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Title: Multiscale drivers of carabid beetle (Coleoptera: Carabidae) assemblages in small European woodlands

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AUTHOR'S CONTRIBUTIONS

GD, KV, MD, VLR, LM, BG, and PDS designed the study.

RM, LM, GD, and VLR wrote the manuscript.

RM, LM, and JoL ran the analyses.

LM, PDS, VLR, and BG sorted arthropods from the traps and identified the species.

LM, VLR, AV, JoL, GD, BG, MD, PDS, KV, JB, SC, JaL, MD, AK, MW, TN, and JeL collected data in the field and contributed to write the manuscript.

EGM managed the databases and conducted GIS analyses.

BIOSKETCH

Ronan Marrec is an Assistant Professor at the UMR 7058 CNRS EDYSAN (Ecology and Dynamics of Anthropogenic Systems), Jules Verne University of Picardy, France. As a landscape ecologist he is interested in evaluating the role of the spatial structure and temporal dynamics of landscapes and human activities on biodiversity and ecosystem services. For more information: <https://ronanmarrec.weebly.com>.

All authors are members of the research project smallFOREST (<http://www.u-picardie.fr/smallforest/uk/>), which is devoted to studying biodiversity and ecosystem services of small forest patches in European landscapes.

1 **Journal:** Global Ecology and Biogeography

2

3 **Title:** Multiscale drivers of carabid beetle (Coleoptera: Carabidae) assemblages in small
4 European woodlands

5 **Running title:** Carabid assemblages in small forests

6

7 **ABSTRACT**

8 **Aim** The spatiotemporal connectivity of forest patches in lowland agricultural landscapes and
9 their age matter to explain current biodiversity patterns across regional as well as biogeographical
10 extents, to the point that it exceeds the contribution of macroclimate for plant diversity in the
11 understory of temperate forests. Whether this holds true for other taxonomic groups remains
12 largely unknown. Yet, it has important consequences for ecosystem functioning and the delivery
13 of ecosystem services. Focusing on carabid beetle assemblages, we assessed the relative
14 importance of macroclimatic, landscape, and patch attributes on driving local species richness (α -
15 diversity) and species dissimilarity between patches (β -diversity).

16 **Location** Deciduous forest patches in seven regions along a 2,100-km long latitudinal gradient
17 across the European temperate forest biome, from southern France to central Sweden.

18 **Methods** We sampled 221 forest patches in two 5×5-km landscape windows with contrasting
19 management intensities. Carabid beetles were classified into four habitat-preference guilds:
20 forest-specialist, forest-generalist, eurytopic, and open-habitat species. We quantified the multi-
21 level environmental influence using mixed-effects models and variation partitioning analysis.

22 **Results** We found that both α - and β -diversity were primarily determined by macroclimate, acting
23 as a large-scale ecological filter on carabid assemblages among regions. Forest-patch conditions,
24 including biotic and abiotic heterogeneity as well as patch age (but not patch size), increased α -
25 diversity of forest species. Landscape management intensity weakly influenced α -diversity of
26 forest species, but increased the number of non-forest species in forest patches. Beta-diversity of
27 non-forest species increased with patch heterogeneity and decreased with landscape management
28 intensity.

29 **Main conclusions** Our results highlight the leading role of broad macroclimatic gradients over
30 local and landscape factors in determining the composition of local carabid communities, thereby
31 shedding light on macroecological patterns of arthropod assemblages. This study emphasizes the
32 urgent need for preserving ancient forest patches embedded in agricultural landscapes, even the
33 small and weakly connected ones.

34 **Keywords**

35 **Agricultural landscapes, arthropods, biogeographic gradient, carabid beetles, habitat**
36 **quality, landscape composition, macroclimate, metacommunity dynamics, smallFOREST,**
37 **species turnover**

38 INTRODUCTION

39 The cover of present-day forests in European lowland mainly consists of forest patches of various
40 size, age, tree species composition, and degree of isolation, that are embedded in a more or less
41 intensively managed agricultural matrix (Estreguil *et al.*, 2013). Forest loss and fragmentation are
42 widely acknowledged as major threats to biodiversity and ecosystem functioning through their
43 effects on habitat availability, quality, and connectivity (Fahrig, 2003; Foley *et al.*, 2005; Haddad
44 *et al.*, 2015). In particular, increased fragmentation reduces the amount of forest interior habitat
45 which is available for habitat specialist species (Pfeifer *et al.*, 2017). Therefore, patch-level biotic
46 homogenization (i.e., loss of genetic, taxonomic, and functional diversity of species assemblages)
47 due to edge effects is generally observed, which increases in importance as patch size decreases
48 (McKinney & Lockwood, 1999; Olden & Rooney, 2006). At the same time, forest edges can
49 offer suitable conditions for a number of animal and plant generalist species originating from
50 neighboring, more open or/and disturbed habitats (e.g., Cousins & Eriksson, 2002; González *et*
51 *al.*, 2017; De Smedt *et al.*, 2018), thereby potentially enhancing the delivery of multiple
52 ecosystem services in small forest patches (Kütt *et al.*, 2018; Valdés *et al.*, 2020). Another
53 consequence of forest loss and fragmentation is that remnant forest patches are increasingly
54 distant from each other. Moreover, the landscape matrix into which forest patches are embedded
55 may be more or less permeable to species movements. Patch isolation and matrix composition
56 both determine landscape connectivity, i.e., the degree to which landscape mosaics facilitate
57 movement of organisms and their genes between distinct forest patches (Taylor *et al.*, 1993;
58 Ricotta *et al.*, 2000; Tischendorf & Fahrig, 2000). In particular, a low management intensity of
59 the agricultural matrix (e.g., with grasslands, which are expected to be more permeable than
60 intensively cultivated croplands) and the presence of ecological corridors (e.g., hedgerows, which
61 are thought to facilitate dispersal of forest species among forest patches) will increase

62 colonization rates, while decreasing local extinction rates, in many taxa, including arthropods
63 (e.g., Baudry & Burel, 2019; Seibold *et al.*, 2019). Reduced connectivity between forest patches
64 represents a major threat to species that are forest specialists, including arthropods, and which
65 often exhibit low dispersal abilities (Aviron *et al.*, 2018). As a result, colonization rate of forest
66 patches may be disproportionately low compared to extinction rate and metacommunity
67 functioning could be disrupted. In case of neutral (Hubbell, 2005) or niche differentiation
68 processes (MacArthur & Levins, 1967; Maire *et al.*, 2012), such a disequilibrium can ultimately
69 lead to an increased dissimilarity in species composition between forest patches, due to species
70 loss or/and species replacement (Hendrickx *et al.*, 2009), thereby increasing the magnitude of
71 difference between the regional species pool and composition of local assemblages. On the
72 contrary, in case of landscape-level filtering, species with similar trait values might be selected,
73 leading to species homogenization at the landscape scale (Keddy, 1992; Maire *et al.*, 2012).

74 In addition to the degree of spatial connectivity, temporal connectivity through the age of
75 forest patches has repeatedly been shown to influence community composition, with ancient
76 forest patches (i.e., patches that have continuously existed for centuries) harboring a higher
77 number of forest-specialist species with limited dispersal abilities than recent forest patches (i.e.,
78 patches that have established on former agricultural lands in the last decades) (Dekoninck *et al.*,
79 2005; Desender *et al.*, 2005; Debnár *et al.*, 2016; Lelli *et al.*, 2019). Ancient forest patches
80 usually support more diverse plant assemblages than recent ones, given their higher habitat
81 heterogeneity (Brunet, 2007; Burrascano *et al.*, 2018) and benefit from longer duration for
82 accumulating forest specialist species (i.e., the species-time relationship; Almoussawi *et al.*,
83 2020; Valdés *et al.*, 2020). However, compared to plant species, arthropod species have received
84 little attention with respect to species richness in ancient vs. recent forest patches (Schowalter,
85 2017). Besides, to the best of our knowledge, only few studies have compared the diversity

86 patterns of such arthropod assemblages in different contexts of landscape mosaic (e.g., Hendrickx
87 *et al.*, 2009; De Smedt *et al.*, 2018).

88 Among major arthropod groups living in forest ecosystems, carabid beetles (Coleoptera:
89 Carabidae) are important for ecosystem functioning and biocontrol (Thiele, 1977; Kromp, 1999;
90 Kotze *et al.*, 2011), and are often used as bioindicators of good forest management practices
91 ensuring healthy and sustainable forest systems (e.g., Rainio & Niemelä, 2003; Pearce & Venier,
92 2006). Forest carabid species are highly sensitive to reduction of forest patch size, as smaller
93 patches exhibit lower habitat quality and greater edge effects than larger patches. Forest
94 fragmentation usually induces a complete replacement of large specialist species characterized by
95 their low mobility by small, generalist, and highly mobile species coming from surrounding
96 habitats (Niemelä, 2001; Rainio & Niemelä, 2003; Lövei *et al.*, 2006; Do & Joo, 2013; Jung *et*
97 *al.*, 2018). Variations in carabid composition and diversity between mature and young forest
98 stands have previously been shown (e.g., Fountain-Jones *et al.*, 2015), as well as the interaction
99 with forest management (e.g., Sroka & Finch, 2006; Barkley *et al.*, 2016). Surprisingly, the role
100 of historical continuity (i.e., forest patch age) has been largely neglected so far (but see Assmann,
101 1999; Desender *et al.*, 2005; Hülsmann *et al.*, 2019).

