Macroecology of ground beetles: species richness, range size and body size show different geographical patterns across a climatically heterogeneous area

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Abstract

Aim Ecogeographical patterns have been widely studied in endothermic vertebrates, but relatively few studies have simultaneously examined patterns and causes of gradients in species richness, range size and body size in ectothermic insects. We examined patterns in species richness, mean range size and mean body size of ground beetle assemblages across the biogeographical provinces of Northern Europe, a region that was mostly covered by ice sheets during the latest Ice Age and that presents strong contemporary climatic gradients.

Location Northern Europe

Methods We used literature information on the occurrence of ground beetles, and analysed patterns in species richness, mean range size and mean body size across the provinces using generalized linear models and boosted regression tree analysis.

Results We found a strongly decreasing gradient in species richness with increasing latitude, a strongly unimodal range size-latitude relationship, and a weak unimodal body size-latitude relationship in entire ground beetle assemblages. These gradients also varied among four major genera, suggesting that the overall patterns result from the nuances of smaller clades of ground beetles. The relative importance of contemporary environmental drivers also varied between species richness, mean range size and mean body size in boosted regression tree analysis. While species richness increased with mean annual temperature, mean range size showed an opposite relationship. Mean body size was most clearly associated with the precipitation of the driest month.

Main Conclusions Our findings showed that the latitudinal species richness gradient was strong, and it was closely related to concomitant variation in temperature, whereas variations in mean range size and mean body size were more complex. These findings suggest that the causes for range size and body size variation in insects may be complex, requiring additional insights from studies conducted at local, regional and continental scales.

Keywords

Biodiversity, Carabidae, climatic forcing, ecogeographical rules, Fennoscandia, insects, latitudinal patterns.

Biosketch

The authors are interested in the biodiversity of terrestrial and aquatic organisms, using biogeographical and ecological approaches to unravel patterns and underlying mechanisms.

1 | INTRODUCTION

Macroecology seeks for recurring patterns in diversity, distribution and abundance of organisms at broad spatial and temporal scales (Brown, 1995; Gaston & Blackburn, 2000). This field of research has proven to be highly successful in overcoming the inherent complexity of community ecology (Lawton, 1999), disclosing patterns that typically only emerge in broad-scale analyses (Gaston & Blackburn, 2000). These patterns include relationships of species richness, range size and body size with ecogeographical variables, such as latitude (e.g. Hillebrand, 2004), elevation (e.g. Rahbek, 1995), productivity (e.g. Evans, James & Gaston, 2016), temperature (e.g. Currie et al., 2004), and land cover (e.g. Higgins, 2007). A number of studies have found support for the effects of these ecogeographical variables on species richness, range size and body size, either alone or in combination at the assemblage level (e.g. Gaston, Chown & Evans, 2008).

Species richness in a number of taxonomic groups tends to decrease from low latitudes toward the poles (e.g. Rosenzweig, 1995). This latitudinal diversity pattern occurs especially in many groups of terrestrial vertebrates and vascular plants (e.g. Willig, Kaufman & Stevens, 2003), whereas there are notable exceptions among various small-bodied animal groups (e.g. Kouki, Niemelä & Viitasaari, 1994). While latitude *per se* does not explain patterns of species richness, it has served as an important background for understanding variation in the diversity of life (Blackburn & Gaston, 2000; Willig & Presley, 2018). Although some authors attempted to explain this species richness gradient in terms of 'geometric constraints' that limit the geographical ranges of species, this model explains very little variation in species richness at broad scales (Hawkins & Diniz-Filho, 2002; Zapata, Gaston & Chown, 2003). Instead, correlations between species richness and latitude are typically considered to be a result of contemporary (e.g. climate, environmental heterogeneity) and historical (e.g. evolutionary diversification, Ice Age history) factors (Currie et al. 2004; Fattorini & Baselga, 2012; Hawkins et al., 2003; Hewitt, 2004; Hillebrand, 2004; Svenning & Skov, 2007; Whittaker et al., 2007). We here particularly focus on the contemporary mechanisms related to climate forcing on species richness in the geographic area of Northern Europe that shows heterogeneous climatic conditions and that was almost entirely covered by ice during the last glacial maximum (e.g. Hewitt, 1999). In such deglaciated areas, colonization after the ice sheets receded (Fattorini & Ulrich, 2012; Ulrich & Fattorini, 2013), current climatic conditions and environmental productivity can be assumed to be the main drivers of species richness at broad scales (e.g. Heino, Alahuhta & Fattorini, 2015) because evolutionary time (< 12,000 years) may have been too limited for extensive speciation in most macroscopic organisms (e.g. Homburg, Schuldt, Drees & Assmann, 2012).

