in multiple spatially restricted refugia within the projected potential distribution area in the Alps and some neighbouring mountain ranges. It appears less important whether there is a significant difference between the historical and the recent distribution range. The fact that the study species tended to have cryptic refugia north of the Alps seems to be of greater importance. While cold-tolerant species, e.g. some mammalian herbivores, have long been believed to have survived in Central European steppe tundra surrounding the glacial ice-sheets, cryptic refugia were surprisingly also found for more temperate animal and tree species (Willis *et al.* 2000; Stewart and Lister 2001). Topographically sheltered sites are assumed to have provided suitable climate conditions and stable microclimates for species with differing habitat requirements (Stewart and Lister 2001; Stewart *et al.* 2010).

Species distribution modelling is a relatively new but already frequently used method for inferring species potential distribution ranges from occurrence data. The method has been criticised for including abiotic factors only and not taking biotic parameters such as competition and dispersal into account, which might explain discrepancies between the documented range and the projected species range (Elith and Leathwick 2009; Rebelo *et al.* 2012). Nonetheless, the high model quality of our simulations (AUC = 0.92 and 0.98) represented high consistence between actual and predicted occurrence. Another uncertainty, especially of past predictive modelling, is the accuracy of past climate data. We used data processed by the downscaling method, which is currently the best large-scale data available but still requires further validation (Waltari *et al.* 2007). Additionally, the modelling approach is based on niche conservatism and does not consider changes in habitat requirements. Nevertheless, past predictive models are useful tools to visualise species distribution patterns and potential glacial refugia. More traditional approaches to identifying refugia are pollen and (sub-)fossil analyses (Elias 1994). Since no subfossils are known for *Platycarabus* species (Breuning 1932-1937), we chose a molecular method (mtDNA analysis) to supplement our findings from modelling and to review assumptions concerning potential glacial refugia.

4.5.2 Genetic evidence for glacial refugia

Phylogenetic analyses (using BI, MP and ML approaches) revealed two well-supported and spatially congruent major clades: one Central European (B) with three subclades and one Carpathian clade (A) with two subclades. The ages of all major phylogenetic splits predating the last ice age, the absence of shared haplotypes and high genetic intraspecific differentiation between clades as well as subclades implied that the ancestors of phylogenetic (sub)clades in *C. irregularis* survived many glacial-interglacial cycles isolated from each other. The Central European clade consisted of three independent and genetically distinct Central European subclades: one subclade with a more southern distribution (Bs: with populations from southern Germany, France and Slovenia), one Slovenian subclade (Bsl) and another one including haplotypes from the northern part of the species' distribution range (Bn: central to northern Germany).

Thus, the assumption of multiple refugia of *C. irregularis* in Central Europe inferred from past predictive models was supported by our phylogenetic results, with at least two refugia located close to the Alps or on the Balkan Peninsula and one northern refugium, potentially in central Germany. However, phylogenetic analyses indicated the existence of independent Carpathian refugia, which were hardly evident from the western European distribution model for LGM conditions (Figure 4.2c, arrows). The past predictive model using the eastern records showed several potential refugia in the Carpathian mountain system (Figure 2d). These potential refugia coincide with the finding of two subclades of clade A one from the eastern (Ae) and one from the southern Carpathians (As), with divergence times dating back more than one million years BP. Species records from the eastern distribution range represented higher altitudes than known from the western range, indicating potential differences also in habitat preferences between the eastern (A) and western clade (B).

As well as refugia in northern Central Europe, Carpathian refugia are not accepted as classical refugial areas and phylogeographic studies including the Carpathian region are still rare. However, since the Carpathians have faced a different glacial history with more local glaciers and larger areas of suitable alpine habitats than the well-studied Alps (Ronikier *et al.* 2008; Ronikier 2011), investigation of the southeastern European mountain range appears likely to be very interesting. Some recent studies (on mountainous plant and animal species) detected low-level differentiation between the Carpathians and the Alps and assumed the Carpathians to have been colonised by adjacent refugia e.g. in the western Alps (Kropf *et al.* 2012) or the Balkans (Pauls *et al.* 2006). In contrast, an increasing number of phylogeographic studies have found very old and divergent phylogenetic lineages, suggesting a major refugium for plants (Ronikier *et al.* 2008; Ronikier 2011) as well as for vertebrates (Babik *et al.* 2004; Babik *et al.* 2005; Deffontaine *et al.* 2005; Kotlik *et al.* 2006) in the Carpathian region. In congruence with our phylogeographic results for *C. irregularis*, alpine plants, namely *Hypochaeris uniflor* and *Campanula alpina*, showed distinct and strongly differentiated genetic groups within the Carpathians, also pointing to long-term isolation and restricted gene flow between several areas within the mountain system (Mráz *et al.* 2007; Ronikier *et al.* 2008; Ronikier 2011). While Ronikier *et al.* (2008) discovered the strongest differentiation between western and eastern Carpathian samples, results of Mráz *et al.* (2007) resembled our findings in that they also showed high differentiation between southern and eastern Carpathian populations. Examples from animals also revealed genetically distinct and long-term isolated phylogenetic groups in the Carpathians (Babik *et al.* 2004; Babik *et al.* 2005; Deffontaine *et al.* 2005; Kotlik *et al.* 2006).

4.5.3 DNA barcoding and systematic delineation

The phylogenetic results of our study agreed only in part with subspecies systematics: Whereas the Carpathian subspecies *C. i. montandoni* was monophyletic (clade A), the other two subspecies (*C. i. irregularis* and *C. i. bucephalus*) were paraphyletic (clade B) and we suggest to rank the populations belonging to clade B as one subspecies. The high proportion of polymorphic sites within ND5 (7.70%) and also within the CO1 loci (8.52%), which is commonly used as a barcoding marker (Hebert *et al.* 2003) – also for ground beetles (Maddison 2012), questions the conventional taxonomy. DNA barcoding using the CO1 locus for rapid species delineation (Wiemers and Fiedler 2007), implies that inter-clade K-2P distances higher than 2.8 to 3.4% indicate species rather than subspecies or populations. Following these thresholds, the divergence of 0.042 ± 0.004 between clade A (taxonomic subspecies *C. i. montandoni*) and B (*irregularis* s. str.) points to independent species rather than subspecies of the same species. Although the commonly used Kimura's two-parameter substitution model (K-2P) has been repeatedly criticised (Collins *et al.* 2012; Srivathsana and Meier 2012), estimates using other substitution models showed similar results for species delineation (Collins *et al.* 2012). For *C. irregularis*, the calculation of other (simpler as well as more complex) genetic distance metrics shows a consistent pattern with K-2P (*p* distance between clade A and B = 0.042; Tamura-Nei distance between clade A and B = 0.044). However, due to the fact that substitution rates can vary even within the same species (Caccone and Valerio 2001) it is necessary to exercise caution when defining a species from nucleotide rates alone.

Using morphological and molecular data Casale *et al.* (1998) reconstructed the phylogeny of the subgenus *Platycarabus*. Following their phylogeny *C. irregularis* shows the strongest differentiation from all other species within the subgenus (basal split) and *C. depressus* and *C. creutzeri* are the second major diverged species pair. Surprisingly, the split between the two main lineages of *C. irregularis* we found is older than the divergence between the latter species pair. This underlines both (i) the possible species status of the Carpathian populations and the (ii) need to incorporate a population-based approach to understand the phylogeny of these highly differentiated ground beetles with their ancient lineages, even below or at the species level.

4.6 Conclusion

Past predictive modelling and phylogenetic analyses acted as supplements and imply that *C. irregularis* survived the last glacial periods in long-term isolated classical refugia on the edges of the Alps as well as in other refugia (in Central Europe and some parts of the Carpathian Mountains). Altogether our results indicate that the Carpathian subspecies of *C. irregularis* differs not only in terms of its geographical and altitudinal distribution, but also genetically and (due to differing habitat preferences as revealed from the poorly overlapping SDMs) ecologically from rest of the species. Thus we conclude that *C. irregularis* comprises at least two evolutionarily significant units (ESUs, *sensu* Moritz 1994) indicating that the species has a very interesting history, which should be investigated in more detail by further phylogeographic analyses – also in the framework of the *Platycarabus* group.

4.7 Acknowledgements

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4.8 Supplementary Material

Table S4.1. Species records of *Carabus irregularis* and subspecies affiliation (according to Turin et al. (2003a) used for species distribution modelling.

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
1	*Carabus irregularis irregularis*	Austria	48.21	16.01	304	1969	Janczyk
2	*Carabus irregularis irregularis*	Austria	48.09	14.44	308	1969	Janczyk
3	*Carabus irregularis irregularis*	Austria	47.13	15.99	357	1969	Janczyk
4	*Carabus irregularis irregularis*	Austria	48.14	16.11	385	1969	Janczyk
5	*Carabus irregularis irregularis*	Austria	47.88	16.49	388	1969	Janczyk
6	*Carabus irregularis irregularis*	Austria	48.28	16.27	390	1969	Janczyk
7	*Carabus irregularis irregularis*	Austria	48.23	16.08	398	1969	Janczyk
8	*Carabus irregularis irregularis*	Austria	48.12	16.17	409	1969	Janczyk
9	*Carabus irregularis irregularis*	Austria	48.18	15.95	411	1969	Janczyk
10	*Carabus irregularis irregularis*	Austria	48.30	14.23	418	1969	Janczyk
11	*Carabus irregularis irregularis*	Austria	48.01	13.80	422	1969	Janczyk
12	*Carabus irregularis irregularis*	Austria	47.99	13.94	429	1969	Janczyk
13	*Carabus irregularis irregularis*	Austria	47.03	15.53	442	1969	Janczyk
14	*Carabus irregularis irregularis*	Austria	48.31	14.20	457	1969	Janczyk
15	*Carabus irregularis irregularis*	Austria	46.14	14.19	463	1943	Eckart Meyer
16	*Carabus irregularis irregularis*	Austria	48.27	16.31	469	1969	Janczyk
17	*Carabus irregularis irregularis*	Austria	48.12	16.24	469	1949	J. Böhme
18	*Carabus irregularis irregularis*	Austria	48.22	16.10	480	1969	Janczyk
19	*Carabus irregularis irregularis*	Austria	46.73	14.91	490	1969	Janczyk
20	*Carabus irregularis irregularis*	Austria	48.11	16.22	500	1969	Janczyk
21	*Carabus irregularis irregularis*	Austria	48.25	16.25	508	1969	Janczyk
22	*Carabus irregularis irregularis*	Austria	48.03	14.50	510	1969	Janczyk
23	*Carabus irregularis irregularis*	Austria	47.56	13.69	513	1976	W. Höhner
24	*Carabus irregularis irregularis*	Austria	46.78	14.88	542	1969	Janczyk
25	*Carabus irregularis irregularis*	Austria	47.14	15.27	554	1984	Wolf
26	*Carabus irregularis irregularis*	Austria	47.70	16.34	555	1969	Janczyk
27	*Carabus irregularis irregularis*	Austria	48.05	16.25	556	1969	Janczyk
28	*Carabus irregularis irregularis*	Austria	47.13	15.47	581	1969	Janczyk
29	*Carabus irregularis irregularis*	Austria	47.92	15.51	581	1969	Janczyk
30	*Carabus irregularis irregularis*	Austria	47.24	9.61	586	1969	Janczyk
31	*Carabus irregularis irregularis*	Austria	48.00	14.57	586	1969	Janczyk
32	*Carabus irregularis irregularis*	Austria	47.69	14.60	587	1969	Janczyk
33	*Carabus irregularis irregularis*	Austria	48.03	15.35	596	1969	Janczyk
34	*Carabus irregularis irregularis*	Austria	48.05	15.84	600	1969	Janczyk
35	*Carabus irregularis irregularis*	Austria	47.98	14.44	601	1969	Janczyk
36	*Carabus irregularis irregularis*	Austria	47.95	14.51	619	1969	Janczyk
37	*Carabus irregularis irregularis*	Austria	47.88	13.83	620	1969	Janczyk
38	*Carabus irregularis irregularis*	Austria	47.33	9.65	624	1969	Janczyk
39	*Carabus irregularis irregularis*	Austria	47.94	13.96	628	1969	Janczyk
40	*Carabus irregularis irregularis*	Austria	47.11	15.35	633	1969	Janczyk
41	*Carabus irregularis irregularis*	Austria	47.94	14.32	637	1969	Janczyk
42	*Carabus irregularis irregularis*	Austria	47.95	14.46	647	1969	Janczyk
43	*Carabus irregularis irregularis*	Austria	47.16	15.28	671	1969	Janczyk
44	*Carabus irregularis irregularis*	Austria	48.05	13.31	677	1969	Janczyk
45	*Carabus irregularis irregularis*	Austria	47.84	14.47	684	1969	Janczyk
46	*Carabus irregularis irregularis*	Austria	46.68	14.88	686	1969	Janczyk
47	*Carabus irregularis irregularis*	Austria	47.57	16.06	690	1969	Janczyk
48	*Carabus irregularis irregularis*	Austria	47.93	13.91	692	1969	Janczyk
49	*Carabus irregularis irregularis*	Austria	47.86	14.18	698	1969	Janczyk
50	*Carabus irregularis irregularis*	Austria	47.29	15.30	699	1969	Janczyk

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
51	*Carabus irregularis irregularis*	Austria	47.90	15.90	700	1969	Janczyk
52	*Carabus irregularis irregularis*	Austria	48.01	14.46	707	1969	Janczyk
53	*Carabus irregularis irregularis*	Austria	47.68	14.68	709	1969	Janczyk
54	*Carabus irregularis irregularis*	Austria	47.85	16.04	711	1969	Janczyk
55	*Carabus irregularis irregularis*	Austria	47.92	14.02	721	1969	Janczyk
56	*Carabus irregularis irregularis*	Austria	47.84	14.87	722	1969	Janczyk
57	*Carabus irregularis irregularis*	Austria	47.09	15.38	725	1969	Janczyk
58	*Carabus irregularis irregularis*	Austria	48.08	15.90	730	1969	Janczyk
59	*Carabus irregularis irregularis*	Austria	47.82	13.74	737	1969	Janczyk
60	*Carabus irregularis irregularis*	Austria	47.87	14.50	741	1969	Janczyk
61	*Carabus irregularis irregularis*	Austria	47.91	13.63	741	1969	Janczyk
62	*Carabus irregularis irregularis*	Austria	47.79	14.76	750	1969	Janczyk
63	*Carabus irregularis irregularis*	Austria	47.84	14.30	754	1969	Janczyk
64	*Carabus irregularis irregularis*	Austria	47.82	14.61	756	1969	Janczyk
65	*Carabus irregularis irregularis*	Austria	47.45	13.18	761	1969	Janczyk
66	*Carabus irregularis irregularis*	Austria	47.60	13.30	764	1969	Janczyk
67	*Carabus irregularis irregularis*	Austria	47.39	9.91	775	1969	Janczyk
68	*Carabus irregularis irregularis*	Austria	47.30	15.92	775	1969	Janczyk
69	*Carabus irregularis irregularis*	Austria	47.22	15.37	778	1969	Janczyk
70	*Carabus irregularis irregularis*	Austria	47.83	14.52	783	1969	Janczyk
71	*Carabus irregularis irregularis*	Austria	47.91	14.34	795	1969	Janczyk
72	*Carabus irregularis irregularis*	Austria	47.93	13.73	796	1969	Janczyk
73	*Carabus irregularis irregularis*	Austria	47.60	13.73	797	1969	Janczyk
74	*Carabus irregularis irregularis*	Austria	47.75	13.24	798	1969	Janczyk
75	*Carabus irregularis irregularis*	Austria	47.72	14.19	803	1969	Janczyk
76	*Carabus irregularis irregularis*	Austria	47.46	9.82	807	1969	Janczyk
77	*Carabus irregularis irregularis*	Austria	47.92	14.56	814	1969	Janczyk
78	*Carabus irregularis irregularis*	Austria	47.91	14.22	815	1969	Janczyk
79	*Carabus irregularis irregularis*	Austria	46.47	14.60	821	1969	Janczyk
80	*Carabus irregularis irregularis*	Austria	47.68	15.00	829	1969	Janczyk
81	*Carabus irregularis irregularis*	Austria	47.89	14.62	830	1969	Janczyk
82	*Carabus irregularis irregularis*	Austria	47.83	13.68	835	1969	Janczyk
83	*Carabus irregularis irregularis*	Austria	47.64	13.66	840	1969	Janczyk
84	*Carabus irregularis irregularis*	Austria	47.39	9.75	855	1969	Janczyk
85	*Carabus irregularis irregularis*	Austria	47.56	14.78	857	1969	Janczyk
86	*Carabus irregularis irregularis*	Austria	47.85	14.11	867	1969	Janczyk
87	*Carabus irregularis irregularis*	Austria	47.95	15.85	871	1969	Janczyk
88	*Carabus irregularis irregularis*	Austria	47.62	14.82	872	1969	Janczyk
89	*Carabus irregularis irregularis*	Austria	47.80	13.82	876	1969	Janczyk
90	*Carabus irregularis irregularis*	Austria	47.81	14.28	884	1969	Janczyk
91	*Carabus irregularis irregularis*	Austria	46.43	14.55	894	1976	J. Böhme
92	*Carabus irregularis irregularis*	Austria	47.88	13.48	896	1969	Janczyk
93	*Carabus irregularis irregularis*	Austria	47.88	13.90	898	1969	Janczyk
94	*Carabus irregularis irregularis*	Austria	47.78	13.70	905	1969	Janczyk
95	*Carabus irregularis irregularis*	Austria	47.78	15.84	910	1969	Janczyk
96	*Carabus irregularis irregularis*	Austria	47.60	14.44	910	1969	Janczyk
97	*Carabus irregularis irregularis*	Austria	47.54	14.59	921	1969	Janczyk
98	*Carabus irregularis irregularis*	Austria	47.60	14.63	950	1969	Janczyk
99	*Carabus irregularis irregularis*	Austria	47.88	14.41	983	1969	Janczyk
100	*Carabus irregularis irregularis*	Austria	47.34	9.75	984	1969	Janczyk
101	*Carabus irregularis irregularis*	Austria	48.39	15.05	989	1969	Janczyk
102	*Carabus irregularis irregularis*	Austria	47.79	14.68	996	1969	Janczyk
103	*Carabus irregularis irregularis*	Austria	47.83	15.41	1002	1969	Janczyk
104	*Carabus irregularis irregularis*	Austria	47.85	14.56	1002	1969	Janczyk
105	*Carabus irregularis irregularis*	Austria	47.75	14.32	1010	1969	Janczyk

