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

7

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19

20 **BIOSKETCH**

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

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35 **Abstract**

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

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

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

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

55 **Main conclusions:** Our findings suggest that the study of the determinants of biodiversity  
56 patterns benefits from the partitioning of beta diversity into different components and from  
57 comparing terrestrial and aquatic groups. For example, our findings suggest that the strong  
58 climatic and land use-related gradients in beta diversity have important implications for

59 predicting and mitigating the effect of ongoing global change on the composition of regional  
60 biotas.

61

62 **KEYWORDS**

63 biodiversity, climate, generalized dissimilarity modelling, land cover, land use, mean annual

64 temperature.

## 65 1 | INTRODUCTION

66

67 Owing to the fact that ongoing global change is threatening the diversity of populations,  
68 species and assemblages (Sala *et al.*, 2000; Heino *et al.*, 2009), understanding the factors  
69 underlying spatial variation of biodiversity remains at the heart of biogeography, ecology and  
70 conservation biology. However, different components of biodiversity may respond differently  
71 to global change and natural environmental variation (Socolar *et al.*, 2016). Species diversity  
72 can be decomposed into alpha, beta and gamma components (Whittaker, 1960), all of which  
73 may respond to various historical, environmental and geographical factors (Mittelbach,  
74 2012). While most previous studies focused on patterns in alpha or gamma diversity  
75 (Hillebrand, 2004; Field *et al.*, 2009), beta diversity has received considerable renewed  
76 interest in recent years (Tuomisto, 2010; Anderson *et al.*, 2011).

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

89 components (Podani & Schmera, 2011) because we were interested in any variation related to  
90 richness differences between sites instead of nestedness-related patterns (Carvalho *et al.*  
91 2012; Legendre, 2014).

92         Although beta diversity is gaining increasing, comparative studies on beta diversity  
93 patterns between biological assemblages inhabiting contrasting environments are mostly  
94 lacking (but see Fattorini, 2010; Heino & Alahuhta, 2015). For example, terrestrial  
95 assemblages are typically driven by climate-related variables (e.g., Hortal *et al.*, 2011),  
96 whereas local habitat conditions, such as water quality, often structure variation in aquatic  
97 assemblages even at broad spatial scales (e.g., Alahuhta, 2015). One possible explanation  
98 may be that not only the terrestrial ecosystems are directly influenced by climate (i.e. air  
99 temperature), whereas actual water temperature is naturally more important than air  
100 temperature to aquatic organisms (e.g. water may buffer extreme changes in air  
101 temperatures), but also the role of water is fundamentally different for aquatic species  
102 distributions (e.g., Heino, 2011). For instance, terrestrial assemblages are mainly affected by  
103 the accessibility of water in the ground for primary producers, drinking water for animals and  
104 different moisture conditions for different animal species (e.g., Begon *et al.*, 2006), whereas  
105 the survival of aquatic species depends more on the quality and movement of water in  
106 freshwater environments (Wetzel, 2001; Allan & Castillo, 2007). Because the underlying  
107 structuring factors for terrestrial versus aquatic assemblages do not necessarily co-vary  
108 geographically, aquatic organisms can be used to disentangle and contrast some of the  
109 mechanisms believed to underlie the most pervasive diversity patterns in the world (Brown,  
110 2014).

111         Beetles are a hyperdiverse group of insects, with different families inhabiting  
112 terrestrial, semi-aquatic and aquatic environments (Thomas, 2008). A highly diverse  
113 terrestrial family of beetles, ground beetles (Coleoptera: Carabidae), has been studied from