Patterns in species ranges have been widely examined from different angles (Gaston, 2003), but one particularly fruitful approach is to understand how interspecific variation in range size is related to latitude (Stevens, 1989). In general, one may assume that species inhabiting high latitudes have larger ranges than those occurring in low-latitude areas, which is also known as Rapoport's rule (Stevens, 1989). The average smaller ranges of species at low latitudes would also be an explanation of the higher species richness values observed for most groups around the equator (smaller ranges allow more species to occur in a given area) and its decrease towards the poles. This pattern has gained variable support in empirical examinations (Rohde, 1998): some studies have found support for the rule, but probably a larger number of studies have found discrepancies with regard to its existence in nature (Gaston, Blackburn & Spicer, 1998; Pintor, Schwarzkopf & Krockenberger, 2015). Rapoport's rule, when it is supported, has been hypothesised to result from the following set of three underlying factors (Stevens, 1996): (1) species that experience variable temperatures are temperature generalists; (2) temperature generalists have broader ranges than temperature specialists along latitudinal gradients, and (3) high latitudes have highest temperature seasonality and, therefore, high latitudes are inhabited by temperature generalist species that possess large ranges.

Body size variations may also occur along latitudinal gradients (Gaston et al., 2008; Horne, Hirst & Akinson, 2015). One of the most widely considered hypotheses assumes that within a given clade larger-sized species are found in colder regions, whereas smaller-sized species occur in warmer regions, because larger animals tend to radiate less body heat per unit of mass (Blackburn et al., 1999). There are examples of this pattern in intraspecific analyses of birds and mammals (Ashton, Tracy & Queiroz, 2000; Meiri & Dayan, 2003), but its existence in interspecific and assemblage-level analyses of arthropods is less well known (Cushman, Lawton & Manly, 1993; Gérard et al., 2018), and even reversed patterns have been found in arthropods along latitudinal gradients (Blackenhorn & Demont, 2004; Heino & Alahuhta, 2019; Shelomi, 2012).

Several hypotheses have been proposed to explain an increase in body size at lower latitudes in arthropods. First, an increase in body size increases the volume-surface area ratio, which reduces transpiration, and hence water loss, allowing larger arthropods to better cope with arid climatic conditions that characterize Southern Europe, where the Mediterranean biome prevails (Fattorini, Lo Monaco, Giulio & Ulrich, 2014). Alternatively, arid climates do not drive body size evolution, but rather select, from a wider fauna containing species of any size, those that have larger bodies. This causes drier regions in southern areas to harbour faunas that contain, on average, larger species, as found for the European tenebrionid beetles (Fattorini et al., 2014). Moreover, the semi-passive or passive oxygen dissipation that is ubiquitous in insects involves a more effective respiration and cell functioning at higher temperatures, which would allow species to attain larger body sizes at higher ambient temperature and, hence, at lower latitudes (Fattorini, Lo Monaco, Giulio & Ulrich, 2013). Finally, an increase in body size at lower latitudes might be due to increased productivity and metabolic rates in regions with high energy availability (Homburg et al., 2012; Heino & Alahuhta, 2019). However, studies on temperature relationships and latitudinal trends in arthropod body size have provided variable results, pointing to taxon and life history specific factors that constrain body size, such as taxon-specific desiccation resistance, resource storage and starvation resistance, resource limitation, food availability, freezing resistance, net primary productivity, seasonality, and metabolic constraints (Fattorini et al., 2013; Heino & Alahuhta, 2019). The multiple and possibly contrasting effects of different environmental variables on body size may also lead to non-linear relationships (Shelomi, 2012). For example, in ground beetles, Homburg et al. (2012) found a hump-shaped relationship between body size and latitude, as a result of positive correlations with ambient energy (which decreases northwards) and precipitation (which decreases southwards) across the Western Palaearctic.

Ground beetles are a speciose family of beetles that has been the focal group in a multitude of ecological studies (Kotze et al., 2011; Koivula, 2011; Lövei & Sunderland, 1996). These studies have found that their species richness and assemblage composition are sensitive to local (Lövei & Sunderland, 1996), land cover (Eyre, Luff, Staley & Telfer, 2003; Kotze et al., 2011) and climatic variables (Eyre, Ruston, Luff & Telfer, 2005; Heino & Alahuhta, 2015). However, to our knowledge, no study to date has simultaneously studied macroecological patterns in species richness, range size and body size of ground beetles across large geographical regions. Here, we examined variation in these biotic variables across the climatically heterogeneous region of Northern Europe. We first examined latitudinal gradients in species richness, range size and body size, and subsequently modelled variation in these biotic variables using current climatic and land use variables assumed to be important for ground beetle distributions at broad scales. We specifically hypothesized that (1) species richness should decline with increasing latitude (Rosenzweig, 1995), (2) mean range size in an assemblage should increase with increasing latitude (Stevens, 1989), and (3) mean body size in an assemblage should exhibit a hump-shaped relationship as a result of contrasting responses to different climatic factors as was found previously specifically for Western Palaearctic ground beetles (Homburg et al., 2012). In addition to entire ground beetle faunas, we also analysed these same latitudinal relationships for four relatively speciose and ecologically different genera, *Carabus*, *Bembidion*, *Pterostichus* and *Amara* (Lindroth, 1985, 1986). We further examined the effects of current climatic and land use drivers of these biotic variables for entire ground beetle assemblages. Understanding these relationships is important because ecogeographical patterns in insects are generally poorly described, yet it is essential for increasing knowledge of causes and consequences of biodiversity loss in the face of global change.