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
106	*Carabus irregularis irregularis*	Austria	47.58	16.00	1014	1969	Janczyk
107	*Carabus irregularis irregularis*	Austria	47.83	15.45	1057	1969	Janczyk
108	*Carabus irregularis irregularis*	Austria	47.82	15.14	1066	1969	Janczyk
109	*Carabus irregularis irregularis*	Austria	47.59	14.90	1073	1969	Janczyk
110	*Carabus irregularis irregularis*	Austria	47.63	13.87	1074	1969	Janczyk
111	*Carabus irregularis irregularis*	Austria	47.32	9.70	1076	1969	Janczyk
112	*Carabus irregularis irregularis*	Austria	47.68	14.53	1097	1969	Janczyk
113	*Carabus irregularis irregularis*	Austria	47.41	15.53	1106	1969	Janczyk
114	*Carabus irregularis irregularis*	Austria	47.40	15.46	1106	1969	Janczyk
115	*Carabus irregularis irregularis*	Austria	47.73	15.64	1108	1969	Janczyk
116	*Carabus irregularis irregularis*	Austria	47.65	13.45	1115	1969	Janczyk
117	*Carabus irregularis irregularis*	Austria	47.82	15.80	1123	1969	Janczyk
118	*Carabus irregularis irregularis*	Austria	47.73	13.74	1149	1969	Janczyk
119	*Carabus irregularis irregularis*	Austria	47.55	14.85	1152	1969	Janczyk
120	*Carabus irregularis irregularis*	Austria	47.55	14.35	1154	1969	Janczyk
121	*Carabus irregularis irregularis*	Austria	47.65	13.93	1163	1969	Janczyk
122	*Carabus irregularis irregularis*	Austria	47.63	14.85	1180	1969	Janczyk
123	*Carabus irregularis irregularis*	Austria	47.69	14.42	1198	1969	Janczyk
124	*Carabus irregularis irregularis*	Austria	47.70	15.18	1200	1969	Janczyk
125	*Carabus irregularis irregularis*	Austria	47.42	15.59	1200	1969	Janczyk
126	*Carabus irregularis irregularis*	Austria	47.64	15.59	1218	1969	Janczyk
127	*Carabus irregularis irregularis*	Austria	47.65	14.61	1228	1969	Janczyk
128	*Carabus irregularis irregularis*	Austria	47.68	13.79	1235	1969	Janczyk
129	*Carabus irregularis irregularis*	Austria	47.57	14.75	1250	1969	Janczyk
130	*Carabus irregularis irregularis*	Austria	47.38	11.65	1254	1982	J. Böhme
131	*Carabus irregularis irregularis*	Austria	47.58	14.28	1269	1969	Janczyk
132	*Carabus irregularis irregularis*	Austria	46.79	14.92	1271	1969	Janczyk
133	*Carabus irregularis irregularis*	Austria	47.47	14.45	1277	1969	Janczyk
134	*Carabus irregularis irregularis*	Austria	47.49	10.56	1286	1969	Janczyk
135	*Carabus irregularis irregularis*	Austria	47.62	14.67	1296	1969	Janczyk
136	*Carabus irregularis irregularis*	Austria	47.22	12.82	1296	1969	Janczyk
137	*Carabus irregularis irregularis*	Austria	47.35	13.24	1303	1969	Janczyk
138	*Carabus irregularis irregularis*	Austria	46.44	14.52	1317	1969	Janczyk
139	*Carabus irregularis irregularis*	Austria	47.88	13.99	1325	1969	Janczyk
140	*Carabus irregularis irregularis*	Austria	47.27	11.04	1337	1969	Janczyk
141	*Carabus irregularis irregularis*	Austria	47.55	13.56	1342	1969	Janczyk
142	*Carabus irregularis irregularis*	Austria	47.62	14.73	1350	1969	Janczyk
143	*Carabus irregularis irregularis*	Austria	47.72	15.60	1361	1969	Janczyk
144	*Carabus irregularis irregularis*	Austria	46.45	14.37	1367	1969	Janczyk
145	*Carabus irregularis irregularis*	Austria	47.43	14.47	1368	1969	Janczyk
146	*Carabus irregularis irregularis*	Austria	47.56	13.79	1369	1969	Janczyk
147	*Carabus irregularis irregularis*	Austria	47.72	15.69	1378	1969	Janczyk
148	*Carabus irregularis irregularis*	Austria	47.27	13.50	1382	1969	Janczyk
149	*Carabus irregularis irregularis*	Austria	47.21	12.73	1403	1969	Janczyk
150	*Carabus irregularis irregularis*	Austria	47.05	9.86	1421	1969	Janczyk
151	*Carabus irregularis irregularis*	Austria	47.50	13.15	1425	1969	Janczyk
152	*Carabus irregularis irregularis*	Austria	46.50	14.53	1433	1969	Janczyk
153	*Carabus irregularis irregularis*	Austria	47.49	10.63	1438	1969	Janczyk
154	*Carabus irregularis irregularis*	Austria	47.17	12.92	1452	1969	Janczyk
155	*Carabus irregularis irregularis*	Austria	47.55	14.40	1454	1969	Janczyk
156	*Carabus irregularis irregularis*	Austria	46.75	13.38	1456	1969	Janczyk
157	*Carabus irregularis irregularis*	Austria	47.28	11.07	1460	1969	Janczyk
158	*Carabus irregularis irregularis*	Austria	46.73	13.47	1489	1969	Janczyk
159	*Carabus irregularis irregularis*	Austria	47.67	14.25	1499	1969	Janczyk
160	*Carabus irregularis irregularis*	Austria	47.13	10.14	1509	1969	Janczyk

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
106	*Carabus irregularis irregularis*	Austria	47.58	16.00	1014	1969	Janczyk
107	*Carabus irregularis irregularis*	Austria	47.83	15.45	1057	1969	Janczyk
108	*Carabus irregularis irregularis*	Austria	47.82	15.14	1066	1969	Janczyk
109	*Carabus irregularis irregularis*	Austria	47.59	14.90	1073	1969	Janczyk
110	*Carabus irregularis irregularis*	Austria	47.63	13.87	1074	1969	Janczyk
111	*Carabus irregularis irregularis*	Austria	47.32	9.70	1076	1969	Janczyk
112	*Carabus irregularis irregularis*	Austria	47.68	14.53	1097	1969	Janczyk
113	*Carabus irregularis irregularis*	Austria	47.41	15.53	1106	1969	Janczyk
114	*Carabus irregularis irregularis*	Austria	47.40	15.46	1106	1969	Janczyk
115	*Carabus irregularis irregularis*	Austria	47.73	15.64	1108	1969	Janczyk
116	*Carabus irregularis irregularis*	Austria	47.65	13.45	1115	1969	Janczyk
117	*Carabus irregularis irregularis*	Austria	47.82	15.80	1123	1969	Janczyk
118	*Carabus irregularis irregularis*	Austria	47.73	13.74	1149	1969	Janczyk
119	*Carabus irregularis irregularis*	Austria	47.55	14.85	1152	1969	Janczyk
120	*Carabus irregularis irregularis*	Austria	47.55	14.35	1154	1969	Janczyk
121	*Carabus irregularis irregularis*	Austria	47.65	13.93	1163	1969	Janczyk
122	*Carabus irregularis irregularis*	Austria	47.63	14.85	1180	1969	Janczyk
123	*Carabus irregularis irregularis*	Austria	47.69	14.42	1198	1969	Janczyk
124	*Carabus irregularis irregularis*	Austria	47.70	15.18	1200	1969	Janczyk
125	*Carabus irregularis irregularis*	Austria	47.42	15.59	1200	1969	Janczyk
126	*Carabus irregularis irregularis*	Austria	47.64	15.59	1218	1969	Janczyk
127	*Carabus irregularis irregularis*	Austria	47.65	14.61	1228	1969	Janczyk
128	*Carabus irregularis irregularis*	Austria	47.68	13.79	1235	1969	Janczyk
129	*Carabus irregularis irregularis*	Austria	47.57	14.75	1250	1969	Janczyk
130	*Carabus irregularis irregularis*	Austria	47.38	11.65	1254	1982	J. Böhme
131	*Carabus irregularis irregularis*	Austria	47.58	14.28	1269	1969	Janczyk
132	*Carabus irregularis irregularis*	Austria	46.79	14.92	1271	1969	Janczyk
133	*Carabus irregularis irregularis*	Austria	47.47	14.45	1277	1969	Janczyk
134	*Carabus irregularis irregularis*	Austria	47.49	10.56	1286	1969	Janczyk
135	*Carabus irregularis irregularis*	Austria	47.62	14.67	1296	1969	Janczyk
136	*Carabus irregularis irregularis*	Austria	47.22	12.82	1296	1969	Janczyk
137	*Carabus irregularis irregularis*	Austria	47.35	13.24	1303	1969	Janczyk
138	*Carabus irregularis irregularis*	Austria	46.44	14.52	1317	1969	Janczyk
139	*Carabus irregularis irregularis*	Austria	47.88	13.99	1325	1969	Janczyk
140	*Carabus irregularis irregularis*	Austria	47.27	11.04	1337	1969	Janczyk
141	*Carabus irregularis irregularis*	Austria	47.55	13.56	1342	1969	Janczyk
142	*Carabus irregularis irregularis*	Austria	47.62	14.73	1350	1969	Janczyk
143	*Carabus irregularis irregularis*	Austria	47.72	15.60	1361	1969	Janczyk
144	*Carabus irregularis irregularis*	Austria	46.45	14.37	1367	1969	Janczyk
145	*Carabus irregularis irregularis*	Austria	47.43	14.47	1368	1969	Janczyk
146	*Carabus irregularis irregularis*	Austria	47.56	13.79	1369	1969	Janczyk
147	*Carabus irregularis irregularis*	Austria	47.72	15.69	1378	1969	Janczyk
148	*Carabus irregularis irregularis*	Austria	47.27	13.50	1382	1969	Janczyk
149	*Carabus irregularis irregularis*	Austria	47.21	12.73	1403	1969	Janczyk
150	*Carabus irregularis irregularis*	Austria	47.05	9.86	1421	1969	Janczyk
151	*Carabus irregularis irregularis*	Austria	47.50	13.15	1425	1969	Janczyk
152	*Carabus irregularis irregularis*	Austria	46.50	14.53	1433	1969	Janczyk
153	*Carabus irregularis irregularis*	Austria	47.49	10.63	1438	1969	Janczyk
154	*Carabus irregularis irregularis*	Austria	47.17	12.92	1452	1969	Janczyk
155	*Carabus irregularis irregularis*	Austria	47.55	14.40	1454	1969	Janczyk
156	*Carabus irregularis irregularis*	Austria	46.75	13.38	1456	1969	Janczyk
157	*Carabus irregularis irregularis*	Austria	47.28	11.07	1460	1969	Janczyk
158	*Carabus irregularis irregularis*	Austria	46.73	13.47	1489	1969	Janczyk
159	*Carabus irregularis irregularis*	Austria	47.67	14.25	1499	1969	Janczyk
160	*Carabus irregularis irregularis*	Austria	47.13	10.14	1509	1969	Janczyk

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
161	*Carabus irregularis irregularis*	Austria	47.52	13.83	1526	1969	Janczyk
162	*Carabus irregularis irregularis*	Austria	47.66	13.91	1557	1969	Janczyk
163	*Carabus irregularis irregularis*	Austria	47.11	13.61	1593	1969	Janczyk
164	*Carabus irregularis irregularis*	Austria	47.40	13.04	1608	1969	Janczyk
165	*Carabus irregularis irregularis*	Austria	46.65	12.83	1649	1969	Janczyk
166	*Carabus irregularis irregularis*	Austria	47.72	14.13	1654	1969	Janczyk
167	*Carabus irregularis irregularis*	Austria	47.71	15.74	1669	1969	Janczyk
168	*Carabus irregularis irregularis*	Austria	47.02	10.75	1747	1969	Janczyk
169	*Carabus irregularis irregularis*	Austria	47.52	13.68	1788	1969	Janczyk
170	*Carabus irregularis irregularis*	Austria	47.61	14.18	1822	1969	Janczyk
171	*Carabus irregularis irregularis*	Austria	47.19	10.11	1867	1969	Janczyk
172	*Carabus irregularis irregularis*	Austria	47.45	11.77	1910	1975	G. Hofmann
173	*Carabus irregularis irregularis*	Austria	47.07	10.76	1934	1969	Janczyk
174	*Carabus irregularis irregularis*	Austria	47.40	11.70	2065	1992	J. Böhme
175	*Carabus irregularis irregularis*	Belgium	50.65	5.63	60	1881	Desender et al. (2008)
176	*Carabus irregularis irregularis*	Belgium	50.18	5.55	253	1882	Desender et al. (2008)
177	*Carabus irregularis irregularis*	Belgium	50.55	5.98	402	1868	Desender et al. (2008)
178	*Carabus irregularis irregularis*	Belgium	50.54	6.06	579	1950	Desender et al. (2008)
179	*Carabus irregularis irregularis*	Belgium	50.52	6.06	665	1868	Desender et al. (2008)
180	*Carabus irregularis irregularis*	Belgium	50.52	6.06	665	1937	Desender et al. (2008)
181	*Carabus irregularis irregularis*	Belgium	50.52	6.06	665	1890	Desender et al. (2008)
182	*Carabus irregularis irregularis*	Belgium	50.52	6.06	665	1868	Desender et al. (2008)
183	*Carabus irregularis irregularis*	Czech Republic	49.51	17.62	271	2003	Hejda
184	*Carabus irregularis irregularis*	Czech Republic	50.71	14.38	272	1990	Hejda
185	*Carabus irregularis irregularis*	Czech Republic	50.31	13.02	334	2002	Hejda
186	*Carabus irregularis irregularis*	Czech Republic	49.91	13.70	373	1989	Hejda
187	*Carabus irregularis irregularis*	Czech Republic	49.91	13.87	388	1981	Hejda
188	*Carabus irregularis irregularis*	Czech Republic	49.02	14.38	390	2010	Hejda
189	*Carabus irregularis irregularis*	Czech Republic	49.30	16.64	428	1982	leg. Hanousek, Hrusa
190	*Carabus irregularis irregularis*	Czech Republic	49.71	16.60	463	2007	Hejda
191	*Carabus irregularis irregularis*	Czech Republic	49.41	13.02	464	1973	Hejda
192	*Carabus irregularis irregularis*	Czech Republic	49.07	14.43	466	1992	Budka
193	*Carabus irregularis irregularis*	Czech Republic	49.02	15.75	467	1991	Hejda
194	*Carabus irregularis irregularis*	Czech Republic	49.69	17.44	471	1995	leg. L. Mazal, Hrusa
195	*Carabus irregularis irregularis*	Czech Republic	49.96	13.79	480	1982	leg. Hanousek, Hrusa
196	*Carabus irregularis irregularis*	Czech Republic	49.61	17.45	487	2009	Hejda
197	*Carabus irregularis irregularis*	Czech Republic	49.91	17.11	523	2003	Hejda
198	*Carabus irregularis irregularis*	Czech Republic	49.30	13.69	550	1976	leg. J. Riha, Hrusa
199	*Carabus irregularis irregularis*	Czech Republic	49.31	15.58	553	1991	Hejda
200	*Carabus irregularis irregularis*	Czech Republic	50.55	13.94	557	1980	leg. J. Slaba, Hrusa
201	*Carabus irregularis irregularis*	Czech Republic	49.41	15.92	561	2010	Hejda
202	*Carabus irregularis irregularis*	Czech Republic	49.31	16.77	569	1990	Hejda
203	*Carabus irregularis irregularis*	Czech Republic	49.80	16.40	572	1850	Letzner
204	*Carabus irregularis irregularis*	Czech Republic	50.11	12.85	599	2002	Hejda
205	*Carabus irregularis irregularis*	Czech Republic	49.61	17.62	605	1989	Hejda
206	*Carabus irregularis irregularis*	Czech Republic	50.01	17.11	620	2003	Hejda
207	*Carabus irregularis irregularis*	Czech Republic	48.92	14.21	689	2008	Hejda
208	*Carabus irregularis irregularis*	Czech Republic	50.21	13.02	707	2002	Hejda
209	*Carabus irregularis irregularis*	Czech Republic	50.21	17.28	800	2003	Hejda
210	*Carabus irregularis irregularis*	Czech Republic	50.01	17.28	827	1900	Hejda
211	*Carabus irregularis irregularis*	Czech Republic	50.11	17.28	841	2010	Hejda
212	*Carabus irregularis irregularis*	Czech Republic	48.82	13.87	930	2010	Hejda
213	*Carabus irregularis irregularis*	Czech Republic	50.10	17.23	1225	1850	Letzner
214	*Carabus irregularis irregularis*	France	48.75	7.14	291	1993	Callot & Schott
215	*Carabus irregularis irregularis*	France	48.75	7.23	345	1993	Callot & Schott

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
216	*Carabus irregularis irregularis*	France	48.36	7.26	351	1993	Callot & Schott
217	*Carabus irregularis irregularis*	France	46.24	6.04	444	1995	Franzen
218	*Carabus irregularis irregularis*	France	47.82	7.09	449	1993	Callot & Schott
219	*Carabus irregularis irregularis*	France	48.36	7.34	472	1993	Callot & Schott
220	*Carabus irregularis irregularis*	France	48.48	7.08	539	1993	Callot & Schott
221	*Carabus irregularis irregularis*	France	47.75	6.62	556	1993	Callot & Schott
222	*Carabus irregularis irregularis*	France	47.48	7.28	570	1993	Callot & Schott
223	*Carabus irregularis irregularis*	France	48.12	6.65	580	1995	Franzen
224	*Carabus irregularis irregularis*	France	48.41	7.33	614	1993	Callot & Schott
225	*Carabus irregularis irregularis*	France	47.87	7.01	629	1993	Callot & Schott
226	*Carabus irregularis irregularis*	France	46.32	5.50	632	1995	Franzen
227	*Carabus irregularis irregularis*	France	47.44	7.28	656	1993	Callot & Schott
228	*Carabus irregularis irregularis*	France	48.58	7.23	660	1993	Callot & Schott
229	*Carabus irregularis irregularis*	France	48.35	7.19	663	1993	Callot & Schott
230	*Carabus irregularis irregularis*	France	48.59	7.32	687	1993	Callot & Schott
231	*Carabus irregularis irregularis*	France	47.86	6.79	719	1993	Callot & Schott
232	*Carabus irregularis irregularis*	France	47.86	6.93	725	1993	Callot & Schott
233	*Carabus irregularis irregularis*	France	48.02	7.16	728	1995	Franzen
234	*Carabus irregularis irregularis*	France	47.94	6.94	747	1993	Callot & Schott
235	*Carabus irregularis irregularis*	France	48.00	7.00	750	2001	http://www.gbif.org/
236	*Carabus irregularis irregularis*	France	46.13	6.20	768	1837	Heer
237	*Carabus irregularis irregularis*	France	47.97	7.07	789	1993	Callot & Schott
238	*Carabus irregularis irregularis*	France	48.44	7.09	816	1993	Callot & Schott
239	*Carabus irregularis irregularis*	France	46.01	5.58	826	1995	Franzen
240	*Carabus irregularis irregularis*	France	47.95	6.99	839	1993	Callot & Schott
241	*Carabus irregularis irregularis*	France	48.54	7.16	839	1993	Callot & Schott
242	*Carabus irregularis irregularis*	France	46.14	5.60	853	1854	Fairemaire & Laboulbène
243	*Carabus irregularis irregularis*	France	45.99	6.61	870	1995	Franzen
244	*Carabus irregularis irregularis*	France	47.91	7.00	876	1993	Callot & Schott
245	*Carabus irregularis irregularis*	France	46.40	5.75	904	1995	Franzen
246	*Carabus irregularis irregularis*	France	46.79	6.18	951	1995	Franzen
247	*Carabus irregularis irregularis*	France	47.90	6.93	979	1993	Callot & Schott
248	*Carabus irregularis irregularis*	France	48.41	7.26	1025	1993	Callot & Schott
249	*Carabus irregularis irregularis*	France	47.90	6.84	1046	1993	Callot & Schott
250	*Carabus irregularis irregularis*	France	47.91	7.08	1050	1993	Callot & Schott
251	*Carabus irregularis irregularis*	France	48.12	6.98	1063	1993	Callot & Schott
252	*Carabus irregularis irregularis*	France	46.78	6.38	1129	2010	Lassalle
253	*Carabus irregularis irregularis*	France	46.79	6.43	1192	2010	Lassalle
254	*Carabus irregularis irregularis*	France	46.54	6.13	1229	1995	Franzen
255	*Carabus irregularis irregularis*	France	46.79	6.46	1281	1982	Delaporte
256	*Carabus irregularis irregularis*	Germany	52.36	10.52	80	1907	Petry
257	*Carabus irregularis irregularis*	Germany	52.06	10.69	84	1995	Franzen
258	*Carabus irregularis irregularis*	Germany	51.90	8.50	91	1966	Lit
259	*Carabus irregularis irregularis*	Germany	52.02	8.90	112	1995	Franzen
260	*Carabus irregularis irregularis*	Germany	52.11	9.82	129	1995	Franzen
261	*Carabus irregularis irregularis*	Germany	52.09	10.14	135	1982	Staven
262	*Carabus irregularis irregularis*	Germany	52.15	9.65	137	1994	Staven
263	*Carabus irregularis irregularis*	Germany	52.16	9.60	170	1986	Staven
264	*Carabus irregularis irregularis*	Germany	51.47	9.89	172	1995	Franzen
265	*Carabus irregularis irregularis*	Germany	52.02	8.44	175	1995	Franzen
266	*Carabus irregularis irregularis*	Germany	51.95	8.72	187	1995	Franzen
267	*Carabus irregularis irregularis*	Germany	51.50	9.22	192	1995	Franzen
268	*Carabus irregularis irregularis*	Germany	51.89	8.87	203	1995	Franzen
269	*Carabus irregularis irregularis*	Germany	52.08	10.21	205	1982	Staven
270	*Carabus irregularis irregularis*	Germany	52.12	9.39	208	1982	Staven