102 Local climatic conditions (Park *et al.*, 2017), as well as current large-scale macroclimatic
103 gradients (e.g., Heino & Alahuhta, 2015) and the biogeographic history of the continent since the
104 Pleistocene glaciations (Calatayud *et al.*, 2016, 2019), are widely acknowledged as important
105 drivers of local carabid species assemblages. Together with local and landscape features,
106 macroclimatic factors were shown to affect carabid assemblages individually, but their relative
107 importance is still unknown, despite their crucial importance for understanding all processes
108 underlying local arthropod, assemblages. Whether common patterns are observed across various
109 carabid guilds remains an unanswered question. Given the importance of small deciduous forest

110 patches as biodiversity reservoirs in agricultural landscapes (De Blois *et al.*, 2002) and in
111 delivering multiple ecosystem services to human societies (Decocq *et al.*, 2016), understanding
112 community assembly processes in these habitats embedded in patchy landscapes is particularly
113 relevant to conservation ecology and sustainable landscape planning.

114 Here we aim at explaining patch-scale species richness (hereafter α -diversity) and magnitude
115 of difference between landscape-scale species pool and patch-scale carabid assemblages
116 (hereafter β -diversity) in small forest patches embedded in contrasted agricultural landscapes
117 along a broad macroclimatic gradient across temperate Europe. We separated carabid
118 assemblages into four different guilds based on habitat preferences, namely: forest specialists,
119 forest generalists, open-habitat species, and eurytopic species. The first two guilds group “forest
120 species”, whilst the latter two group “non-forest species”. More specifically, we address the
121 following research hypotheses: (i) macroclimatic conditions act as the main ecological filter on
122 all carabid beetle assemblages; (ii) landscape management intensity decreases local species
123 richness (α -diversity), and increases the magnitude of difference between the landscape species
124 pool and local assemblages (β -diversity) of forest species (particularly for specialists), whilst the
125 reverse is true for non-forest species (particularly for open-habitat species); and (iii) patch size
126 and patch age both positively affect α -diversity, especially for forest species, and forest
127 specialists in particular. To test these hypotheses, we quantified the relative importance of
128 potential environmental drivers acting at different spatial scales (patch, landscape, continent) on
129 local carabid assemblages, using a large, dedicated field survey which encompasses seven
130 regions distributed along a transect running from southern France to central Sweden.

131

132 **METHODS**

133 **Study sites**

134 We collected data across a total of 221 deciduous forest patches, distributed among seven
135 European regions. Regions were distributed along a south-west-to-north-east gradient of ca.
136 2,100 km across the European temperate forest biome (Fig. 1). In each region, we selected two 5
137 km × 5 km landscape windows differing by their degree of landscape permeability (see Valdés *et*
138 *al.*, 2015 for more details). The first window was characterized by forest patches embedded in an
139 intensively cultivated open field landscape (hereafter “open field”). The second window
140 contained forest patches more or less connected by woody corridors (e.g., hedgerows) within a
141 less intensively managed landscape, dominated by grasslands and small crop fields (hereafter
142 “bocage”). A detailed and updated list of landscape and macroclimatic variables associated with
143 each landscape window can be found in Vanneste *et al.* (2019).

144 For each landscape window, we computed area, perimeter, and age of all forest patches using
145 digitized maps (one contemporary map at a scale of 1:25,000 and historical maps from the 17th,
146 18th, 19th, and 20th centuries) in a Geographic Information System (GIS; ARCGIS 9.3, ESRI).
147 Patches were subsequently distributed among four classes according to their area and age: small
148 (< median patch area value for the focal window) and recent (< 150 years); large (> median patch
149 area value for the focal window) and recent; small and ancient (> 150 years); and large and
150 ancient.

151 # Figure 1 here #

152 **Carabid sampling and habitat preference**

153 Whenever possible, we selected four forest patches (i.e., four repetitions) per level of patch size-
154 age combination ($n = 4$) and per landscape window ($n = 14$). A perfect balanced design was
155 achieved in five out of seven regions, to finally include a total of 221 forest patches to trap

156 carabid beetles (i.e., 16 forest patches in each window, except 14 in the openfield window in
157 eastern Germany and 15 in the openfield window in southern Sweden). For this purpose, we used
158 10-cm diameter pitfall traps installed for 14 consecutive days in both spring (ca. April) and
159 summer (ca. August) 2013. Traps were filled with 200 mL of a 50 % conservative solution of
160 ethylene-glycol and a few drops of detergent, and protected from litter and rain fall by aluminum
161 roofs. A total of four pairs of traps were disposed in each patch as follows. A first pair, consisting
162 of two traps separated by a plastic barrier (100-cm long, 18-cm high), was disposed into the inner
163 part of a south-facing edge (or, when not possible, first a west-, and then an east-facing edge was
164 chosen). This setup was replicated 5-m apart along the same edge. A third pair was installed at
165 the barycenter of the forest patch (except in eastern Germany, where all traps were located in the
166 edge), and similarly replicated (fourth pair). The plastic barrier was always parallel to the
167 selected forest edge. To make data comparable among the seven studied regions, and because of
168 the latitudinal climatic gradient covered by our study, the two sampling sessions carried out in
169 each region started when local growing degree hours (GDH ; Graae *et al.*, 2012) reached values
170 of ca. 10,000°C h and 20,000°C h, respectively. Following trap collection, carabid beetles were
171 sorted in the lab in a 70% ethanol solution and identified to the species level following Jeannel
172 (1941, 1942). Species names follow *Fauna Europaea* (de Jong *et al.*, 2014). Data from all pitfall
173 traps of a given patch and from the two trapping sessions were pooled in all subsequent statistical
174 analyses.

175 Species were distributed among four guilds, according to their habitat preference and using
176 knowledge from the scientific literature (Hůrka, 1996; Sadler *et al.*, 2006; Gaublomme *et al.*,
177 2008; Bräunicke & Trautner, 2009): forest-specialist species, limited to stable, mature forest
178 stands; forest-generalist species, occurring in any type of forest stand, in ancient as well as recent
179 forest; open-habitat species, associated with non-forest habitats such as grasslands and arable

180 lands; and eurytopic species, occurring in open habitats and tolerating transiently forest habitats.
181 We could not assign only one species (*Oodes helopioides*, $n = 1$ individual) to any group because
182 of a lack of information in the literature.

183 **Environmental variables**

184 Three groups of explanatory variables (patch, landscape, and macroclimatic variables) were
185 derived from field observations, historical archives, or global climatic layers, for and around each
186 forest patch using a GIS.

187 *Macroclimatic variables*

188 To assess the influence of macroclimate on species diversity, we extracted 10 candidate
189 bioclimatic variables from the WorldClim global database (1-km resolution,
190 <http://www.worldclim.org>), and averaged each variable for each forest patch using all 1-km²
191 pixels intersecting it. Four macroclimatic variables were retained for further analyses, based on a
192 principal component analysis (PCA; see Valdés *et al.*, 2015), namely maximum temperature of
193 the warmest month (MaTWm; BIO5); minimum temperature of the coldest month (MiTCm;
194 BIO6); precipitation of the wettest month (PWm; BIO13); and precipitation of the driest month
195 (PDm; BIO14). The selection was made in a way to minimize the correlation between variables
196 and to maximize the correlation with the PCA axes. Our variables were correlated (Pearson's r)
197 as follow with the PC1 (67.0 % of explained variance) and PC2 (17.2 %): BIO5 (PC1: $r = -0.64$;
198 PC2: $r = -0.12$), BIO6 (PC1: -0.93 ; PC2: 0.34), BIO13 (PC1: -0.52 ; PC2: -0.85), and BIO14
199 (PC1: -0.94 ; PC2: -0.04).

200 *Landscape variables*

201 Landscape variables were computed for five concentric 'doughnut'-like buffers of increasing
202 width around each forest patch: 50; 100; 250; 500; and 1,000 m width. We used Corine Land

203 Cover 2006 (Büttner & Kosztra, 2007) to map the distribution of woodland, cropland, and
204 grassland. We digitized hedgerows from aerial photographs. As proposed by Martin & Fahrig
205 (2012) and Fahrig (2013), we considered composition-based measurements of spatial isolation
206 for each forest patch, by calculating the proportion of each cover type and the hedgerow density
207 within each buffer.

208 *Patch-scale attributes*

209 We included patch area and patch age as covariates in our analyses, to account for both the
210 species-area and species-time relationship (Rosenzweig, 1995). We took the coefficient of
211 variation in elevation values (C_{Ve}) within a given forest patch using the ASTER Global Digital
212 Elevation Map at 30-m resolution (see Valdés *et al.*, 2015 for further details), as a proxy for
213 heterogeneity of abiotic conditions (incl. microclimate, soil conditions, and light availability)
214 (Lenoir *et al.*, 2017; Graae *et al.*, 2018). Finally, we computed a dissimilarity index in understory
215 plant species composition within each forest patch (i.e., intra-patch β -diversity; see Valdés *et al.*,
216 2015 for details on computation), separately for forest plant specialists and generalists following
217 distinction criteria as in Valdés *et al.* (2015).

218

219 **Data analysis**

220 All statistical analyses were performed in R 3.5.0 (R. Core Team, 2018).

221 *Multiple-site dissimilarities*

222 To evaluate whether between-patches differences in carabid composition were due to
223 replacement of species or to nestedness (since the same sampling effort was applied irrespective
224 to patch size), we computed multiple-site dissimilarities, separating the turnover and nestedness-
225 resultant components of overall Sørensen-based multiple-site dissimilarity as proposed by

226 Baselga (2010, 2012). Dissimilarities were evaluated at two different scales: (1) between-patch
227 dissimilarity within each landscape window, and (2) between-region dissimilarity along the
228 European gradient. We used the ‘betapart’ package (Baselga *et al.*, 2018).

