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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 ( $\alpha$ -  
15 diversity) and species dissimilarity between patches ( $\beta$ -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  $\alpha$ - and  $\beta$ -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  $\alpha$ -  
25 diversity of forest species. Landscape management intensity weakly influenced  $\alpha$ -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  $\alpha$ -diversity) and magnitude  
115 of difference between landscape-scale species pool and patch-scale carabid assemblages  
116 (hereafter  $\beta$ -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 ( $\alpha$ -diversity), and increases the magnitude of difference between the landscape species  
124 pool and local assemblages ( $\beta$ -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  $\alpha$ -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 17<sup>th</sup>,  
146 18<sup>th</sup>, 19<sup>th</sup>, and 20<sup>th</sup> 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-km<sup>2</sup>  
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<sub>Ve</sub>) 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  $\beta$ -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  $\alpha$ -diversity, defined as the total number of species trapped per forest  
231 patch; landscape-level  $\gamma$ -diversity, defined as the total number of species retrieved in all patches  
232 of a given landscape window; and  $\beta$ -diversity, defined as the magnitude of difference between  
233 the landscape-level species pool ( $\gamma$ -diversity) and the composition of the local assemblage  
234 ( $\alpha$ -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  $\alpha$ -diversity and  
237  $\beta$ -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  $\alpha$ -diversity.  
240 Gaussian error distributions with an identity link were used for  $\beta$ -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 ( $\alpha$  and  $\beta$ -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 ( $\alpha$ -diversity) or LMMs ( $\beta$ -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 ( $\alpha$ -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 ( $\alpha$ -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<sub>Wm</sub>) increased,  $\alpha$ -  
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<sub>Cm</sub>), except for open-habitat species, for which  $\alpha$ -diversity peaked  
315 in regions with intermediate values along the studied gradient of MiT<sub>Cm</sub> 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  $\beta$ -diversity of forest-specialist plant species (but  
330 negatively affected by local  $\beta$ -diversity of generalist plant species). The effect of topographic  
331 variability (CVe) on  $\alpha$ -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  $\beta$ -  
333 diversity of generalist plants and with decreasing local  $\beta$ -diversity of forest-specialist plants.

#### 334 **Magnitude of difference between local assemblages and the landscape pool ( $\beta$ -diversity)**

335 Overall, we found high values of  $\beta$ -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  $\beta$ -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,  $\beta$ -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  $\beta$ -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  $\beta$ -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  $\beta$ -diversity.

357 Landscape characteristics affected  $\beta$ -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<sub>V</sub>e) had a negative effect on forest-specialist  
365  $\beta$ -diversity, but a positive effect on eurytopic and open-habitat  $\beta$ -diversity. Beta-diversity of  
366 forest-generalist species increased with  $\beta$ -diversity of generalist plant species in the herb layer but  
367 decreased with increasing  $\beta$ -diversity of forest specialist plants. The opposite pattern was found  
368 for open-habitat  $\beta$ -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  $\alpha$ - and  $\beta$ -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  $\alpha$ - and  $\beta$ -diversity patterns. More precisely,  
385 extremes of temperature (cf. MaTW<sub>m</sub>, MiTC<sub>m</sub>) 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  $\alpha$ -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  $\beta$ -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  $\alpha$ -diversity) and precipitation (cf. negative effect of both PWm

410 and PDM on  $\alpha$ -diversity), while open-habitat  $\alpha$ -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  $\alpha$ - and  $\beta$ -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  $\beta$ -diversity of forest-generalist species, which increases with hedgerow  
460 density and forest cover in the surrounding landscape, landscape factors do not affect the  $\alpha$ - and  
461  $\beta$ -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  $\alpha$ - and  $\beta$ -diversity patterns of forest  
478 carabid species. Patch characteristics were even the primary drivers of  $\alpha$ -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  $\beta$ -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  $\beta$ -diversity of forest generalists was influenced by the same patch-scale factors as  $\alpha$ -  
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  $\beta$ -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  $\beta$ -  
519 diversity of forest plant specialists. This suggests that open-habitat species, and, to a lesser  
520 degree, eurytopic species (see positive relationship between  $\beta$ -diversity of eurytopic species and  
521 CVe) hardly colonize heterogeneous forests established on complex terrains. Consistently, the  
522 number of open-habitat species ( $\alpha$ -diversity) decreased with increasing vegetation heterogeneity  
523 (cf.  $\beta$ -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  $\alpha$ -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

## 556 REFERENCES

- 557 Almoussawi, A., Lenoir, J., Jamoneau, A., Hattab, T., Wasof, S., Gallet-Moron, E., Garzon-Lopez, C.X.,  
558 Spicher, F., Kobaissi, A. & Decocq, G. (2020) Forest fragmentation shapes the alpha–gamma  
559 relationship in plant diversity. *Journal of Vegetation Science*, **31**, 63–74.
- 560 Assmann, T. (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of north-  
561 west Germany (Coleoptera, Carabidae). *Biodiversity & Conservation*, **8**, 1499–1517.
- 562 Aviron, S., Lalechère, E., Dufлот, R., Parisey, N. & Poggi, S. (2018) Connectivity of cropped vs. semi-natural  
563 habitats mediates biodiversity: a case study of carabid beetles communities. *Agriculture,  
564 Ecosystems & Environment*, **268**, 34–43.
- 565 Bale, J.S. (1996) Insect cold hardiness: a matter of life and death. *European Journal of Entomology*, **93**,  
566 369–382.
- 567 Bale, J.S. & Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of Experimental  
568 Biology*, **213**, 980–994.
- 569 Barkley, E.P., Malcolm, J.R., Smith, S.M. & Bellocq, M.I. (2016) Does variable stand structure associated  
570 with multi-cohort forests support diversity of ground beetle (Coleoptera, Carabidae)  
571 communities in the central Nearctic boreal forest? *Journal of Forestry Research*, **27**, 1191–1202.
- 572 Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology  
573 and Biogeography*, **19**, 134–143.
- 574 Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness,  
575 and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.
- 576 Baselga, A., Orme, D., Villeger, S., De Bortoli, J. & Leprieur, F. (2018) betapart: Partitioning beta diversity  
577 into turnover and nestedness components. R package version 1.5.1. [https://CRAN.R-  
578 project.org/package=betapart](https://CRAN.R-project.org/package=betapart).
- 579 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4.  
580 *Journal of Statistical Software*, **67**, 1–48.
- 581 Baudry, J. & Burel, F. (2019) *Multi-Scale Control of Carabid Assemblages in Hedgerow Network  
582 Landscapes. The Ecology of Hedgerows and Field Margins* (ed. by J.W. Dover), CRC Press.
- 583 Bräunicke, M. & Trautner, J. (2009) Lebensraumpräferenzen der Laufkäfer Deutschlands–  
584 Wissensbasierter Katalog. *Angewandte Carabidologie Supplement*, **1**, 45.
- 585 Brunet, J. (2007) Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration  
586 of broadleaved forest vegetation. *Journal of Applied Ecology*, **44**, 563–572.