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
271	*Carabus irregularis irregularis*	Germany	52.12	9.39	209	1937	Rensch & Graebner
272	*Carabus irregularis irregularis*	Germany	51.98	10.23	212	1981	Staven
273	*Carabus irregularis irregularis*	Germany	52.17	8.84	218	1995	Franzen
274	*Carabus irregularis irregularis*	Germany	49.83	6.39	219	1995	Franzen
275	*Carabus irregularis irregularis*	Germany	51.90	9.00	220	1966	http://www.gbif.org/
276	*Carabus irregularis irregularis*	Germany	51.90	9.00	220	1937	Lit
277	*Carabus irregularis irregularis*	Germany	52.22	9.26	222	1949	Schramm
278	*Carabus irregularis irregularis*	Germany	51.98	10.22	224	2010	Schäfer, Homburg & Rabe
279	*Carabus irregularis irregularis*	Germany	52.09	9.09	226	1995	Franzen
280	*Carabus irregularis irregularis*	Germany	51.95	9.94	228	1997	Staven
281	*Carabus irregularis irregularis*	Germany	52.13	8.95	230	1973	Franzisket
282	*Carabus irregularis irregularis*	Germany	51.92	9.17	233	1973	Franzisket
283	*Carabus irregularis irregularis*	Germany	51.52	10.17	234	1995	Franzen
284	*Carabus irregularis irregularis*	Germany	51.85	9.43	238	1973	Franzisket
285	*Carabus irregularis irregularis*	Germany	51.60	8.83	241	1966	http://www.gbif.org/
286	*Carabus irregularis irregularis*	Germany	51.60	8.83	241	1966	Lit
287	*Carabus irregularis irregularis*	Germany	52.22	9.35	243	1937	Rensch & Graebner
288	*Carabus irregularis irregularis*	Germany	52.16	8.13	245	1998	Sendker
289	*Carabus irregularis irregularis*	Germany	51.70	8.83	246	1966	http://www.gbif.org/
290	*Carabus irregularis irregularis*	Germany	51.70	8.83	246	1966	Lit
291	*Carabus irregularis irregularis*	Germany	51.79	9.03	248	1973	Franzisket
292	*Carabus irregularis irregularis*	Germany	52.20	9.27	248	2009	Schäfer, Homburg & Rabe
293	*Carabus irregularis irregularis*	Germany	52.05	9.56	249	1971	Nowotschyn
294	*Carabus irregularis irregularis*	Germany	51.95	9.13	253	1973	Franzisket
295	*Carabus irregularis irregularis*	Germany	51.97	10.00	255	1997	Staven
296	*Carabus irregularis irregularis*	Germany	52.16	8.10	258	1998	Sendker
297	*Carabus irregularis irregularis*	Germany	50.96	13.62	260	1970	Nüssler
298	*Carabus irregularis irregularis*	Germany	52.21	9.16	261	1973	http://www.gbif.org/
299	*Carabus irregularis irregularis*	Germany	52.15	8.18	263	1998	Sendker
300	*Carabus irregularis irregularis*	Germany	51.90	9.17	265	1923	http://www.gbif.org/
301	*Carabus irregularis irregularis*	Germany	51.90	9.17	265	1924	Lit
302	*Carabus irregularis irregularis*	Germany	51.10	10.51	268	1995	Franzen
303	*Carabus irregularis irregularis*	Germany	52.14	8.18	268	2010	Schäfer & Weber
304	*Carabus irregularis irregularis*	Germany	50.88	12.06	269	1933	Erbe
305	*Carabus irregularis irregularis*	Germany	51.84	9.01	270	1973	Franzisket
306	*Carabus irregularis irregularis*	Germany	49.86	6.35	271	1995	Franzen
307	*Carabus irregularis irregularis*	Germany	51.30	11.16	272	1933	Petry
308	*Carabus irregularis irregularis*	Germany	51.70	9.03	275	1973	Franzisket
309	*Carabus irregularis irregularis*	Germany	51.55	10.07	277	1979	Staven
310	*Carabus irregularis irregularis*	Germany	51.82	9.01	281	1973	Franzisket
311	*Carabus irregularis irregularis*	Germany	49.85	6.44	281	1995	Franzen
312	*Carabus irregularis irregularis*	Germany	51.68	8.83	281	1973	Franzisket
313	*Carabus irregularis irregularis*	Germany	51.40	9.16	286	1995	Franzen
314	*Carabus irregularis irregularis*	Germany	51.67	9.04	287	1973	Franzisket
315	*Carabus irregularis irregularis*	Germany	52.10	9.17	288	1937	http://www.gbif.org/
316	*Carabus irregularis irregularis*	Germany	51.64	9.37	292	1973	Franzisket
317	*Carabus irregularis irregularis*	Germany	51.77	9.04	292	1995	Franzen
318	*Carabus irregularis irregularis*	Germany	52.12	9.63	299	1971	Hahlbohm
319	*Carabus irregularis irregularis*	Germany	52.20	10.74	299	1974	Staven
320	*Carabus irregularis irregularis*	Germany	51.94	8.70	299	1998	Sendker
321	*Carabus irregularis irregularis*	Germany	52.12	8.28	300	1998	Sendker
322	*Carabus irregularis irregularis*	Germany	52.20	9.33	300	1937	Rensch & Graebner
323	*Carabus irregularis irregularis*	Germany	51.63	8.84	301	1973	Franzisket
324	*Carabus irregularis irregularis*	Germany	52.00	10.32	304	1981	Staven
325	*Carabus irregularis irregularis*	Germany	52.20	10.81	307	1836	Panzer

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
326	*Carabus irregularis irregularis*	Germany	52.01	9.90	310	1997	Staven
327	*Carabus irregularis irregularis*	Germany	51.83	10.16	311	1980	Staven
328	*Carabus irregularis irregularis*	Germany	51.36	10.64	315	1933	Jänner
329	*Carabus irregularis irregularis*	Germany	51.10	10.47	317	1995	Hartmann
330	*Carabus irregularis irregularis*	Germany	51.10	10.47	317	1979	Stumpf
331	*Carabus irregularis irregularis*	Germany	51.10	10.47	317	1997	Weigel
332	*Carabus irregularis irregularis*	Germany	51.10	10.47	317	1979	Körner
333	*Carabus irregularis irregularis*	Germany	51.10	10.47	317	1983	Körner
334	*Carabus irregularis irregularis*	Germany	51.10	10.47	317	2008	Grübel
335	*Carabus irregularis irregularis*	Germany	51.79	8.90	317	1973	Franzisket
336	*Carabus irregularis irregularis*	Germany	49.90	11.00	319	2001	FRI
337	*Carabus irregularis irregularis*	Germany	51.33	9.98	319	1995	Franzen
338	*Carabus irregularis irregularis*	Germany	52.23	9.53	319	1937	Rensch & Graebner
339	*Carabus irregularis irregularis*	Germany	48.52	9.15	320	1995	Franzen
340	*Carabus irregularis irregularis*	Germany	51.82	10.16	321	2010	Schäfer, Homburg & Rabe
341	*Carabus irregularis irregularis*	Germany	51.21	10.39	322	2009	Goßner
342	*Carabus irregularis irregularis*	Germany	52.19	9.36	323	1937	Rensch & Graebner
343	*Carabus irregularis irregularis*	Germany	51.90	9.17	323	1973	Franzisket
344	*Carabus irregularis irregularis*	Germany	50.78	9.99	324	1995	Franzen
345	*Carabus irregularis irregularis*	Germany	51.10	10.46	324	1930	Jahn
346	*Carabus irregularis irregularis*	Germany	50.82	9.84	326	1995	Franzen
347	*Carabus irregularis irregularis*	Germany	49.85	6.39	326	1995	Franzen
348	*Carabus irregularis irregularis*	Germany	51.20	10.25	328	2000	Sparnberg
349	*Carabus irregularis irregularis*	Germany	51.57	8.85	328	1998	Sendker
350	*Carabus irregularis irregularis*	Germany	51.25	10.56	330	1933	Kellner
351	*Carabus irregularis irregularis*	Germany	48.57	9.26	331	1995	Franzen
352	*Carabus irregularis irregularis*	Germany	50.95	9.88	332	1995	Franzen
353	*Carabus irregularis irregularis*	Germany	51.09	10.51	335	1995	Hartmann
354	*Carabus irregularis irregularis*	Germany	51.18	10.38	335	2009	Goßner
355	*Carabus irregularis irregularis*	Germany	51.55	9.02	336	1973	Franzisket
356	*Carabus irregularis irregularis*	Germany	51.92	8.78	339	1998	Sendker
357	*Carabus irregularis irregularis*	Germany	48.80	13.00	342	1988	Lit
358	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1985	Gebert
359	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1963	Jahn
360	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1984	Körner
361	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1986	Körner
362	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1933	Möller
363	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1983	Müller
364	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1992	Platt
365	*Carabus irregularis irregularis*	Germany	51.19	10.37	344	1987	Platt
366	*Carabus irregularis irregularis*	Germany	51.54	9.78	345	1995	Franzen
367	*Carabus irregularis irregularis*	Germany	51.37	10.84	347	1994	Bößnek
368	*Carabus irregularis irregularis*	Germany	52.20	9.35	348	1937	Rensch & Graebner
369	*Carabus irregularis irregularis*	Germany	49.70	11.17	348	1905	Lit
370	*Carabus irregularis irregularis*	Germany	51.77	8.90	348	1973	Franzisket
371	*Carabus irregularis irregularis*	Germany	51.70	8.91	351	1998	Sendker
372	*Carabus irregularis irregularis*	Germany	51.94	8.73	358	1998	Sendker
373	*Carabus irregularis irregularis*	Germany	51.93	8.74	360	1998	Sendker
374	*Carabus irregularis irregularis*	Germany	51.21	10.17	364	1988	Staven
375	*Carabus irregularis irregularis*	Germany	51.39	10.74	367	1933	Petry
376	*Carabus irregularis irregularis*	Germany	51.23	10.72	368	2000	Sparnberg
377	*Carabus irregularis irregularis*	Germany	51.05	10.41	369	1999	Brüggemann
378	*Carabus irregularis irregularis*	Germany	51.05	10.41	369	2007	Weigel
379	*Carabus irregularis irregularis*	Germany	51.05	10.41	369	2008	Weigel
380	*Carabus irregularis irregularis*	Germany	51.05	10.41	369	1998	Weigel

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
381	*Carabus irregularis irregularis*	Germany	51.60	8.86	370	1995	Franzen
382	*Carabus irregularis irregularis*	Germany	51.21	10.37	370	2009	Goßner
383	*Carabus irregularis irregularis*	Germany	48.65	9.21	371	1995	Franzen
384	*Carabus irregularis irregularis*	Germany	51.18	10.37	373	2009	Goßner
385	*Carabus irregularis irregularis*	Germany	51.55	8.90	373	1998	Sendker
386	*Carabus irregularis irregularis*	Germany	51.06	10.40	374	2002	Apfel
387	*Carabus irregularis irregularis*	Germany	51.06	10.40	374	2003	Apfel
388	*Carabus irregularis irregularis*	Germany	51.06	10.40	374	1961	Jahn
389	*Carabus irregularis irregularis*	Germany	51.06	10.40	374	1999	Weigel
390	*Carabus irregularis irregularis*	Germany	51.06	10.40	374	2000	Weigel
391	*Carabus irregularis irregularis*	Germany	51.06	10.40	374	2001	Weigel
392	*Carabus irregularis irregularis*	Germany	51.21	10.37	377	1987	Platt
393	*Carabus irregularis irregularis*	Germany	48.60	13.17	378	1988	Lit
394	*Carabus irregularis irregularis*	Germany	51.04	10.46	381	2003	Apfel
395	*Carabus irregularis irregularis*	Germany	51.04	10.46	381	2001	Weigel
396	*Carabus irregularis irregularis*	Germany	51.08	10.50	383	2009	Goßner
397	*Carabus irregularis irregularis*	Germany	51.15	10.38	386	1933	Kellner
398	*Carabus irregularis irregularis*	Germany	51.15	10.38	386	1930	Petry
399	*Carabus irregularis irregularis*	Germany	51.15	10.38	386	1933	Weipert
400	*Carabus irregularis irregularis*	Germany	51.17	10.36	386	1995	Franzen
401	*Carabus irregularis irregularis*	Germany	51.11	10.41	398	2009	Goßner
402	*Carabus irregularis irregularis*	Germany	49.30	12.33	400	1999	MKR
403	*Carabus irregularis irregularis*	Germany	47.47	7.76	401	1995	Franzen
404	*Carabus irregularis irregularis*	Germany	51.22	10.27	401	2000	Sparnberg
405	*Carabus irregularis irregularis*	Germany	46.29	6.16	402	1995	Franzen
406	*Carabus irregularis irregularis*	Germany	48.70	11.00	402	2002	Lit
407	*Carabus irregularis irregularis*	Germany	51.33	10.16	404	2001	Weipert
408	*Carabus irregularis irregularis*	Germany	51.32	10.12	406	2001	Weipert
409	*Carabus irregularis irregularis*	Germany	51.39	9.31	406	1963	SMF Hessen
410	*Carabus irregularis irregularis*	Germany	51.39	9.31	406	1943	SMF Hessen
411	*Carabus irregularis irregularis*	Germany	51.39	9.31	406	1943	SMF Hessen
412	*Carabus irregularis irregularis*	Germany	51.13	10.38	407	2009	Goßner
413	*Carabus irregularis irregularis*	Germany	50.58	10.40	408	1933	Brückner
414	*Carabus irregularis irregularis*	Germany	51.05	10.49	408	2009	Goßner
415	*Carabus irregularis irregularis*	Germany	51.36	10.15	408	1989	Arndt
416	*Carabus irregularis irregularis*	Germany	51.14	10.38	411	2009	Goßner
417	*Carabus irregularis irregularis*	Germany	51.40	10.30	417	1989	Arndt
418	*Carabus irregularis irregularis*	Germany	51.43	10.53	419	1911	Liebmann
419	*Carabus irregularis irregularis*	Germany	51.43	10.53	419	1933	Petry
420	*Carabus irregularis irregularis*	Germany	51.10	10.40	420	2009	Goßner
421	*Carabus irregularis irregularis*	Germany	51.35	10.80	422	1933	Jänner
422	*Carabus irregularis irregularis*	Germany	48.75	9.17	423	1995	Franzen
423	*Carabus irregularis irregularis*	Germany	51.26	10.19	425	1982	Arndt
424	*Carabus irregularis irregularis*	Germany	50.69	9.99	425	1995	Franzen
425	*Carabus irregularis irregularis*	Germany	51.26	10.22	428	1987	Albrecht
426	*Carabus irregularis irregularis*	Germany	51.26	10.22	428	1933	Petry
427	*Carabus irregularis irregularis*	Germany	51.27	10.31	429	2009	Goßner
428	*Carabus irregularis irregularis*	Germany	48.84	10.09	430	1974	W. Höhner
429	*Carabus irregularis irregularis*	Germany	49.01	9.71	431	1995	Franzen
430	*Carabus irregularis irregularis*	Germany	51.44	10.54	431	1989	Arndt
431	*Carabus irregularis irregularis*	Germany	51.50	10.38	432	1933	Eigen
432	*Carabus irregularis irregularis*	Germany	51.27	10.24	433	2009	Goßner
433	*Carabus irregularis irregularis*	Germany	48.60	12.33	436	2004	BY, MAT*
434	*Carabus irregularis irregularis*	Germany	51.17	10.33	438	1989	Arndt
435	*Carabus irregularis irregularis*	Germany	47.32	7.78	444	1995	Franzen

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
436	*Carabus irregularis irregularis*	Germany	51.14	10.36	447	2009	Goßner
437	*Carabus irregularis irregularis*	Germany	51.23	10.06	453	1988	Staven
438	*Carabus irregularis irregularis*	Germany	50.56	9.86	454	1995	Franzen
439	*Carabus irregularis irregularis*	Germany	48.50	10.17	455	1960	Lit
440	*Carabus irregularis irregularis*	Germany	51.19	10.32	457	2009	Goßner
441	*Carabus irregularis irregularis*	Germany	51.34	10.37	457	2009	Goßner
442	*Carabus irregularis irregularis*	Germany	50.73	13.07	457	1979	Zerche
443	*Carabus irregularis irregularis*	Germany	51.27	10.24	462	2009	Goßner
444	*Carabus irregularis irregularis*	Germany	51.34	10.36	465	2009	Goßner
445	*Carabus irregularis irregularis*	Germany	50.45	7.02	465	1995	Franzen
446	*Carabus irregularis irregularis*	Germany	51.46	10.34	467	1999	Sparnberg
447	*Carabus irregularis irregularis*	Germany	48.60	12.30	469	1992	Heinz
448	*Carabus irregularis irregularis*	Germany	51.05	10.48	470	2009	Goßner
449	*Carabus irregularis irregularis*	Germany	48.50	13.50	472	1988	Lit
450	*Carabus irregularis irregularis*	Germany	47.78	7.65	473	1982	Staven
451	*Carabus irregularis irregularis*	Germany	50.17	6.67	474	1995	Franzen
452	*Carabus irregularis irregularis*	Germany	51.20	10.34	477	2009	Goßner
453	*Carabus irregularis irregularis*	Germany	48.51	12.34	477	1995	Franzen
454	*Carabus irregularis irregularis*	Germany	51.20	10.33	480	1963	Jahn
455	*Carabus irregularis irregularis*	Germany	51.35	10.51	484	2009	Goßner
456	*Carabus irregularis irregularis*	Germany	50.40	10.00	484	2004	BY
457	*Carabus irregularis irregularis*	Germany	48.33	10.98	491	1995	Franzen
458	*Carabus irregularis irregularis*	Germany	48.73	10.49	492	1995	Franzen
459	*Carabus irregularis irregularis*	Germany	51.20	10.32	494	2009	Goßner
460	*Carabus irregularis irregularis*	Germany	51.35	10.52	498	1993	Weise
461	*Carabus irregularis irregularis*	Germany	51.37	10.53	502	2009	Goßner
462	*Carabus irregularis irregularis*	Germany	50.67	12.99	504	1995	Franzen
463	*Carabus irregularis irregularis*	Germany	48.90	10.83	506	1980	BY
464	*Carabus irregularis irregularis*	Germany	48.30	10.83	507	1859	LOR
465	*Carabus irregularis irregularis*	Germany	50.30	9.83	509	1991	BY
466	*Carabus irregularis irregularis*	Germany	51.36	10.53	511	2009	Goßner
467	*Carabus irregularis irregularis*	Germany	51.28	10.23	512	2009	Goßner
468	*Carabus irregularis irregularis*	Germany	51.29	10.23	514	2009	Goßner
469	*Carabus irregularis irregularis*	Germany	51.36	10.52	516	2009	Goßner
470	*Carabus irregularis irregularis*	Germany	51.36	10.52	520	2009	Goßner
471	*Carabus irregularis irregularis*	Germany	51.36	10.52	523	1908	Petry
472	*Carabus irregularis irregularis*	Germany	48.10	12.33	524	2000	LOR
473	*Carabus irregularis irregularis*	Germany	50.90	14.26	532	1926	MTD
474	*Carabus irregularis irregularis*	Germany	50.90	14.26	532	2003	Riebe
475	*Carabus irregularis irregularis*	Germany	50.15	6.68	535	1980	F. Ermisch
476	*Carabus irregularis irregularis*	Germany	47.37	8.76	548	1995	Franzen
477	*Carabus irregularis irregularis*	Germany	48.80	13.33	550	1988	Lit
478	*Carabus irregularis irregularis*	Germany	48.70	10.50	554	1949	Lit
479	*Carabus irregularis irregularis*	Germany	47.86	9.11	555	1980	Staven
480	*Carabus irregularis irregularis*	Germany	46.80	7.52	560	1995	Franzen
481	*Carabus irregularis irregularis*	Germany	51.25	10.05	560	1994	SMF Entomologie 2
482	*Carabus irregularis irregularis*	Germany	47.45	9.02	580	1995	Franzen
483	*Carabus irregularis irregularis*	Germany	50.50	10.00	584	1995	BY
484	*Carabus irregularis irregularis*	Germany	48.03	11.51	588	1972	G. Hofmann
485	*Carabus irregularis irregularis*	Germany	46.71	7.64	591	1995	Franzen
486	*Carabus irregularis irregularis*	Germany	50.72	10.08	591	1999	Gharadjedaghi
487	*Carabus irregularis irregularis*	Germany	50.72	10.08	591	1983	Schmidt
488	*Carabus irregularis irregularis*	Germany	50.51	9.28	591	1963	SMF Hessen
489	*Carabus irregularis irregularis*	Germany	48.10	10.83	593	2005	BUS, BY*
490	*Carabus irregularis irregularis*	Germany	50.64	10.16	598	1983	Blochwitz

