Knitting patterns of biodiversity, range size and body size in aquatic beetle

faunas: significant relationships but slightly divergent drivers

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Abstract. 1. Ecogeographical rules refer to recurring patterns in nature, including the latitudinal diversity gradient (LDG), Rapoport's rule and Bergmann's rule, among others. We examined the existence of these rules for diving beetles (Coleoptera: Dytiscidae), a family of aquatic predatory beetles.

2. We analysed assemblage-level data for diving beetles, focusing on species richness, local contribution to beta diversity (LCBD), mean range size and mean body size across the biogeographical provinces of Northern Europe. We first correlated each of these variables with latitude, and then modelled variation in each variable using actual environmental variables in boosted regression tree (BRT) analysis.

3. We found that species richness decreased with latitude, LCBD increased with latitude, mean range size did not show a significant relationship with latitude and mean body size decreased with latitude. The latter finding was contrary to Bergmann's rule. The actual environmental variables best predicting variation in these four response variables varied among the models, but generally included temperature-related and land use variables as the most influential ones.

4. Our results suggested that diving beetles conformed to the LDG, did not follow Rapoport's rule, and showed a reversed latitudinal gradient in the context of Bergmann's rule. In addition, species-poor provinces harboured ecologically most unique faunas, suggesting that species richness and LCBD are complementary measures of biodiversity.

5. Even though we did not find general support for most ecogeographical rules we examined, our findings are interesting because they suggest that aquatic ectothermic invertebrates may show patterns different from those originally described for terrestrial endothermic vertebrates.

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Introduction

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45   Ecogeographical rules are recurring patterns in species features that are assumed to be

46   generally prevailing in nature (Gaston *et al*., 2008). These rules typically occur at large

47   spatial and temporal scales rather than within local communities, and this is one of the

48   reasons why Lawton (1999) suggested moving from local-scale approaches in community

49   ecology to broad-scale pattern-seeking endeavours in macroecology (Brown, 1995). Indeed,

50   macroecological investigations have led to a few general rules which are found across a

51   number of taxa at broad spatial scales (Gaston & Blackburn, 2000; Gaston *et al*., 2008).

52   However, most tests of these ecogeographical rules have been done with data from well-

53   known organisms, such as mammals, birds, fish and terrestrial plants (Brown, 1995; Gaston

54   & Blackburn, 2000), while many hyperdiverse organism groups, such as insects and microbes

55   have received little research thus far (Heino, 2011; Soininen, 2012). This somewhat biased

56   emphasis on few organism groups limits our understanding of the generality of major

57   ecogeographical rules, such as the latitudinal diversity gradient (e.g. Rosenzweig, 1995),

58   Rapoport's rule (e.g. Stevens, 1989) and Bergmann's rule (e.g. Bergmann, 1847). In addition,

59   knitting these patterns together, i.e., if, how and why these seemingly independent rules

60   might be correlated, remains inadequately understood for many organism groups. Knitting

61   these ecogeographical rules is especially interesting at the assemblage level because general

62   patterns exist over and above individual species (Gaston *et al*., 2008). Next, these three major

63   ecogeographical rules and how they are potentially interlinked are shortly reviewed.

64   The latitudinal diversity gradient (LDG) refers to the decrease of species richness

65   from the equator toward the poles (e.g. Rosenzweig, 1995). This pattern has been found in a

66   broad variety of taxa, ranging from terrestrial plants and butterflies to birds and mammals

67   (e.g. Hillebrand, 2004). However, there are also notable exceptions to the general rule that

68   species richness should decrease from low to high latitudes (Kinlock *et al.*, 2017), including

69   taxa such as sawflies (e.g. Kouki *et al*., 1994), some groups of aquatic insects (e.g. Pearson &

70   Boyero, 2009) and many microbial groups (e.g. Soininen, 2012). These taxa deviating from

71   the general LDG are typically smaller groups of larger taxonomic entities that may follow the

72   general pattern (Gaston & Blackburn, 2000). The general LDG has been hypothesised to

73   result from the combined effects of biome area (e.g. Rosenzweig, 2003), climate (e.g. Currie

74   *et al*., 2004) and history (e.g. Hortal *et al*., 2011) on species richness, to name three broad

75   classes of hypotheses. For example, the larger area of tropical biomes in comparison to those

76   at higher latitudes might explain greater diversity close to the equator, because of both

77   reduced extinction risk and increased speciation probability in larger areas (Rosenzweig,

78   2003). Second, warmer, milder and less variable climate in the low latitudes provide more

79   energy and less harsh conditions to support more species compared with areas at high

80   latitudes (Currie *et al*., 2004). Third, the realised evolutionary history should have been

81   longer at low latitudes than at high latitudes because high-latitude areas have undergone

82   recurring ice ages (Brown & Lomolino, 1998). Ice ages have resulted in the elimination of

83   most plants and animals in high-latitude areas (Hewitt, 1999) and have necessitated re-

84   colonisation of these denuded areas after the ice sheets receded (Pielou, 1991). However, the

85   degree to which these hypotheses hold for most organism groups in general and those that

86   may have specific habitat requirements in particular remains to be studied.