114 ecological, evolutionary and biogeographical perspectives for a long time (Lindroth, 1985;  
115 Lövei & Sunderland, 1996; Dajoz, 2002; Kotze *et al.*, 2011). Previous studies have found  
116 clear geographical patterns in their regional diversity and assemblage composition, which  
117 have been associated with concurrently varying climate conditions (Heino & Alahuhta,  
118 2015). In particular, temperature and humidity are two important environmental factors  
119 influencing the behaviour and ecology of ground beetles (e.g., Rainio & Niemelä, 2003), for  
120 which reason these insects are regarded as a model group for research on the effects of  
121 climate change (e.g., Müller-Kroehling, 2014). For example, temperature may influence their  
122 flight, speed of digestion, larval survival and life-history phenology (Thiele, 1977;  
123 Butterfield, 1996; Lövei and Sunderland, 1996), whereas humidity may be important in  
124 regulating behavioural patterns and habitat affinity (e.g., Kagawa & Maeto, 2009). However,  
125 landscape features and more localised environmental variations also affect the distributions of  
126 ground beetles (Thiele, 1977; Lindroth, 1985; Lövei & Sunderland, 1996). Ground beetle  
127 assemblages are strongly influenced by habitat structure, especially as reflected by vegetation  
128 (Brose 2003; Koivula *et al.*, 1999; Taboada *et al.* 2008; Koivula, 2011). Thus, ground beetle  
129 assemblages host species characteristic of particular habitats, reflect variation in structural  
130 features (e.g. soil characteristics), and may be particularly sensitive to anthropogenic  
131 alterations (Rainio & Niemelä, 2003; Koivula, 2011). For these reasons, ground beetle  
132 distributional patterns can be strongly influenced by land use (Eyre *et al.*, 2003; Eyre & Luff,  
133 2004; Kotze *et al.*, 2011). Thus, it is important to examine the influence of land cover on  
134 ground beetle assemblages in a broad-scale biogeographical context (Heino & Alahuhta,  
135 2015). A highly diverse aquatic family of beetles, diving beetles (Coleoptera: Dytiscidae), has  
136 also been the focus of numerous ecological and biogeographical studies. Some studies,  
137 addressed to associate their distributions and diversity to local environmental variables  
138 (Nilsson, Elmberg and Sjöberg, 1994; Nilsson & Söderberg, 1996), have emphasised that

139 diving beetle assemblages are mostly driven by vegetation characteristics, invertebrate prey  
140 abundance, fish predation and geographical location of water bodies. On the other hand,  
141 studies at broad scales have suggested that assemblage composition of diving beetles is  
142 mostly driven by climatic variables, with additional influences by landscape features (Heino  
143 & Alahuhta, 2015). However, no previous study has aimed to find out if and how geography,  
144 climate, land cover and anthropogenic land use variables affect the replacement and richness  
145 difference components of beta diversity in these two major beetle groups inhabiting different  
146 environments.

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



164 scale latitudinal and longitudinal patterns in Northern Europe. Our findings should contribute  
165 to discussion of the ongoing global change effects on insect biodiversity in high-latitude  
166 areas.

167

## 168 **2 | METHODS**

169

### 170 **2.1 | Study area**

171

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

181

### 182 **2.2 | Species data**

183

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

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

207

### 208 **2.3 | Predictor variables**

209

210 Among the multiple correlated climatic variables available in WorldClim (Hijmans *et al.*,  
211 2005), we selected those that are presumably the most important for insect distributions.  
212 These climate variables were: average annual temperature (°C), maximum temperature of the  
213 warmest month (°C), minimum temperature of the coldest month (°C), precipitation of the  
214 wettest month (mm) and precipitation of the driest month (mm). The climate variables were  
215 averaged values for the period 1960-1990 for each biogeographical province and were  
216 derived from WorldClim with 0.93 km × 0.93 km resolution (Hijmans *et al.*, 2005). Because  
217 most of the aforementioned climate variables were strongly intercorrelated ( $r \geq 0.80$ ), we  
218 used only average annual temperature and precipitation of the wettest month in the statistical  
219 analyses. These two are also conceptually the most important climatic variables affecting  
220 biodiversity at high latitudes. Land cover and land use variables were percentages of fresh  
221 water, forests, open areas, wetlands, agricultural areas and urban areas. These variables were  
222 obtained from European CORINE 2006 with 100m resolution. For the suitability of  
223 CORINE-based land use and land cover variables in these types of studies in northern  
224 Europe, see Heino & Alahuhta (2015). Although the land cover data is from the mid-2000s,  
225 most drastic changes in the land cover happened in Northern Europe between 1950 and 1980,  
226 when the current road and peatland drainage networks were established and a large  
227 proportion of people moved from the countryside to urban environments (Seppälä, 2005).  
228 Development of agriculture changed landscapes already thousands of years ago in Southern  
229 Fennoscandia (Eriksson *et al.*, 2002), after which changes in the quantity of agricultural land  
230 has been considerably modest. Finally, average elevation and elevation range within the  
231 province were also considered as land cover variables, as these variables are related to the  
232 environmental variation along elevation gradients. Elevation variables were obtained from  
233 3D Digital Elevation Model over Europe with 25m resolution. Because these two variables  
234 were strongly correlated ( $r = 0.95$ ), only average elevation was used in the statistical analysis.

