Predicting beta diversity of terrestrial and aquatic beetles using ecogeographical variables: insights from the replacement and richness difference components

Jani Heino[1*], Janne Alahuhta[2], Simone Fattorini[3] & Dénes Schmera[4,5]

[1] Finnish Environment Institute, Biodiversity Centre. P.O. Box 413, FI–90014 Oulu, Finland.

[2] Geography Research Unit, University of Oulu. P.O. Box 3000, FI–90014 Oulu, Finland.

[3]Department of Life, Health & Environmental Sciences, University of L'Aquila, Via Vetoio, Coppito, 67100 L'Aquila, Italy

[4]MTA Centre for Ecological Research, Balaton Limnological Institute, Klebelsberg K. u. 3, H-8237 Tihany, Hungary

[5]MTA Centre for Ecological Research, GINOP Sustainable Ecosystem Group, Klebelsberg K. u. 3, H-8237 Tihany, Hungary

*Correspondence: jani.heino@environment.fi

BIOSKETCH

The authors are interested in all aspects of biodiversity, ranging from spatial patterns in species distributions through different facets of biodiversity to their conservation implications.

Author contributions: JH devised the original ideas, analysed the data, and led the writing. JA contributed the predictor variable data. All authors contributed to the ideas and writing of the manuscript.

ACKNOWLEDGEMENTS

We dedicate this paper to all people who have contributed to the faunistics of beetles in Northern Europe. We would like to express our gratitude to three anonymous referees for their comments on a previous version of this paper. This research was supported by the OTKA K128496 and GINOP 2.3.3-15-2016-00019 grants.

ORCID

Jani Heino: orcid.org/0000-0003-1235-6613

Janne Alahuhta: orcid.org/0000-0001-55149361

Simone Fattorini: orcid.org/0000-0002-4517-2135

Dénes Schmera: orcid.org/0000-0003-1248-8413

Abstract

Aim: We examined the responses of the beta diversity of aquatic and terrestrial beetles to ecogeographical variables, including climate, land cover and land use, across Northern Europe.

Location: Northern Europe (Denmark, Sweden, Norway and Finland).

Methods: Information on the occurrence of ground beetles and diving beetles across Northern European biogeographic provinces was collated from literature sources. Beta diversity was examined using Jaccard dissimilarity coefficient as well as its replacement and richness difference components. Each of the three dissimilarity matrices (responses) was modelled using various ecogeographical variables (predictors) by generalized dissimilarity modelling (GDM).

Results: The magnitude of total beta diversity was relatively similar between ground beetles and diving beetles, but the richness difference component contributed more than the replacement component to total beta diversity in ground beetles, whereas the opposite was true for diving beetles. The predictor variables most influential in GDM in accounting for spatial variation in beta diversity varied between the two beetle groups as well as between the replacement and richness difference components. In general, the richness difference component of ground beetles responded strongly to latitude and associated climatic variables, whereas the replacement component of diving beetles varied strongly along the same geographical gradient.

Main conclusions: Our findings suggest that the study of the determinants of biodiversity patterns benefits from the partitioning of beta diversity into different components and from comparing terrestrial and aquatic groups. For example, our findings suggest that the strong climatic and land use-related gradients in beta diversity have important implications for predicting and mitigating the effect of ongoing global change on the composition of regional biotas.

KEYWORDS

biodiversity, climate, generalized dissimilarity modelling, land cover, land use, mean annual temperature.

1 | INTRODUCTION

Owing to the fact that ongoing global change is threatening the diversity of populations, species and assemblages (Sala *et al*., 2000; Heino *et al*., 2009), understanding the factors underlying spatial variation of biodiversity remains at the heart of biogeography, ecology and conservation biology. However, different components of biodiversity may respond differently to global change and natural environmental variation (Socolar *et al*., 2016). Species diversity can be decomposed into alpha, beta and gamma components (Whittaker, 1960), all of which may respond to various historical, environmental and geographical factors (Mittelbach, 2012). While most previous studies focused on patterns in alpha or gamma diversity (Hillebrand, 2004; Field *et al*., 2009), beta diversity has received considerable renewed interest in recent years (Tuomisto, 2010; Anderson *et al*., 2011).

Beta diversity can be defined as the variation in assemblage composition among sampling units or the extent of change in assemblage composition along gradients (Legendre *et al*., 2005; Tuomisto *et al*., 2006), and it can further include different components (e.g. replacement and richness difference components; Podani & Schmera, 2011). Species replacement is related to factors affecting changes in species identities between sites, whereas richness difference informs about factors determining differences in the number of species (Legendre, 2014). However, given the paucity of empirical studies using this approach (Baiser *et al*., 2012; Tonial *et al*., 2012; Vad *et al*., 2017), it is difficult to (i) make conclusions about the relative importance of these components, and (ii) if these components respond differently to environmental and geographical gradients. An alternative approach would be to decompose total beta diversity into turnover and nestedness components (Baselga, 2010), but we opted to focus on the replacement and richness difference components (Podani & Schmera, 2011) because we were interested in any variation related to richness differences between sites instead of nestedness-related patterns (Carvalho *et al.* 2012; Legendre, 2014).

Although beta diversity is gaining increasing interest among ecologists and biogeographers, comparative studies on beta diversity patterns between biological assemblages inhabiting contrasting environments are mostly lacking (but see Fattorini, 2010; Heino & Alahuhta, 2015). For example, terrestrial assemblages are typically driven by climate-related variables (e.g., Hortal *et al.*, 2011), whereas local habitat conditions, such as water quality, often structure variation in aquatic assemblages even at broad spatial scales (e.g., Alahuhta, 2015). One possible explanation may be that not only the terrestrial ecosystems are directly influenced by climate (i.e. air temperature), whereas actual water temperature is naturally more important than air temperature to aquatic organisms (e.g. water may buffer extreme changes in air temperatures), but also the role of water is fundamentally different for aquatic species distributions (e.g., Heino, 2011). For instance, terrestrial assemblages are mainly affected by the accessibility of water in the ground for primary producers, drinking water for animals and different moisture conditions for different animal species (e.g., Begon *et al*., 2006), whereas the survival of aquatic species depends more on the quality and movement of water in freshwater environments (Wetzel, 2001; Allan & Castillo, 2007). Because the underlying structuring factors for terrestrial versus aquatic assemblages do not necessarily co-vary geographically, aquatic organisms can be used to disentangle and contrast some of the mechanisms believed to underlie the most pervasive diversity patterns in the world (Brown, 2014).