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
491	*Carabus irregularis irregularis*	Germany	47.80	12.33	600	1994	BY*, LEI
492	*Carabus irregularis irregularis*	Germany	47.04	7.44	600	1995	Franzen
493	*Carabus irregularis irregularis*	Germany	47.02	7.54	601	1995	Franzen
494	*Carabus irregularis irregularis*	Germany	48.63	9.78	603	1971	Putzler
495	*Carabus irregularis irregularis*	Germany	47.64	13.00	611	1972	W. Höhner
496	*Carabus irregularis irregularis*	Germany	50.17	6.69	616	1995	Franzen
497	*Carabus irregularis irregularis*	Germany	47.60	11.17	628	2001	HRY
498	*Carabus irregularis irregularis*	Germany	47.37	7.43	631	1995	Franzen
499	*Carabus irregularis irregularis*	Germany	48.75	10.19	632	1995	Franzen
500	*Carabus irregularis irregularis*	Germany	50.52	9.21	634	1992	SMF Entomologie 2
501	*Carabus irregularis irregularis*	Germany	50.52	9.21	634	1992	SMF Hessen
502	*Carabus irregularis irregularis*	Germany	48.03	10.88	641	1975	G. Hofmann
503	*Carabus irregularis irregularis*	Germany	46.82	9.40	645	1995	Franzen
504	*Carabus irregularis irregularis*	Germany	47.30	7.67	649	1995	Franzen
505	*Carabus irregularis irregularis*	Germany	47.67	11.28	660	1968	W. Höhner
506	*Carabus irregularis irregularis*	Germany	48.90	13.17	661	1988	Lit
507	*Carabus irregularis irregularis*	Germany	50.87	10.45	662	1999	Bellstedt
508	*Carabus irregularis irregularis*	Germany	48.32	9.58	668	1995	Franzen
509	*Carabus irregularis irregularis*	Germany	47.96	10.99	672	1995	Franzen
510	*Carabus irregularis irregularis*	Germany	47.75	9.42	686	1980	Staven
511	*Carabus irregularis irregularis*	Germany	48.90	13.33	695	1988	Lit
512	*Carabus irregularis irregularis*	Germany	48.47	9.25	695	1971	Hrusa
513	*Carabus irregularis irregularis*	Germany	48.50	13.67	697	1988	Lit
514	*Carabus irregularis irregularis*	Germany	48.41	9.36	699	2009	Goßner
515	*Carabus irregularis irregularis*	Germany	47.80	12.83	702	1988	LOR
516	*Carabus irregularis irregularis*	Germany	47.84	8.34	713	2010	Schäfer, Rabe
517	*Carabus irregularis irregularis*	Germany	50.47	10.09	720	1991	W. Höhner
518	*Carabus irregularis irregularis*	Germany	50.47	10.09	720	1998	W. Höhner
519	*Carabus irregularis irregularis*	Germany	46.65	6.70	726	1995	Franzen
520	*Carabus irregularis irregularis*	Germany	47.11	7.78	731	1995	Franzen
521	*Carabus irregularis irregularis*	Germany	47.83	11.03	734	1995	Franzen
522	*Carabus irregularis irregularis*	Germany	47.19	7.16	734	1995	Franzen
523	*Carabus irregularis irregularis*	Germany	50.73	13.54	739	1966	Arndt
524	*Carabus irregularis irregularis*	Germany	48.40	9.25	741	2009	Goßner
525	*Carabus irregularis irregularis*	Germany	47.70	10.83	745	2001	LOR
526	*Carabus irregularis irregularis*	Germany	48.75	9.93	748	1975	Ivanovs
527	*Carabus irregularis irregularis*	Germany	47.47	11.03	749	1957	J. Böhme
528	*Carabus irregularis irregularis*	Germany	48.40	9.45	750	2009	Goßner
529	*Carabus irregularis irregularis*	Germany	47.80	10.83	753	1999	LOR, OEK
530	*Carabus irregularis irregularis*	Germany	48.38	9.35	754	2009	Goßner
531	*Carabus irregularis irregularis*	Germany	48.37	9.42	768	2009	Goßner
532	*Carabus irregularis irregularis*	Germany	50.65	10.88	769	1860	Schaum
533	*Carabus irregularis irregularis*	Germany	47.80	11.00	771	1994	BY(LOR)
534	*Carabus irregularis irregularis*	Germany	47.01	7.32	772	1995	Franzen
535	*Carabus irregularis irregularis*	Germany	47.60	10.67	781	1951	LOR
536	*Carabus irregularis irregularis*	Germany	47.70	11.00	782	2002	LOR
537	*Carabus irregularis irregularis*	Germany	50.77	13.77	783	1899	Hänel
538	*Carabus irregularis irregularis*	Germany	50.77	13.77	783	1963	Nüssler
539	*Carabus irregularis irregularis*	Germany	50.77	13.77	783	2001	Lorenz
540	*Carabus irregularis irregularis*	Germany	50.77	13.77	783	2004	Lorenz
541	*Carabus irregularis irregularis*	Germany	50.77	13.77	783	1963	MTD
542	*Carabus irregularis irregularis*	Germany	48.18	9.12	788	1949	J. Böhme
543	*Carabus irregularis irregularis*	Germany	48.18	9.12	788	1949	J. Böhme
544	*Carabus irregularis irregularis*	Germany	47.06	7.92	789	1995	Franzen
545	*Carabus irregularis irregularis*	Germany	47.06	7.69	793	1995	Franzen

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
546	*Carabus irregularis irregularis*	Germany	47.60	11.33	798	1975	LOR
547	*Carabus irregularis irregularis*	Germany	46.74	7.23	799	1995	Franzen
548	*Carabus irregularis irregularis*	Germany	47.10	7.11	802	1995	Franzen
549	*Carabus irregularis irregularis*	Germany	47.80	10.50	803	1986	BY(LOR)
550	*Carabus irregularis irregularis*	Germany	48.42	9.42	806	2009	Goßner
551	*Carabus irregularis irregularis*	Germany	48.44	9.42	829	1995	Franzen
552	*Carabus irregularis irregularis*	Germany	47.73	7.84	837	1995	Franzen
553	*Carabus irregularis irregularis*	Germany	47.50	10.33	838	1936	LOR
554	*Carabus irregularis irregularis*	Germany	46.84	7.41	839	1995	Franzen
555	*Carabus irregularis irregularis*	Germany	51.79	10.67	839	1995	Franzen
556	*Carabus irregularis irregularis*	Germany	47.55	10.22	852	1991	Hemmer & Terlutter
557	*Carabus irregularis irregularis*	Germany	46.53	7.06	881	1995	Franzen
558	*Carabus irregularis irregularis*	Germany	46.55	6.92	885	1995	Franzen
559	*Carabus irregularis irregularis*	Germany	46.92	7.79	920	1995	Franzen
560	*Carabus irregularis irregularis*	Germany	47.60	11.50	968	1994	LOR
561	*Carabus irregularis irregularis*	Germany	47.03	6.80	1014	1995	Franzen
562	*Carabus irregularis irregularis*	Germany	47.70	12.53	1029	1995	Franzen
563	*Carabus irregularis irregularis*	Germany	47.55	10.21	1033	1991	Hemmer & Terlutter
564	*Carabus irregularis irregularis*	Germany	47.66	12.08	1044	1967	Drovenik
565	*Carabus irregularis irregularis*	Germany	47.70	12.67	1067	2000	BY
566	*Carabus irregularis irregularis*	Germany	47.70	12.50	1091	2003	LOR
567	*Carabus irregularis irregularis*	Germany	48.91	13.03	1102	1929	Eckart Meyer
568	*Carabus irregularis irregularis*	Germany	47.50	10.17	1142	1989	LOR
569	*Carabus irregularis irregularis*	Germany	47.60	11.67	1151	2002	BY(LOR)
570	*Carabus irregularis irregularis*	Germany	47.12	6.95	1163	1995	Franzen
571	*Carabus irregularis irregularis*	Germany	47.60	11.83	1217	2002	BY(LOR)*, FRI
572	*Carabus irregularis irregularis*	Germany	46.68	7.29	1226	1995	Franzen
573	*Carabus irregularis irregularis*	Germany	47.50	10.83	1229	1984	LOR
574	*Carabus irregularis irregularis*	Germany	46.45	6.96	1230	1995	Franzen
575	*Carabus irregularis irregularis*	Germany	46.96	6.64	1244	1995	Franzen
576	*Carabus irregularis irregularis*	Germany	47.70	12.00	1257	1991	BY(FRA)
577	*Carabus irregularis irregularis*	Germany	47.70	11.67	1262	1990	LOR
578	*Carabus irregularis irregularis*	Germany	47.40	10.17	1299	1944	LOR
579	*Carabus irregularis irregularis*	Germany	47.54	10.21	1301	1991	Hemmer & Terlutter
580	*Carabus irregularis irregularis*	Germany	47.74	12.34	1302	1995	Franzen
581	*Carabus irregularis irregularis*	Germany	47.65	11.99	1327	1995	Franzen
582	*Carabus irregularis irregularis*	Germany	47.60	11.00	1340	2005	LOR, MAT*
583	*Carabus irregularis irregularis*	Germany	47.19	9.11	1343	1995	Franzen
584	*Carabus irregularis irregularis*	Germany	47.50	10.67	1670	1919	LOR
585	*Carabus irregularis irregularis*	Germany	47.50	11.00	1697	1978	LOR
586	*Carabus irregularis irregularis*	Germany	47.06	9.12	1732	1995	Franzen
587	*Carabus irregularis irregularis*	Germany	47.50	12.83	1746	2003	Lit, BY*
588	*Carabus irregularis irregularis*	Germany	46.82	7.95	1831	1995	Franzen
589	*Carabus irregularis irregularis*	Germany	46.47	7.38	1846	1995	Franzen
590	*Carabus irregularis irregularis*	Germany	47.40	10.33	1854	2003	LOR
591	*Carabus irregularis irregularis*	Germany	46.54	7.75	1910	1995	Franzen
592	*Carabus irregularis irregularis*	Germany	46.97	10.99	1977	1995	Franzen
593	*Carabus irregularis irregularis*	Germany	46.89	9.66	2077	1995	Franzen
594	*Carabus irregularis irregularis*	Germany	46.40	7.50	2139	1995	Franzen
595	*Carabus irregularis irregularis*	Germany	47.40	11.00	2206	1999	BY, LEI*, LOR
596	*Carabus irregularis irregularis*	Germany	46.64	9.23	2532	1995	Franzen
597	*Carabus irregularis irregularis*	Hungary	48.00	20.00	239	2001	http://www.gbif.org/
598	*Carabus irregularis irregularis*	Hungary	47.39	16.50	417	1980	Rozner
599	*Carabus irregularis irregularis*	Italy	46.62	12.20	1611	1995	Franzen
600	*Carabus irregularis irregularis*	Italy	46.70	12.13	1683	1995	Franzen

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
601	*Carabus irregularis irregularis*	Italy	46.71	11.37	2172	1995	Franzen
602	*Carabus irregularis irregularis*	Luxembourg	49.82	6.33	294	1998	Evelyne Carrières
603	*Carabus irregularis irregularis*	Luxembourg	49.82	6.33	294	1999	Marc Meyer
604	*Carabus irregularis irregularis*	Luxembourg	49.83	6.32	297	1957	Desender et al. (2008)
605	*Carabus irregularis irregularis*	Luxembourg	49.83	6.32	297	1950	Desender
606	*Carabus irregularis irregularis*	Luxembourg	49.83	6.32	297	1997	M. Delwaide
607	*Carabus irregularis irregularis*	Luxembourg	49.69	6.27	302	1988	Franzen
608	*Carabus irregularis irregularis*	Luxembourg	49.74	6.27	321	1941	Alfred Mousset
609	*Carabus irregularis irregularis*	Luxembourg	49.80	6.32	323	1998	Marc Meyer
610	*Carabus irregularis irregularis*	Luxembourg	49.80	6.32	323	1998	Marc Meyer
611	*Carabus irregularis irregularis*	Luxembourg	49.81	6.33	336	1999	Marc Meyer
612	*Carabus irregularis irregularis*	Luxembourg	49.81	6.33	336	1999	Marc Meyer
613	*Carabus irregularis irregularis*	Luxembourg	49.77	6.32	338	1950	Desender
614	*Carabus irregularis irregularis*	Luxembourg	49.62	6.22	354	1950	Desender et al. (2008)
615	*Carabus irregularis irregularis*	Luxembourg	49.76	6.31	367	1988	Franzen
616	*Carabus irregularis irregularis*	Poland	50.71	16.34	562	1850	Letzner
617	*Carabus irregularis irregularis*	Poland	50.60	16.59	632	1850	Letzner
618	*Carabus irregularis irregularis*	Poland	50.87	16.71	675	1850	Letzner
619	*Carabus irregularis irregularis*	Poland	50.47	16.41	691	1850	Letzner
620	*Carabus irregularis irregularis*	Poland	50.39	16.40	748	1850	Letzner
621	*Carabus irregularis irregularis*	Poland	50.69	16.27	820	1850	Letzner
622	*Carabus irregularis irregularis*	Poland	50.23	16.79	844	1850	Letzner
623	*Carabus irregularis irregularis*	Poland	50.25	16.86	846	1850	Letzner
624	*Carabus irregularis irregularis*	Poland	50.79	15.62	940	1860	Schaum
625	*Carabus irregularis irregularis*	Poland	50.20	16.83	1152	2007	Sienkiewicz
626	*Carabus irregularis irregularis*	Switzerland	47.58	8.90	396	1956	Hugent.
627	*Carabus irregularis irregularis*	Switzerland	47.55	8.89	411	1961	Hugent.
628	*Carabus irregularis irregularis*	Switzerland	47.03	8.44	431	1989	Vetter
629	*Carabus irregularis irregularis*	Switzerland	47.46	8.38	436	1981	Osterw.
630	*Carabus irregularis irregularis*	Switzerland	47.13	7.23	457	1980	Marggi
631	*Carabus irregularis irregularis*	Switzerland	47.37	9.54	465	1966	Spälti
632	*Carabus irregularis irregularis*	Switzerland	47.37	9.54	465	1959	Spälti
633	*Carabus irregularis irregularis*	Switzerland	47.29	8.56	480	1950	Zuber
634	*Carabus irregularis irregularis*	Switzerland	47.48	8.70	489	1940	Allenspach V
635	*Carabus irregularis irregularis*	Switzerland	47.40	7.12	494	1973	Ammann
636	*Carabus irregularis irregularis*	Switzerland	46.96	7.39	507	1994	Hoess
637	*Carabus irregularis irregularis*	Switzerland	46.96	7.39	507	1988	Hoess
638	*Carabus irregularis irregularis*	Switzerland	46.96	7.39	507	1988	Hoess
639	*Carabus irregularis irregularis*	Switzerland	47.67	8.57	523	1976	Ettmüll.
640	*Carabus irregularis irregularis*	Switzerland	46.52	6.67	526	1960	Toumayeff
641	*Carabus irregularis irregularis*	Switzerland	46.95	7.37	531	1988	Hoess
642	*Carabus irregularis irregularis*	Switzerland	46.88	7.50	533	1986	R.Scherl
643	*Carabus irregularis irregularis*	Switzerland	47.04	7.29	542	1882	Frey
644	*Carabus irregularis irregularis*	Switzerland	47.05	7.62	543	1970	Kiener
645	*Carabus irregularis irregularis*	Switzerland	47.45	8.05	545	1994	Hoess
646	*Carabus irregularis irregularis*	Switzerland	47.43	7.33	548	1982	Osterw.
647	*Carabus irregularis irregularis*	Switzerland	47.03	8.27	566	1970	Ammann
648	*Carabus irregularis irregularis*	Switzerland	47.76	8.51	587	1951	Allenspach V
649	*Carabus irregularis irregularis*	Switzerland	47.76	8.51	587	1940	BänningerM
650	*Carabus irregularis irregularis*	Switzerland	46.42	6.19	589	1943	Poluzzi
651	*Carabus irregularis irregularis*	Switzerland	46.42	6.19	589	1945	Poluzzi
652	*Carabus irregularis irregularis*	Switzerland	47.03	8.24	600	1972	Ammann
653	*Carabus irregularis irregularis*	Switzerland	47.03	8.24	600	1972	Ammann
654	*Carabus irregularis irregularis*	Switzerland	47.03	8.24	600	1963	Ammann
655	*Carabus irregularis irregularis*	Switzerland	46.98	7.33	608	1984	Hoess