235

## 236 2.4. | Statistical methods

237

238 We first calculated beta diversity components for each beetle group based on Jaccard  
239 dissimilarity coefficient. We thus followed the approach devised by Podani & Schmera  
240 (2011) and Carvalho *et al.* (2012). In this scheme, total beta diversity is decomposed into  
241 replacement and richness difference components: **Btotal** = **Brepl** + **Brich**. **Btotal** reflects  
242 both species replacement and loss-gain; **Brepl** refers to replacement of species identities  
243 alone, and **Brich** relates to species loss-gain or richness differences alone. A recent review  
244 found this decomposition a suitable approach for addressing complex issues in beta diversity  
245 (Legendre, 2014). We thus produced dissimilarity matrices based on each of the three  
246 components for each beetle group using the ‘beta’ function in the R package BAT (Cardoso *et*  
247 *al.*, 2015).

248         Second, we modelled variation in biological dissimilarities using Generalized  
249 Dissimilarity Modelling (GDM: Ferrier *et al.*, 2007). GDM is a technique for modelling  
250 spatial variation in assemblage composition between pairs of geographical locations, and it  
251 can be based on any dissimilarity matrix as response. These were, in our case, pairwise  
252 **Btotal**, **Brepl** and **Brich** dissimilarity matrices for each beetle group. GDM is based on matrix  
253 regression, and it can accommodate nonlinearities typical in ecogeographical datasets. These  
254 nonlinearities occur for two reasons: (i) the curvilinear response between increasing  
255 ecological distance and observed compositional dissimilarity, and (ii) the variation in the rate  
256 of compositional dissimilarity at different position along ecogeographical gradients (Ferrier *et*  
257 *al.*, 2007). It is thus a highly useful technique for large-scale assessments of assemblage  
258 composition. In consistency with other generalized linear models, the GDM model is

259 specified based on two functions: (i) a link function (in our case,  $1 - \exp[-y]$ ) defining the  
260 relationship between the response (i.e. compositional dissimilarity between sites) and the  
261 linear predictor (i.e. inter-site distances based on any ecogeographical variable, including  
262 geographical distance between sites), and (ii) a variance function defining how the variance  
263 of the response depends on the predicted mean (Ferrier *et al.*, 2007). We ran the GDM  
264 models, plotted the I-splines (which are monotone cubic spline functions) for each predictor  
265 variable (and geographical distance) and assessed the impacts of the predictor variables  
266 (which are estimated as the variance explained by the predictor when all the others are kept  
267 constant) on the response dissimilarities using the functions ‘gdm’ and ‘gdm.varImp’  
268 available in the R package gdm (Manion *et al.*, 2017). Prior to running GDMs, we checked  
269 for multicollinearity among the predictor variables. The highest correlation was between  
270 agriculture and mean annual temperature (Pearson  $r = 0.80$ ), but the other correlations were  
271 lower ( $r < 0.70$  or  $r > -0.70$ ). Hence, we did not remove any of the predictor variables shown  
272 in the final models. Also, GDM is known to be robust to multicollinearity among predictor  
273 variables (e.g., Glassman *et al.*, 2018). We did not standardize the predictor variables in our  
274 focal analyses, as a number of authors have followed a similar approach (e.g., Fitzpatrick *et*  
275 *al.*, 2013), and because this facilitates understanding variation in beta diversity along actual  
276 environmental gradients. However, we also ran the analyses using standardized predictor  
277 variables (mean = 0, SD = 1), but the main inferences did not change (i.e. the same predictor  
278 variables were the most important irrespective of whether or not we standardized the  
279 variables, and the explained deviance did not differ too much between the two approaches).  
280 For all above analyses, we assessed the uncertainty in the fitted I-splines by plotting I-splines  
281 with error bands using a bootstrapping approach (Shyrock *et al.*, 2015). We used 100  
282 iterations in bootstrapping, and 70% of the sites were retained from the full site-pair table  
283 when subsampling the data.