229 *Species diversity*

230 We computed patch-level α -diversity, defined as the total number of species trapped per forest
231 patch; landscape-level γ -diversity, defined as the total number of species retrieved in all patches
232 of a given landscape window; and β -diversity, defined as the magnitude of difference between
233 the landscape-level species pool (γ -diversity) and the composition of the local assemblage
234 (α -diversity): $(\gamma-\alpha)/\gamma$. Diversity values were calculated separately for each of the four carabid
235 guilds, using the ‘vegan’ package (Oksanen *et al.*, 2018).

236 *Model selection.* The effects of patch, landscape, and macroclimatic attributes on α -diversity and
237 β -diversity were quantified using generalized linear mixed-effects models (GLMMs) and the
238 ‘lme4’ package (Bates *et al.*, 2015). Negative binomial distribution models (including an
239 observation level factor to account for overdispersion) were used for patch-level α -diversity.
240 Gaussian error distributions with an identity link were used for β -diversity. Distribution families
241 were chosen using the functions *descdist* and *fitdist* of the ‘fitdistrplus’ package (Delignette-
242 Muller & Dutang, 2015). To address possible multi-collinearity issues between macroclimatic,
243 landscape, and patch attributes, we computed pairwise Pearson correlation tests between all
244 continuous variables, and considered a threshold of 0.70 to consider two independent predictors
245 as correlated (Dormann *et al.*, 2013; Appendix S1). All explanatory variables were standardized
246 prior to analyses by subtracting the mean and dividing by the standard deviation. We included
247 ‘region’ and ‘window type’ (nested within ‘region’) as random intercept terms in all models to

248 account for the hierarchical structure of the sampling design and potential spatial autocorrelation
249 between assemblages occurring in the same region and landscape window.

250 In a first step, we selected the most relevant spatial scale (from 50 to 1,000 m) to consider for
251 each landscape variable (i.e., hedgerow density, grassland, crop, and forest relative proportion) at
252 each diversity level (α and β -diversity) and for each guild. For each landscape variable, we ran a
253 model at each spatial scale (one variable at a time) and retained the one scale from the model
254 with the lowest Akaike Information Criterion (AIC; Burnham & Anderson, 2004).

255 In a second step, we constructed complete models regrouping all explanatory variables (see
256 ‘Environmental variables’): first order (BIO_X) and second order (BIO_X^2 ; to allow for non-linear
257 macroclimatic variation) macroclimatic variables ($n = 8$); landscape variables ($n = 4$); and patch
258 variables ($n = 5$). Because of the large number of variables, we could not compare candidate
259 models with all possible combinations of variables. We thus performed a backward stepwise
260 selection of fixed explanatory variables: the full model was simplified step-by-step by removing
261 the most non-significant explanatory variables based on likelihood-ratio tests. The ML estimation
262 was used during model selection, and then REML was used for fitting the final model.

263 *Variation partitioning*

264 We ran a variation partitioning procedure including all response variables to quantify the
265 respective explanatory power of the three groups of explanatory variables (patch, $n = 5$ variables;
266 landscape, $n = 4$; and macroclimatic, $n = 8$) according to Legendre & Legendre (2012) and
267 Valdés *et al.* (2015). We constructed GLMMs (α -diversity) or LMMs (β -diversity) including
268 combinations of one, two, or three variable groups plus the random effects, and determined the
269 proportion of variation explained by the fixed variables (marginal R^2 ; R^2_m) according to
270 Nakagawa & Schielzeth (2013). We quantified the proportion of this variation explained by the

271 unique and shared contribution of patch, landscape, and macroclimatic variables, and expressed
272 this relative to the total amount of variation explained by the fixed factors in the global model
273 (containing all three groups of explanatory variables).

274

275 **RESULTS**

276 A total of 35,072 individuals corresponding to 159 species were collected from the 221 forest
277 patches. Seven highly frequent species were retrieved in more than 100 patches (*Abax*
278 *parallelepipedus* ($n = 2,443$ individuals), *Carabus hortensis* ($n = 968$), *C. nemoralis* ($n = 1,206$),
279 *Nebria brevicollis* ($n = 1,605$), *Pterostichus melanarius* ($n = 6,583$), *P. niger* ($n = 2,095$), and *P.*
280 *oblongopunctatus* ($n = 2,926$)). Ten species ($n = 5,270$ individuals) were forest specialist (FS), 24
281 species ($n = 12,350$) forest generalist (FG), 51 species ($n = 14,803$) eurytopic (EU), and 72
282 species ($n = 2,613$) open-habitat (OH) (see Appendix S2 for the full list of species together with
283 their associated habitat-preference guild and total abundance).

284 We observed important dissimilarities in species composition among regions along the European
285 gradient, irrespective of the guild considered (Sørensen dissimilarity: 0.62-0.72). These were
286 mainly driven by species turnover (Simpson dissimilarity: 0.50-0.61) (Fig. 2). Similar results
287 were found among patches within each landscape window and for each guild, except for forest-
288 specialist species, for which the nestedness component of Sørensen dissimilarity almost equaled
289 the turnover component (Fig. 2).

290 # Figure 2 here #

291 **Species richness (α -diversity)**

292 Species richness varied along the latitudinal gradient for all guilds, with a trend toward more
293 species at intermediate than at extreme latitudes along our European gradient (Fig. 3). In most

294 regions, open-habitat species richness was (or tended to be) higher in open field than in bocage
295 windows (Fig. 3d). We found no significant difference in mean species richness of the three other
296 guilds between open field and bocage windows, irrespective of the region considered (except in
297 northern France: less eurytopic species in bocage than open field window; Fig. 3c).

298 *# Figure 3 here #*

299 Based on the marginal and conditional R^2 difference derived from mixed-effects models, and
300 contrary to other guilds, variance in forest-specialist species richness was mostly explained by
301 random factors (i.e., region and window type nested in region) (Fig. 4a-d; Table 1a). Among all
302 groups of explanatory variables, the pure effect of macroclimate explained the largest proportion
303 of local species richness (α -diversity) for all guilds (89.8%, 84.3%, and 75.5% of the explained
304 variance for forest-specialist, eurytopic, and open-habitat species, within the fixed part of the
305 model, respectively; Fig. 4a,c,d) except forest generalists. The percentage of variation explained
306 by patch-scale attributes and landscape variables was negligible. Variation in forest-generalist
307 species richness was better explained by the pure (50.3%) and total (86.5%) effect of patch-scale
308 attributes, than by pure (19.0%) and total (49.2%) effects of macroclimatic variables (Fig. 4b).

309 *# Figure 4 here #*

310 Local carabid species richness was chiefly affected by temperature condition, across all guilds
311 (Table 1a). As the maximum temperature during the warmest month (MaT_{Wm}) increased, α -
312 diversity of forest-generalist and open-habitat species increased whilst the one of eurytopic
313 species decreased. Alpha-diversity of all guilds decreased with increased minimum temperature
314 during the coldest month (MiT_{Cm}), except for open-habitat species, for which α -diversity peaked
315 in regions with intermediate values along the studied gradient of MiT_{Cm} and steeply decreased
316 towards mildest temperatures (Table 1a). Extremes in rainfall conditions only affected eurytopic
317 and open-habitat species richness (Table 1a). Alpha-diversity of eurytopic species decreased with

318 increasing amount of precipitation during the wettest (PWm) and driest (PDm) months. Alpha-
319 diversity of open-habitat species was the lowest in regions with intermediate amount of
320 precipitations during the driest month and increased towards both extremes of the latitudinal
321 gradient.

322 *# Table 1 here #*

323 Landscape characteristics only affected eurytopic and open-habitat species richness (Table
324 1a), with both eurytopic and open-habitat species richness decreasing with increasing proportion
325 of forest in the landscape (500 m). Alpha-diversity of open-habitat species further decreased with
326 increasing amount of grassland in the landscape (100 m).

327 Guilds were impacted differently by patch conditions, but none was influenced by patch area
328 (Table 1a). Species richness for forest-generalists was higher in ancient than recent forest
329 patches, and was positively affected by local β -diversity of forest-specialist plant species (but
330 negatively affected by local β -diversity of generalist plant species). The effect of topographic
331 variability (CVe) on α -diversity was positive for forest-specialist, but negative for eurytopic and
332 open-habitat species. Richness for open-habitat species further increased with increasing local β -
333 diversity of generalist plants and with decreasing local β -diversity of forest-specialist plants.

334 **Magnitude of difference between local assemblages and the landscape pool (β -diversity)**

335 Overall, we found high values of β -diversity among fragments, irrespective of guild, landscape
336 type and region considered (Fig. 5). We found the lowest magnitude of difference between the
337 landscape pool and local assemblages for forest-specialists, especially at intermediate latitudes
338 (Fig. 5a).

339 *# Figure 5 here #*

340 Our model explained a low proportion of the observed variation in β -diversity of carabid
341 species assemblages for all guilds and especially for open-habitat species ($R^2_m = 0.096$; $R^2_c =$
342 0.232) (Fig. 4e-h; Table 1b).

343 For all guilds, β -diversity was mostly explained by the pure effect of macroclimatic variables
344 (from 31.9% to 71.7% of the explained variance; Fig. 3e-h), except for open-habitat species (pure
345 effect of patch-scale attributes: 41.2%). For all guilds except forest-specialist species, landscape
346 variables had a non-negligible effect on β -diversity (pure effect from 13.4% to 22.9%; Fig. 4f-h).

