

Modelling the effects of global warming on the ground beetle (Coleoptera: Carabidae) fauna of beech forests in Bavaria, Germany

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Abstract. We studied the effects of global warming and rising temperatures on the ground beetle fauna of Bavarian beech forests using the space for time approach at two geographical scales. The first was a Bavarian-wide gradient of 50 plots in beech forests and the second a regional gradient in the Bavarian Forest in the mountains in eastern Bavaria consisting of 48 plots, which also included subalpine spruce forests. For purposes of validation, we used backdrop data from 413 additional plots all across Bavaria from a wide range of forest habitats. We found five species that would be favoured and six species that would be disadvantaged by rising temperatures in beech forests. For another five species the conditions within the gradient studied reach both their minimum and their maximum temperatures. As a consequence of increasing temperatures there will be winners and losers in these forests and the species composition of ground beetle communities will change. Approximately the same number of species is likely to profit as will be affected negatively. However, when considering the “global responsibility species” for Germany, the balance is negative. Species may react differently in different habitats and at different regional scales, which must be taken into consideration when applying the results.

INTRODUCTION

Although the scope of global warming and its regional effects are subject to some uncertainty, there has been a clear general increase in temperature over the last 100 years (IPCC, 2007). Temperatures are also increasing in central Europe and many parts of this region are becoming dryer, with an increase in precipitation in winter months and a change from snow to rain. It is also likely there will be an increase in the frequency of extreme events like drought. Among the consequences will be effects on ecosystem functions and biodiversity, since a loss of species (if not replaced by others) can alter ecosystem functioning and reduce biodiversity.

Cold-adapted species are expected to be the first to suffer and are already suffering (Müller-Kroehling et al., 2009). Little is known about the likely consequences of rising temperatures and corresponding changes in water availability on widespread species and habitats like European beech forests, the most prominent type of forest in central Europe. Geographically, Germany is situated in the center of the distribution of *Fagus sylvatica* and forests dominated by this species. In the absence of human inference it is likely that beech forests would cover large parts of central Europe, including most of Bavaria (Ellenberg, 1996). Currently, however, only about 36% of Bavaria is forested and only 10% of the forested area is covered by European beech (*Fagus sylvatica*) (Walentowski et al., 2004). Beech forests would dominate on almost all types of soil from acidic to base-rich (with a

high degree of base saturation), from hills to high mountain ranges. Beech forests are absent only in small areas of other habitats like ravine forests, bogs, floodplain forests, pure stands of Scots pine on sand dunes, or oak forests on pure clay soils.

Ground beetles (Carabidae including Cicindelidae) are one of the best studied insect groups worldwide. They occur worldwide wherever insects live, well above the timber line and in arctic habitats, in lightless caves as well as in deserts, along the seashore and in water-logged bogs. Standardized methods for sampling are available for soil-dwelling species, which make up the majority of this taxonomic group. Their taxonomy is well established. Müller-Kroehling (2009) has presented an overview of the ground beetles characteristic of Bavarian beech forests. About one tenth of the roughly 500 species living in Bavaria can live in beech forests (Müller-Kroehling, 2009), although only a few strongly prefer this type of forest (Walentowski et al., 2010).

Ground beetles are good indicators of palaeo-climate (De Lapouge, 1902; Atkinson et al., 1987; Coope, 1987; Ashworth, 1996; Kuzmina & Sher, 2006; Whitehouse, 2006; Zinovyev, 2011) and their habitat relations have been used to reconstruct ancient faunal habitats comparable to pollen diagrams (Lindroth, 1960; Coope, 1967, 1978; Lavoie, 2001). They are regarded as a model group for doing research on the effects of climate change (Müller-Motzfeld, 1982, 1995). There is a strong link between the occurrence of carabid species and climate along a steep gradient around the rim of the Mediterra-

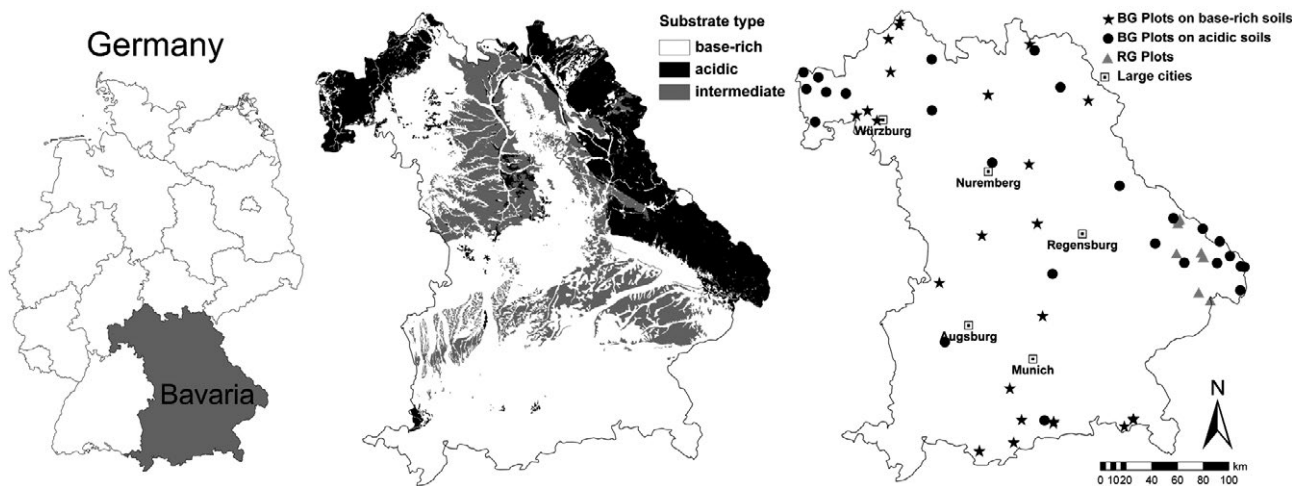


Fig. 1. Maps showing the location of Bavaria in Germany, the distribution of the different types of substrates in Bavaria and the location of study sites along the BG and RG gradients. Source of data for the type of substrate map: Bayerisches Landesamt für Umwelt und Bayerische Landesanstalt für Wald und Forstwirtschaft. (Borders of Germany and the federal states © Bundesamt für Kartographie und Geodäsie, Frankfurt/Main, used with permission.)

nean and in mountain ranges (Brandmayr et al., 1983). Several species occur only in mountain ranges and boreo-alpine habitats (e.g. Holdhaus, 1954; Hurka, 1980), although most species can be found in more than one altitudinal belt. The distribution of some more sedentary thermophilous species can be explained in terms of the history of the vegetation caused by historic shifts in climate (Becker, 1972), whereas others rapidly react to an increase in temperature (Horion, 1939).

For some species their developmental biology is directly linked to climatic factors (De Zordo, 1979; Butterfield, 1986, 1996; Refseth, 1986; Vainikainen et al., 1998), which is obligatorily biannual in some and facultatively so in others. Another adaptation is the altering of phenology, which is more “condensed” at high altitudes. This can be combined with higher levels of melanism and a relatively small body size, which both speed up development.

General trends in abundance and distribution of ground beetles have been recorded over long time spans in parts of Europe (e.g. Turin & Peters, 1986; Turin & den Boer, 1988). However, it is difficult to unravel the different interacting effects of changes in climate, habitat management and changing trophic conditions.

Because of the excellent knowledge of ground beetle distribution and ecology we selected this group for this climate change-related study.

The questions we will address in this paper, with particular reference to Bavaria, are:

- How do ground beetles living in beech forests behave in a temperature gradient? (i.e. What is their reaction to changing temperature?)
- In what way will the expected temperature increase affect and alter the fauna of beech forest habitats?
- Do the distributions of species in regional (whole Bavaria) and local gradients (from the foothills to the top of the Bavarian Forest mountain range) differ?

- What conclusions should be drawn regarding practical measures? Are there hints as to what forest managers can do about the effects found?

METHODS

General approach and sampling design

Due to a lack of standardized historical ground beetle data we used the “space for time” approach in our study. In this approach, a temperature gradient is used as a surrogate for a change in temperature in situ over time. This is a common approach in situations where a true time series with data of comparable quality is unavailable, which is most often the case for invertebrate species. We discuss the limitations and reasoning of this approach in the discussion.

We worked at two different geographic levels (Fig. 1):

- a Bavarian-wide data set (BG) with an even distribution of 50 plots along a temperature gradient, which is based on a subset of 140 vegetation plots (Jantsch et al., in press). The 50 faunal plots selected from this pool are representative of the regional temperature and distribution of different types of soil.
- a regional gradient (RG) in the Bavarian Forest mountain range in SE Bavaria (48 plots, Blaschke et al., 2011).