87   Rapoport's rule states that species occurring near the equator have, on average,

88   smaller ranges than those occurring in high latitudes (Stevens, 1989; Gaston, 2003). Stevens

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89   (1989) also suggested that owing to this pattern, there is higher species richness in the tropics

90   because species there have smaller ranges that facilitate more species to occur in an area. In

91   contrast, species in high latitudes are assumed to have large ranges, resulting in the possibility

92   that only the same rather limited sets of species to occur in an area. The link between range

93   size and species richness can also be approached from a different angle (Šizling *et al.*, 2009).

94   For example, it is actually possible that Stevens' (1989) model works only when larger range

95   sizes would covary with reduced range overlap, and Šizling *et al*. (2009) indeed showed that

96   Rapoport's pattern will not generate the LDG if this assumption is not met. In fact, the

97   inverse of Rapoport's rule will generate a normal LDG because more broad-ranging species

98   in the tropics will mean stronger range overlap (Tomašových *et al.*, 2015).

99   Support for the generality of Rapoport's rule has been quite variable (Gaston *et al.*,

100   1998; Pintor *et al.*, 2015; Tomašových *et al.*, 2016): findings for (e.g. Rohde *et al.*, 1993) and

101   against (e.g. Rohde, 1992) the existence of the rule have emerged. In general, Rapoport's

102   rule, when it exists, is typically the most prevalent above latitudes north of 40° to 50° (Rohde,

103   1996), which may be related to two main hypotheses suggested to explain the existence of

104   this rule. First, there is the hypothesis of the effects of ice glaciations that have eliminated

105   species with narrow ranges at high latitudes (Brown, 1995). Second, there is the hypothesis of

106   climatic variability, whereby seasonal variability selects for higher climatic tolerances and

107   subsequently leads to broader latitudinal ranges at high latitudes (Stevens, 1996). The logic

108   behind the climatic variability hypothesis is as follows (Stevens, 1996): (1) species

109   experiencing variable temperatures will be temperature generalists; (2) along geographical

110   gradients with changing temperature, temperature generalists will have broader ranges than

111   temperature specialists; (3) higher latitudes have highest temperature seasonality and,

112   therefore, higher latitudes are inhabited by broad-ranging species. Thus, the abrupt changes in

113   the area of the latest ice age maxima and present-day climatic conditions might explain the

114   prevalence of large ranges of species in high latitudes.

115   Bergmann's rule proposes that within a group of closely-related species (e.g. a

116   family), larger-sized species are found in colder areas, whereas smaller-size species are found

117   in warmer areas across the world (Bergmann, 1847; Blackburn *et al*., 1999). This rule would

118   thus suggest a general latitudinal gradient in body size in a taxonomic group because high-

119   latitude areas are colder than low-latitude areas (Gaston & Blackburn, 2000). Bergmann's

120   rule has been shown to exist in many taxa of mammals and birds (e.g. Ashton *et al*., 2000),

121   although there have also been clear exceptions to the rule in intraspecific (e.g. Meiri &

122   Dayan, 2003), interspecific (e.g. Clauss *et al*., 2013) and assemblage-level (e.g. Olalla-

123   Tarraga *et al*., 2006) analyses. As already suggested above, a latitudinal gradient in body size

124   should be related to temperature, with lower temperatures selecting for larger body size. The

125   mechanistic basis for this pattern comes from the original idea of Bergmann (1847) that large

126   endothermic animals have a lower surface area-to-volume ratio than small animals, the

127   former radiating less heat per unit of body mass. Hence, large animals can maintain warmer

128   body temperatures in cold climates compared with smaller animals. While this idea has been

129   subsequently tested with endothermic vertebrates with some successful examples in

130   intraspecific analyses of birds and mammals (Ashton *et al*., 2000; Meiri & Dayan, 2003), it is

131   less certain if it occurs frequently in assemblage-level analyses in general (Olalla-Tarraga *et*

132   *al*., 2006; Rodríguez *et al*., 2008) and those in ectothermic invertebrates in particular

133   (Cushman *et al*., 1993; Gérard *et al*., 2018). In addition, even if there is some support for

134   Bergmann's rule in ectothermic invertebrates, the underlying mechanisms do not necessarily

135   need to be the same as in mammals and birds (Cushman *et al*., 1993; Gérard *et al*., 2018).

