Received: 15 March 2024 | Revised: 14 October 2024 | Accepted: 17 October 2024

DOI: 10.1111/jvs.13318

Journal of Vegetation Science
IAVS

RESEARCH ARTICLE

Patterns of local plant diversity and community saturation in deciduous forests in Europe

Jolina Paulssen[1] | Jörg Brunet[2] | Sara A. O. Cousins[3] | Guillaume Decocq[4] | Pieter De Frenne[5] | Pallieter De Smedt[5] | Per-Ola Hedwall[2] | Jonathan Lenoir[4] | Jaan Liira[6] | Jessica Lindgren[3] | Tobias Naaf[7] | Taavi Paal[6] | Alicia Valdés[8] | Kris Verheyen[5] | Monika Wulf[7] | Martin Diekmann[1]

[1]Vegetation Ecology and Conservation Biology, Institute of Ecology, University of Bremen, Bremen, Germany

[2]Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Lomma, Sweden

[3]Department of Physical Geography, Stockholm University, Stockholm, Sweden

[4]UMR CNRS 7058 Ecologie et Dynamique Des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, Amiens, France

[5]Forest & Nature Lab, Ghent University, Gontrode, Belgium

[6]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

[7]Research Area 2, Leibniz Centre for Agricultural Landscape Research, ZALF, Müncheberg, Germany

[8]Department of Ecology, Environment and Plant Sciences (DEEP), Stockholm University, Stockholm, Sweden

Correspondence
Jolina Paulssen, Vegetation Ecology and Conservation Biology, Institute of Ecology, University of Bremen, James-Watt-Straße 1, Bremen D-28359, Germany.
Email: jolina@uni-bremen.de

Funding information
BIODIVERSA; FWO; Deutsche Forschungsgemeinschaft; Agence Nationale de la Recherche; MINECO; Svenska Forskningsrådet Formas; Eesti Teadusagentuur; Deutsches Zentrum für Luft- und Raumfahrt; Belgian Federal Science Policy Office

Co-ordinating Editor: Kerry Woods

Abstract

Questions: How do local forest conditions and characteristics at the forest patch - scale and landscape - scale affect plot-scale plant diversity in Europe? Do these patterns vary between forest specialists and generalists? Do community saturation patterns differ between forests varying in their surrounding landscape type?

Location: Deciduous forests sampled along a European gradient from southwest to northeast comprising eight regions in five countries (France, Belgium, Germany, Sweden, Estonia).

Methods: We examined the effects of local conditions assessed by means of Ellenberg indicator values (soil moisture, soil nitrogen, soil pH, light availability), patch-scale characteristics (patch-scale plant diversity, forest patch age, forest patch size) and a landscape-scale variable (representing low and high connectivity of forest patches) on plot-scale plant diversity, separately for forest specialist and generalist species. Additionally, we ran regression models to examine community saturation patterns.

Results: We found patterns of niche partitioning among forest specialists and generalists. Low light availability and medium soil moisture favored forest specialists, while generalists were mostly present at higher light availability and medium and high soil moisture. In general, we found the highest plot-scale diversity at medium soil pH. Patch-scale diversity showed a positive impact on plot-scale diversity and plots in the high-connectivity landscape had a higher diversity than plots in the low-connectivity landscape. Further, we observed a high degree of community saturation in both landscape types.

Conclusion: The positive impact of a high connectivity of forest patches on local plant diversity emphasizes the importance of small semi-natural habitats like tree lines, unused field margins and hedgerows to enhance the potential dispersal of forest plants across agricultural landscapes. Community saturation patterns revealed the increasing relevance of local conditions and processes for plot-scale diversity when patch-scale diversity increases.

KEYWORDS
agricultural landscapes, Ellenberg indicator values, forest generalists, forest specialists, habitat fragmentation, landscape connectivity, niche partitioning, plant community saturation

1 | INTRODUCTION

Anthropogenic land-cover change represents a major threat for species diversity (Tscharntke et al., 2005), and large areas of the world are now modified by agriculture, forestry, road construction or urbanization (Kennedy et al., 2019). While traditional low-intensity land uses often harbor high biological values, further agricultural intensification leads to habitat loss and fragmentation (Tscharntke et al., 2005), resulting in a decline of biodiversity (Wilcox & Murphy, 1985; Wilson et al., 2016; Fahrig, 2017).

In the European Union, landscapes with poorly connected forest patches (forest connectivity index <30%) represent 70% of the total area (see Joint Research Centre, 2012 for details). Land-cover changes not only affect the spatial distribution of forest patches, but also the landscape matrix surrounding those patches (Deckers et al., 2005; Poschlod & Braun-Reichert, 2017). This matrix—being a more or less hostile environment to many forest plant species—is usually composed of grasslands and crop fields, but may also include small and linear semi-natural habitats like unused margins, tree rows and hedgerows (Jamoneau et al., 2011; Poschlod & Braun-Reichert, 2017). However, due to agricultural expansion, these matrix elements have been considerably reduced since the 19th century (Deckers et al., 2005; Poschlod & Braun-Reichert, 2017). The enlargement and consolidation of single fields has contributed to extended and homogeneous zones of agricultural land as well as less natural habitats in between (Tscharntke et al., 2005). Therefore, it is essential to evaluate the importance of habitat fragmentation and of the surrounding landscape matrix across broad environmental gradients to examine patterns of community assembly of forest species across large spatial extents.

Generally, the local number of plant species that co-occur in a community (e.g., alpha [α] diversity; Whittaker, 1960) is influenced by local conditions as well as processes operating across larger spatial extents (Ricklefs, 1987; Brunet et al., 2011). Processes like competition, parasitism and herbivory, collectively referred to as biotic interactions, take place within smaller local areas at the community level, whereas long-distance dispersal operates at larger spatial extents (Cornell & Lawton, 1992; He et al., 2005). Many environmental variables have been shown to affect the local plant species richness in forests (Schuster & Diekmann, 2005). For example, light availability was reported to influence herbaceous cover and species richness (Vockenhuber et al., 2011; Márialigeti et al., 2016; Depauw et al., 2020). Among the edaphic variables, herbaceous plant species richness often shows a hump-shaped or positive relationship with soil pH (Mölder et al., 2008; Vockenhuber et al., 2011), and soil nutrient availability and soil moisture are also important determinants of plant diversity (Gazol & Ibáñez, 2010; Szymura et al., 2014; Chudomelová et al., 2017; Raduła et al., 2018; Gilliam, 2019). However, the response of plant species to environmental gradients may differ between species groups with different habitat requirements, for example forest specialist species and generalist species (Valdés et al., 2015; Heinken et al., 2022). Moreover, the fragmentation of forest patches and the conditions of the surrounding matrix strongly affect dispersal processes and thereby also the species richness in forests (Brunet et al., 2011; Uroy et al., 2019). In northern France, hedgerow length in the surrounding landscape had a positive impact on forest herb species richness, emphasizing the relevance of small semi-natural habitats in the matrix (Jamoneau et al., 2011). Forest patch size and forest patch age have also been found to affect the local number of plant species (Kolb & Diekmann, 2004; Valdés et al., 2020). Species diversity across larger spatial extents (e.g., gamma [γ] diversity; Whittaker, 1960) may also be an important driver of local species richness (Ricklefs, 1987; Harrison & Cornell, 2008).

