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The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe

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ABSTRACT

Aim Macroclimate is a major determinant of large-scale diversity patterns. However, the influence of smaller-scale factors on local diversity across large spatial extents is not well documented. Here, we quantify the relative importance of local (patch-scale), landscape-scale and macroclimatic drivers of herbaceous species diversity in small forest patches in agricultural landscapes across Europe.

Location Deciduous forest patches in eight regions along a macroclimatic gradient from southern France to central Sweden and Estonia.

Methods The diversity of forest specialists and generalists at three levels (whole forest patch, sampling plots within patches and between scales) was related to patch-scale (forest area, age, abiotic and biotic heterogeneity), landscape-scale (amount of forest, grasslands and hedgerows around the patch, patch isolation) and macroclimatic variables (temperature and precipitation) using generalized linear mixed models and variation partitioning for each group of variables.

Results The total amount of explained variation in diversity ranged from 8% for plot-scale diversity of generalists to 54% for patch-scale diversity of forest specialists. Patch-scale variables always explained more than 60% of the explained variation in diversity, mainly due to the positive effect of within-patch heterogeneity on patch-scale and between-scale diversities and to the positive effect of patch age on plot-scale diversity of forest specialists. Landscape-scale variables mainly contributed to the amount of explained variation in plot-scale diversity, being more important for forest specialists (21%) than for generalists (18%). Macroclimatic variables contributed a maximum of 11% to the plot-scale diversity of generalists.

Main conclusions Macroclimate poorly predicts local diversity across Europe, and herbaceous diversity is mainly explained by habitat features, less so by landscape structure. We show the importance of conserving old forest patches as refugia for typical forest species, and of enhancing the landscape context around the patches by reducing the degree of disturbance caused by agriculture.

Keywords

Agricultural landscapes, biodiversity, forest, habitat fragmentation, habitat history, local conditions, macroclimate, macroclimatic gradient, smallFOREST, vegetation.

INTRODUCTION

It is widely accepted that large-scale biodiversity gradients are strongly related to macroclimate (Francis & Currie, 2003; Hawkins *et al.*, 2003; Kreft & Jetz, 2007). The latitudinal diversity gradient (the decline in species richness with latitude) is a relatively general spatial pattern with few exceptions (Willig *et al.*, 2003; Kindlmann *et al.*, 2007). However, the spatial scale of biodiversity assessments matters, since the processes driving diversity patterns may change with grain size and the extent of the analyses (Siefert *et al.*, 2012). Macroclimate (i.e. large-scale climate extending 200 km or more, governed by large-scale atmospheric circulation systems, *sensu* Geiger *et al.*, 2009) has been acknowledged as a dominant determinant of regional species richness (gamma diversity) at large grain sizes and large (continental or global) extents (Hawkins *et al.*, 2003). Nevertheless, the importance of small-scale biotic and abiotic drivers for species richness in local habitats (alpha diversity) increases at small grain sizes and local extents (Field *et al.*, 2009), and can even override the influence of climate (Siefert *et al.*, 2012). Landscape attributes may make a considerable contribution to explaining variations in broad-scale diversity gradients, although less so than climate (Xu *et al.*, 2014). However, the influence of local and landscape factors on alpha and gamma diversity is not well documented at broad (e.g. continental) extents since ecological data sampled at small grain sizes are not well studied over such spatial extents. Hence, the influence of small-scale factors on large-extent studies may have been underestimated so far, as these studies are generally coarse-grained.

Habitat fragmentation may alter large-scale biodiversity patterns and increase the importance of local factors for biodiversity (Jamoneau *et al.*, 2012). Alpha diversity in fragmented forests has been demonstrated to depend on local habitat characteristics, like habitat area, heterogeneity and history, and on landscape structure (Jacquemyn *et al.*, 2001; Jamoneau *et al.*, 2011), although these relationships have neither been tested over large extents nor compared with the influence of global-scale drivers like climate. In Europe, the original forest cover is strongly reduced and fragmented due to human activities such as the conversion of forests into agricultural land (Foley, 2005). Most present-day forests appear as small patches embedded in landscapes dominated by an agricultural matrix with varying intensities of disturbance (Honnay *et al.*, 2005). These patches are refugia for typical forest plant species and provide ecosystem services to humans (e.g. food production, pollination, pest control, carbon storage, water retention; Foley, 2005). Assessing biodiversity and its drivers in these small refugia across Europe is crucial if we are to understand the ecological value of cultural landscapes.

The diversity of species that are either strictly associated with forest habitats (i.e. 'forest specialists') or that have their optimum in non-forest habitats but may survive in forests (further referred to as 'generalists') can respond differently to variations of the same drivers across a regional extent (Jamoneau *et al.*, 2011). Yet, it is still unknown whether this pattern still applies over larger extents. Forest specialists are strongly dispersal-limited and slow colonizers (Honnay *et al.*,

2005), depending on a long-term continuous forest cover, and only infrequently occur in recent, post-agricultural forests (De Frenne *et al.*, 2011). A higher diversity of forest specialists is expected in more connected patches, due to facilitation of propagule flows, sometimes promoted by habitat corridors (e.g. hedgerows or streams; Roy & de Blois, 2008; Araujo Calçada *et al.*, 2013). On the contrary, the diversity of faster-colonizing generalists depends more on landscape composition and management, being higher in patches located in heterogeneous landscapes with scattered small crop fields and dominated by grasslands (Jamoneau *et al.*, 2011).

