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

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26

27 **BIOSKETCH**

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

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Predicting beta diversity of terrestrial and aquatic beetles using ecogeographical

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variables: insights from the replacement and richness difference components

49 **Abstract**

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

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

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

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

69 **Main conclusions:** Our findings showed that the magnitudes of the replacement and richness
70 difference components varied slightly between ground beetles and diving beetles, and that the
71 best ecogeographical predictors of total beta diversity, replacement and richness difference
72 varied strongly between these two beetle families. These findings suggest that the study of

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

78

79 **KEYWORDS**

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

82 1 | INTRODUCTION

83

84 Owing to the fact that ongoing global change is threatening the diversity of populations,
85 species and assemblages (Sala *et al.*, 2000; Heino *et al.*, 2009), understanding the factors
86 underlying spatial variation of biodiversity remains at the heart of biogeography, ecology and
87 conservation biology. However, different components of biodiversity may respond differently
88 to global change and natural environmental variation (Socolar *et al.*, 2016), suggesting that
89 these different components should be given due attention. Species diversity can be
90 decomposed into alpha, beta and gamma components (Whittaker, 1960), all of which may
91 respond to various historical, environmental and geographical factors (Mittelbach, 2012).
92 While most previous studies focused on patterns in alpha or gamma diversity (Hillebrand,
93 2004; Field *et al.*, 2009), beta diversity has received considerable renewed interest in recent
94 years (Tuomisto, 2010; Anderson *et al.*, 2011).

95 Beta diversity can be defined as spatial variation or spatial turnover in assemblage
96 composition (Legendre *et al.*, 2005; Tuomisto *et al.*, 2006), and it can further include
97 different components (e.g. replacement and richness difference components; Podani &
98 Schmera, 2011). These components may provide more information than total beta diversity
99 about the mechanisms structuring variations in assemblage composition, species replacement
100 being related to factors affecting true changes in species identities between sites and richness
101 difference informing about factors determining differences in the number of species between
102 sites (Legendre, 2014). However, given the paucity of empirical studies using this approach
103 (Baiser *et al.*, 2012; Tonial *et al.*, 2012; Vad *et al.*, 2017), it is difficult to (i) make
104 conclusions about the relative importance of these components, and (ii) if these components
105 respond differently to environmental and geographical gradients. An alternative approach

106 would be to decompose total beta diversity into turnover and nestedness components
107 (Baselga, 2010), but we opted to focus on the replacement and richness difference
108 components (Podani & Schmera, 2011) because we were interested in any variation related to
109 richness differences between sites instead of nestedness-related patterns (Carvalho *et al.*
110 2012; Legendre, 2014).

111 Although beta diversity is gaining increasing interest among ecologists and
112 biogeographers, comparative studies on beta diversity patterns between biological
113 assemblages inhabiting contrasting environments are mostly lacking (but see Fattorini, 2010;
114 Heino & Alahuhta, 2015). For example, terrestrial and aquatic realms support highly different
115 environments for species assemblages, further influencing how assemblage composition in
116 each realm responds to environmental gradients. Terrestrial assemblages are typically driven
117 by climate-related variables (e.g. Hortal *et al.*, 2011), whereas local habitat conditions, such
118 as water quality, often structure variation in aquatic assemblages even at broad spatial scales
119 (e.g. Alahuhta, 2015). One possible explanation why aquatic assemblages respond differently
120 to climate gradients may be that the terrestrial ecosystems are directly influenced by climate
121 (i.e. air temperature), whereas actual water temperature is naturally more important than air
122 temperature to aquatic organisms (e.g. water may buffer extreme changes in air temperatures)
123 and (ii) the role of water is fundamentally different for aquatic species distributions (e.g.
124 Heino, 2011). For instance, to illustrate this latter difference, terrestrial assemblages are
125 mainly affected by the accessibility of water in the ground for primary producers, drinking
126 water for animals and different moisture conditions for different animal species (e.g. Begon *et*
127 *al.*, 2006), whereas the survival of aquatic species depends more on the quality and
128 movement of water in freshwater environments (Wetzel, 2001; Allan & Castillo, 2007).
129 Because the underlying structuring factors for terrestrial versus aquatic assemblages do not
130 necessarily co-vary strongly in geographically, aquatic organisms can be used to disentangle

131 and contrast some of the mechanisms believed to underlie the most pervasive diversity
132 patterns in the world (Brown, 2014).