An alpha–gamma relationship (AGR) is an analysis in which α diversity is regressed on γ diversity (a local population obtains species from the species pool at a larger spatial scale) to assess the relative importance of local and large-scale processes for α diversity (Cornell & Lawton, 1992; He et al., 2005; Damschen & Brudvig, 2012). There are two theoretical extremes of AGRs. In type I communities, α diversity increases proportionally with increasing γ diversity ("proportional sampling"), indicating an unsaturated dependency of local species richness on the species pool. In contrast, in type II communities, α diversity does not increase proportionally with increasing γ diversity, but levels off and reaches a plateau (saturated). Beyond this point, α diversity is predominantly determined by local conditions and processes (soil and light conditions, competition, parasitism, etc.) (Cornell & Lawton, 1992; Szava-Kovats et al., 2013).

However, this classic AGR regression has been criticized because of several statistical constraints. First, the extent of the area at which local α diversity is recorded matters, with smaller extents contributing to curvilinear AGR shapes (Loreau, 2000; He et al., 2005). Second, α and γ diversity are not independent as α is nested within γ, which results in a tendency to observe linear relationships, just by chance (Szava-Kovats et al., 2012; Gonçalves-Souza et al., 2013). Even in interactive communities where local processes are dominating, linear AGRs were identified (Hillebrand, 2005; Gonçalves-Souza et al., 2013). To overcome the limitations of the classic AGR regression, Szava-Kovats et al. (2012) proposed a log-ratio transformation, where the natural logarithm (ln) of $[\alpha/(\gamma-\alpha)]$ (hereafter: *ratio*) serves as the dependent variable and is regressed on the natural logarithm (ln) of γ diversity. The slope of the regression serves as a measure of the degree of saturation, meaning that a regression line with a steeper (more) negative slope reflects a higher degree of community saturation. Significantly negative slopes indicate saturated communities (Szava-Kovats et al., 2012). Whereas mainly unsaturated relationships were identified with the traditional AGR regression, saturated and unsaturated patterns were similarly common when applying the log-ratio method (Szava-Kovats et al., 2013). Different environmental conditions may influence these saturation patterns and therefore the relationship between α and γ diversity (Michalet et al., 2015). Focusing on a gradient of forest fragmentation in northern France, Almoussawi et al. (2020) found a higher degree of community saturation in highly fragmented landscapes for forest specialists, likely due to their low dispersal abilities. In contrast, generalist species were observed to be more saturated in landscapes with no fragmentation.

Here, we examined the effects of several environmental variables on the variation in plot-scale (α) diversity in deciduous temperate forests in eight study regions along a gradient from SW to NE Europe. We examined community saturation patterns based on the relationship between plot-scale diversity and patch-scale (γ) diversity in forests differing in their surrounding landscape matrix. To our knowledge there have been few other studies on the AGRs of plant species applying the log-ratio method, while simultaneously considering various environmental variables (see Almoussawi et al., 2020, which was restricted to northern France only), and none that did so at a continental extent.

We distinguished two groups of plant species varying in their forest affinity, forest specialists and generalists, to evaluate potential differences in their responses to environmental drivers. We focused on two main research questions:

1. Are there general patterns in the effects of local conditions (soil variables, light availability), patch-scale characteristics (patch-scale plant diversity, forest patch age, forest patch size) and a landscape-scale variable (landscape type) on plot-scale plant diversity in Europe? Do these patterns vary between forest specialists and generalists?
2. Do community saturation patterns differ between forests that vary in their surrounding landscape type? Do these patterns vary between forest specialist and generalist plant species?

We expected similar relationships between species diversity and environmental variables in all regions, i.e. no systematic change in these relationships along the geographic gradient.

2 | METHODS

2.1 | Study area

The study was carried out along a geographic gradient including eight study regions in five countries (France, Belgium, Germany, Sweden, Estonia, Figure 1a). The mean annual temperature in the regions ranged from 3.7°C (Estonia) to 14.3°C (southern France), while the mean annual precipitation varied between 558 mm (central Sweden) and 793 mm (Belgium) (EuroLST Bioclim data, long-term averages from 1950 to 2000).

In each study region, two landscape windows of 5 km × 5 km were selected, representing contrasting landscape configuration types. One landscape window was characterized by a relatively high density of small semi-natural habitats in the matrix such as hedgerows, shrubs and tree alignments connecting the forest patches, in the following called “bocage” to allow for a short expression (according to Baudry et al., 2000) (Figure 1b). In contrast, the “open” landscape window corresponds to a landscape with more isolated forest fragments with fewer small semi-natural habitats between the patches (Figure 1c). The open landscapes were mainly characterized by arable fields, whereas the bocage landscapes showed a dominance of grasslands. The landscape windows were positioned in areas that are rich in deciduous forests. Also, the selection of the landscape windows was based on a visual graphic inspection (QGIS, 2012) of the landscapes and semi-natural habitats (hedgerows, shrubs, tree alignments) in the vicinity of the institutes/universities in the respective study regions. Specifically, we considered the proportion of forest cover in a 100–500 m buffer around the forest patch and the proportion of hedgerows in a 0–50 m buffer. For example, for western Germany (Figure 1b,c), the proportions of hedgerows in the bocage and open landscape were 0.42% and 0.30%, respectively, and the proportions of forest amounted to 20.2% and 7.3%, respectively. Based on historical maps, each forest patch was assigned to a historical forest age category being either ancient or recent and to a forest size category being either small or large (see Valdés et al., 2020 for details). Forest age describes the forest continuity since afforestation and if forest patches appeared on maps dating back more than 100 years, they were categorized as ancient (see Appendix S1 for details about the historical maps). As the average size of forest patches varied considerably between regions (central Sweden 1.2 ha; southern France 8.2 ha), we decided to base the differentiation of small and large forest patches on median values in the respective landscape windows. The boundary between small and large forests thus varies slightly between regions, but this procedure ensured a balanced number of small and large patches in each region.

2.2 | Vegetation surveys

The vegetation was surveyed in 2012 and 2013 as part of the smallFOREST project (www.biodiversa.eu/2022/10/31/smallforest, Valdés et al., 2015, Valdés et al., 2020) conducted with the help of the FLEUR network (www.fleur.ugent.be). All deciduous forests larger than 1 ha were sampled within a landscape window. The investigated plots had a circular shape with a radius of 10 m, resulting in an area of 314 m^2. The plots were located along transects that were arranged parallel to the longer axis of the forest patch with a distance of 50 m between them. The plots were positioned along the transects at intervals of 100 m. The number of transects and plots thus varied depending on the area and shape of the forest patch. In total, the study comprised 3538 vegetation plots distributed across 699 deciduous forest patches. The number of forest patches within a region ranged from 55 (Estonia) to 123 (Belgium), while the number of plots varied between 174 (southern Sweden) and 929 (eastern Germany) (Table 1).