Here, we present a comprehensive dataset of local records sampled along a wide macroclimatic gradient in the temperate forest biome of western Europe. The study of natural environmental gradients provides invaluable insights into community and ecosystem responses (De Frenne *et al.*, 2013). The gradient of our study is unique because it covers a broad (continental) extent with a very fine grain size (individual vegetation plots within forest patches), contrasting with former studies on latitudinal gradients (Willig *et al.*, 2003) which generally have a coarser grain. This allows us to simultaneously compare the relative strengths of spatial associations between broad-scale diversity patterns and potential environmental (macroclimatic, landscape-scale, patch-scale) drivers acting at different spatial grains. We focus on herbaceous species, which constitute the greater part of temperate forest biodiversity and maintain ecosystem functioning (Gilliam, 2007). Previous studies on the herbaceous layer along similar geographic extents have focused on the species richness–productivity relationship (Oberle *et al.*, 2009; Axmanová *et al.*, 2012). Using a correlation-based approach, our study aims to compare the relative importance of patch-scale, landscape-scale and macroclimatic drivers in determining local herbaceous species diversity of forest patches. More specifically, we addressed the following hypotheses.

1. Patch-scale drivers do matter as potential determinants of herbaceous diversity (from plot- to patch-scale diversity) in small forest patches along this macroclimatic gradient.
2. The main drivers of diversity are scale dependent: for example, the strength of the relationships between macroclimatic drivers and diversity is higher at the patch-scale than at the plot-scale.
3. Forest specialists and generalists respond differently to the drivers, for example patch age and connectivity are more important for forest specialists, while generalists are more susceptible to landscape composition and management.

METHODS

Study area

We compiled occurrences of plant species in deciduous forest patches in eight regions along a macroclimatic gradient spanning c. 2500 km across the temperate forest biome of western Europe (Fig. 1) and covering a large range of macroclimatic conditions and several forest types (Appendix S1 in Supporting Information). In each region, two 5 km × 5 km landscape

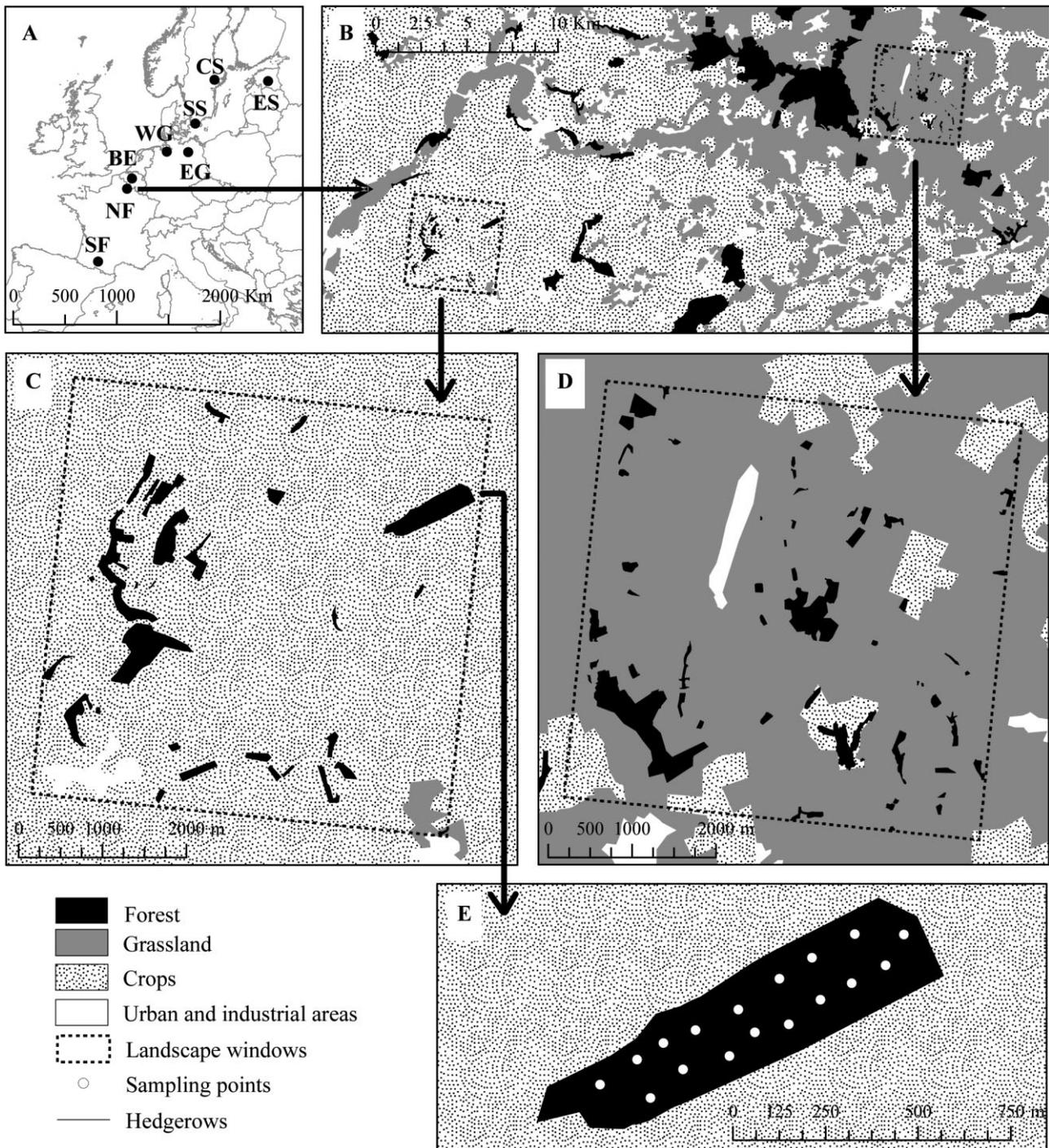


Figure 1 Sampling design. (a) Location of the eight study regions along a macroclimatic gradient in Europe (SF, southern France; NF, northern France; BE, Belgium; WG, western Germany; EG, eastern Germany; SS, southern Sweden; CS, central Sweden; ES, Estonia). (b) Detail of the area including the two windows in northern France, showing the most important land uses. Details of the ‘high-disturbance’ (c) and ‘low-disturbance’ (d) landscape windows with forest patches, land uses and hedgerows. (e) Detail of a forest patch in one of the landscape windows, showing the distribution of the sampling plots (white dots) used for the vegetation surveys. Note that for the sake of clarity the road network is not depicted on any of the maps.

windows (16 in total) with two contrasting agricultural disturbance intensities were selected.