133 Beetles are a hyperdiverse group of insects, with different families inhabiting
134 terrestrial, semi-aquatic and aquatic environments (Thomas, 2008). A highly diverse
135 terrestrial family of beetles, ground beetles (Coleoptera: Carabidae), has been studied from
136 ecological, evolutionary and biogeographical perspectives for a long time (Lindroth, 1985;
137 Lövei & Sunderland, 1996; Dajoz, 2002; Kotze *et al.*, 2011). Previous studies have found
138 clear geographical patterns in their regional diversity and assemblage composition, which
139 have been mostly associated with concurrently varying climate conditions (Heino &
140 Alahuhta, 2015). In particular, temperature and humidity are two important environmental
141 factors influencing ground beetle behaviour and ecology (Rainio & Niemelä, 2003) and these
142 insects are regarded as a model group for doing research on the effects of climate change
143 (e.g., Müller-Kroehling, 2014). For example, temperature may influence their flight, speed of
144 digestion, larval survival and phenology (e.g. Thiele, 1977; Butterfield, 1996; Lövei and
145 Sunderland, 1996), whereas humidity may be important in regulating behavioural patterns
146 and habitat affinity (e.g. Andersen, 1985; Eyre *et al.* 1990; Kagawa & Maeto, 2009).

147 However, as landscape features and more localised environmental variations also
148 affect the distributions of ground beetles (Thiele, 1977; Lindroth, 1985; Lövei & Sunderland,
149 1996). Ground beetle assemblages are strongly influenced by habitat structure, especially as
150 reflected by vegetation (Brose 2003; Koivula *et al.* 1999; 2003; Taboada *et al.* 2008). Thus
151 ground beetle assemblages host species characteristic of particular habitats, reflect variation
152 in structural features (e.g. soil characteristics), and may be particularly sensitive to
153 anthropogenic alterations (Rainio & Niemelä, 2003; Koivola, 2011). For these reasons,
154 ground beetle distributional patterns can be strongly influenced by land use (Eyre *et al.*, 2003,
155 2004; Eyre & Luff, 2004; Kotze *et al.*, 2011). Thus, it is important that land cover variables

156 are examined in broad-scale biogeographical studies (Heino & Alahuhta, 2015). Another
157 highly diverse aquatic family of beetles, diving beetles (Coleoptera: Dytiscidae), has also
158 been the focus of numerous ecological and biogeographical studies. Some studies focusing on
159 diving beetles have been more local in scope, with the aim to associate their distribution and
160 diversity to local environmental variables (Nilsson, Elmberg and Sjöberg, 1994; Nilsson &
161 Söderberg, 1996). These studies have emphasised that diving beetle assemblages are mostly
162 driven by vegetation characteristics, invertebrate prey abundance, fish predation and
163 geographical location of water bodies. However, studies at broad scales have suggested that
164 assemblage composition of diving beetles is mostly driven by climatic variables, with
165 additional influences by landscape features (Heino & Alahuhta, 2015). However, no previous
166 study has aimed to find out if and how geography, climate, land cover and anthropogenic land
167 use variables affect the replacement and richness difference components of beta diversity in
168 these two major beetle groups inhabiting different environments.

169 Here, we focused on beta diversity of ground beetles and diving beetles through
170 examining the responses of total beta diversity and its replacement and richness difference
171 components to climate, land cover and geographical gradients across Northern Europe. Our
172 previous study found that both ground beetle and diving beetle assemblages were mostly
173 driven by mean annual temperature and, secondarily, by various other climatic and land cover
174 variables (Heino & Alahuhta, 2015). However, in our previous study, we used constrained
175 ordination and constrained clustering methods, and did not examine the drivers of
176 replacement and richness difference components. In the present study, we expected that
177 terrestrial ground beetle assemblages would be more strongly driven by different land cover
178 and human land use variables compared with aquatic diving beetle assemblages, but their
179 response to climatic variables would be similar (because both are groups of ectothermic
180 animals). We also expected that the replacement component would be driven by land cover

181 and land use variables (because species composition typically shows turnover along long
182 environmental gradients; e.g. Gaston & Blackburn, 2000; Qian & Ricklefs, 2012; König *et*
183 *al.*, 2017) and the richness difference component would be driven by geographical and
184 climatic variables (because history and climate shape variation in species richness at large
185 scales; e.g. Hillebrand, 2004; Field *et al.*, 2009). In the final stage, we mapped the observed
186 responses of beta diversity and its components to show their broad-scale latitudinal and
187 longitudinal patterns in Northern Europe. As our main analytical tool, we used generalized
188 dissimilarity modelling because it (i) allows using different biological dissimilarity matrices
189 as responses and (ii) facilitates comparing the impacts of different predictor variables on
190 these response matrices (Ferrier *et al.*, 2007). Our findings should contribute to discussion of
191 the ongoing global change effects on insect biodiversity in high-latitude areas.