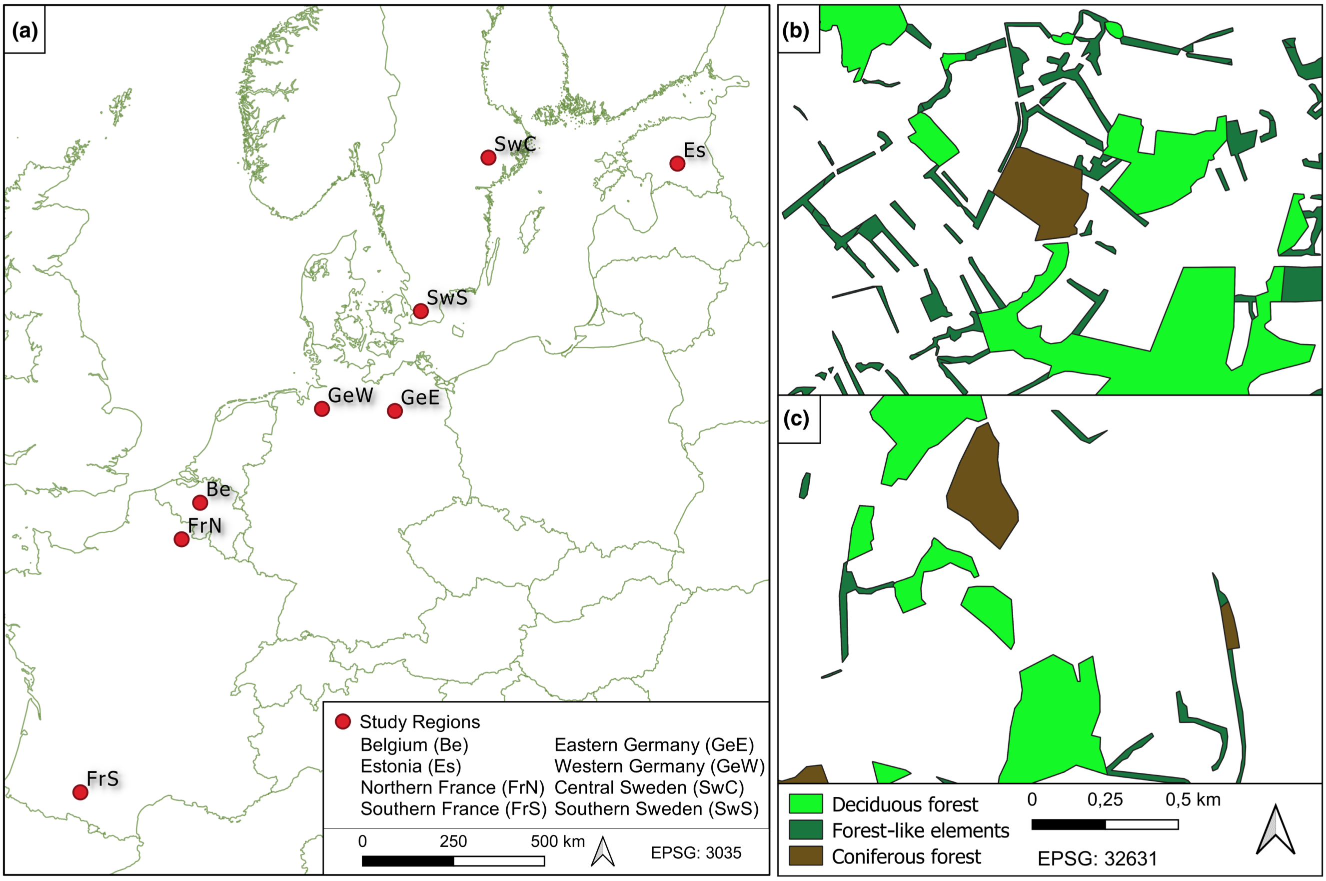

FIGURE 1 Map of the study regions (a, Shapefile retrieved from @EuroGeographics). Exemplary section of a bocage (b) and open landscape (c) in western Germany.

TABLE 1 Overview of the number of studied forest patches and plots per region and of the cumulative number of plant species (total, and separately for forest specialists and generalists).

Study regions	FrS	FrN	Be	GeW	GeE	SwS	SwC	Es
Forests patches	102	91	123	88	64	68	108	55
Plots	239	239	550	884	929	174	264	259
All species	340	239	281	263	257	189	292	204
Forest specialists	49 (14%)	56 (23%)	53 (19%)	67 (25%)	58 (23%)	44 (23%)	31 (11%)	51 (25%)
Generalists	196 (58%)	159 (67%)	163 (58%)	165 (63%)	177 (69%)	127 (67%)	215 (74%)	127 (62%)
No. species/plot	25.3	28.9	14.1	20.0	20.5	21.1	26.0	23.6
No. species/patch	77.1	104.5	85.4	101.4	95.3	101.0	84.9	78.4

Note: For the two subcategories of species, the proportions relative to all species are given in parenthesis. Also, the average numbers (No.) of observed species per plot and per patch are given for each study region. Regions: FrS, southern France; FrN, northern France; Be, Belgium; GeW, western Germany; GeE, eastern Germany; SwS, southern Sweden; SwC, central Sweden; Es, Estonia.

In each plot, all vascular plant species were recorded. The taxonomy follows the database for Euro-Mediterranean vascular plant diversity (Euro+Med Plant Base, n.d., https://www.emplantbase.org/home.html). All herbaceous vascular plant species as well as individuals of potentially woody species (tree and shrub species) less than 1 m in height were considered as part of the herb layer. Woody species reaching the upper canopy were assigned to the tree layer, while trees and shrubs below the dominant canopy (including saplings ≥1 m) were defined as the shrub layer. Taxonomic aggregates were treated as single species (e.g., *Rubus fruticosus* agg.). When moving between plots along a transect in a forest, additional vascular plant species not occurring in any of the plots were noted so that a nearly complete list of vascular plant species was obtained for each forest patch. We defined plot-scale diversity as the number of observed plant species per plot and patch-scale diversity as the number of observed plant species per forest patch.

2.3 | Data analysis

All analyses were performed for the total number of plant species and additionally for two contrasting subcategories of plant species, based on the values of forest affinity defined for the different study regions in the list of European forest species (Heinken et al., 2022): forest plant specialist species, which mainly occur in closed-canopy forests (1.1) and generalist plant species, which grow equally well both inside and outside forests (2.1, 2.2). As local measurements of climatic or edaphic conditions in the plots were not available, local environmental conditions were assessed by means of Ellenberg indicator values (EIVs) for light (m*L*), soil moisture (m*F*), soil nitrogen (m*N*) and soil pH (m*R*) (Ellenberg et al., 1991; Ellenberg & Leuschner, 2010). The mean EIV for each plot was calculated based on the presence/absence of plant species, meaning that species abundance was not weighed. As the number of species is often related to environmental conditions in a hump-shaped manner, quadratic terms were also included in the statistical models when a hump-shaped relation was observed during the graphical data exploration (see, for example, Cornwell & Grubb, 2003; Vockenhuber et al., 2011).

Prior to the modeling, we examined multicollinearity of the explanatory variables (Pearson correlation coefficient with a threshold of 0.65 and conditional boxplots). We excluded m*N* from the models based on collinearity with m*R*. (We additionally performed the analyses with m*N* instead of m*R*, obtaining highly similar results and higher Akaike information criterion (AIC) values; see Appendix S2. We therefore decided to maintain the analysis with m*R* in the main text.) Also, forest patch age and forest patch size both had to be omitted based on collinearity with patch-scale diversity (Appendix S3). The values for patch-scale diversity and local explanatory variables were standardized prior to the analysis by subtracting the mean and dividing by the standard deviation.

Generalized linear mixed-effects models (GLMM) with Poisson distribution (log link function) were run to examine the impact of m*L*, m*F*, m*R* (local scale), patch-scale diversity (patch scale) and landscape type (landscape scale) on plot-scale diversity of all species, and separately of forest specialists and generalists. We also included the interaction between patch-scale diversity and landscape type. A stepwise backward model selection was used based on the AIC. A difference in the AIC larger than 2 was considered relevant to select the best model. For differences in AIC lower than 2, the more simple model (without interaction) was selected. The dispersion of the GLMMs with Poisson distribution was assessed using the package *DHARMa* (Hartig, 2022). Model assumptions were validated by plotting the residuals.