136   Also, even for endothermic vertebrates, the mechanisms underlying body size variation may

137   be more complex than originally proposed in the context of Bergmann's rule (Geist, 1987;

138   Clauss *et al*., 2013).

139   While the LDG, Rapoport's rule and Bergmann's rule have received considerable

140   interest (Gaston *et al*., 2008), their relationships with other aspects of biodiversity have thus

141   far been largely neglected. One aspect of biodiversity that would be highly interesting to

142   address in this context is beta diversity in terms of the variation in species composition

143   among sites (Anderson *et al*., 2011). Recently, Legendre and De Cáceres (2013) devised a

144   method to decompose total beta diversity in the contributions of species or sites, whereby the

145   relative ecological uniqueness of sites can be evaluated (i.e., local contribution to beta

146   diversity, LCBD). Empirical research on the topic has thus far revealed that species richness

147   is typically negatively correlated with LCBD across local ecological assemblages, although

148   there is some variation around the relationship (Legendre & De Caceres, 2013, Heino *et al*.,

149   2017, Vilmi *et al*., 2017, Landeiro *et al*., 2018, da Silva *et al*., 2018). This relationship thus

150   shows that species poor assemblages contribute the most to the regional beta diversity in

151   various taxonomic groups. However, how mean body size and mean range size relate to

152   LCBD has not been previously examined, although LCBD could be related to the LDG,

153   Bergmann's rule and Rapoport's rule through the influences of latitude and associated

154   environmental variations on species ranges.

155   Tying together species richness, range size, body size and LCBD patterns can be most

156   easily done by focusing on a major master gradient, i.e., latitude (Gaston *et al*., 2008). Then,

157   based on what was described above (Fig. 1), we assumed that (A) species richness would

158   decline with latitude, (B) mean range size would increase with latitude (if temperature

159   variability increases monotonically with latitude) and (C) mean body size should increase

160   with latitude. Thus, in general, we could expect to find faunas with low species richness,

161   large average range size and large average body size at high latitudes (Rosenzweig, 1995;

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Stevens, 1989). Regarding the mechanisms, we expected that in the case of species richness, climate, history and habitat area would affect variation in species richness in combination (Gaston & Blackburn, 2000). For mean range size, we expected that climate and history would be the underlying reasons (Brown, 1995). Third, we assumed that temperature variation would explain geographical variation in body size (Bergmann, 1847). Finally, we assumed that if LCBD is negatively correlated to species richness, it should increase with latitude and be affected by a complex set of actual predictor variables. We tested these predictions using data for diving beetles (Coleoptera: Dytiscidae) collated for the biogeographical provinces in Northern Europe (54°N to 71°N). Diving beetles occur mostly in freshwater environments (Nilsson & Holmen, 1995), thus adding an interesting test case for examining the covariation of species richness, range size and body size in a group of aquatic insects (Vamosi *et al*., 2007). These beetles are primarily predaceous (Nilsson & Holmen, 1995), thereby providing a suitable case of examining if ecogeographical rules exist in ectothermic aquatic predators (Vamosi *et al*., 2007).

We asked the following specific questions when studying the major ecogeographical rules at the assemblage level (Gaston *et al*., 2008). (1) Are there latitudinal gradients in species richness, mean range size and mean body size across provincial diving beetle assemblages? (2) Which actual environmental variables account for variation in species richness, mean range size, mean body size and LCBD of diving beetles across the biogeographical provinces of Northern Europe? We also discussed if diving beetle faunas follow any ecogeographical rules, and if not, which alternative explanations could fit with patterns found for this diverse family of aquatic insects. We built this study on our previous research, where we found that the variation in the provincial species composition of diving beetles was mostly accounted for by temperature along latitudinal and longitudinal gradients across this climatically heterogeneous region of Northern Europe (Heino & Alahuhta, 2015).