347 The magnitude of difference between the landscape pool and local assemblages was primarily
348 explained by extreme temperature (forest-specialist, generalist, and eurytopic species) and
349 extreme rainfall (forest-specialist, eurytopic, and open-habitat species) conditions (Table 1b).
350 Beta-diversity of forest-generalist species decreased with increasing maximum temperature
351 during the warmest month (MaTWm), whilst the reverse pattern was observed for eurytopic
352 species. Both forest-specialist and forest-generalist β -diversity increased with minimum
353 temperature during the coldest month (MiTCm). Beta-diversity of eurytopic species peaked in
354 regions with intermediate amount of precipitation during the wettest month (PWm), and
355 increased with the amount of precipitation during the driest month (PDM). The latter also had a
356 positive effect on forest-specialist β -diversity.

357 Landscape characteristics affected β -diversity of all guilds except forest-specialist species
358 (Table 1a). Beta-diversity of forest-generalist species increased with hedgerow density (50 m)
359 and the proportion of forest (500 m) in the landscape. Beta-diversity of eurytopic species
360 decreased with increasing proportion of crops (250 m) and grassland (1,000 m) in the
361 surrounding landscape. Beta-diversity of open-habitat species decreased with the increasing
362 amount of crops (500 m) and forest (50 m) in the surrounding landscape.

363 Beta-diversity of forest specialists and forest generalists was higher in recent than ancient
364 forest patches (Table 1a). Topographic variability (C_Ve) had a negative effect on forest-specialist
365 β -diversity, but a positive effect on eurytopic and open-habitat β -diversity. Beta-diversity of
366 forest-generalist species increased with β -diversity of generalist plant species in the herb layer but
367 decreased with increasing β -diversity of forest specialist plants. The opposite pattern was found
368 for open-habitat β -diversity.

369

370 **DISCUSSION**

371 In this study, we have quantified the respective importance of forest patch characteristics,
372 landscape features, and macroclimate in driving α - and β -diversities of carabid beetle
373 assemblages. Both within and between small forest patches embedded in contrasted agricultural
374 landscapes. We showed that both diversity components were primarily determined by
375 macroclimate, likely via the size and composition of regional species pools. Local carabid species
376 assemblages differed because of habitat preferences. While the diversity of non-forest species
377 (open-habitat and eurytopic) in forest patches was mostly influenced by landscape features,
378 especially proportion of different land-cover types, the diversity of forest species (specialist and
379 generalist) was on the other hand positively affected by patch-scale attributes, such as patch age
380 and heterogeneity in patch properties (abiotic and biotic).

381 **Macroclimate: a prominent ecological filter**

382 We found support for our first research hypothesis: macroclimatic conditions act as the main
383 ecological filter on carabid beetle diversity patterns, as implied by the high relative importance
384 values of macroclimatic factors in explaining local α - and β -diversity patterns. More precisely,
385 extremes of temperature (cf. MaTW_m, MiTC_m) and, to a lesser degree, extremes of precipitation

386 (cf. PWm, PDm), emerge as crucial drivers of carabid diversity. This is consistent with earlier
387 studies, showing that the strong effect of latitude on carabid species richness is mediated by
388 climate, and then more by temperature than precipitation (e.g., Schuldt & Assmann, 2009; Ernst
389 & Buddle, 2015). In addition, and congruently, regional species pools of all species guilds tend to
390 show a hump-shaped relationship with lower regional species richness at both extremes of the
391 latitudinal gradient (Appendix S3), while a high species turnover is observed among regions
392 along this gradient (Fig. 2). Furthermore, distinct carabid species respond differently to
393 macroclimatic factors, depending on habitat preference.

394 Forest species mostly respond to annual extreme temperatures, with the α -diversity of
395 specialist and generalist species increasing as MiTCm and MaTWm decreased and increased,
396 respectively. Cold temperatures (cf. MiTCm) are known to exert strong physiological constraints
397 on overwintering poikilothermous species (Thiele, 1977; Lövei & Sunderland, 1996). The
398 majority of temperate carabid species require winter diapause to complete larval development or
399 gonad maturation and cannot survive environments with too mild winter temperatures, since
400 diapause is not triggered (Kotze *et al.*, 2011). On the other hand, cold induces physiological costs
401 and only few species have adapted mechanisms to survive very harsh winter conditions (Bale,
402 1996). High temperature (cf. MaTWm) usually increases activity and development rates (e.g.,
403 Taylor, 1963; Forrest, 2016) and throughout the active period of the year, insects that face warm
404 conditions during their ontogenetic development can acclimate to even higher temperatures
405 (Sheikh *et al.*, 2017). Warmer weather conditions may thus promote species movements within
406 landscapes, thereby affecting β -diversity patterns (here defined as the magnitude of difference
407 between the landscape-level species pool and the composition of local assemblages).

408 Among non-forest species, eurytopic species respond to both temperature (cf. negative effect
409 of both MaTWm and MiTCm on α -diversity) and precipitation (cf. negative effect of both PWm

410 and PDM on α -diversity), while open-habitat α -diversity rather show a unimodal relationship with
411 MiTCm and PDM. Eurytopic species can live and disperse in most habitats, but may not have
412 developed adaptations for extreme climatic conditions. Moreover, as non-forest species,
413 eurytopic and open-habitat species cannot benefit from canopy-induced microclimatic conditions
414 of the understory, which is typically moister over the year, cooler in summer, and milder in
415 winter (De Frenne *et al.*, 2019). When the temperature is too high or the environment too dry,
416 these species are thus more prone to enter into summer diapause or quiescence to face unsuitable
417 conditions (Masaki, 1980). Because of reduced activity, these species likely disperse less
418 efficiently, thereby increasing compositional dissimilarity among patches.

419 As a consequence of the current climate change and because of physiological constraints of
420 species to their regional climate, the elevational range of some carabid species has changed in the
421 past 30 years, to track the shifting isotherms (e.g., Pizzolotto *et al.*, 2014; Moret *et al.*, 2016).
422 Movement of species northward (in the Northern Hemisphere) can also be expected, but changes
423 in latitudinal distributions can be hard to predict as the dominant diapause-inducing cue
424 (photoperiod) will not be affected by climate change while other cues (temperature, moisture)
425 will (Huffeltdt, 2020). Species may indeed suffer from mismatched information between critical
426 photoperiod for diapause induction and other environmental conditions acting on the physiology,
427 development, or behavior of specific life stages, which could affect their survival (Bale &
428 Hayward, 2010; Tougeron *et al.*, 2019). In addition, by causing species-specific shifts in
429 phenology, climate change can alter interspecific interactions as well (Damien & Tougeron,
430 2019).

431 The legacy of the biogeographical history of Europe (particularly glaciations of the
432 Pleistocene and the subsequent post-glacial recolonization of northern regions) may confound the
433 pure effect of current climatic conditions in explaining the macroecological diversity patterns we

434 observed. This is particularly true for dispersal-limited organisms such as carabid beetles
435 (Calatayud *et al.*, 2016, 2019), and may explain the lower species richness recorded in the
436 northern regions.

437 **Landscape features explain the contribution of non-forest species to local assemblages**

438 Our results reveal that the composition of the landscape matrix into which forest patches are
439 embedded significantly explains the α - and β -diversity of non-forest carabid species (cf.
440 eurytopic and open-habitat guilds). In particular, focal patches surrounded by forest and grassland
441 have a negative effect on species richness for these species. Consistently, the number of open-
442 habitat species was higher in open field landscapes compared to bocage landscapes. This may be
443 explained by the diversity of crops cultivated in the surrounding fields (e.g., cereals, sugar beet,
444 potato, rapeseed), each associated with a particular pool of species (Holland *et al.*, 2005; Marrec
445 *et al.*, 2015), whilst grasslands may harbor less specific carabid assemblages and benefit from
446 spillover from adjacent habitats, including forests (Schneider *et al.*, 2016; Dufлот *et al.*, 2018).
447 Moreover, arable lands may allow beetles to move more easily on the ground than grasslands,
448 particularly because of differences in vegetation density (Thomas *et al.*, 2006). Our results are
449 consistent with previous studies, which showed that landscape attributes affect biodiversity in
450 important ways (see Fletcher *et al.*, 2016 for a review). Open-habitat and eurytopic species use
451 forest habitats as alternative, temporary habitat, but are less competitive there than in more open
452 habitats (e.g., Niemelä *et al.*, 1993). In particular, they enter forest edges to find a shelter, to
453 search for food or to seek overwintering sites (Knapp *et al.*, 2019). The decreased magnitude of
454 difference between the landscape-level species pool and the composition of local assemblages
455 with increasing crop or/and grassland cover in the landscape suggests that these habitats allow a
456 large suite of non-forest species to enter forest patches. However, the high turnover observed

457 among patches of a given landscape window suggests that they are not present at the same time in
458 most patches.

459 With the exception of β -diversity of forest-generalist species, which increases with hedgerow
460 density and forest cover in the surrounding landscape, landscape factors do not affect the α - and
461 β -diversity patterns of forest-specialist and generalist carabid species. This result indicates that
462 hedgerows are not always positive for species movement (e.g., Baudry & Burel, 2019).

463 Alternatively, hedgerows in the studied landscapes may be too recent or scarce to serve as high-
464 quality corridors (Closset-Kopp *et al.*, 2016; Lenoir *et al.*, 2020) for forest carabid species, that
465 are well known for their very low dispersal capacities (Rainio & Niemelä, 2003). However,
466 hedgerows can allow some forest species to disperse between forest patches as previously
467 suggested (e.g., Baudry & Burel, 2019), increasing the probability that more species will reach
468 forest patches. However, the high nestedness we found for forest-specialist species compared to
469 other guilds suggests that only a few species are actually able to colonize new forest patches.