1. A ‘high-disturbance landscape’: isolated forest patches surrounded by an intensively cultivated matrix, dominated by large

open fields with intensive use of pesticides and high energy input through fertilizers.

2. A ‘low-disturbance landscape’: forest patches more or less connected by different types of hedgerows and surrounded by a

less disturbed matrix with fewer and smaller crop fields. This landscape was expected to be more permeable to the movement of species between patches. Although typical hedgerow landscapes are absent in the northern part of the gradient, we have considered other types of linear forest elements, for example deciduous forest borders between crop fields and coniferous forest (hereafter referred to as hedgerows).

Our aim was to sample all forest patches dominated by temperate deciduous forest stands in the area of each landscape window. Thus, purely coniferous plantations and recently afforested lands were not sampled. Whenever deciduous forest patches were embedded in a large coniferous plantation, the coniferous part was not surveyed, and deciduous stands were considered as single patches. Deciduous forest patches containing scattered individuals or small stands of coniferous trees were included unless the proportion of coniferous trees exceeded 40% of the patch area. We sampled between 19 and 67 patches per window (mean = 44). The total number of patches sampled was 708.

Vegetation surveys

All forest patches were surveyed for all vascular plant species at the peak of phenology of the vegetation (May–July, depending on region), including all herbaceous species, shrubs and trees (Appendix S2). Herbaceous species were subsequently split into two non-overlapping groups: we classified as ‘forest specialists’ those species belonging to forest phytosociological classes according to Oberdorfer *et al.* (1990), modified to include some species restricted to forests in our study area, and as ‘generalists’ those having their optimum either in forest-associated habitats (e.g. edges, clear-cuts) or in non-forest habitats (e.g. grasslands, crop fields). To comprehensively survey vegetation, we walked along parallel transects located 10 m apart from each other and recorded all vascular plant species. We thus obtained, for each herbaceous plant group as well as for woody plants, a value of species richness per patch (hereafter, ‘patch-scale diversity’). Secondly, we walked along parallel transects located 50 m apart from each other and established sampling plots every 100 m along a given transect line (Fig. 1e). The number of sampling plots per patch ranged from 1 (for patches smaller than 0.5 ha) to 128 (mean \pm SE = 5 ± 0.41). We recorded all herbaceous species within a sampling plot of radius 10 m. This survey provided us with values of species richness for both forest specialists and generalists at each plot within each patch.

Calculation of explanatory variables

Three groups of explanatory variables (patch-scale, landscape-scale and macroclimatic variables) were calculated for each patch. To avoid overweighting of one group over the others during model selection simply because one group contained more explanatory variables, we selected the four most meaningful and representative variables per group (details in Appendix S3).

Patch-scale variables

We used patch area (AREA) and age (AGE) as potential local (patch-scale) drivers because smaller forest patches might host fewer species (Jacquemyn *et al.*, 2001), according to the species–area relationship (Rosenzweig, 1995) and since forest age is key for understorey communities: more forest specialists are found in ancient forests (having existed continuously since *c.* 1750 in Europe; Hermy & Verheyen, 2007) than in recent forests (established on previously cultivated soils; De Frenne *et al.*, 2011).

Abiotic conditions (microclimatic, edaphic) within a patch may vary depending on topography. Complex terrains offer more thermal variability than flat areas (Lenoir *et al.*, 2013), and present different degrees of litter decomposition and differences in soil texture, leading to heterogeneity in soil development (Dwyer & Merriam, 1981). Canopy heterogeneity could also affect herbaceous diversity through stand structure and diversity (influenced by forest management; Barbier *et al.*, 2008) by modifying local environmental conditions. Indeed, trees modify the local abiotic conditions below the canopy with strong implications for herbaceous plants (Nieto-Lugilde *et al.*, 2015). To address these effects, we chose topographic heterogeneity (coefficient of variation of altitude) and the total number of tree species within each patch as proxies for abiotic (ABIO_H) and biotic (BIO_H) heterogeneity. These variables are meant to capture local environmental heterogeneity in the availability of light, microclimatic conditions and soil properties.

Landscape-scale variables

Agricultural intensification generally reduces landscape heterogeneity. Forest patches in heterogeneous landscapes may host more generalist herbaceous species than patches within homogeneous, highly disturbed landscapes dominated by large crop fields (Jamoneau *et al.*, 2011). We also expect a higher diversity of forest specialists in more connected patches where propagule density is higher. Therefore, we computed 20 candidate variables representing patch isolation and the landscape around each patch. In order to keep the same number of variables as in the previous group, and to facilitate between-group comparisons, we retained four of the candidate landscape-scale variables for further analyses (see details in Appendix S3): proportion of forest (F500) and grasslands (G500) in a 500-m buffer ring around each patch, proportion of hedgerows in a 50-m buffer ring around each patch (H50) and proximity index (PROX, increasing with patch isolation).