192

193 **2 | METHODS**

194

195 **2.1 | Study area**

196

197 We analysed beetle distribution and environmental data derived from the 101 biogeographic
198 provinces belonging to Denmark, Sweden, Norway and Finland (Väisänen *et al.*, 1992;
199 Väisänen & Heliövaara, 1994). Prior to the analyses, we merged various small coastal
200 provinces in Norway to provide a better and more accurate representation of species ranges
201 (Heino & Alahuhta, 2015; Heino *et al.*, 2015). After these modifications, the number of
202 provinces remaining in the analyses was 79. Each province has typical characteristics of
203 climate and land cover, and “biogeographic province” is thus a relatively homogeneous study

204 unit. We used the 79 provinces as sampling units (i.e. grain size), and all the species found in
205 a biogeographic province were pooled to represent a single assemblage.

206

207 **2.2 | Species data**

208

209 We analysed the same literature data as in Heino and Alahuhta (2015) for two adepagan
210 beetle groups: ground beetles (Carabidae; Lindroth, 1985; 1986) and diving beetles
211 (Dytiscidae; Nilsson & Holmen, 1995). Ground beetles are mainly terrestrial insects, which
212 are predatory, omnivorous, granivorous or herbivorous species as adults and mostly predatory
213 as larvae (Lindroth, 1985; Lövei & Sunderland, 1996; Dajoz, 2002). Diving beetles dwell in
214 fresh waters and sometimes in brackish waters, and they are mostly predatory as larvae and
215 predators or scavengers as adults (Nilsson & Holmen, 1995). These two beetle groups are
216 relatively species rich in Northern Europe. However, Carabidae comprised more species
217 (total number of species = 388; mean number of species per province = 159, sd = 56.9) than
218 Dytiscidae (total number of species = 155; mean = 78.9, sd = 19.3; paired t-test; $p < 0.001$)
219 based on the literature data (Lindroth, 1985, 1986; Nilsson & Holmen, 1995). Although these
220 biological data are already rather old, they represent good information about species
221 distributions across Northern Europe and can be easily associated with predictor variable data
222 derived for a period between 1960s and 1990s.

223

224 **2.3 | Predictor variables**

225

226 Climate variables were average annual temperature (°C), maximum temperature of the
227 warmest month (°C), minimum temperature of the coldest month (°C), precipitation of the
228 wettest month (mm) and precipitation of the driest month (mm). The climate variables were
229 average values of period 1960-1990 for each biogeographical province and were derived
230 from WorldClim with 0.93 km × 0.93 km resolution (Hijmans *et al.* 2005). Because most of
231 the aforementioned climate variables were strongly intercorrelated ($r \geq 0.80$), we used only
232 average annual temperature and precipitation of the wettest month in the statistical analyses.
233 These two are also conceptually the most important climatic variables affecting biodiversity
234 at high latitudes. Land cover and land use variables were percentages of fresh water, forests,
235 open areas, wetlands, agricultural areas and urban areas. These variables were obtained from
236 European CORINE 2006 with 100m resolution. For the suitability of CORINE-based land
237 use and land cover variables in these types of studies in northern Europe, see Heino &
238 Alahuhta (2015). Finally, average elevation and elevation range within the province were also
239 considered as land cover variables, as these variables are related to the environmental
240 variation along elevation gradients. Elevation variables were obtained from 3D Digital
241 Elevation Model over Europe with 25m resolution. Because these two variables were
242 strongly correlated ($r = 0.95$), only average elevation was used in the statistical analysis.

243

244 **2.4. | Statistical methods**

245

246 We first calculated beta diversity components for each beetle group based on Jaccard
247 dissimilarity coefficient. We thus followed the approach devised by Podani & Schmera
248 (2011) and Carvalho *et al.* (2012). In this scheme, total beta diversity is decomposed into
249 replacement and richness difference components: **Btotal** = **Brepl** + **Brich**. **Btotal** reflects

250 both species replacement and loss-gain; **Brepl** refers to replacement of species identities
251 alone, and **Brich** relates to species loss-gain or richness differences alone. A recent review
252 found this decomposition a suitable approach for addressing complex issues in beta diversity
253 (Legendre, 2014). We thus produced dissimilarity matrices based on each of the three
254 components for each beetle group using the ‘beta’ function in the R package BAT (Cardoso *et*
255 *al.*, 2015).