470 Increased magnitude of difference between the landscape-level species pool and the composition
471 of local assemblages in bocage landscapes could then be linked to random local species
472 replacement due to competition, or neutral processes. In summary, we found little support to our
473 second research hypothesis: landscape management intensity only weakly influences the diversity
474 of forest carabid species, but instead increases the number of non-forest species in small forest
475 patches.

476 **Forest patch characteristics drive forest carabid species diversity**

477 We found that patch-scale attributes mostly influence the α - and β -diversity patterns of forest
478 carabid species. Patch characteristics were even the primary drivers of α -diversity for forest-
479 generalist species. This includes patch age and various proxies for local environmental

480 heterogeneity. The higher number of forest generalists in ancient compared to recent forest
481 patches likely reflects the accumulation of weaker dispersers over time, according to the species-
482 time relationship (Rosenzweig, 1995), which has already been showed for vascular plant species
483 in the same study system (Valdés *et al.*, 2015). Similarly, forest carabid species are large species,
484 with poor dispersal abilities, and long life cycles (Thiele, 1977; Rainio & Niemelä, 2003).
485 Ancient forests are thought to be more stable, allowing these species to persist (Driscoll & Weir,
486 2005; Schowalter, 2017). Moreover, ancient forest patches are also thought to exhibit more
487 heterogeneous environmental conditions than recent patches (Lawesson *et al.*, 1998; Honnay *et*
488 *al.*, 1999; Schowalter, 2017), thereby providing carabid beetles with more potential niches. This
489 is confirmed by the positive effect of plant diversity (cf. intra-patch β -diversity of forest
490 specialists) on the species richness of forest generalist carabid beetles, since plant species
491 richness has also been shown to increase with patch heterogeneity (Jamoneau *et al.*, 2011).
492 Carabid beetles are proven to be very sensitive to variations in forest characteristics, so that their
493 assemblages change during the forestry cycle, according to variation in forest structure and
494 composition (e.g., Butterfield, 1997; Koivula *et al.*, 2002; Magura *et al.*, 2003).

495 The β -diversity of forest generalists was influenced by the same patch-scale factors as α -
496 diversity, but in the opposite direction. This indicates that the few forest-generalist species
497 present in a given landscape window tend to occupy all ancient, heterogeneous forest patches of
498 this window. Interestingly, the β -diversity of forest specialists also decreased as patch age
499 increased, consistent with species accumulation over time. However, local species richness was
500 mostly determined by region and landscape-window type (i.e., random factors in our models).
501 This result suggests that the colonization of forest patches within landscape windows occurs at
502 random in such fragmented systems where metapopulation dynamics for these dispersal-limited

503 species are likely disrupted. The positive effect of local topography (another proxy for intra-patch
504 heterogeneity) on local species richness can be explained by the fact that small-scale variation in
505 topography offers more thermal variability than flat areas (Lenoir *et al.*, 2013), as well as more
506 micro-habitats (e.g. various depth and quality of litter, coarse woody debris, snags, different soil
507 texture; Dwyer & Merriam, 1981). These features have already been shown to affect carabid
508 assemblages (Latty *et al.*, 2006; Tyler, 2008), and other arthropods such as ticks, *Ixodes ricinus*
509 (Ehrmann *et al.*, 2017).

510 It is noteworthy that patch area was not significant in our models, which is likely a
511 consequence of our sampling design, since we applied the same sampling effort irrespective of
512 patch size, using traps that can catch beetles over a very limited area relative to patch size.
513 Nonetheless, recent reviews suggested that small and isolated habitat patches can have similar
514 ecological values as large patches, especially when they encompass the same overall area at the
515 landscape to regional scale (Fahrig, 2017; Wintle *et al.*, 2019).

516 To a lesser extent, patch-scale attributes also impact the diversity of open-habitat species. In
517 particular, the magnitude of difference between the landscape-level species pool and the
518 composition of their local assemblages was positively affected by local topography and β -
519 diversity of forest plant specialists. This suggests that open-habitat species, and, to a lesser
520 degree, eurytopic species (see positive relationship between β -diversity of eurytopic species and
521 CVe) hardly colonize heterogeneous forests established on complex terrains. Consistently, the
522 number of open-habitat species (α -diversity) decreased with increasing vegetation heterogeneity
523 (cf. β -diversity of forest specialist plants) and increasing elevational heterogeneity (cf. CVe).

524 Based on these results, we can partly confirm our third research hypothesis: patch age, not
525 patch size (at least when a similar sampling effort is applied irrespective of patch size), increases

526 α -diversity of forest species, but local abiotic and biotic heterogeneities have an even more
527 positive effect.

528

529 **CONCLUSION**

530 We show that composition of carabid assemblages in small forest patches is strongly driven by
531 macroclimatic conditions (and possibly by confounding historical factors) for all habitat-
532 preference guilds. This result indicates the importance of considering macroecological factors as
533 the main drivers of local carabid species assemblages. This novel result was yet unknown for
534 most arthropods including carabid beetles, and much needed to improve our knowledge in
535 arthropod macroecological patterns. Indeed, in the current climate change context, integrating
536 climatic information in large-scale (both temporal and spatial) ecology studies is required. If
537 species facing climate change are not sufficiently plastic or adaptable in their climatic tolerance
538 range, they would have to move northward (in the Northern Hemisphere) or upward in
539 mountainous systems to track the shifting isotherms and survive, and consequently impact local
540 species assemblages.

541 Species assembly was also importantly altered by patch environmental heterogeneity and age, as
542 previously observed in the same forest networks for other arthropods and plants (Valdés *et al.*,
543 2015; De Smedt *et al.*, 2018). Yet, we did not find any evidence on an influence of forest size.

544 These results highlight the major need of protecting old forest patches embedded in agricultural
545 landscapes, even the small ones. Finally, landscape management intensity weakly influences the
546 diversity of forest carabid species, but increases the number of non-forest species in small forest
547 patches, while decreasing their turnover among patches. These results invalidate our previous
548 assumptions and instead made us consider that observed patterns, at multiple spatial scales, are

549 likely linked to functional traits, more than species habitat preference only. Congruently, Le
550 Provost *et al.* (2020) recently showed that mobility, resource-acquisition, and body-size traits
551 drive local species assembly through environmental filtering acting at the landscape and patch
552 levels, especially in landscapes suffering high short and long-term turnover such as agricultural
553 landscapes. Such evidence has not been provided yet on assemblages living in small forest
554 patches embedded in these agricultural landscapes.

555

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857 DATA AVAILABILITY STATEMENT

858 Full data are available in the Dryad data repository (<https://doi.org/10.5061/dryad.g79cnp5ns>)
859 while total abundances per species and species habitat preferences are listed in Appendix S2.

860 **Table 1.** Results of the mixed model backward stepwise selection of fixed explanatory variables: macroclimatic, landscape, and patch-scale
861 attributes (see ‘Data analysis’). Models were computed for **(a)** α -diversity and **(b)** β -diversity of the four habitat-preference species groups
862 independently: forest-specialist, forest-generalist, eurytopic, and open-habitat species. The values inside the table represent marginal R^2 (R^2_m),
863 conditional R^2 (R^2_c), and parameter estimates (\pm standard error of the regression) for the best model. For landscape attributes, we also indicated
864 the selected spatial scale. The significance of each explanatory variable was obtained from a χ^2 test, and is indicated as: ***, $p < 0.001$; **, $p <$
865 0.01 ; *, $p < 0.05$; ;, $p < 0.10$. All variables were standardized prior to analysis. Spaces with a dash indicate that the variable was not included in
866 the best model. Abbreviations are explained under the table.

Explanatory variables	Forest specialist	Forest generalist	Eurytopic	Open habitat	
	Estimate (\pm SE)	Estimate (\pm SE)	Estimate (\pm SE)	Estimate (\pm SE)	
(a) α-diversity					
	$R^2_m = 0.361$	$R^2_m = 0.653$	$R^2_m = 0.582$	$R^2_m = 0.438$	
	$R^2_c = 0.825$	$R^2_c = 0.653$	$R^2_c = 0.582$	$R^2_c = 0.638$	
Macroclimate	MaTWm	-	-0.06 (\pm 0.05)	-0.17 (\pm 0.07)*	-0.39 (\pm 0.20)
	MaTWm^2	-	0.32 (\pm 0.04)***	-	0.22 (\pm 0.10)*
	MiTcm	-1.11 (\pm 0.36)**	-0.31 (\pm 0.06)***	-0.07 (\pm 0.12)	1.31 (\pm 0.33)***
	MiTcm^2	-	-0.55 (\pm 0.05)***	-0.13 (\pm 0.03)***	-0.62 (\pm 0.13)***
	PWm	-	-	-0.11 (\pm 0.03)***	-
	PWm^2	-	-	-	-
	PDm	-	-	-0.21 (\pm 0.09)*	-1.19 (\pm 0.20)***
	PDm^2	-	-	-0.18 (\pm 0.04)***	0.31 (\pm 0.11)**
Landscape	Hedgerow length	-	-	-	-
	Crops (%)	-	-	-	-
	Grassland (%)	-	-	-	100 m -0.15 (\pm 0.05)**