587 Burnham, K.P. & Anderson, D.R. (2004) Multimodel inference: understanding AIC and BIC in model  
588 selection. *Sociological Methods and Research*, **33**, 261–304.

589 Burrascano, S., Ripullone, F., Bernardo, L., Borghetti, M., Carli, E., Colangelo, M., Gangale, C., Gargano, D.,  
590 Gentilesca, T. & Luzzi, G. (2018) It's a long way to the top: Plant species diversity in the transition  
591 from managed to old-growth forests. *Journal of Vegetation Science*, **29**, 98–109.

592 Butterfield, J. (1997) Carabid community succession during the forestry cycle in conifer plantations.  
593 *Ecography*, **20**, 614–625.

594 Büttner, G. & Kosztra, B. (2007) CLC2006 technical guidelines. *European Environment Agency, Technical  
595 Report*.

596 Calatayud, J., Hortal, J., Medina, N.G., Turin, H., Bernard, R., Casale, A., Ortuño, V.M., Penev, L. &  
597 Rodríguez, M.Á. (2016) Glaciations, deciduous forests, water availability and current  
598 geographical patterns in the diversity of European Carabus species. *Journal of Biogeography*, **43**,  
599 2343–2353.

600 Calatayud, J., Rodríguez, M.Á., Molina-Venegas, R., Leo, M., Horreo, J.L. & Hortal, J. (2019) Pleistocene  
601 climate change and the formation of regional species pools. *Proceedings of the Royal Society B*,  
602 **286**, 20190291.

603 Closset-Kopp, D., Wasof, S. & Decocq, G. (2016) Using process-based indicator species to evaluate  
604 ecological corridors in fragmented landscapes. *Biological Conservation*, **201**, 152–159.

605 Cousins, S.A. & Eriksson, O. (2002) The influence of management history and habitat on plant species  
606 richness in a rural hemiboreal landscape, Sweden. *Landscape Ecology*, **17**, 517–529.

607 Damien, M. & Tougeron, K. (2019) Prey-predator phenological mismatch under climate change. *Current  
608 Opinion in Insect Science*, **35**, 60–68.

609 De Blois, S., Domon, G. & Bouchard, A. (2002) Landscape issues in plant ecology. *Ecography*, **25**, 244–  
610 256.

611 De Frenne, P., Zellweger, F., Rodriguez-Sanchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M.,  
612 Verheyen, K. & Lenoir, J. (2019) Global buffering of temperatures under forest canopies. *Nature  
613 Ecology & Evolution*, **3**, 744–749.

614 De Smedt, P., Baeten, L., Proesmans, W., Berg, M.P., Brunet, J., Cousins, S.A., Decocq, G., Deconchat, M.,  
615 Diekmann, M. & Gallet-Moron, E. (2018) Linking macrodetritivore distribution to desiccation  
616 resistance in small forest fragments embedded in agricultural landscapes in Europe. *Landscape  
617 Ecology*, **33**, 407–421.

618 Debnár, Z., Magura, T., Horváth, R., D Nagy, D., Mizser, S., Demkó, A., Tajthi, B. & Tóthmérész, B. (2016)  
619 Group selection harvesting supports the diversity of epigeic arthropod assemblages  
620 (Coleoptera: Carabidae; Araneidae: Araneae; Isopoda: Oniscidae). *Periodicum Biologorum*, **118**,  
621 311–314.

622 Decocq, G., Andrieu, E., Brunet, J., Chabrierie, O., De Frenne, P., De Smedt, P., Deconchat, M., Diekmann,  
623 M., Ehrmann, S. & Giffard, B. (2016) Ecosystem services from small forest patches in agricultural  
624 landscapes. *Current Forestry Reports*, **2**, 30–44.

625 Dekoninck, W., Pals, P. & Grootaert, P. (2005) Hoverfly communities on former agricultural fields: a study  
626 of afforestation and planted forests stands in the Voeren region. *Bulletin de L'Institut Royal des  
627 Sciences Naturelles de Belgique-Entomologie*, **75**, 281–290.

628 Delignette-Muller, M.L. & Dutang, C. (2015) fitdistrplus: An R package for fitting distributions. *Journal of  
629 Statistical Software*, **64**, 1–34.

630 Desender, K., Dekoninck, W. & Grootaert, P. (2005) Diversity and assemblages of Carabid beetles in  
631 ancient forests and afforested former agricultural land. *Bull. Konin. Belg. Inst.  
632 Natuurwet.(Entomol.)*, **75**, 253–265.

633 Do, Y. & Joo, G.J. (2013) The effect of fragmentation and intensive management on carabid beetles in  
634 coniferous forest. *Applied Ecology and Environmental Research*, **11**, 451–461.

635 Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B.,  
636 Lafourcade, B. & Leitão, P.J. (2013) Collinearity: a review of methods to deal with it and a  
637 simulation study evaluating their performance. *Ecography*, **36**, 27–46.

638 Driscoll, D.A. & Weir, T.O.M. (2005) Beetle responses to habitat fragmentation depend on ecological  
639 traits, habitat condition, and remnant size. *Conservation Biology*, **19**, 182–194.

640 Duflot, R., Daniel, H., Aviron, S., Alignier, A., Beaujouan, V., Burel, F., Cochard, A., Ernoult, A., Pain, G. &  
641 Pithon, J.A. (2018) Adjacent woodlands rather than habitat connectivity influence grassland  
642 plant, carabid and bird assemblages in farmland landscapes. *Biodiversity and Conservation*, **27**,  
643 1925–1942.

644 Dwyer, L.M. & Merriam, G. (1981) Influence of topographic heterogeneity on deciduous litter  
645 decomposition. *Oikos*, **37**, 228–237.

646 Ehrmann, S., Liira, J., Gärtner, S., Hansen, K., Brunet, J., Cousins, S.A., Deconchat, M., Decocq, G., De  
647 Frenne, P. & De Smedt, P. (2017) Environmental drivers of *Ixodes ricinus* abundance in forest  
648 fragments of rural European landscapes. *BMC Ecology*, **17**, 31.

649 Ernst, C.M. & Buddle, C.M. (2015) Drivers and patterns of ground-dwelling beetle biodiversity across  
650 Northern Canada. *PloS one*, **10**, e0122163.

651 Estreguil, C., Caudullo, G., de Rigo, D. & San-Miguel-Ayanz, J. (2013) Forest landscape in Europe: pattern,  
652 fragmentation and connectivity. *EUR Scientific and Technical Research*, **25717**.

653 Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology,  
654 Evolution, and Systematics*, **48**, 1–23.

655 Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution,  
656 and Systematics*, **34**, 487–515.

657 Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of  
658 Biogeography*, **40**, 1649–1663.

659 Fletcher, R.J., Burrell, N.S., Reichert, B.E., Vasudev, D. & Austin, J.D. (2016) Divergent perspectives on  
660 landscape connectivity reveal consistent effects from genes to communities. *Current Landscape  
661 Ecology Reports*, **1**, 67–79.

662 Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily,  
663 G.C. & Gibbs, H.K. (2005) Global consequences of land use. *Science*, **309**, 570–574.