2 | MATERIALS AND METHODS

2.1 | Ground beetle data and response variables

We used ground beetle (Coleoptera: Carabidae) incidence data for the 79 biogeographic provinces of Denmark, Sweden, Norway and Finland (54°N to 71°N; 5°E to 32°E) in Northern Europe (Heino & Alahuhta, 2015; Heino et al., 2015) using data reported in Lindroth (1985, 1986). These data are based on literature reviews, examination of museum specimens, Carl H. Lindroth's own field work and collections, and more. Each province has characteristic climate, land cover and land use features, and they can thus be considered as relatively homogeneous study units (Väisänen, Heliövaara & Immonen, 1992; Väisänen & Heliövaara, 1994). Even though these species records are relatively old, they represent good information about ground beetle species distributions across Northern Europe up to mid-1980s and can thus be used in association with predictor data derived for the period between 1960s and 1990s (Heino & Alahuhta, 2019; Heino, Alahuhta, Fattorini & Schmera, 2019). Thus, our study represents a benchmark for future investigations in the face of climate change.

We analysed the responses of species richness, mean range size of species per province and mean body size of species per province to the predictor variables (see below).

Species range size was calculated as the number of provinces occupied by a species as given by the species-by-province tables in Lindroth (1985, 1986). It has to be noted that the number of provinces occupied by species was strongly correlated with their areal extent ($r = 0.993$, P < 0.001, $N = 388$). Because no species occurs all over a given province, we considered that the number of provinces was a more realistic measure of range size than the real spatial extent of the occupied provinces. These specific values were used to calculate the arithmetic means of range size for each province of the study region. For each species, we used as a measure of body size the maximum value of total body length (from tip of mandibles to tip of elytra) for a species as given in Lindroth (1985, 1986). Then, we calculated arithmetic means of body length for each province. It has to be noted that the minimum body length and maximum body length were very strongly correlated ($r = 0.986$, P < 0.001, $N = 388$; Supporting Information Fig. S1) in the ground beetle dataset. In addition to entire ground beetle fauna (N = 388 species), we also analysed data separately for four biologically (e.g. body size) and ecologically (e.g. feeding modes) different genera, *Carabus* (N = 16 species), *Bembidion* (N = 70 species), *Pterostichus* (N = 23 species) and *Amara* (N = 43 species), across Northern Europe (Lindroth, 1985, 1986). As we used the assemblage approach (*sensu* Gaston *et al*., 2008), each species contributes to mean range size and mean body size values in a number of provinces. The idea of ‘community weighted means’ is thus inherent in the assemblage approach and should be considered when interpreting variation in the response variables.

2.2 | Predictor variables

Latitude and longitude for each province were based on a province centroid. Of the many possible climatic variables, we used the ecologically meaningful mean annual temperature (°C), maximum temperature of the warmest month (°C), minimum temperature of the coldest month (°C), temperature range (°C), precipitation of the wettest month (mm) and precipitation of the driest month (mm). The climate variables were mean values of a period from 1960 to 1990 for each biogeographical province and were derived from WorldClim with 0.93 km × 0.93 km resolution (Hijmans, Cameron, Parra, Jones & Jarvis, 2005). The two precipitation variables were strongly correlated ($r = 0.966$, $P < 0.001$, $N = 79$), and we thus omitted precipitation of the wettest month from the analyses. In addition, minimum temperature was strongly correlated with temperature range ($r = -0.899$, $P < 0.001$, $N = 79$), so we used only temperature range in the modelling analyses. Land cover variables were relative cover (%) of open, forested, urban and agricultural areas in each province and were obtained from European CORINE 2006 with 100m resolution (https://land.copernicus.eu/pan-european/corine-land-cover/). Finally, average elevation and elevation range within the province were also used, which were obtained from 3D Digital Elevation Model over Europe with 25m resolution (https://www.eea.europa.eu/data-and-maps/data/eu-dem). Because these two elevation variables were very strongly correlated ($r = 0.955$, $P < 0.001$, $N = 79$), we omitted average elevation from the statistical analysis. The remaining predictor variables were not generally strongly correlated (Supporting Information, Table S1).

2.3 | Modelling variation in species richness, mean range size and mean body size across the biogeographic provinces

We first examined latitudinal trends in ground beetle species richness, mean range size and mean body size using generalised linear modelling (GLM) with first and second order terms of the predictor variable included. We also analysed these same latitudinal relationships for four relatively speciose and ecologically different genera, *Carabus*, *Bembidion*, *Pterostichus* and *Amara* (Lindroth, 1985, 1986). We drew scatterplots of the relationships between the response and latitude, as well as compared model fits using adjusted deviance explained (D^2 adj.) and Akaike's Information Criterion (AIC). These analyses we conducted using the R package stats and the R package modEvA (Barbosa, Brown, Jimenez-Valverde & Real, 2016).