	Forest (%)	-	-	500 m	-0.14 (± 0.03)***	500 m	-0.16 (± 0.07)*	
Patch	Age (recent vs. old)	-	-0.11 (± 0.05)*		-		-	
	Area	-	-		-		-	
	Cve	0.12 (± 0.04)**	-		-0.10 (± 0.02)***		-0.19 (± 0.05)***	
	β-div. generalist plants	-	-0.68 (± 0.27)*		-		0.19 (± 0.06)**	
	β-div. forest spec. plants	-	0.95 (± 0.38)*		-		-0.14 (± 0.04)**	
(b) β-diversity								
		$R^2_m = 0.284$	$R^2_m = 0.153$		$R^2_m = 0.285$		$R^2_m = 0.096$	
		$R^2_c = 0.653$	$R^2_c = 0.359$		$R^2_c = 0.286$		$R^2_c = 0.232$	
Macroclimate	MaTWm	-	-0.08 (± 0.02)*		0.02 (± 0.01)*		-	
	MaTWm^2	-	-		-		-	
	MiTcm	0.38 (± 0.12)*	0.09 (± 0.04)*		-		-	
	MiTcm^2	-	-		-		-	
	PWm	-	-		0.03 (± 0.01)**		-	
	PWm^2	-	-		-0.03 (± 0.01)*		-	
	PDm	-0.18 (± 0.09)	-		0.04 (± 0.01)**		-	
	PDm^2	0.18 (± 0.06)**	-		0.02 (± 0.01)*		-	
Landscape	Hedgerow length	500 m	-	50 m	0.02 (± 0.01)**		-	
	Crops (%)	-	-		250 m	-0.04 (± 0.01)***	500 m	-0.02 (± 0.01)*
	Grassland (%)	-	-		1,000 m	-0.04 (± 0.01)**		-
	Forest (%)	-	-	500 m	0.03 (± 0.01)*		50 m	-0.02 (± 0.01)*
Patch	Age (recent vs. old)	0.07 (± 0.02)**	0.03 (± 0.01)*		-		-	
	Area	-	-		-		-	
	CVe	-0.06 (± 0.01)***	-		0.03 (± 0.01)***		0.03 (± 0.01)***	
	β-div. generalist plants	-	0.03 (± 0.01)**		-		-0.03 (± 0.01)**	
	β-div. forest spec. plants	-	-0.03 (± 0.01)***		-		0.03 (± 0.01)**	

867 MaTWm (BIO5): maximum temperature of the warmest month; MiTcm (BIO6): minimum temperature of the coldest month; PWm (BIO13):

868 precipitation of the wettest month; PDm (BIO14): precipitation of the driest month; Cve: coefficient of variation in elevation.

869 **Figure captions**

870 **Figure 1** Study area and sampling design. **(a)** Location of the bocage (green dot) and open-field
871 (yellow dot) landscape windows of the seven study regions across the European gradient (Fr_S =
872 southern France; Fr_N = northern France; Be = Belgium; Ge_W = western Germany; Ge_E =
873 eastern Germany; Sw_S = southern Sweden; Sw_C = central Sweden). **(b)** Detail of landscape
874 windows of western Germany showing the different land-cover types and the forest fragments
875 selected for sampling (red dots: sampling locations). **(c)** Sampling design at the forest-fragment
876 level, with one sampling site in the core area and one another at the edge. Are represented the
877 contours of the concentric buffers (red line), from 50 to 1,000-m radius around focus forest
878 patches.

879 **Figure 2** Among-region along the European gradient (“All gradient”) and among-patch within
880 each region multiple-site dissimilarities. Turnover (blue; Simpson dissimilarity) and nestedness
881 components (yellow; nestedness-resultant fraction of Sørensen dissimilarity) are distinguished.

882 **Figure 3** Mean (\pm SD) carabid species richness (α -diversity) sampled in each forest patch,
883 grouped based on region and window type (orange: ‘bocage’; blue: open-field). Statistical
884 differences between each pair of groups were evaluated using an analysis of variance model
885 followed by a Tukey post-hoc test. FS: forest specialists; FG: forest generalists; EU: eurytopic
886 species; OH: open-habitat species.

887 **Figure 4** Results of the variation partitioning for each combination of diversity levels and
888 habitat-preference groups as the response variable. The amount of variation explained by pure
889 and shared contributions of each variable group was calculated as a percentage of the total
890 variation explained by the fixed factors in the global model (including the three groups of
891 explanatory variables). Values of marginal R^2 (R^2_m) and conditional R^2 (R^2_c) of the global models
892 are shown for each response variable. Variation partitioning was based on generalized (GLMM;
893 α -diversity) or linear mixed-effect models (LMM; β -diversity) with the predictor variables as
894 fixed effects and ‘region’ as well as ‘window type’ (nested within ‘region’) as random intercept
895 terms.

896 **Figure 5** Mean (\pm SD) between-patch carabid species dissimilarity (β -diversity), grouped based
897 on region and window type (black: ‘bocage’; gray: open-field). Statistical differences between
898 each pair of groups were evaluated using an analysis of variance model followed by a Tukey
899 post-hoc test. FS: forest specialists; FG: forest generalists; EU: eurytopic species; OH: open-
900 habitat species.

901

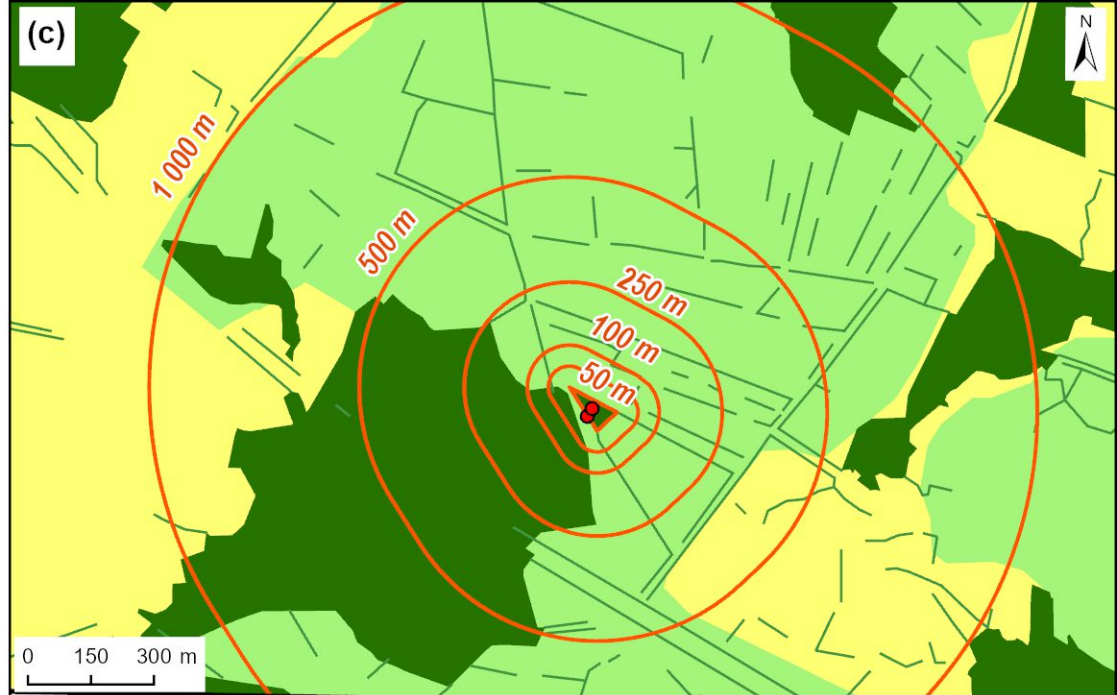
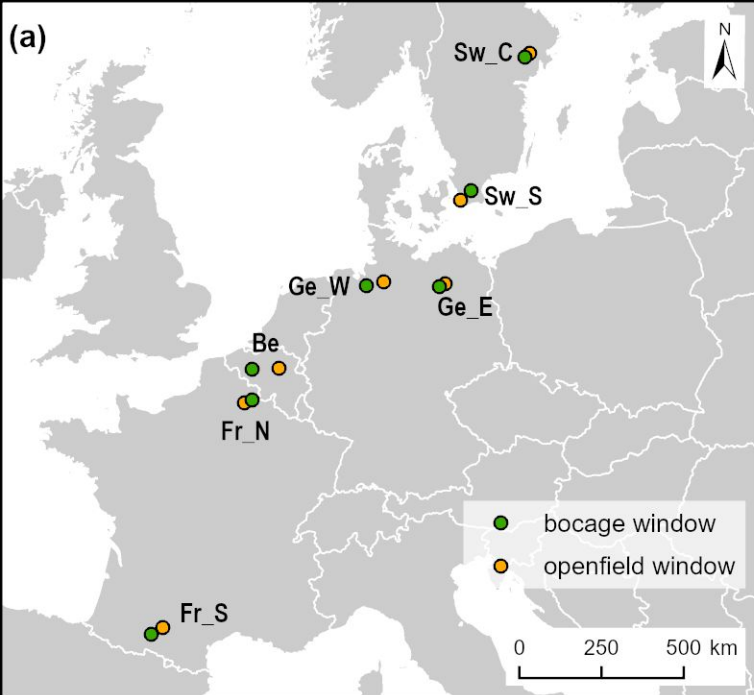
902 **SUPPORTING INFORMATION**

903 Additional supporting information may be found in the online version of this article at the
904 publisher's website.

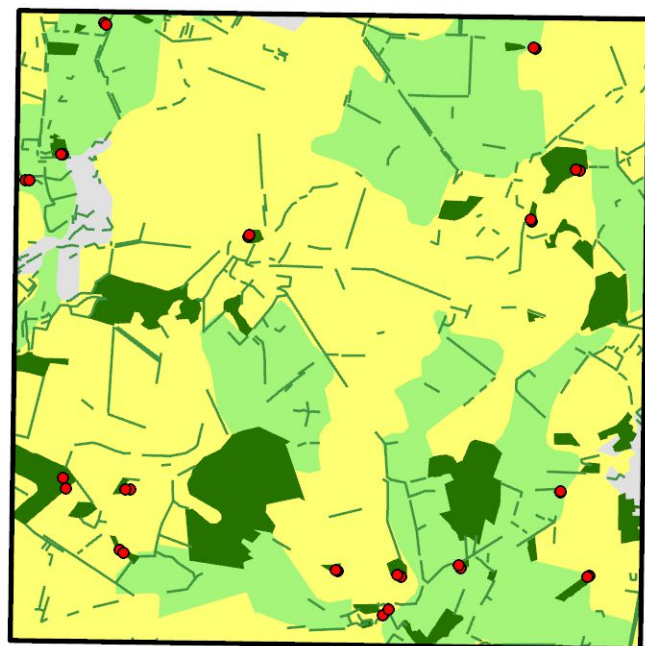
905 **Appendix S1** Correlation table between all patch, landscape, and macroclimatic-level variables.