For the Bavarian-wide gradient (BG; Table 1) 25 plots were selected on acidic soils and 25 on base-rich soils. All plots are slightly south facing, have a continuous forest history and a beech cover of at least 50%. Beech forests are a rather homogeneous habitat, and since we wanted to isolate the possible effects of climate change, we tried to minimize the effect of all other factors like canopy closure, large age differences etc. by selecting sampling sites in closed-canopy, medium-aged, strongly beech dominated plots with at least a minimal quantity of deadwood. Apart from classifying soils as acidic or base-rich as a basis for stratification, we also classified the type of humus and the rockiness of the sites. However, we found these variables to be of little explanatory value for the questions asked, at least for beech forests, and hence will not refer to these parameters.

For the regional gradient (RG; Table 1), from the colline level to the subalpine crest of the Bavarian Forest mountains, six plots each in eight strictly protected forest reserves (“natural forest reservations” with non-intervention regime) were sampled. The plots represent the different types of forest in the

TABLE 1. Data sets generated for and used in this study.

Project	Bavarian temperature gradient	Regional Bavarian Forest Mts. gradient	“All forests” (Backdrop)	“All beech” (BG and beech forests from AF)
Abbreviation of dataset	BG	RG	AF	AB
Number of plots	50	48	413	120
Number of beech forest plots	50	33	70	120
Distribution	Bavaria	Bavarian Forest Mts.	Bavaria	Bavaria
Study years	2010	2009	1999–2010	1999–2010

region, including 33 beech forests (Luzulo- and Galio-Fagetum) but also three Tilio-Acerion ravine forests, nine subalpine spruce forests and three conifer plantations on beech forest sites. For a more detailed description of this data set refer to Blaschke et al. (2011).

Sampling was done in 2009 (RG) and 2010 (BG). Ground beetles were sampled at each plot using six 7 × 7 cm plastic cups, dug in flush to the surface and filled to two thirds with a 10% solution of sodium benzoate of neutral pH. Cups were spaced 5 m apart in a line in the center of the study plot and emptied about every three weeks. The traps were active between the end of April and the beginning of October, excluding a “summer break” in July and August. This standard program allows for the trapping of spring breeding and autumn breeding species. For the regional gradient, a slight modification of the trap was used in order to obtain data compatible with that gathered by the National Park in their gradient project in which a single large 0.5 liter trap was used. We complemented these traps with three of the traps described above giving an equivalent of six small traps in terms of the circumferences of the traps per plot. The drawbacks of the large traps were a much larger by-catch of vertebrates (shrews, voles, mice and amphibians), greater disturbance of soil when installing the trap into often rocky or shallow soils and greater danger of the trap being pushed out of the soil by a rise in the water table at wetter sites. This should be noted and will be discussed elsewhere.

Identification of all the carabids to species was performed by the first author using Müller-Motzfeld (2006). All voucher material is stored at LWF.

Data sets used

We used the two gradient datasets and further data for validation (Table 1). Additionally we used data from 413 plots in Bavarian forests or naturally open (bogs, scree slopes, sand dunes) habitats, which were gathered using the same field methods since 1999, as backdrop information. This is a compilation of carabid data from forests and associated habitats occurring at all the altitudes covered by forest and in all types of stands including plantation forests. Out of these, we also used the data from 70 additional beech forests along with the BG data giving a combined total of 120 beech forest stands.

In this paper, we focus on the results of the Bavarian temperature gradient (BG) and use the regional gradient data (RG) and backdrop datasets (AF and AB) only to compare and test the validity and robustness of the model predictions for the species found in beech forests. A more in-depth analysis of the results for other habitats studied in the Bavarian forest regional project, including habitats other than beech forests, will be presented elsewhere.

Climatic parameters for our plots were interpolated from daily measurements from climate stations of the German Meteorological Service collected over a period of 30 years from 1971 to 2000 (Hera et al., 2012).

For the expected future climate we used the WETTREG B1 scenario for the time period 2071 to 2100 (Spekat et al., 2007).

An increase of 1.8 Kelvin (K) in the annual average temperature is assumed by WETTREG B1 until 2100 and so it can be regarded as a moderate warming scenario. Since our gradient was established on the basis of the average annual temperature, this is the sole variable we analyzed. We also conducted tests with the annual precipitation, but since it is strongly correlated with temperature, we chose to omit the results for this factor.

Data analysis

Generalized linear models for mean annual temperature

We calculated a sigmoidal model and a unimodal generalized linear model (GLM) for all species. For the sigmoidal models we used a t-test to identify species with a significant different mean annual temperature in plots in which the species was present and absent, respectively. The final selection of the model is based on the significance of the regression coefficients and the explained deviance. Our strategy in model selection was parsimonious, so a more complex model was selected only if it constituted a substantially better description than the simpler model of the behaviour of a species.

The upper and lower bound of the preferred temperature range is the intersection of the modelled probability of occurrence with the priori probability of occurrence of the selected species (Fischer, 1994). In the case of unimodal (optimum) models, the lower and upper bound of the ecological amplitude can be determined. In the case of sigmoidal models, i.e. for species with an ecological optimum outside the observed temperature range, only the upper or lower bound can be identified.

All analyses were performed using R package (R Development Core Team, 2012). The maptools-package (Lewin-Koh et al., 2012) was used to process raster files. We used a significance level of 95% for all decisions.

Procedure used to model future distribution

The result of the GLM was used to develop habitat suitability maps for the different species under the recent climate 1971–2000 and the expected future climate in 2071–2100 using the dismo-package (Hijmans et al., 2012). With the calculated logit-transformed priori probability, the threshold for the potential occurrence is:

$$threshold = \frac{\log\left(\frac{p_i}{p_n}\right)}{1 - \left(\frac{p_i}{p_n}\right)}$$

p_i = number of presences, p_n = number of plots

The dark grey coloured areas in our habitat suitability maps show where the conditional probability was higher than the a priori probability.

The accuracy of the model was assessed using the AUC (area under the receiver operating curve) value, which was calculated using the PresenceAbsence-package (Freeman & Moisen, 2008). Best models have an AUC near to 1, whereas random models have an AUC near 0.5. We considered only species with an AUC ≥ 0.80 for modelling the species distribution.

Species found in at least two locations were considered for the analyses. Only species with a significant temperature rela-

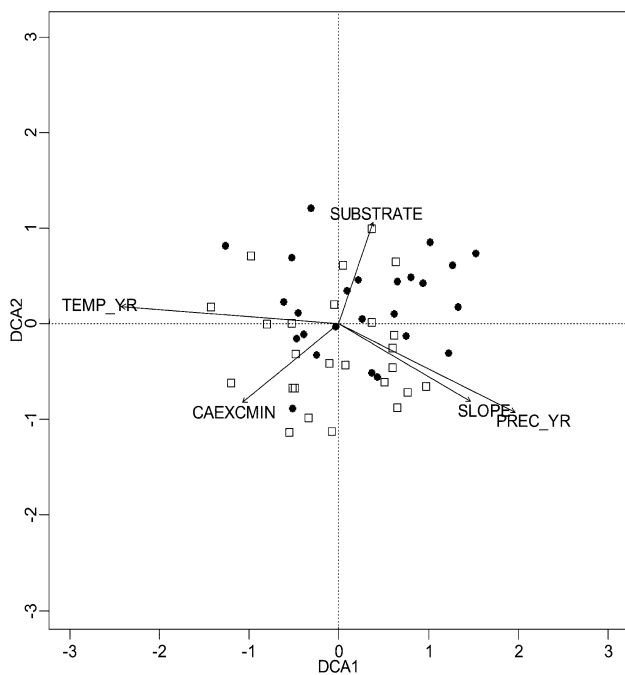


Fig. 2. DCA ordination of the ground beetle data in the BG data set (Eigenvalues: 1: 0.3623, 2: 0.2806, 3: 0.2022); black dots: plots on acidic soils, white squares: plots on base-rich soils. TEMP_YR – annual mean air temperature; Substrate: classification of the substrate (acidic or base-rich), Caexcmn – exchangeable Calcium stock in the mineral soil; Slope – slope in degrees; Prec_Yr – annual precipitation.

tion in beech forests are relevant for this study and are presented in the results section. Since all temperature relations can be assumed to be shaped like optimum curves in nature, sigmoidal curves are indeed part of optimum curves limited and truncated by the length of the gradient. If both the optimum and sigmoidal models are significant, we selected the model with the higher explained deviance. All species with no optimum model in beech forests were then tested in the groups “warm adapted” or “cold adapted”.