664 Forrest, J.R. (2016) Complex responses of insect phenology to climate change. *Current opinion in insect  
665 science*, **17**, 49–54.

666 Fountain-Jones, N.M., Jordan, G.J., Baker, T.P., Balmer, J.M., Wardlaw, T. & Baker, S.C. (2015) Living near  
667 the edge: being close to mature forest increases the rate of succession in beetle communities.  
668 *Ecological Applications*, **25**, 800–811.

669 Gaublomme, E., Hendrickx, F., Dhuyvetter, H. & Desender, K. (2008) The effects of forest patch size and  
670 matrix type on changes in carabid beetle assemblages in an urbanized landscape. *Biological  
671 Conservation*, **141**, 2585–2596.

672 González, E., Salvo, A. & Valladares, G. (2017) Natural vegetation cover in the landscape and edge  
673 effects: differential responses of insect orders in a fragmented forest. *Insect Science*, **24**, 891–  
674 901.

675 Graae, B.J., De Frenne, P., Kolb, A., Brunet, J., Chabrierie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel,  
676 M. & Shevtsova, A. (2012) On the use of weather data in ecological studies along altitudinal and  
677 latitudinal gradients. *Oikos*, **121**, 3–19.

678 Graae, B.J., Vandvik, V., Armbruster, W.S., Eiserhardt, W.L., Svenning, J.-C., Hylander, K., Ehrlén, J.,  
679 Speed, J.D., Klanderud, K. & Bråthen, K.A. (2018) Stay or go—how topographic complexity  
680 influences alpine plant population and community responses to climate change. *Perspectives in  
681 Plant Ecology, Evolution and Systematics*, **30**, 41–50.



682 Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O.,  
683 Austin, M.P. & Collins, C.D. (2015) Habitat fragmentation and its lasting impact on Earth's  
684 ecosystems. *Science Advances*, **1**, e1500052.

685 Heino, J. & Alahuhta, J. (2015) Elements of regional beetle faunas: faunal variation and compositional  
686 breakpoints along climate, land cover and geographical gradients. *Journal of Animal Ecology*, **84**,  
687 427–441.

688 Hendrickx, F., Maelfait, J.-P., Desender, K., Aviron, S., Bailey, D., Diekotter, T., Lens, L., Liira, J., Schweiger,  
689 O. & Speelmans, M. (2009) Pervasive effects of dispersal limitation on within-and among-  
690 community species richness in agricultural landscapes. *Global Ecology and Biogeography*, **18**,  
691 607–616.

692 Holland, J.M., Thomas, C.F.G., Birkett, T., Southway, S. & Oaten, H. (2005) Farm-scale spatiotemporal  
693 dynamics of predatory beetles in arable crops. *Journal of Applied Ecology*, **42**, 1140–1152.

694 Honnay, O., Hermy, M. & Coppin, and P. (1999) Effects of area, age and diversity of forest patches in  
695 Belgium on plant species richness, and implications for conservation and reforestation. *Biological  
696 Conservation*, **87**, 73–84.

697 Hubbell, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence.  
698 *Functional Ecology*, **19**, 166–172.

699 Huffeldt, N.P. (2020) Photic Barriers to Poleward Range-shifts. *Trends in Ecology & Evolution*.

700 Hülsmann, M., Boutaud, E., Buse, J., Schuldt, A. & Assmann, T. (2019) Land-use legacy and tree age in  
701 continuous woodlands: weak effects on overall ground beetle assemblages, but strong effects on  
702 two threatened species. *Journal of Insect Conservation*, **23**, 623–633.

703 Hůrka, K. (1996) *Carabidae of the Czech and Slovak Republics*, Vit Kabourek Editors, Zlin.

704 Jamoneau, A., Sonnier, G., Chabrierie, O., Closset-Kopp, D., Saguez, R., Gallet-Moron, E. & Decocq, G.  
705 (2011) Drivers of plant species assemblages in forest patches among contrasted dynamic  
706 agricultural landscapes. *Journal of Ecology*, **99**, 1152–1161.

707 Jeannel, R. (1941) *Coléoptères Carabiques, Faune de France*, Lechevalier, Paris.

708 Jeannel, R. (1942) *Coléoptères Carabiques II, Faune de France*, Lechevalier, Paris.

709 de Jong, Y., Verbeek, M., Michelsen, V., de Place Bjørn, P., Los, W., Steeman, F., Bailly, N., Basire, C.,  
710 Chylarecki, P. & Stloukal, E. (2014) Fauna Europaea—all European animal species on the web.  
711 *Biodiversity Data Journal*, e4034.

712 Jung, J.-K., Lee, S.K., Lee, S.-I. & Lee, J.-H. (2018) Trait-specific response of ground beetles (Coleoptera:  
713 Carabidae) to forest fragmentation in the temperate region in Korea. *Biodiversity and  
714 Conservation*, **27**, 53–68.

715 Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of  
716 Vegetation Science*, **3**, 157–164.

717 Knapp, M., Seidl, M., Knappová, J., Macek, M. & Saska, P. (2019) Temporal changes in the spatial  
718 distribution of carabid beetles around arable field-woodlot boundaries. *Scientific Reports*, **9**,  
719 8967.

720 Koivula, M., Kukkonen, J. & Niemelä, J. (2002) Boreal carabid-beetle (Coleoptera, Carabidae)  
721 assemblages along the clear-cut originated succession gradient. *Biodiversity & Conservation*, **11**,  
722 1269–1288.

723 Kotze, D.J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M.J., Lövei, G.L.,  
724 Mossakowski, D., Noordijk, J. & Paarmann, W. (2011) Forty years of carabid beetle research in  
725 Europe—from taxonomy, biology, ecology and population studies to bioindication, habitat  
726 assessment and conservation. *ZooKeys*, 55.

727 Kromp, B. (1999) Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation  
728 impacts and enhancement. *Agriculture, Ecosystems & Environment*, **74**, 187–228.

729 Kütt, L., Paal, T., Löhmus, K., Rammi, I.-J., Zobel, K. & Liira, J. (2018) Multi-user quality of floral services  
730 along a gradient of margin habitats between semi-natural grasslands and forests. *Applied*  
731 *Vegetation Science*, **21**, 363–372.

732 Latty, E.F., Werner, S.M., Mladenoff, D.J., Raffa, K.F. & Sickley, T.A. (2006) Response of ground beetle  
733 (Carabidae) assemblages to logging history in northern hardwood–hemlock forests. *Forest*  
734 *Ecology and Management*, **222**, 335–347.

735 Lawesson, J.E., de Blust, G., Grashof, C., Firbank, L., Honnay, O., Hermy, M., Hobitz, P. & Jensen, L.M.  
736 (1998) Species diversity and area-relationships in Danish beech forests. *Forest Ecology and*  
737 *Management*, **106**, 235–245.

738 Le Provost, G., Badenhausser, I., Le Bagousse-Pinguet, Y., Clough, Y., Henckel, L., Violle, C., Bretagnolle,  
739 V., Roncoroni, M., Manning, P. & Gross, N. (2020) Land-use history impacts functional diversity  
740 across multiple trophic groups. *Proceedings of the National Academy of Sciences*.