284 Third, we produced RGB colour maps using province scores from three non-metric  
285 multidimensional (NMDS) axes simultaneously. NMDS is considered as a highly robust  
286 unconstrained ordination method that can be utilised in ecology and biogeography (Minchin,  
287 1987). For our present purpose, we ran 20 3-dimensional NMDS solutions based on random  
288 starts, and selected for mapping the solution of three NMDS axes with the lowest stress  
289 value. These NMDS axes were calculated separately based on total beta diversity,  
290 replacement and richness difference dissimilarity matrices for each beetle group using the  
291 function ‘metaMDS’ with the R package *vegan* (Oksanen *et al.*, 2017). The stress values were  
292 acceptable and ranged from 0.016 to 0.199, with the exception of the replacement  
293 component-related ordination of ground beetles for which the stress value was 0.242. The  
294 colour mapping routines were conducted using the functions ‘recluster.col’ and  
295 ‘recluster.plot.sites.col’ from the R package *recluster* (Dapporto *et al.*, 2015) and the results  
296 were plotted on the maps of the study area.

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

302

### 303 **3 | RESULTS**

304

305 Regarding the decomposition of total beta diversity into replacement and richness difference  
306 components, there were no clear differences between ground beetles and diving beetles (Fig.  
307 1). Total beta diversity hardly differed between the beetle groups, with average values being

308 very similar (ground beetles: 0.52; diving beetles: 0.49). However, while the richness  
309 difference component was slightly more important than the replacement component for  
310 ground beetles (average replacement = 0.23, average richness difference = 0.29), the opposite  
311 was true for diving beetles (average replacement = 0.28, average richness difference = 0.21).

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

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

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

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

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



358 63°N, after which the species compositional variation increased rapidly (Fig. 3b). Similarly,  
359 there was a clear break, followed by a plateau, in the richness difference component of diving  
360 beetles at a longitude of 10°E to 11°E (Fig. 3f). These visual inspections were corroborated by  
361 the numerical results of the GDM analysis (Table 2).

362

#### 363 **4 | DISCUSSION**

364

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

370 We found that different factors drove the most variation in the assemblages of ground  
371 beetles and diving beetles, and these differences were also contingent on the beta diversity  
372 measure in question. Total beta diversity of ground beetles responded most strongly to (i)  
373 geographic distance between provinces, which expresses the importance biogeographical and  
374 historical factors (such as the presence of geographical barriers, the distribution of suitable  
375 habitats, and the effects of glaciations); (ii) mean annual temperature, indicating the role of  
376 current climatic forcing; and (iii) urban land use, suggesting that provinces with varying  
377 degrees of urbanization harbour different ground beetle assemblages. For diving beetles, total  
378 beta diversity was mostly related to (i) precipitation of the wettest month, describing a  
379 gradient from the Atlantic coast of Norway in the west to continental areas in Eastern Finland  
380 in the east; (ii) mean annual temperature, which varies markedly from south to north across  
381 the study area (Heino *et al.*, 2015); and (iii) open areas, implying that the provinces having

382 open areas versus forested areas harbour different diving beetle assemblages. The weak  
383 impact of geographical distance in diving beetles may be due to their dispersal capabilities.  
384 Diving beetles live in spatially discrete and sometimes ephemeral habitat patches, and many  
385 species are therefore assumed to be very active dispersers, able to move between suitable  
386 localities sometimes even on multiple occasions within an individual's lifetime (Bilton,  
387 2014). Although large-sized ground beetles move relatively speedily on the ground, being  
388 able to disperse over distances in the order of kilometres, and many species are able to fly,  
389 high habitat fragmentation and geographical barriers are known to prevent many species from  
390 colonizing most patches (Kotzke *et al.*, 2011; Elek *et al.*, 2014). This can be especially true  
391 for flightless ground beetle species, which are constrained by habitat fragmentation at larger  
392 spatial scales. For these cases, geographical distance is likely to exert increased importance in  
393 comparison to diving beetles that are better dispersers, as observed in our study.

