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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

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Running title: Carabid assemblages in small forests

ABSTRACT

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

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

Methods We sampled 221 forest patches in two 5×5-km landscape windows with contrasting management intensities. Carabid beetles were classified into four habitat-preference guilds: forest-specialist, forest-generalist, eurytopic, and open-habitat species. We quantified the multi-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.

Keywords

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

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

In addition to the degree of spatial connectivity, temporal connectivity through the age of forest patches has repeatedly been shown to influence community composition, with ancient forest patches (i.e., patches that have continuously existed for centuries) harboring a higher number of forest-specialist species with limited dispersal abilities than recent forest patches (i.e., patches that have established on former agricultural lands in the last decades) (Dekoninck *et al.*, 2005; Desender *et al.*, 2005; Debnár *et al.*, 2016; Lelli *et al.*, 2019). Ancient forest patches usually support more diverse plant assemblages than recent ones, given their higher habitat heterogeneity (Brunet, 2007; Burrascano *et al.*, 2018) and benefit from longer duration for accumulating forest specialist species (i.e., the species-time relationship; Almoussawi *et al.*, 2020; Valdés *et al.*, 2020). However, compared to plant species, arthropod species have received little attention with respect to species richness in ancient *vs.* recent forest patches (Schowalter, 2017). Besides, to the best of our knowledge, only few studies have compared the diversity patterns of such arthropod assemblages in different contexts of landscape mosaic (e.g., Hendrickx *et al.*, 2009; De Smedt *et al.*, 2018).

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

Local climatic conditions (Park *et al.*, 2017), as well as current large-scale macroclimatic gradients (e.g., Heino & Alahuhta, 2015) and the biogeographic history of the continent since the Pleistocene glaciations (Calatayud *et al.*, 2016, 2019), are widely acknowledged as important drivers of local carabid species assemblages. Together with local and landscape features, macroclimatic factors were shown to affect carabid assemblages individually, but their relative importance is still unknown, despite their crucial importance for understanding all processes underlying local arthropod, assemblages. Whether common patterns are observed across various carabid guilds remains an unanswered question. Given the importance of small deciduous forest patches as biodiversity reservoirs in agricultural landscapes (De Blois *et al.*, 2002) and in delivering multiple ecosystem services to human societies (Decocq *et al.*, 2016), understanding community assembly processes in these habitats embedded in patchy landscapes is particularly relevant to conservation ecology and sustainable landscape planning.

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

METHODS

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

Species were distributed among four guilds, according to their habitat preference and using knowledge from the scientific literature (Hůrka, 1996; Sadler *et al.*, 2006; Gaublomme *et al.*, 2008; Bräunicke & Trautner, 2009): forest-specialist species, limited to stable, mature forest stands; forest-generalist species, occurring in any type of forest stand, in ancient as well as recent forest; open-habitat species, associated with non-forest habitats such as grasslands and arable lands; and eurytopic species, occurring in open habitats and tolerating transiently forest habitats. We could not assign only one species (*Oodes helopioides*, *n* = 1 individual) to any group because of a lack of information in the literature.

Environmental variables

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

Macroclimatic variables

To assess the influence of macroclimate on species diversity, we extracted 10 candidate bioclimatic variables from the WorldClim global database (1-km resolution, http://www.worldclim.org), and averaged each variable for each forest patch using all 1-km^2 pixels intersecting it. Four macroclimatic variables were retained for further analyses, based on a principal component analysis (PCA; see Valdés *et al.*, 2015), namely maximum temperature of the warmest month (MaTWm; BIO5); minimum temperature of the coldest month (MiTCm; BIO6); precipitation of the wettest month (PWm; BIO13); and precipitation of the driest month (PDm; BIO14). The selection was made in a way to minimize the correlation between variables and to maximize the correlation with the PCA axes. Our variables were correlated (Pearson's *r*) as follow with the PC1 (67.0 % of explained variance) and PC2 (17.2 %): BIO5 (PC1: r = -0.64; PC2: r = -0.12), BIO6 (PC1: -0.93; PC2: 0.34), BIO13 (PC1: -0.52; PC2: -0.85), and BIO14 (PC1: -0.94; PC2: -0.04).

Landscape variables

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

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

Patch-scale attributes

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

Data analysis

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

Multiple-site dissimilarities

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

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

Species diversity

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

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

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

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

Variation partitioning

We ran a variation partitioning procedure including all response variables to quantify the respective explanatory power of the three groups of explanatory variables (patch, n = 5 variables; landscape, n = 4; and macroclimatic, n = 8) according to Legendre & Legendre (2012) and Valdés *et al.* (2015). We constructed GLMMs (α–diversity) or LMMs (β–diversity) including combinations of one, two, or three variable groups plus the random effects, and determined the proportion of variation explained by the fixed variables (marginal R^2; R^2_m) according to Nakagawa & Schielzeth (2013). We quantified the proportion of this variation explained by the unique and shared contribution of patch, landscape, and macroclimatic variables, and expressed this relative to the total amount of variation explained by the fixed factors in the global model (containing all three groups of explanatory variables).