Beetles are a hyperdiverse group of insects, with different families inhabiting terrestrial, semi-aquatic and aquatic environments (Thomas, 2008). A highly diverse terrestrial family of beetles, ground beetles (Coleoptera: Carabidae), has been studied from ecological, evolutionary and biogeographical perspectives for a long time (Lindroth, 1985; Lövei & Sunderland, 1996; Dajoz, 2002; Kotze *et al.*, 2011). Previous studies have found clear geographical patterns in their regional diversity and assemblage composition, which have been associated with concurrently varying climate conditions (Heino & Alahuhta, 2015). In particular, temperature and humidity are two important environmental factors influencing the behaviour and ecology of ground beetles (e.g., Rainio & Niemelä, 2003), for which reason these insects are regarded as a model group for research on the effects of climate change (e.g., Müller-Kroehling, 2014). For example, temperature may influence their flight, speed of digestion, larval survival and life-history phenology (Thiele, 1977; Butterfield, 1996; Lövei and Sunderland, 1996), whereas humidity may be important in regulating behavioural patterns and habitat affinity (e.g., Kagawa & Maeto, 2009). However, landscape features and more localised environmental variations also affect the distributions of ground beetles (Thiele, 1977; Lindroth, 1985; Lövei & Sunderland, 1996). Ground beetle assemblages are strongly influenced by habitat structure, especially as reflected by vegetation (Brose 2003; Koivula *et al.*, 1999; Taboada *et al.* 2008; Koivula, 2011). Thus, ground beetle assemblages host species characteristic of particular habitats, reflect variation in structural features (e.g. soil characteristics), and may be particularly sensitive to anthropogenic alterations (Rainio & Niemelä, 2003; Koivula, 2011). For these reasons, ground beetle distributional patterns can be strongly influenced by land use (Eyre *et al.*, 2003; Eyre & Luff, 2004; Kotze *et al.*, 2011). Thus, it is important to examine the influence of land cover on ground beetle assemblages in a broad-scale biogeographical context (Heino & Alahuhta, 2015). A highly diverse aquatic family of beetles, diving beetles (Coleoptera: Dytiscidae), has also been the focus of numerous ecological and biogeographical studies. Some studies, addressed to associate their distributions and diversity to local environmental variables, have emphasised that diving beetle assemblages are mostly driven by vegetation characteristics, invertebrate prey abundance, fish predation and geographical location of water bodies (Nilsson, Elmberg and Sjöberg, 1994; Nilsson & Söderberg, 1996). On the other hand, studies at broad scales have suggested that assemblage composition of diving beetles is mostly driven by climatic variables, with additional influences by landscape features (Heino & Alahuhta, 2015). However, no previous study has aimed to find out if and how geography, climate, land cover and anthropogenic land use variables affect the replacement and richness difference components of beta diversity in these two major beetle groups inhabiting different environments.

Here, we focused on the beta diversity of ground beetles and diving beetles through examining the responses of total beta diversity and its replacement and richness difference components to climate, land cover and geographical gradients across Northern Europe. Our previous study found that both ground beetle and diving beetle assemblages were mostly driven by mean annual temperature and, secondarily, by various other climatic and land cover variables (Heino & Alahuhta, 2015). However, it is still not clear whether this assemblage differentiation across Northern Europe is manifested by species replacement, richness difference or both, and whether the identified ecogeographical drivers have similar effects on these beta diversity components. In our previous study, we used constrained ordination and constrained clustering methods, and did not examine the drivers of replacement and richness difference components. In the present study, we expected that (i) the replacement component would be driven by land cover and land use variables (because species composition typically shows turnover along long environmental gradients; e.g., Gaston & Blackburn, 2000; Qian & Ricklefs, 2012; König *et al.*, 2017) and (ii) the richness difference component would be driven by geographical and climatic variables (because history and climate shape variation in species richness at large scales; e.g., Hillebrand, 2004; Field *et al.*, 2009). In the final stage, we mapped the observed responses of beta diversity and its components to show their broad-scale latitudinal and longitudinal patterns in Northern Europe. Our findings should contribute to discussion of the ongoing global change effects on insect biodiversity in high-latitude areas.

2 | METHODS

2.1 | Study area

We analysed beetle distribution and environmental data derived from the 101 biogeographic provinces belonging to Denmark, Sweden, Norway and Finland (Väisänen *et al.*, 1992; Väisänen & Heliövaara, 1994). Prior to the analyses, we merged various small coastal provinces in Norway to provide a better and more accurate representation of species ranges (Heino & Alahuhta, 2015; Heino *et al*., 2015). After these modifications, the number of provinces remaining in the analyses was 79. Each province has typical characteristics of climate and land cover, and “biogeographic province” is thus a relatively homogeneous study unit. We used the 79 provinces as sampling units (i.e. grain size), and all the species found in a biogeographic province were pooled to represent a single assemblage.

2.2 | Species data

We analysed the same literature data as in Heino and Alahuhta (2015) for two adephagan beetle groups: ground beetles (Carabidae; Lindroth, 1985; 1986) and diving beetles

(Dytiscidae; Nilsson & Holmen, 1995). Ground beetles are mainly terrestrial insects, which are predatory, omnivorous, granivorous or herbivorous species as adults and mostly predatory as larvae (Lindroth, 1985; Lövei & Sunderland, 1996; Dajoz, 2002). Diving beetles live in fresh waters and sometimes in brackish waters, and they are mostly predatory as larvae and predators or scavengers as adults (Nilsson & Holmen, 1995). These two beetle groups are relatively species rich in Northern Europe. However, Carabidae comprised more species (total number of species = 388; mean number of species per province = 159, sd = 56.9) than Dytiscidae (total number of species = 155; mean = 78.9, sd = 19.3; paired t-test; $p < 0.001$) based on the literature data (Lindroth, 1985, 1986; Nilsson & Holmen, 1995). Although these biological data are already rather old, they represent good information about species distributions across Northern Europe and can be easily associated with predictor variable data derived for a period between 1960s and 1990s. Although additional beetle distributional data may be available in more recent faunistic publications, we opted to not use them because our predictor variable are older in comparison to these recent assessments. The presence-absence data we used are based on various faunistic and ecological surveys across Northern Europe and comprise the work of a large number of scientists and amateur entomologists. For this reason, the sampling effort might be different among the provinces to an unknown extent, and this variation cannot be accounted for in the present analyses. However, the very long time of sampling effort, the multitude of people that collected data, the variety of used techniques and sampled habitats, and the relatively small number of species occurring in the study area, suggest that faunal inventories were comprehensive by the dates the books were published.

2.3 | Predictor variables

Among the multiple correlated climatic variables available in WorldClim (Hijmans *et al*., 2005), we selected those that are presumably the most important for insect distributions. These climate variables were: average annual temperature (°C), maximum temperature of the warmest month (°C), minimum temperature of the coldest month (°C), precipitation of the wettest month (mm) and precipitation of the driest month (mm). The climate variables were averaged values for the period 1960-1990 for each biogeographical province and were derived from WorldClim with 0.93 km × 0.93 km resolution (Hijmans *et al*., 2005). Because most of the aforementioned climate variables were strongly intercorrelated ($r \geq 0.80$), we used only average annual temperature and precipitation of the wettest month in the statistical analyses. These two are also conceptually the most important climatic variables affecting biodiversity at high latitudes. Land cover and land use variables were percentages of fresh water, forests, open areas, wetlands, agricultural areas and urban areas. These variables were obtained from European CORINE 2006 with 100m resolution. For the suitability of CORINE-based land use and land cover variables in these types of studies in northern Europe, see Heino & Alahuhta (2015). Although the land cover data is from the mid-2000s, most drastic changes in the land cover happened in Northern Europe between 1950 and 1980, when the current road and peatland drainage networks were established and a large proportion of people moved from the countryside to urban environments (Seppälä, 2005). Development of agriculture changed landscapes already thousands of years ago in Southern Fennoscandia (Eriksson *et al*., 2002), after which changes in the quantity of agricultural land has been considerably modest. Finally, average elevation and elevation range within the province were also considered as land cover variables, as these variables are related to the environmental variation along elevation gradients. Elevation variables were obtained from 3D Digital Elevation Model over Europe with 25m resolution. Because these two variables were strongly correlated ($r = 0.95$), only average elevation was used in the statistical analysis.