Macroclimatic variables

Because diversity has been largely related to macroclimate (Francis & Currie, 2003), we extracted ten candidate bioclimatic variables (see Appendix S1) from the WorldClim global database (1-km resolution, <http://www.worldclim.org/>) and averaged each variable for each patch using all 1-km² pixels intersecting it. As for landscape-scale variables, we retained four of the candidate macroclimatic variables for further analyses (see details in

Appendix S3): maximum temperature of the warmest month (MaTWm), minimum temperature of the coldest month (MiTCm), precipitation of the wettest month (PWm) and precipitation of the driest month (PDm).

Data analysis

Species diversity

Diversity values were calculated separately for forest specialists and generalists. For each patch, we calculated patch-scale diversity as the total number of species recorded in the entire patch; plot-scale diversity as the average number of species recorded in all sampling plots per patch and between-scale diversity as $1 - (\text{plot-scale diversity}/\text{patch-scale diversity})$. This formula is derived from that proposed by Ricotta (2008) to calculate beta diversity independently from species richness, with plot-scale and patch-scale diversity representing alpha and gamma diversity, respectively. The spatial grains used here are finer than those used in most studies [but see Kraft *et al.* (2011) for another non-standard use of the terms alpha, gamma and beta diversity], but appropriate for capturing responses to local environmental conditions. However, to avoid misinterpretations, we use the terms patch-scale diversity, plot-scale diversity and between-scale diversity throughout the text.

Model selection and averaging

The effects of patch-scale, landscape-scale and macroclimatic variables on patch-scale, plot-scale and between-scale diversity were examined using generalized linear mixed models (GLMMs) with maximum-likelihood estimation. Poisson-lognormal models (including an individual-level random effect to avoid overdispersion; see Elston *et al.*, 2001) were used for patch-scale diversity. Gaussian error distributions with an identity link were used for plot-scale diversity and between-scale diversity, as these are continuous variables (plot-scale diversity is an average of counts per plot). All explanatory variables were standardized prior to analyses by subtracting the mean and dividing by the standard deviation. 'Region' and 'window type' (nested within region) were used as random effects in all models to account for the nested structure of the sampling design (Fig. 1) and for regional variation in species diversity values not due to macroclimatic, landscape-scale or patch-scale factors, but to random effects such as observer bias (Milberg *et al.*, 2008) and measurement errors. A set of candidate models was constructed for each of the six studied response variables, which are a combination of diversity levels (patch-scale, plot-scale and between-scale diversity) and species groups (forest specialists and generalists). We used 12 explanatory variables (see Methods): four patch-scale (AREA, AGE, ABIO_H and BIO_H); four landscape-scale (F500, G500, H50 and PROX); and four macroclimatic (MaTWm, MiTCm, PWm and PDm) variables. There was no important collinearity between them (see Appendix S4 for a correlation matrix and Appendix S3 for discussion on the correlation between MiTCm and PDm). For each of the

six response variables, we built candidate model sets with all combinations of terms from simple models to a global model including all 12 explanatory variables, and ranked the models using the corrected version of the second-order Akaike information criterion (AICc). To account for model uncertainty, we performed model averaging of parameter estimates across all models with $\Delta\text{AICc} < 2$ (Appendix S5).

Variation partitioning

We followed a variation partitioning procedure to determine the proportion of variation in the global model for each response variable which was explained by pure and shared effects of patch-scale, landscape-scale and macroclimatic variables. We constructed a series of GLMMs (see Appendix S6 for an alternative analysis using generalized linear models) including combinations of one, two or three variable groups plus the random effects. The proportion of variation explained by the fixed factors (i.e. the three variable groups) was represented by the R^2 of the global model, calculated based on likelihood ratio test statistics comparing the log-likelihood of this model with the log-likelihood of a null model including only the intercept plus the random factors (Magee, 1990). We determined the proportion of this variation explained by fixed factors that was respectively explained by each variable group, following Legendre & Legendre (1998).

Statistical analyses were carried out in R 3.0.1 (R Core Team, 2013) using the packages lme4 (Bates *et al.*, 2013), lmerTest (Kuznetsova *et al.*, 2013) and MuMIn (Bartoń, 2013).

RESULTS

A total of 163 forest specialist species and 620 generalist species were found in the 708 sampled forest patches of the 16 landscape windows. Descriptive statistics for all variables used in the analyses are shown in Appendix S7.

For patch-scale diversity (Table 1), the proportion of variance explained by fixed factors (R^2 fixed) of the best candidate model was 54% and 29% for forest specialists and generalists, respectively. Patch-scale diversity of specialists was positively correlated with forest area, age and abiotic and biotic heterogeneity. It responded positively to an increasing proportion of forest around the patch and negatively to an increasing proportion of hedgerows. We found a similar pattern of response to patch-scale variables for generalists, but in this case none of the landscape-scale variables showed a significant effect. In both cases, biotic heterogeneity had the greatest effect on patch-scale diversity, and none of the macroclimatic variables were significant.