Secondly, Boosted Regression Tree (BRT) analysis (Elith, Leathwick & Hastie, 2008) was employed to analyse variation in species richness, mean range size and mean body size of entire ground beetle assemblages using the environmental variables measured across the provinces. We did not model genus-level biotic variables separately because they would have been based on a relatively low numbers of species. BRT is a robust machine learning method that is able to handle various types of data, has no need for a priori data transformation or elimination of outliers, considers non-linear relationships between response and predictor variables, and automatically takes into account interactions between predictor variables (Elith et al., 2008). Here, we used BRTs to obtain the unique contributions of each environmental variable (see above) to the three response variables based on Poisson (species richness) or Gaussian (mean range size and mean body size) error distributions. The following parameters were used in all BRTs: tree.complexity = 5, learning.rate = 0.01, and bag.fraction = 0.5. Of these parameters, 'tree.complexity' sets the complexity of individual trees, 'learning.rate' sets the weight applied to individual trees, and 'bag.fraction' sets the proportion of observations used in selecting variables (Hijmans, Phillips, Leathwick & Elith, 2017). We also tried different learning rates (from 0.001 to 0.01) and bag fractions (from 0.5 to 0.75) in the trial analyses, but the main findings did not change. We calculated the explained deviance of the BRT models as model strength and showed the partial dependency plots to examine the relative contribution of each predictor variable on species richness, mean range size and mean body size. BRTs were conducted using the function ‘gbm.step’ in the R package dismo version 1.1-4 (Hijmans et al., 2017).

We used Moran’s I correlograms to examine spatial autocorrelation patterns in species richness, mean range size and mean body size as well as the respective residuals from the BRT models. The correlograms were drawn using the function ‘correlog’ in the R package pgirmess version 1.6.9 (Giraudoux, 2018).

3 | RESULTS

There was a lot of variation among species in both occupancy and body size (Supporting Information, Fig. S2). Similar patterns of occupancy were detected among the four genera analysed separately (not shown), but body size distributions varied to some extent. For example, while the entire ground beetle assemblage showed a right-skewed pattern in body size, the patterns for separate genera were more unimodal with mid-sized species being most typical within each genus.

Species richness was negatively correlated with province area (r = -0.642, P < 0.001, N = 79), owing to the fact that the species-poor northernmost provinces were the largest in size. Hence, we did not correct for the effect of province area on species richness because there was no significant positive relationship between these two variables. In addition, observed species richness and residuals from species richness-province area regression were strongly correlated ($r = 0.766$, $P < 0.001$, $N = 79$), suggesting that correcting for province area in the species richness analyses would not affect the results too much.

There were clear relationships between some environmental or biological variables and latitude (Fig. 1, Table 1). We found that the species richness of ground beetles was strongly negatively and almost linearly related to latitude, with both linear and quadratic models showing a similar fit. Mean range size increased with latitude, but the quadratic model showed a far better fit. Mean body size showed a moderately strong quadratic relationship with latitude, with first an increasing and then a decreasing trend along the latitudinal gradient. The four genera analysed separately, *Carabus*, *Bembidion*, *Pterostichus* and *Amara*, showed clearly decreasing trends of species richness with latitude (Supporting Information, Table S2, Fig. S3). In addition, all four genera showed a quadratic relationship between mean range size and latitude, although the exact form of these relationships varied among the genera. Finally, the mean body size-latitude relationships were non-significant for *Carabus*, generally increasing for *Bembidion* and *Amara*, and quadratic for *Pterostichus*.

The BRT models were strong (Table 2), and the most important environmental variables varied among the models of species richness, mean range size and mean body size (Fig. 2). Species richness was most clearly affected by mean annual temperature (relative impact: 43.4% out of 100%), followed by agriculture (20.2%) and urban land use (16.3%). Of these predictor variables, mean annual temperature had a generally positive relationship with species richness, whereas agriculture and urban land uses had increasing effects before reaching a plateau in the graph (Fig. 2). Mean range size was best predicted by mean annual temperature (41.9%), which was generally negatively related to the response variable and agricultural land use (33.4%) that first had a negative effect and then reached a plateau in the graph (Fig 3). Mean body size showed the clearest relationship with precipitation of the driest month (32.3%), the effect of which was first increasing and then reached a plateau in the graph (Fig. 2). Other environmental variables were clearly less important for mean body size in terms of their relative impacts.

Species richness, mean range size and mean body size were spatially structured across Northern Europe (Fig. 3). However, the environmental variables in the BRT models captured most spatial patterns in the response variables, as was evidenced by Moran’s I correlograms. Only for mean body size, the residuals of the BRT model showed some minor signs of significant spatial autocorrelation (Fig. 3).

4 | DISCUSSION

We found variable support for our three hypotheses. First, species richness declined with increasing latitude (Fig. 4), which corroborated a large body of evidence for various systems (Rosenzweig, 1995, Willig & Presley, 2018). Second, mean range size in the study area did not increase linearly with increasing latitude (Stevens, 1989), but rather showed a unimodal response that has been previously detected in the same study area for aquatic diving beetles (Heino & Alahuhta, 2019). Third, mean body size in entire assemblages showed a unimodal response to latitude, which is accordance with the overall pattern observed for ground beetles in the Western Palaearctic (Homburg et al., 2012). We further found that the effects of climatic drivers on these response variables varied, with mean annual temperature being important for species richness (a positive relationship) and mean range size (a negative relationship), whereas mean body size correlated most strongly with precipitation of the driest month (a mainly positive relationship). Finally, we observed that the four major genera we examined separately showed partly different patterns in range size and body size across the biogeographic provinces of Northern Europe, although their species richness declined strongly with latitude.