2.4. | Statistical methods

We first calculated beta diversity components for each beetle group based on Jaccard dissimilarity coefficient. We thus followed the approach devised by Podani & Schmera (2011) and Carvalho *et al*. (2012). In this scheme, total beta diversity is decomposed into replacement and richness difference components: **Btotal** = **Brepl** + **Brich**. **Btotal** reflects both species replacement and loss-gain; **Brepl** refers to replacement of species identities alone, and **Brich** relates to species loss-gain or richness differences alone. A recent review found this decomposition a suitable approach for addressing complex issues in beta diversity (Legendre, 2014). We thus produced dissimilarity matrices based on each of the three components for each beetle group using the 'beta' function in the R package BAT (Cardoso *et al*., 2015).

Second, we modelled variation in biological dissimilarities using Generalized Dissimilarity Modelling (GDM: Ferrier *et al.*, 2007). GDM is a technique for modelling spatial variation in assemblage composition between pairs of geographical locations, and it can be based on any dissimilarity matrix as response. These were, in our case, pairwise Btotal, Brepl and Brich dissimilarity matrices for each beetle group. GDM is based on matrix regression, and it can accommodate nonlinearities typical in ecogeographical datasets. These nonlinearities occur for two reasons: (i) the curvilinear response between increasing ecological distance and observed compositional dissimilarity, and (ii) the variation in the rate of compositional dissimilarity at different position along ecogeographical gradients (Ferrier *et al.*, 2007). It is thus a highly useful technique for large-scale assessments of assemblage composition. In consistency with other generalized linear models, the GDM model is specified based on two functions: (i) a link function (in our case, 1-exp[y]) defining the relationship between the response (i.e. compositional dissimilarity between sites) and the linear predictor (i.e. inter-site distances based on any ecogeographical variable, including geographical distance between sites), and (ii) a variance function defining how the variance of the response depends on the predicted mean (Ferrier *et al*., 2007). We ran the GDM models, plotted the I-splines (which are monotone cubic spline functions) for each predictor variable (and geographical distance) and assessed the impacts of the predictor variables (which are estimated as the variance explained by the predictor when all the others are kept constant) on the response dissimilarities using the functions ‘gdm’ and ‘gdm.varImp’ available in the R package gdm (Manion *et al*., 2017). Prior to running GDMs, we checked for multicollinearity among the predictor variables. The highest correlation was between agriculture and mean annual temperature (Pearson $r = 0.80$), but the other correlations were lower ($r < 0.70$ or $r > - 0.70$). Hence, we did not remove any of the predictor variables shown in the final models. Also, GDM is known to be robust to multicollinearity among predictor variables (e.g., Glassman *et al*., 2018). We did not standardize the predictor variables in our focal analyses, as a number of authors have followed a similar approach (e.g., Fitzpatrick *et al*., 2013), and because this facilitates understanding variation in beta diversity along actual environmental gradients. However, we also ran the analyses using standardized predictor variables (mean = 0, SD = 1), but the main inferences did not change (i.e. the same predictor variables were the most important irrespective of whether or not we standardized the variables, and the explained deviance did not differ too much between the two approaches). For all above analyses, we assessed the uncertainty in the fitted I-splines by plotting I-splines with error bands using a bootstrapping approach (Shyrock *et al*., 2015). We used 100 iterations in bootstrapping, and 70% of the sites were retained from the full site-pair table when subsampling the data.

Third, we produced RGB colour maps using province scores from three non-metric multidimensional (NMDS) axes simultaneously. NMDS is considered as a highly robust unconstrained ordination method that can be utilised in ecology and biogeography (Minchin, 1987). For our present purpose, we ran 20 3-dimensional NMDS solutions based on random starts, and selected for mapping the solution of three NMDS axes with the lowest stress value. These NMDS axes were calculated separately based on total beta diversity, replacement and richness difference dissimilarity matrices for each beetle group using the function 'metaMDS' with the R package vegan (Oksanen *et al.*, 2017). The stress values were acceptable and ranged from 0.016 to 0.199, with the exception of the replacement component-related ordination of ground beetles for which the stress value was 0.242. The colour mapping routines were conducted using the functions 'recluster.col' and 'recluster.plot.sites.col' from the R package recluster (Dapporto *et al.*, 2015) and the results were plotted on the maps of the study area.

Finally, we used GDM to examine latitudinal and longitudinal patterns in total beta diversity and its components across the study area. We thus ran GDM to regress each dissimilarity matrix, **Btotal**, **Brepl** and **Brich**, with both latitudinal distance and longitudinal distance. We again used bootstrapping as above to assess the uncertainty in the resulting I-splines.

3 | RESULTS

Regarding the decomposition of total beta diversity into replacement and richness difference components, there were no clear differences between ground beetles and diving beetles (Fig. 1). Total beta diversity hardly differed between the beetle groups, with average values being very similar (ground beetles: 0.52; diving beetles: 0.49). However, while the richness difference component was slightly more important than the replacement component for ground beetles (average replacement = 0.23, average richness difference = 0.29), the opposite was true for diving beetles (average replacement = 0.28, average richness difference = 0.21).

There were some differences in the explained deviance between the beetle groups and the components of beta diversity when using the selected 10 predictor variables (Table 1). Total beta diversity of ground beetles was slightly better explained than that of diving beetles, but the opposite was true for the replacement component. The richness difference component of ground beetles was slightly better explained than that of diving beetles.

The total beta diversity of ground beetles was best explained by geographical distance, followed by mean annual temperature, urban land use and open areas (Table 1). Of these variables, geographical distance and mean annual temperature had almost linear relationships with beta diversity variation, urban areas first had an increasing relationship and then reached a plateau, and open areas had a slightly curvilinear increasing relationship (Supporting Information, Fig. S1). Other variables had only weak or no relationships with total beta diversity of ground beetles. The replacement component of ground beetles was most strongly impacted by geographic distance, followed by precipitation, mean annual temperature, forest cover and wetland cover (Fig. S2). Of these, geographic distance showed a relationship that first increased rapidly after which the pattern levelled off. Mean annual temperature had a closely similar relationship to that of geographic distance, and the other important variables had slightly curvilinear increasing impacts on the replacement component. The richness differences component of ground beetles was most clearly related to urban land use and mean annual temperature, of which the former had a very steep increasing effect that decreased with higher urban land uses (Fig. S3). Mean annual temperature had almost a linear relationship with the richness difference component.

The total beta diversity of diving beetles was mostly impacted by precipitation, followed by mean annual temperature and open areas (Table 1). These variables showed slightly curvilinear, almost sigmoidal and almost linear relationships, respectively, with total beta diversity (Fig. S4). The replacement component of diving beetles was mostly related to mean annual temperature and geographic distance, which had almost linear relationships with this component (Fig. S5). Finally, the richness difference component was mostly driven by precipitation, followed by open areas and urban land use. These variables showed slightly curvilinear relationships with richness difference (Fig. S6).