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Materials and methods

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190 *Study area and diving beetle data*

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192 We considered diving beetle (Coleoptera: Dytiscidae) occurrence and environmental data for

193 the 101 biogeographic provinces of Denmark, Sweden, Norway and Finland (54ºN to 71ºN,

194 5ºE to 32ºE). As in our previous studies, we merged various small coastal provinces in

195 Norway to provide a better and more accurate representation of species ranges (Heino &

196 Alahuhta, 2015; Heino *et al.*, 2015). After these modifications, the number of provinces for

197 the analyses was 79. Each province has typical characteristics of climate, land cover and land

198 use, and biogeographic provinces are thus relatively homogeneous study units, so they can be

199 used for biogeographical studies, assuming that they provide a homogeneous grain size

200 (Väisänen et al., 1992; Väisänen & Heliövaara, 1994). A biogeographical province can thus

201 be defined as having generally similar climatic conditions and natural vegetation patterns. We

202 here analysed the same data on diving beetles as in Heino and Alahuhta (2015). These data

203 were derived from the literature (Nilsson & Holmen, 1995). Although these data for diving

204 beetles are already relatively old, they represent good information about species distributions

205 across Northern Europe up to mid-1990s and can thus be directly correlated with predictor

206 variable data collated between 1960s and 1990s.

207

208 *Predictor variables*

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210   To represent climate, we used average annual temperature (°C), maximum temperature of the

211   warmest month (°C), minimum temperature of the coldest month (°C), temperature range

212   (°C), precipitation of the wettest month (mm) and precipitation of the driest month (mm). The

213   climate variables were mean values of a period from 1960 to 1990 for each biogeographical

214   province and were derived from WorldClim with 0.93 km × 0.93 km resolution (Hijmans *et*

215   *al*., 2005). Because the two precipitation variables were strongly correlated ($r = 0.966$, P <

216   0.001), we only used the precipitation of the driest month in the analyses. In addition,

217   minimum temperature was strongly correlated with temperature range ($r = -0.899$, P < 0.001),

218   so we excluded temperature range from the analysis. Land cover variables were relative cover

219   (%) of fresh water, wetlands and agricultural areas in a province. These variables were

220   obtained from European CORINE 2006 with 100m resolution that is freely available from

221   Copernicus Land Monitoring Service (https://land.copernicus.eu/pan-european/corine-land-

222   cover/). Finally, average elevation and elevation range within the province were also

223   considered as land cover variables, as these variables are related to the environmental

224   variation along elevation gradients (Hof *et al*., 2012). Elevation variables were obtained from

225   3D Digital Elevation Model over Europe with 25m resolution. Because these two variables

226   were strongly correlated ($r = 0.955$), only elevation range was used in the statistical analysis.

227

228   *Response variables*

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230   As response variables, we used species richness, mean range size of species per province and

231   mean body size of species per province. All these data were collated from information given

232   in Nilsson & Holmen (1995). Species richness was the number of species per province, and it

233   was not significantly and positively correlated with province area ($r = -0.197$). Mean range

234 size was the average number of provinces occupied by all species detected in a given

235 province. Mean body size per province was calculated from the maximum body length for

236 each species reported in the literature (Nilsson & Holmen, 1995). As it is generally the case

237 in diving beetles, within-species variation in body size is low (Vamosi *et al*., 2007), and

238 minimum body length correlated strongly with maximum body length across species in the

239 dataset ($r = 0.990$). Finally, we also calculated local contribution to beta diversity (LCBD) as

240 a measure of beta diversity (Legendre & De Cáceres, 2013). To do so, we first Hellinger-

241 transformed province-by-species matrix (Legendre & Gallagher, 2001), and thereafter

242 calculated the total beta diversity (BD total, i.e. total variation in a site-by-species matrix) and

243 LCBD value for each site (i.e. the contribution of each site to total variation). This novel

244 approach is thus based on the total variance in the assemblage matrix, which is the total sum

245 of squares (the sum, over all species and all sites, of the squared deviations from the species

246 means) divided by n-1. This measure, in turn, can be decomposed into the contribution of the

247 sites (or the species) to total beta diversity (Legendre & De Cáceres, 2013). To complement

248 the Hellinger distance-based analysis, we also calculated LCBD values using Simpson

249 dissimilarity coefficient, a measure immune to species richness variation (Koleff *et al*., 2003).

250 For further details of calculating LCBD values and the R function 'beta.div' for conducting

251 the statistical analysis involved, see Legendre and De Cáceres (2013). LCBD represents the

252 ecological uniqueness of a province, i.e., it provides a measure of the relative contribution of

253 the given province to regional beta diversity of diving beetles. Large LCBD values indicate

254 high importance of the given province to the overall beta diversity. For recent applications of

255 the LCBD approach, see Tonkin *et al*. (2016), Heino & Grönroos (2017), Vad *et al.* (2017)

256 and da Silva *et al*. (2018).