Map model validation

To validate the habitat suitability maps based on the climate preferences of the species, we used distributional data for Bavaria in the online atlas provided by Lorenz (2004a). These grid maps use data up to the present, including historical records if no recent records are available for a particular grid. For the species analyzed, there were no solely historical records. When comparing the modelled maps and the grid maps of the actual distribution, the effect of the grid and questions of scale must be taken into consideration.

TABLE 2. Species with an optimum (unimodal) temperature relation in beech forests, indicating a preference for intermediate temperatures.

Ground beetle species	AUC – ecological amplitude	Left inflection point	Optimum	Right inflection point	Significance of regression coefficients	Explained deviance	Frequency	Significant difference box plots	Interrelation temperature and substrate	Data set
<i>Carabus linnei</i>	0.88; 3.9–6.7	4.3	5.3	6.3	0.0172	0.35	18	<0.0001	–	AB
<i>Carabus hortensis</i>	0.58; 6.2–8.5	6.3	7.3	8.3	0.0189	0.11	25	0.0290	–	AB
<i>Molops elatus</i>	0.68; 6.8–8.6	6.7	7.7	8.7	0.0093	0.18	28	<0.0001	–	AB
<i>Carabus nemoralis</i>	0.67; 6.8–9.3	6.5	8.0	9.5	0.0372	0.13	37	<0.0001	–	AB
<i>Abax parallelus</i>	0.89; 7.2–9.7	7.7	8.5	9.3	0.0245	0.53	16	<0.0001	0.0417	BG

For the red data book of endangered species, the Bavarian list was used (Lorenz et al., 2004b), for the list of species of high global responsibility Müller-Motzfeld et al. (2004). These are species with a central European distribution and hence their protection is mainly the responsibility of central European countries.

RESULTS

Influence of non-climatic factors

A total of 51 species and 3673 individuals were recorded in the Bavarian-wide (BG) and 41 species and 6534 individuals in the regional (RG) plots.

Very few of the species found are endangered according to the Bavarian Red Data Book (Lorenz, 2004b). The rare *Carabus intricatus* and *Carabus arvensis*, which are both “endangered” in Bavaria (category 3 in the RDB) and the “strongly endangered” (cat. 2) *Trechus alpicola* were found as singletons in one plot each.

34 of the species recorded in the BG dataset were common enough for their occurrence in relation to climate and substrate to be statistically analyzed. The results for all species showing a correlation to temperature or substrate are listed in Appendix 1.

A large overlap of beech forests on acidic and base-rich soils is evident in the DCA ordination (Fig. 2).

For four species, there is a significant interrelation between climate and substrate. Two of these prefer base-rich substrates (*Abax parallelus*, *Carabus coriaceus*), while two others (*Pterostichus pumilio* and *P. unctulatus*) are specialists of acidic soils. The latter are known to be dwellers of well-developed litter layers (moder, raw humus types; Trautner, 1992), while the former are species preferring broadleaved forests at low altitudes (Riecken & Rath, 1996; Abmann, 1999).

Only one species, *Molops elatus*, is entirely restricted to one of the two substrates, occurring only on base-rich soils, which is in accordance with the literature (Müller-Kroehling, 2013). However, in some parts of its range, e.g. southwestern Germany, this species is apparently less restricted in this regard, as it is recorded in acidic mixed mountain forests (e.g. Trautner et al., 1998).

Temperature-relationships of species

Intermediate species

All species with a significant optimum model of their temperature relations in beech forests are listed in Table 2. These species display both an upper and a lower tem-

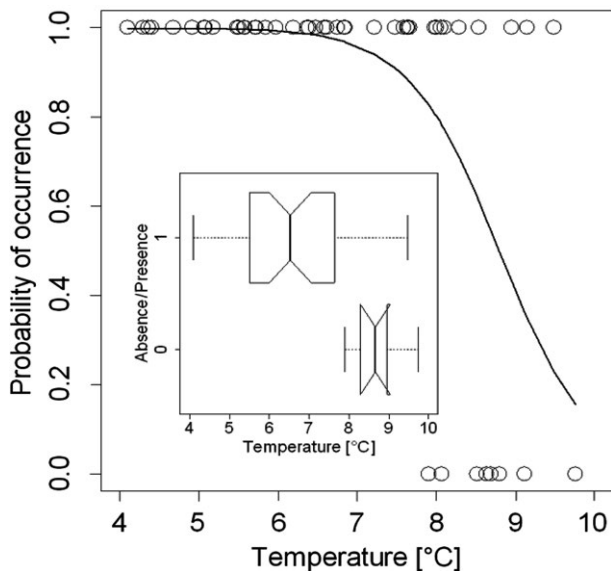


Fig. 3. Relationship between the probability of occurrence of *Pterostichus burmeisteri* and temperature in the BG data set.

perature bounds to their occurrence in Bavarian beech forests.

These five species show a temperature relation in the AB or BG dataset with both a left and right inflection point, meaning a temperature optimum which lies within the gradient studied, and a higher “explained deviation” for the unimodal model than for the sigmoidal model. This relationship is strongest for most of these species in the AB dataset, indicating that this broader dataset is even better suited to describe this relationship than BG. This group contains species that will benefit to some degree from rising temperatures in beech forests. However, of these five species, four have temperature amplitudes that will allow them to prosper under slightly raised temperatures in beech forests. *Carabus linnei* is restricted to the mountains of eastern Bavaria and the Alps will be affected in the near future at least in parts of Bavaria. In the BG dataset, it is a cold-adapted species with an optimum model relation only in the larger AB dataset. This species could arguably be placed in the next group.

There are three species (*C. linnei*, *M. elatus*, *A. parallelus*) in this group that are of global responsibility (Müller-Motzfeld et al., 2004).

Cold-adapted (mountain range) species

For six species (Table 3) the fit of a sigmoidal model with a right but no left inflection point is significant, meaning that there is an upper temperature limit to their distribution in the gradient studied and are thus “cold-adapted”. For some of these species the fit of the optimum curve is significant, but weaker (see Appendix 1).

All these species show the same trend in the backdrop dataset of “all beech forests” (AB in Table 1). For *Calathus micropterus*, *Pterostichus pumilio* and *P. unctulatus* the explained deviance and significance values are slightly higher in that dataset. *Cychrus attenuatus* is another species belonging to this group, albeit with a significant value only for the backdrop data set and a barely non-significant value for the BG gradient.

All these species have been classified as “mountain range” species in the literature (i.e. Horion, 1941) because they are not recorded as occurring at low altitudes in Germany. However, *Calathus micropterus* is also known to occur in lowland Pine forests (see below), but this differs regionally.

The range of *Carabus auronitens* does extend into the Westphalian lowlands and the Forêt de Soignes region in Belgium, but it still can be said to have an overall “mountain range” distribution, which is most certainly true for Bavaria (see maps in Lorenz, 2004a).

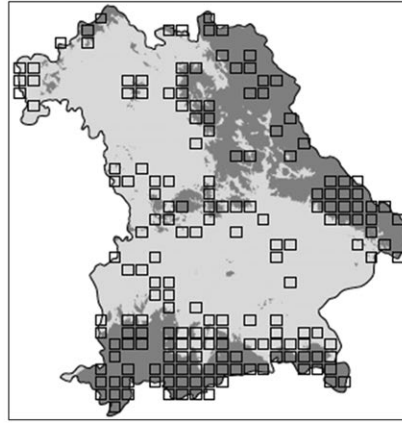
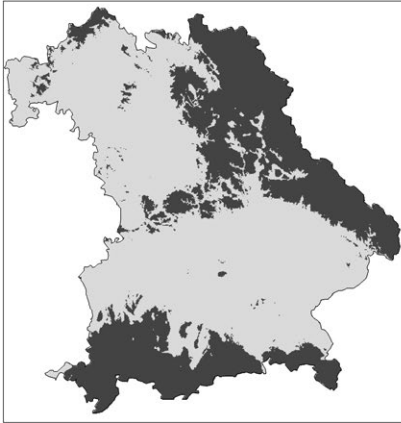
Some of these species also exhibit an upper limit to their distributions in beech forests only regionally, as in the RG dataset. One such species is *Abax ovalis*, a species with a two-year developmental cycle (Löser, 1972; Lampe, 1975). In the Bavarian-wide beech forest data (BG, AB) no temperature relation is evident.