256 Second, we modelled variation in biological dissimilarities using Generalized
257 Dissimilarity Modelling (GDM: Ferrier *et al.*, 2007). GDM is a technique for modelling
258 spatial variation in assemblage composition between pairs of geographical locations, and it
259 can be based on any dissimilarity matrix as response. These were, in our case, pairwise
260 Btotal, Brepl and Brich dissimilarity matrices for each beetle group. GDM is based on matrix
261 regression, and it can accommodate nonlinearities typical in ecogeographical datasets. These
262 nonlinearities occur for two reasons: (i) the curvilinear response between increasing
263 ecological distance and observed compositional dissimilarity, and (ii) the variation in the rate
264 of compositional dissimilarity at different position along ecogeographical gradients (Ferrier *et*
265 *al.*, 2007). It is thus a highly useful technique for large-scale assessments of assemblage
266 composition. In consistency with other generalized linear models, the GDM model is
267 specified based on two functions: (i) a link function defining the relationship between the
268 response (i.e. compositional dissimilarity between sites) and the linear predictor (i.e. inter-site
269 distances based on any ecogeographical variable, including geographical distance between
270 sites), and (ii) a variance function defining how the variance of the response depends on the
271 predicted mean (Ferrier *et al.*, 2007). Following previous suggestions, we used the
272 appropriate default link and the binomial variance function (Ferrier *et al.*, 2007). We ran the
273 GDM models, plotted the I-splines (which are monotone cubic spline functions) for each
274 predictor variable (and geographical distance) and assessed the impacts of the predictor

275 variables on the response dissimilarities using the functions ‘gdm’ and ‘gdm.varImp’
276 available in the R package gdm (Manion *et al.*, 2017). Prior to running GDMs, we checked
277 for multicollinearity among the predictor variables. The highest correlation was between
278 agriculture and mean annual temperature (Pearson $r = 0.80$), but the other correlations were
279 lower ($r < 0.70$ or $r > -0.70$). Hence, we did not remove any of the predictor variables shown
280 in the final models. Also, GDM is known to be robust to multicollinearity among predictor
281 variables (e.g, Glassman *et al.*, 2018). We did not standardize the predictor variables in our
282 focal analyses, as many authors have followed a similar approach (e.g. Fitzpatrick *et al.*,
283 2013), and because this facilitates understanding variation in beta diversity along actual
284 environmental gradients. However, we also ran the analyses using standardized predictor
285 variables (mean = 0, SD = 1), but the main inferences did not change (i.e. the same predictor
286 variables were the most important irrespective of whether or not we standardized the
287 variables, and the explained deviance did not differ too much between the two approaches).
288 For all above analyses, we assessed the uncertainty in the fitted I-splines by plotting I-splines
289 with error bands using a bootstrapping approach (Shyrock *et al.*, 2015). We used 100
290 iterations in bootstrapping, and 70% of the sites were retained from the full site-pair table
291 when subsampling the data.

292 Third, we produced RGB colour maps using province scores from three non-metric
293 multidimensional (NMDS) axes simultaneously. NMDS is considered as a highly robust
294 unconstrained ordination method that can be utilised in ecology and biogeography (Minchin,
295 1987). For our present purpose, we ran 20 3-dimensional NMDS solutions based on random
296 starts, and selected for mapping the solution of three NMDS axes with the lowest stress
297 value. These NMDS axes were calculated separately based on total beta diversity,
298 replacement and richness difference dissimilarity matrices for each beetle group using the
299 function ‘metaMDS’ with the R package vegan (Oksanen *et al.*, 2017). The stress values were

300 acceptable and ranged from 0.016 to 0.199, with the exception of the replacement
301 component-related ordination of ground beetles for which the stress value was 0.242. The
302 colour mapping routines were conducted using the functions ‘recluster.col’ and
303 ‘recluster.plot.sites.col’ from the R package recluster (Dapporto *et al.*, 2015) and the results
304 were plotted on the maps of the study area.

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

310

311 **3 | RESULTS**

312

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

320 There were some differences in the explained deviance between the beetle groups and
321 the components of beta diversity when using the selected 10 predictor variables (Table 1).

322 Total beta diversity of ground beetles was slightly better explained than that of diving beetles,

323 but the opposite was true for the replacement component. The richness difference component
324 of ground beetles was slightly better explained than that of diving beetles.

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

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

347 precipitation, followed by open areas and urban land use. These variables showed slightly
348 curvilinear relationships with richness difference (Fig. S6).