A number of hypotheses have been coined to account for variation in species richness at broad spatial scales. These hypotheses revolve around historical and contemporary explanations, of which evolutionary changes, Ice Age history and various climatic factors have been most often cited as important causes for variation in species richness (Schuldt & Assmann, 2009; Willig & Presley, 2018). In our present study area, we can very likely exclude the possibility that speciation has occurred amongst ground beetles in the last 12,000 years after the latest Ice Age. In addition, given that almost the entire study area was covered by ice sheets, these areas have been colonized in a relatively short time period and, most likely, by species that have relatively good dispersal powers, as is also shown by the lack flightless species in northern faunas (Homburg et al., 2012). Hence, provided that most species have been able to reach most provinces, their distributions and thereby species richness variation should be mostly under contemporary climatic conditions and land cover features. Indeed, we found that mean annual temperature was clearly the most important predictor of species richness variation in ground beetles, followed by generally positive effects of agriculture and urban land use on species richness. The latter two relationships seem to be counterintuitive because they refer to strongly modified land uses, which should decrease rather than increase species richness. As already mentioned in a study on beta diversity of ground beetles in the same study area (Heino et al., 2019), this pattern is most easily explicable in terms of the most climatically suitable provinces in the southern parts of the study area being also most strongly affected by human land use. It is thus possible that 'favorable climate' overcomes the effects of 'poor land use' because small organisms can find at least some suitable habitats even within relatively degraded landscapes (Fattorini et al., 2016).

Mean range size showed an interesting unimodal response to latitude. This pattern was previously detected for diving beetles in the same study area, although the latitude at which the highest mean range size occurred varied between diving beetles (Heino & Alahuhta, 2019) and ground beetles (this study). The reason for the unimodal latitudinal gradient in the mean range size of beetles may be related to the fact that there are some northern species not occurring south of central Sweden and central Finland. Thus, even though most ground beetle species have large ranges in the northern parts of the study area, the restricted-range species occurring in the north result in the fact that mean range size at the assemblage level starts to decrease approximately north of 64ºN. However, this is the pattern in our study area, and actually many of these northern species have large ranges at high latitudes in the Palaearctic realm and even the Nearctic realm (Lindroth, 1985, 1986). This finding underscores the importance to consider whether the entire or partial distribution ranges of species are considered. In addition, it has to be noted that the four major genera analyzed separately showed partly different range size-latitude relationships (Supporting Information, Table S2 and Fig. S2). These findings suggest that the unimodal latitudinal pattern in range size may also stem from different patterns shown by smaller clades of ground beetles.

As expected because of a relatively strong latitudinal gradient in mean annual temperature in the study area (Fig. 1), mean range size was also relatively strongly affected by this predictor variable. The relationship was generally negative, suggesting that species in warmer southern provinces have smaller ranges compared with species in colder northern provinces, yet temperature range was weakly related to mean range size. This finding was partly conflicting with the idea of Rapoport's rule that there is (1) a latitudinal range size pattern, and (2) that this pattern is caused by species responses to temperature variability (Stevens, 1989).

Mean body size also showed a unimodal relationship with latitude, although the relationship was not particularly strong. This finding is thus partly counter to the hypothesis that animal body size should be larger in cold climates at high latitudes (Blackburn, Gaston & Loder, 1999). However, the unimodal pattern found in our study also contrasts with studies showing a negative correlation between latitude and body size (Shelomi, 2012), but is consistent with the pattern outlined for ground beetles in the Western Palaearctic (Homburg et al., 2012). In fact, this is a rather unusual pattern: out of 108 studies on body size variations at interspecific level along latitudinal and altitudinal gradients revised by Shelomi (2012), only four studies found a hump-shaped pattern for elevational interspecific variation and none for the latitudinal gradient. A partial reason for our finding may be that we focused on assemblage-level measure of body size rather than the interspecific analysis (*sensu* Gaston et al., 2008). In addition, even though the overall pattern across all ground beetle species was unimodal, the genera *Bembidion* and *Amara* showed increasing mean body size with latitude, whereas the genera *Carabus* and *Pterostichus* did not show significant linear body size relationships with latitude.

The causes for the discrepancies between different animal groups in the relationships between body size and latitude may stem from differences not only in temperature conditions, but also in resource availability and habitat-specific factors (Clauss, Dittmann, Müller, Meloro & Codron, 2013; Geist, 1987). For ground beetles, mean body size in a provincial assemblage was mostly strongly affected by the precipitation of the driest month, suggesting that in provinces with limited amounts of rainfall, ground beetle body size may, on average, be small. This is logical because resources may be in short supply in dry areas (e.g. prey for predaceous species, seeds for granivorous species; Lindroth, 1985; 1986), and small body size is a characteristic of ground beetles that inhabit harsh environments, probably because of poor food availability (Blake, Foster, Eyre & Luff, 1994; Hiramatsu & Usio, 2018; Lövei &

Magura, 2006). However, this idea may also fall short in explaining patterns across local ground beetle assemblages, i.e., those scales where resource limitation truly occurs, because we focused only on provincial patterns in ground beetle body size.