741 Legendre, P. & Legendre, L.F. (2012) *Numerical ecology. Third edition*, Elsevier, Amsterdam, The  
742 Netherlands.

743 Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, Ö., Goldberg, I., Nascimbene, J.,  
744 Tøttrup, A.P. & Rahbek, C. (2019) Biodiversity response to forest structure and management:  
745 Comparing species richness, conservation relevant species and functional diversity as metrics in  
746 forest conservation. *Forest Ecology and Management*, **432**, 707–717.

747 Lenoir, J., Decocq, G., Spicher, F., Gallet-Moron, E., Buridant, J. & Closset-Kopp, D. (2020) Historical  
748 continuity and spatial connectivity ensure hedgerows are effective corridors for forest plants:  
749 evidence from the species-time-area relationship. *Journal of Vegetation Science*.

750 Lenoir, J., Graae, B.J., Aarrestad, P.A., Alsos, I.G., Armbruster, W.S., Austrheim, G., Bergendorff, C., Birks,  
751 H.J.B., Bråthen, K.A. & Brunet, J. (2013) Local temperatures inferred from plant communities  
752 suggest strong spatial buffering of climate warming across Northern Europe. *Global Change*  
753 *Biology*, **19**, 1470–1481.

754 Lenoir, J., Hattab, T. & Pierre, G. (2017) Climatic microrefugia under anthropogenic climate change:  
755 implications for species redistribution. *Ecography*, **40**, 253–266.

756 Lövei, G.L., Magura, T., Tóthmérész, B. & Ködöböcz, V. (2006) The influence of matrix and edges on  
757 species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Global*  
758 *Ecology and Biogeography*, **15**, 283–289.

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

761 MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting  
762 species. *The American Naturalist*, **101**, 377–385.

763 Magura, T., Tóthmérész, B. & Elek, Z. (2003) Diversity and composition of carabids during a forestry  
764 cycle. *Biodiversity & Conservation*, **12**, 73–85.

765 Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L. da S., Soussana, J.-F. & Louault, F. (2012)  
766 Habitat filtering and niche differentiation jointly explain species relative abundance within  
767 grassland communities along fertility and disturbance gradients. *New Phytologist*, **196**, 497–509.

768 Marrec, R., Badenhausser, I., Bretagnolle, V., Börger, L., Roncoroni, M., Guillon, N. & Gauffre, B. (2015)  
769 Crop succession and habitat preferences drive the distribution and abundance of carabid beetles  
770 in an agricultural landscape. *Agriculture, Ecosystems & Environment*, **199**, 282–289.

771 Martin, A.E. & Fahrig, L. (2012) Measuring and selecting scales of effect for landscape predictors in  
772 species–habitat models. *Ecological Applications*, **22**, 2277–2292.

773 Masaki, S. (1980) Summer diapause. *Annual Review of Entomology*, **25**, 1–25.

774 McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in  
775 the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450–453.

776 Moret, P., Aráuz, M. de los Á., Gobbi, M. & Barragán, Á. (2016) Climate warming effects in the tropical  
777 Andes: first evidence for upslope shifts of Carabidae (Coleoptera) in Ecuador. *Insect Conservation*  
778 *and Diversity*, **9**, 342–350.

779 Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R<sup>2</sup> from generalized  
780 linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.

781 Niemelä, J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review.  
782 *European Journal of Entomology*, **98**, 127–132.

783 Niemelä, J., Langor, D. & Spence, J.R. (1993) Effects of clear-cut harvesting on boreal ground-beetle  
784 assemblages (Coleoptera: Carabidae) in western Canada. *Conservation biology*, **7**, 551–561.

785 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B.,  
786 Simpson, G.L., Solymos, P., Stevens, H.H., Szoecs, E. & Wagner, H. (2018) vegan: Community  
787 Ecology Package. R package version 2.5-2. <https://CRAN.R-project.org/package=vegan>.

788 Olden, J.D. & Rooney, T.P. (2006) On defining and quantifying biotic homogenization. *Global Ecology and*  
789 *Biogeography*, **15**, 113–120.

790 Park, Y., Kim, J., Jang, T., Chae, H. & Takami, Y. (2017) Local climate mediates spatial and temporal  
791 variation in carabid beetle communities in three forests in Mount Odaesan, Korea. *Ecological*  
792 *Entomology*, **42**, 184–194.

793 Pearce, J.L. & Venier, L.A. (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders  
794 (Araneae) as bioindicators of sustainable forest management: a review. *Ecological Indicators*, **6**,  
795 780–793.

796 Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-  
797 Rodríguez, V., Barlow, J. & Cerezo, A. (2017) Creation of forest edges has a global impact on  
798 forest vertebrates. *Nature*, **551**, 187–191.

799 Pizzolotto, R., Gobbi, M. & Brandmayr, P. (2014) Changes in ground beetle assemblages above and below  
800 the treeline of the D olomites after almost 30 years (1980/2009). *Ecology and Evolution*, **4**, 1284–  
801 1294.

802 R. Core Team (2018) *R: A language and environment for statistical computing*. R Foundation for  
803 *Statistical Computing, Vienna, Austria*. URL <https://www.R-project.org/>.

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

806 Ricotta, C., Stanisci, A., Avena, G.C. & Blasi, C. (2000) Quantifying the network connectivity of landscape  
807 mosaics: a graph-theoretical approach. *Community Ecology*, **1**, 89–94.

808 Rosenzweig, M.L. (1995) *Species diversity in space and time*, Cambridge University Press.

809 Sadler, J.P., Small, E.C., Fiszpan, H., Telfer, M.G. & Niemelä, J. (2006) Investigating environmental  
810 variation and landscape characteristics of an urban–rural gradient using woodland carabid  
811 assemblages. *Journal of Biogeography*, **33**, 1126–1138.

812 Schneider, G., Krauss, J., Boetzel, F.A., Fritze, M.-A. & Steffan-Dewenter, I. (2016) Spillover from adjacent  
813 crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural  
814 grasslands. *Oecologia*, **182**, 1141–1150.

815 Schowalter, T. (2017) Arthropod Diversity and Functional Importance in Old-Growth Forests of North  
816 America. *Forests*, **8**, 97.

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

819 Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J.,  
820 Fischer, M. & Habel, J.C. (2019) Arthropod decline in grasslands and forests is associated with  
821 landscape-level drivers. *Nature*, **574**, 671–674.

822 Sheikh, A.A., Rehman, N.Z. & Kumar, R. (2017) Diverse adaptations in insects: A Review. *J. Entomol. Zool.*  
823 *Stud.*, **5**, 343–350.