906 **Appendix S2** Complete list of species that were found in the sampled forest patches, along with
907 their habitat preference.

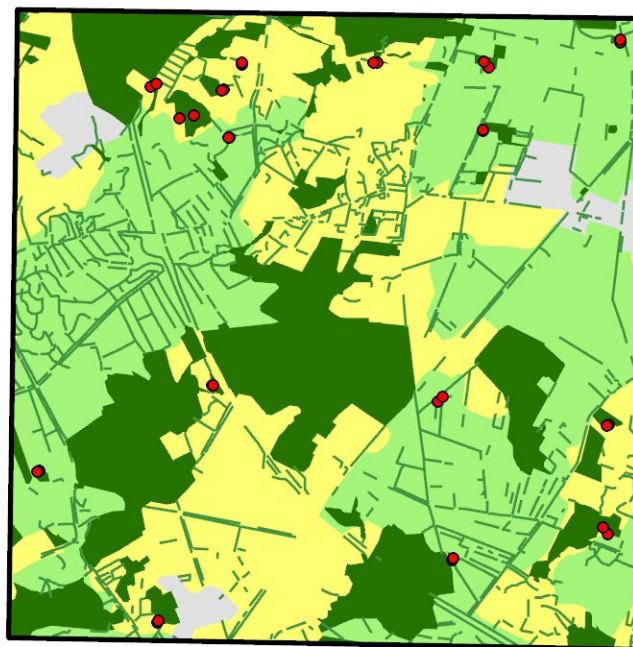
908 **Appendix S3** Gamma-diversity of all species together and per habitat-preference guild.



(b) openfield 5x5 km window (Ge_W)



bocage 5x5 km window (Ge_W)



Land use

cropland

woodland

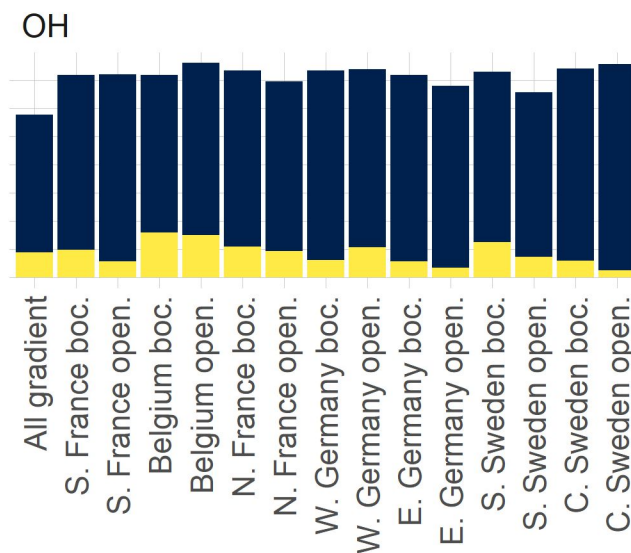
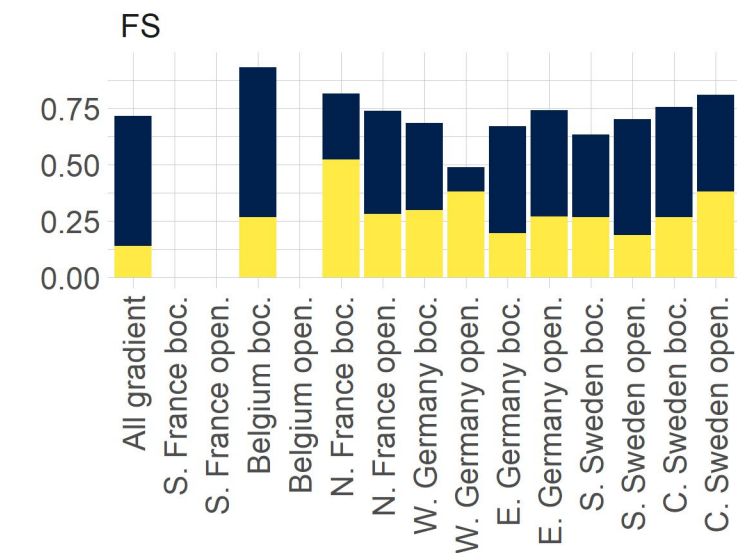
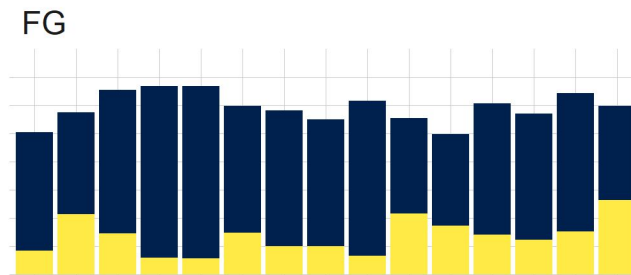
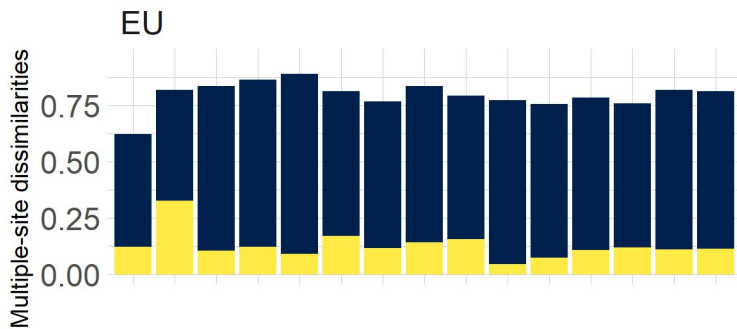
grassland

other

hedgerows

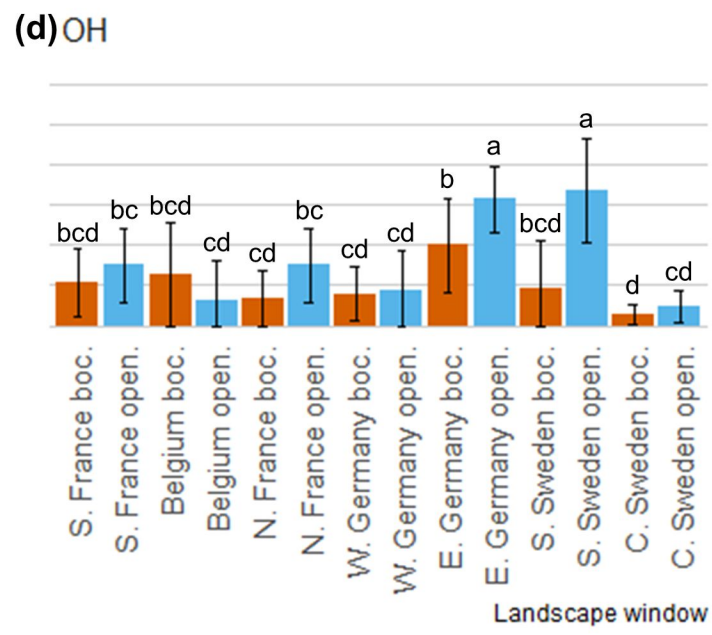
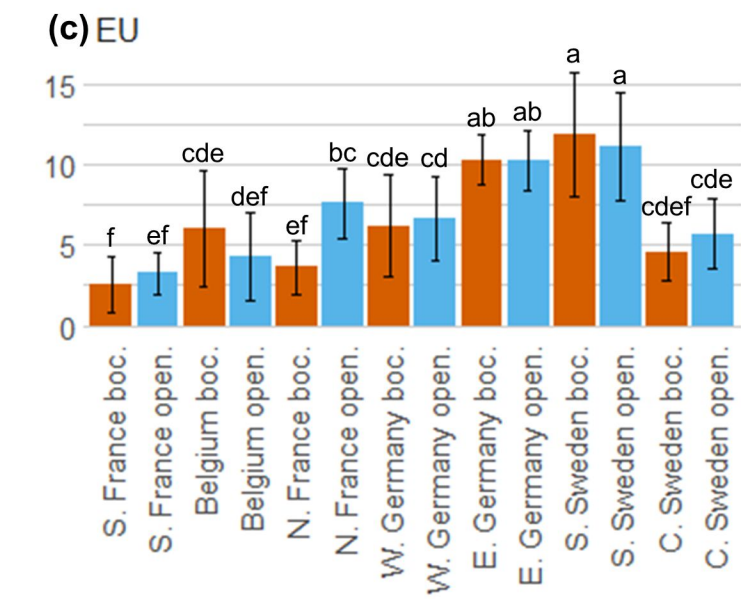
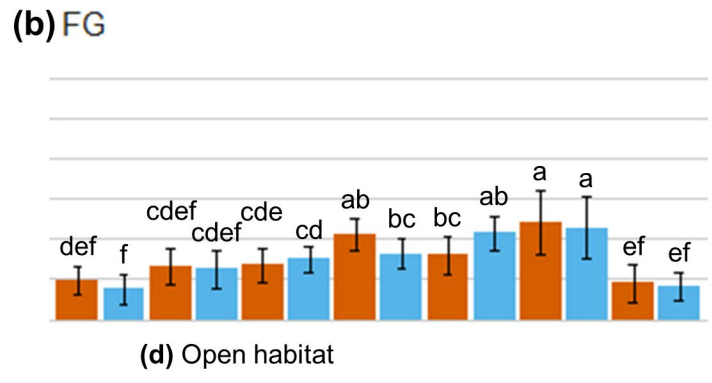
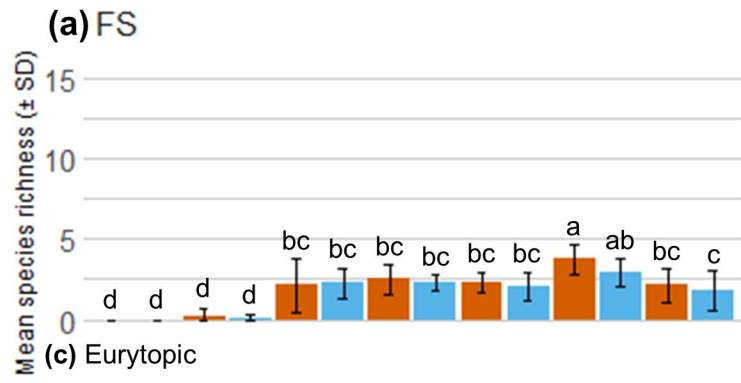
carabid beetle traps