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
656	*Carabus irregularis irregularis*	Switzerland	46.70	7.62	608	1974	Marggi
657	*Carabus irregularis irregularis*	Switzerland	46.70	7.62	608	1978	Marggi
658	*Carabus irregularis irregularis*	Switzerland	47.45	7.93	609	1991	Reutiman
659	*Carabus irregularis irregularis*	Switzerland	47.45	7.93	609	1991	Reutiman
660	*Carabus irregularis irregularis*	Switzerland	47.26	9.12	637	1981	Schiller
661	*Carabus irregularis irregularis*	Switzerland	47.43	8.95	639	1882	Täschler
662	*Carabus irregularis irregularis*	Switzerland	46.88	7.62	660	1967	Blatti
663	*Carabus irregularis irregularis*	Switzerland	47.16	7.25	666	1986	R.Scherl
664	*Carabus irregularis irregularis*	Switzerland	46.66	7.61	679	1988	Scherler
665	*Carabus irregularis irregularis*	Switzerland	47.34	7.49	681	1977	Marggi
666	*Carabus irregularis irregularis*	Switzerland	47.48	8.37	684	1949	Allenspach V
667	*Carabus irregularis irregularis*	Switzerland	47.48	8.37	684	1949	BänningerM
668	*Carabus irregularis irregularis*	Switzerland	47.02	6.91	693	1950	Toumayeff
669	*Carabus irregularis irregularis*	Switzerland	46.82	7.62	695	1972	Marggi
670	*Carabus irregularis irregularis*	Switzerland	46.57	6.63	697	1988	Scherler
671	*Carabus irregularis irregularis*	Switzerland	46.53	6.67	699	1978	Toumayeff
672	*Carabus irregularis irregularis*	Switzerland	46.46	6.25	704	1970	Poluzzi
673	*Carabus irregularis irregularis*	Switzerland	46.99	7.56	715	1993	Scherler
674	*Carabus irregularis irregularis*	Switzerland	47.01	7.60	718	1993	Scherler
675	*Carabus irregularis irregularis*	Switzerland	47.02	8.61	730	1975	Staven
676	*Carabus irregularis irregularis*	Switzerland	46.82	7.31	735	1960	Toumayeff
677	*Carabus irregularis irregularis*	Switzerland	46.79	7.71	736	1980	Marggi
678	*Carabus irregularis irregularis*	Switzerland	46.50	6.31	745	1899	Marggi
679	*Carabus irregularis irregularis*	Switzerland	46.74	7.50	745	1986	R.Scherl
680	*Carabus irregularis irregularis*	Switzerland	46.74	7.50	745	1987	Scherler
681	*Carabus irregularis irregularis*	Switzerland	47.00	7.57	747	1993	Scherler
682	*Carabus irregularis irregularis*	Switzerland	46.72	6.78	767	1943	Comelli.
683	*Carabus irregularis irregularis*	Switzerland	46.72	6.78	767	1970	Poluzzi
684	*Carabus irregularis irregularis*	Switzerland	46.70	7.58	804	1973	Marggi
685	*Carabus irregularis irregularis*	Switzerland	47.15	9.14	805	1983	Osterw.
686	*Carabus irregularis irregularis*	Switzerland	47.15	9.14	805	1965	Spälti
687	*Carabus irregularis irregularis*	Switzerland	46.57	6.75	823	1963	Toumayeff
688	*Carabus irregularis irregularis*	Switzerland	47.76	8.57	823	1985	Agosti Donat
689	*Carabus irregularis irregularis*	Switzerland	47.76	8.57	823	1978	BesuchetCl
690	*Carabus irregularis irregularis*	Switzerland	47.76	8.57	823	1979	Grimm
691	*Carabus irregularis irregularis*	Switzerland	47.76	8.57	823	1967	Toumayeff
692	*Carabus irregularis irregularis*	Switzerland	47.76	8.57	823	1988	Pedroli
693	*Carabus irregularis irregularis*	Switzerland	46.79	7.40	831	1987	Hoess
694	*Carabus irregularis irregularis*	Switzerland	46.79	7.40	831	1987	Hoess
695	*Carabus irregularis irregularis*	Switzerland	47.00	9.49	837	1960	Toumayeff
696	*Carabus irregularis irregularis*	Switzerland	46.57	7.66	857	1973	Marggi
697	*Carabus irregularis irregularis*	Switzerland	46.25	7.33	861	1899	Marggi
698	*Carabus irregularis irregularis*	Switzerland	46.99	8.03	869	1982	Burckhar
699	*Carabus irregularis irregularis*	Switzerland	46.94	7.65	875	1989	R.Scherl
700	*Carabus irregularis irregularis*	Switzerland	47.37	7.78	883	2002	Straumann
701	*Carabus irregularis irregularis*	Switzerland	46.89	7.69	897	1973	Marggi
702	*Carabus irregularis irregularis*	Switzerland	46.89	7.69	897	1973	Marggi
703	*Carabus irregularis irregularis*	Switzerland	46.95	7.86	914	1981	Marggi
704	*Carabus irregularis irregularis*	Switzerland	47.37	7.77	915	2003	Straumann
705	*Carabus irregularis irregularis*	Switzerland	47.02	8.23	928	1998	Roman Graf
706	*Carabus irregularis irregularis*	Switzerland	47.13	7.16	928	1987	Scherler
707	*Carabus irregularis irregularis*	Switzerland	46.98	7.60	933	1993	Scherler
708	*Carabus irregularis irregularis*	Switzerland	47.13	6.78	948	1945	Aellen
709	*Carabus irregularis irregularis*	Switzerland	46.85	6.61	963	1958	Rappo
710	*Carabus irregularis irregularis*	Switzerland	46.85	6.61	963	1958	Rappo

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
711	*Carabus irregularis irregularis*	Switzerland	47.14	7.20	970	1899	Mathey
712	*Carabus irregularis irregularis*	Switzerland	46.80	7.74	984	1992	Scherler
713	*Carabus irregularis irregularis*	Switzerland	46.82	7.70	984	1992	Scherler
714	*Carabus irregularis irregularis*	Switzerland	46.61	7.27	986	1985	Osterw.
715	*Carabus irregularis irregularis*	Switzerland	46.92	7.69	986	1988	Scherler
716	*Carabus irregularis irregularis*	Switzerland	46.79	7.44	1004	1988	Scherler
717	*Carabus irregularis irregularis*	Switzerland	46.46	6.94	1007	1964	Toumayeff
718	*Carabus irregularis irregularis*	Switzerland	47.01	8.23	1009	2001	Roman Graf
719	*Carabus irregularis irregularis*	Switzerland	47.03	7.82	1013	1974	Marggi
720	*Carabus irregularis irregularis*	Switzerland	47.03	7.82	1013	1974	Marggi
721	*Carabus irregularis irregularis*	Switzerland	46.82	7.77	1014	1992	Scherler
722	*Carabus irregularis irregularis*	Switzerland	46.82	8.41	1015	1972	Ammann F.
723	*Carabus irregularis irregularis*	Switzerland	46.82	8.41	1015	1971	Ammann F.
724	*Carabus irregularis irregularis*	Switzerland	46.82	8.41	1015	1975	Ammann F.
725	*Carabus irregularis irregularis*	Switzerland	46.64	6.37	1026	1979	Sermet
726	*Carabus irregularis irregularis*	Switzerland	47.39	9.51	1032	1965	Hugent.
727	*Carabus irregularis irregularis*	Switzerland	47.13	7.18	1045	1986	R.Scherl
728	*Carabus irregularis irregularis*	Switzerland	46.94	6.73	1053	1941	Aellen
729	*Carabus irregularis irregularis*	Switzerland	46.93	7.69	1060	1988	R.Scherl
730	*Carabus irregularis irregularis*	Switzerland	47.34	7.58	1060	1960	Toumayeff
731	*Carabus irregularis irregularis*	Switzerland	46.66	7.65	1089	1837	Heer
732	*Carabus irregularis irregularis*	Switzerland	46.48	6.90	1130	1921	Comelli.
733	*Carabus irregularis irregularis*	Switzerland	46.77	7.75	1150	1959	Kobel
734	*Carabus irregularis irregularis*	Switzerland	46.99	7.94	1159	1979	Kiener
735	*Carabus irregularis irregularis*	Switzerland	46.99	7.94	1159	1974	Marggi
736	*Carabus irregularis irregularis*	Switzerland	46.99	7.94	1159	1982	Osterw.
737	*Carabus irregularis irregularis*	Switzerland	46.79	8.46	1178	1971	Ammann F.
738	*Carabus irregularis irregularis*	Switzerland	46.99	7.95	1193	1974	Marggi
739	*Carabus irregularis irregularis*	Switzerland	46.48	6.92	1199	1958	Zuber
740	*Carabus irregularis irregularis*	Switzerland	46.77	7.77	1218	1976	Marggi
741	*Carabus irregularis irregularis*	Switzerland	46.98	8.21	1233	2004	Graf Roman
742	*Carabus irregularis irregularis*	Switzerland	46.74	8.29	1234	1978	Ammann
743	*Carabus irregularis irregularis*	Switzerland	47.21	7.24	1244	1899	Mathey
744	*Carabus irregularis irregularis*	Switzerland	46.81	8.40	1250	1882	Stierlin
745	*Carabus irregularis irregularis*	Switzerland	46.33	10.05	1252	1987	Brägger
746	*Carabus irregularis irregularis*	Switzerland	46.95	6.78	1270	1969	Gut
747	*Carabus irregularis irregularis*	Switzerland	47.30	7.43	1280	1964	Allenspach V
748	*Carabus irregularis irregularis*	Switzerland	46.98	8.17	1312	2004	Graf Roman
749	*Carabus irregularis irregularis*	Switzerland	46.80	7.92	1354	1978	Marggi
750	*Carabus irregularis irregularis*	Switzerland	46.45	7.70	1360	1951	Allenspach V
751	*Carabus irregularis irregularis*	Switzerland	46.98	8.20	1369	1998	Graf Roman
752	*Carabus irregularis irregularis*	Switzerland	46.98	8.20	1369	2004	Graf Roman
753	*Carabus irregularis irregularis*	Switzerland	46.74	7.45	1387	1975	Marggi
754	*Carabus irregularis irregularis*	Switzerland	46.83	8.42	1393	1975	Ammann F.
755	*Carabus irregularis irregularis*	Switzerland	46.83	8.42	1393	1971	Ammann F.
756	*Carabus irregularis irregularis*	Switzerland	46.77	6.46	1398	1949	Rappo
757	*Carabus irregularis irregularis*	Switzerland	46.47	7.70	1400	1979	Marggi
758	*Carabus irregularis irregularis*	Switzerland	46.47	7.70	1400	1978	Marggi
759	*Carabus irregularis irregularis*	Switzerland	47.12	7.04	1418	1988	BesuchetCl
760	*Carabus irregularis irregularis*	Switzerland	47.13	7.04	1434	1970	Kiener
761	*Carabus irregularis irregularis*	Switzerland	47.13	7.04	1434	1992	Marggi
762	*Carabus irregularis irregularis*	Switzerland	47.13	7.04	1434	1977	Marggi
763	*Carabus irregularis irregularis*	Switzerland	47.13	7.04	1434	1979	Marggi
764	*Carabus irregularis irregularis*	Switzerland	47.13	7.04	1434	1982	Sond.
765	*Carabus irregularis irregularis*	Switzerland	46.45	6.97	1438	1899	Marggi

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
766	*Carabus irregularis irregularis*	Switzerland	46.85	6.53	1462	1963	Zuber
767	*Carabus irregularis irregularis*	Switzerland	46.80	8.37	1481	1964	Ammann
768	*Carabus irregularis irregularis*	Switzerland	46.80	8.37	1481	1975	Ammann
769	*Carabus irregularis irregularis*	Switzerland	46.62	7.27	1491	1960	BänningerM
770	*Carabus irregularis irregularis*	Switzerland	46.57	7.56	1495	2009	Marggi
771	*Carabus irregularis irregularis*	Switzerland	46.42	6.10	1589	1972	Vit
772	*Carabus irregularis irregularis*	Switzerland	46.54	7.78	1615	1941	Naef
773	*Carabus irregularis irregularis*	Switzerland	46.64	7.50	1626	1974	Haefeli
774	*Carabus irregularis irregularis*	Switzerland	46.63	9.18	1652	1960	Jörger
775	*Carabus irregularis irregularis*	Switzerland	46.43	6.97	1731	1946	BänningerM
776	*Carabus irregularis irregularis*	Switzerland	46.98	8.25	1760	1970	Ammann
777	*Carabus irregularis irregularis*	Switzerland	46.53	7.50	1903	1977	Marggi
778	*Carabus irregularis irregularis*	Switzerland	45.64	6.79	2000	1995	Franzen
779	*Carabus irregularis irregularis*	Switzerland	46.52	7.78	2182	1960	BänningerM
780	*Carabus irregularis irregularis*	Switzerland	46.33	7.28	2238	1964	Besuchet
781	*Carabus irregularis irregularis*	Switzerland	46.89	9.34	2980	1986	Osterw.
782	*Carabus irregularis irregularis*	Switzerland	46.89	9.34	2980	1961	Spälti
783	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	44.33	17.13	823	1984	Dovenik
784	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	44.54	16.47	977	1982	Drovenik
785	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	43.68	18.55	980	1976	Drovenik
786	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	43.33	18.69	997	1976	Drovenik
787	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	44.50	16.35	1000	1981	Staven
788	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	44.29	18.10	1020	1976	Drovenik
789	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	43.48	18.46	1068	1976	Drovenik
790	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	44.18	18.67	1072	1976	Drovenik
791	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	43.81	18.24	1148	1976	Drovenik
792	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	43.53	18.43	1234	1984	Dovenik
793	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	44.29	18.09	1256	1976	Drovenik
794	*Carabus irregularis bucephalus*	Bosnia/Herzegovina	43.72	18.28	1382	1976	Drovenik
795	*Carabus irregularis bucephalus*	Croatia	47.39	7.82	618	2006	Straumann
796	*Carabus irregularis bucephalus*	Croatia	45.92	15.96	662	2001	Seric-Jelaska
797	*Carabus irregularis bucephalus*	Croatia	46.20	16.10	670	1932	Seric-Jelaska
798	*Carabus irregularis bucephalus*	Croatia	45.53	17.60	777	2008	Seric-Jelaska
799	*Carabus irregularis bucephalus*	Croatia	45.21	14.75	791	1905	Csiki et al.
800	*Carabus irregularis bucephalus*	Croatia	45.92	15.97	810	2001	Seric-Jelaska
801	*Carabus irregularis bucephalus*	Croatia	45.44	14.75	821	1928	Seric-Jelaska
802	*Carabus irregularis bucephalus*	Croatia	45.26	14.72	827	1928	Seric-Jelaska
803	*Carabus irregularis bucephalus*	Croatia	45.42	14.76	864	1905	Csiki et al.
804	*Carabus irregularis bucephalus*	Croatia	44.53	15.23	916	2007	Seric-Jelaska
805	*Carabus irregularis bucephalus*	Croatia	45.78	15.39	925	1905	Csiki et al.
806	*Carabus irregularis bucephalus*	Croatia	45.91	15.97	930	1969	Seric-Jelaska
807	*Carabus irregularis bucephalus*	Croatia	45.37	15.00	950	1935	Seric-Jelaska
808	*Carabus irregularis bucephalus*	Croatia	45.91	15.97	972	2001	Seric-Jelaska
809	*Carabus irregularis bucephalus*	Croatia	45.31	14.66	1079	1905	Csiki et al.
810	*Carabus irregularis bucephalus*	Croatia	44.59	15.14	1185	2009	Seric-Jelaska
811	*Carabus irregularis bucephalus*	Croatia	45.42	14.57	1205	1968	Seric-Jelaska
812	*Carabus irregularis bucephalus*	Montenegro	42.63	19.25	959	NA	J. Böhme
813	*Carabus irregularis bucephalus*	Montenegro	42.90	19.59	1121	1984	Dovenik
814	*Carabus irregularis bucephalus*	Montenegro	43.20	19.09	1154	1984	Dovenik
815	*Carabus irregularis bucephalus*	Montenegro	43.14	19.09	1427	1976	Drovenik
816	*Carabus irregularis bucephalus*	Montenegro	43.26	18.72	1557	1984	Dovenik
817	*Carabus irregularis bucephalus*	Serbia	43.88	19.88	560	1932	Breuning
818	*Carabus irregularis bucephalus*	Serbia	43.88	19.88	560	2004	Deuve
819	*Carabus irregularis bucephalus*	Serbia	43.57	19.83	1240	1984	Dovenik
820	*Carabus irregularis bucephalus*	Slovenia	46.70	15.66	286	2006	A. Kapla

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
821	*Carabus irregularis bucephalus*	Slovenia	46.70	15.66	286	2006	A. Kapla
822	*Carabus irregularis bucephalus*	Slovenia	46.70	15.66	287	1972	Drovenik
823	*Carabus irregularis bucephalus*	Slovenia	46.07	14.86	333	1972	Drovenik
824	*Carabus irregularis bucephalus*	Slovenia	46.58	15.32	484	1996	Vrezec
825	*Carabus irregularis bucephalus*	Slovenia	45.90	14.22	531	1988	Vrezec
826	*Carabus irregularis bucephalus*	Slovenia	46.08	15.46	537	1972	Drovenik
827	*Carabus irregularis bucephalus*	Slovenia	46.19	15.07	620	1980	Drovenik
828	*Carabus irregularis bucephalus*	Slovenia	46.18	15.08	623	1997	A. Kapla
829	*Carabus irregularis bucephalus*	Slovenia	45.93	14.31	624	1969	Drovenik
830	*Carabus irregularis bucephalus*	Slovenia	45.93	14.31	624	1991	Vrezec
831	*Carabus irregularis bucephalus*	Slovenia	46.10	15.10	632	1997	A. Kapla
832	*Carabus irregularis bucephalus*	Slovenia	46.10	15.10	632	2001	A. Kapla
833	*Carabus irregularis bucephalus*	Slovenia	46.10	15.10	632	1997	A. Kapla
834	*Carabus irregularis bucephalus*	Slovenia	46.18	15.09	639	2000	A. Kapla
835	*Carabus irregularis bucephalus*	Slovenia	46.28	15.60	641	2006	A. Vrezec
836	*Carabus irregularis bucephalus*	Slovenia	46.28	15.60	641	2006	A. Vrezec
837	*Carabus irregularis bucephalus*	Slovenia	46.47	14.85	679	1982	T. Jeseničnik
838	*Carabus irregularis bucephalus*	Slovenia	46.47	14.85	679	1982	T. Jeseničnik
839	*Carabus irregularis bucephalus*	Slovenia	46.64	15.21	681	1972	Drovenik
840	*Carabus irregularis bucephalus*	Slovenia	46.28	15.62	693	2009	A. Vrezec
841	*Carabus irregularis bucephalus*	Slovenia	45.81	14.10	699	2004	A. Kapla
842	*Carabus irregularis bucephalus*	Slovenia	46.51	15.46	707	2005	A. Kapla
843	*Carabus irregularis bucephalus*	Slovenia	46.28	15.63	708	2006	A. Vrezec
844	*Carabus irregularis bucephalus*	Slovenia	46.28	15.63	708	2006	A. Vrezec
845	*Carabus irregularis bucephalus*	Slovenia	45.86	14.40	721	1905	P.M. Giachino
846	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1986	Furlan (1988)
847	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1985	Slapnik (1986)
848	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1985	Slapnik (1986)
849	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1985	Slapnik (1986)
850	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1991	Vrezec
851	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1991	Vrezec
852	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1985	Slapnik (1986)
853	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1985	Slapnik (1986)
854	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1990	Vrezec
855	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1986	Furlan (1988)
856	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1986	Furlan (1988)
857	*Carabus irregularis bucephalus*	Slovenia	46.32	14.60	736	1985	Slapnik (1986)
858	*Carabus irregularis bucephalus*	Slovenia	46.29	15.61	739	1993	Vrezec
859	*Carabus irregularis bucephalus*	Slovenia	46.29	15.61	739	1996	Vrezec
860	*Carabus irregularis bucephalus*	Slovenia	46.28	15.60	748	1953	Drovenik
861	*Carabus irregularis bucephalus*	Slovenia	46.07	15.28	766	1999	A. Kapla
862	*Carabus irregularis bucephalus*	Slovenia	46.19	14.97	842	1989	Vrezec
863	*Carabus irregularis bucephalus*	Slovenia	45.53	15.10	849	1972	Drovenik
864	*Carabus irregularis bucephalus*	Slovenia	46.33	15.37	853	1992	Vrezec
865	*Carabus irregularis bucephalus*	Slovenia	46.33	15.37	853	1992	B. Drovenik
866	*Carabus irregularis bucephalus*	Slovenia	46.42	14.64	855	1981	Broder, Hrusa
867	*Carabus irregularis bucephalus*	Slovenia	45.62	15.10	856	1970	Drovenik
868	*Carabus irregularis bucephalus*	Slovenia	46.42	14.62	864	1967	Drovenik
869	*Carabus irregularis bucephalus*	Slovenia	45.94	14.47	869	2004	A. Vrezec
870	*Carabus irregularis bucephalus*	Slovenia	45.91	14.47	882	2001	A. Kapla
871	*Carabus irregularis bucephalus*	Slovenia	45.91	14.47	883	2001	A. Kapla
872	*Carabus irregularis bucephalus*	Slovenia	46.47	15.53	883	1991	Vrezec
873	*Carabus irregularis bucephalus*	Slovenia	46.39	15.22	898	2000	A. Kapla
874	*Carabus irregularis bucephalus*	Slovenia	46.48	13.80	937	1992	Drovenik
875	*Carabus irregularis bucephalus*	Slovenia	46.48	13.80	937	1974	Hrusa

