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

Ronan Marrec, Vincent Le Roux, Ludmilla Martin, Jonathan Roger Michel Henri Lenoir, Jorg Brunet, Sara Cousins, Pallieter de Smedt, Marc Deconchat, Martin Diekmann, Steffen Ehrmann, et al.

HAL Id: hal-03025668
https://hal.inrae.fr/hal-03025668

Submitted on 3 Oct 2021

Journal: Global Ecology and Biogeography

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

Authors: Ronan MARREC[1,*], Vincent LE ROUX[1], Ludmilla MARTIN[1], Jonathan LENOIR[1], Jörg BRUNET[2], Sara A. O. COUSINS[3,4], Pallieter DE SMEDT[5], Marc DECONCHAT[6], Martin DIEKMANN[7], Steffen EHRMANN[8,9], Emilie GALLET-MORON[1], Brice GIFFARD[6], Jaan LIIRA[10], Jessica LINDGREN[3], Alicia VALDES[1,4,11], Kris VERHEYEN[5], Monika WULF[12], Guillaume DECOCQ[1]

Affiliations:

[1] EDYSAN (*Ecologie et Dynamique des Systèmes Anthropisés*), UMR CNRS 7058, Université de Picardie Jules Verne, 33 rue Saint Leu, F-80039 Amiens, France

[2] Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Box 49, SE-230 53 Alnarp, Sweden

[3] Biogeography and Geomatics, Department of Physical Geography, Stockholm University, SE-106 91 Stockholm, Sweden

[4] Bolin Centre of Climate Research, Stockholm University, Stockholm, Sweden

[5] Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode, Belgium

[6] Université de Toulouse, Dynafor, INRAE, INPT ENSAT, , F-31320 Castanet Tolosan, France

[7] Vegetation Ecology and Conservation Biology, Institute of Ecology, FB2, University of Bremen, Leobener Str., D-28359 Bremen, Germany

[8] Faculty of Biology, Department of Geobotany, University of Freiburg, Schänzlestr. 1, D-79104 Freiburg im Breisgau, Germany

[9] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[10] Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, EE-51005 Tartu, Estonia

[11] Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91, Stockholm, Sweden

[12] Research Area 2, Leibniz-ZALF (e.V.), Eberswalder Strasse 84, D-15374 Müncheberg, Germany

E-mail addresses (in the same order as authors): ronan.marrec@u-picardie.fr, vincent.leroux@u-picardie.fr, ludmilla.martin0109@gmail.com, jonathan.lenoir@u-picardie.fr, jorg.brunet@slu.se, sara.cousins@natgeo.su.se, pallieter.desmedt@ugent.be, marc.deconchat@inrae.fr, mdiekman@uni-bremen.de, steffen.ehrmann@idiv.de, emilie.moron@u-picardie.fr, brice.giffard@gmail.com, jaan.liira@ut.ee, jessica.lindgren@natgeo.su.se, aliciavaldes1501@gmail.com, kris.verheyen@ugent.be, mwulf@zalf.de, guillaume.decocq@u-picardie.fr

* Corresponding author: Ronan MARREC (ronan.marrec@u-picardie.fr)

ORCID Numbers

R. Marrec, 0000-0003-1607-4939

Vincent LE ROUX, 0000-0001-5443-3707

Jörg BRUNET, 0000-0003-2667-4575

Sara A. O. COUSINS, 0000-0003-2656-2645

Pallieter DE SMEDT, 0000-0002-3073-6751

Marc DECONCHAT, 0000-0002-4638-3858

Martin DIEKMANN, 0000-0001-8482-0679

Steffen EHRMANN, 0000-0002-2958-0796

Emilie GALLET-MORON, 0000-0003-1579-5013

Brice GIFFARD, 0000-0003-4367-1245

Jonathan LENOIR, 0000-0003-0638-9582

Jaan LIIRA, 0000-0001-8863-0098

Jessica LINDGREN, 0000-0001-7219-4359

Alicia VALDES, 0000-0001-9281-2871

Kris VERHEYEN, 0000-0002-2067-9108

Monika WULF, 0000-0001-6499-0750

Guillaume DECOCQ, 0000-0001-9262-5873

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.