When the plot-scale diversity analyses indicated differences in optimum local conditions between forest specialists and generalists, we performed a GLMM with beta distribution to statistically evaluate this difference in optimum conditions. This was relevant for light availability (m*L*). Therefore, we analyzed the impact of m*L*, group (forest specialist/generalist) and the interaction of m*L* and group on the proportion of specialists and generalists relative to the total number of species. The use of the interaction term enabled us to investigate if the impact of light conditions on plant species differs between forest specialist and generalist species. Raw data values had to be slightly adapted to avoid values of 0 and 1 in the dataset, which are not allowed in a beta model. Stepwise backward model selection was used based on the AIC.

To identify community saturation patterns, we applied the log-ratio method based on Szava-Kovats et al. (2012). We performed GLMMs with a Gaussian distribution to analyze the impact of the environmental variables with the natural logarithm (ln) of patch-scale diversity as main explanatory variable on the response variable *ratio* (ln{plot-scale diversity/[patch-scale diversity − plot-scale diversity]}) for all species, forest specialists and generalists. We used maximum-likelihood estimation for model selection and re-ran the best candidate model using restricted maximum likelihood (REML) for extracting the model parameters (Zuur et al., 2009). We included the interaction term between ln(patch-scale diversity) and landscape type to test for differences in community saturation patterns between forests varying in their surrounding landscape. An interaction is associated with different slope estimates of the two levels investigated per factor variable (bocage/open) in the log-ratio model and implies differences in community saturation. The slopes of the regression lines quantify the degree of saturation, so that a regression line with a steeper (more) negative slope reflects a higher degree of community saturation. Significantly negative slopes are associated with saturated communities (Szava-Kovats et al., 2012, 2013; Gonçalves-Souza et al., 2013; Michalet et al., 2015). Model selection and validation were carried out similarly to the plot-scale diversity model.

To account for the nested study design, three variables were used as random terms: study region, landscape type (nested within study region) and forest patch (nested within landscape type). As we are interested in the effect of landscape type on plot-scale diversity in the study regions, landscape type was incorporated in the model formula as both fixed and random intercept terms simultaneously. We additionally carried out the analysis with only study region and forest patch as random intercept terms (Appendix S4). This analysis produced highly similar patterns of results and the models fitted the data equally well. We therefore decided to maintain the analysis with three random intercept terms (study region, landscape type, forest patch).

The statistical analyses were carried out in R (4.0.4, R Core Team, 2021). The GLMMs were performed with the package *glmmTMB* (Brooks et al., 2017) and R-squared values (R^2) were extracted with the package *performance*(Lüdecke et al., 2021).

3 | RESULTS

3.1 | Drivers of plot-scale diversity

Across all regions, 749 different vascular plant species were recorded. The cumulative number of species per region ranged from 189 (southern Sweden) to 340 (southern France) (Table 1). The number of forest specialists per region varied between 31 (central Sweden) and 67 (western Germany). On average, the share of specialist and generalist species relative to all observed species in a region was 20 ± 5% and 65 ± 6%, respectively. The mean number of species per plot ranged from 14.1 (Belgium) to 28.9 (northern France), while the mean number of species per patch was more constant across regions, varying between 77.1 (southern France) and 104.5 (northern France).

For the plot-scale diversity of all species, forest specialists and generalists, the variance explained by fixed factors of the final model was 27%, 59%, and 37%, respectively (Table 2; detailed statistical results for the GLMMs are given in Appendix S5). Plot-scale diversity increased with increasing patch-scale diversity for all species and for both of the two sub-groups (Figure 2). Plots located in the bocage landscape had a higher plot-scale diversity for all species, forest specialists and generalists, than plots located in the open landscape (Figure 2). Among the local environmental factors, light availability (m*L*), soil moisture (m*F*) and soil pH (m*R*) contributed to the final models in a consistent way, all showing hump-shaped relationships between plot-scale diversity and the environmental variables (Figure 3). The optimum light availability differed between forest specialists and generalists: while a high plot-scale diversity of forest specialists was associated with low light availability, the opposite was true for the generalist species (Figure 3). This pattern is also confirmed by the statistical results of a GLMM that revealed a relevant interaction of m*L* and group (forest specialist/generalist) (Appendix S6). This emphasizes that the relation between the proportion of plant species and light availability differs between forest specialists and generalists (Figure 4). The optima along the soil pH gradient were positioned at intermediate values when considering all species together and the two sub-groups separately. A difference in optimum position between specialists and generalists was observed along the soil moisture gradient with the former showing an optimum at medium values and the latter at medium and high values.

Also, additional visual examinations of the influence of local environmental conditions on plot-scale diversity for the individual study regions showed highly consistent patterns (Appendix S7). Accordingly, the relationships between plot-scale diversity and EIVs for the single study regions largely reflect the overall pattern shown in Figure 3. In a few study regions, however, optimum curves could not be observed due to short environmental gradients.

3.2 | Community saturation

For the *ratio* of all species, forest specialists and generalists, the amount of variance explained by fixed factors of the final model was 53%, 43%, and 55%, respectively (Table 2). The interaction between ln(patch-scale diversity) and landscape did not remain in any of the final models, which resulted in the same slope estimate for both landscape types (Figure 5). This indicates a similar degree of community saturation in the bocage and in the open landscape. All three slope coefficients were significantly negative (−1.17 to −1.33, Table 2). The slope coefficient was higher for forest specialists (−1.17), suggesting a lower degree of saturation for this species group compared to generalists and all species.

TABLE 2 Results (model estimates) of the final GLMMs for plot-scale diversity and the *ratio* (natural logarithm of (plot-scale diversity/[patch-scale diversity − plot-scale diversity])), separately given for all plant species, forest specialist species and generalist species.

	Plot-scale diversity			Ratio		
	Total	**Specialists**	**Generalists**	**Total**	**Specialists**	**Generalists**
Intercept	3.16	1.69	2.73	5.00	2.74	4.36
Patch-scale diversity	0.07	0.14	0.07			
Ln(patch-scale diversity)				−1.33	−1.17	−1.32
Landscape open	−0.14	(−0.18)	−0.12	(−0.18)	−0.27	[−0.17]
m*L*	0.96	2.45	1.64	1.30	2.26	2.18
mL^2	−0.87	−2.91	−1.41	−1.18	−2.70	−1.89
m*F*	0.88	1.06	0.81	1.36	1.02	1.38
mF^2	−0.83	−1.03	−0.75	−1.29	−0.97	−1.29
m*R*	1.26	1.64	1.11	1.54	2.04	0.22
mR^2	−1.13	−1.55	−0.98	−1.39	−1.95	
Fixed R^2	0.27	0.59	0.37	0.53	0.43	0.55
Overall R^2	0.73	0.74	0.68	0.81	0.75	0.81

Note: For the plot-scale diversity models, patch-scale diversity was included as explanatory variable, while for the *ratio* models ln(patch-scale diversity) was included. For the landscape type, the estimates are given with regard to the open-landscape category. Further explanatory variables include light availability (m*L*), soil moisture (m*F*), soil pH (m*R*) and their quadratic terms. Parentheses and square brackets show marginally significant ($p < 0.1$) and non-significant effects, respectively. As model simplification was performed based on the Akaike information criterion (AIC), the final model also included non-significant variables.