Pterostichus burmeisteri is the dominant species in beech forests (Müller-Kroehling 2009; Walentowski et al., 2010), accounting for 35.5% of the total catch and occurring in 84% of the BG plots. Its association with a mountain range climate manifests itself in the fact that it is a species with an obligatory biannual life cycle and mountain range distribution (Weidemann, 1971). In our BG data set, this species declines with increasing temperature above a certain threshold (Fig. 3). However, of the tabulated mountain range species, it has the highest inflection point, indicating that it may be able to survive in a warmer climate to some degree.

TABLE 3. Species with an upper limit to their sigmoidal temperature relation in beech forests, indicating a preference for cold conditions.

Ground beetle species	AUC – upper ecological bound	Right inflection point	Significance of regression coefficients	Explained deviance	Frequency	Significant difference boxplots	Interrelation temperature and substrate	Data set
<i>Calathus micropterus</i>	0.95; <5.4	4.5	0.0308	0.52	4	0.0009	0.1389	BG
<i>Pterostichus unctulatus</i>	0.86; <6.1	4.7	0.0068	0.28	8	<0.0001	0.0306	BG
<i>Pterostichus pumilio</i>	0.82; <6.3	4.9	0.0044	0.25	10	0.0012	0.0387	BG
<i>Carabus auronitens</i>	0.81; <6.4	5.1	0.0043	0.21	12	0.0003	0.4620	BG
<i>Cychrus attenuatus</i>	0.78; <6.9	6.3	<0.0001	0.15	44	<0.0001	–	AB
<i>Pterostichus burmeisteri</i>	0.91; <7.9	8.8	0.0069	0.40	42	<0.0001	0.0806	BG

Pterostichus burmeisteri 1971-2000



Pterostichus burmeisteri 2071-2100

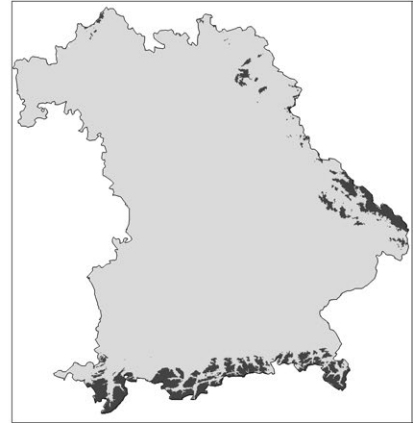


Fig. 4. Distributions of *Pterostichus burmeisteri* in beech forests predicted by a model based on present and future climate and BG data (left and right) and its current distribution in Bavaria according to Lorenz, 2004a (basis: 12×12 km grid; center).

Fig. 4 shows the modelled potential distribution based on the temperature preferences derived from the temperature data for Bavaria over the period 1971 to 2000 (left), the same for the expected temperature during 2071–2100 (right), and the recent distribution on a 12×12 km grid of *Pterostichus burmeisteri* (center). Bearing in mind the fundamental differences in the maps, and the fact that the modelling is based solely on temperature, the fit is reasonably good and identifies even the smaller mid-altitude mountain ranges where this species lives, including the Franconian Keuper mountains of the Frankenhöhe and northern Steigerwald.

The model of the future distribution is plausible since the modelled present distribution is situated, to a large extent, within the actual (measured) present distribution and because the models are based on the same temperature relationships. With a change in temperature, the future distribution will be dramatically reduced to a fraction of the original potential distribution in beech forests. In northern Bavaria, the species will be restricted to the high Rhön and Fichtelgebirge mountains. In the Bavarian Forest mountain range the species will become a dweller of high altitudes. Even in the Alps it will all but vanish from the foothills and only persist at high altitudes. It is unlikely to gain terrain at high altitudes, since living conditions there are limited orographically and by soil development.

The results for this species using the BG data set and the 120 beech forests in the AB data set produce curves

of a similar direction and shape. In Bavaria as a whole its distribution indicates it is not a species that prefers the warmest regions and habitats. This species has clear limits to its vertical distribution in the mountain range and does not occur at low altitudes. The RG data set in contrast indicates a curve ascending with increase in temperature with a left inflection point at 4.9°C . In this gradient, the species was present in every single beech (and ravine) plot but one, and largely absent from the subalpine spruce forests. Hence, in the continental and precipitation rich, mid-altitude mountains in this region, it is not a species that prefers the coldest sites.

All the other species are not linked as closely to beech forests. While the temperature relationship holds true for these species in beech forests, when one looks at “all forests” (the AF data set), including natural and artificial conifer stands, the results change for some of the species mentioned:

(1) *Carabus auronitens*, *Pterostichus burmeisteri* and *Cychrus attenuatus* in this dataset have optimum curve temperature distributions. This means that in other types of forest they also occur at the colder end of the gradient studied, possibly in subalpine coniferous forests.

(2) *Pterostichus unctulatus* and *Calathus micropterus* distributions do not have significant relationships with temperature when data for “all forests” are considered. *C. micropterus* prefers conifer stands and ranges from low-altitude pine forests to high-altitude spruce forests (Müller-Kroehling et al., 2009), while in Italy it is a spe-

TABLE 4. Species with a lower limit to their sigmoidal temperature relation in beech forests, indicating they are thermophilous species.

Ground beetle species	AUC – ecological bound	Left inflection point	Significance of regression coefficients	Explained deviance	Frequency	Significant difference boxplots	Interrelation temperature and substrate	Data set
<i>Carabus coriaceus</i>	0.76; >7.2	8.6	0.0102	0.14	14	0.0061	0.0356	BG
<i>Harpalus latus</i>	0.85; >7.6	8.8	0.0059	0.29	9	<0.0001	0.8808	BG
<i>Limodromus assimilis</i>	0.87; >7.8	9.5	0.0042	0.24	7	0.0003	–	AB
<i>Pterostichus strenuus</i>	0.97; >8.1	9.8	0.0302	0.37	2	0.0064	–	AB
<i>Notiophilus rufipes</i>	0.92; > 8.2	9.1	0.0214	0.44	5	0.0011	0.3142	BG

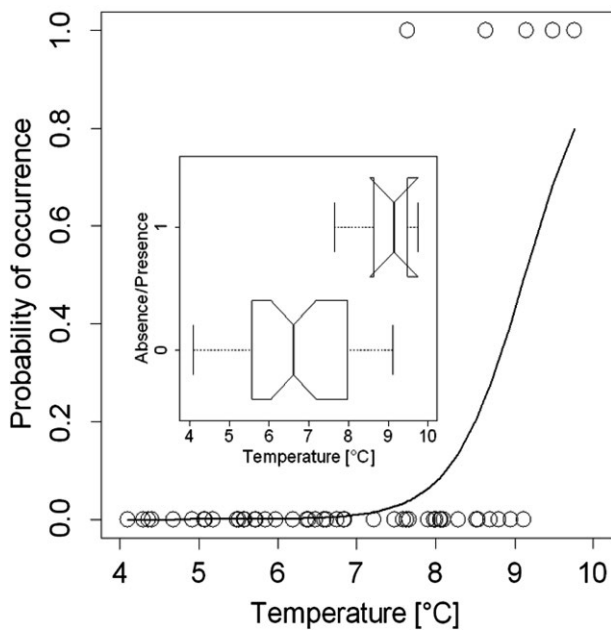


Fig. 5. Relationship between the probability of occurrence of *N. rufipes* and temperature in the BG data set.

cies typical of subalpine spruce forests of the class Vaccinio-Piceetea in the Dolomites (Brandmayr & Zetto Brandmayr, 1988). *P. unctulatus* prefers areas with a well-developed litter layer and often occurs in admixed coniferous forests, also on wet soils (Trautner, 1992; Müller-Kroehling, 2013).

Germany has a particular responsibility (Müller-Motzfeld et al., 2004) to protect three species in this group (*P. unctulatus*, *C. auronitens* and *P. burmeisteri*).

Thermophilous species

The distribution of a third group of species is positively associated with the temperature recorded in beech forests and hence will benefit from the projected temperature increase based on their current living conditions in beech forests (Table 4).

Again, none of these species is restricted to beech forests, although some of them occur frequently in this habitat (Müller-Kroehling, 2009). All of them inhabit a wide range of different types of forest including oak-hornbeam forests, floodplain forests, lowland Scots pine plantations etc., and most of them are widely distributed. Although beech forests are mentioned as a particular habitat of *Notiophilus rufipes* (Müller-Motzfeld, 2006), it is not in any way restricted to this habitat or even shows a strong preference for it (Koch, 1989).