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.

Results We found that both α- and β-diversity were primarily determined by macroclimate, acting

as a large-scale ecological filter on carabid assemblages among regions. Forest-patch conditions,

including biotic and abiotic heterogeneity as well as patch age (but not patch size), increased α-

diversity of forest species. Landscape management intensity weakly influenced α-diversity of

forest species, but increased the number of non-forest species in forest patches. Beta-diversity of

non-forest species increased with patch heterogeneity and decreased with landscape management

intensity.

Main conclusions Our results highlight the leading role of broad macroclimatic gradients over

local and landscape factors in determining the composition of local carabid communities, thereby

shedding light on macroecological patterns of arthropod assemblages. This study emphasizes the

urgent need for preserving ancient forest patches embedded in agricultural landscapes, even the

small and weakly connected ones.

INTRODUCTION

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

6

Study sites

We collected data across a total of 221 deciduous forest patches, distributed among seven

European regions. Regions were distributed along a south-west-to-north-east gradient of ca.

2,100 km across the European temperate forest biome (Fig. 1). In each region, we selected two 5

km $\times$ 5 km landscape windows differing by their degree of landscape permeability (see Valdés *et*

al., 2015 for more details). The first window was characterized by forest patches embedded in an

intensively cultivated open field landscape (hereafter "open field"). The second window

contained forest patches more or less connected by woody corridors (e.g., hedgerows) within a

less intensively managed landscape, dominated by grasslands and small crop fields (hereafter

"bocage"). A detailed and updated list of landscape and macroclimatic variables associated with

each landscape window can be found in Vanneste *et al.* (2019).

For each landscape window, we computed area, perimeter, and age of all forest patches using

digitized maps (one contemporary map at a scale of 1:25,000 and historical maps from the 17th,

18th, 19th, and 20th centuries) in a Geographic Information System (GIS; ARCGIS 9.3, ESRI).

Patches were subsequently distributed among four classes according to their area and age: small

($<$ median patch area value for the focal window) and recent ($<$ 150 years); large ($>$ median patch

area value for the focal window) and recent; small and ancient ($>$ 150 years); and large and

ancient.

 # Figure 1 here #

Carabid sampling and habitat preference

Whenever possible, we selected four forest patches (i.e., four repetitions) per level of patch size-

age combination ($n = 4$) and per landscape window ($n = 14$). A perfect balanced design was

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^2

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 (CVe) 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

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 #*

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 (MaTWm) 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 (MiTCm), except for open-habitat species, for which α-diversity peaked

315   in regions with intermediate values along the studied gradient of MiTCm 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 #*

15

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-sale 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 (CVe) 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. MaTWm, MiTCm) and, to a lesser degree, extremes of precipitation

17

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 (Huffeldt, 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.

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; Duflot *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

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., Duflot, 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.
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 epigaeic arthropod assemblages
620   (Coleoptera: Carabidae; Araneidae: Araneae; Isopoda: Oniscidae). *Periodicum Biologorum*, **118**,
621   311–314.
622 Decocq, G., Andrieu, E., Brunet, J., Chabrerie, 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., Chabrerie, 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., Chabrerie, 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., Lõhmus, 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 N orthern E urope. *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 R2 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., McGlinn, 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., Boetzl, 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., Chabrerie, 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., Chabrerie, 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)** 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 Estimate (± SE)	Forest generalist Estimate (± SE)	Eurytopic Estimate (± SE)	Open habitat Estimate (± 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 (± 0.05)	**-0.17 (± 0.07)***	-0.39 (± 0.20)˙	
	MaTWm^2	-	**0.32 (± 0.04)*****	-	**0.22 (± 0.10)***	
	MiTCm	**-1.11 (± 0.36)****	**-0.31 (± 0.06)*****	-0.07 (± 0.12)	**1.31 (± 0.33)*****	
	MiTCm^2	-	**-0.55 (± 0.05)*****	**-0.13 (± 0.03)*****	**-0.62 (± 0.13)*****	
	PWm	-	-	**-0.11 (± 0.03)*****	-	
	PWm^2	-	-	-	-	
	PDm	-	-	**-0.21 (± 0.09)***	**-1.19 (± 0.20)*****	
	PDm^2	-	-	**-0.18 (± 0.04)*****	**0.31 (± 0.11)****	
Landscape	**Hedgerow length**	-	-	-	-	
	Crops (%)	-	-	-	-	
	Grassland (%)	-	-	-	100 m	**-0.15 (± 0.05)****