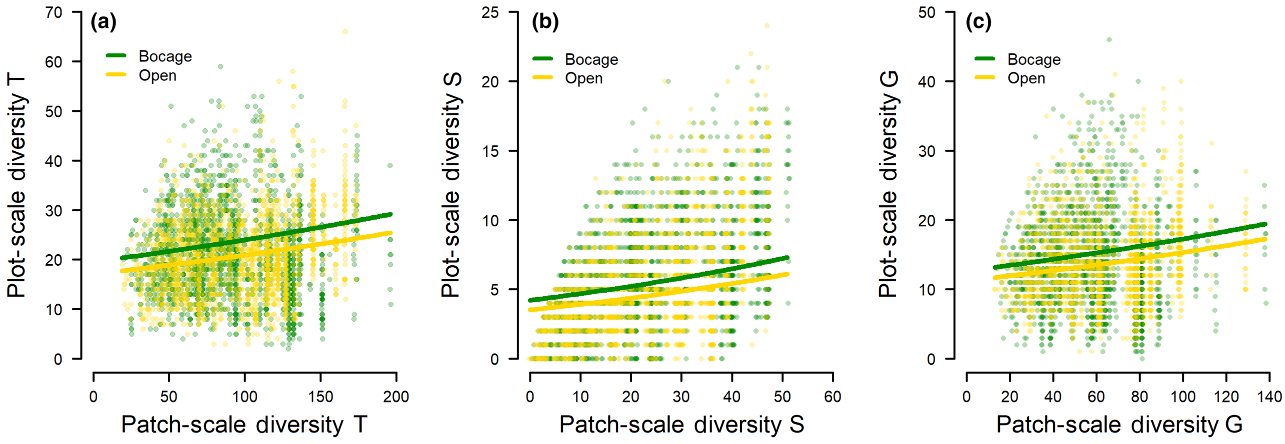

FIGURE 2 Relationship between plot-scale diversity and patch-scale diversity for (a) the total of plant species, (b) forest specialists and (c) generalist species (abbreviated with T, S, G, respectively). Plots located in the bocage landscape are visualized in green and plots in the open landscape in yellow. The data points were jittered and are displayed with increased transparency for visualization. Trendlines are based on model estimates.

4 | DISCUSSION

4.1 | Patch- and landscape-scale drivers of plot-scale diversity

The results revealed a positive impact of patch-scale diversity on plot-scale diversity for all species, forest specialists and generalists. Such a positive relationship emerges, because local populations obtain their species from a species pool at relatively larger scales (He et al., 2005). Whether a species of this pool actually inhabits a local community depends on its dispersal ability and on the ability to thrive under the specific local environmental conditions (Pärtel et al., 2013). The concept of hierarchical filters stresses that species have to pass a "dispersal" filter, a "habitat" filter and a filter of "biotic interactions" in order to be part of a local community (Zobel, 2016). In our study, patch-scale diversity was highly correlated with both patch size and patch age and therefore these were not included as predictors in our models. Positive species–area and species–time–area relationships have frequently been reported (e.g., Rosenzweig, 1995; Kolb & Diekmann, 2004; Valdés et al., 2015; Lenoir et al., 2021), as well as a higher overall diversity of species and of forest specialist species in ancient forest patches compared to recent forests (Flinn & Vellend, 2005; Valdés et al., 2015). For generalist species, different studies have found contrasting patterns, with a higher diversity observed in either ancient or recent forests (Valdés et al., 2015; Vinter et al., 2016).

In general, plots in the bocage landscape had a higher plot-scale diversity (taking into account the varying edaphic and light conditions), both when looking at all species and when distinguishing forest specialists from generalists (Table 2, Figure 2). This indicates that small semi-natural habitats such as hedgerows, tree rows and shrubs in the surrounding landscape matrix enhance the connectivity between forest patches and enable dispersion of forest plants between forest patches (Jamoneau et al., 2011; Lenoir et al., 2021). These corridors increase the dispersal possibilities for plant species by increasing habitat accessibility and create a generally higher permeability of the landscape. As a consequence, this might offer several different opportunities to reach and enter a forest patch and accordingly provides more chances for forest plant species to establish local populations within a forest patch. Our findings coincide with a large-scale analysis of fragmentation and connectivity patterns of natural areas in the United States, which revealed a supportive effect of landscape corridors on species' movements across fragmented habitats with large anthropogenic impact (McGuire et al., 2016). Vanneste et al. (2020) found that linear landscape elements generally form a suitable habitat for many forest species, and this was also shown in a recent review on forest plant species in European hedgerows (Litza et al., 2022). Although generalists appear to have higher dispersal abilities and to be less sensitive to habitat fragmentation than specialists (Verheyen & Hermy, 2001; Brunet et al., 2011), the results of our study show that generalist species can also be negatively affected by habitat fragmentation, when the connectivity between the forest patches is low.

4.2 | Local drivers of plot-scale diversity

The relationship between plot-scale diversity and light availability (m*L*) was hump-shaped. Figures 3 and 4 emphasize different optima for forest specialists and generalists, indicating suitable light conditions for specialists under relatively shady conditions and for generalists at relatively high light values. For forest specialist species, this result coincides with previous studies, which reported an increase in forest specialists with increasing canopy cover or shade-casting ability (Vockenhuber et al., 2011; Govaert et al., 2020). Specialists mainly grow in closed-canopy forests (Heinken et al., 2022), suggesting a higher shade tolerance of the species in this group. However, Márialigeti et al. (2016) found an opposite pattern in temperate forests in Hungary, possibly explained by a very low general light availability that caused even forest specialists to respond