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

359 The visual inspections were also largely corroborated by the results of additional
360 GDMs, with total beta diversity being strongly related to latitude in both beetle groups,
361 whereas the replacement and richness difference components showed differences between the
362 beetle groups (Fig. 3). For ground beetles, the richness difference component was strongly
363 correlated to latitude, whereas the replacement component of diving beetles showed a strong
364 relationship with latitude.

365

366 **4 | DISCUSSION**

367

368 There is a substantial lack of studies that have compared the beta diversity patterns of
369 multiple insect groups based on the same study units and identical statistical methods
370 (Fattorini, 2010; Heino & Alahuhta, 2015). Here, we contrasted biogeographical patterns in

371 the total beta diversity and its replacement and richness difference components for terrestrial
372 (ground beetles) and aquatic (diving beetles) insects.

373 We found that different factors drove the most variation in assemblages of ground
374 beetles and diving beetles, and these differences were also contingent on the beta diversity
375 measure in question. Total beta diversity of ground beetles responded most strongly to (1)
376 geographic distance between provinces, suggesting biogeographical and historical factors
377 (such as the presence of geographical barriers, the distribution of suitable habitats and the
378 effects of glaciations) drive ground beetle distributions, (2) mean annual precipitation,
379 suggesting climatic forcing on species distributions, and (3) urban land use, suggesting that
380 provinces with varying degree of urbanization harboured different ground beetle
381 assemblages. For diving beetles, total beta diversity was mostly related to (1) precipitation of
382 the wettest month, describing a gradient from the Atlantic coast of Norway to continental
383 areas in Eastern Finland, (2) mean annual temperature, which varies markedly from south to
384 north across the study area (Heino *et al.*, 2015), and (3) by open areas, implying that the
385 provinces having open areas versus forested areas harboured different diving beetle
386 assemblages. The low impact of geographical distance in diving beetles may be due to their
387 dispersal capabilities. Diving beetles live in spatially discrete and sometime ephemeral
388 habitat patches, and many species are therefore very active dispersers, able to move between
389 suitable localities sometimes even on multiple occasions within individual's lifetime (Bilton,
390 2014). Ground beetles may disperse both by moving on the ground and (for winged species)
391 by flying. Large-sized species can move quite speedily on the ground and can be able to
392 move over distances in the order of kilometers, but high habitat fragmentation and
393 geographical barriers are likely to prevent them from colonizing most uninhabited habitat
394 patches (Lövei *et al.*, 2006; Kotze *et al.*, 2011; Elek *et al.*, 2014). Thus, geographic distance

395 may an important driver of species distributions, especially for flightless species, that are
396 constrained by habitat fragmentation.

397 The few previous studies that have decomposed total beta diversity into the
398 replacement and richness difference components have found that the importance (i.e. the
399 relative contribution of the two components to their sum) of these components varies among
400 study systems and organisms (Baiser *et al.*, 2012; Tonial *et al.*, 2012; Victorero *et al.*, 2018).
401 Using an alternative approach to partition beta diversity into the turnover and nestedness
402 components (Baselga, 2010), Soininen *et al.* (2018) observed that the turnover component
403 was clearly more important than the nestedness component in a meta-analysis of 269
404 datapoints. This finding is similar to that of a global comparative study of lake macrophytes
405 that showed the preponderance of the turnover component over the nestedness component
406 (Alahuhta *et al.*, 2017). In our study, the predictors of the replacement component varied
407 somewhat between the two beetle groups. For ground beetles, geographic distance was by far
408 the most important variable affecting differences in species composition between provinces.
409 This effect is plausible given the rather large geographical area and the legacy of historical
410 influences in the study area (e.g. post-ice age colonization may still be ongoing; Hortal *et al.*,
411 2011). Geographical distance was followed by precipitation, mean annual temperature, forest
412 cover and wetland cover. These variables were likely to be related to effects of climate and
413 habitat differences on species compositional differences among provinces, as has been
414 observed in previous accounts on ground beetle distributions in the study area (Lindroth
415 1985, 1986). For diving beetles, the replacement component was mostly driven by mean
416 annual temperature and geographic distance, suggesting strong south-north changes in
417 species identities along a temperature gradient. These findings are in accordance with
418 previous accounts of species distributions, emphasising that diving beetle species are

419 sensitive to temperature that may strongly contribute to their distributions at both local and
420 regional scales (Nilsson & Holmen, 1995; Heino & Alahuhta, 2015).

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

444 spatial resolutions as that used in this study, because remnants of suitable biotopes can be
445 found even where human population density is high (Fattorini *et al.*, 2016).