For plot-scale diversity (Table 1), the proportion of variance explained by fixed factors (R^2 fixed) of the best candidate model was 12% and 8% for specialists and generalists, respectively. Plot-scale diversity of specialists increased with age, biotic heterogeneity and with increasing proportions of forest and grassland around the patch. Age was the variable showing the greatest effect on plot-scale diversity of specialists. Conversely, plot-scale diversity of generalists decreased with age and biotic

| | | Diversity | | |
|-----------------|--------|--|--|--|
| | | Patch-scale | Plot-scale | Between-scale |
| Specialists | | logLik = -2107 R^2 fixed = 0.54 R^2 all = 0.97 | logLik = -1576 R^2 fixed = 0.12 R^2 all = 0.46 | logLik = 185 R^2 fixed = 0.21 R^2 all = 0.40 |
| Patch-scale | AREA | 0.031 (\pm 0.013)* | -0.120 (\pm 0.097) | 0.018 (\pm 0.008)* |
| | AGE | 0.165 (\pm 0.016)*** | 0.516 (\pm 0.100)*** | 0.018 (\pm 0.008)* |
| | ABIO_H | 0.118 (\pm 0.027)*** | 0.125 (\pm 0.156) | 0.033 (\pm 0.012)** |
| | BIO_H | 0.285 (\pm 0.017)*** | 0.424 (\pm 0.102)*** | 0.068 (\pm 0.009)*** |
| Landscape-scale | F500 | 0.090 (\pm 0.025)*** | 0.401 (\pm 0.145)** | |
| | G500 | | 0.323 (\pm 0.154)* | -0.031 (\pm 0.012)** |
| | H50 | -0.061 (\pm 0.020)** | -0.121 (\pm 0.097) | |
| | PROX | 0.022 (\pm 0.015) | 0.046 (\pm 0.086) | 0.013 (\pm 0.007). |
| Macroclimatic | MaTWm | -0.171 (\pm 0.107) | -0.639 (\pm 0.571) | -0.016 (\pm 0.024) |
| | MiTCm | 0.165 (\pm 0.123) | -0.929 (\pm 0.721) | 0.076 (\pm 0.023)** |
| | PWm | 0.127 (\pm 0.076) | 0.345 (\pm 0.350) | 0.007 (\pm 0.019) |
| | PDm | 0.203 (\pm 0.113) | 0.900 (\pm 0.663) | |
| Generalists | | logLik = -2761 R^2 fixed = 0.29 R^2 all = 1.00 | logLik = -2038 R^2 fixed = 0.08 R^2 all = 0.35 | logLik = 291 R^2 fixed = 0.31 R^2 all = 0.37 |
| Patch-scale | AREA | 0.076 (\pm 0.018)*** | 0.081 (\pm 0.190) | 0.009 (\pm 0.007) |
| | AGE | 0.055 (\pm 0.019)** | -0.748 (\pm 0.194)*** | 0.043 (\pm 0.007)*** |
| | ABIO_H | 0.118 (\pm 0.029)*** | 0.263 (\pm 0.298) | 0.025 (\pm 0.010)* |
| | BIO_H | 0.199 (\pm 0.020)*** | -0.769 (\pm 0.192)*** | 0.082 (\pm 0.007)*** |
| Landscape-scale | F500 | | -0.268 (\pm 0.279) | 0.010 (\pm 0.009) |
| | G500 | 0.035 (\pm 0.030) | 0.792 (\pm 0.297)** | -0.017 (\pm 0.010) |
| | H50 | -0.033 (\pm 0.023) | -0.515 (\pm 0.233)* | 0.006 (\pm 0.008) |
| | PROX | 0.019 (\pm 0.016) | 0.044 (\pm 0.169) | 0.005 (\pm 0.006) |
| Macroclimatic | MaTWm | 0.040 (\pm 0.059) | 0.878 (\pm 0.707) | -0.009 (\pm 0.014) |
| | MiTCm | 0.111 (\pm 0.099) | -1.449 (\pm 0.779) | 0.043 (\pm 0.015)** |
| | PWm | -0.089 (\pm 0.052) | -0.894 (\pm 0.588) | 0.008 (\pm 0.012) |
| | PDm | -0.137 (\pm 0.100) | -1.575 (\pm 0.762)* | 0.012 (\pm 0.024) |

AREA, patch area; AGE, patch age; ABIO_H, abiotic heterogeneity; BIO_H, biotic heterogeneity; F500, proportion of forest in the 500-m buffer ring; G500, proportion of grasslands in the 500-m buffer ring; H50, proportion of hedgerows in the 50-m buffer ring; PROX, proximity index; MaTWm, maximum temperature of the warmest month; MiTCm, minimum temperature of the coldest month; PWm, precipitation of the wettest month; PDm, precipitation of the driest month.

Values in the table are β coefficients \pm their standard errors, resulting from model averaging across all models with $\Delta AICc < 2$. Values are left blank where a variable was not included in the model. Satterthwaite's approximation was used to calculate P -values: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; $P < 0.1$. $n = 708$ forest patches. See Appendix S5 for a ranking of each individual candidate model with $\Delta AICc < 2$.

heterogeneity. It was higher in patches surrounded by high proportions of grasslands, and low proportions of hedgerows, and decreased with precipitation of the driest month (thus increasing with latitude and longitude; see Appendix S1). In this case, precipitation had the greatest effect on plot-scale diversity of generalists.

Finally, for between-scale diversity (Table 1), the proportion of variance explained by fixed factors (R^2 fixed) of the best candidate model was 21% and 31% for specialists and generalists, respectively. Between-scale diversity of specialists increased with area, age, biotic and abiotic heterogeneity, decreased in patches surrounded by high proportions of grassland, and

Table 1 Results of model selection and model averaging for the best candidate models relating diversity at each of the three scales considered to patch-scale, landscape-scale and macroclimatic variables. Region and window type (nested within region) were used as random factors, and an individual-level random effect was included.

Log-likelihood (logLik) and values of R^2 representing the total variation explained by fixed effects (R^2 fixed, likelihood-ratio based R^2 of the global model calculated using a null model including the intercept plus random factors; Magee, 1990) and by fixed plus random effects (R^2 all, likelihood-ratio based R^2 of the global model calculated using a null model including only the intercept; Magee, 1990) are shown for the best model resulting from model selection.