- 824 Sroka, K. & Finch, O.-D. (2006) Ground beetle diversity in ancient woodland remnants in north-western  
825 Germany (Coleoptera, Carabidae). *Journal of Insect Conservation*, **10**, 335.
- 826 Taylor, L.R. (1963) Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology*,  
827 **32**, 99–117.
- 828 Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape  
829 structure. *Oikos*, **68**, 571–573.
- 830 Thiele, H.-U. (1977) *Carabid Beetles in Their Environments. A Study on Habitat Selection by Adaptations in*  
831 *Physiology and Behaviour*, Springer-Verlag, Berlin.
- 832 Thomas, C.F.G., Brown, N.J. & Kendall, D.A. (2006) Carabid movement and vegetation density:  
833 Implications for interpreting pitfall trap data from split-field trials. *Agriculture, Ecosystems &*  
834 *Environment*, **113**, 51–61.
- 835 Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**,  
836 7–19.
- 837 Tougeron, K., Brodeur, J., Le Lann, C. & van Baaren, J. (2019) How climate change affects the seasonal  
838 ecology of insect parasitoids. *Ecological Entomology*.
- 839 Tyler, G. (2008) Differences in abundance, species richness, and body size of ground beetles (Coleoptera:  
840 Carabidae) between beech (*Fagus sylvatica* L.) forests on Podzol and Cambisol. *Forest Ecology*  
841 *and Management*, **256**, 2154–2159.
- 842 Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrierie, O., Cousins, S.A., Deconchat, M., De  
843 Smedt, P. & Diekmann, M. (2020) High ecosystem service delivery potential of small woodlands  
844 in agricultural landscapes. *Journal of Applied Ecology*, **57**, 4–16.
- 845 Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrierie, O., Closset-Kopp, D., Cousins,  
846 S.A., Deconchat, M. & De Frenne, P. (2015) The contribution of patch-scale conditions is greater  
847 than that of macroclimate in explaining local plant diversity in fragmented forests across E  
848 urope. *Global Ecology and Biogeography*, **24**, 1094–1105.
- 849 Vanneste, T., Valdés, A., Verheyen, K., Perring, M.P., Bernhardt-Römermann, M., Andrieu, E., Brunet, J.,  
850 Cousins, S.A., Deconchat, M. & De Smedt, P. (2019) Functional trait variation of forest  
851 understorey plant communities across Europe. *Basic and Applied Ecology*, **34**, 1–14.
- 852 Wintle, B.A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A.,  
853 Lentini, P.E. & Cadenhead, N.C. (2019) Global synthesis of conservation studies reveals the  
854 importance of small habitat patches for biodiversity. *Proceedings of the National Academy of*  
855 *Sciences*, **116**, 909–914.
- 856

## 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)**  $\alpha$ -diversity and **(b)**  $\beta$ -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  $\chi^2$  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)
<b>(a) <math>\alpha</math>-diversity</b>				
	$R^2_m = 0.361$	$R^2_m = 0.653$	$R^2_m = 0.582$	$R^2_m = 0.438$
	$R^2_c = 0.825$	$R^2_c = 0.653$	$R^2_c = 0.582$	$R^2_c = 0.638$
	-	-0.06 ( $\pm$ 0.05)	<b>-0.17 (<math>\pm</math> 0.07)*</b>	-0.39 ( $\pm$ 0.20)
	-	<b>0.32 (<math>\pm</math> 0.04)***</b>	-	<b>0.22 (<math>\pm</math> 0.10)*</b>
	<b>-1.11 (<math>\pm</math> 0.36)**</b>	<b>-0.31 (<math>\pm</math> 0.06)***</b>	-0.07 ( $\pm$ 0.12)	<b>1.31 (<math>\pm</math> 0.33)***</b>
Macroclimate	-	<b>-0.55 (<math>\pm</math> 0.05)***</b>	<b>-0.13 (<math>\pm</math> 0.03)***</b>	<b>-0.62 (<math>\pm</math> 0.13)***</b>
	-	-	<b>-0.11 (<math>\pm</math> 0.03)***</b>	-
	-	-	-	-
	-	-	<b>-0.21 (<math>\pm</math> 0.09)*</b>	<b>-1.19 (<math>\pm</math> 0.20)***</b>
	-	-	<b>-0.18 (<math>\pm</math> 0.04)***</b>	<b>0.31 (<math>\pm</math> 0.11)**</b>
	-	-	-	-
Landscape	-	-	-	-
	-	-	-	-
	-	-	-	100 m <b>-0.15 (<math>\pm</math> 0.05)**</b>

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

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 ( $\alpha$ -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  $\alpha$ -diversity) or linear mixed-effect models (LMM;  $\beta$ -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 ( $\beta$ -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**