446 We also found that latitude (Table S1) strongly affected the richness difference
447 component of beta diversity in ground beetles, but not in diving beetles. Effects of post- Ice
448 Age recolonization are expected to be higher for the richness difference component (see
449 Hortal *et al.*, 2011), since few species (especially the most tolerant and mobile) were able to
450 recolonize or disperse to areas strongly affected by historical climatic changes, especially
451 those located at high latitudes (see Fattorini & Ulrich, 2011, 2012). Thus, the influence of
452 latitude on the richness difference component of beta diversity of ground beetles is consistent
453 with the hypothesis that the spatial distribution of restricted-range species is still
454 significantly affected by historical processes (Schuldt & Assmann, 2009). By contrast, the
455 possible impact of Ice Age on the current distribution of diving beetles seems to be virtually
456 erased by their ability to long dispersal to reach scattered suitable habitat patches. In diving
457 beetles, species loss-gain most likely occurs along a gradient from coastal (higher
458 precipitation) to continental (lower precipitation) provinces. Especially the amount of
459 precipitation may influence habitat availability and habitat types for diving beetles, with
460 temporary ponds and pools, as important habitats for some diving beetle species (Nilsson &
461 Holmen, 1995), being probably uncommon in provinces with continuously high precipitation.
462 In addition, water level fluctuations in permanent lakes and rivers may affect aquatic
463 vegetation, thereby affecting habitat availability for and structure of diving beetle habitats.
464 Finally, increased precipitation may result in nutrient leaching to aquatic ecosystems
465 (Soininen *et al.*, 2015), which might determine the chemical environment for diving beetles
466 and affect the geographical distributions of these species.

467 Our findings showed that the magnitudes of the replacement and richness difference
468 components varied slightly between ground beetles and diving beetles. We also found that the

469 best predictors of total beta diversity, replacement and richness difference varied, sometimes
470 strongly, between these two beetle groups inhabiting contrasting environments. These
471 findings thus suggest that the study of the determinants of biodiversity patterns will benefit
472 from the partitioning of beta diversity into different components (Podani & Schmera, 2011;
473 Legendre, 2014), as these components are determined by different ecogeographical factors.
474 Knowing which ecogeographical factors affect present-day biodiversity patterns is also a
475 prerequisite for predicting alterations in species distributions in the face of global change. For
476 example, our findings suggest that the strong climatic gradients in beta diversity have
477 important implications for predicting, adapting and mitigating the effect of ongoing climate
478 change on the composition of biological assemblages: (i) the species composition in areas of
479 cold climates will likely become to resemble that currently present in more southerly regions
480 (Hickling *et al.*, 2006) and (ii) some species may go extinct with climate change (Thomas *et*
481 *al.*, 2006). However, these two topics deserve further and more direct modelling studies in the
482 context of hyperdiverse insect groups. Although we analysed patterns at the scale of
483 biogeographic provinces, our findings do point out that various factors should be taken into
484 account in the conservation biogeography of highly diverse organism groups in terrestrial and
485 aquatic realms to facilitate understanding nuances in biodiversity patterns.