	Forest (%)		-		-	500 m	-0.14 (± 0.03)***	500 m	-0.16 (± 0.07)*
	Age (recent vs. old)		-		-0.11 (± 0.05)*		-		-
	Area		-		-		-		-
Patch	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
	MaTWm		-		-0.08 (± 0.02)*		0.02 (± 0.01)*		-
	MaTWm^2		-		-		-		-
	MiTCm		0.38 (± 0.12)*		0.09 (± 0.04)*		-		-
Macroclimate	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)*		-
	Hedgerow length	500 m	-	50 m	0.02 (± 0.01)**		-		-
Landscape	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)*
	Age (recent vs. old)		0.07 (± 0.02)**		0.03 (± 0.01)*		-		-
	Area		-		-		-		-
Patch	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.

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 (± 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 (± 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-
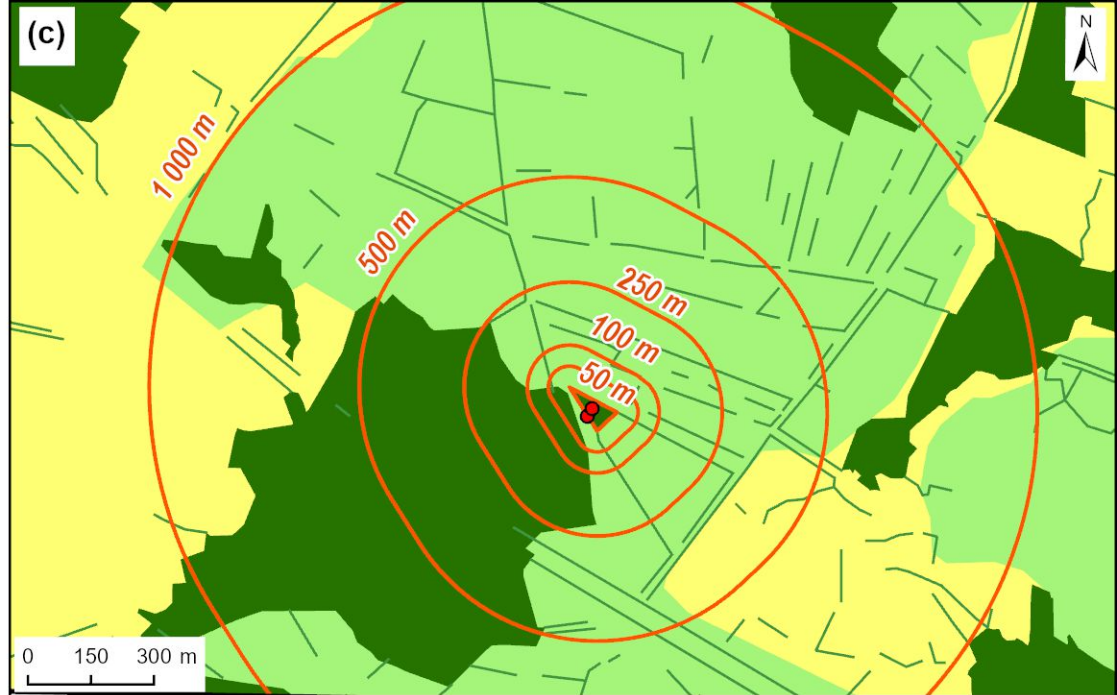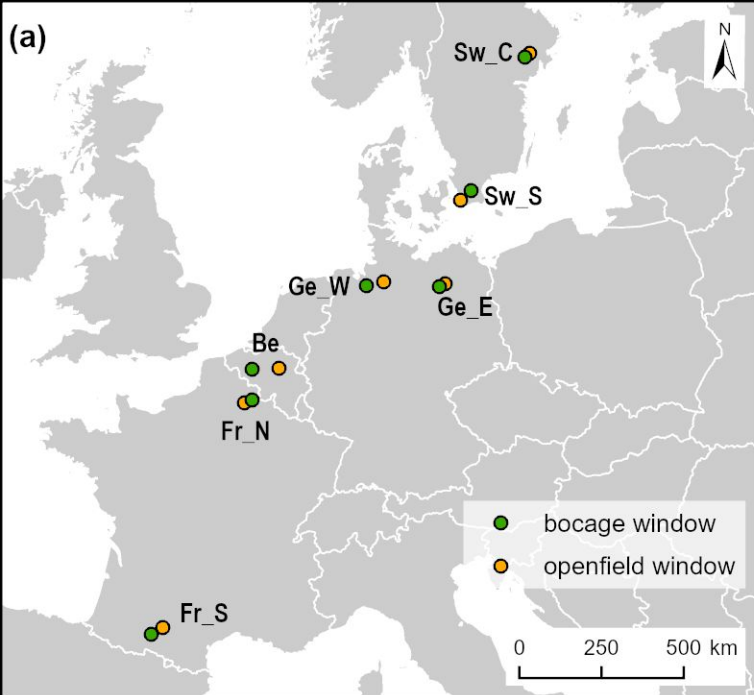900 habitat species.