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
876	*Carabus irregularis bucephalus*	Slovenia	45.65	15.03	946	1967	Drovenik
877	*Carabus irregularis bucephalus*	Slovenia	46.36	15.33	949	1992	Vrezec
878	*Carabus irregularis bucephalus*	Slovenia	46.34	15.37	987	1970	Drovenik
879	*Carabus irregularis bucephalus*	Slovenia	45.89	14.53	990	1994	Vrezec
880	*Carabus irregularis bucephalus*	Slovenia	45.89	14.53	990	1994	Vrezec
881	*Carabus irregularis bucephalus*	Slovenia	45.89	14.53	990	1993	Vrezec
882	*Carabus irregularis bucephalus*	Slovenia	45.89	14.53	990	1996	Vrezec
883	*Carabus irregularis bucephalus*	Slovenia	45.63	15.10	993	1979	Drovenik
884	*Carabus irregularis bucephalus*	Slovenia	46.08	15.08	1001	1997	A. Kapla
885	*Carabus irregularis bucephalus*	Slovenia	45.73	14.29	1017	1971	Tombesi, Hrusa
886	*Carabus irregularis bucephalus*	Slovenia	46.57	14.98	1018	1972	Drovenik
887	*Carabus irregularis bucephalus*	Slovenia	45.89	14.52	1020	1978	Hrusa
888	*Carabus irregularis bucephalus*	Slovenia	45.89	14.53	1024	1968	Drovenik
889	*Carabus irregularis bucephalus*	Slovenia	46.32	14.58	1026	1983	Broder
890	*Carabus irregularis bucephalus*	Slovenia	45.93	14.47	1052	2001	A. Vrezec
891	*Carabus irregularis bucephalus*	Slovenia	45.93	14.47	1052	2006	A. Kapla
892	*Carabus irregularis bucephalus*	Slovenia	45.93	14.47	1052	2001	A. Vrezec
893	*Carabus irregularis bucephalus*	Slovenia	45.93	14.47	1052	2006	A. Kapla
894	*Carabus irregularis bucephalus*	Slovenia	46.08	15.07	1067	1999	A. Kapla
895	*Carabus irregularis bucephalus*	Slovenia	46.08	15.07	1067	1995	A. Kapla
896	*Carabus irregularis bucephalus*	Slovenia	46.19	15.11	1075	1992	Vrezec
897	*Carabus irregularis bucephalus*	Slovenia	46.49	15.51	1086	1990	Vrezec
898	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1986	Furla (1988)
899	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1991	Vrezec
900	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1986	Furlan (1988)
901	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1986	Furla (1988)
902	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1991	Vrezec
903	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1990	Vrezec
904	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1988	Vrezec
905	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1986	Furlan (1988)
906	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1991	Vrezec
907	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1991	Vrezec
908	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1991	Vrezec
909	*Carabus irregularis bucephalus*	Slovenia	45.92	14.47	1092	1990	B. Drovenik
910	*Carabus irregularis bucephalus*	Slovenia	46.36	14.03	1092	1969	Drovenik
911	*Carabus irregularis bucephalus*	Slovenia	46.09	15.07	1131	1969	Drovenik
912	*Carabus irregularis bucephalus*	Slovenia	46.34	14.38	1197	1990	J. Broder
913	*Carabus irregularis bucephalus*	Slovenia	45.94	13.81	1217	1973	Drovenik (1978)
914	*Carabus irregularis bucephalus*	Slovenia	45.94	13.81	1217	1973	Drovenik (1978)
915	*Carabus irregularis bucephalus*	Slovenia	45.94	13.81	1217	1973	Drovenik (1978)
916	*Carabus irregularis bucephalus*	Slovenia	45.94	13.81	1217	1973	Drovenik (1978)
917	*Carabus irregularis bucephalus*	Slovenia	45.59	14.74	1252	1995	F. Kljun
918	*Carabus irregularis bucephalus*	Slovenia	45.59	14.74	1252	1992	Vrezec
919	*Carabus irregularis bucephalus*	Slovenia	46.35	14.39	1291	1990	J. Broder
920	*Carabus irregularis bucephalus*	Slovenia	45.98	13.87	1296	1975	Drovenik (1978)
921	*Carabus irregularis bucephalus*	Slovenia	45.98	13.87	1312	1975	Drovenik (1978)
922	*Carabus irregularis bucephalus*	Slovenia	45.98	13.87	1317	1975	Drovenik (1978)
923	*Carabus irregularis bucephalus*	Slovenia	46.25	14.79	1367	1992	Vrezec
924	*Carabus irregularis bucephalus*	Slovenia	45.57	14.41	1382	1979	Staven
925	*Carabus irregularis bucephalus*	Slovenia	46.25	14.82	1386	1975	Drovenik

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
926	*Carabus irregularis montandoni*	Czech Republic	49.71	18.64	342	1900	Hejda
927	*Carabus irregularis montandoni*	Czech Republic	49.61	18.64	504	1900	Hejda
928	*Carabus irregularis montandoni*	Czech Republic	49.21	18.13	563	1983	Hejda
929	*Carabus irregularis montandoni*	Czech Republic	49.41	18.30	602	2003	Hejda
930	*Carabus irregularis montandoni*	Czech Republic	49.51	18.47	619	2003	Hejda
931	*Carabus irregularis montandoni*	Czech Republic	49.41	18.47	718	2003	Hejda
932	*Carabus irregularis montandoni*	Czech Republic	49.51	18.64	831	2004	Hejda
933	*Carabus irregularis montandoni*	Poland	50.21	19.83	381	2003	Aleksandrowicz
934	*Carabus irregularis montandoni*	Poland	49.53	21.53	544	2008	Pawlowski
935	*Carabus irregularis montandoni*	Poland	49.46	20.77	711	1991	Sienkiewicz
936	*Carabus irregularis montandoni*	Poland	49.16	19.51	719	1999	Skalski T.
937	*Carabus irregularis montandoni*	Poland	49.42	20.40	760	2008	Pawlowski
938	*Carabus irregularis montandoni*	Poland	49.60	19.54	826	2008	Pawlowski
939	*Carabus irregularis montandoni*	Poland	49.11	22.68	854	1983	Sienkiewicz
940	*Carabus irregularis montandoni*	Poland	49.58	20.07	874	2008	Wojas
941	*Carabus irregularis montandoni*	Poland	49.11	22.52	886	2008	Pawlowski
942	*Carabus irregularis montandoni*	Poland	49.41	18.99	896	1997	Paweł Szafraniec
943	*Carabus irregularis montandoni*	Poland	49.49	20.25	950	2008	Pawlowski
944	*Carabus irregularis montandoni*	Poland	49.59	19.54	954	2000	Marek Przewoźny
945	*Carabus irregularis montandoni*	Poland	49.32	20.10	959	1999	Skalski T.
946	*Carabus irregularis montandoni*	Poland	49.27	19.93	1035	1991	Andrzej Melke
947	*Carabus irregularis montandoni*	Poland	49.28	20.04	1168	2007	Sienkiewicz
948	*Carabus irregularis montandoni*	Poland	49.26	20.00	1267	2008	Pawlowski
949	*Carabus irregularis montandoni*	Romania	45.76	23.88	830	1890	Hopffgarten
950	*Carabus irregularis montandoni*	Romania	47.51	24.68	1014	1882	Buysson
951	*Carabus irregularis montandoni*	Romania	47.70	23.79	1043	2003	Prunar, Barloy, Prunar
952	*Carabus irregularis montandoni*	Romania	45.50	25.51	1126	2009	Schäfer & Aßmann
953	*Carabus irregularis montandoni*	Romania	47.60	25.49	1146	1890	Hopffgarten
954	*Carabus irregularis montandoni*	Romania	47.70	23.87	1223	2009	Prunar et. al.
955	*Carabus irregularis montandoni*	Romania	45.63	24.61	1244	2009	Schäfer & Aßmann
956	*Carabus irregularis montandoni*	Romania	45.54	24.80	1307	2009	Prunar et. al.
957	*Carabus irregularis montandoni*	Romania	47.61	24.65	1440	2009	Schäfer & Aßmann
958	*Carabus irregularis montandoni*	Romania	47.45	25.56	1471	2009	Schäfer & Aßmann
959	*Carabus irregularis montandoni*	Romania	47.51	24.65	1474	2008	Nitzu et al.
960	*Carabus irregularis montandoni*	Romania	47.45	25.56	1505	2009	Schäfer & Aßmann
961	*Carabus irregularis montandoni*	Romania	45.60	24.57	1620	1890	Hopffgarten
962	*Carabus irregularis montandoni*	Romania	45.59	24.42	1705	1909	Hoffmann
963	*Carabus irregularis montandoni*	Romania	45.46	25.46	1854	1909	Hoffmann
964	*Carabus irregularis montandoni*	Romania	45.56	24.48	1870	1915	Hoffmann
965	*Carabus irregularis montandoni*	Romania	45.45	25.44	2074	1915	Hoffmann
966	*Carabus irregularis montandoni*	Slovakia	48.85	22.19	360	2000	Lohaj
967	*Carabus irregularis montandoni*	Slovakia	49.29	21.31	421	1983	leg. J.Hron, Hrusa
968	*Carabus irregularis montandoni*	Slovakia	49.29	21.31	422	1985	Hron, Hrusa
969	*Carabus irregularis montandoni*	Slovakia	48.76	21.24	450	2000	Lohaj
970	*Carabus irregularis montandoni*	Slovakia	49.04	22.29	547	2000	Lohaj
971	*Carabus irregularis montandoni*	Slovakia	49.35	21.26	682	2000	Lohaj
972	*Carabus irregularis montandoni*	Slovakia	49.35	21.25	730	1983	Dr. M. Resi
973	*Carabus irregularis montandoni*	Slovakia	49.04	19.68	753	1984	Hron, Hrusa
974	*Carabus irregularis montandoni*	Slovakia	49.03	19.67	759	2000	Lohaj
975	*Carabus irregularis montandoni*	Slovakia	48.69	19.05	769	2000	Lohaj
976	*Carabus irregularis montandoni*	Slovakia	49.13	19.15	802	2000	Lohaj
977	*Carabus irregularis montandoni*	Slovakia	48.87	20.34	805	1978	J. Böhme
978	*Carabus irregularis montandoni*	Slovakia	48.87	20.34	805	1977	J. Böhme
979	*Carabus irregularis montandoni*	Slovakia	49.01	19.67	822	1984	Hron, Hrusa
980	*Carabus irregularis montandoni*	Slovakia	49.02	19.58	858	2000	Lohaj

Table S4.1. *Continued.*

REC	SUBSPECIES	COUNTRY	LAT	LONG	ELEV	DATE	COLL/SOURCE
981	*Carabus irregularis montandoni*	Slovakia	48.93	20.27	903	1986	Dr. M. Resi
982	*Carabus irregularis montandoni*	Slovakia	48.93	13.91	910	1975	Slaba, Hrusa
983	*Carabus irregularis montandoni*	Slovakia	49.10	19.97	927	2000	Lohaj
984	*Carabus irregularis montandoni*	Slovakia	49.24	19.05	977	2000	Lohaj
985	*Carabus irregularis montandoni*	Slovakia	49.26	20.29	1008	2000	Lohaj
986	*Carabus irregularis montandoni*	Ukrain	48.56	22.46	188	2003	Rizun
987	*Carabus irregularis montandoni*	Ukrain	49.70	23.98	295	2003	Rizun
988	*Carabus irregularis montandoni*	Ukrain	48.22	23.53	382	2003	Rizun
989	*Carabus irregularis montandoni*	Ukrain	48.75	22.64	398	2003	Rizun
990	*Carabus irregularis montandoni*	Ukrain	48.77	22.99	470	2003	Rizun
991	*Carabus irregularis montandoni*	Ukrain	48.52	23.14	479	2003	Rizun
992	*Carabus irregularis montandoni*	Ukrain	49.21	23.22	497	2003	Rizun
993	*Carabus irregularis montandoni*	Ukrain	48.66	22.71	524	2003	Rizun
994	*Carabus irregularis montandoni*	Ukrain	49.27	23.42	529	2003	Rizun
995	*Carabus irregularis montandoni*	Ukrain	48.91	23.43	691	2003	Rizun
996	*Carabus irregularis montandoni*	Ukrain	48.34	23.63	748	2003	Rizun
997	*Carabus irregularis montandoni*	Ukrain	49.04	23.16	809	2003	Rizun
998	*Carabus irregularis montandoni*	Ukrain	48.19	24.70	858	2003	Rizun
999	*Carabus irregularis montandoni*	Ukrain	48.93	23.51	1011	2003	Rizun
1000	*Carabus irregularis montandoni*	Ukrain	48.21	24.82	1082	2003	Rizun
1001	*Carabus irregularis montandoni*	Ukrain	48.21	24.20	1213	2003	Rizun
1002	*Carabus irregularis montandoni*	Ukrain	47.95	24.27	1346	2003	Rizun
1003	*Carabus irregularis montandoni*	Ukrain	48.15	24.41	1400	2003	Rizun
1004	*Carabus irregularis montandoni*	Ukrain	48.59	23.91	1610	2003	Rizun
1005	*Carabus irregularis montandoni*	Ukrain	48.16	24.50	1807	2000	Putchkov

Table S4.2. Climate data (monthly temperature and rainfall values) generated according to Hijmans et al. (2005) (Hijmans *et al.* 2005) to 19 bioclimatic variables.

Abbreviation	Parameter denotation
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Table S4.3. Summary of statistical analyses on measures of DNA sequence variation within clades, subclades and in all sequences together (total) for CO1 and ND5 separately: N = sample size, S = number of polymorphic/segregating sites, Eta = total number of mutations, k = average pairwise nucleotide difference per sequence, H = number of haplotypes, h = haplotype diversity, π = nucleotide diversity, θG = mutation parameter per sequence).

CO1 (786 bp)									
Clade/Subclade	N	S	Eta	k	H	h	Var(h)	π	θG
Clade A	14	32	34	129.341	7	0.857	0.00426	0.01646	106.914
Subclade Ae	7	12	12	44.762	4	0.714	0.03272	0.00569	48.980
Subclade As	7	15	16	75.238	3	0.667	0.02554	0.00957	65.306
Clade B	76	30	30	72.993	12	0.742	0.00148	0.00929	61.208
Subclade Bn	38	4	4	0.4922	3	0.240	0.00737	0.00063	0.9520
Subclade Bs	30	7	7	11.241	5	0.566	0.00798	0.00143	17.669
Subclade Bsl	8	12	12	50.714	6	0.929	0.00711	0.00645	46.281
Total	90	67	70	141.985	19	0.813	0.00098	0.01806	138.027

ND5 (999 bp)									
Clade/Subclade	N	S	Eta	k	H	h	Var(h)	π	θG
Clade A	14	41	42	159.451	8	0.901	0.00331	0.01596	132.070
Subclade Ae	7	11	11	39.048	4	0.714	0.03272	0.00391	44.898
Subclade As	7	24	24	129.524	4	0.857	0.01047	0.01297	97.959
Clade B	76	31	33	80.182	19	0.786	0.00137	0.00803	67.328
Subclade Bn	38	6	6	0.5590	6	0.376	0.00958	0.00056	14.280
Subclade Bs	30	10	10	21.540	8	0.628	0.00890	0.00216	25.242
Subclade Bsl	8	13	13	49.286	7	0.964	0.00596	0.00493	50.138
Total	90	77	83	164.729	27	0.846	0.00086	0.01649	163.661

Table S4.4. Genetic differentiation (Φ_{ST}; in the upper part of the matrix) and intraspecific genetic divergence (K-2P distances; in the lower part of the matrix) of *Carabus irregularis*. K-2P distances greater than the threshold value assumed for species identification by Wiemers and Fiedler (2007) are printed in bold.

	Teu	Sue	Hz I	Hz II	Hai I	Hai II	Hai III	Sw I	Sw II	Sw III	Bla	Jur II	Slo I	Slo II	Slo III	Car II	Car III
Teu		*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	*n.s.*	0.999	0.992	0.984	0.932	0.992	0.966	0.839	0.892	0.968	0.992
Sue	0		0.629	0.629	*n.s.*	0.114	*n.s.*	0.993	0.986	0.978	0.932	0.986	0.962	0.852	0.896	0.969	0.991
Hz I	0	0		0.696	*n.s.*	0.143	*n.s.*	0.999	0.993	0.986	0.938	0.993	0.97	0.86	0.904	0.972	0.993
Hz II	0.001	0.001	0.001		0.572	0.464	0.55	0.978	0.971	0.961	0.917	0.971	0.942	0.821	0.871	0.96	0.983
Hai I	0	0	0	0.001		0.094	*n.s.*	0.986	0.979	0.97	0.927	0.979	0.954	0.844	0.889	0.967	0.988
Hai II	0.001	0.001	0.001	0.002	0.001		*n.s.*	0.966	0.959	0.947	0.904	0.959	0.927	0.802	0.855	0.956	0.979
Hai III	0.001	0.001	0.001	0.002	0.001	0.001		0.979	0.97	0.958	0.908	0.971	0.936	0.789	0.853	0.956	0.982
Sw I	0.015	0.015	0.015	0.016	0.015	0.015	0.015		*n.s.*	0.934	*n.s.*	*n.s.*	0.826	0.654	0.826	0.969	0.992
Sw II	0.015	0.015	0.015	0.016	0.015	0.015	0.015	0		0.902	*n.s.*	*n.s.*	0.788	0.635	0.81	0.967	0.989
Sw III	0.015	0.015	0.015	0.016	0.015	0.016	0.016	0.004	0.004		0.492	0.902	0.727	*n.s.*	0.774	0.957	0.983
Bla	0.015	0.015	0.015	0.016	0.015	0.015	0.015	0.001	0.001	0.003		*n.s.*	0.46	0.488	0.712	0.947	0.965
Jur II	0.015	0.015	0.015	0.016	0.015	0.015	0.015	0	0	0.004	0.001		0.788	0.639	0.813	0.967	0.989
Slo I	0.014	0.014	0.014	0.015	0.014	0.015	0.015	0.003	0.003	0.003	0.003	0.003		0.469	0.714	0.953	0.977
Slo II	0.015	0.015	0.015	0.016	0.015	0.016	0.016	0.006	0.006	0.006	0.006	0.006	0.005		0.103	0.898	0.917
Slo III	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.008	0.008	0.009	0.008	0.009	0.008	0.006		0.928	0.948
Car II	**0.04**	**0.04**	**0.04**	**0.04**	**0.04**	**0.041**	**0.041**	**0.042**	**0.042**	**0.04**	**0.041**	**0.042**	**0.041**	**0.041**	**0.041**		0.919
Car III	**0.044**	**0.044**	**0.044**	**0.043**	**0.044**	**0.044**	**0.044**	**0.041**	**0.041**	**0.04**	**0.041**	**0.041**	**0.041**	**0.041**	**0.041**	0.022	

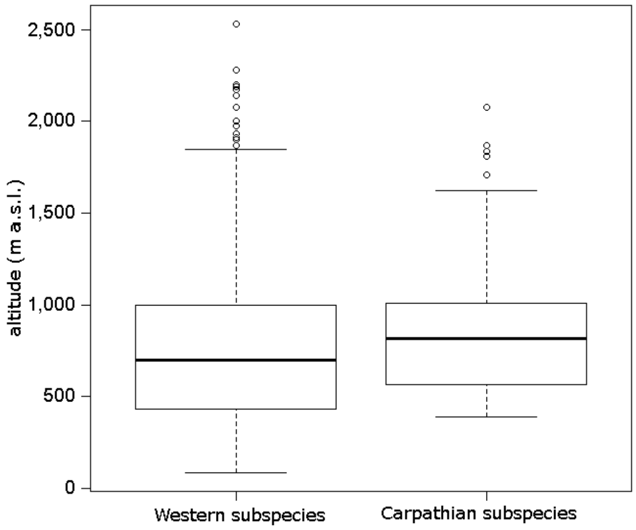

Figure S4.1. Altitudinal distribution range of the western and the Carpathian ESU of *Carabus irregularis*. (p < 0.001; Mann-Whitney-U-test).