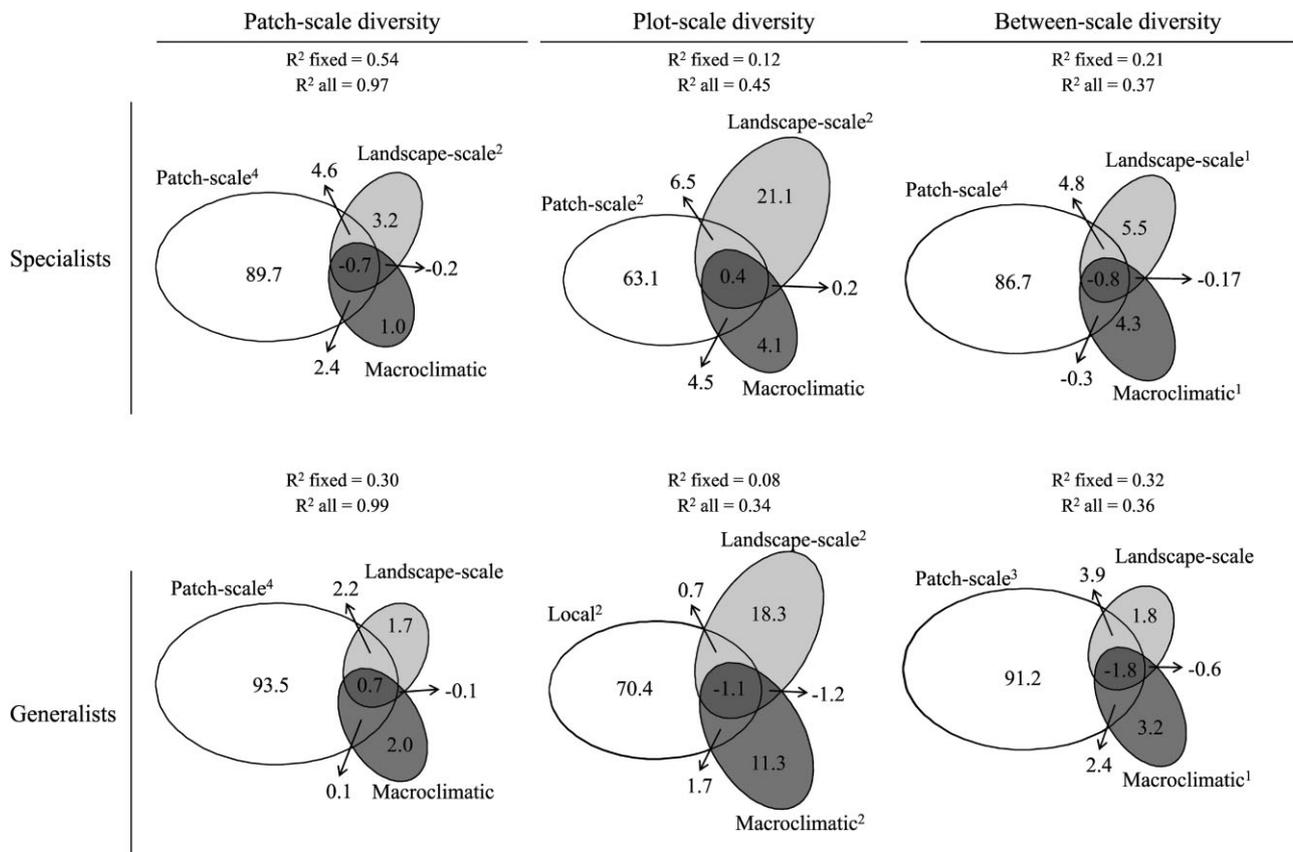


Figure 2 Results of the variation partitioning for each combination of diversity levels and herbaceous species groups. Values shown inside the ellipses are the percentages of the total variation explained by fixed factors (R^2 fixed of the global model including all the variables). Pure as well as shared contributions by patch-scale, landscape-scale and macroclimatic variables are depicted by the ellipses, with the ellipse area proportional to the percentage of variation explained. Values of R^2 for fixed effects (R^2 fixed) and for fixed plus random effects (R^2 all) of the global models are shown (see explanation in the caption to Table 1). Numerical exponents indicate the number of significant variables for each group in the averaged GLMM (Table 1).

increased with minimum temperature of the coldest month (thus decreasing with latitude and longitude; see Appendix S1). Temperature was the variable that had the greatest effect on between-scale diversity of specialists. Between-scale diversity of generalists increased with age, biotic and abiotic heterogeneity and with minimum temperature of the coldest month, but none of the landscape-scale variables was significant. In this case, biotic heterogeneity had the greatest effect on between-scale diversity of generalists.

The pure effect of patch-scale variables contributed the most to explaining variation in all three levels of diversity (Fig. 2). The pure effect of landscape-scale variables contributed to low percentages of variation in diversity, except for plot-scale diversity, where landscape-scale variables contributed to a significant percentage of variation (21% for specialists and 19% for generalists), although this was still lower than that of patch-scale variables. The pure effect of macroclimatic variables contributed in general to low percentages of variation (always lower than the pure contribution of patch-scale variables). The percentages of variation shared by combinations of variables were generally low.

DISCUSSION

This study quantified the relative importance of patch-scale, landscape-scale and macroclimatic drivers of herbaceous biodiversity in small forest patches along a wide macroclimatic gradient. Patch-scale drivers explained the highest proportion of variation, followed by landscape-scale drivers, whilst macroclimatic drivers contributed little to the variation in patch-scale herbaceous diversity measures along the studied gradient. We observed a scale dependence in the drivers of biodiversity, as it responded to different drivers acting at different scales. Finally, forest specialists and generalists responded to different drivers, with landscape-scale effects being more important for specialists.