Two of the species, *Notiophilus rufipes* (Table 4) and *Leistus rufomarginatus*, which is not listed in Table 4 because it was recorded at only a few locations, are currently geographically limited in their distribution to Bavaria and appear to be in the process of spreading in Europe (e.g. Rushton et al., 1996) as well as in Bavaria. Both show similar distributions in Bavaria (Lorenz, 2004a) in that they occur in the warmest regions such as the extreme northwest and southeast, most likely because of their thermophily.

Kittel (1874) records *N. rufipes* only from Passau where it possibly entered Bavaria by spreading along the warm slopes of the River Danube valley from Linz in Austria. He also mentions the species occurring in Darmstadt in southern Hesse, and thus at two opposite ends of Bavaria, both of which are among the warmest parts of Bavaria. Horion (1941) mentions this species occurring in “Aschaffenburg” on the Bavarian side of the border with Hesse (Horion, 1941). From there it seems to have spread over the following decades into all of northwestern Bavaria where climatic conditions are favourable. Hence, *N. rufipes* is still limited to the warmest regions of Bavaria but is expanding its range. It is able to fly (Turin, 2000). The distribution of *N. rufipes* is western and southern Europe up to Asia Minor. It is widespread in Italian beech forests (Brandmayr & Pizzolotto, 1988; Comandini & Vigna Taglianti, 1990; Vigna Taglianti & De Felici, 1994). According to Müller-Motzfeld (2006) it prefers beech forests on soils with a neutral pH (and thus base-rich soils) in Germany, although this is not reflected

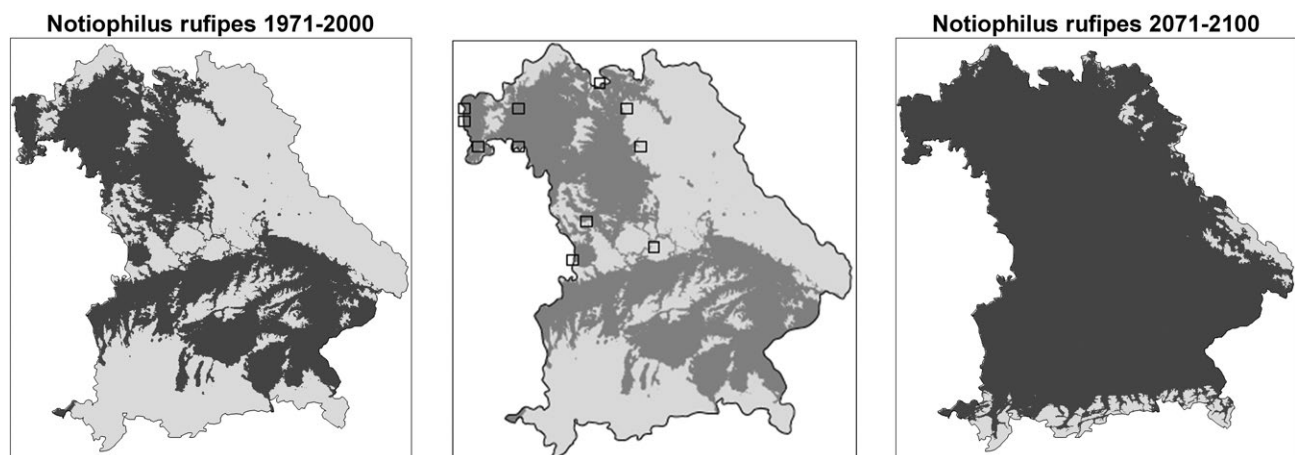


Fig. 6. Distributions of *Notiophilus rufipes* in beech forests predicted by the model based on present and future climates and BG data (left and right) and its current distribution based on atlas data (center) for validation purposes (for further explanations see Fig. 4).

in the BG data set. The temperature-occurrence relation (Fig. 5) is strong and positive.

The geographic model (Fig. 6) provides a rather good fit for northern Bavaria, considering this species is still spreading. It seems that the beetle has not yet been able to colonize all habitats that are climatically favourable in southern Bavaria (south of the Danube). The reasons could be: (1) not enough time has elapsed since climatic conditions became favourable for this thermophilous species and the southern Bavarian part of the modelled suitable range is not quite as warm as the northwestern Bavarian part. (2) Since this species prefers broadleaved forests according to the literature, the dominant conifer plantations in southern Bavaria, often pure stands, might have additionally hampered its spread. Thus, it is reasonable to assume that this species will indeed spread to large parts of the Bavarian landscape where suitable habitats are available and within reach. With the exception of the highest altitudes, following an increase in temperature this species might colonize beech forest all over Bavaria (Fig. 6).

In this group there are no species for which Germany is globally responsible for their protection (Müller-Motzfeld et al., 2004).

DISCUSSION

Beech forest-dwellers will react to climate change differently

Species will react differently to a changing temperature regime, so we tested the effects at the species level. Six species have optimum temperature relations in Bavarian beech forests in terms of both their upper and a lower temperature limits. A further six species prefer the colder and another five the warmer parts of Bavarian beech forests. Only one of these species is largely restricted to beech forests (Walentowski et al., 2010). For the others, their reaction to warmer temperatures might be different in other habitats. For the cold-preferring species, habitats at high altitudes, i.e. in subalpine forests or beyond the timber line could provide suitable living conditions in those regions where beech does not form the highest vegetation belt. In regions where there are no high altitude refuges, cold-preferring species might find a climate refuge on north-facing slopes and in cool ravines. If they can utilize such habitats, they might be able to survive there even in regions where beech forests might no longer be suitable habitats.

On the other hand, for those species that prefer warmer areas, the (positive) effects of warmer temperatures might be even stronger in less shady and cool habitats than beech forests.

This must be considered when predicting future distributions because our results are only valid for beech forests.

Regionality of gradients is reflected in the results

Systematically sampled data on the historical distribution of species are rare and are a prerequisite of a true time series. There are only a few possible ways of over-

coming this problem. The “space for time” approach used in this study (RG, BG) is one of them. Clearly, it has disadvantages when compared with a true time series. This arises since no species is bound or regulated by just one factor and all regions differ by a multitude of factors or unique combinations of factors. Adding to the complexity, most regions have distinct faunal elements that are missing in other regions due to distributional boundaries, which need not be climate-driven. Species preferences and ecological requirements shift between regions due to the “law of regionally stenoeccious behaviour” (Kühnelt, 1943).

Data gathered in all parts of Bavaria will provide a better basis for predicting the effects climate change will have on the beetles living in Bavarian beech forests than data gathered only along a regional gradient.

Comparison of the BG and RG gradients, application of backdrop data (AF and AB) and distribution maps reveal that:

- data collected at a smaller scale (like RG) will provide more reliable results for predictions at that scale than data collected at a larger scale (like BG) (and vice versa);
- the results of a regional gradient analysis should therefore only be applied at that particular regional scale;
- data gathered in one habitat should only be applied with caution and restraint to other habitats, if at all. This is true especially if the species is not restricted to or specialist of the habitat studied

We used annual mean air temperature as the relevant factor for the reaction of species to climate change. It could be argued that precipitation is just as likely to be as important as temperature. Both factors are highly collinear, and more so at the regional than at the Bavarian-wide scale. Although for some species there is a strong association with precipitation reflected in the results, both factors combine to determine the humidity regime, which is the most likely factor influencing the reaction of the majority of species of carabids to climate.

To obtain a better separation of the effects of temperature and precipitation, results from “cool and dry” and “warm and wet” plots, which do not occur in Bavarian beech forests, would have to be included from outside Bavaria. For the scope of this study, temperature is used as a proxy of “climate” because temperature and precipitation are so highly correlated.

In particular, the reaction of species in one habitat (here: beech forest) may not be the same in other habitats, due to habitat-specific differences in microclimate and other reasons. As we demonstrated by using the whole Bavarian backdrop data, some species (like *Calathus micropterus*) are linked to the coldest stands within the beech forests studied, but live in other habitats at lower altitudes. It would be misleading to include these species in a calculation of the share of beech forest species endangered by climate change.

Both gradients have shortcomings. In the Bavarian-wide dataset, there were only a few beech forests with a high amount of deadwood, so that the habitat prerequisite of sufficient deadwood was at least for some species (e.g.

Carabus irregularis, Müller-Kroehling, 2009) often not met (e.g., only four to five plots with deadwood of more than 10 m³ per hectare). This factor, however, was not limiting in the regional dataset as it consisted of forest reserves with comparatively high amounts of dead wood. On the other hand, the results for this gradient suffered from the fact that there were no strict requirements for the beech habitat properties of the plots. On the upside, including subalpine species in that gradient takes into consideration some highly sensitive subalpine and alpine habitats that will experience or are currently experiencing, severe stress and loss of territory as a result of increasing temperature (Sømme et al., 1993). Therefore it is likely that natural spruce forests will be adversely affected (Müller-Kroehling et al., 2009).