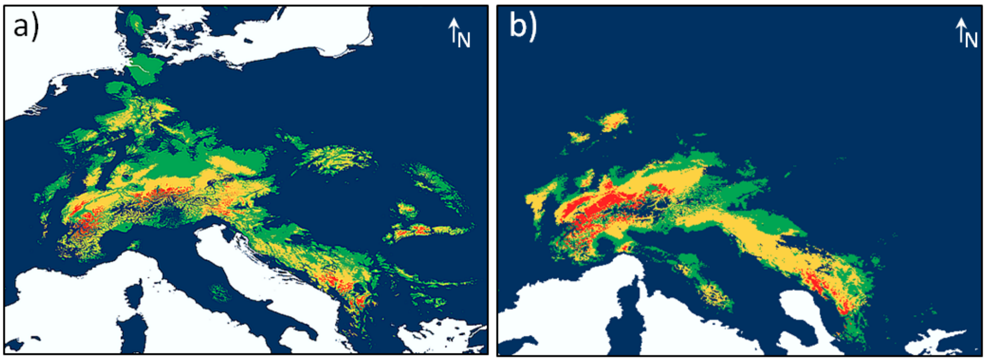

Figure S4.2. Entire distribution model for (a) current and (c) past climate conditions. Past distribution is shown for the Last Glacial Maximum (LGM, 21,000 BP). Warmer colors show areas with better predicted conditions (green: p > 0.3, yellow: p > 0.5, red: p > 0.7).

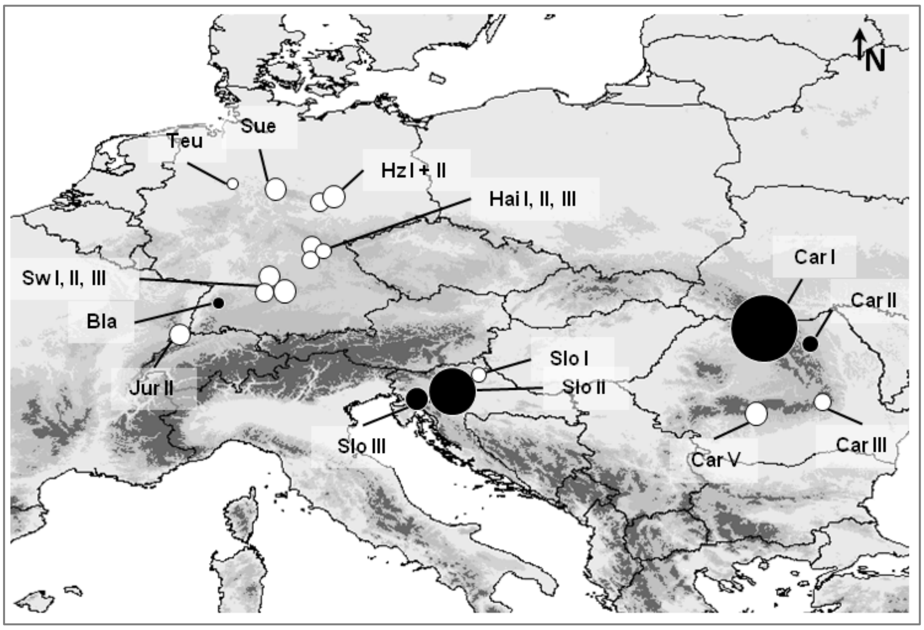

Figure S4.3. Nucleotide diversity of 19 studied *Carabus irregularis* populations. Black circles symbolise values higher than the global mean nucleotide diversity; white circles stand for lower than mean diversity. Circle size is proportional to the difference from the mean diversity. Three populations (Dei, Jur I, Car IV) are omitted due to insufficient sample sizes.

5 EVOLUTIONARILY SIGNIFICANT UNITS IN A FLIGHTLESS GROUND BEETLE SHOW DIFFERENT CLIMATE NICHES AND HIGH EXTINCTION RISK DUE TO GLOBAL WARMING

Submitted Manuscript

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5.1 Abstract

Species distribution models (SDMs), especially those basing on climatic parameters, have frequently been used to project future species ranges and to develop conservation strategies. As suggested by several authors, we considered both different dispersal abilities and different evolutionarily significant units (ESUs, as determined in an earlier genetic survey). For our study species, the flightless ground beetle *Carabus irregularis*, SDMs for two ESUs from the western and the Carpathian area of the distribution range showed immense, and deviating future range contractions reflecting divergent ecological requirements. As minimal dispersal SDMs resulted in a stronger decline of future ranges than the maximal dispersal models, low dispersal ability tended to strengthen the already high vulnerability of the cold-adapted mountain species to global warming. Areas shown in our maximal dispersal models as offering climatically suitable habitats for *C. irregularis* in the future should be considered as potential areas of action in future conservation planning (e.g. assisted migration or assisted colonisation). Thus, both dispersal scenarios and different (if applicable) ESUs should be considered when developing SDMs as useful tools for species conservation strategies adapted to species' performance and differentiation patterns.

5.2 Introduction

Recent climate change is one of the most powerful drivers of biodiversity loss (MEA 2005). Warming temperatures have already led to shifts in species' distribution ranges to higher altitudes or latitudes (Parmesan and Yohe 2003; Hickling *et al.* 2006). To assess these range shifts, new methods such as species distribution models (SDMs) have been used to project future distribution by relating current species occurrence with climatic variables (Guisan and Thuiller 2005; Elith and Leathwick 2009). However, SDMs have been criticised due to their limitation to climate conditions and the disregard of other ecological factors such as species dispersal (Araújo and Guisan 2006; Heikkinen *et al.* 2006). Most SDMs are capable to predict future climatically suitable habitats but do not consider whether species can actually reach the predicted areas. Limited dispersal abilities can even enhance the retraction of species' distribution ranges (Svenning and Skov 2004; Schloss *et al.* 2012). Range retractions can then be associated with even more severe consequences such as the loss of genetic diversity, e.g. when genetically unique subgroups of a species are predicted to disappear (Habel *et al.* 2011). The dispersal ability of species might play a crucial role for a better understanding of species' vulnerability against global change (Schweiger *et al.* 2008; Schweiger *et al.* 2012) and for the development of suitable conservation activities such as assisted migration/colonisation) The necessity of biodiversity conservation at the levels of ecosystems and species as well as at the genetic level is recognised as highly important (IUCN 1980). As genetic diversity is essential to the long-time survival of species and their ability to adapt to changing environmental conditions (Frankham 2003; Reed and Frankham 2003), the preservation of genetically unique subgroups (i.e. evolutionarily significant units = ESUs) appears crucial in terms of conservation management. The concept of ESUs has become an important part of conservation biology – especially in conservation genetics – over the last decades (Moritz 1994; Frankham *et al.* 2005). The existence and importance of ESUs has been demonstrated for many endangered species (Mateus *et al.* 2011; Reilly *et al.* 2012). Most studies focus on the analysis of genetic characteristics rather than on assessing the extinction risk of ESUs or the conservation of these differentiated entities. However, the concept of ESUs implies not only the implementation of (neutral) molecular markers (e.g. allozymes, DNA sequences) but also ecological and other species traits, which could be important for conservation management (Vogler *et al.* 1993a; Vogler and DeSalle 1994; Crandall *et al.* 2000).

Mountain species often show highly differentiated genetic subgroups, due to disjunct recent distribution in rutted landscapes (Matern *et al.* 2009; Dieker *et al.* 2012) but also when they have survived ice-ages in isolated refugia (Schönswetter *et al.* 2004; Haubrich and Schmitt 2007; Wachter *et al.* 2012). Additionally, mountain inhabiting species are mostly adapted to cool and moist climate conditions and are considered as particularly sensitive to global warming (Settele *et al.* 2009; Konvička *et al.* 2010; Dieker *et al.* 2011). The cold-adapted mountainously distributed *Carabus irregularis* might belong to these strongly vulnerable species. A former phylogeographic study revealed strongly differentiated subgroups within *C. irregularis*, which can be considered as ESUs. These ESUs are assumed to have survived the last glacial period in multiple refugia in south-eastern Europe and in Central Europe north of the Alps (Homburg *et al.* 2013b). The low dispersal ability (due to flightlessness) of *C. irregularis* might have caused strong genetic differentiation of several genetic lineages within its distribution range.

In this study, we combine modern SDMs with different dispersal scenarios in the framework of the ESU concept. SDMs were calculated for the entire species and for the two ESUs according to Homburg *et al.* (2013b) and also for two different future climate scenarios (A2a and B2a, IPCC) to predict possible future distribution ranges. In addition, each set of SDMs was used to analyse the assumption of maximum and minimum dispersal.

We addressed the following specific study questions: (1) Do the SDMs of the most differentiated phylogeographic units (ESUs) differ from each other and from those of the entire distribution range, especially in respect to the possible future distribution ranges? (2) How do potential future distribution patterns vary when different dispersal scenarios are considered? (3) Which consequences can result from these findings for species conservation?

5.3 Material and methods

5.3.1 Study species

Carabus (*Platycarabus*) *irregularis* Fabricius, 1792 shows a disjunct distribution range from Lower Saxony and Westphalia in the north to the Dinaric Mountains in the south and from the Jura Mountains in the west to the Carpathians in the east (Turin *et al.* 2003a). In the taxonomic literature, three subspecies are well-accepted (Bousquet *et al.* 2003; Casale and Kryzhanovskij. 2003) but only two of them are well recognisable on the molecular level (Homburg *et al.* 2013b): the populations from the Carpathians (ssp. *montandoni* Buysson, 1882) and all others (including ssp. *irregularis*, Central Europe and north of the Balkan Peninsula, and ssp. *bucephalus* Kraatz, 1879 from the Balkan). Suitable habitats are predominantly on limestone and are rich in snails, the preferred food of *C. irregularis*. The study species is adapted to cold and moist habitats in montane to subalpine altitudes (e.g. beech forests and high mountain meadows; Turin *et al.* 2003a) and thus belongs to a group of species which is highly vulnerable to global warming due to the resulting loss or shift of suitable habitats (Pauli *et al.* 2007). Actually, the species is already declining in some regions (Lorenz 2003) and became extinct in some parts of its former distribution range (e.g. in Belgium; Desender *et al.* 2008).

5.3.2 Species distribution modelling

Species data

We compiled 1,000 data points of observed occurrences of *C. irregularis* from museum and private entomological collections and from the literature and databases (e.g. Sokolár 1909; Weber 1966a; Franzen 1995; Hartmann 1998; Flechtner 2000; Gebert 2006; Köhler and Flechtner 2007; Hejda 2011). Redundant localities were excluded by the model software to avoid spatial clumping; the final locality input included 645 records. The species records comprised a western and a Carpathian subgroup of *C. irregularis* – two divergent phylogenetic lineages which can be considered as ESUs (Homburg *et al.* 2013b). Species records were not only used for modelling as entire data set, but also split into two sets: one with the western European species records (from Central Europe and the Balkan; hereafter western ESU, comprising the populations of the nominate subspecies and *C. i. bucephalus*) and one with the eastern European part of the species distribution (Carpathians; hereafter Carpathian ESU, comprising the populations of the subspecies *C. i. montandoni*).

Predictors

Climate data were generated according to Hijmans et al. (2005). Nineteen bioclimatic variables (BIO1-BIO19) represent temperature and humidity measures which are particularly significant in determining species' distributions (Waltari *et al.* 2007). Current climate data (i.e. period 1950-2000) were downloaded with a spatial resolution of 30 arc s (~ 1 x 1 km) from the WorldClim database (http://www.worldclim.org/). Future climate data (2080s, averages 2070-2099) were downscaled from general circulation models to the required spatial resolution and provided by Ramirez and Jarviz (2008) (http://www.ccafs-climate.org/). Data were derived from the GCM HadCM3 (Gordon *et al.* 2000) according to two different emission scenarios A2a and B2a (SRES - Special Report on Emission Scenarios; Nakićenović and Swart 2000) of the Intergovernmental Panel on climate change (IPCC). The "business-as-usual" scenario A2a reflects rapid global warming due to unreduced CO_2 emission. The B2a scenario projects reduced CO_2 emission and slower climate change. We included only uncorrelated variables with high explanatory power and ecological relevance (cf. Araújo and Guisan 2006; Rödder and Dambach 2010) which are most likely to influence the occurrence of *C. irregularis*. Therefore, we performed a principal component analysis (PCA), compiled a correlation matrix and excluded all strongly correlated variables (Pearson's $r^2 > 0.75$; Guisan and Thuiller 2005). Final models included five predictor variables: 'Isothermality' (BIO3), 'temperature seasonality' (BIO4), 'minimum temperature of coldest month' (BIO6), 'precipitation of wettest month' (BIO13) and 'precipitation of driest month' (BIO14) – climatic measures reflecting habitat conditions which are likely to affect the occurrence of *C. irregularis* (Weber 1966a; Hartmann 1998).

Model building and validation

SDMs were generated using MAXENT 3.3.3 (www.cs.princeton.edu/~schapire/maxent), with automatically sampled random background points and species records split into 75% model training and 25% model evaluation data randomly permutated in each model. The predictive performance of our models was evaluated by the Area Under Curve (AUC) method averaged over 100 model replicate runs. An AUC higher than 0.7 indicates ecologically meaningful model results (Fielding and Bell 1997).

We calculated three sets of SDMs for *C. irregularis*: (i) current, A2a and B2a distribution projected by use of the entire set of species records (hereafter “entire distribution model”), (ii) current, A2a and B2a distribution projected by use of the western European species records and (iii) current, A2a and B2a distribution projected by use of the eastern European species records.

Dispersal scenarios

The logistic model outputs were processed in ArcGIS v10.1 (ESRI, Redlands, California) and transformed into binary maps only showing areas that are suitable for *C. irregularis* under current climate conditions (baseline niche). Thresholds were selected based on the ‘10th percentile training presence’ rule cutting off all raster cells with lower suitabilities than the 10th percentile of presence points used for model training (cf. Nazeri *et al.* 2012). This relatively conservative rule was chosen based on the assumption that the predominant majority of included presences used to train the model should indicate regions suitable for *C. irregularis*.

Subsequent binary outputs were used to develop two dispersal scenarios. In the first one, maximum dispersal is assumed thus all areas indicated as climatically suitable are and potentially will be occupied; the second one relies on the assumption of minimum dispersal. Here only regions documented to be actually occupied according to Turin *et al.* (2003a) and our occurrence data collected for modelling will be colonised in the future.

5.4 Results

5.4.1 Baseline niche and future climatically suitable conditions

In the western part of its distribution range, *C. irregularis* has been recorded in high as well as low altitudes (interquartile range: ~ 450 - 1,000m a.s.l.; median altitude: 709m a.s.l.). In contrast, the species was less often recorded from altitudes below 600m a.s.l. (interquartile range: ~ 600 - 1,100m a.s.l.; median altitude: 842m a.s.l.) in the eastern part of the range in the Carpathian mountain system. Figure 5.1 shows differences in the altitudinal distribution of the western and the eastern (= Carpathian) records. The differences in altitudinal distribution patterns of the western and the Carpathian group are consistent with two ancient phylogenetic lineages found in *C. irregularis* (Homburg *et al.* 2013b).

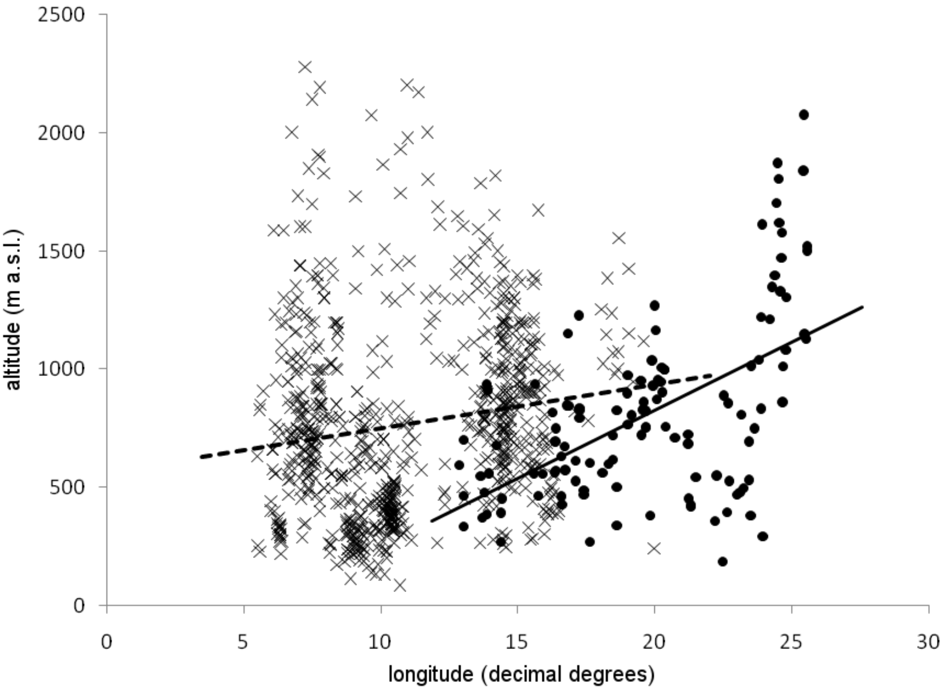

Figure 5.1. Altitudinal and longitudinal distribution of the western (crosses; dashed line) and the Carpathian (dots; black line) records of *Carabus irregularis*. Trendlines indicate differences in altitudinal distribution patterns of the two ESUs (p = 0.0003, slope comparison according to Sachs (1997).

High average training AUC values over all replicate runs ranging from 0.93 ± 0.002 for the entire distribution to 0.94 ± 0.002 for the western ESU and 0.98 ± 0.002 for the Carpathian ESU reflected the high accuracy of our models. Based on the selected threshold rule, included presence points were correctly classified (sensitivity) with at least 86% for the Carpathian ESU. Background points created by Maxent were correctly classified (specifity) with a minimum rate of 88% for the entire species (Table 5.1).

Table 5.1. Sensitivity (correctly classified presences) and specifity (correctly classified background points) values for all computed Maxent models .

	Sensitivity	Specifity
Entire species	0.878	0.883
Western ESU	0.870	0.908
Carpathian ESU	0.868	0.956

Figure 5.2 shows maps of the baseline niche (potential current distribution) and future distribution of *C. irregularis* projected for the overlap of both scenarios, and for the A2a and B2a scenarios separately. The SDMs for the western (Figure 5.2c) and the Carpathian ESU (Figure 5.2e) of *C. irregularis* differed markedly from each other, with suitable climate

conditions for the western ESU displayed mainly in the western part of the entire distribution model and the Carpathian ESU shown mainly in the eastern part. The entire distribution model (Figure 5.2a) showed characteristics of both, the western and the Carpathian ESU model.