RESULTS

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

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

 # Figure 2 here #

Species richness (*α*-diversity)

Species richness varied along the latitudinal gradient for all guilds, with a trend toward more species at intermediate than at extreme latitudes along our European gradient (Fig. 3). In most regions, open-habitat species richness was (or tended to be) higher in open field than in bocage windows (Fig. 3d). We found no significant difference in mean species richness of the three other guilds between open field and bocage windows, irrespective of the region considered (except in northern France: less eurytopic species in bocage than open field window; Fig. 3c).

 # Figure 3 here #

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

 # Figure 4 here #

Local carabid species richness was chiefly affected by temperature condition, across all guilds (Table 1a). As the maximum temperature during the warmest month (MaTWm) increased, α-diversity of forest-generalist and open-habitat species increased whilst the one of eurytopic species decreased. Alpha-diversity of all guilds decreased with increased minimum temperature during the coldest month (MiTCm), except for open-habitat species, for which α-diversity peaked in regions with intermediate values along the studied gradient of MiTCm and steeply decreased towards mildest temperatures (Table 1a). Extremes in rainfall conditions only affected eurytopic and open-habitat species richness (Table 1a). Alpha-diversity of eurytopic species decreased with increasing amount of precipitation during the wettest (PWm) and driest (PDm) months. Alpha-diversity of open-habitat species was the lowest in regions with intermediate amount of precipitations during the driest month and increased towards both extremes of the latitudinal gradient.

 # Table 1 here #

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

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

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

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

 # Figure 5 here #

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

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

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

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

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

DISCUSSION

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

Macroclimate: a prominent ecological filter

We found support for our first research hypothesis: macroclimatic conditions act as the main ecological filter on carabid beetle diversity patterns, as implied by the high relative importance values of macroclimatic factors in explaining local α- and β-diversity patterns. More precisely, extremes of temperature (cf. MaTWm, MiTCm) and, to a lesser degree, extremes of precipitation (cf. PWm, PDm), emerge as crucial drivers of carabid diversity. This is consistent with earlier studies, showing that the strong effect of latitude on carabid species richness is mediated by climate, and then more by temperature than precipitation (e.g., Schuldt & Assmann, 2009; Ernst & Buddle, 2015). In addition, and congruently, regional species pools of all species guilds tend to show a hump-shaped relationship with lower regional species richness at both extremes of the latitudinal gradient (Appendix S3), while a high species turnover is observed among regions along this gradient (Fig. 2). Furthermore, distinct carabid species respond differently to macroclimatic factors, depending on habitat preference.

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

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

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

The legacy of the biogeographical history of Europe (particularly glaciations of the Pleistocene and the subsequent post-glacial recolonization of northern regions) may confound the pure effect of current climatic conditions in explaining the macroecological diversity patterns we observed. This is particularly true for dispersal-limited organisms such as carabid beetles (Calatayud *et al.*, 2016, 2019), and may explain the lower species richness recorded in the northern regions.

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

Our results reveal that the composition of the landscape matrix into which forest patches are embedded significantly explains the α- and β-diversity of non-forest carabid species (cf. eurytopic and open-habitat guilds). In particular, focal patches surrounded by forest and grassland have a negative effect on species richness for these species. Consistently, the number of open-habitat species was higher in open field landscapes compared to bocage landscapes. This may be explained by the diversity of crops cultivated in the surrounding fields (e.g., cereals, sugar beet, potato, rapeseed), each associated with a particular pool of species (Holland *et al.*, 2005; Marrec *et al.*, 2015), whilst grasslands may harbor less specific carabid assemblages and benefit from spillover from adjacent habitats, including forests (Schneider *et al.*, 2016; Duflot *et al.*, 2018). Moreover, arable lands may allow beetles to move more easily on the ground than grasslands, particularly because of differences in vegetation density (Thomas *et al.*, 2006). Our results are consistent with previous studies, which showed that landscape attributes affect biodiversity in important ways (see Fletcher *et al.*, 2016 for a review). Open-habitat and eurytopic species use forest habitats as alternative, temporary habitat, but are less competitive there than in more open habitats (e.g., Niemelä *et al.*, 1993). In particular, they enter forest edges to find a shelter, to search for food or to seek overwintering sites (Knapp *et al.*, 2019). The decreased magnitude of difference between the landscape-level species pool and the composition of local assemblages with increasing crop or/and grassland cover in the landscape suggests that these habitats allow a large suite of non-forest species to enter forest patches. However, the high turnover observed among patches of a given landscape window suggests that they are not present at the same time in most patches.

With the exception of β-diversity of forest-generalist species, which increases with hedgerow density and forest cover in the surrounding landscape, landscape factors do not affect the α- and β-diversity patterns of forest-specialist and generalist carabid species. This result indicates that hedgerows are not always positive for species movement (e.g., Baudry & Burel, 2019). Alternatively, hedgerows in the studied landscapes may be too recent or scarce to serve as high-quality corridors (Closset-Kopp *et al.*, 2016; Lenoir *et al.*, 2020) for forest carabid species, that are well known for their very low dispersal capacities (Rainio & Niemelä, 2003). However, hedgerows can allow some forest species to disperse between forest patches as previously suggested (e.g., Baudry & Burel, 2019), increasing the probability that more species will reach forest patches. However, the high nestedness we found for forest-specialist species compared to other guilds suggests that only a few species are actually able to colonize new forest patches. Increased magnitude of difference between the landscape-level species pool and the composition of local assemblages in bocage landscapes could then be linked to random local species replacement due to competition, or neutral processes. In summary, we found little support to our second research hypothesis: landscape management intensity only weakly influences the diversity of forest carabid species, but instead increases the number of non-forest species in small forest patches.