We validated the temperature relation by comparing the measured distributions with the modelled potential distributions based on present-day temperatures. Since the habitat suitability models only show the potential distribution in beech forests, all grids representing occurrences in other habitats are not directly relevant. However, information about the habitats represented by the grid cells in the distribution maps is not available. On the other hand, beech forests are not present in all grid cells, so that the actual distribution could not be compared directly with the modelled distribution for those species preferring or restricted to beech forests. Overall, a direct comparison of the modelled and measured distributions must be done with caution, bearing in mind the limitations of the data. This validation by comparison is, however, a necessary step.

Changing habitat composition will alter beech forest habitats

The trends reported here for ground beetles are similar to those reported for plants (Jantsch et al., in press).

Substrate is an important habitat factor for several species of ground beetles (Knopf, 1962; Thiele, 1977), and could have been expected to play a larger role when comparing base-rich and acidic beech forests. This is possibly because of the “unifying effect” of the moder layer that develops in pure, even-aged stands of beech growing on any substrate. As a result, even base-rich soils often have an acidic litter layer of some depth, providing a habitat for species adapted to soils with a high mineral composition. This combination might even be particularly well-suited for some of the species in question since the high nutrient content provides for a rich soil life while at the same time the slowly decomposing acidic beech leaves provide the right pH and moder layer depth. The cool and moist climate conditions of these shady types of stand are another positive feature for these species.

Habitat types defined on a phytosociological basis are models used to structure and classify the many variations found in nature, for which only a few hard boundaries are known. Although they constitute models, they contain species assemblages that can be considered characteristic. Each and every species, however, has its own “niche” or profile of demands that are catered for at every location the species occupies. With changing climate conditions,

habitats will change in terms of composition and distribution. We might not have the same “habitat types” in the future, not because they will necessarily vanish altogether or shift their range, but because of compositional shifts (Fischer, 2008).

Some ground beetle species are currently not regularly found in beech forests but prefer warmer habitats like vineyards. Such a species is *Leistus spinibarbis*, which is occasionally recorded in beech forests in northwestern Bavaria (Müller-Kroehling, 2009) and for which a few records are included in the AF data set. Since the species can regularly be found in Italian beech forests (Vigna Taglianti & De Felici, 1994) and is well adapted to living in this kind of habitat, it is likely that it will be found more frequently in Bavarian beech forests in the future and will eventually become a regular component of this habitat.

Conservation implications

The results show that there will be “winners and losers” among ground beetles in beech forests as a consequence of changing temperature regimes. Based on the classification of Müller-Motzfeld et al. (2004), most of the mountain range species that will gradually become extinct in parts of their range are central and eastern European species and therefore from a global point of view are most in need of protection (Müller-Kroehling, 2012). The three “central European responsibility species” linked to cold climates are *Pterostichus burmeisteri*, *Carabus auronitens* and *Pterostichus unctulatus*. Three other species have an intermediate temperature preference (*Abax parallelus*, *Molops elatus*, *Carabus linnei*), of which the latter is predicted to have a rather strong preference for mountain range climate conditions based on the optimum curve model. Of the warm temperature preferring species, none is a responsibility species. Hence the balance for this category of species is negative. Even if the “global responsibility species” were to be replaced by other, more tolerant species (which is likely), a biodiversity conservation concern would remain. According to the Convention on Biological Diversity, we must seek to protect the species of this group first and foremost since our failure to do so will leave them globally vulnerable. Although these species are not entirely restricted to beech forests, the other habitats used by them (e.g. subalpine spruce forests) are facing a similar problem.

Beech forests only became the dominant type of vegetation in central Europe rather recently during the post-glacial vegetational phase. As a consequence, there are no endemic species inhabiting Bavarian beech forests, in sharp contrast to some other European regions with a much longer occurrence of this type of forest, like the Italian mountains or Carpathians (Walentowski et al., 2010). There, the consequences for biodiversity in a comparable setting are likely to be considerably worse.

In most parts of Bavaria the majority of the characteristic species of ground beetles in beech forests will not be affected by the effects of global warming for quite some time. However, the distributions of some of them are likely to shrink, and this process will start (and likely is

already under way) on the “mountain range frontier” of their distributions in the foreseeable future. Here, mountain range conditions are already marginal and so it is not possible for these species to “move upward”, as they are at the very limit of their tolerance and will likely become extinct. These regions could aptly be named the “mountain range frontier”.

In regard to nature conservation and forestry, the results show that some species will be vulnerable to rising temperatures. The protection of these species, especially near the borders of their acceptable temperature ranges, will most likely benefit from habitats in optimal condition in terms of site characteristics, size and connectivity.

Species have adapted to an ever changing climate regime throughout the Holocene almost exclusively by moving with their preferred climate and its associated habitats (Coope, 1995). Coope (1995) has rightfully called for a network of habitats that will quintessentially serve to protect species against the consequences of climate change in a fragmented environment.

In this context, the following measures are likely to help preserve central European beech forest biodiversity in the future:

- preserve or establish habitat corridors along which species can spread, i.e. to higher altitudes and locations where in the future suitable habitats are likely to occur;

- do not use silvicultural practices like large-scale clear cuts or coppicing that result in sudden and abrupt changes in light intensity and local climatic conditions. This is likely to be stressful for specialized forest species with low dispersal ability;

- preserve existing pure and mixed beech and beech-fir or beech-maple forest stands, especially those at high altitudes that are not necessarily unmanaged but should be managed in such a way that preserves the overall characteristics of the habitat.

As the quantities of deadwood at most the sites included in our dataset were insufficient for this factor to be included in the analysis, it is likely that this habitat factor is important for at least some species and also a possible “buffer” against adverse climatic conditions. We recommend maintaining sufficient levels of deadwood, which the larvae of some of the highly specialized species use as shelters, which enable them to successfully survive droughts.

Within the EU, the Natura 2000 network is a key element in this strategy (Fischer, 2008), as it aims at the preservation of natural or near-natural habitats in functioning and interconnected networks.

Although our results are only predictions based on models they nevertheless provide a solid baseline for future research on this topic using a true time series approach.

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APPENDIX 1. Results for all species showing a correlation to temperature or substrate.

Species	Data set	AUC – ecological bound	Left inflection point	Optimum	Right inflection point	Significance of regression coefficients in the GLM	Variance accounted for by the GLM	Frequency of species in the data set	Significant differences between presences and absences	Interrelation temperature and substrate
<i>Abax ovalis</i> Duftschmid, 1812	BG		8.2			0.5010	0.01	23	0.5107	0.5040
	BG		–	3.8	–	0.8720	0.01	23		
	RG		6.8			0.0004	0.34	22	<0.0001	
	RG		6.9	7.8	8.7	0.0499	0.47	22		
	AB		8.2			0.1297	0.01	52	0.1247	
	AB		6.1	13.5	20.9	0.8690	0.01	52		
	AF		10.8			0.0002	0.04	73	<0.0001	
<i>Abax parallelepipedus</i> Piller & Mitterpacher, 1783	AF		6.6	7.3	8.0	<0.0001	0.20	73		
	BG		–6.6			0.6260	0.01	42	0.6332	0.9940
	BG		–	6.0	–	0.6540	0.01	42		
	RG		4.9			0.0048	0.51	39	<0.0001	
	RG		–	3.0	–	0.5790	0.52	39		
	AB		1.3			0.1100	0.03	108	0.1342	
	AB		–	4.2	–	0.6690	0.04	108		
<i>Abax parallelus</i> Duftschmid, 1812	AF		6.6			<0.0001	0.20	226	<0.0001	
	AF		6.4	7.9	9.4	0.0003	0.24	226		
	BG		7.9			0.0005	0.40	16	<0.0001	0.0078
	BG	0.89; 7.2–9.7	7.7	8.5	9.3	0.0245	0.53	16		0.0417
	RG		8.1			0.0005	0.52	11	<0.0001	
	RG		10.4	12.7	15	0.8410	0.52	11		
	AB		7.7			<0.0001	0.34	41	<0.0001	
	AB		7.7	8.6	9.5	0.0042	0.41	41	<0.0001	
	AF		8.1			<0.0001	0.28	108	<0.0001	
	AF		7.3	8.4	9.5	0.0018	0.30	108		
<i>Bembidion deletum</i> Audinet-Serville, 1821	BG		27.1			0.7430	0.01	2	0.7885	0.8710
	BG		5.7	7.3	8.9	0.4870	0.05	2		
	AB		17.3			0.5010	0.02	3	0.5510	
	AB		5.8	8.6	11.4	0.7680	0.02	3		
	AF		14.4			0.0741	0.04	12	0.0026	
<i>Bembidion lampros</i> Herbst, 1784	AF		6.6	7.5	8.4	0.0548	0.09	12		
	BG		11.1			0.1240	0.11	4	0.0032	0.7264
	BG		7.4	8.1	8.8	0.2350	0.29	4		