The NMDS-based maps of total beta diversity and its replacement and richness difference components showed some differences (Fig. 2). While total beta diversity varied quite similarly along latitudinal and longitudinal gradients across Northern Europe, the replacement and richness difference components showed some striking differences between the two beetle groups. The replacement component of ground beetles and diving beetles showed clear differences between Denmark and southern Sweden, whereas the richness difference component showed different patterns for ground beetles and diving beetles. As a result, ground beetles showed a latitudinal gradient in richness difference, whereas a longitudinal gradient was more pronounced in the case of diving beetles across the provinces based on visual inspections.

The visual inspections were also largely corroborated by the results of additional GDMs, with total beta diversity being strongly related to latitude in both beetle groups, whereas the replacement and richness difference components showed differences between the beetle groups (Fig. 3). For ground beetles, the richness difference component was strongly correlated to latitude, whereas the replacement component of diving beetles showed a strong relationship with latitude. These relationships were almost linear. There was also a major geographical break in the replacement component of ground beetles at latitude of 62^{o}N to

63°N, after which the species compositional variation increased rapidly (Fig. 3b). Similarly, there was a clear break, followed by a plateau, in the richness difference component of diving beetles at a longitude of 10°E to 11°E (Fig. 3f). These visual inspections were corroborated by the numerical results of the GDM analysis (Table 2).

4 | DISCUSSION

There is a substantial lack of studies that have compared the beta diversity patterns of multiple insect groups based on the same study units and identical statistical methods (Fattorini, 2010; Heino & Alahuhta, 2015). Here, we contrasted biogeographical patterns in the total beta diversity and its replacement and richness difference components for terrestrial (ground beetles) and aquatic (diving beetles) insects.

We found that different factors drove the most variation in the assemblages of ground beetles and diving beetles, and these differences were also contingent on the beta diversity measure in question. Total beta diversity of ground beetles responded most strongly to (i) geographic distance between provinces, which expresses the importance of biogeographical and historical factors (such as the presence of geographical barriers, the distribution of suitable habitats, and the effects of glaciations); (ii) mean annual temperature, indicating the role of current climatic forcing; and (iii) urban land use, suggesting that provinces with varying degrees of urbanization harbour different ground beetle assemblages. For diving beetles, total beta diversity was mostly related to (i) precipitation of the wettest month, describing a gradient from the Atlantic coast of Norway in the west to continental areas in Eastern Finland in the east; (ii) mean annual temperature, which varies markedly from south to north across the study area (Heino *et al.*, 2015); and (ii) open areas, implying that the provinces having open areas versus forested areas harbour different diving beetle assemblages. The weak impact of geographical distance in diving beetles may be due to their dispersal capabilities. Diving beetles live in spatially discrete and sometimes ephemeral habitat patches, and many species are therefore assumed to be very active dispersers, able to move between suitable localities sometimes even on multiple occasions within an individual's lifetime (Bilton, 2014). Although large-sized ground beetles move relatively speedily on the ground, being able to disperse over distances in the order of kilometres, and many species are able to fly, high habitat fragmentation and geographical barriers are known to prevent many species from colonizing most habitat patches (Kotzke *et al*., 2011; Elek *et al*., 2014). This can be especially true for flightless ground beetle species, which are constrained by habitat fragmentation at larger spatial scales. For these cases, geographical distance is likely to exert increased importance in comparison to diving beetles that are better dispersers, as observed in our study.

The few previous studies that have decomposed total beta diversity into the replacement and richness difference components have found that their relative importance varies among study systems and organisms (Baiser *et al*., 2012; Tonial *et al*., 2012; Victorero *et al*., 2018). Using an alternative approach to partition beta diversity into the turnover and nestedness components (Baselga, 2010), Soininen *et al*. (2018) observed that the turnover component was clearly more important that the nestedness component in a meta-analysis of 269 data points. This finding is similar to that of a global comparative study of lake macrophytes that showed the preponderance of the turnover component over the nestedness component (Alahuhta *et al*., 2017). In our study, the predictors of the replacement component varied somewhat between the two beetle groups. For ground beetles, geographic distance was by far the most important variable affecting differences in species composition between provinces. This effect is plausible given the rather large geographical area and the legacy of historical influences in the study region (e.g. post-Ice Age colonization may still be ongoing; Hortal *et al*., 2011). Geographical distance was followed by precipitation, mean annual temperature, forest cover and wetland cover. These variables were likely to be related to effects of climate and habitat differences on species composition, as already observed in previous accounts on ground beetle distributions in the study area (Lindroth 1985, 1986). For diving beetles, the replacement component was mostly driven by mean annual temperature and geographic distance, suggesting strong south-north changes in species identities along a temperature gradient. These findings are in accordance with previous accounts of species distributions, emphasising that diving beetles are sensitive to temperature that may strongly contribute to their distributions at both local and regional scales (Nilsson & Holmen, 1995; Heino & Alahuhta, 2015).

The variables best explaining the richness difference components of ground beetles and diving beetles were strikingly different. While the richness difference component of ground beetles was mostly related to urban land use (impact: 10.8) and mean annual temperature (impact: 3.4), that of diving beetles was mostly impacted by precipitation (impact: 28.8) and cover of open areas (impact: 11.9). These findings suggest that species loss-gain occurs mostly along urbanization and temperature gradients in ground beetles, with more species occurring in southernmost provinces with a higher urban land use cover than in more northerly provinces in the study area. While the positive effect of temperature on species richness is consistent with geographical patterns observed in most organisms (Currie *et al*., 2004; Hawkins *et al*., 2004; Lomolino *et al*., 2010), the increase of ground beetle richness with urbanization is counter-intuitive, because urbanization has typically negative effects on insect diversity (McKinney, 2002; Martinson & Raupp, 2013; New, 2015). This unexpected positive association can be explained by assuming that species richness and human settlements both respond positively to energy availability, because the higher the energy, the greater the biomass and the number of individuals to be sustained, which, in turn, allow more species to maintain viable populations within an area (Gaston, 2005; Evans & Gaston, 2005). Thus, it can be hypothesised that early human populations settled in a clumped fashion and grew more readily in the warmer and more productive areas represented by southern provinces, where there is high abundance and diversity of plants and animals that can be used as food or for other purposes, and where climate is milder. This hypothesis is supported by the fact that the richness difference component of ground beetles was also related to mean annual temperature, which increases southwards. As regards the negative effects of urbanization, they can really operate, but their influence may be masked at coarse spatial resolutions as that used in this study, because remnants of suitable biotopes can be found even where human population density is high (Fattorini *et al*., 2016).