257

258 *Modelling variation in species richness, LCBD, mean range size and mean body* size *using*

259 *boosted regression trees*

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261 We used Boosted Regression Tree (BRT) analysis (Elith *et al*., 2008) to model variation in

262 species richness, LCBD, mean range size and mean body size across the provinces. BRTs can

263 handle various types of data, have no need for prior data transformation or elimination of

264 outliers, consider non-linear relationships between response and predictor variables, and

265 automatically take into account interaction effects between predictors (Elith *et al*., 2008).

266 Here, we used BRTs to obtain the unique contributions of each actual environmental variable

267 (see above) to the four response variables based on Gaussian error. We used the following

268 parameters in all BRTs: tree.complexity = 5, learning.rate = 0.01, and bag.fraction = 0.5.

269 BRTs were conducted using the function 'gbm.step' in the R package dismo (Hijmans *et al*.,

270 2016). We showed the explained deviance of the BRT models and the partial dependency

271 plots to examine the model fits and contributions of predictor variables on species richness,

272 LCBD, mean range size and mean body size. We assumed that more complex models would

273 have smaller amount of explained deviance and that no single variable should have a large

274 unique impact on the response variable. In contrast, a model was deemed less complex if

275 explained deviance was high and if a single predictor variable had a high relative impact on

276 the response variable compared with other predictor variables.

277

278 **Results**

279

280 There was a lot of variation in range size and body size at the species level (Fig. S1), with the

281 histograms showing a uniform distribution for the former (i.e., there were similar numbers of

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282 species with small, intermediate and large ranges) and a right-skewed pattern for the latter

283 (i.e., most species were small).

284   Both the environmental predictors and response variables varied considerably across

285 the provinces (Table 1). For example, species richness ranged from 32 to 113, mean range

286 size from 46 to 61 and mean body size from 7.38 to 10.14 mm per province (Fig. 2). The

287 studied region shows high variations in climate, with steep temperature and precipitation

288 gradients from temperate to arctic regions, and from marine coasts to continental zones,

289 respectively. This facilitates finding explanations for climatically-driven ecogeographical

290 rules.

291   The response variables were variably correlated (Fig. 3). Species richness and LCBD

292 were strongly negatively correlated, and this relationship was relatively robust to using

293 different distance measures for calculating LCBD (Hellinger distance: $r = -0.820$, $P < 0.001$;

294 Simpson dissimilarity: $r = -0.520$, $p < 0.001$). Species richness and mean range size were

295 similarly negatively correlated. However, LCBD, range size and body size showed weaker,

296 yet significant correlations. Interesting relationships were, however, a negative correlation

297 between mean range size and mean body size, and a positive correlation between species

298 richness and mean body size. These correlations suggested complex relationships among the

299 response variables.

300   Species richness and mean body size decreased with latitude, whereas LCBD did the

301 opposite (Fig. 4). Mean range size did not vary linearly with latitude, but it was unimodally

302 related to latitude, with largest mean range sizes being detected at ca. 60°N. These response

303 variables also showed different relationships with the actual predictor variables (Table 2),

304 with explained deviance varying from 0.656 for mean body size to 0.887 for LCBD. Species

305 richness variation was mostly driven by maximum temperature, followed by elevation range

306 and precipitation (Fig. 5a). LCBD showed the strongest relationships with maximum

307 temperature, minimum temperature and water area, with LCBD decreasing with maximum

308 temperature, increasing with minimum temperature and first decreasing with water area

309 before reaching a plateau (Fig. 5b). Mean range size model was most strongly contributed by

310 mean annual temperature, which first had an increasing and then decreasing effect on the

311 response variable (Fig. 5c). This model was also complex in other ways because many

312 predictor variables had quite similar contributions to mean range size and their effects were

313 far from linear. Finally, mean body size model was mostly strongly contributed by agriculture

314 which increased mean body size to a certain level and then levelled off (Fig. 5d). In addition,

315 mean body size was contributed relatively strongly by maximum temperature, with a

316 unimodal response, and by mean annual temperature, with mostly increasing response.

317 Finally, it should be noted that the variables mostly directly related with diving beetle

318 habitats (i.e. water area and wetlands) were not generally positively and strongly contributing

319 to the variation in the response variables (contribution < 10%).