Species	Data set	AUC – ecological bound	Left inflection point	Optimum	Right inflection point	Significance of regression coefficients in the GLM	Variance accounted for by the GLM	Frequency of species in the data set	Significant differences between presences and absences	Interrelation temperature and substrate	
<i>Calathus micropterus</i> Duftschmid, 1812	AB		11.5			0.0943	0.06	7	0.0483		
	AB		7.0	9.0	11.0	0.5290	0.07	7			
	AF		10.5			0.0002	0.10	28	0.0001		
	AF		–	5.4	–	0.0042	0.14	28			
	BG	0.95; <5.4				0.0308	0.52	4	0.0009	0.1389	
	BG		–	8.6	–	0.5100	0.53	4			
	RG					0.0238	0.62	8	<0.0001		
	RG		2.6	3.5	4.4	0.5770	0.63	8			
	AB					0.0146	0.57	4	0.0028		
	AB		–	8.3	–	0.4400	0.58	4			
<i>Carabus arvensis</i> Herbst, 1784	AF				–0.5	0.0042	0.06	16	0.0800		
	AF		–	6.5	–	<0.0001	0.21	16			
	BG				–0.1	0.3250	0.05	3	0.5476	0.9360	
	BG		–	7.4	–	0.2770	0.10	3			
	AB					0.1520	0.08	3	0.4965		
<i>Carabus auronitens</i> Fabricius, 1792	AB		–	7.2	–	0.0719	0.17	3			
	AF				–1.5	0.0108	0.02	40	0.0255		
	AF		–	10.2	–	0.6360	0.03	40			
	BG	0.81; <6.4				0.0043	0.21	12	0.0003	0.4620	
	BG		2.5	4.5	6.5	0.3310	0.23	12			
	RG		–0.9			0.3580	0.03	43	0.3850		
	RG		–	4.4	–	0.7250	0.03	43			
	AB					0.0011	0.08	46	0.0004		
	AB		3.7	5.6	7.5	0.0594	0.10	46			
	AF					0.0509	0.01	134	0.0412		
<i>Carabus coriaceus</i> Linnaeus, 1758	AF		3.3	5.8	8.3	0.0018	0.03	134			
	BG	0.76; >7.2	8.6			0.0102	0.14	14	0.0061	0.0356	
	BG		–	3.0	–	0.6350	0.14	14			
	RG		8.4			0.0032	0.27	10	<0.0001		
	RG		7.2	8.0	8.8	0.2140	0.34	10			
	AB		7.8			<0.0001	0.21	43	<0.0001		
	AB		12.6	16.6	20.6	0.7620	0.21	43			
	AF		8.2			<0.0001	0.22	102	<0.0001		
	AF		7.1	8.4	9.7	0.0059	0.24	102			
	BG		14.6			0.3860	0.04	3	0.5458	0.4710	
<i>Carabus glabratus</i> Paykull, 1790	BG		–	5.6	–	0.6480	0.04	3			
	RG		22.3			0.8050	0.00	15	0.7310		
	RG		6.1	6.5	6.9	0.0449	0.60	15			
	AB					0.0714	0.03	16	0.0493		
	AB		4.1	5.9	7.7	0.1440	0.06	16			
	AF					–0.9	0.2280	0.00	57	0.0455	
	AF		5.3	6.4	7.5	<0.0001	0.17	57			
	BG		21.7			0.6400	0.01	3	0.3491	0.5170	
	BG		6.8	7.3	7.8	0.2010	0.31	3			
	RG		15.6			0.4670	0.01	7	0.1020		
<i>Carabus hortensis</i> Linnaeus, 1758	RG		6.8	7.3	7.8	0.1330	0.48	7			
	AB		11.4			0.1178	0.02	25	0.0290		
	AB	0.58; 6.2–8.5	6.3	7.3	8.3	0.0189	0.11	25			
	AF		11.0			0.0003	0.04	65	<0.0001		
	AF		6.4	7.4	8.4	0.0001	0.12	65			
	BG					0.0430	0.25	4	0.0042	0.9960	
	BG		3.8	4.8	5.8	0.4020	0.30	4			
	RG		85.7			0.9420	0.00	10	0.9046		
	RG		5.7	6.5	7.3	0.1026	0.33	10			
	AB					5.1	<0.0001	0.26	18	<0.0001	
<i>Carabus linnei</i> Panzer, 1810	AB	0.88; 3.9–6.7	4.3	5.3	6.3	0.0172	0.35	18			
	AF					1.5	<0.0001	0.08	35	<0.0001	
	AF		4.0	5.3	6.6	0.0003	0.18	35			
	BG		10.2			0.0589	0.10	8	0.0320	0.5264	
	BG		6.7	9.2	11.7	0.5130	0.11	8			
	RG		7.0			0.0427	0.69	19	<0.0001		
	RG		–	–5.9	–	0.9550	0.69	19			
	AB		8.4			0.0012	0.09	37	<0.0001		
	AB	0.67; 6.8–9.3	6.5	8.0	9.5	0.0372	0.13	37			
	AF		8.1			<0.0001	0.19	119	<0.0001		
<i>Cychrus attenuatus</i> Fabricius, 1792	AF		6.8	7.9	9.0	<0.0001	0.23	119			
	BG					0.0716	0.05	20	0.0582	0.9477	
	BG		3.6	5.8	8.0	0.1990	0.08	20			
	RG		4.9			0.0083	0.58	39	<0.0001		
	RG		–	4.4	–	0.1080	0.84	39			