394         The few previous studies that have decomposed total beta diversity into the  
395 replacement and richness difference components have found that their relative importance  
396 varies among study systems and organisms (Baiser *et al.*, 2012; Tonial *et al.*, 2012; Victorero  
397 *et al.*, 2018). Using an alternative approach to partition beta diversity into the turnover and  
398 nestedness components (Baselga, 2010), Soininen *et al.* (2018) observed that the turnover  
399 component was clearly more important than the nestedness component in a meta-analysis of  
400 269 data points. This finding is similar to that of a global comparative study of lake  
401 macrophytes that showed the preponderance of the turnover component over the nestedness  
402 component (Alahuhta *et al.*, 2017). In our study, the predictors of the replacement component  
403 varied somewhat between the two beetle groups. For ground beetles, geographic distance was  
404 by far the most important variable affecting differences in species composition between  
405 provinces. This effect is plausible given the rather large geographical area and the legacy of  
406 historical influences in the study region (e.g. post-Ice Age colonization may still be ongoing;

407 Hortal *et al.*, 2011). Geographical distance was followed by precipitation, mean annual  
408 temperature, forest cover and wetland cover. These variables were likely to be related to  
409 effects of climate and habitat differences on species composition, as already observed in  
410 previous accounts on ground beetle distributions in the study area (Lindroth 1985, 1986). For  
411 diving beetles, the replacement component was mostly driven by mean annual temperature  
412 and geographic distance, suggesting strong south-north changes in species identities along a  
413 temperature gradient. These findings are in accordance with previous accounts of species  
414 distributions, emphasising that diving beetles are sensitive to temperature that may strongly  
415 contribute to their distributions at both local and regional scales (Nilsson & Holmen, 1995;  
416 Heino & Alahuhta, 2015).

417         The variables best explaining the richness difference components of ground beetles  
418 and diving beetles were strikingly different. While the richness difference component of  
419 ground beetles was mostly related to urban land use (impact: 10.8) and mean annual  
420 temperature (impact: 3.4), that of diving beetles was mostly impacted by precipitation  
421 (impact: 28.8) and cover of open areas (impact: 11.9). These findings suggest that species  
422 loss-gain occurs mostly along urbanization and temperature gradients in ground beetles, with  
423 more species occurring in southernmost provinces with a higher urban land use cover than in  
424 more northerly provinces in the study area. While the positive effect of temperature is  
425 consistent with geographical patterns observed in most organisms (Currie *et al.*, 2004;  
426 Hawkins *et al.*, 2004; Lomolino *et al.*, 2010), the increase of ground beetle richness with  
427 urbanization is counter-intuitive, because urbanization has typically negative effects on insect  
428 diversity (McKinney, 2002; Martinson & Raupp, 2013; New, 2015). This unexpected positive  
429 association can be explained by assuming that species richness and human settlements both  
430 respond positively to energy availability, because the higher the energy, the greater the  
431 biomass and the number of individuals to be sustained, which, in turn, allow more species to

432 maintain viable populations within an area (Gaston, 2005; Evans & Gaston, 2005). Thus, it  
433 can be hypothesised that early human populations settled in a clumped fashion and grew  
434 more readily in the warmer and more productive areas represented by southern provinces,  
435 where there is high abundance and diversity of plants and animals that can be used as food or  
436 for other purposes, and where climate is milder. This hypothesis is supported by the fact that  
437 the richness difference component of ground beetles was also related to mean annual  
438 temperature, which increases southwards. As regards the negative effects of urbanization,  
439 they can really operate, but their influence may be masked at coarse spatial resolutions as that  
440 used in this study, because remnants of suitable biotopes can be found even where human  
441 population density is high (Fattorini *et al.*, 2016).

442         We also found that latitude strongly affected the richness difference component of  
443 beta diversity in ground beetles, but not so much in diving beetles. The effects of  
444 recolonization after the Ice Age are expected to be higher for the richness difference  
445 component (see also Hortal *et al.*, 2011), since few species (especially the most tolerant and  
446 mobile) were able to recolonize or disperse to areas strongly affected by historical climatic  
447 changes, especially those located at high latitudes (Fattorini & Ulrich, 2012a; 2012b). Thus,  
448 the influence of latitude on the richness difference component of beta diversity of ground  
449 beetles is consistent with the hypothesis that the spatial distribution of dispersal-limited  
450 species is still significantly affected by historical processes, as observed for ground beetles  
451 (see also Schuldt & Assmann, 2009). By contrast, the possible impact of Ice Age history on  
452 the current distribution of diving beetles seems to have been erased by their ability to long  
453 dispersal to reach scattered suitable habitat patches. In diving beetles, species loss-gain most  
454 likely occurs along a gradient from coastal (higher precipitation) to continental (lower  
455 precipitation) provinces. Especially the amount of precipitation may influence habitat  
456 availability and habitat types for diving beetles, with temporary ponds and pools, as