Local patch characteristics are crucial for determining herbaceous species diversity in small forests

Contrary to previous broad-extent studies which have highlighted the dominant role of macroclimate in determining biodiversity (Francis & Currie, 2003; Hawkins *et al.*, 2003; Kreft & Jetz, 2007), our results suggest that herbaceous diversity in forest

patches is mainly driven by local patch characteristics. Patch-scale variables alone always contributed more than 60% of the total amount of explained variation in diversity. Macroclimatic variables contributed little to the explanation of variation in diversity (although more in the models with no random factors; see Appendix S6), and they never contributed the highest percentage of variation. Therefore, macroclimatic variables are poor predictors of local herbaceous diversity in forest patches embedded in agricultural landscapes across Europe. The contrast between this finding and most of the previous broad-extent studies might be the result of differences in grain size (Siefert *et al.*, 2012). Here, the grain size is forest patch area, which is on average 0.04 km²; this is very small compared with the extent of the study area (i.e. c. 2500 km) and with the spatial resolution of the widely used WorldClim bioclimatic variables. Weak correlations between biodiversity and macroclimate have also been reported for other small-grained studies (< 10 km²; Field *et al.*, 2009), but most of these were conducted over small spatial extents. In contrast, studies conducted over large extents (> 1000 km; Field *et al.*, 2009) showed strong correlations of biodiversity with macroclimate, but they usually considered larger grain sizes. Thus, the prevalence of patch-scale over macroclimatic drivers in determining local biodiversity across our gradient could be explained by the combination of small grain size and large spatial extent, allowing for a sound testing of the effect of local-scale variables compared with coarser-grained studies. Furthermore, some of the studies that claim macroclimate is dominant in determining biodiversity patterns consider biodiversity in general, for all habitats (e.g. Kreft & Jetz, 2007), while we focused on a very specific habitat. Fragmented habitats are potentially strongly influenced by local and landscape characteristics (e.g. Collinge *et al.*, 2003), and the influence of large-scale factors seems to play a secondary role.

The poor contribution of macroclimate to explaining local herbaceous diversity is corroborated by the fact that the regional herbaceous species pool size (i.e. the cumulated species richness per window) is not strongly related to latitude (Appendix S8). This can be due to an impoverishment and homogenization of the current herbaceous species pools across regions due to human-related disturbances (agriculture, management) leading to spatial and temporal isolation of patches (Jamoneau *et al.*, 2012). Trees might depend more strongly on macroclimate than understorey plants, as shown by the stronger decrease in size of the regional tree species pool with latitude and longitude in our data (Appendix S8), while they then modify the within-forest microclimate (i.e. the climate of an individual site, with characteristic horizontal dimensions between 10⁻³ and 10² m, *sensu* Geiger *et al.*, 2009) and lessen the effect of macroclimate on understorey plant diversity, as has already been pointed out by Oberle *et al.* (2009).

Scale dependence in the drivers of herbaceous diversity

We found a scale dependence (Siefert *et al.*, 2012) in the drivers of herbaceous diversity in forest patches, as patch-scale,

plot-scale and between-scale diversity respond differently to patch-scale, landscape-scale and macroclimatic drivers. Patch-scale drivers contributed the most to the variation in the three diversity scales, although landscape-scale drivers contributed to a considerable part of the variation in plot-scale diversity. Our set of drivers explains a relatively low percentage of variation in plot-scale diversity (12% for forest specialists and 8% for generalists). As plot-scale diversity is an averaged value for all the plots within a patch, it could happen that herbaceous diversity at this very fine scale (a circle of radius 10 m) is mostly determined by plot-scale drivers not considered in this study, such as light availability (Axmanová *et al.*, 2012), stand age (Brunet *et al.*, 2011), distance from the forest edge (Chabrierie *et al.*, 2013), soil conditions (Pepller-Lisbach & Kleyer, 2009), limited dispersal (De Frenne *et al.*, 2011) and by random factors.

As expected, our results suggest that the relative importance of patch-scale drivers is very high for between-scale diversity (accounting for 88% and 92% of the explained variation for specialists and generalists, respectively). This is particularly due to higher heterogeneity in the patch promoting not only species diversity per se (Barbier *et al.*, 2008; Hofer *et al.*, 2008) but also species dissimilarity within the patch (e.g. if there are many rare species, patch-scale diversity will be higher than plot-scale diversity, leading to high between-scale diversity).

Contrary to our hypothesis, landscape-scale drivers do not seem very important for patch-scale diversity. However, they contributed significantly to explaining variation in plot-scale diversity, meaning that not only the measured patch characteristics but also the characteristics of the environment around the patch are important for explaining local diversity. This emphasizes the importance of including the landscape context, not just the characteristics of the habitat patch, in studies of fragmented landscapes (Mazerolle & Villard, 1999).

Differences between forest specialists and generalists in the response to drivers

For both species groups, patch-scale and between-scale diversity within the patches were higher in patches with higher biotic and abiotic heterogeneity. This reflects how understorey vegetation is influenced by the increased environmental complexity and higher niche diversity generated by many tree species and heterogeneous topographies (Pausas & Austin, 2001; Hofer *et al.*, 2008). The influence of the overstorey can be due to either changes in microclimatic conditions or in resource availability (light, soil water and nutrients), as well as in the physical and chemical properties of the litter layer (Barbier *et al.*, 2008). The positive influence of overstorey diversity was maintained for plot-scale diversity of forest specialists, but turned negative for generalists. Diversified overstoreys may result in multi-layered, denser canopies, and the plot-scale diversity of generalist herbaceous species, generally light-demanding, is therefore higher in recent forests (with less diversified overstoreys) due to incomplete canopy closure (Chabrierie *et al.*, 2013). We acknowledge that the strong effect of biotic heterogeneity could be partly due to overstorey and understorey diversities responding similarly

to the same environmental factors that are not fully accounted for here, for example light and soil characteristics. However, overstorey and understorey diversities can also show very different responses to other factors (e.g. forest management practices directly influence tree diversity, but only indirectly affect understorey diversity; Decocq, 2000).