To conclude, we found support for some ecogeographical rules (*sensu* Gaston et al., 2008) in the ground beetle faunas of Northern Europe. In particular, the latitudinal species richness gradient was strong, and it was closely related to concomitant variation in mean annual temperature. However, variations in mean range size and mean body size were more complex, often showing unimodal responses to latitude. These findings and other evidence suggest that the causes for range size and body size variation in insects may be complex, requiring additional insights from studies at local, regional and continental scales. These insights are all more important in the face of climate change, which is likely to reform floras and faunas as well as modify the ranges and body sizes of the ground beetle species in regional faunas.

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AUTHORS’ CONTRIBUTIONS

JH devised the original study ideas, ran the statistical analyses and led the writing. JA collated the predictor variable data. JA and SF contributed to the ideas and writing.

DATA ACCESSIBILITY

All biological data are available as species-by-province tables in the books on Northern European ground beetles (Lindroth 1985, 1986). Climatic data were derived from WorldClim (Hijmans et al., 2005) and land use variables from CORINE database, both freely available in the Internet.

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Supporting Information

Table S1. Pearson correlations between the predictor variables.

Table S2. Summaries of linear and quadratic regression models for the four genera of ground beetles.

Fig. S1. The relationship between minimum and maximum body size of species in the ground beetle fauna of Northern Europe.

Fig. S2. Frequency histograms of occupancy and body length for ground beetle species in our study.

Fig. S3. Latitudinal gradients in species richness, mean range size and mean body size for the ground beetle genera.

Tables and Figures

Table 1. Generalized linear models (GLMs) for species richness, mean range size and mean body size in relation to latitude (as distance from the equator). Both linear and unimodal models are shown. Poisson error distribution was used for species richness, and Gaussian error distribution for mean range size and mean body size. Also shown are adjusted deviance explained (D^2 adj.) and Akaike Information Criterion (AIC) values for model comparisons.

Species richness	Estimate	SE	z	P	D^2 adj.	AIC
(Intercept)	8.037	0.086	93.780	<0.001		
Latitude	-3.45e -06	1.01e -08	-34.200	<0.001	0.791	873.845
(Intercept)	9.674	0.719	13.443	< 0.001		
Latitude	-7.19e -07	1.63e -07	-4.391	< 0.001		
Latitude^2	2.12e -14	9.25e -15	2.292	0.022	0.792	870.637

Mean range size	Estimate	SE	t	P	D^2 adj.	AIC
(Intercept)	18.817	4.699	4.004	< 0.001		
Latitude	3.87e -06	5.33e -07	7.277	< 0.001	0.392	472.509
(Intercept)	-27.102	2.365	-11.47	< 0.001		
Latitude	6.89e -05	5.28e -06	13.06	<0.001		
Latitude^2	-3.60e -12	2.92e -13	-12.35	< 0.001	0.795	387.571

Mean body size	Estimate	SE	t	P	D^2 adj.	AIC
(Intercept)	10.868	0.386	28.165	< 0.001		
Latitude	-1.87e -07	4.38e -08	-4.275	< 0.001	0.171	77.562
(Intercept)	-1.815	3.032	-0.599	0.551		
Latitude	2.66e -06	6.77e -07	3.928	< 0.001		
Latitude^2	-1.57e -13	3.74e -14	-4.212	< 0.001	0.319	62.989

Table 2. Summaries of boosted regression tree analyses for species richness, mean range size and mean body size in ground beetle faunas of Northern Europe.

	Species richness	Mean range size	Mean body size
Mean total deviance	20.268	36.258	0.179
Mean residual deviance	1.703	4.796	0.057
Deviance explained (D^2)	**0.947**	**0.868**	**0.682**
Estimated cv deviance	4.414	9.510	0.110
Estimated cv deviance (se)	0.765	0.975	0.019
Training data correlation	0.958	0.933	0.836
cv correlation	0.876	0.825	0.642
cv correlation (se)	0.027	0.053	0.072