Forest patch characteristics drive forest carabid species diversity

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

The β-diversity of forest generalists was influenced by the same patch-scale factors as α-diversity, but in the opposite direction. This indicates that the few forest-generalist species present in a given landscape window tend to occupy all ancient, heterogeneous forest patches of this window. Interestingly, the β-diversity of forest specialists also decreased as patch age increased, consistent with species accumulation over time. However, local species richness was mostly determined by region and landscape-window type (i.e., random factors in our models). This result suggests that the colonization of forest patches within landscape windows occurs at random in such fragmented systems where metapopulation dynamics for these dispersal-limited species are likely disrupted. The positive effect of local topography (another proxy for intra-patch heterogeneity) on local species richness can be explained by the fact that small-scale variation in topography offers more thermal variability than flat areas (Lenoir *et al.*, 2013), as well as more micro-habitats (e.g. various depth and quality of litter, coarse woody debris, snags, different soil texture; Dwyer & Merriam, 1981). These features have already been shown to affect carabid assemblages (Latty *et al.*, 2006; Tyler, 2008), and other arthropods such as ticks, *Ixodes ricinus* (Ehrmann *et al.*, 2017).

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

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

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

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

CONCLUSION

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

Species assembly was also importantly altered by patch environmental heterogeneity and age, as previously observed in the same forest networks for other arthropods and plants (Valdés *et al.*, 2015; De Smedt *et al.*, 2018). Yet, we did not find any evidence on an influence of forest size. These results highlight the major need of protecting old forest patches embedded in agricultural landscapes, even the small ones. Finally, landscape management intensity weakly influences the diversity of forest carabid species, but increases the number of non-forest species in small forest patches, while decreasing their turnover among patches. These results invalidate our previous assumptions and instead made us consider that observed patterns, at multiple spatial scales, are likely linked to functional traits, more than species habitat preference only. Congruently, Le Provost *et al.* (2020) recently showed that mobility, resource-acquisition, and body-size traits drive local species assembly through environmental filtering acting at the landscape and patch levels, especially in landscapes suffering high short and long-term turnover such as agricultural landscapes. Such evidence has not been provided yet on assemblages living in small forest patches embedded in these agricultural landscapes.

REFERENCES

Almoussawi, A., Lenoir, J., Jamoneau, A., Hattab, T., Wasof, S., Gallet-Moron, E., Garzon-Lopez, C.X., Spicher, F., Kobaissi, A. & Decocq, G. (2020) Forest fragmentation shapes the alpha–gamma relationship in plant diversity. *Journal of Vegetation Science*, **31**, 63–74.

Assmann, T. (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of north-west Germany (Coleoptera, Carabidae). *Biodiversity & Conservation*, **8**, 1499–1517.

Aviron, S., Lalechère, E., Duflot, R., Parisey, N. & Poggi, S. (2018) Connectivity of cropped vs. semi-natural habitats mediates biodiversity: a case study of carabid beetles communities. *Agriculture, Ecosystems & Environment*, **268**, 34–43.

Bale, J.S. (1996) Insect cold hardiness: a matter of life and death. *European Journal of Entomology*, **93**, 369–382.

Bale, J.S. & Hayward, S.A.L. (2010) Insect overwintering in a changing climate. *Journal of Experimental Biology*, **213**, 980–994.

Barkley, E.P., Malcolm, J.R., Smith, S.M. & Bellocq, M.I. (2016) Does variable stand structure associated with multi-cohort forests support diversity of ground beetle (Coleoptera, Carabidae) communities in the central Nearctic boreal forest? *Journal of Forestry Research*, **27**, 1191–1202.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Baselga, A. (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, **21**, 1223–1232.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J. & Leprieur, F. (2018) betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.5.1. https://CRAN.R-project.org/package=betapart.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1–48.

Baudry, J. & Burel, F. (2019) *Multi-Scale Control of Carabid Assemblages in Hedgerow Network Landscapes*. *The Ecology of Hedgerows and Field Margins* (ed. by J.W. Dover), CRC Press.

Bräunicke, M. & Trautner, J. (2009) Lebensraumpräferenzen der Laufkäfer Deutschlands–Wissensbasierter Katalog. *Angewandte Carabidologie Supplement*, **1**, 45.

Brunet, J. (2007) Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology*, **44**, 563–572.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, **4**, 133–142.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Sroka, K. & Finch, O.-D. (2006) Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). *Journal of Insect Conservation*, **10**, 335.

Taylor, L.R. (1963) Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology*, **32**, 99–117.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571–573.

Thiele, H.-U. (1977) *Carabid Beetles in Their Environments. A Study on Habitat Selection by Adaptations in Physiology and Behaviour*, Springer-Verlag, Berlin.

Thomas, C.F.G., Brown, N.J. & Kendall, D.A. (2006) Carabid movement and vegetation density: Implications for interpreting pitfall trap data from split-field trials. *Agriculture, Ecosystems & Environment*, **113**, 51–61.

Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7–19.

Tougeron, K., Brodeur, J., Le Lann, C. & van Baaren, J. (2019) How climate change affects the seasonal ecology of insect parasitoids. *Ecological Entomology*.

Tyler, G. (2008) Differences in abundance, species richness, and body size of ground beetles (Coleoptera: Carabidae) between beech (Fagus sylvatica L.) forests on Podzol and Cambisol. *Forest Ecology and Management*, **256**, 2154–2159.

Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrerie, O., Cousins, S.A., Deconchat, M., De Smedt, P. & Diekmann, M. (2020) High ecosystem service delivery potential of small woodlands in agricultural landscapes. *Journal of Applied Ecology*, **57**, 4–16.

Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrerie, O., Closset-Kopp, D., Cousins, S.A., Deconchat, M. & De Frenne, P. (2015) The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across E urope. *Global Ecology and Biogeography*, **24**, 1094–1105.

Vanneste, T., Valdés, A., Verheyen, K., Perring, M.P., Bernhardt-Römermann, M., Andrieu, E., Brunet, J., Cousins, S.A., Deconchat, M. & De Smedt, P. (2019) Functional trait variation of forest understorey plant communities across Europe. *Basic and Applied Ecology*, **34**, 1–14.

Wintle, B.A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A., Gordon, A., Lentini, P.E. & Cadenhead, N.C. (2019) Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the National Academy of Sciences*, **116**, 909–914.

DATA AVAILABILITY STATEMENT

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

Table 1. Results of the mixed model backward stepwise selection of fixed explanatory variables: macroclimatic, landscape, and patch-scale attributes (see 'Data analysis'). Models were computed for **(a)** *α*-diversity and **(b)** *β*-diversity of the four habitat-preference species groups independently: forest-specialist, forest-generalist, eurytopic, and open-habitat species. The values inside the table represent marginal R^2 (R^2_m), conditional R^2 (R^2_c), and parameter estimates (± standard error of the regression) for the best model. For landscape attributes, we also indicated the selected spatial scale. The significance of each explanatory variable was obtained from a χ^2 test, and is indicated as: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ·, $p < 0.10$. All variables were standardized prior to analysis. Spaces with a dash indicate that the variable was not included in 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)***
Patch	**Age (recent vs. old)**		-		**-0.11 (± 0.05)***		-		-
	Area		-		-		-		-
	Cve		**0.12 (± 0.04)****		-		**-0.10 (± 0.02)*****		**-0.19 (± 0.05)*****
	β-div. generalist plants		-		**-0.68 (± 0.27)***		-		**0.19 (± 0.06)****
	β-div. forest spec. plants		-		**0.95 (± 0.38)***		-		**-0.14 (± 0.04)****
(b) β-diversity									
			R^2_m = 0.284		R^2_m = 0.153		R^2_m = 0.285		R^2_m = 0.096
			R^2_c = 0.653		R^2_c = 0.359		R^2_c = 0.286		R^2_c = 0.232
Macroclimate	**MaTWm**		-		**-0.08 (± 0.02)***		**0.02 (± 0.01)***		-
	MaTWm^2		-		-		-		-
	MiTCm		**0.38 (± 0.12)***		**0.09 (± 0.04)***		-		-
	MiTCm^2		-		-		-		-
	PWm		-		-		**0.03 (± 0.01)****		-
	PWm^2		-		-		**-0.03 (± 0.01)***		-
	PDm		-0.18 (± 0.09)·		-		**0.04 (± 0.01)****		-
	PDm^2		**0.18 (± 0.06)****		-		**0.02 (± 0.01)***		-
Landscape	**Hedgerow length**	500 m	-	50 m	**0.02 (± 0.01)****		-		-
	Crops (%)		-		-	250 m	**-0.04 (± 0.01)*****	500 m	**-0.02 (± 0.01)***
	Grassland (%)		-		-	1,000 m	**-0.04 (± 0.01)****		-
	Forest (%)		-	500 m	**0.03 (± 0.01)***		-	50 m	**-0.02 (± 0.01)***
Patch	**Age (recent vs. old)**		**0.07 (± 0.02)****		**0.03 (± 0.01)***		-		-
	Area		-		-		-		-
	CVe		**-0.06 (± 0.01)*****		-		**0.03 (± 0.01)*****		**0.03 (± 0.01)*****
	β-div. generalist plants		-		**0.03 (± 0.01)****		-		**-0.03 (± 0.01)****
	β-div. forest spec. plants		-		**-0.03 (± 0.01)*****		-		**0.03 (± 0.01)****

MaTWm (BIO5): maximum temperature of the warmest month; MiTCm (BIO6): minimum temperature of the coldest month; PWm (BIO13): precipitation of the wettest month; PDm (BIO14): precipitation of the driest month; Cve: coefficient of variation in elevation.