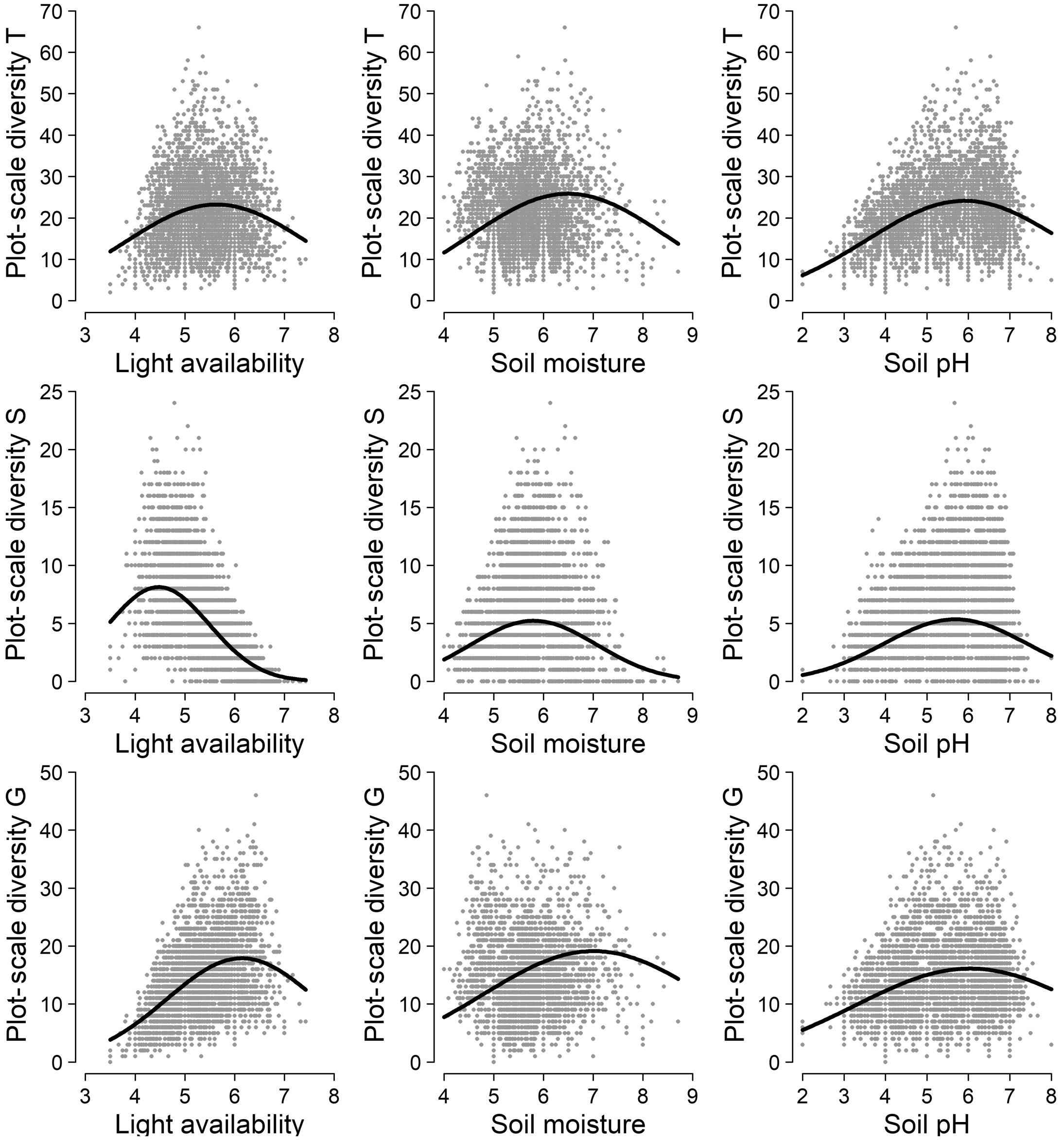

FIGURE 3 Relationships between plot-scale diversity and light availability (m*L*), soil moisture (mF) and soil pH (m*R*) (derived from Ellenberg indicator values). Top: total of species; middle: specialist species; bottom: generalist species (abbreviated with T, S, G, respectively). Trendlines are based on model estimates.

positively to increasing radiation. For generalist species, our findings are in accordance with studies of Brunet et al. (2011) and Govaert et al. (2020), who observed a negative effect of increasing canopy cover and shade-casting ability on species richness. Many generalists with higher light demand grow primarily in more open forest habitats (successional stages, edges, clearings) as well as in open landscapes (Heinken et al., 2022). When combining all species together, the relationship between plot-scale diversity and light availability showed a rather wide optimum range (Figure 3) that likely reflects the different habitat requirements of the subcategories of species and their mixture in forests with medium light availability.

Soil nitrogen was highly positively correlated with soil pH and therefore not included as a predictor. Soil pH and nutrient availability in fact form a complex gradient in most temperate forest habitats, with base-rich sites usually being nutrient-rich and acidic sites nutrient-poor (Schuster & Diekmann, 2005). One of the few exceptions to the positive pH-fertility relationship in forests includes forests on calcareous slopes with shallow soils that have a high pH, but owing to drought a low nutrient availability. Hump-shaped relationships between plot-scale diversity and soil pH were observed for all species as well as for forest specialists and generalists. Our findings agree with some previous studies, which also reported hump-shaped relations (Schuster & Diekmann, 2005; Peppler-Lisbach & Kleyer, 2009; Vockenhuber et al., 2011). Other studies, in contrast, showed linear and logarithmic increases in plant species richness in forests with increasing soil pH (Schuster & Diekmann, 2003; Zarfos et al., 2019). Generally, soil pH is an important soil chemical variable for plants, because it influences the solubility and availability of nutrients. A decrease in soil pH below 4.5 increases the aluminum concentration and contributes to aluminum (Al^3) toxicity, which may result in inhibited root growth (Tyler, 2003; Rahman et al., 2018; Penn & Camberato, 2019). The strong correlation of soil pH and nutrient availability (see above) suggests also a hump-shaped relation between plot-scale diversity and soil nutrients. Overall, soil nitrogen is known to be a major driver of species composition and richness in forests (Chudomelová et al., 2017; Melliger et al., 2018; Hrivnák et al., 2022). A hump-shaped relationship of forest species richness and soil nutrients was also reported on a broad scale for central Europe (Cornwell & Grubb, 2003). High nutrient availability is associated with the competitive displacement of many smaller-statured plants by a few tall vigorous species (Gilliam, 2006), while nutrient deficiency allows only few species with a tolerance strategy to occur.

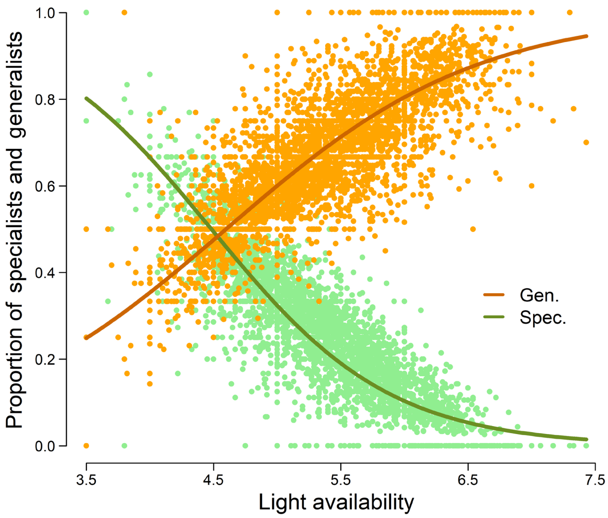

FIGURE 4 Relationship between the proportion of forest specialists and generalists (relative to the total number of species) and light availability (m*L*). Forest specialists (Spec.) and generalists (Gen.) are visualized in light green and orange, respectively. Trendlines are based on model estimates.

The relationship between plot-scale diversity and soil moisture (m*F*) was also in all cases hump-shaped. Previous studies emphasized the importance of soil moisture for species composition in forests (Gilbert & Lechowicz, 2004; Gazol & Ibáñez, 2010; Melliger et al., 2018). It affects plant species by controlling the availability of resources and regulating photosynthetic activity (D'Odorico et al., 2010; Wang et al., 2019). Forest specialists and generalists both thrive under medium soil moisture conditions, but only generalists appear to grow also at very high soil moisture levels (m*F* 8–9). Likely, forests on moist or wet soils are relatively open and offer suitable sites for generalists typical of wet grasslands and reed communities. These results indicate potential niche partitioning of forest specialists and generalists along the soil moisture gradient (Dawson, 1990; Silvertown et al., 2015).

4.3 | Community saturation

Based on the significance of the slope coefficient in the log-ratio model, communities can be classified as either saturated or unsaturated. As significant negative slopes are associated with saturated communities (Szava-Kovats et al., 2012; Gonçalves-Souza et al., 2013), plant communities combining all species together as well as both the forest specialists and generalists can be classified as saturated. According to the categories defined by Szava-Kovats et al. (2013), our slope coefficients can be assigned to the type II category (slope < −1, saturated). Patterns of community saturation were also reported previously for plants (Michalet et al., 2015; Alroy, 2018) and several animal taxa (Alroy, 2018). Given that plot-scale diversity levels off at some point and does no longer depend on patch-scale diversity, our findings suggest that local factors and