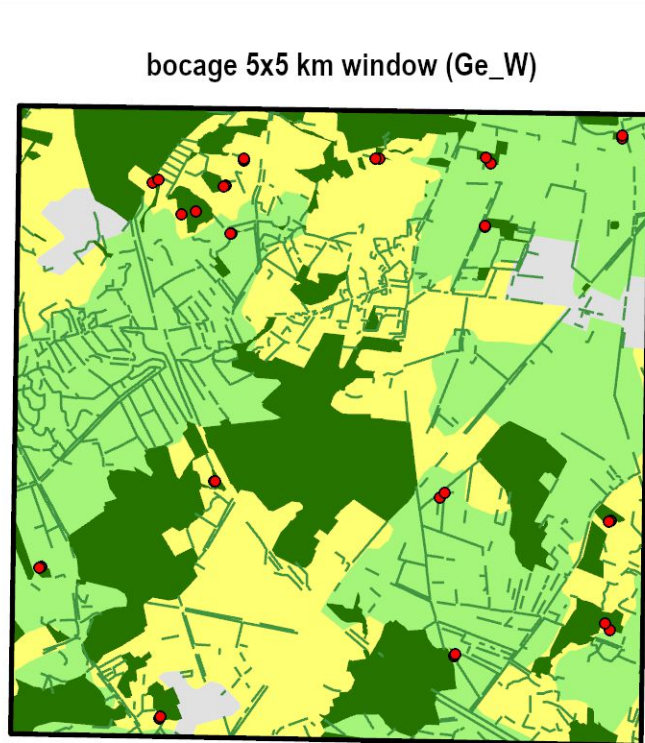
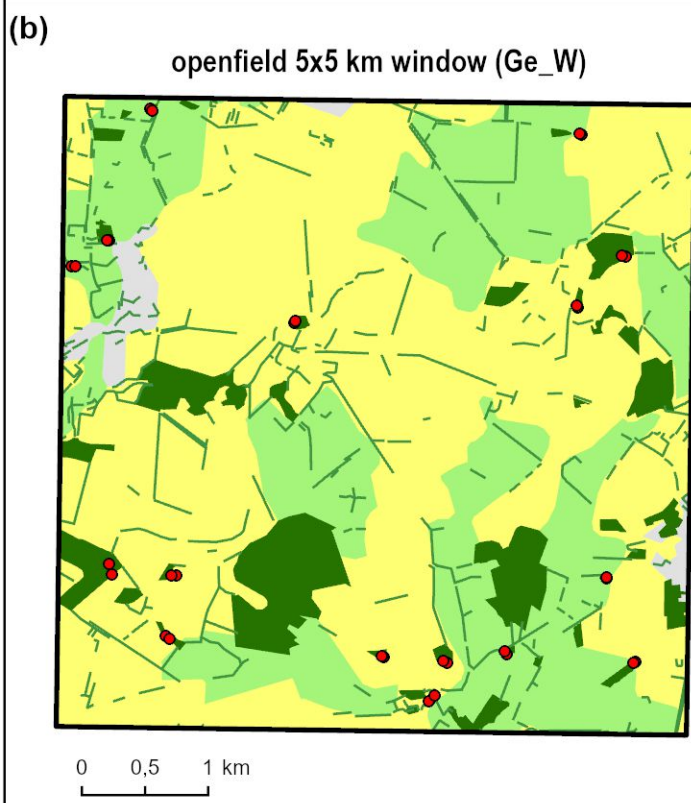
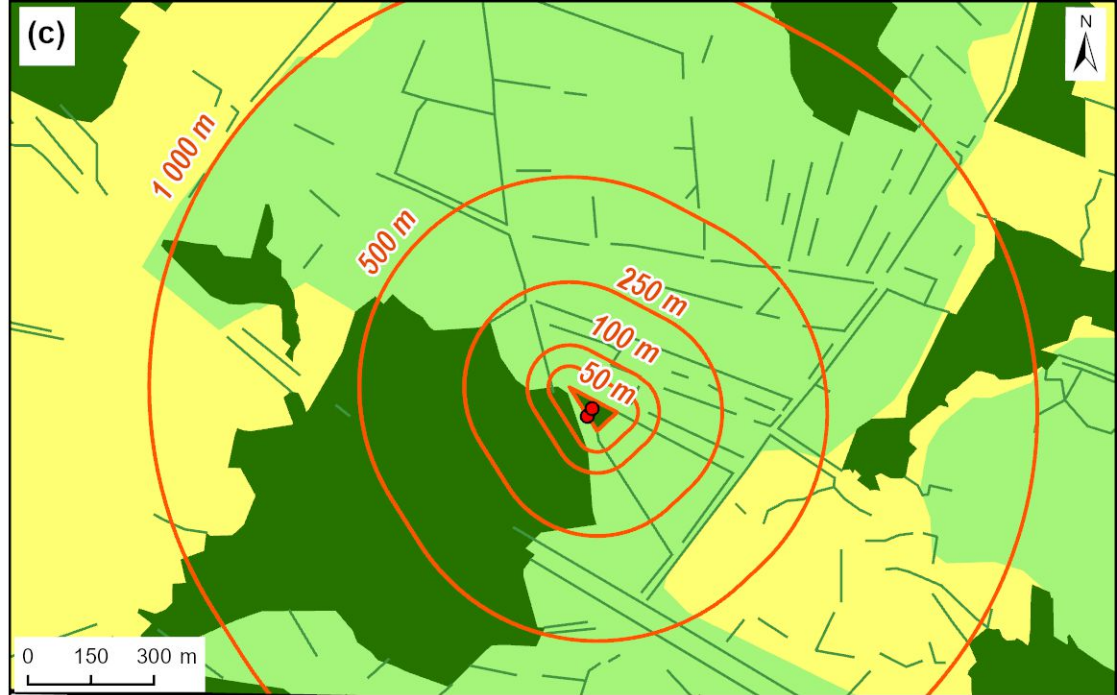
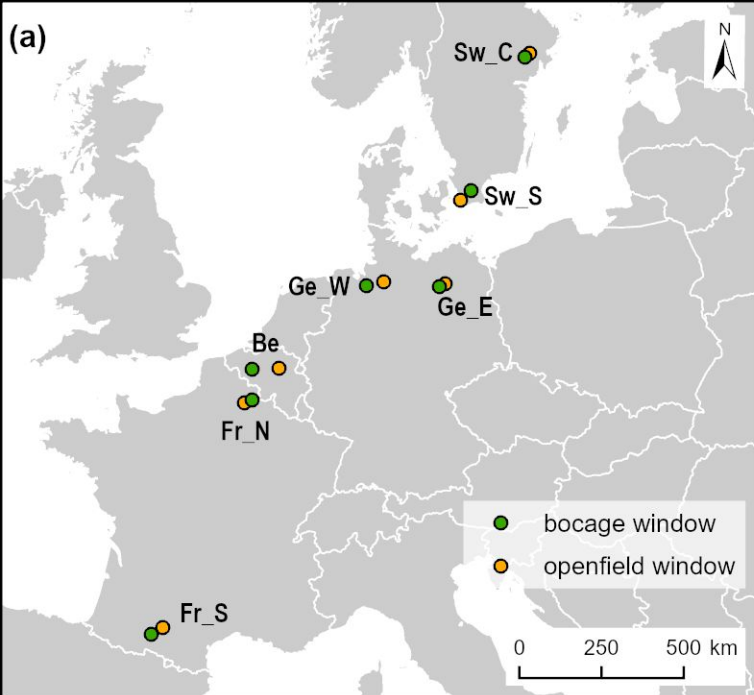
903 Additional supporting information may be found in the online version of this article at the  
904 publisher's website.

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.





**Land use**

cropland

woodland

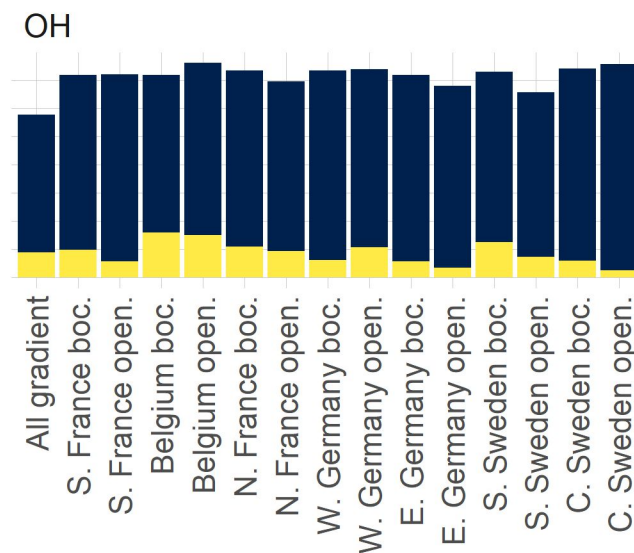
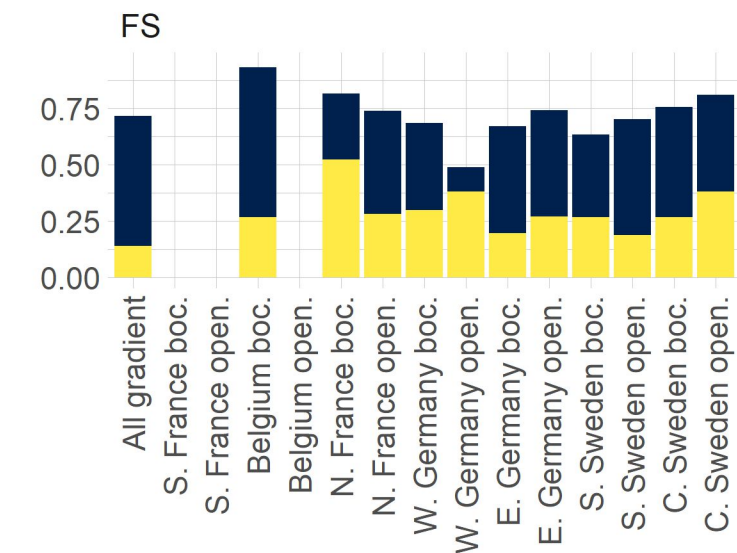
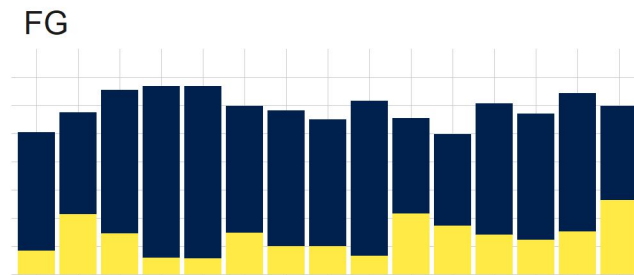
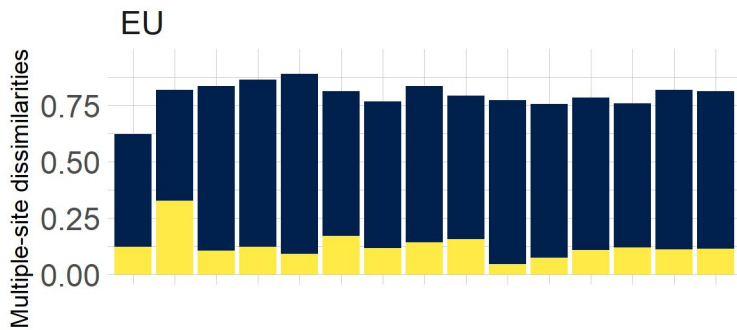
grassland