Figure captions

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

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

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

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

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

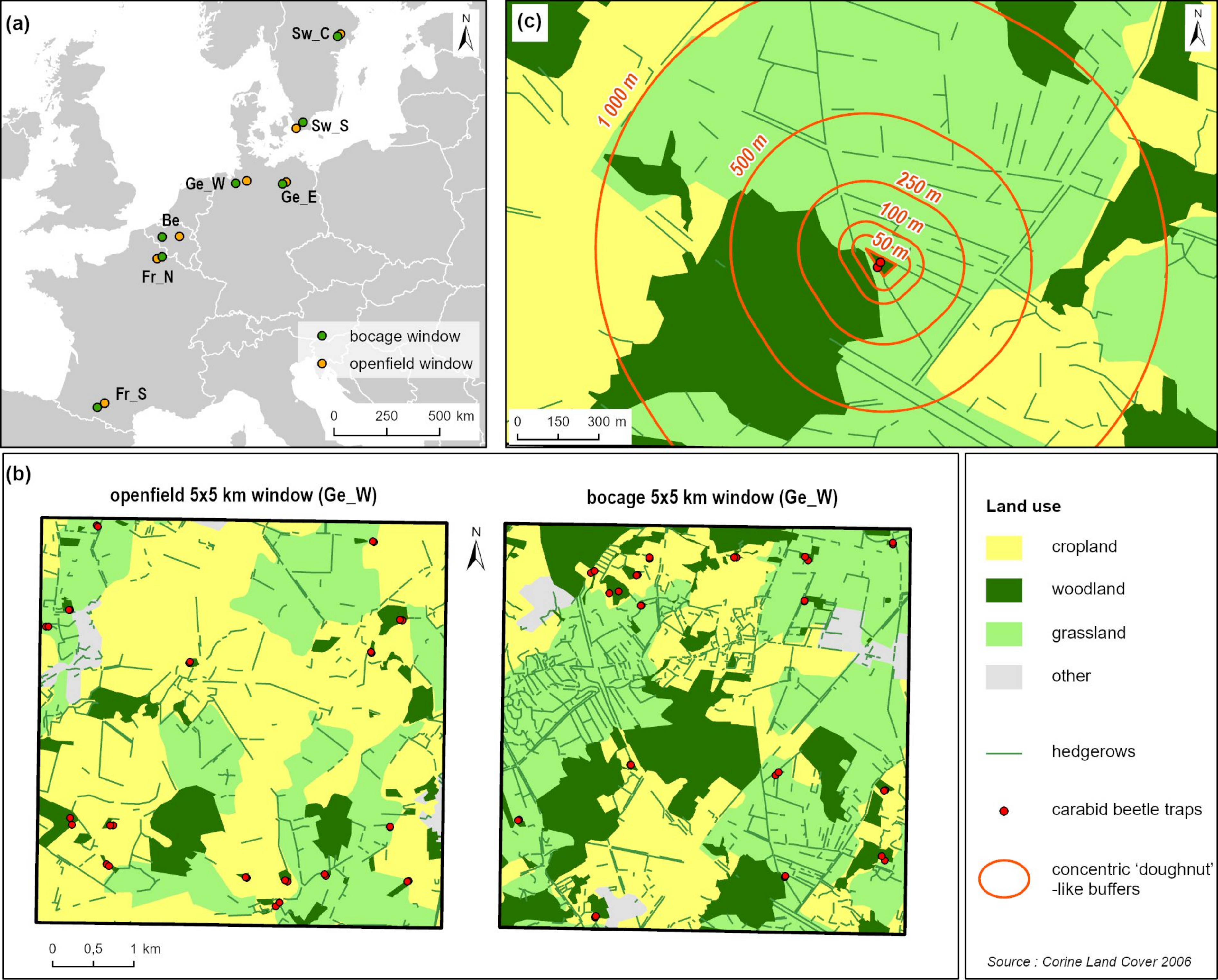