320

321 **Discussion**

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323 Few studies have tried to unravel the patterns and causes of multiple ecogeographical rules at

324 the same time (Gaston *et al*., 2008). Our aim was to test the occurrence of general patterns in

325 diving beetles faunas in a climatically heterogeneous region. We first found that the

326 correlations between species richness, local contribution to beta diversity (LCBD), mean

327 range size and mean body size varied clearly, and some of the correlations seemed to run

328 counter to what could be expected based on theory (e.g. species richness and mean body size

329 were positively related; Fig. 3). We also found that species richness decreased with latitude,

thereby lending support for the latitudinal diversity gradient (Rosenzweig, 1995; Hillebrand, 2004), and that LCBD exhibited the opposite trend, showing the species-poor northern (and western) provinces have more ecologically unique diving beetle assemblages. In contrast, mean range size showed a unimodal relationship with latitude, suggesting that diving beetles do not conform to Rapoport's rule (Stevens, 1989; Gaston, 2003). Finally, mean body size in diving beetle assemblages decreased with increasing latitude, showing a trend opposite to that suggested by Bergmann's rule (Bergmann, 1847; Blackburn *et al*., 1999). Moreover, the main actual environmental predictors varied somewhat among species richness, LCBD, mean range size and mean body size in the boosted regression tree models.

The latitudinal diversity gradient (LDG) is typically assumed to result from three main groups of hypothesised mechanisms (e.g. Hurlbert & Stegen, 2014). These include the effects of biome area (e.g. Rosenzweig, 2003), climate (e.g. Currie *et al*., 2004) and history (e.g. Hewitt, 1999) on species richness. The species richness of diving beetles decreased with latitude, although the correlation was not particularly strong, possibly owing to the heterogeneous climatic conditions across the study area (e.g. Heino *et al.,* 2015) and the fact that various aquatic insect groups may not exhibit clear classical latitudinal gradients (e.g. Pearson & Boyero, 2009). Also, some smaller clades of diving beetles may peak at mid latitudes (e.g. Morinière *et al*., 2016). Given that the predictor variables most strongly associated with diving beetle habitats, i.e. water area and wetlands, did not contribute strongly to species richness, we can refute the hypothesis that habitat area per se accounts for variation in species richness at this spatial scale. A potential explanation to this finding is that diving beetles typically inhabit small water bodies and the vegetated margins of large water bodies (Nilsson *et al*., 1994; Nilsson & Söderberg, 1996; Vamosi *et al*., 2007), which were more difficult to detect at this study resolution and, hence, water area or wetlands did not contribute strongly to provincial species richness. Instead, although we cannot completely

355 rule out the effects of ice age history on the species richness pattern of diving beetles in an

356 area where ice sheet of the Last Glaciation Maximum retreated in a stepwise way between

357 25,000 and 8,000 years before present (Denton & Hughes, 1981; Kleman & Hättestrand,

358 1999; Houmark-Nielsen *et al.*, 2012), we can nevertheless suggest that climate affects the

359 most variation in species richness across the study area. In that regard, it was notable that

360 maximum temperature of the warmest month contributed the most to the species richness

361 variation. It is hence possible that warmer climates support higher species richness of diving

362 beetles because the distributions of aquatic insects are strongly affected by temperature (e.g.

363 Vannote & Sweeney, 1980). It is also likely that, owing to warmer air and water

364 temperatures, freshwater ecosystems in the southern part of the study area are much more

365 productive that those in the northern parts, thereby providing more energy to support more

366 species (e.g. Currie *et al*., 2004). How this more energy hypothesis relates to the resources for

367 diving beetles can only be speculated, but it is possible that warmer and more productive

368 freshwater ecosystems provide more invertebrate prey for predaceous diving beetles. A large

369 prey availability might thus account for the indirect effect of temperature on diving beetle

370 species richness. A second explanation why temperature appeared important in our models is

371 simply physiological (e.g. Calosi *et al*., 2009), with more species being physiologically more

372 able to occur in southern provinces with warmer and less seasonally variable climates than

373 those in the northern provinces with more seasonal variability (e.g. Willig *et al.,* 2003).

374 However, this latter assumption may not hold because some provinces on the coast of the

375 Atlantic Ocean (Central Norway) have less seasonal climates than those in the more

376 continental areas of the study area (Eastern Finland), yet the latter provinces harboured more

377 species than the former (Fig. 2). It thus appears that the species richness pattern of diving

378 beetles is complex, and that multiple mechanisms are likely to act in concert in accounting for

379 this variation.