901

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the

publisher's website.
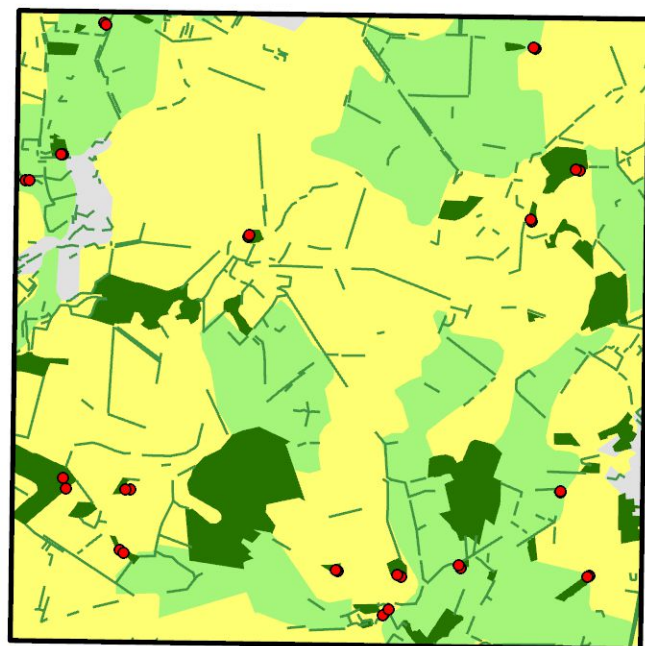
Appendix S1 Correlation table between all patch, landscape, and macroclimatic-level variables.