486

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675

676 **DATA AVAILABILITY STATEMENT**

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

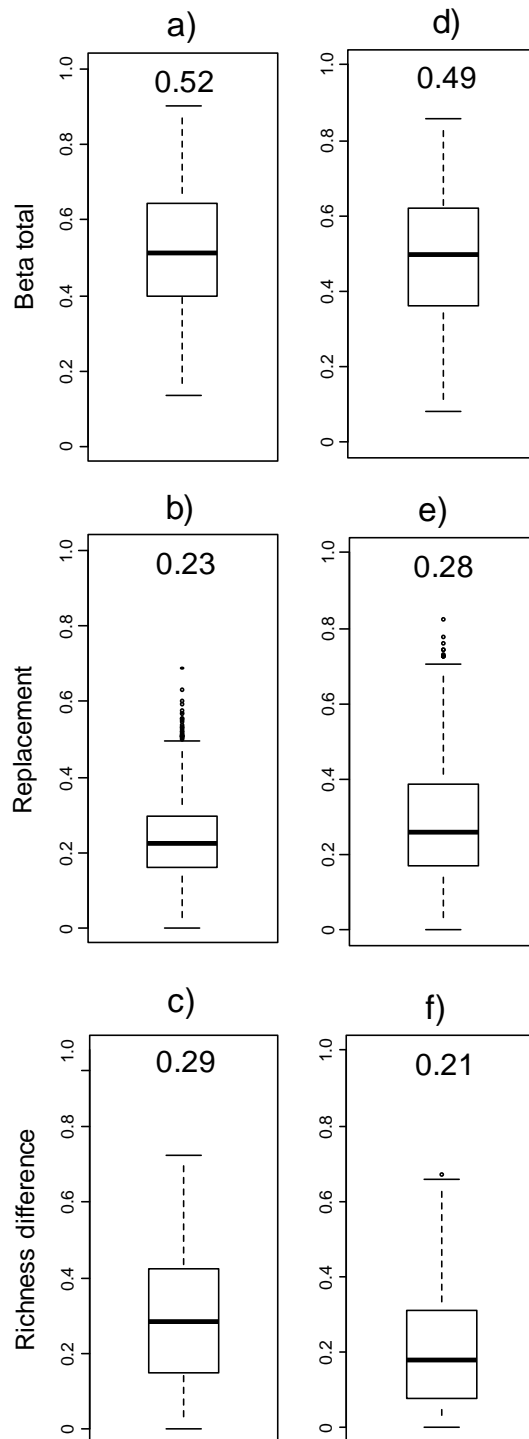
679

680 **Supporting Information**

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

682 Table 1. Summaries of GDM models for each beetle group and component of beta diversity. Also, shown are the 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