SUPPORTING INFORMATION

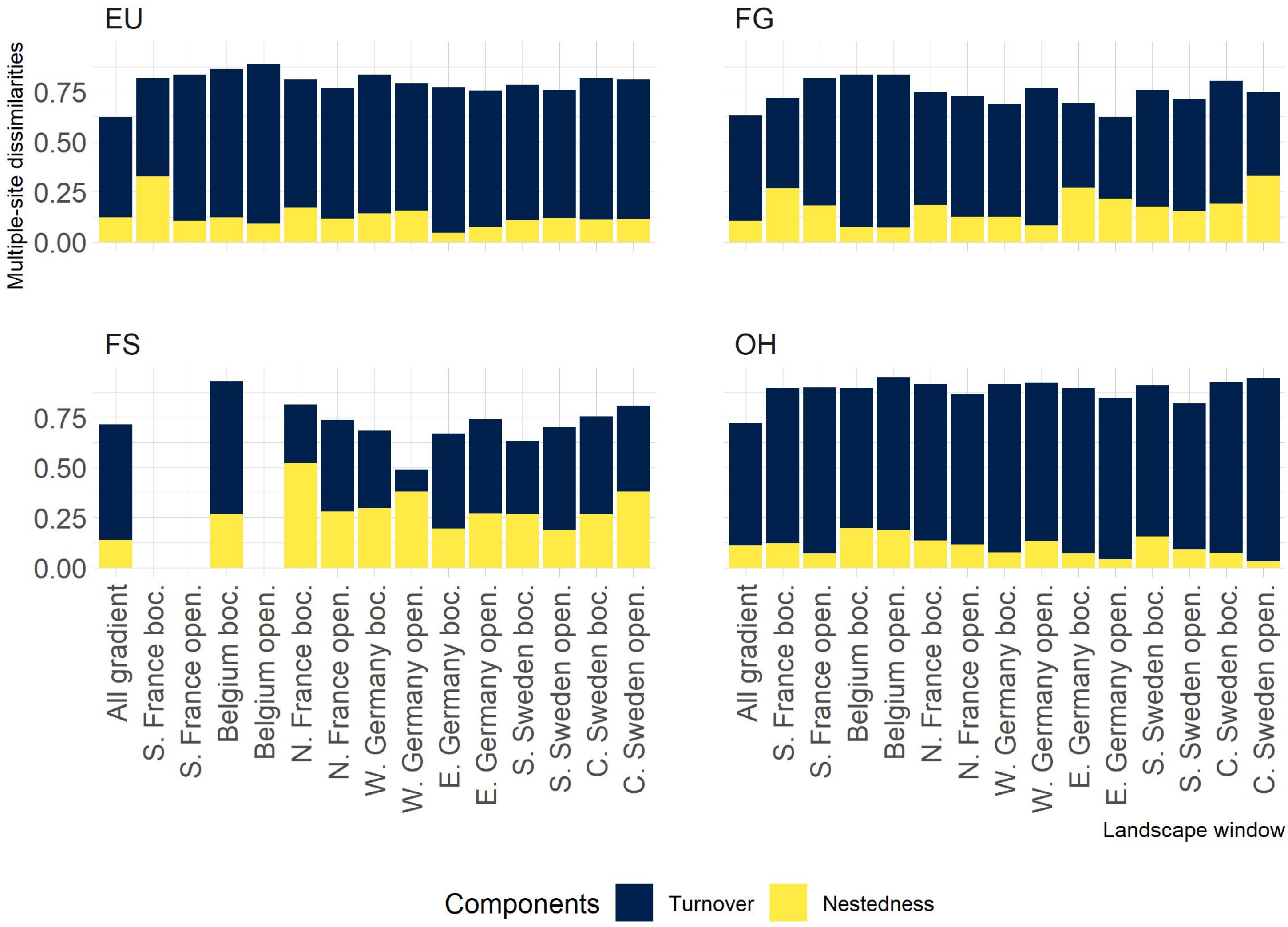
Additional supporting information may be found in the online version of this article at the publisher’s website.

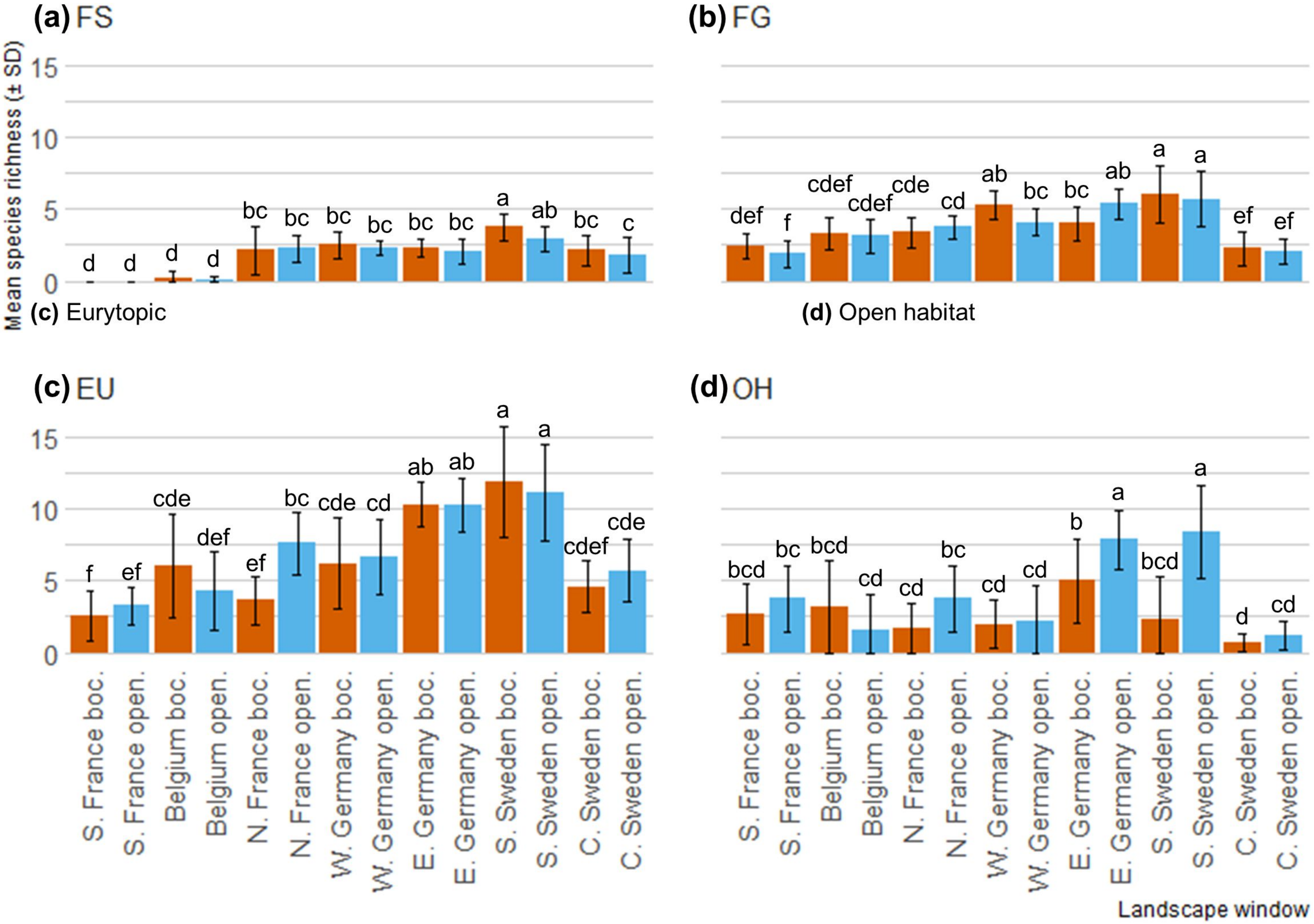
Appendix S1 Correlation table between all patch, landscape, and macroclimatic-level variables.