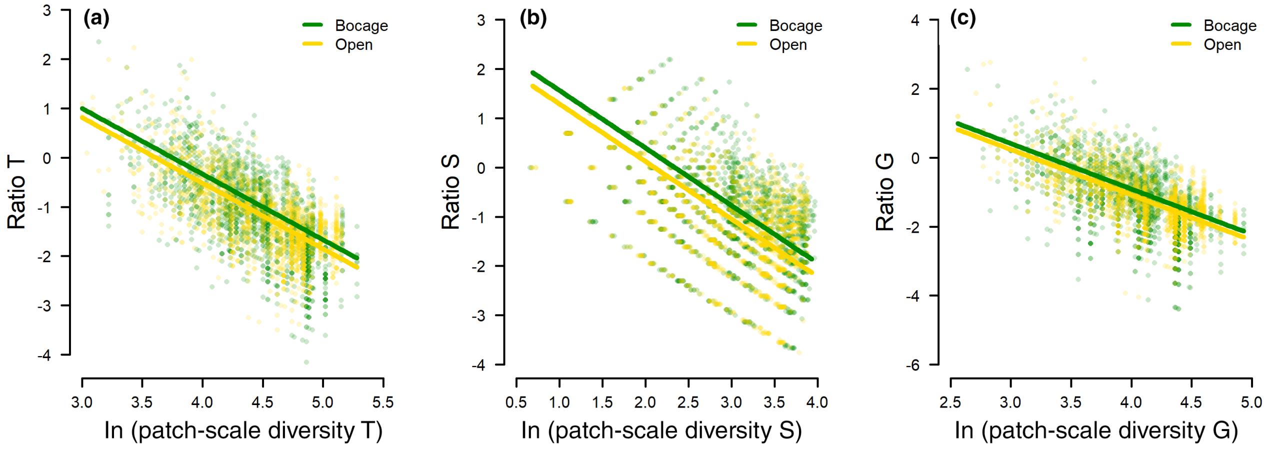

FIGURE 5 Relationship between the *ratio* (natural logarithm of [plot-scale diversity/(patch-scale diversity − plot-scale diversity)]) and natural logarithm of patch-scale diversity for (a) the total of plant species, (b) forest specialists and (c) generalist species (abbreviated with T, S, G, respectively). The slope of the regression serves as a measure of the degree of saturation and significantly negative slopes indicate saturated communities. Note that the axis length of the figures varies. Plots located in the bocage landscape are visualized in green and plots in the open landscape in yellow. The data points were jittered and are displayed with increased transparency for visualization. Trendlines are based on model estimates.

processes play a major role for plot-scale diversity (Ricklefs, 1987; Cornell & Lawton, 1992).

Plant communities in the bocage and in the open landscape had a similar degree of community saturation for all species as well as for the subcategories. This is contradictory to findings of Almoussawi et al. (2020) who found differences in plant community saturation between different landscape types in northern France. These different findings may be explained by the fact that three landscape types were observed in the latter study (open, bocage, continuous forest). The latter type, acting as a control or baseline for comparative purposes, is associated with highly suitable environmental conditions for forest specialists and less favorable conditions for generalists, which may have contributed to unsaturated specialist communities and saturated generalist communities (Almoussawi et al., 2020).

Moreover, there was a higher degree of community saturation for generalists compared to forest specialists. Generalist species were more frequent than forest specialists at the plot scale as well as at the patch scale, which coincides with findings of Brown (1984). Based on high competitive abilities, generalist species can thrive under various environmental conditions (Boulangeat et al., 2012). Due to restricted resources and limited resource variability, local plots can only hold a limited number of species. Most likely, generalist species, which use resources more efficiently (for example, attaining greater height or leaf area to intercept light, Garnier et al., 2016), may outcompete other generalists at the local scale when a certain plot-scale diversity is exceeded, leading to a higher degree of community saturation.

5 | CONCLUSION

Our study demonstrated consistent patterns in the effects of patch-scale and landscape-scale variables on plot-scale diversity of forest species in deciduous forests across a geographical gradient from southwest to northeast Europe. Plot-scale diversity increased with increasing patch-scale diversity and plots located in the bocage landscape contained a higher diversity than plots in the open landscape. This is a relevant finding, because it shows how the biodiversity of forest plant species can be supported in forests embedded in agricultural landscapes. The latter emphasizes not only the importance to retain but also to expand small semi-natural habitats like tree rows, unused field margins, and hedgerows to promote the dispersal of forest specialists and generalists across agricultural landscapes. Moreover, patterns of niche partitioning were present among forest specialists and generalists. Forest specialists were mostly present under low light availability and medium soil moisture levels, while generalists thrived best at high light availability and at medium and high soil moisture. Generally, plot-scale diversity was highest in the middle of the soil pH gradient. We conclude that forest specialists and generalists are similarly affected by landscape type, patch-scale diversity and soil pH (and also nutrient availability based on the high correlation with soil pH) and differently by light and soil moisture conditions. We found equally saturated plant communities in both landscape types. When plot-scale diversity levels off with increasing patch-scale diversity, it is likely influenced to a high extent by local variables and processes (e.g. light conditions, soil variables, competition).

To our knowledge, this is the first study in which the effects of landscape-scale, patch-scale and local factors on species richness and saturation have been studied across many regions at a continental scale, using more than 3500 forest vegetation plots. The findings extend our understanding of factors and processes that shape local plant diversity and help to comprehend the different responses of generalist and specialist species.

AUTHOR CONTRIBUTIONS

Jolina Paulssen and Martin Diekmann designed the project. Jörg Brunet, Sara Cousins, Guillaume Decocq, Pieter De Frenne, Pallieter De Smedt, Martin Diekmann, Per-Ola Hedwall, Jonathan Lenoir, Jaan Liira, Jessica Lindgren, Tobias Naaf, Taavi Paal, Alicia Valdés, Kris Verheyen, and Monika Wulf carried out the data collection. Jolina Paulssen performed the statistical analyses and wrote the first draft of the paper. All authors made substantial contributions to the revision of the manuscript and provided their final consent for its publication.

ACKNOWLEDGEMENTS

This work was supported by the Research Foundation—Flanders (FWO) by funding the scientific research network FLEUR (W000322N, www.fleur.ugent.be).

FUNDING INFORMATION

This research was funded by the ERA-Net BiodivERsA project smallFOREST, with the national funders ANR (France), MINECO (Spain), FORMAS (Sweden), ETAG (Estonia), DFG/DLR (Germany) and BELSPO (Belgium) as part of the 2011 BiodivERsA call for research proposals. In addition, this work was supported by the Research Foundation—Flanders (FWO) by funding the scientific research network FLEUR (W000322N, www.fleur.ugent.be).

DATA AVAILABILITY STATEMENT

The data used for the analyses will be stored publicly at figshare https://doi.org/10.6084/m9.figshare.27315078.v1, https://doi.org/10.6084/m9.figshare.27315072.v1.

ORCID

Jolina Paulssen https://orcid.org/0009-0008-7622-0751
Jörg Brunet https://orcid.org/0000-0003-2667-4575
Sara A. O. Cousins https://orcid.org/0000-0003-2656-2645
Guillaume Decocq https://orcid.org/0000-0001-9262-5873
Pieter De Frenne https://orcid.org/0000-0002-8613-0943
Per-Ola Hedwall https://orcid.org/0000-0002-0120-7420
Jonathan Lenoir https://orcid.org/0000-0003-0638-9582
Jaan Liira https://orcid.org/0000-0001-8863-0098
Jessica Lindgren https://orcid.org/0000-0001-7219-4359

Tobias Naaf https://orcid.org/0000-0002-4809-3694
Alicia Valdés https://orcid.org/0000-0001-9281-2871
Kris Verheyen https://orcid.org/0000-0002-2067-9108
Monika Wulf https://orcid.org/0000-0001-6499-0750
Martin Diekmann https://orcid.org/0000-0001-8482-0679

REFERENCES

Almoussawi, A., Lenoir, J., Jamoneau, A., Hattab, T., Wasof, S., Gallet, E. et al. (2020) Forest fragmentation shapes the alpha–gamma relationship in plant diversity. *Journal of Vegetation Science*, 31(3), 63–74. Available from: https://doi.org/10.1111/jvs.12817

Alroy, J. (2018) Limits to species richness in terrestrial communities. *Ecology Letters*, 21(12), 1781–1789. Available from: https://doi.org/10.1111/ele.13152

Baudry, J., Bunce, R.G.H. & Burel, F. (2000) Hedgerows: an international perspective on their origin, function and management. *Journal of Environmental Management*, 60(1), 7–22. Available from: https://doi.org/10.1006/jema.2000.0358

Boulangeat, I., Lavergne, S., Es, J., Garraud, L. & Thuiller, W. (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal of Biogeography*, 39, 204–214. Available from: https://doi.org/10.1111/j.1365-2699.2011.02581.x

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. Available from: https://doi.org/10.32614/RJ-2017-066

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist*, 124(2), 255–279.