Species	Data set	AUC – ecological bound	Left inflection point	Optimum	Right inflection point	Significance of regression coefficients in the GLM	Variance accounted for by the GLM	Frequency of species in the data set	Significant differences between presences and absences	Interrelation temperature and substrate
<i>Cychnus caraboides</i> Linnaeus, 1758	AB	0.78; <6.9			6.3	<0.0001	0.15	44	<0.0001	
	AB		3.3	5.1	6.9	0.0677	0.17	44		
	AF				-9.4	0.2440	0.00	60	0.0847	
	AF		5.0	6.3	7.6	<0.0001	0.12	60		
	BG				-6.5	0.6190	0.02	2	0.3554	0.9970
	BG		5.8	6.3	6.8	0.3790	0.28	2		
	AB				-21.3	0.7610	0.00	14	0.6449	
<i>Harpalus laevipes</i> Zetterstedt, 1828	AB	0.85; >7.6	5.9	6.8	7.7	0.0329	0.12	14		
	AF		20.1			0.1785	0.01	47	0.0497	
	AF		5.4	6.9	8.4	0.0045	0.06	47		
	BG				0.8	0.3010	0.08	2	0.0286	0.9530
	BG		5.4	5.8	6.2	0.3220	0.39	2		
<i>Harpalus latus</i> Linnaeus, 1758	AB		15.6			0.3369	0.01	11	0.2931	
	AB		5.3	8.2	11.1	0.5950	0.02	11		
	AF	15.1				0.0372	0.02	40	0.0151	
	AF	4.9	9.0	13.1	0.5190	0.02	40			
	BG	8.8				0.0059	0.29	9	<0.0001	0.8808
	BG	7.8	9.1	10.4	0.2870	0.33	9			
	AB	9.0				0.0007	0.20	15	<0.0001	
<i>Leistus rufomarginatus</i> Duftschmid, 1812	AB		8.0	9.4	10.8	0.2850	0.22	15		
	AF	10.5				0.0001	0.09	36	0.0001	
	AF	-	5.7	-	-	<0.0001	0.16	36		
	BG		9.5			0.0919	0.54	2	0.0468	0.9970
	BG	12.5	14.2	15.9	0.9280	0.54	2			
	AB	9.5			0.0360	0.61	2	0.0907		
	AB	9.9	10.9	11.9	0.7870	0.61	2			
<i>Limodromus assimilis</i> Paykull, 1790	AF		15.1			0.2403	0.04	4	0.1749	
	AF		6.5	8.8	11.1	0.7330	0.04	4		
	BG		9.5			0.0568	0.39	3	<0.0001	0.1349
	BG	8.9	9.1	9.3	0.1620	0.74	3			
	AB	0.87; >7.8	9.5			0.0042	0.24	7	0.0003	
	AB		8.2	9.1	10.0	0.2800	0.27	7		
	AF	9.3				<0.0001	0.15	53	<0.0001	
<i>Molops elatus</i> Fabricius, 1801	AF		192.1	212.3	232.5	0.9870	0.15	53		
	BG		9.2			0.1620	0.08	6	0.1303	only base-rich
	BG	6.3	8.5	10.7	0.5830	0.10	6		only base-rich	
	RG	7.9				0.0003	0.58	12	<0.0001	
	RG	7.7	8.1	8.5	0.1160	0.67	12			
	AB	9.2				0.0047	0.07	28	<0.0001	
	AB	0.68; 6.8–8.6	6.7	7.7	8.7	0.0093	0.18	28	<0.0001	
<i>Molops piceus agg.</i> Panzer, 1793	AF	10.3				<0.0001	0.06	66	<0.0001	
	AF	6.8	7.5	8.2	<0.0001	0.20	66	<0.0001		
	BG	12.1			0.8050	0.00	22	0.8097	0.0001	
	BG	-	0.8	-	0.9760	0.00	22			
	AB	8.8			0.1048	0.02	47	0.1024		
	AB	-	4.1	-	0.6630	0.02	47			
	AF	9.0				<0.0001	0.13	77	<0.0001	
<i>Notiophilus biguttatus</i> Fabricius, 1779	AF	6.7	8.0	9.3	0.0085	0.15	77	<0.0001		
	BG	5.0			0.3590	0.01	29	0.3553	0.0774	
	BG	-	6.2	-	0.2850	0.03	29			
	RG	6.6			0.4250	0.01	24	0.4340		
	RG	-	6.0	-	0.3420	0.02	24			
	AB	12.7			0.7860	0.00	53	0.7960		
	AB	-	6.7	-	0.0052	0.06	53			
<i>Notiophilus palustris</i> Duftschmid, 1812	AF	9.1				<0.0001	0.06	109	<0.0001	
	AF	-	3.2	-	0.2180	0.07	109			
	BG	11.2			0.1937	0.15	2	0.0708	0.7016	
	BG	8.0	8.5	9.0	0.3830	0.30	2			
	AB	10.3			0.0519	0.18	3	0.0085		
	AB	8.2	8.6	9.0	0.2130	0.34	3			
	AF	9.8				<0.0001	0.14	34	<0.0001	
<i>Notiophilus rufipes</i> Curtis, 1829	AF	9.1				<0.0001	0.20	34	<0.0001	
	BG	0.92; >8.2	9.1			0.0214	0.44	5	0.0011	0.3142
	BG	-	4.8	-	0.4770	0.45	5			
	AB	9.1				0.0023	0.49	5	0.0046	
	AB	-	5.6	-	0.2360	0.50	5			
	AF	9.0				0.0008	0.61	5	0.0001	
	AF	-	5.6	-	0.0113	0.63	5			
<i>Pterostichus aethiops</i> Panzer, 1796	BG		11.7			0.1692	0.06	6	0.1753	0.0562
	BG		7.2	11.6	16.0	0.8230	0.06	6		

Species	Data set	AUC – ecological bound	Left inflection point	Optimum	Right inflection point	Significance of regression coefficients in the GLM	Variance accounted for by the GLM	Frequency of species in the data set	Significant differences between presences and absences	Interrelation temperature and substrate
<i>Pterostichus burmeisteri</i> Heer, 1838	RG				1.3	0.2020	0.07	4	0.1954	
	RG		2.6	4.8	7.0	0.5640	0.08	4		
	AB		68.7			0.8890	0.00	11	0.8963	
	AB		–	5.5	–	0.9360	0.00	11		
	AF				1.1	0.0001	0.05	41	<0.0001	
	AF		4.3	5.5	6.7	<0.0001	0.19	41		
	BG	0.91; <7.9				0.0069	0.40	42	<0.0001	0.0806
	BG		–	9.1	–	0.2320	0.45	42		
	RG		4.9			0.0126	0.61	39	<0.0001	
	RG		7.7	9.3	10.9	0.6560	0.62	39		
<i>Pterostichus niger</i> Schaller, 1783	AB				9.0	0.0007	0.28	109	0.0001	
	AB		–	322.6	–	0.9950	0.28	109		
	AF		9.2			0.0005	0.02	142	<0.0001	
	AF		6.1	7.1	8.1	<0.0001	0.18	142		
	BG		12.2			0.2113	0.04	7	0.1611	0.2204
	BG		5.9	8.0	10.1	0.3660	0.07	7		
	RG		8.8			0.0110	0.17	10	0.0009	
	RG		6.9	8.0	9.1	0.2550	0.23	10		
	AB		22.2			0.5980	0.00	18	0.5551	
	AB		4.9	7.2	9.5	0.3300	0.01	18		
<i>Pterostichus oblongopunctatus</i> Fabricius, 1787	AF		10.0			<0.0001	0.04	97	<0.0001	
	AF		5.5	7.7	9.9	0.0145	0.06	97		
	BG		2.2			0.2940	0.02	37	0.3214	0.4910
	BG		4.6	9.5	14.4	0.7740	0.02	37		
	RG		–	5.3	–	0.1820	0.16	36		
	AB		–49.1			0.9140	0.00	89	0.9148	
	AB		–	6.3	–	0.8710	0.00	89		
	AF		5.4			0.0006	0.02	240	0.0007	
	AF		4.3	9.4	14.5	0.3990	0.02	240		
	BG	0.82; <6.3				0.0044	0.25	10	0.0012	0.0387
<i>Pterostichus pumilio</i> Dejean, 1828	BG		–	10.9	–	0.6210	0.26	10		
	RG				6.4	0.0005	0.46	22	<0.0001	
	RG		–	23.2	–	0.8750	0.46	22		
	AB				5.2	<0.0001	0.29	19	<0.0001	
	AB		–	35.0	–	0.9210	0.29	19		
	AF				4.4	<0.0001	0.31	59	<0.0001	
	AF		–0.7	1.9	4.5	0.1720	0.32	59		
	BG		10.0			0.1180	0.31	2	<0.0001	0.9960
	BG		8.8	9.0	9.2	0.3850	0.61	2		
	AB	0.97; >8.1		9.8			0.0302	0.37	2	0.0064
<i>Pterostichus strenuus</i> Panzer, 1796	AB		8.8	9.0	9.2	0.3900	0.67	2		
	AF		10.8			0.0005	0.09	26	<0.0001	
	AF		–	–3.1	–	0.7970	0.09	26		
	BG	0.86; <6.1				0.0068	0.28	8	<0.0001	0.0306
	BG		3.8	4.9	6.0	0.2300	0.34	8		
	AB				4.4	0.0006	0.32	8	0.0001	
	AB		3.5	4.6	5.7	0.2580	0.36	8		
	AF				894.8	0.9874	0.00	5	0.9798	
	AF		5.5	6.7	7.9	0.2700	0.06	5		
	BG		14.1			0.3850	0.05	2	0.0265	0.8600
<i>Trechus obtusus</i> Erichson, 1837	BG		7.5	7.8	8.1	0.5290	0.37	2		
	AB		15.5			0.3917	0.02	4	0.3445	
	AB		6.2	8.0	9.8	0.5610	0.04	4		
	AF		19.7			0.3139	0.02	7	0.2145	
	AF		5.4	7.7	10.0	0.5240	0.02	7		
	BG		17.0			0.5360	0.01	9	0.5026	0.9260
	BG		5.1	7.3	9.5	0.3130	0.03	9		
	RG		8.8			0.0128	0.16	10	0.0110	
	RG		–	4.2	–	0.4950	0.17	10		
	AB				–2.5	0.4490	0.00	25	0.4375	
<i>Trichotichnus laevicollis</i> Duftschmid, 1812	AB		3.2	6.1	9.0	0.4240	0.01	25		
	AF		45.4			0.6550	0.00	69	0.5507	
	AF		5.0	6.6	8.2	0.0001	0.07	69		
	BG		20.4			0.6020	0.01	4	0.6626	0.4630
	BG		5.2	13.8	22.4	0.9550	0.01	4		
	AB		45.0			0.8270	0.00	6	0.8570	
	AB		–	6.3	–	0.7330	0.00	6		
	AF		27.4			0.4344	0.01	13	0.1134	
	AF		6.4	7.1	7.8	0.0113	0.13	13		