other

hedgerows

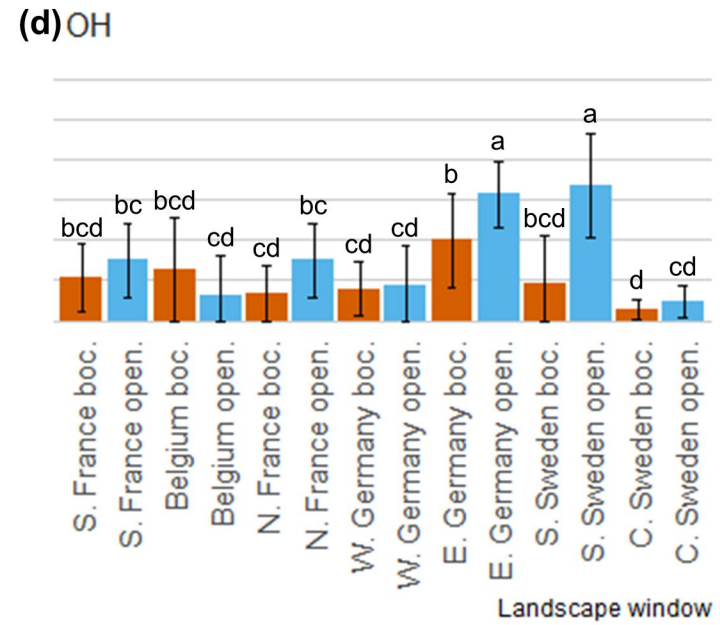
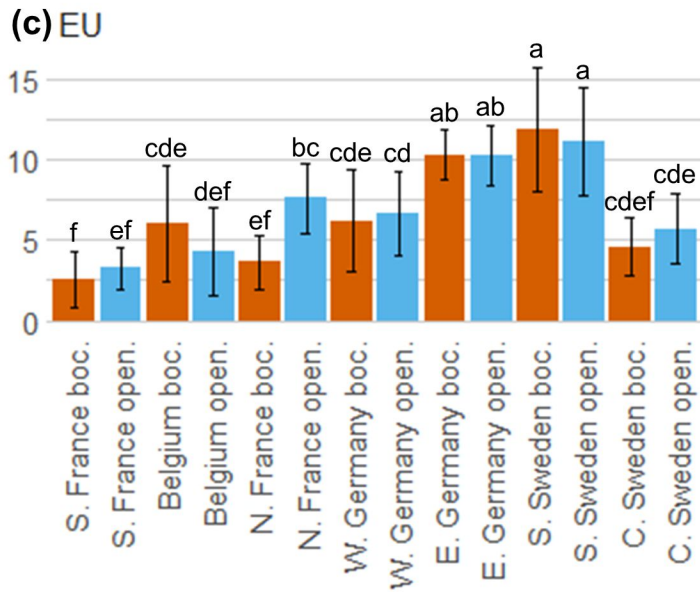
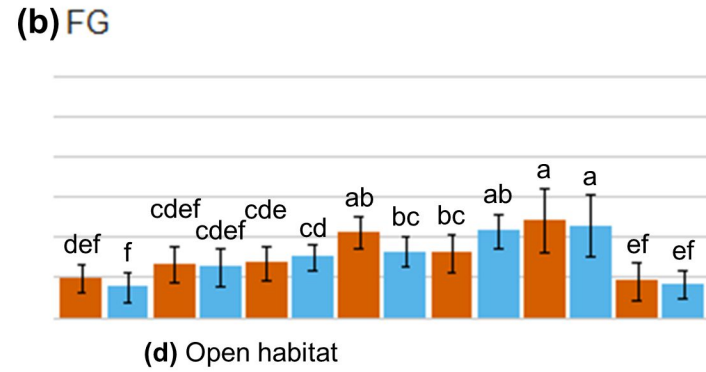
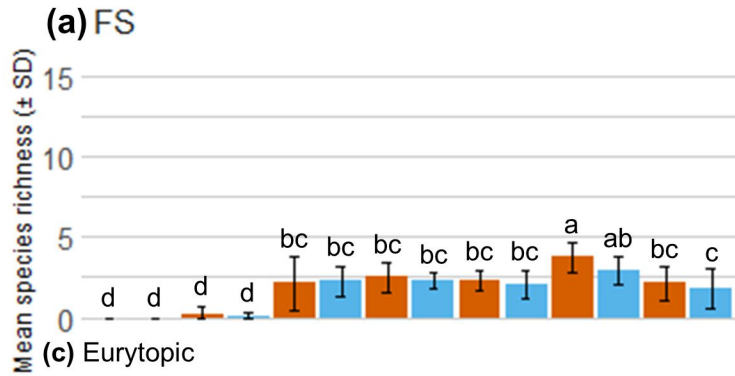
carabid beetle traps