Higher diversities of forest specialists at both patch and plot scales were found in older patches, as these species are dispersal limited and thus less capable of colonizing recently established patches (Honnay *et al.*, 2005). The effect of patch age was weaker or even negative (at the plot scale) for generalists. Thus, older patches had higher plot-scale diversity of specialists and less of generalists. Generalists are usually shade-intolerant species, and thus have a disadvantage after canopy closure in older patches. Habitat age seems to be more important than current habitat area for explaining species diversity of low-dispersal taxa like forest specialists. Thus, our study proves the existence of a species–time relationship (Rosenzweig, 1995) for forest specialists, as older patches had more time to accumulate species and thus are less temporally isolated, but provides no clear evidence of the existence of a species–area relationship (Rosenzweig, 1995).

Landscape effects on diversity were more evident for forest specialists. For both patch and plot scales, specialist diversity was favoured by a higher connectivity provided by a greater amount of surrounding forest (Boscolo & Metzger, 2011). However, increasing the number of hedgerows around a patch did not increase patch-scale diversity of specialists (on the contrary, the effect was negative). The potential of linear habitats to support species-rich native plant communities increases with time (Roy & de Blois, 2008), and hedgerows in our windows may be still too young to act as efficient corridors and promote connectivity between forest patches (Jamoneau *et al.*, 2012). Conversely, a greater amount of grasslands in the vicinity of the patch favoured plot-scale diversity of both species groups. Compared with an intensively cultivated matrix, a grassland-dominated matrix is more permeable for the dispersal of specialist species between patches (Jamoneau *et al.*, 2012). Moreover, grasslands harbour in general many more species than crops, and their presence in the neighbourhood can increase generalist diversity into forest patches by allowing the penetration of matrix species into them (Ås, 1999).

Macroclimate contributed to plot-scale diversity of generalists and between-scale diversity of both groups. While between-scale diversity was higher in regions with a higher minimum temperature during the coldest month (i.e. it decreased with latitude and longitude) in accordance with the energy–water hypothesis (Hawkins *et al.*, 2003), plot-scale diversity of generalists was higher in regions with lower precipitation during the driest month (i.e. it increased with latitude and longitude). Although some cases of inverse latitudinal gradients have been reported (Kindlmann *et al.*, 2007), this increase in plot-scale diversity of generalists towards the north-east could be due to some other environmental factor related to the studied gradient, not to macroclimate itself. In particular, patches in central Sweden (the northernmost region in the gradient) had remark-

ably high values of plot-scale diversity of generalists, and also very high values of abiotic heterogeneity (data not shown). We believe that the high diversity at this scale in central Sweden could actually be due to high abiotic heterogeneity within the patches. Central Sweden had also the lowest value of average patch area across the gradient (data not shown), which may have resulted in a relatively larger edge effect, increasing the diversity of generalists.

CONCLUSIONS

Previous studies examining drivers of local understorey diversity have either examined the effect of a small set of predictors along a large geographic extent (Oberle *et al.*, 2009; Axmanová *et al.*, 2012) or the effect of a large set of predictors along a narrower extent (e.g. the south-eastern USA; Peet *et al.*, 2014). However, to our knowledge, no previous study has at the same time analysed such a wide macroclimatic gradient and considered the effect of many drivers nested at multiple scales. Contrary to previous broad-extent studies using larger grain sizes, our fine-grain study concludes that local herbaceous diversity in forest patches across Europe is poorly associated with macroclimatic differences, but mostly associated with local patch characteristics, and to a small extent with characteristics of the surrounding landscape. More large-extent studies with small grain sizes (suitable for testing both global- and local-scale effects) are needed to see if this trend is confirmed for other ecosystems. This study provides important insights for the conservation and management of networks of small habitat patches in agricultural landscapes (Lindborg *et al.*, 2014), particularly highlighting the importance of older forest patches as refugia for forest species. These old patches should be targeted as a conservation priority to preserve native forest floras. We also show the importance of considering the landscape context around these patches (e.g. the degree of connectivity with other patches, the degree of matrix disturbance – patch surrounded by crops versus grasslands). Management measures reducing the isolation of forest patches will enhance their function as refugia for forest flora or even their role as stepping-stones for species migration across the landscape (Collingham & Huntley, 2000). Furthermore, management measures reducing the degree of disturbance in the agricultural matrix may lead to an increase in overall diversity in the forest patches, but not necessarily to an increasing diversity of forest specialists.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Details of the length of the macroclimatic gradient, climatic classification and dominant tree species for the eight studied regions.

Appendix S2 List of all vascular species found in the surveys made in 2013.

Appendix S3 Details of the calculation of explanatory variables and variable reduction procedures.

Appendix S4 Correlation matrix for the 12 retained explanatory variables used in model selection.

Appendix S5 Ranking of candidate models with $\Delta AICc < 2$, used in model averaging.

appendix S6 Results of the variation partitioning analysis based on generalized linear models with no random factors.

Appendix S7 Descriptive statistics for the variables used in the analyses.

Appendix S8 Relationships between the cumulated species richness per window and longitude and latitude.

BIOSKETCH

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