For current climate conditions, the western ESU model assuming maximal dispersal revealed a disjunct distribution of habitats with suitable conditions for the occurrence of *C. irregularis* ranging from lowlands in Denmark in the North to the Dinaric Alps (Albania, Serbia) in the South and from parts of the Massif Central (France) in the West to the Balkan mountain range (Bulgaria) in the East. The maximal dispersal scenario for the Carpathian ESU showed suitable conditions in Norway and Sweden as well as in the western Alps and the Balkan mountain range. According to our models, the western Carpathians (Czech Republic, Slovakia) and the northern and eastern Carpathians (Romania, Ukraine) represented the main distribution of the Carpathian ESU.

All models (the entire as well as the western and the Carpathian ESU models) for future climate conditions showed a strong decline of the distribution range of *C. irregularis* by 2080s. For the entire species, the business-as-usual scenario (A2a) projected a contraction of climatically suitable areas to 13% of the potential current distribution; the more moderate B2a scenario predicted 23% of the potential current range to remain in the future. The overlap of both future scenarios amounted to 11% of the potential current distribution range (Table 5.2). From now until 2080s, scenario overlaps predicted a decline of areas with suitable climate conditions for the western ESU to 12% and for the Carpathian ESU to 5% of the current distribution range (Table 5.2). The entire distribution model (Figure 5.2a) and the western ESU model (Figure 5.2c) pointed to the complete loss of suitable habitats in the species' current northern and eastern distribution range under A2a and B2a future climate conditions. The B2a scenario showed slightly larger remaining suitable conditions at the northern edge of the Alps than the A2a scenario (Figure 5.2a,c). For the Carpathian ESU (Figure 5.2e) suitable future conditions were found for both A2a and B2a conditions only in very small areas in the southern and eastern Carpathians (Romania, Ukraine) as well as in the western Carpathians (Tatra mountains in Slovakia) and in the eastern Alps (Austria).

Table 5.2. Areas and proportions of projected ranges of *Carabus irregularis* under current and future climate conditions for maximal and minimal dispersal scenarios.

Model	max. dispersal range [km^2]	min. dispersal range [km^2]	proportional range max. dispersal [%]	proportional range min. dispersal [%]
Entire species				
Baseline niche (current distribution)	549,934	331,385	**100**	60
Future distribution (B2a)	125,501	102,962	23	19
Future distribution (A2a)	72,373	68,013	13	12
Future overlap (A2a+B2a)	62,803	59,892	11	11
Western ESU				
Baseline niche (current distribution)	426,132	252,158	**100**	59
Future distribution (B2a)	113,209	89,207	27	21
Future distribution (A2a)	54,453	49,054	13	12
Future overlap (A2a+B2a)	49,278	45,921	12	11
Carpathian ESU				
Baseline niche (current distribution)	198,307	64,409	**100**	32
Future distribution (B2a)	28,324	8,923	14	4
Future distribution (A2a)	13,248	4,138	7	2
Future overlap (A2a+B2a)	9,292	3,459	5	2

5.4.2 *Minimal dispersal*

Model outputs subjected to the minimal dispersal assumption exposed smaller baseline niches and projected future distributions than maximum dispersal: 60% of the climatically suitable areas projected by the entire maximal dispersal model lay within the borders of the documented actual distribution range (Table 5.2). For the western ESU, 59% of the projected suitable areas were located within the borders of the documented distribution range, and 32% of the potentially suitable conditions for the Carpathian ESU lay within the actual distribution range (Table 5.2). The entire and the western ESU models for minimal dispersal excluded lowlands of northern Germany and Denmark as well as parts of the Massif Central, the Carpathians, the Balkan mountain range and the western Alps (Austria, Switzerland). The models indicated suitable conditions in higher mountain regions of eastern France (Jura and Vosges Mountains), northern and eastern parts of the Alps, the western Balkan (Dinaric Alps) as well as Romania (Transylvanian Alps). Climatic suitability was also attributed to lower mountain regions of northwestern, Central and southern Germany (e.g. Teutoburg Forest, Weser Mountains, Harz, Black Forest, Bavarian Forest), and the Ardennes (France, Belgium, Luxembourg). The distribution of the Carpathian ESU showed suitable conditions in the eastern and western parts of the Alps under maximum dispersal but not under minimal dispersal conditions (Figure 5.2e,f), and is thus limited to small areas in Slovakia and Romania.

The predictions of the future distribution taking dispersal limitations into account showed a strong decline of reachable, suitable climate conditions by 2080s: The overlap of A2a and B2a scenarios expected that only 11% of the overall currently suitable climate conditions for entire species and western ESU will remain in the future; for the Carpathian ESU, only 2% of the currently suitable area will remain climatically suitable and reachable by minimal dispersal until 2080s (Table 5.2). Consequently, low dispersal of the species appeared to strongly enhance range retractions of *C. irregularis*.

5.5 Discussion

5.5.1 Distribution patterns of the two ESUs

SDMs have been used as a valuable tool for the detection and localisation of potentially suitable habitats for single species (e.g. Habel *et al.* 2010a; Taubmann *et al.* 2011). However, since different distribution patterns of subgroups within a species can result from intraspecific variability in habitat requirements, ecological divergences between subgroups need to be considered in species distribution modelling.

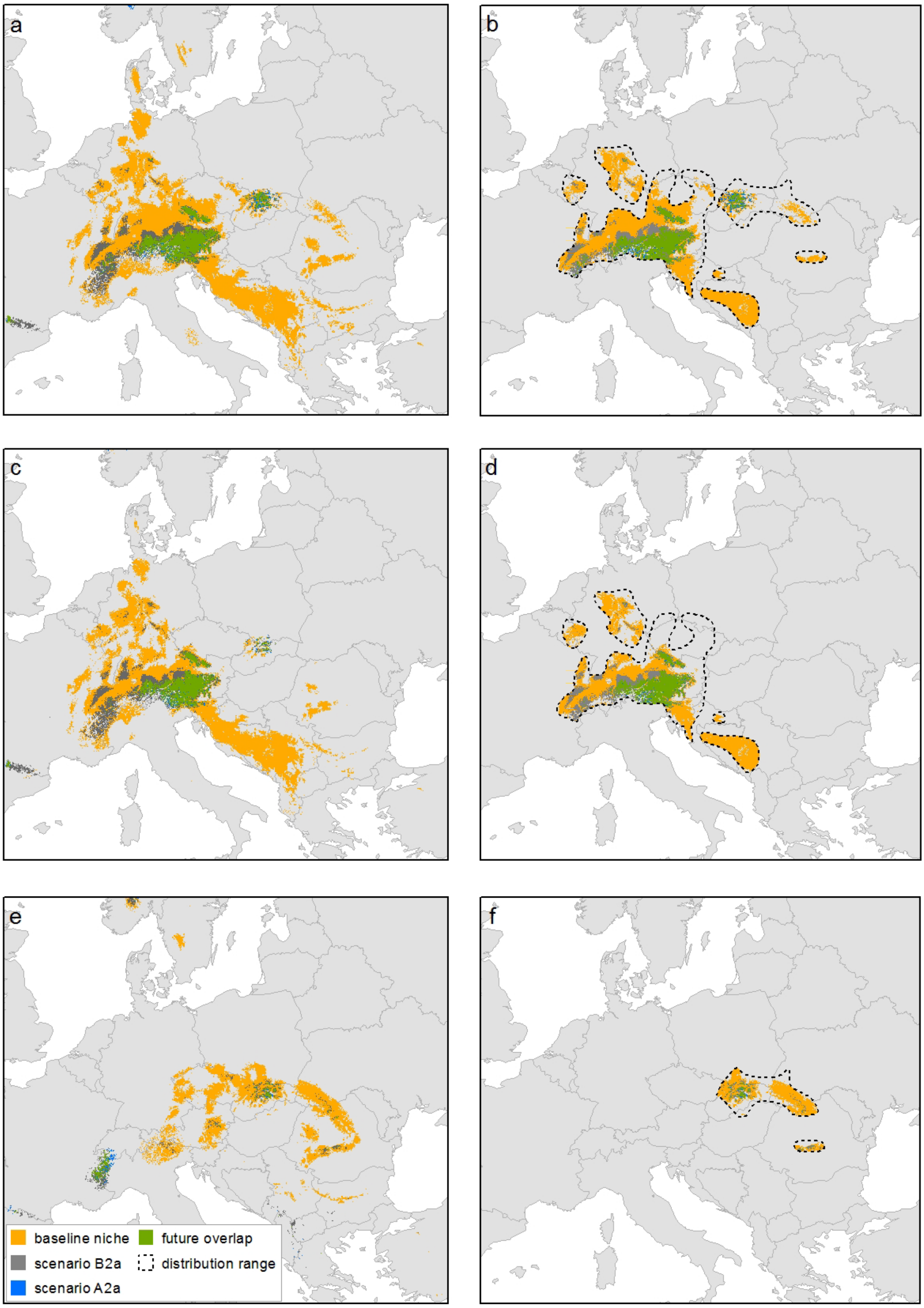

Figure 5.2. Current and future distributions of *Carabus irregularis* modelled with Maxent for (a, b) the entire distribution range of the species and for (c, d) the western and (e, f) the Carpathian ESU separately. Maximal dispersal models are shown the left column. Minimal dispersal models shown in the right column also indicate the area of documented distribution range of the study species (dashed line). Current distribution is shown as the baseline niche. Future distribution is shown for 2080s for A2a and B2a scenarios and for their overlap.

Our findings give point to a differentiation of ESUs detected for *C. irregularis* by Homburg *et al.* (2013b) prior to the development of SDMs. Even though our entire distribution model showed attributes of the two definite ESU models, clear differences between the potential current and future distribution ranges of the two ESUs can be inferred from the models handling the ESUs separately. Especially the potential effect of climate conditions on the Carpathian ESU appeared to be underrepresented in the entire distribution model. The ESUs might not only be characterised by genetic divergence but also by differences in the climatic niche also potentially represented by variation in the altitudinal distribution pattern of the two ESUs (Figure 5.1).

There are other studies revealing strong differences between habitat requirements within species: Tiger beetle as well as ground beetle species showed genetically divergent subgroups, which differed in terms of habitat association (e.g. *Cicindela puritana* and *Cicindela dorsalis*: Vogler *et al.* 1993b; Vogler and DeSalle 1994), for instance represented by differing altitudinal distribution patterns (e.g. in Pyrenean populations of Carabus auronitens: Colas 1969; Assmann 1995; Assmann and Weber 1997). Especially in ancient lineages, evolutionary processes tend to have resulted in high intraspecific ecological differentiation (Rasplus *et al.* 2001). The strict dependence on specific habitat or microhabitat conditions is likely to be a consequence of genetic differentiation, as habitat preference is assumed to be a heritable attribute in ground beetles (Thiele 1977). This aspect points out the importance of considering ecologically divergent units prior to species distribution modelling.

5.5.2 Climate change and dispersal ability

Our SDMs for *C. irregularis* showed only very small remaining areas of suitable climate conditions in relation to the species' recent distribution range. This may be due to the fact that mountain inhabiting species are mostly adapted to cool and moist habitats, which are expected to shrink immensely (Wilson *et al.* 2007; Settele *et al.* 2009; Dieker *et al.* 2011). Consequently mountain species are particularly sensitive to global warming.

In addition, the realised distribution of a species can be restricted by dispersal limitations and cannot be equatable with the distribution of suitable climate conditions (Engler and Guisan 2009; Kharouba *et al.* 2012; Schlaepfer *et al.* 2012). This seems to be true for many wingless mountainous beetles as revealed by a macroecological analysis by Baselga *et al.* (2012). Our two sets of dispersal scenarios for minimal and maximal dispersal based on SMD outputs showed severe differences in future distribution ranges. Since the minimal dispersal scenario (Figure 5.2b,d,f) predicted a stronger contraction of future distribution ranges of *C.*

irregularis than the (climate-only) maximal dispersal scenario (Figure 5.2a,c,e), low dispersal ability tends to strengthen the already high vulnerability of the cold-adapted mountain species against global change.

Hence the SDMs helped to estimate the extinction risk of the studied species in specific regions of its current distribution range by locating regions of potential habitat loss. Nevertheless, modelling results can be more useful to develop conservation strategies for particular species or groups of species with specific characteristics by identifying future suitable habitats (cf. Schwartz 2012). Assisted migration – which has been successfully implemented for other ground beetle species – can be used as conservation strategy to help species colonising suitable habitats which could not be reached self-initiatedly due to low dispersal.

5.5.3 Species conservation strategies

For *C. irregularis* and other low-dispersal species, assisted migration might be an appropriate method to enable long-term survival of a species in regions that are unconnected with recently colonised areas but will provide suitable climate conditions still in the future. Both, accidental introductions (e.g. Lindroth 1957; Vigna-Taglianti *et al.* 2000; Turin *et al.* 2003b; Bousquet 2012) as well as assisted migration (e.g. *Carabus olympiae*: Malausa and Drescher 1991) were shown to successfully found populations of a number of ground beetle species. From a conservation point of view, assisted migration using enclosures and providing thus comparable and controllable settings seems to be the measure of choice (*Poecilus lepidus* and *Olistopus rotundatus*: De Vries 1996; *Carabus auronitens*: Schwöppe *et al.* 1998). However, there are also unsuccessful attempts of assisted migrations (Assmann and Janssen 1999) introductions of *Carabus* species.

The results that rely on the maximal dispersal scenarios indicated that the western Alps recently hold climatically well-suitable habitats for *C. irregularis* that will persist over the future decades. During past dispersal processes, *C. irregularis* might not have been able to pass the crest of the Alps due to its low dispersal ability. Since there is no indication that the western Alps might not offer suitable habitats for *C. irregularis* and other *Platycarabus* species, areas emerging from our models as offering suitable environmental conditions might be taken into consideration as potential destinations of species introduction.

Our models concentrate on climatic parameters as predictors for the current and future distribution range. However, also other ecological factors such as the occurrence of forage species (prey), predators or competitors play an important role for the species survival. Other studies take this aspect into account by the parallel development of projections for host plants (Schweiger *et al.* 2008; Schweiger *et al.* 2012). In addition, the input of further parameters (e.g. land use or land cover) to models regarding species distribution patterns might be useful (Dieker *et al.* 2011). In the specific case of *C. irregularis,* the occurrence of snails, the only or at least preferred prey (cf. Turin *et al.* 2003b), has to be taken into account. Snails are obviously abundant on calcareous soils and seem to indicate a crucial requirement for species occurrence that must not be ignored in the preparation of conservation actions. Other studies have shown that biotic interactions have significant impact on SDM outputs (Linder *et al.* 2012; Pellissier *et al.* 2012). Thus incorporating relevant biotic information such as trophic interactions, for instance by consideration of distribution patterns and climate niches of interacting species, is useful for conservation management. Conservation strategies for a species' long-term survival such as assisted migration cannot solely base on SDMs including only climatic predictors, but certainly on a combination of model projections and more detailed habitat analyses.

Despite the fact that presence-only SDMs cannot project realised distributions, they provide useful indications of regions that might offer suitable environmental conditions in the future, which might be convenient destinations for assisted migration.

Nevertheless, effective species conservation should not be dedicated solely to the transfer of individuals of the species to so far uninhabited prospectively suitable habitats but also to the preservation and management of currently colonised areas that are likely to be affected by climate change (cf. Loss *et al.* 2011). An appropriate habitat management might allow an extended species survival also in regions for which a low probability of future species occurrence has been projected by SDMs. For *C. irregularis*, sustainable silvicultural land use activities might provide suitable micro-habitats in ravine forests facilitating the long-term survival of single populations.

5.6 Conclusions

Models projecting future species distribution ranges proved to be useful tools to prepare species conservation strategies such as assisted migration. Taking account of genetically divergent groups appears appropriate, since evolutionarily significant units might occupy different ecological and hence climatic niches. *C. irregularis* is a possible model species with species' traits such as cold-adaption or low dispersal abilities which increase its vulnerability to climate change.

5.7 Acknowledgements

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LIST OF PUBLICATIONS

Peer-reviewed journals

Homburg, K., Brandt, P., Drees, C. and T. Assmann (*submitted*). Evolutionarily significant units in a flightless ground beetle show different climate niches and high extinction risk due to global warming.

Homburg, K., Homburg, N., Schäfer, F., Schuldt, A. and T. Assmann (2013c). Carabids.org – A dynamic online database of ground beetle species traits (Coleoptera, Carabidae). Insect Conservation and Diversity. Early View. DOI: 10.1111/icad.12045

Homburg, K., Drees, C., Gossner, M.M., Rakosy, L., Vrezec, A. and T. Assmann (2013b). Multiple glacial refugia of the low-dispersal ground beetles *Carabus irregularis*: Molecular data support predictions of species distribution models. PLoS ONE 8(4): e61185. DOI: 10.1371/journal.pone.0061185

Homburg, K., Schuldt, A., Drees, C. and T. Assmann (2013a). Broad-scale geographic patterns in body size and hind wing development of western Palaearctic carabid beetles (Coleoptera: Carabidae). Ecography 36: 166-177. DOI: 10.1111/j.1600-0587.2012.07488.x

Drees, C., Brandmayr, P., Buse, J., Dieker, P., Gürlich, S., Habel, J., Harry, I., Härdtle, W., Matern, A., Meyer, H., Pizzolotto, R., Quante, M., **Schäfer, K.**, Schuldt, A., Taboada, A. and T. Assmann (2011). Poleward range expansion without a southern contraction in *Agonum viridicupreum* (Coleoptera: Carabidae). ZooKeys 100: 333-352.

Conference Contributions and Talks

Homburg, K., Drees, C. and T. Assmann: Linking phylogeography and global change biology: history and future of the cold-adapted ground beetle Carabus irregularis. 42th annual Meeting of the GfÖ. Sept 10 - Sept 14, 2012. Lüneburg, Germany. Talk.

Drees, C., Brandt, P., Dieker, P., **Homburg, K.,** Husemann, M. and T. Assmann: Genetic markers and climate niche models indicate glacial refugia for the flightless ground beetle Carabus sylvestris north of the Alps. 42th annual Meeting of the GfÖ. Sept 10 - Sept 14, 2012. Lüneburg, Germany. Talk.

Schäfer, K., Schuldt, A. and T. Assmann: Do carabids follow Bergmann's rule? – A macroecological study on ground beetles in the western Palaearctic (Coleoptera: Carabidae). The GfÖ 40th Anniversary Meeting. Aug 30 - Sept 3, 2010, Gießen, Germany. Poster.

Schuldt, A., Drees, C. Drescher, N., **Schäfer, K.** and T. Assmann: What determines subterranean ground beetle diversity in the West Palaearctic? - A macroecological approach using country-based distribution data (Coleoptera: Carabidae). 20th International Conference on Subterranean Biology, Aug 29 - Sep 3, 2010, Postojna, Slovenia. Talk.

Drescher, N., Loos, J., Dayan, T., Levanony, T., Schuldt, A., **Schäfer, K.** and T. Assmann: Unexpected rich terrestrial subterranean fauna in Israel: First results from the inventory of 13 caves. 20th International Conference on Subterranean Biology, Aug 29 - Sep 3, 2010, Postojna, Slovenia. Talk.

CURRICULUM VITAE

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STUDIUM

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Lüneburg, 20.12.2013

ERKLÄRUNG

Ich versichere, dass ich die eingereichte Dissertation “Effects of climate on diversity patterns in ground beetles: case studies in macroecology, phylogeography and global change biology“ selbstständig und ohne unerlaubte Hilfsmittel verfasst habe. Anderer als der von mir angegebenen Hilfsmittel und Schriften habe ich mich nicht bedient. Alle wörtlich oder sinngemäß anderen Schriften entnommenen Stellen habe ich kenntlich gemacht.

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Lüneburg, 20.12.2013