457 important habitats for some diving beetle species (Nilsson & Holmen, 1995), being probably  
458 uncommon in provinces with continuously high precipitation. In addition, water level  
459 fluctuations in permanent lakes and rivers may affect aquatic vegetation, thereby affecting  
460 habitat availability for diving beetles. Finally, increased precipitation may result in nutrient  
461 leaching to aquatic ecosystems (Soininen *et al.*, 2015), which influences the chemical  
462 environment for diving beetles and might therefore affect their geographical distribution.  
463 Thus, in addition to historical influences, present-day latitudinal and longitudinal  
464 distributions of beetles may also be affected by environmental factors that vary  
465 geographically (Heino & Alahuhta, 2015). Disentangling the effects of Ice Age history and  
466 contemporary environmental conditions may be especially difficult in a region, such as  
467 Northern Europe, where these two sets of factors co-vary strongly geographically.

468         Our findings showed that the magnitudes of beta diversity changes varied depending  
469 on the beta component considered and in relation with the main habitat of the study group.  
470 These findings suggest that the analysis of the determinants of biodiversity patterns will  
471 benefit from the partitioning of beta diversity into different components (Podani & Schmera,  
472 2011; Legendre, 2014), as these components are determined by different ecogeographical  
473 factors in animals inhabiting contrasting environments. Knowing which ecogeographical  
474 factors affect present-day biodiversity patterns is also a prerequisite for predicting alterations  
475 in species distributions in the face of global change. For example, the presence of strong  
476 climatic gradients in beta diversity have important implications for predicting, adapting and  
477 mitigating the effect of ongoing climate change on the composition of biological  
478 assemblages: (i) the species composition in areas of cold climates will likely become to  
479 resemble that currently present in more southerly regions (Hickling *et al.*, 2006) and (ii) some  
480 species with northern distributions may go extinct with climate change (Thomas *et al.*, 2006).  
481 However, these two topics deserve further and more direct modelling studies in the context of

482 hyperdiverse insect groups. Although we analysed patterns at the scale of biogeographic  
483 provinces, our findings do point out that various factors should be taken into account in the  
484 conservation biogeography of highly diverse organism groups in terrestrial and aquatic  
485 realms to facilitate understanding nuances in biodiversity patterns.

486

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#### 724 **DATA AVAILABILITY STATEMENT**

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

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#### 728 **Supporting Information**

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



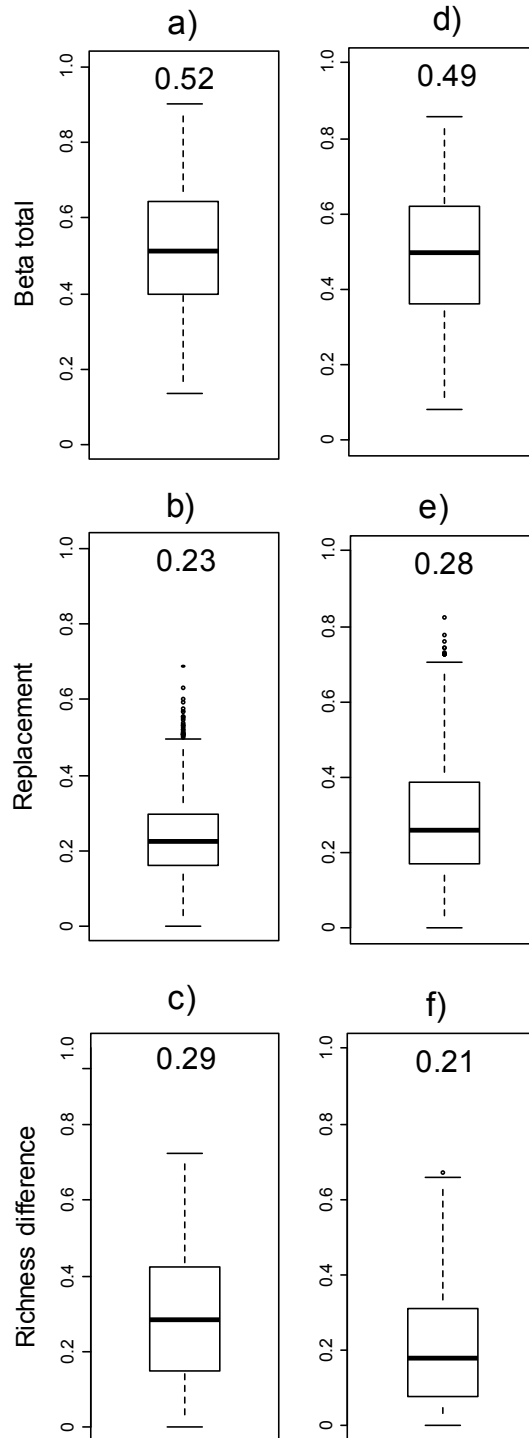
730 Table 1. Summaries of the GDM models for each beetle group and component of beta diversity. Also, shown are the predictor variable impacts in each model.