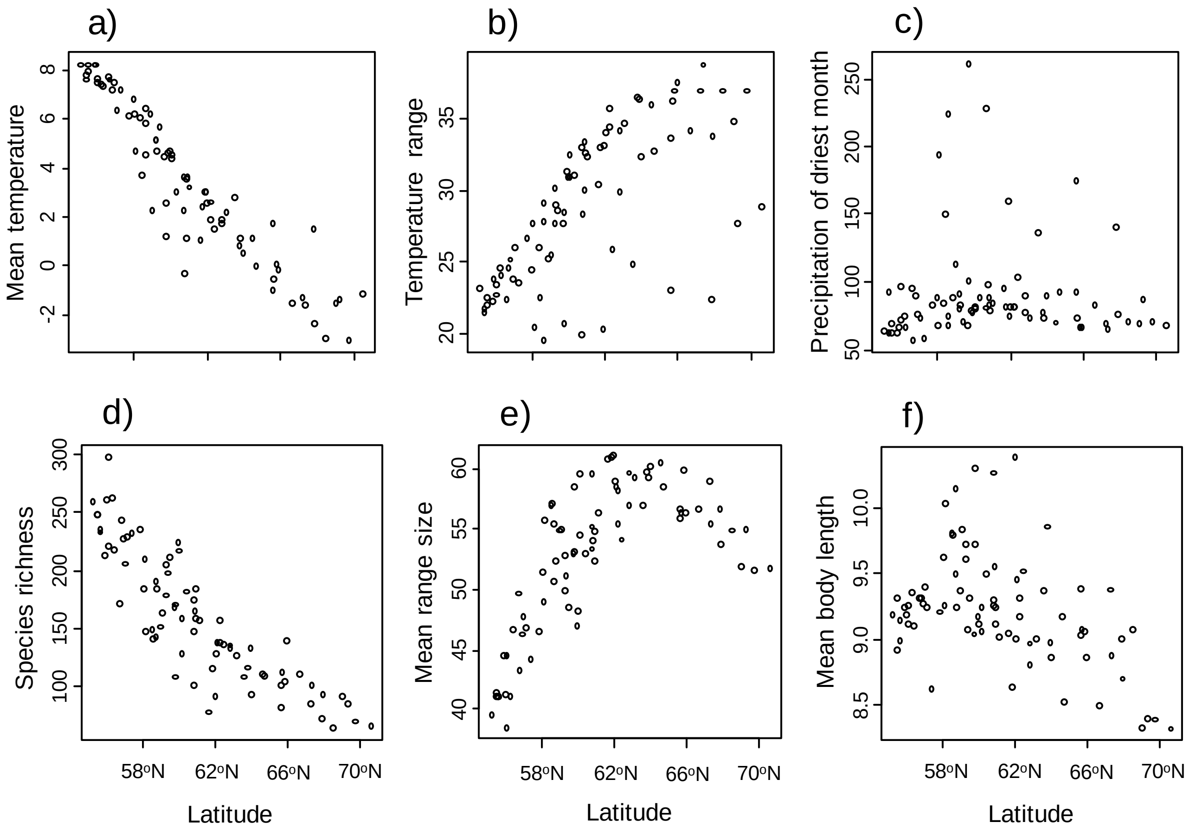
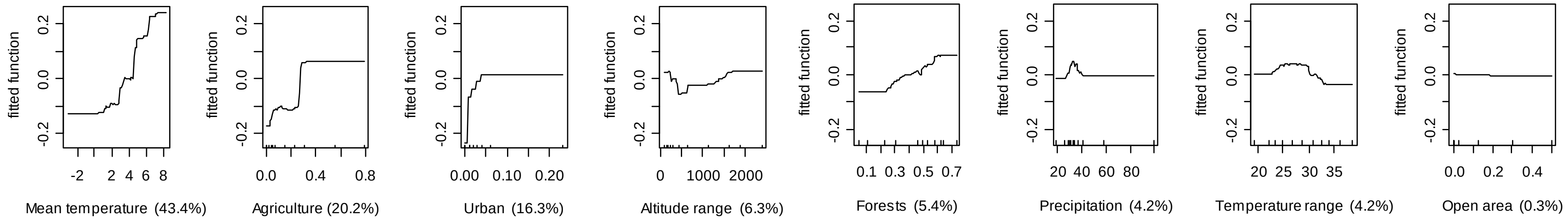
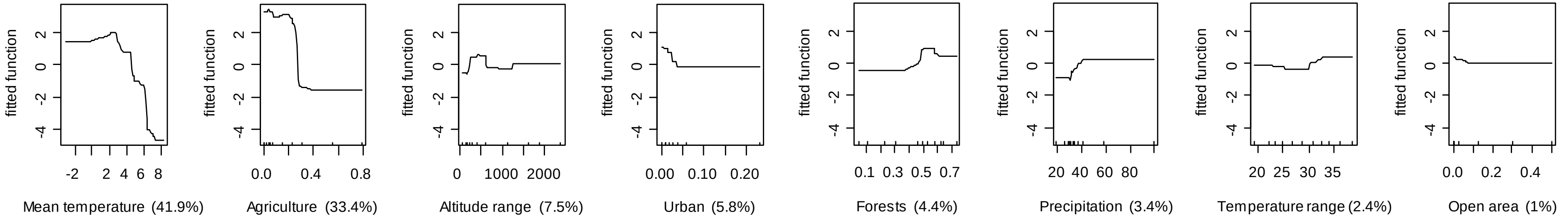


Fig. 1. Latitudinal gradients in main climatic variables (a to c), as well as in species richness (d), mean range size (e) and mean body size (f) in the ground beetle faunas of Northern Europe. N = 79 provinces.

a) Species richness (Poisson)



b) Mean range size (Gaussian)



c) Mean body size (Gaussian)

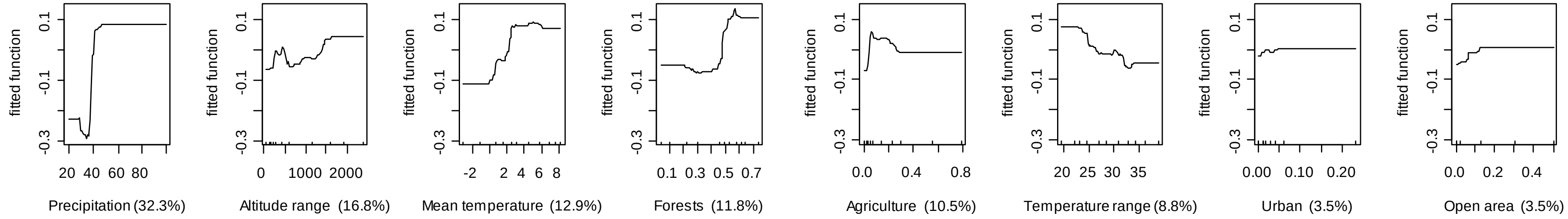


Fig. 2. Partial dependency plots from boosted regression trees (BRT). Also shown are relative contributions to the explained deviance of the predictor variables for species richness (a), mean range size (b) and mean body size (c) variation in the ground beetle faunas of Northern Europe.