concentric 'doughnut'-like buffers

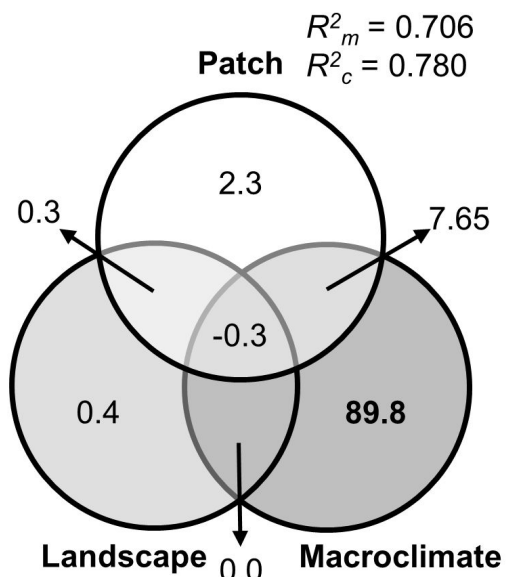


Landscape window

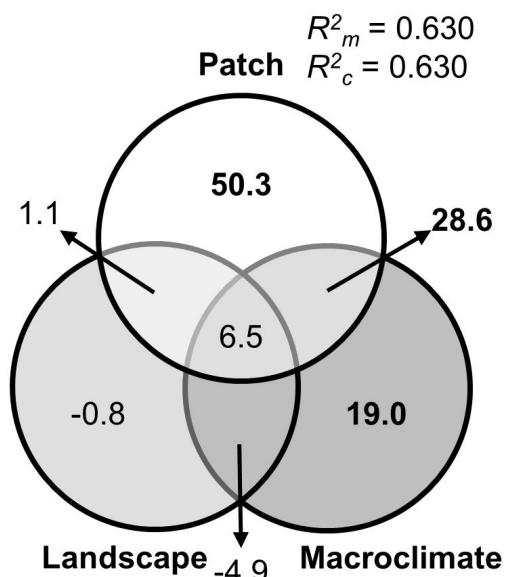
Components Turnover Nestedness



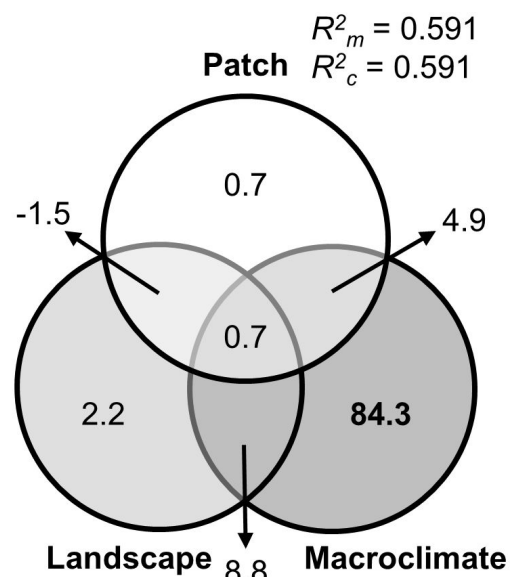
(a) Forest-specialist α -diversity



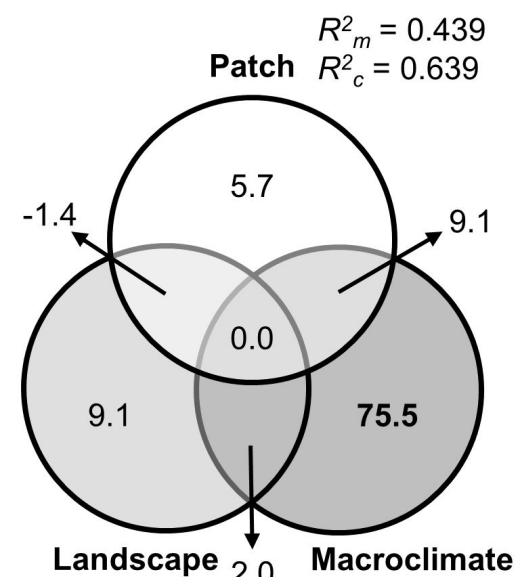
(b) Forest-generalist α -diversity



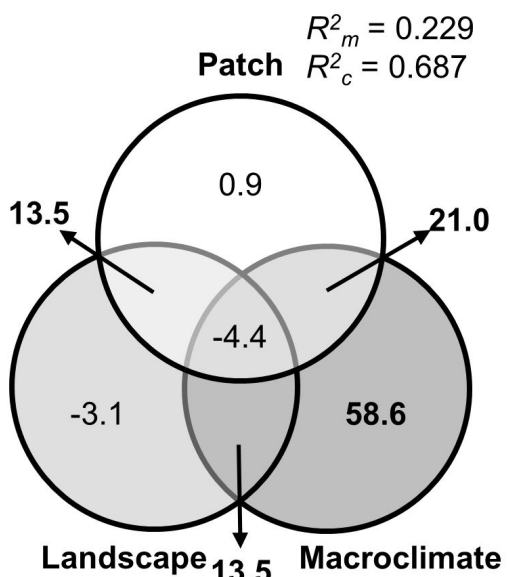
(c) Eurytopic α -diversity



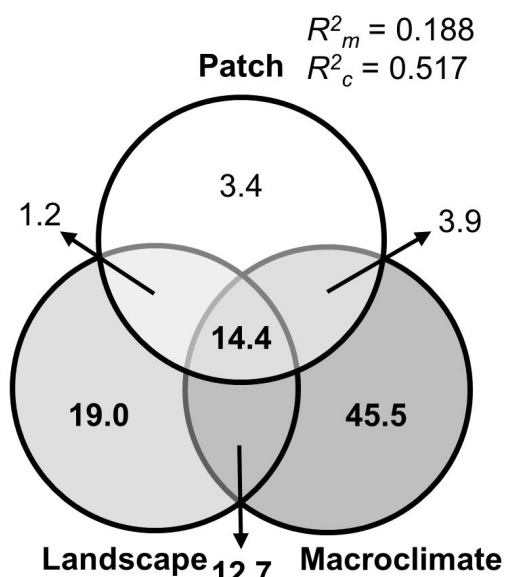
(d) Open-habitat α -diversity



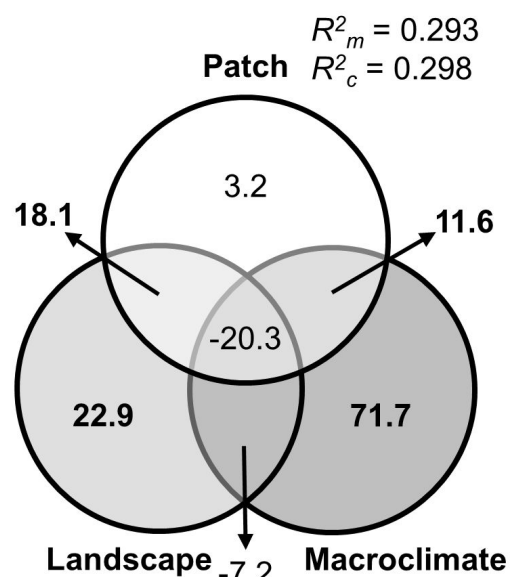
(e) Forest-specialist β -diversity



(f) Forest-generalist β -diversity



(g) Eurytopic β -diversity



(h) Open-habitat β -diversity