380   The spatial pattern of species richness was relatively strongly correlated to that of

381   LCBD, and this relationship was robust to using different distance measures. However, the

382   relationship of LCBD to maximum temperature was generally negative (Fig. 6), suggesting

383   that the species poor provinces with low maximum temperatures contributed the most to

384   regional beta diversity. While the negative relationship between species richness and LCBD

385   has been noted before in empirical studies of local ecological assemblages (Legendre & De

386   Cáceres, 2013; Heino & Grönroos, 2017; Vilmi *et al.,* 2017; Landeiro *et al*., 2018), no study

387   to our knowledge has examined the relationship of LCBD with temperature at large spatial

388   scales across biogeographical provinces. Our finding thus has potentially important

389   implications for understanding spatial variation in biodiversity for two reasons. First, we

390   cannot simply state that the biodiversity in species poor provinces should be ignored. Rather,

391   it contains an important biodiversity resource if species-poor provinces with high LCBD

392   values contain rare species. Second, in terms of climate change, these species poor provinces

393   are likely to gain more species with increasing temperatures in the near future, suggesting

394   that regional beta diversity patterns will also change. These changes in LCBD are thus

395   directly related with alterations in species ranges.

396   We did not find support for Rapoport's rule that range size should increase with

397   latitude (Stevens, 1989) and be linearly correlated with temperature conditions (i.e. mean,

398   maximum, minimum or range) or ice age history (Brown, 1995). Rather, we found that mean

399   range size in diving beetles faunas showed a unimodal relationship with latitude and mean

400   annual temperature that largely follows a latitudinal trend in the study area (Heino *et al*.,

401   2015). Hence, given that there is a rather clear decline in mean temperature (r = -0.936) and

402   increase of temperature range (r = 0.665) with latitude in our study area but no increase in

403   range size, we can refute the hypothesis that Rapoport's rule is occurring in diving beetles in

404   Northern Europe. This is because a precondition for the existence of Rapoport's rule is a clear

latitudinal change in temperature conditions (Gaston & Chown, 1999; Tomašových *et al*.,
2015). In addition, mean range size first increased and then decreased with the amount of
agriculture, and generally increased with minimum temperature and precipitation (Fig. 7).
These main predictors of mean range size suggest that largest average ranges of diving
beetles occur at ca. 60°N, where the temperature conditions are possibly most suitable for
diving beetles in the study area. However, given that we only analysed parts of the species
global ranges (e.g. the ranges of most species expand towards south of the study area), it is
possible that mean range size decreases even more towards south from 60°N because of both
climatic and historical reasons. Indeed, many diving beetle species in faunas of Southern
Europe have smaller ranges than those occurring in Northern Europe (e.g. Calosi *et al*.,
2009). This has been postulated to result from historical influences in southern faunas, which
show relatively recent evolutionary changes and, in northern faunas, which have formed after
the latest ice age (e.g. García-Vázquez *et al*., 2017). Hence, only species able to disperse
across large geographical areas have reached the north and nowadays form northern faunas
(Dehling *et al*., 2010; Gómez-Rodríguez & Baselga, 2018). However, it appears that the
variation of mean range size in diving beetle faunas is a combination of multiple underlying
causes, which may be difficult to unravel.

We neither found support for Bergmann's rule that species body size should be larger
in cold climates (i.e. high latitudes) than in warm climates (i.e. low latitudes) across a broad
geographical gradient (Bergmann, 1847). Rather, we found that mean body size in diving
beetle faunas decreased with latitude and was mostly strongly contributed by mainly
increasing effects of agriculture, maximum temperature and mean annual temperature (Fig.
8). While it is understandable that a hypothesis originally coined to account for body size
variation in endothermic mammals and birds did not apply to ectothermic invertebrates, there
are studies that have found support to Bergmann's rule in ectothermic animals at the

18

430 assemblage level (*sensu* Gaston *et al*., 2008). For example, studies on ants (e.g. Cushman *et*

431 *al*., 1993) and bees (e.g. Gérard *et al*., 2018) found support for Bergmann's rule, whereas

432 partial support has been found for lizards (Olalla-Tarraga *et al*., 2006). However, the studies

433 conducted at the assemblage level are less common than those on intraspecific level (Gaston

434 *et al*., 2008), so it is difficult to compare our present findings of decreasing body size with

435 decreasing latitude to those of intraspecific exercises. However, Olalla-Tarraga *et al*. (2006)

436 found rather similarly that the body size of snake assemblages decreased with decreasing

437 temperatures. These patterns suggest that the determination of body size variation is a

438 complex issue in ectothermic animals, implying that the mechanisms involved are also

439 multifaceted. For mean body size variation in diving beetle faunas, we offer as yet a

440 speculative explanation for further testing. Given that mean body size increased with

441 agriculture and temperature, we could assume that ecosystem productivity, which is relying

442 on temperature and nutrient availability in freshwaters (Wetzel, 2001), is higher in the

443 southern freshwaters compared with northern freshwaters. This higher freshwater

444 productivity is then seen as higher availability of prey for predatory diving beetles. Being

445 predatory, geographical variation in mean body size of diving beetles may thus be related to

446 availability of resources (Geist, 1987; Clauss *et al*., 2013), which are less readily available in

447 the cold and nutrient-poor freshwaters in the north than in the warmer and nutrient-rich

448 freshwater in the south of the study area. Thus, higher productivity could select for larger-

449 sized diving beetles because they would require more energy to attain their final larval and

450 adult size compared with small-bodied species.