We also found that latitude strongly affected the richness difference component of beta diversity in ground beetles, but not so much in diving beetles. The effects of recolonization after the Ice Age are expected to be higher for the richness difference component (see also Hortal *et al.*, 2011), since few species (especially the most tolerant and mobile) were able to recolonize or disperse to areas strongly affected by historical climatic changes, especially those located at high latitudes (Fattorini & Ulrich, 2012a; 2012b). Thus, the influence of latitude on the richness difference component of beta diversity of ground beetles is consistent with the hypothesis that the spatial distribution of dispersal-limited species is still significantly affected by historical processes, as observed for ground beetles (see also Schuldt & Assmann, 2009). By contrast, the possible impact of Ice Age history on the current distribution of diving beetles seems to have been erased by their ability to long dispersal to reach scattered suitable habitat patches. In diving beetles, species loss-gain most likely occurs along a gradient from coastal (higher precipitation) to continental (lower precipitation) provinces. Especially the amount of precipitation may influence habitat availability and habitat types for diving beetles, with temporary ponds and pools, as important habitats for some diving beetle species (Nilsson & Holmen, 1995), being probably uncommon in provinces with continuously high precipitation. In addition, water level fluctuations in permanent lakes and rivers may affect aquatic vegetation, thereby affecting habitat availability for diving beetles. Finally, increased precipitation may result in nutrient leaching to aquatic ecosystems (Soininen *et al*., 2015), which influences the chemical environment for diving beetles and might therefore affect their geographical distributions. Thus, in addition to historical influences, present-day latitudinal and longitudinal distributions of beetles may also be affected by environmental factors that vary geographically (Heino & Alahuhta, 2015). Disentangling the effects of Ice Age history and contemporary environmental conditions may be especially difficult in a region, such as Northern Europe, where these two sets of factors co-vary strongly geographically.

Our findings showed that the magnitudes of beta diversity changes varied depending on the beta diversity component considered and in relation to the main habitat of the studied beetle groups. These findings suggest that the analysis of the determinants of biodiversity patterns will benefit from the partitioning of beta diversity into different components (Podani & Schmera, 2011; Legendre, 2014), as these components are determined by different ecogeographical factors in animals inhabiting contrasting environments. Knowing which ecogeographical factors affect present-day biodiversity patterns is also a prerequisite for predicting alterations in species distributions in the face of global change. For example, the presence of strong climatic gradients in beta diversity have important implications for predicting, adapting and mitigating the effect of ongoing climate change on the composition of biological assemblages: (i) the species composition in areas of cold climates will likely become to resemble that currently present in more southerly regions (Hickling *et al*., 2006) and (ii) some species with northern distributions may go extinct with climate change

(Thomas *et al*., 2006). However, these two topics deserve further and more direct modelling studies in the context of hyperdiverse insect groups. Although we analysed patterns at the scale of biogeographic provinces, our findings do point out that various factors should be taken into account in the conservation biogeography of highly diverse organism groups in terrestrial and aquatic realms to facilitate understanding nuances in biodiversity patterns.

REFERENCES

Alahuhta, J. (2015) Geographic patterns of lake macrophyte communities and species richness at regional scale. *Journal of Vegetation Science,* **26,** 564-575.

Alahuhta, J., Kosten, S., Akasaka, M., Auderset, D., Azzella, M., Bolpagni, R., Bove, C.P., Chambers, P.A., Chappuis, E., Ilg, C., Clayton, J., de Winston, M., Ecke, F., Gacia, E., Gecheva, G., Grillas, P., Hauxwell, J., Hellsten, S., Hjort, J., Hoyer, M.V., Kolada, A., Kuoppala, M., Lauridsen, T., Li, E.-H., Lukács, B.A., Mjelde, M., Mikulyuk, A., Mormul, R.P., Nishihiro, J., Oertli, B., Rhazi, L., Rhazi, M., Sass, L., Schranz, C., Søndergaard, M., Yamanouchi, T., Yu, Q., Wang, H., Willby, N., Zhang, X.-K. & Heino, J. (2017) Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. *Journal of Biogeography,* **44,** 1758-1769.

Allan, J.D. & Castillo, M.M. (2007) *Stream Ecology. Structure and Function of Running Waters*. Second Edition. Springer, New York.

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N.

J., Stegen, J. C. & Swenson, N. G. (2011), Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14,** 19-28.

Baiser, B., Olden, J.D., Record, S., Lockwood, J.L., & M.L. McKinney (2012) Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society B: Biological Sciences*, **279,** 4772-4777.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19,** 134-143.

Begon, M., Townsend, C.R., Harper, J.L. (2005) *Ecology: From Individuals to Ecosystems*. fourth Edition. Wiley-Blackwell, Oxford.

Bilton, D.T. (2014) Dispersal in Dytiscidae, In: Donald, E. (ed.) *Ecology, Systematics, and the Natural History of Predaceous Diving Beetles (Coleoptera: Dytiscidae)*, pp.387-407. Springer, New York.

Brose, U. (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, **135,** 407-413.

Brown, J.H. (2014) Why are there so many species in the tropics? *Journal of Biogeography*, **41,** 8-22.

Butterfield, J.E. (1996) Carabid life-cycle strategies and climate change: a study on an altitude transect. *Ecological Entomology*, **21,** 9-16.

Cardoso, P., Rigal, F. & Carvalho, J. C. (2015) BAT – Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, **6,** 232-236.

Carvalho, J.C., Cardoso, P. & Gomes, P. (2012) Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, **21,** 760-771.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7,** 1121e1134.

Dajoz, R. (2002) *Les Coléoptères Carabides et Ténébrionidés. Ecologie et Biologie*. Lavoisier, Paris.

Dapporto, L., Ramazzotti, M., Fattorini, S., Vila, R., Talavera, G. & Dennis, R.H.L. (2015) Package 'recluster'. Ordination Methods for the Analysis of Beta-Diversity Indices. Version 2.8. https://cran.r-project.org/web/packages/recluster/recluster.pdf

Elek, Z., Drag, L., Pokluda, P., Čížek, L.& Bérces, S. (2014) Dispersal of individuals of the flightless grassland ground beetle, *Carabus hungaricus* (Coleoptera: Carabidae), in three populations and what they tell us about mobility estimates based on mark-recapture. *European Journal of Entomology*, **111,** 663-668.

Eriksson, O., Cousins, S.A.O. & Bruun, H.H. (2002) Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science*, **13,** 743-748.

Eyre, M.D., Luff, M.L., Staley, J.R. & Telfer, M.G. (2003) The relationship between British ground beetles (Coleoptera, Carabidae) and land cover. *Journal of Biogeography*, **30**, 719-730.

Eyre, M.D. & Luff, M.L. (2004) Ground beetle species (Coleoptera, Carabidae) associations with land cover variables in northern England and southern Scotland. *Ecography*, **27,** 417-426.

Evans, K.L. & Gaston, K.J. (2005) People, energy and avian species richness. *Global Ecology and Biogeography*, **14,** 187-196.

Fattorini, S. (2010) The influence of geographical and ecological factors on island beta diversity patterns. *Journal of Biogeography*, **37,** 1061-1070.

Fattorini, S. & Ulrich, W. (2012a) Drivers of species richness in European Tenebrionidae (Coleoptera). *Acta Oecologica*, **36,** 255-258.

Fattorini, S. & Ulrich, W. (2012b) Spatial distributions of European Tenebrionidae point to multiple postglacial colonization trajectories. *Biological Journal of the Linnean Society, London*, **105,** 318-329.

Fattorini, S., Galassi, D.M.P. & Strona, G. (2016) When human needs meet beetle preferences: tenebrionid beetle richness covaries with human population on the Mediterranean islands. *Insect Conservation and Diversity*, **9,** 369-373.

Ferrier, S., Manion, G., Elith, J. & Richardson, K. (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, **13,** 252-264.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36,** 132-147.

Fitzpatrick, M.C., Sanders, N.J., Normand, S., Svenning, J.C., Ferrier, S. Gove, A.D. & Dunn, R.R. (2013) Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. *Proceedings of the Royal Society B*, **280,** 20131201.