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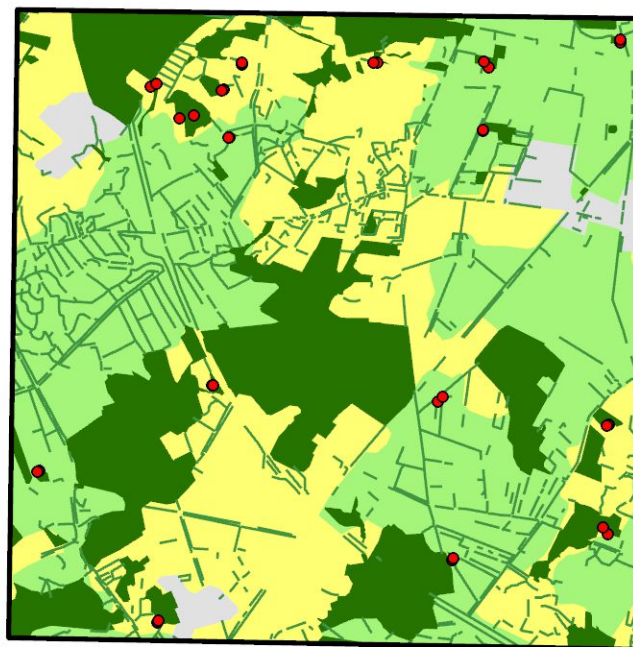
their habitat preference.

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

(a)

Sw_C

Sw_S

Ge_W
Ge_E

Be

Fr_N

Fr_S

● bocage window
● openfield window

0   250   500 km

(c)

1 000 m

500 m

250 m

100 m

50 m

0   150   300 m

(b)

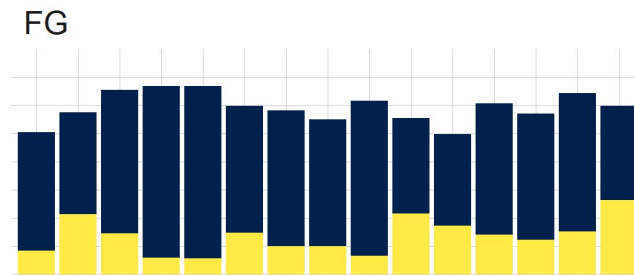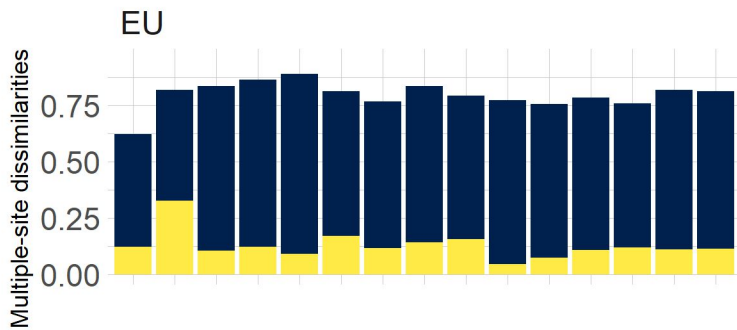**openfield 5x5 km window (Ge_W)**

bocage 5x5 km window (Ge_W)