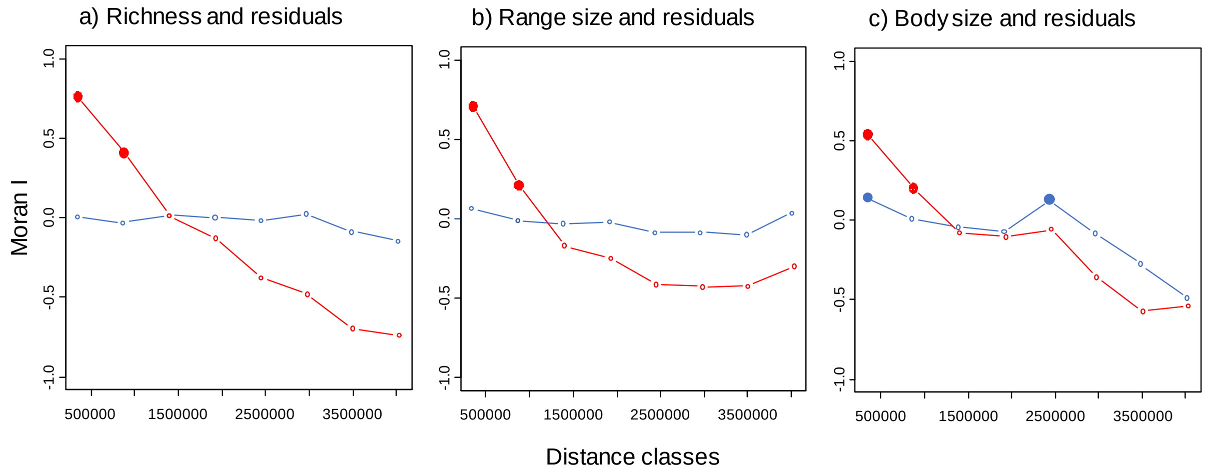


Fig. 3. Moran's I correlograms for species richness (a), mean range size (b) and mean body size (c) (in red), as well as for corresponding residuals from the BRT analysis (in blue). Large filled circles represent significant ($p < 0.05$) spatial autocorrelation in a corresponding distance class.

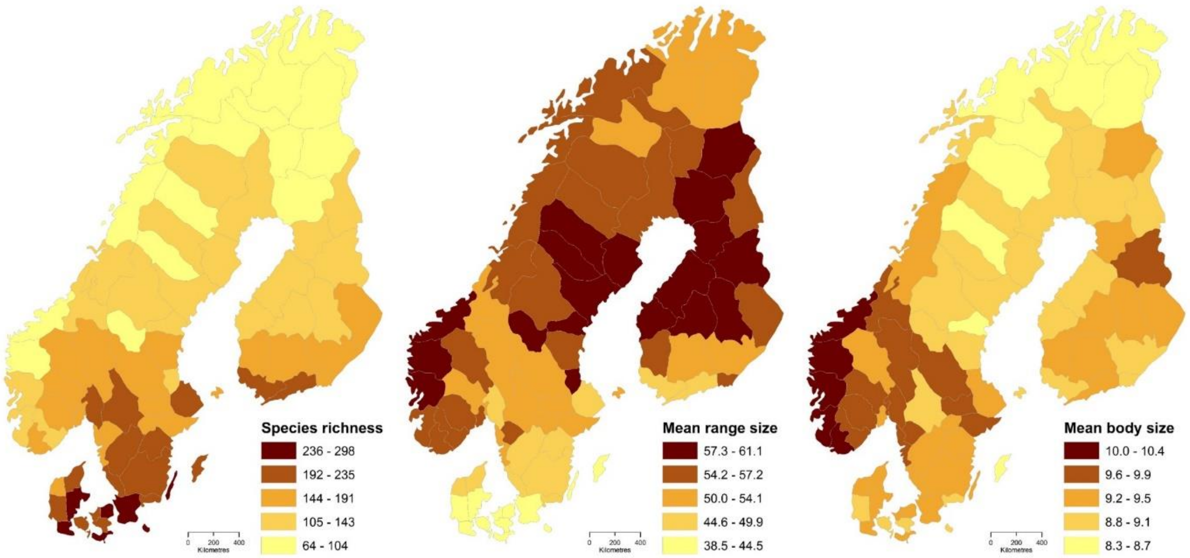


Fig. 4. Maps of species richness, mean range size and mean body size across the entire ground beetle assemblages in Northern Europe. N = 79 provinces.