Gaston, K.J. (2005) Biodiversity and extinction: species and people. *Progress in Physical Geography*, **29,** 239-247.

Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and Process in Macroecology*. Blackwell Science, Oxford.

Glassman, S.I., Wang, I.J. & Bruns, T.D. (2017) Environmental filtering by pH and soil nutrients drives community assembly in fungi at fine spatial scales. *Molecular Ecology*, **26,** 6960-6973.

Hawkins, B.A. & Diniz-Filho, J.A.F. (2004) 'Latitude' and geographic patterns in species richness. *Ecography*, **27,** 268-272.

Heino, J. (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biology,* **56,** 1703–1722.

Heino, J. & Alahuhta, J. (2015) Elements of regional beetle faunas: faunal variation and compositional breakpoints along climate, land cover and geographical gradients. *Journal of Animal Ecology,* **84,** 427-441.

Heino, J., Alahuhta, J. & Fattorini, S. (2015) Phylogenetic diversity of regional beetle faunas at high latitudes: patterns, drivers and chance along ecological gradients. *Biodiversity and Conservation,* **24,** 2751-2767.

Heino, J., Virkkala, R. & Toivonen, H. (2009) Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews,* **84,** 39-54.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R. & Thomas, C. D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12,** 450-455.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25,** 1965-1978.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American Naturalist*, **163,** 192-211.

Hortal, J., Diniz-Filho, J. A., Bini, L. M., Rodríguez, M. Á., Baselga, A., Nogués-Bravo, D., Rangel, T. F., Hawkins, B. A. & Lobo, J. M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741-748.

Kagawa, Y. & Maeto, K. (2014) Ground beetle (Coleoptera: Carabidae) assemblages associated with a satoyama landscape in Japan: the effects of soil moisture, weed height, and distance from woodlands. *Applied Entomology and Zoology*, **49,** 429-436.

Koivula., M., Punttila., P., Haila, Y. & Niemelä, J. (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography*, **22,** 424-435.

Koivula, M. (2011) Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys*, **100,** 287-317.

König, C., P. Weigelt, P. & Kreft, H. (2017) Dissecting global turnover in vascular plants. *Global Ecology and Biogeography*, **26,** 228-242.

Kotze, D. J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M. J., Lövei, G. L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R. & Zetto, T. (2011) Forty years of carabid beetle research in Europe - from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. *ZooKeys*, **100,** 55-148.

Legendre, P. (2014) Replacement and richness difference components. *Global Ecology and Biogeography*, **23,** 1324-1334.

Legendre, P., Borcard, D. & Peres-Neto, P. R. (2005) Analyzing beta diversity: Partitioning the spatial variation of community data. *Ecological Monographs*, **75,** 435-450.

Lindroth, C.H. (1985) The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, **15,** 1-225.

Lindroth, C.H. (1986) The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, **15,** 226-497.

Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010) Biogeography. Fourth Edition. Sinauer, Sunderland.

Lövei, G. L. & Sunderland, K. D. (1996) Ecology and behaviour of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, **41,** 231–256.

Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D., Mokany, K. & Fitzpatrick, M.C. (2017) gdm: Generalized Dissimilarity Modeling. R package version 1.3.4. https://CRAN.R-project.org/package=gdm

Martinson, H. M. & Raupp, M.J. (2013) A meta-analysis of the effects of urbanization on ground beetle communities. Ecosphere 4: 60. http://dx.doi.org/10.1890/ES12-00262

McKinney, M.L. (2002) Urbanization, biodiversity and conservation. *BioScience*, **52,** 883-890.

Minchin, P.R. (1987) An evaluation of relative robustness of techniques for ecological ordinations. *Vegetatio,* **69,** 89-107.

Mittelbach, G.G. (2012) *Community Ecology*. Sinauer, Sunderland.

Müller-Kroehling, S., Jantsch, M.C., Fischer, H.S., & Fischer, A. (2014) Modelling the effects of global warming on the ground beetle (Coleoptera: Carabidae) fauna of beech forests in Bavaria, Germany. *European Journal of Entomology*, **111,** 35-49.

New, T. R. (2015) *Insect Conservation and Urban Environments*. Springer, New York.

Nilsson, A.N., Elmberg, J. & Sjöberg, K. (1994) Abundance and species richness patterns of predaceous diving beetles (Coleoptera, Dytiscidae) in Swedish lakes. *Journal of Biogeography,* **21,** 197-206.

Nilsson, A.N. & Holmen, M. (1995) The Aquatic Adephaga of Fennoscandia and Denmark 2. Dytiscidae. *Fauna Entomologica Scandinavica,* **32,** 1-188.

Nilsson, A.N. & Söderberg, H. (1996) Abundance and species richness patterns of diving beetles (Coleoptera, Dytiscidae) from exposed and protected sites in 98 northern Swedish lakes. *Hydrobiologia,* **321,** 83-88.

Oksanen, J., Blanchet, F.G., Kindt, Friendly, M., R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2017) vegan: Community Ecology Package. R package version 2.4-5. http://CRAN.R-project.org/package=vegan.

Podani, J. & Schmera, D. (2011) A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos*, **120,** 1625-1638.

Qian, H. & Ricklefs, R.E. (2012) Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Global Ecology and Biogeography*, **21,** 341-351.

Rainio, J. & Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity & Conservation*, **12,** 487-506.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. (2000) Global biodiversity scenarios for the year 2100. *Science*, **287,** 1770-1774.

Schuldt, A. & Assmann, T. (2009) Environmental and historical effects on richness and endemism patterns of carabid beetles in the western Palaearctic. *Ecography*, **32,** 705-714.

Seppälä, M. (ed). (2005). *The Physical Geography of Fennoscandia*. Oxford University Press. Oxford.

Shryock, D. F., Havrilla, C.A., DeFalco, L.A., Esque, T.C., Custer, N.A. & T. E. Wood (2015) Landscape genomics of *Sphaeralcea ambigua* in the Mojave Desert: a multivariate, spatially-explicit approach to guide ecological restoration. *Conservation Genetics,* **16,** 1303-1317.

Socolar, J.B.**,** Gilroy, J., W. Kunin, W. & Edwards, D. 2016. How should beta-diversity inform biodiversity conservation? *Trends in Ecology and Evolution*, **31,** 67-80.

Soininen, J., Bartels, P., Heino, J., Luoto, M. & Hillebrand, H. (2015) Toward more integrated ecosystem research in aquatic and terrestrial environments. *BioScience*, **65,** 174-182.

Soininen, J., Heino, J. & Wang, J. (2018) A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography,* **27,** 96-109.

Taboada, A., Kotze, D.J., Tárrega, R. & Salgado, J.M. (2008) Carabids of differently aged reforested pinewoods and a natural pine forest in a historically modified landscape. *Basic and Applied Ecology*, **9**, 161-171.

Thiele, H. U. (1977) *Carabid Beetles in Their Environments*. Springer, Berlin.

Thomas, C.D., France, A.M.A. & Hill J. K. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution*, **21,** 415-416.

Thomas, M.C. (2008) Beetles (Coleoptera). In: Capinera, J.L. (ed.) *Encyclopedia of Entomology.* Second edition, pp. 437-447. Springer, New York.