	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
<b>Variable impacts</b>						
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

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732 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
<b>Variable impacts</b>						
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



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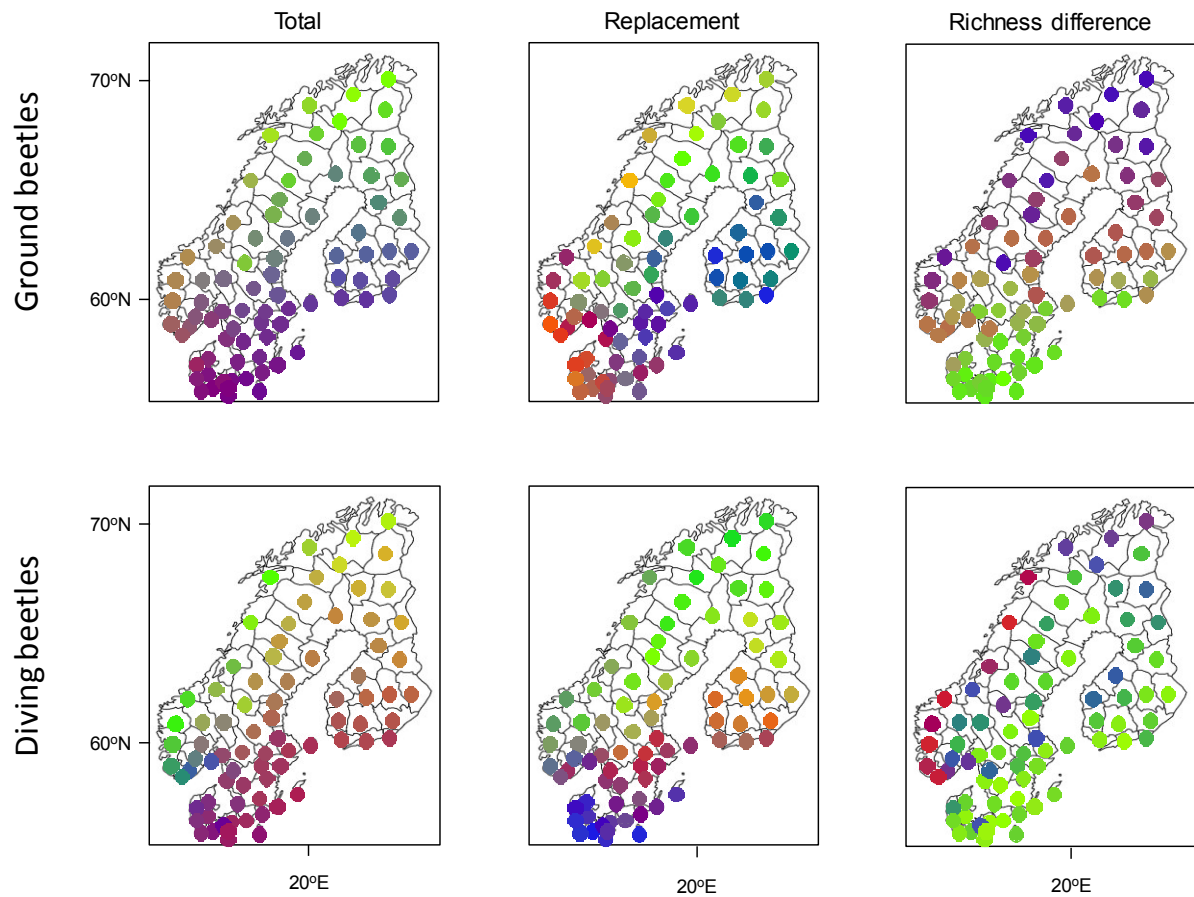
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735 Fig. 1. Boxplots of median pairwise dissimilarities for total, replacement and richness difference