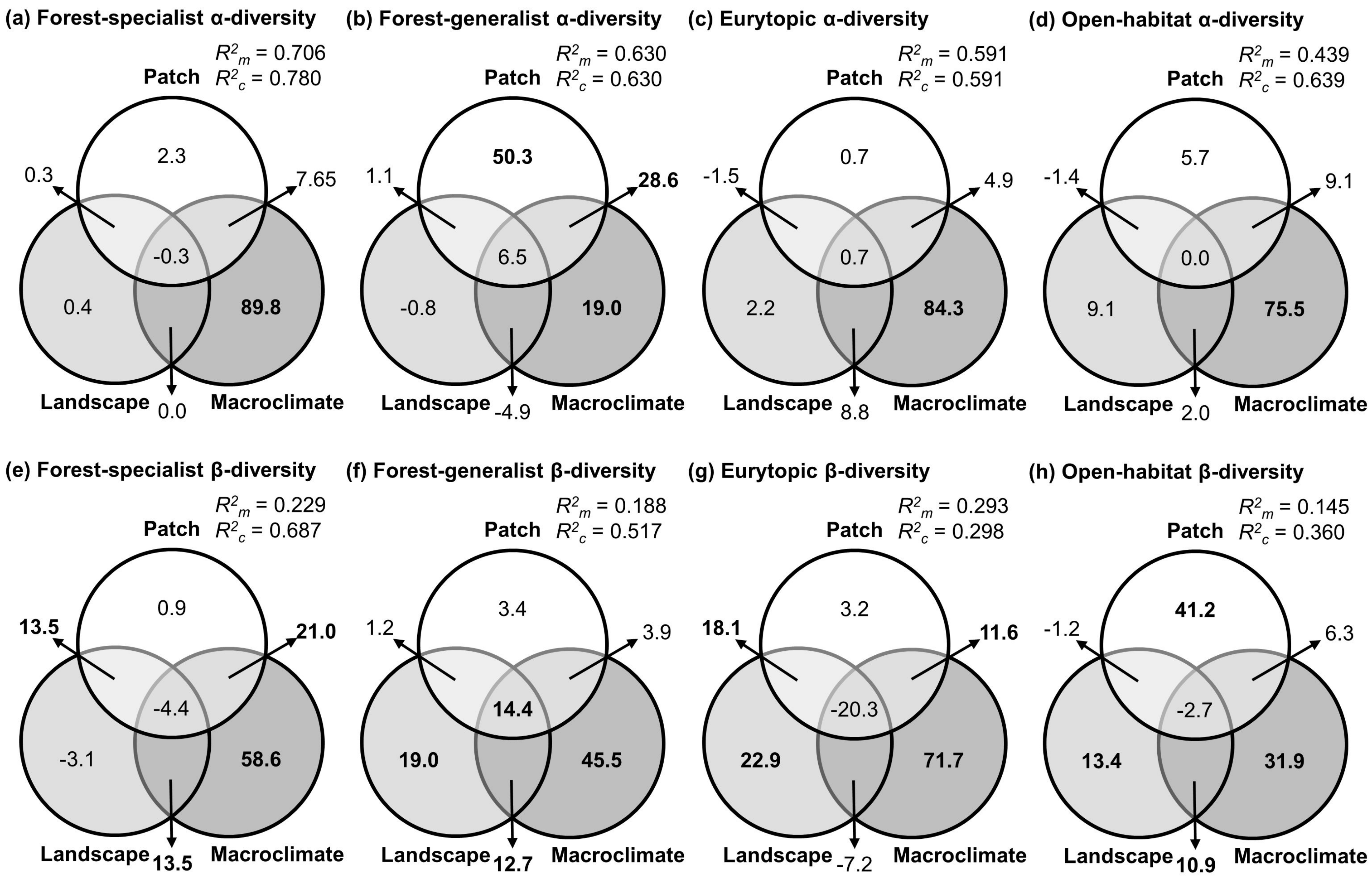
Appendix S2 Complete list of species that were found in the sampled forest patches, along with their habitat preference.