Tonial, M.L.S., Silva, H.L.R., Tonial, I.J., Costa, M.C., Silva Júnior, N.J. & Diniz-Filho, J.A.F. (2012) Geographical patterns and partition of turnover and richness components of beta-diversity in faunas from Tocantins river valley. *Brazilian Journal of Biology,* **72,** 497-504

Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33,** 2-22.

Tuomisto, H. and Ruokolainen, K. (2006) Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. *Ecology*, **87,** 2697-2708.

Väisänen, R. & Heliövaara, K. (1994) Hot-spots of insect diversity in northern Europe. *Annales Zoologici Fennici*, **31,** 71-81.

Väisänen, R., Heliövaara, K. & Immonen, A. (1992) Biogeography of northern European insects: province records in multivariate analysis (Saltatoria, Lepidoptera: Sesiidae; Coleoptera: Bubrestidae, Cerambycidae). *Annales Zoologici Fennici*, **28,** 57-81.

Vad, C. F., A. L. Péntek, N. J. Cozma, A. Földi, A. Tóth, B. Tóth, N. A. Böde, A. Móra, R. Ptacnik, É. Ács, K. Zsuga, and Z. Horváth (2017) Wartime scars or reservoirs of biodiversity? The value of bomb crater ponds in aquatic conservation. *Biological Conservation*, **209,** 253-262.

Victorero, L., Robert, K., Robinson, L.F., Taylor, M.L. & Huvenne, V.A.I. (2018) Species replacement dominates megabenthos beta diversity in a remote seamount setting. *Scientific Reports*, **8,** 4152.

Wetzel, R.G. (2001) *Limnology. Lake and River Ecosystems*. Third Edition. Academic Press, San Diego.

Whittaker, R. H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30,** 279-338.

DATA AVAILABILITY STATEMENT

The datasets utilized in this paper are accessible in published books (Lindroth, 1985; 1986; Nilsson & Holmen, 1995) and the WorldClim database (Hijmans *et al*., 2005).

Supporting Information

Additional Supporting Information can be found in the online version of this article.

Table 1. Summaries of the GDM models for each beetle group and component of beta diversity. Also, shown are the predictor variable impacts in each model.

	Ground beetles			Diving beetles		
	Total beta	Replacement	Richness diff	Total beta	Replacement	Richness diff
GDM deviance	48	144	252	68	162	273
Null deviance	339	181	488	338	350	487
Explained (%)	85.9	20.7	48.2	79.8	53.6	44.0
Intercept	0.177	0.091	0.076	0.165	0.033	0.083
Variable impacts						
Geographic distance	3.636	12.604	0.802	0.985	3.311	0.000
Urban	2.867	0.000	10.848	1.927	0.010	2.537
Agriculture	1.041	0.087	1.474	0.235	1.741	0.000
Forests	0.041	4.260	0.018	0.102	0.192	0.405
Open area	2.066	0.258	1.985	2.993	0.000	11.967
Wetlands	0.761	4.007	0.727	0.519	0.793	0.360
Water	0.000	1.063	0.000	0.000	0.948	0.000
Altitude	0.046	0.581	0.000	0.164	0.131	0.000
Mean annual temperature	2.995	4.575	3.418	3.614	8.705	0.000
Precipitation of wettest month	0.075	5.867	0.080	9.765	0.177	28.872

Table 2. Summaries of the GDM models for each beetle group and component of beta diversity, with only latitude and longitude used as predictor variables.

	Ground beetles			Diving beetles		
	Total beta	Replacement	Richness diff	Total beta	Replacement	Richness diff
GDM deviance	91.7	156	289	153	202	414
Null deviance	339	181	488	338	350	487
Explained (%)	72.9	14.1	40.8	54.7	42.2	14.9
Intercept	0.317	0.192	0.115	0.294	0.126	0.148
Variable impacts						
Latitude	92.873	14.687	33.185	74.922	20.678	18.413
Longitude	3.472	20.237	0.332	32.613	0.000	96.269

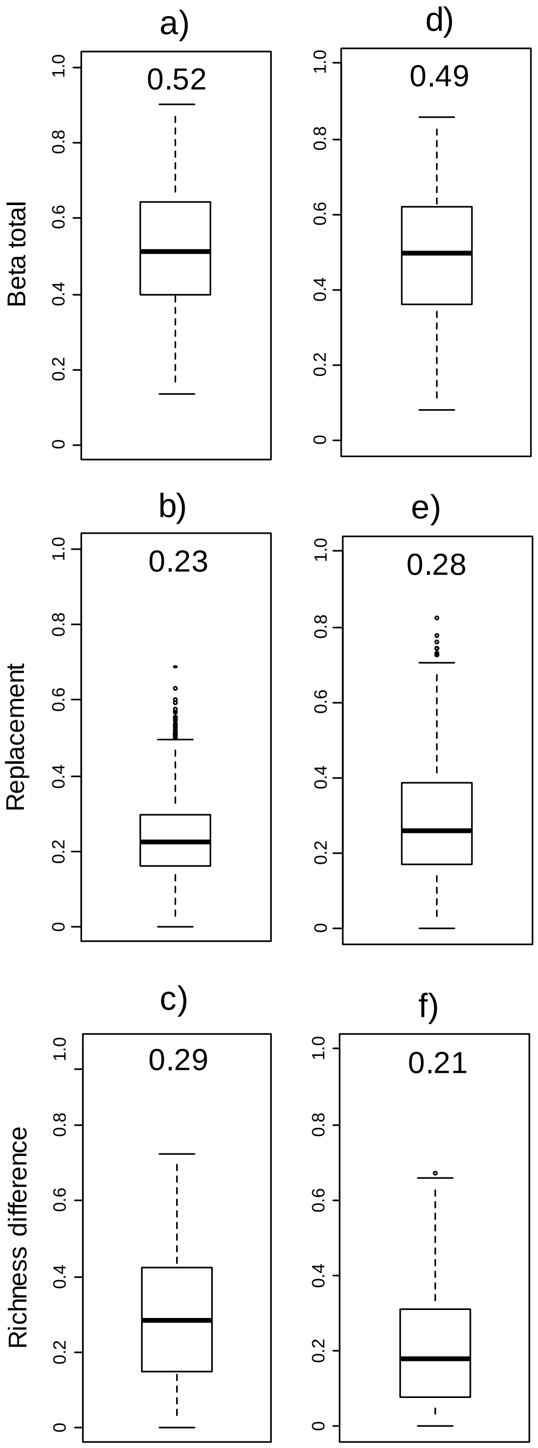

Fig. 1. Boxplots of median pairwise dissimilarities for total, replacement and richness difference component of ground beetles (a to c) and diving beetles (d to f). The horizontal line describes the median value, box denotes first and third quartiles, whiskers denote minimum and maximum values, and dots indicate outliers. Numerical values inside the boxes denote means.