736 component of ground beetles (a to c) and diving beetles (d to f). The horizontal line describes the

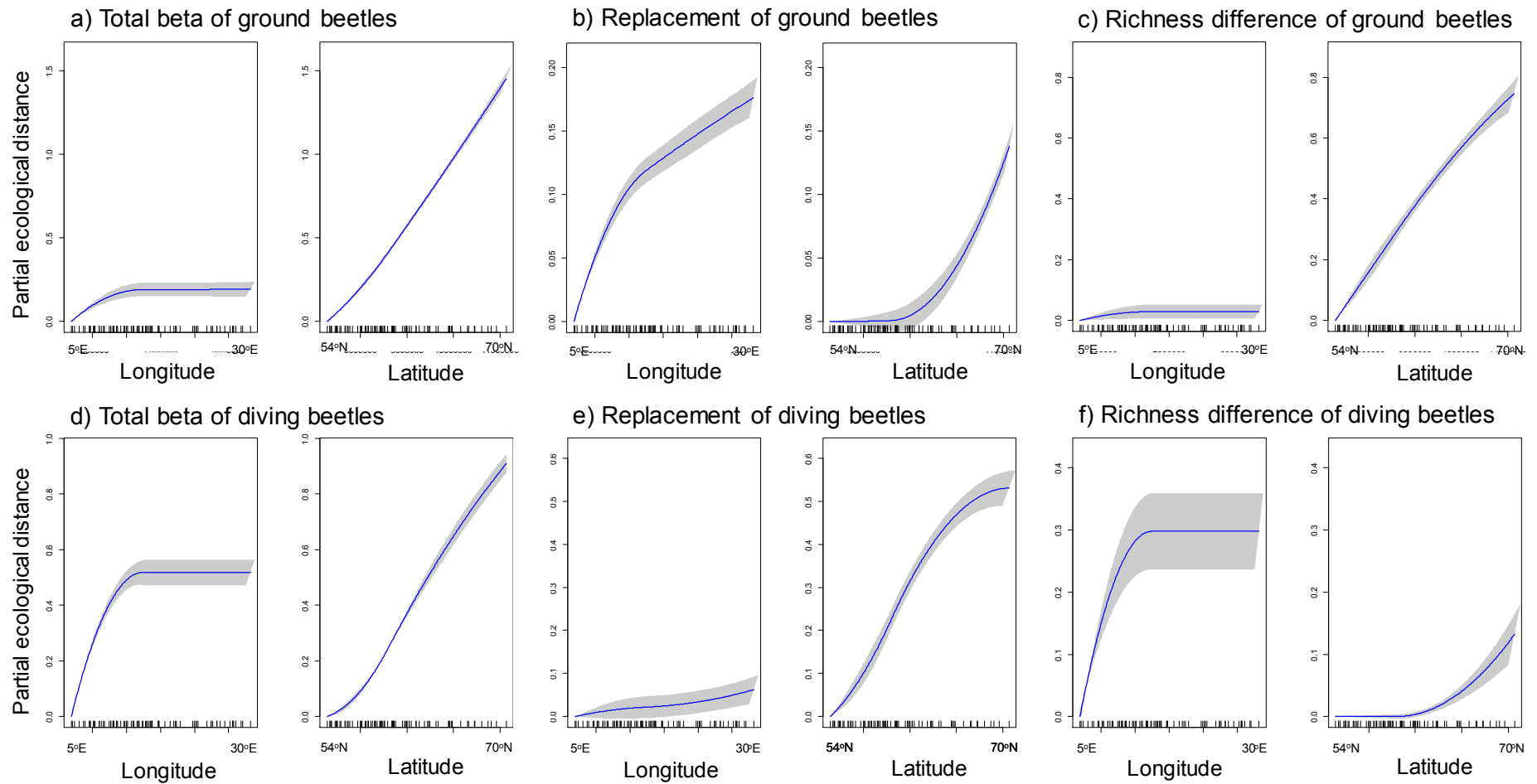
737 median value, box denotes first and third quartiles, whiskers denote minimum and maximum

738 values, and dots indicate outliers. Numerical values inside the boxes denote means.



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



744

745 Fig. 3. Plots of I-splines of the predictor variables (blue) and confidence intervals from bootstrapping (grey) for the beta diversity components of ground  
 746 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)  
 747 and richness differences component (c and f).