451   Tying together various ecogeographical rules can be most easily done by focusing on

452 the latitudinal gradient (Gaston *et al*., 2008). We found some statistically significant

453 relationships between our response variables and latitude, but these did not conform to the

454 original hypotheses in some cases. While species richness decreased with latitude, mean

455   range size did not vary linearly across latitude and mean body size decreased with latitude.

456   Hence, these patterns did not as a whole provide strong support for the existence of

457   ecogeographical rules in ectothermic aquatic invertebrates. However, we can expect to find

458   low species richness, high contribution to beta diversity and small mean body size in diving

459   beetle faunas in the northernmost provinces of the study area, whereas mean range size

460   variation was more complex. This complexity was also identified for the models of all

461   response variables, with temperature and some land use variables attaining slightly different

462   roles in accounting for variation in species richness, LCBD, mean range size and mean body

463   size. These patterns could be tested and tied together in other regions and organism groups to

464   see if they are similarly complex or if more general patterns better conforming to the

465   ecogeographical rules exist.

466

473

Contribution of authors

474

475

476   JH devised the study ideas, ran the statistical analyses and led the writing. JA collated the

477   predictor variable data and contributed to the writing.

478

479 **References**

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655   **Supporting Information**

656   Supporting Information Fig. S1. Species-based histograms of range size and body size for

657   diving beetles in Northern Europe.

658 Table 1. Descriptive statistics of the response variables and predictor variables. SD =

659 standard deviation, CV = coefficient of variation. NA = not applicable because there were

660 negative values. LCBD = local contribution to beta diversity.

	Mean	SD	CV	Min	Max
Species richness	78.873	19.274	0.244	32.000	113.000
LCBD	0.013	0.005	0.375	0.006	0.027
Mean range size per province	54.183	3.731	0.069	46.168	61.837
Mean body size per province	8.742	0.622	0.071	7.382	10.143
Maximum temperature (°C)	18.654	2.406	0.129	13.350	21.870
Mean annual temperature (°C)	3.429	3.185	0.929	-3.050	8.230
Minimum temperature (°C)	-10.101	5.363	NA	-21.105	-1.989
Precipitation of driest month (mm)	37.430	15.175	0.405	19.500	99.860
Agriculture (%)	0.182	0.221	1.210	0.000	0.790
Water area (%)	0.053	0.045	0.837	0.000	0.230
Wetlands (%)	0.048	0.053	1.101	0.000	0.220
Elevation range (m)	775.031	714.219	0.922	62.180	2381.940

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Table 2. Summaries of the boosted regression tree results. LCBD = local contribution to beta diversity.

	Species richness	LCBD	Mean range size	Mean body size
Total fauna				
Mean total deviance	366.794	0.222	13.747	0.381
Mean residual deviance	59.997	0.025	2.417	0.131
Explained deviance	0.836	0.887	0.824	0.656
Estimated cv deviance	164.047	0.08	6.246	0.213
Training data correlation	0.918	0.945	0.913	0.823
cv correlation	0.724	0.713	0.695	0.656

Figure captions

Fig. 1. A schematic view of the ecogeographical rules and latitude. Also shown are the potential actual predictors underlying the geographical gradients in species richness, mean range size and mean body size.

Fig. 2. Maps of the response variables across Northern Europe. Shown are diving beetle species richness, mean range size, mean body size, and local contribution to beta diversity (LCBD).

Fig. 3. Relationships between the response variables. All Pearson correlations were significant at $p < 0.05$.

Fig. 4. Relationships between the four response variables and latitude. LCBD = local contribution to beta diversity. Pearson correlations: (a) Species richness vs latitude: $r = -0.404$, $p < 0.001$; (b) LCBD vs latitude: $r = 0.289$, $p < 0.001$; (c) Mean range size vs latitude: $r = 0.193$, $p = 0.089$; (d) Mean body size vs latitude: $r = -0.638$, $p < 0.001$; (e) Temperature range vs latitude: $r = 0.665$, $p < 0.001$. N = 79 provinces.

Fig. 5. Partial dependency plots from the BRT models. Shown are the predictor variables and their relative influences on the response variable. Subplots: (a) species richness, (b) local contribution to beta diversity (LCBD), (c) mean range size, and (d) mean body size.