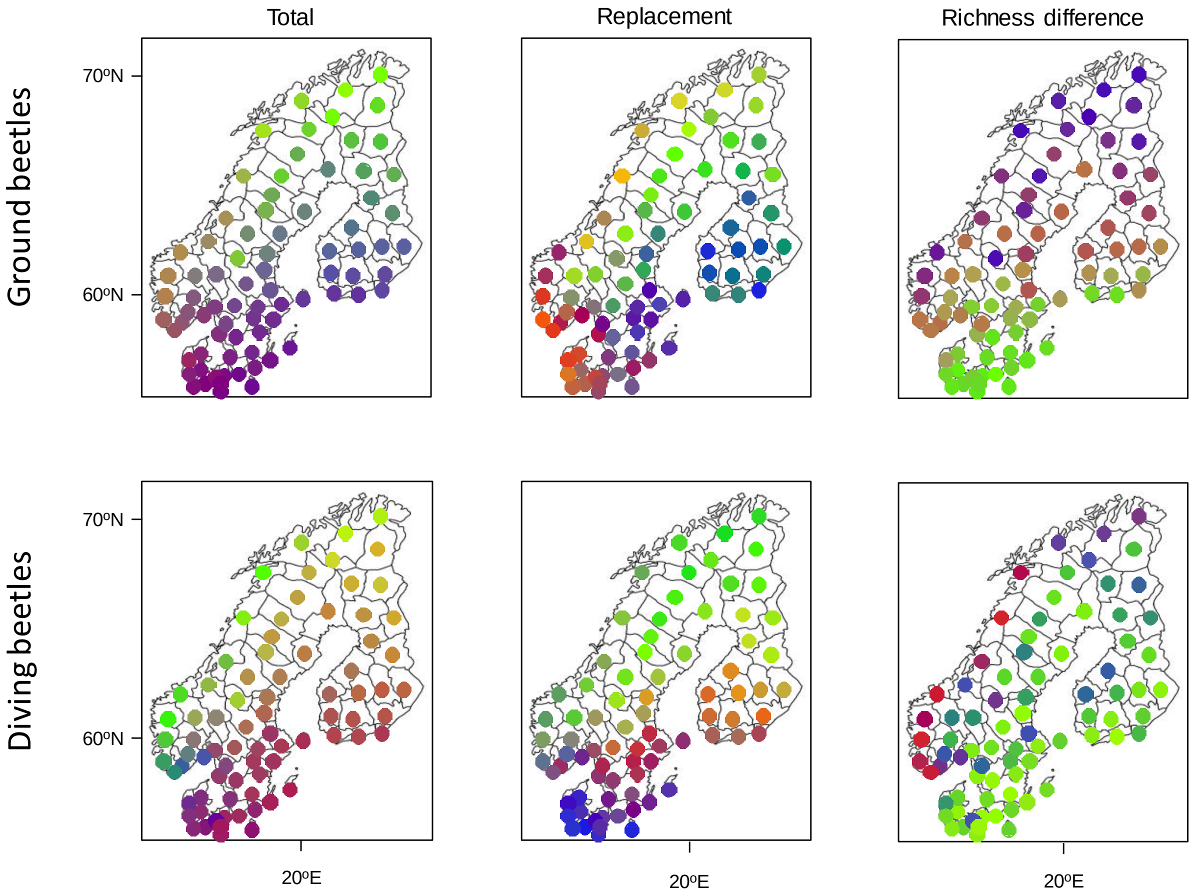

Fig. 2. RGB colour maps based on the first three axes of NMDS for total, replacement and richness difference components across the biogeographical provinces of Northern Europe. First row: ground beetles. Second row: diving beetles. Similar colours represent similarities in assemblage composition between provinces.

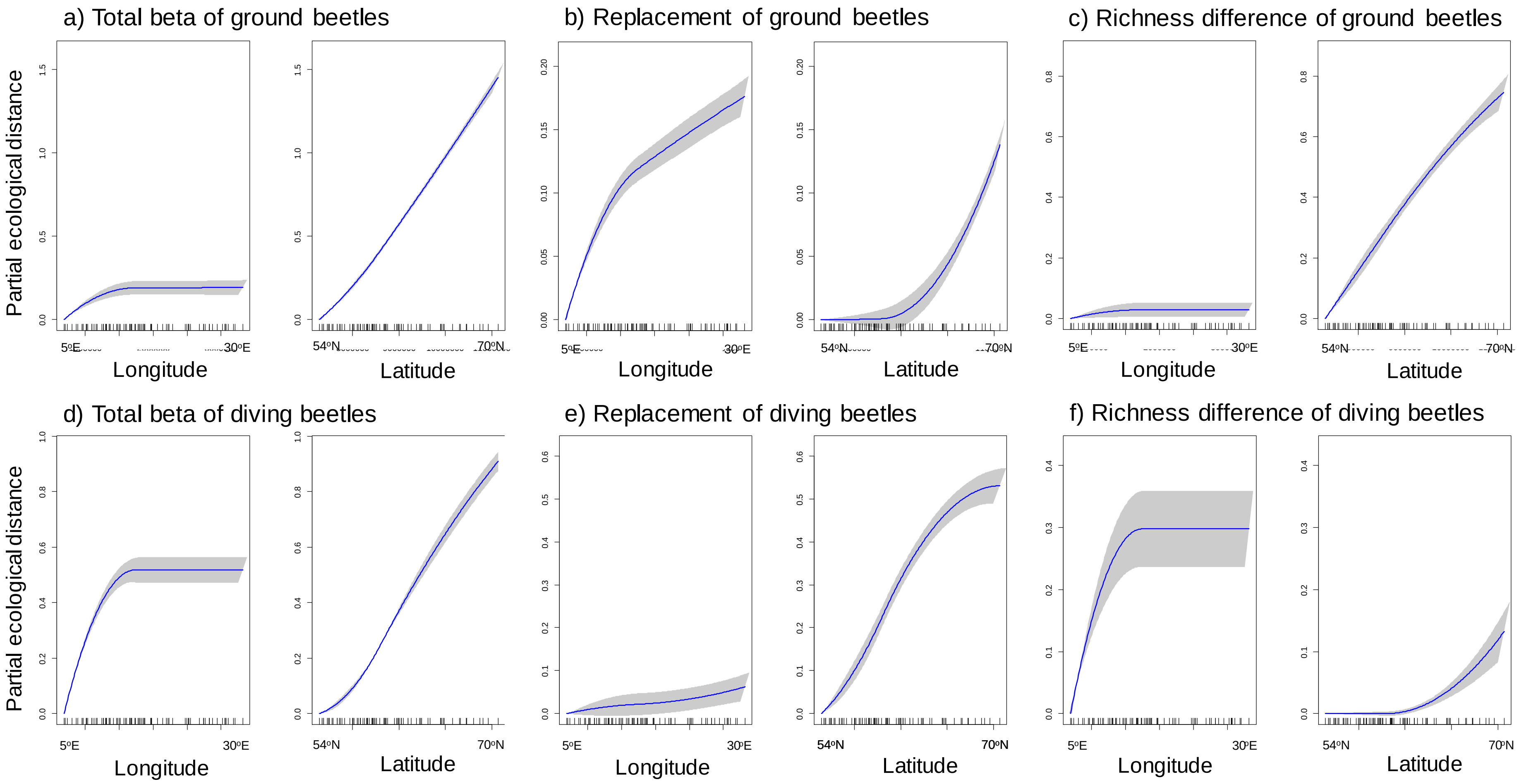

Fig. 3. Plots of I-splines of the predictor variables (blue) and confidence intervals from bootstrapping (grey) for the beta diversity components of ground beetles (a-c) and diving beetles (d-f) along latitudinal and longitudinal gradients. Subfigures: total beta diversity (a and d), replacement component (b and e) and richness differences component (c and f).