N

0   0,5   1 km

Land use

cropland

woodland

grassland

other

hedgerows

● carabid beetle traps

⬭ concentric 'doughnut'
-like buffers

Source : Corine Land Cover 2006

EU

FG

FS

OH

Multiple-site dissimilarities
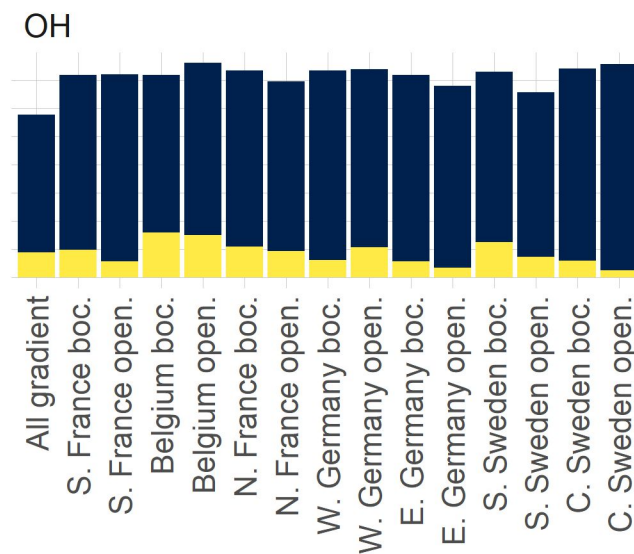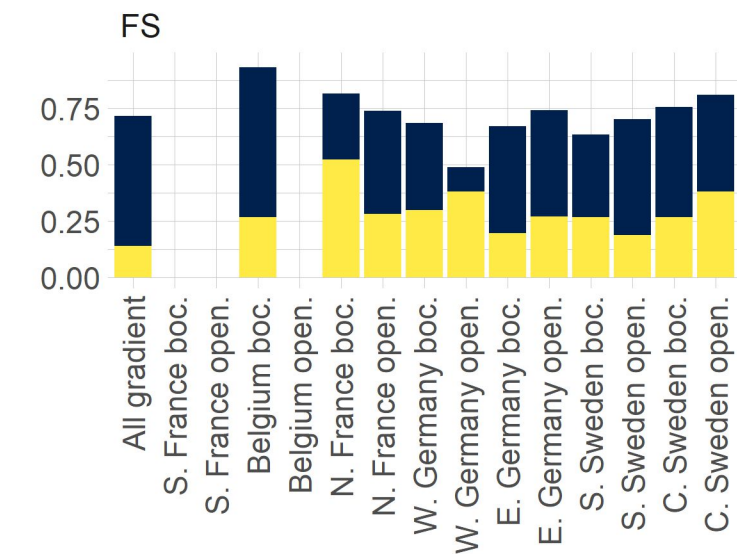
Landscape window

Components ■ Turnover ■ Nestedness

(a) FS

(b) FG

(c) Eurytopic

(d) Open habitat

(c) EU

(d) OH

Mean species richness (± SD)

Landscape window

S. France boc.
S. France open.
Belgium boc.
Belgium open.
N. France boc.
N. France open.
W. Germany boc.
W. Germany open.
E. Germany boc.
E. Germany open.
S. Sweden boc.
S. Sweden open.
C. Sweden boc.
C. Sweden open.

(a) Forest-specialist α-diversity
$R^2_m = 0.706$
$R^2_c = 0.780$
Patch
2.3
0.3
7.65
-0.3
0.4
89.8
Landscape 0.0 Macroclimate

(b) Forest-generalist α-diversity
$R^2_m = 0.630$
$R^2_c = 0.630$
Patch
50.3
1.1
28.6
6.5
-0.8
19.0
Landscape -4.9 Macroclimate

(c) Eurytopic α-diversity
$R^2_m = 0.591$
$R^2_c = 0.591$
Patch
0.7
-1.5
4.9
0.7
2.2
84.3
Landscape 8.8 Macroclimate

(d) Open-habitat α-diversity
$R^2_m = 0.439$
$R^2_c = 0.639$
Patch
5.7
-1.4
9.1
0.0
9.1
75.5
Landscape 2.0 Macroclimate

(e) Forest-specialist β-diversity
$R^2_m = 0.229$
$R^2_c = 0.687$
Patch
0.9
13.5
21.0
-4.4
-3.1
58.6
Landscape **13.5** Macroclimate

(f) Forest-generalist β-diversity
$R^2_m = 0.188$
$R^2_c = 0.517$
Patch
3.4
1.2
3.9
14.4
19.0
45.5
Landscape **12.7** Macroclimate

(g) Eurytopic β-diversity
$R^2_m = 0.293$
$R^2_c = 0.298$
Patch
3.2
18.1
11.6
-20.3
22.9
71.7
Landscape -7.2 Macroclimate

(h) Open-habitat β-diversity
$R^2_m = 0.145$
$R^2_c = 0.360$
Patch
41.2
-1.2
6.3
-2.7
13.4
31.9
Landscape **10.9** Macroclimate

(a) FS   **(b)** FG

(c) EU   **(d)** OH

Mean between-patch dissimilarity (± SD)

Landscape window

S. France boc.
S. France open.
Belgium boc.
Belgium open.
N. France boc.
N. France open.
W. Germany boc.
W. Germany open.
E. Germany boc.
E. Germany open.
S. Sweden boc.
S. Sweden open.
C. Sweden boc.
C. Sweden open.