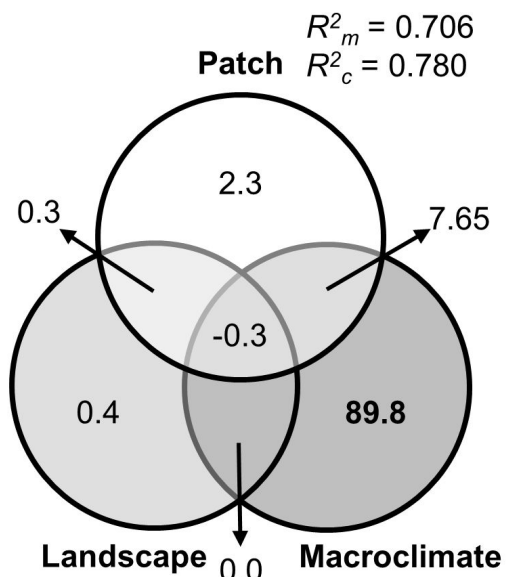
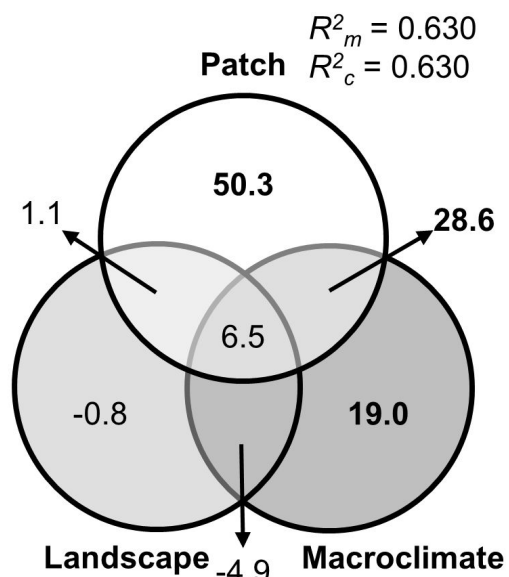
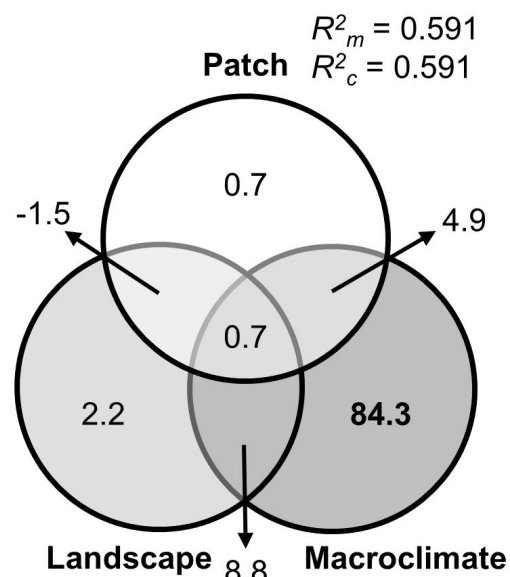
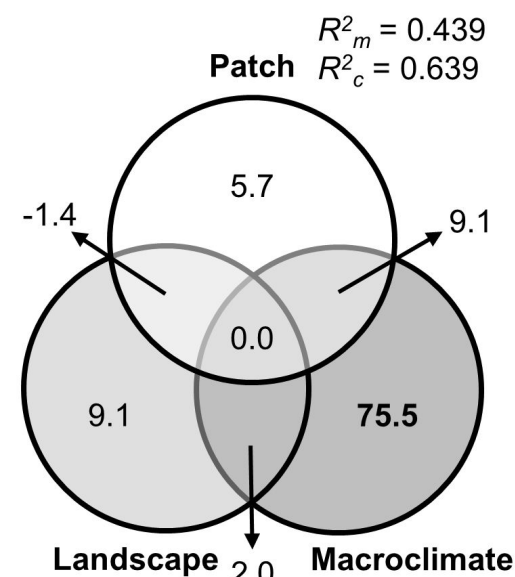
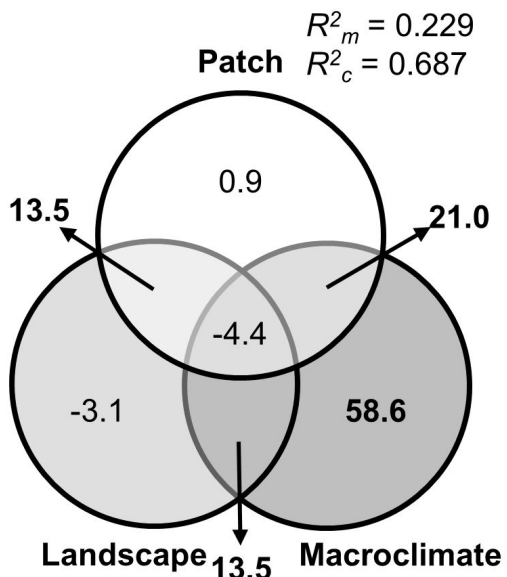
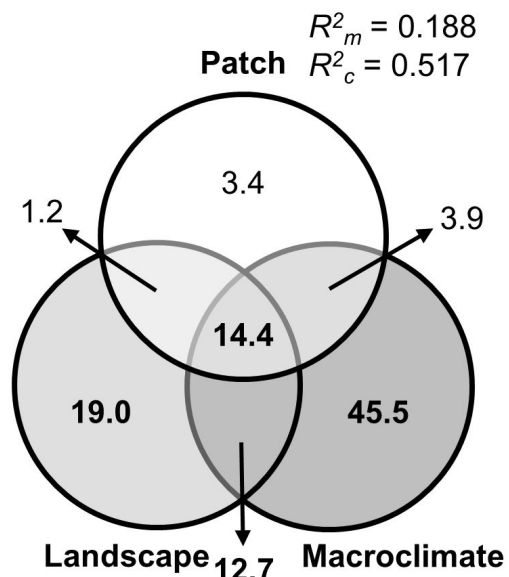
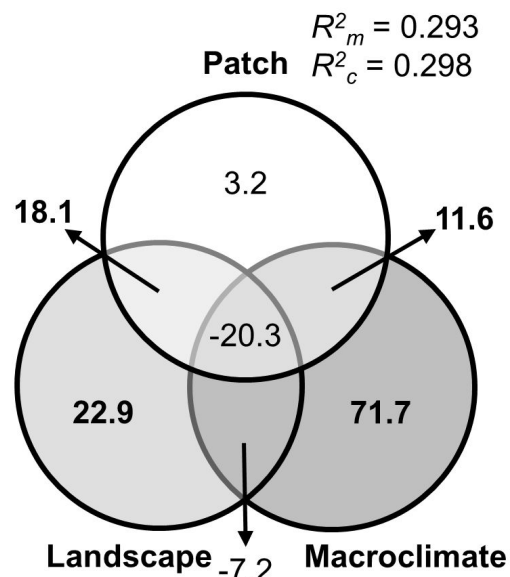
concentric 'doughnut'-like buffers



Landscape window

Components  Turnover  Nestedness



**(a) Forest-specialist  $\alpha$ -diversity****(b) Forest-generalist  $\alpha$ -diversity****(c) Eurytopic  $\alpha$ -diversity****(d) Open-habitat  $\alpha$ -diversity****(e) Forest-specialist  $\beta$ -diversity****(f) Forest-generalist  $\beta$ -diversity****(g) Eurytopic  $\beta$ -diversity****(h) Open-habitat  $\beta$ -diversity**