683

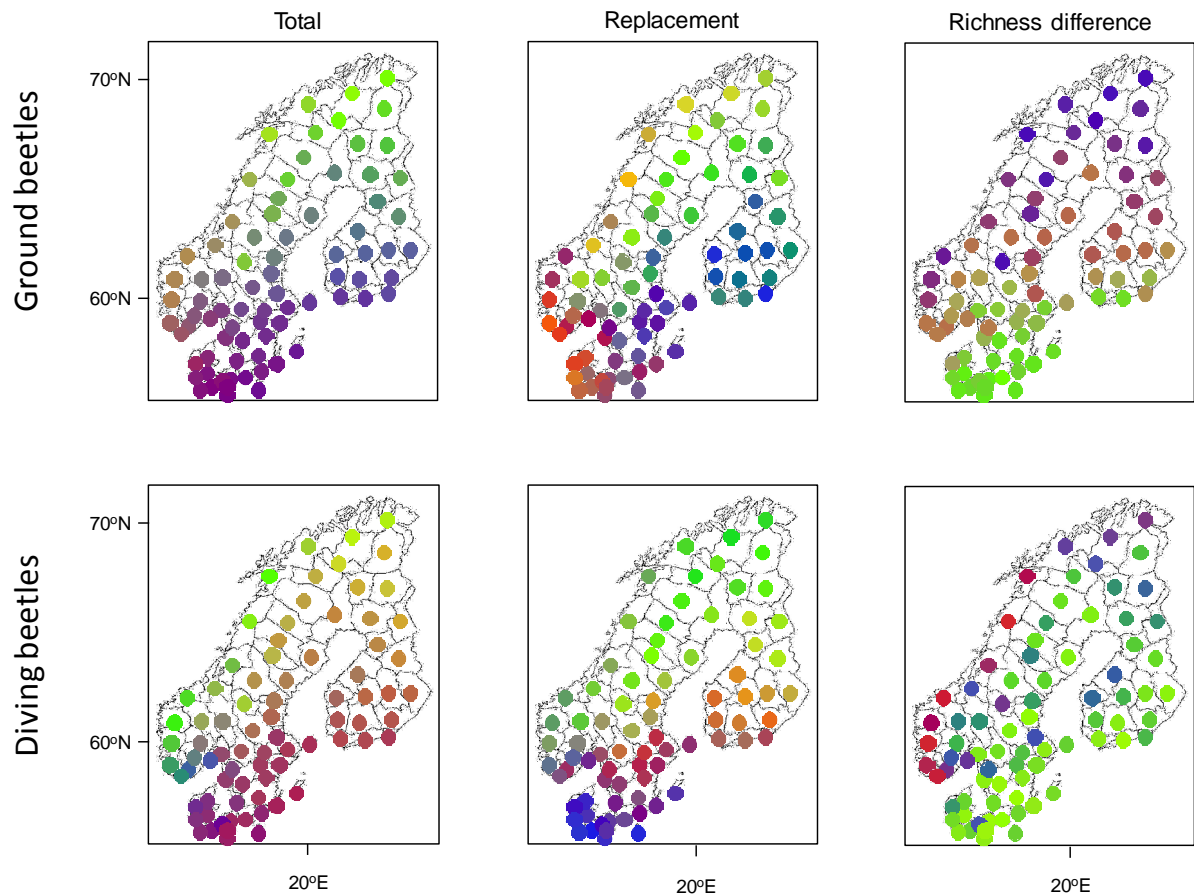
684

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

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

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

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



689

690 Fig. 2. RGB maps based on the first three axes of NMDS for total, replacement and richness

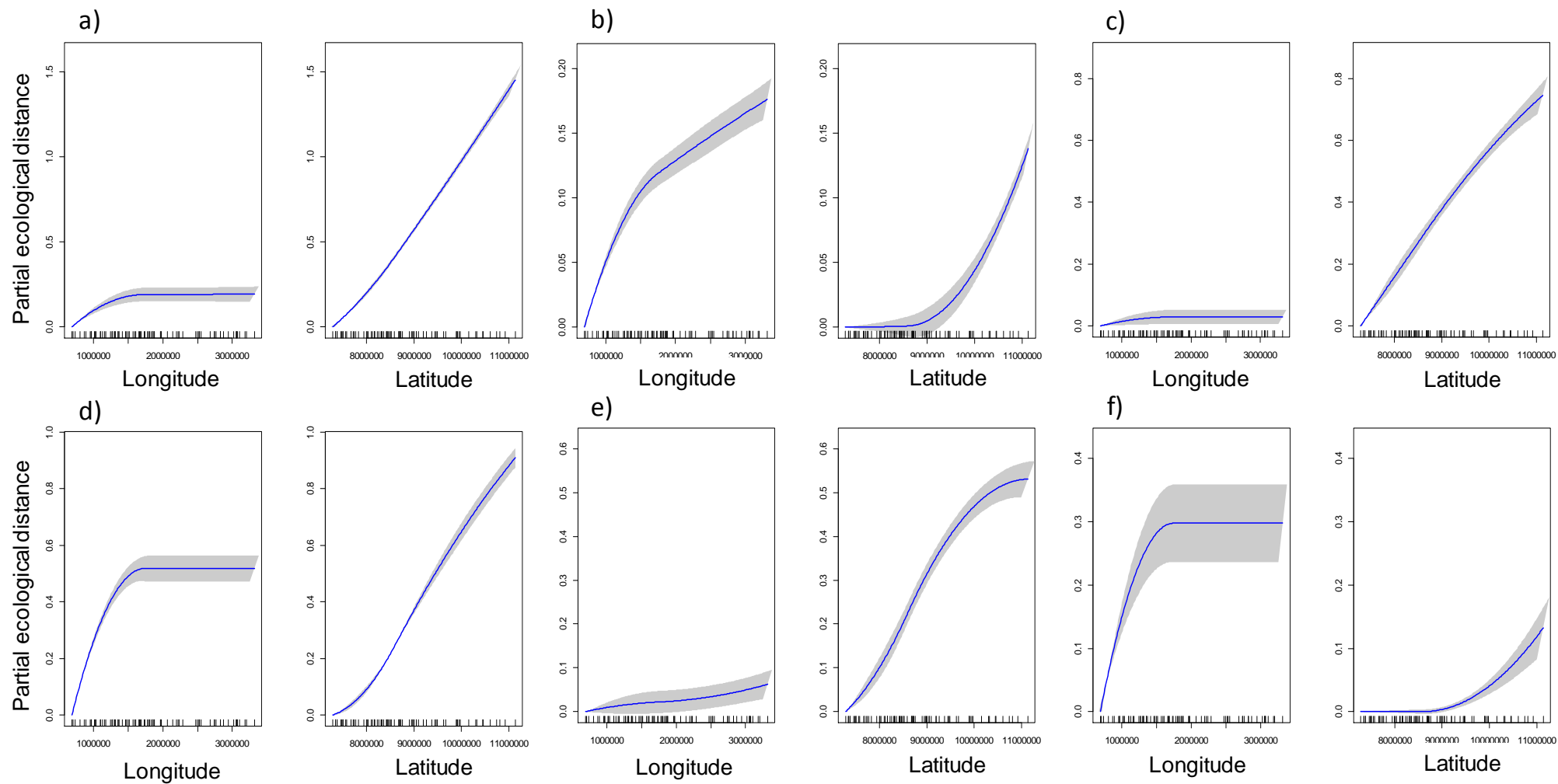
691 difference components across the biogeographical provinces of Northern Europe. First row: ground

692 beetles. Second row: diving beetles. Similar colours represent similarities in assemblage composition

693 between provinces.

694 Not sure of this figure (and associated text) is needed anymore, because we have the I-splines for

695 latitude and longitude as predictors. What do you think?



696
 697 Fig. 3. Plots of I-splines of the predictor variables (blue) and confidence intervals from bootstrapping (grey) for the beta diversity components of ground
 698 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)
 699 and richness differences component (c and f).