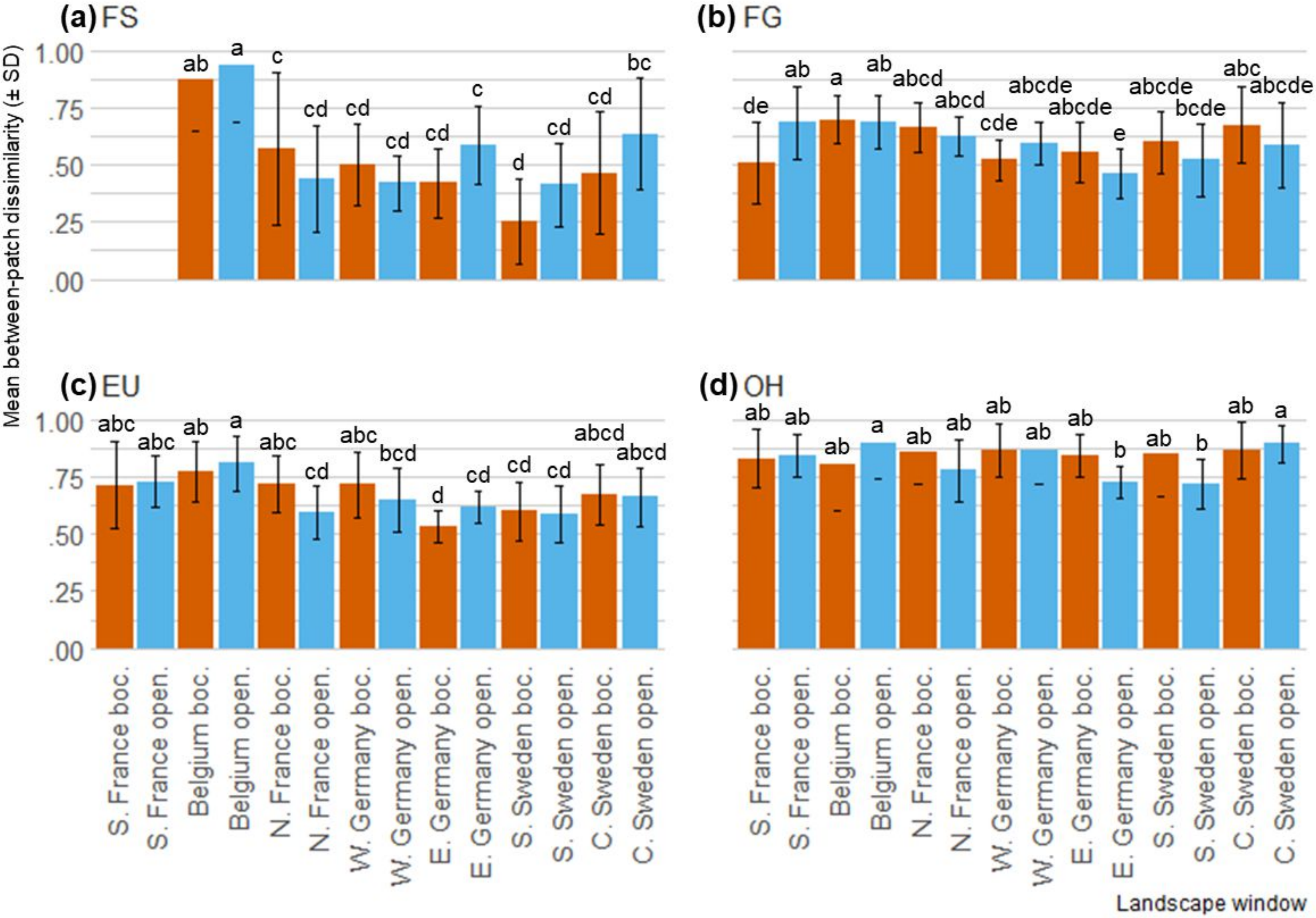
Appendix S3 Gamma-diversity of all species together and per habitat-preference guild.


(a)
N
Sw_C
Sw_S
Ge_W
Ge_E
Be
Fr_N
Fr_S
bocage window
openfield window
0 250 500 km
(c)
N
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
0.00
0.25
0.50
0.75
All gradient
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.
Landscape window
Components
Turnover
Nestedness


(a) FS
(b) FG
(c) Eurytopic
(d) Open habitat
(c) EU
(d) OH
Mean species richness (± SD)
0
5
10
15
d d d d bc bc bc bc bc bc a ab bc c
def f cdef cdef cde cd ab bc bc ab a a ef ef
f ef cde def ef bc cde cd ab ab a a cdef cde
bcd bc bcd cd cd bc cd cd b a bcd a d cd
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.
Landscape window


(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)
1.00
.75
.50
.25
.00
ab
a
c
cd
cd
cd
cd
c
d
cd
cd
bc
de
ab
a
ab
abcd
abcd
cde
abcde
abcde
e
abcde
bcde
abc
abcde
abc
abc
ab
a
abc
cd
abc
bcd
d
cd
cd
cd
abcd
abcd
ab
ab
ab
a
ab
ab
ab
ab
ab
b
ab
b
ab
a
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.
Landscape window