Brunet, J., Valtinat, K., Mayr, M.L., Felton, A., Lindbladh, M. & Bruun, H.H. (2011) Understory succession in post-agricultural oak forests: habitat fragmentation affects forest specialists and generalists differently. *Forest Ecology and Management*, 262(9), 1863–1871. Available from: https://doi.org/10.1016/j.foreco.2011.08.007

Chudomelová, M., Zelený, D. & Li, C.-F. (2017) Contrasting patterns of fine-scale herb layer species composition in temperate forests. *Acta Oecologica*, 80, 24–31. Available from: https://doi.org/10.1016/j.actao.2017.02.003

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *The Journal of Animal Ecology*, 61(1), 5503. Available from: https://doi.org/10.2307/5503

Cornwell, W.K. & Grubb, P.J. (2003) Regional and local patterns in plant species richness with respect to resource availability. *Oikos*, 100(3), 417–428. Available from: https://doi.org/10.1034/j.1600-0706.2003.11697.x

Damschen, E.I. & Brudvig, L.A. (2012) Landscape connectivity strengthens local–regional richness relationships in successional plant communities. *Ecology*, 93(4), 704–710. Available from:https://doi.org/10.1890/11-1797.1

Dawson, T.E. (1990) Spatial and physiological overlap of three Co-occurring alpine willows. *Functional Ecology*, 4(1), 13–25. Available from: https://doi.org/10.2307/2389647

Deckers, B., Kerselaers, E., Gulinck, H., Muys, B. & Hermy, M. (2005) Long-term spatio-temporal dynamics of a hedgerow network landscape in Flanders, Belgium. *Environmental Conservation*, 32(1), 20–29. Available from: https://doi.org/10.1017/S0376892905001840

Depauw, L., Perring, M.P., Landuyt, D., Maes, S.L., Blondeel, H., De Lombaerde, E. et al. (2020) Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. *Journal of Ecology*, 108(4), 1411–1425. Available from: https://doi.org/10.1111/1365-2745.13339

D'Odorico, P., Laio, F., Porporato, A., Ridolfi, L., Rinaldo, A. & Rodriguez-Iturbe, I. (2010) Ecohydrology of terrestrial ecosystems. *Bioscience*, 60(11), 898–907. Available from: https://doi.org/10.1525/bio.2010.60.11.6

Ellenberg, H. & Leuschner, C. (2010) *Vegetation Mitteleuropas mit den Alpen*, 6th edition. Stuttgart: Zusatzmaterial zum UTB-Band. Verlag Eugen Ulmer.

Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, 18, 1–248.

Euro+Med Plant Base. The information resource for Euro-Mediterranean plant diversity. Available from: https://www.emplantbase.org/home.html [Accessed 12 March 2024]

Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 1–23. Available from: https://doi.org/10.1146/annurev-ecolsys-110316-022612

Flinn, K.M. & Vellend, M. (2005) Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment*, 3(5), 243–250. Available from: https://doi.org/10.2307/3868486

Garnier, E., Navas, M.-L. & Grigulis, K. (2016) *Plant functional diversity: organism traits, community structure, and ecosystem properties*. Oxford: Oxford University Press.

Gazol, A. & Ibáñez, R. (2010) Plant species composition in a temperate forest: multi-scale patterns and determinants. *Acta Oecologica*, 36(6), 634–644. Available from: https://doi.org/10.1016/j.actao.2010.09.009

Geoportal of the European Commission (EUROSTAT) EuroGeographics and UN-FAO. (2020) Countries, 2020 - Administrative Units – Dataset. Available from: https://ec.europa.eu/eurostat/web/gisco/geodata/reference-data/administrative-units-statistical-units/countries [Accessed 08 June 2021]

Gilbert, B. & Lechowicz, M.J. (2004) Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences*, 101(20), 7651–7656. Available from: https://doi.org/10.1073/pnas.0400814101

Gilliam, F.S. (2006) Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology*, 94(6), 1176–1191. Available from: https://doi.org/10.1111/j.1365-2745.2006.01155.x

Gilliam, F.S. (2019) Excess nitrogen in temperate forest ecosystems decreases herbaceous layer diversity and shifts control from soil to canopy structure. *Forests*, 10, 10066. Available from: https://doi.org/10.3390/f10010066

Gonçalves-Souza, T., Romero, G.Q. & Cottenie, K. (2013) A critical analysis of the ubiquity of linear local–regional richness relationships. *Oikos*, 122(7), 961–966. Available from: https://doi.org/10.1111/j.1600-0706.2013.00305.x

Govaert, S., Meeussen, C., Vanneste, T., Bollmann, K., Brunet, J., Cousins, S.A.O. et al. (2020) Edge influence on understorey plant communities depends on forest management. *Journal of Vegetation Science*, 31(2), 281–292. Available from: https://doi.org/10.1111/jvs.12844

Harrison, S. & Cornell, H. (2008) Toward a better understanding of the regional causes of local community richness. *Ecology Letters*, 11(9), 969–979. Available from: https://doi.org/10.1111/j.1461-0248.2008.01210.x

Hartig, F. (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression Models. R Package Version 0.4.6. Availalbe from: https://CRAN.R-project.org/package=DHARMa

He, F., Gaston, K.J., Connor, E.F. & Srivastava, D.S. (2005) The local–regional relationship: immigration, extinction, and scale. *Ecology*, 86(2), 360–365. Available from: https://doi.org/10.1890/04-1449

Heinken, T., Diekmann, M., Liira, J., Orczewska, A., Schmidt, M., Brunet, J. et al. (2022) The European forest plant species list (EuForPlant):

concept and applications. *Journal of Vegetation Science*, 33(3), e13132. Available from: https://doi.org/10.1111/jvs.13132

Hillebrand, H. (2005) Regressions of local on regional diversity do not reflect the importance of local interactions or saturation of local diversity. *Oikos*, 110(1), 195–198. Available from: https://doi.org/10.1111/j.0030-1299.2005.14008.x

Hrivnák, R., Bošeľa, M., Slezák, M., Lukac, M., Svitková, I. et al. (2022) Competition for soil resources forces a trade-off between enhancing tree productivity and understorey species richness in managed beech forests. *Science of the Total Environment*, 849, 157825. Available from: https://doi.org/10.1016/j.scitotenv.2022.157825

Jamoneau, A., Sonnier, G., Chabrerie, O., Closset-Kopp, D., Saguez, R., Gallet-Moron, E. et al. (2011) Drivers of plant species assemblages in forest patches among contrasted dynamic agricultural landscapes: local species diversity in forest metacommunities. *Journal of Ecology*, 99(5), 1152–1161. Available from: https://doi.org/10.1111/j.1365-2745.2011.01840.x

Joint Research Centre, Institute for Environment and Sustainability, Estreguil, C., Caudullo, G. & De Rigo, D. (2012) *Forest landscape in Europe: pattern, fragmentation and connectivity*. Luxembourg: Publications Office of the European Union.

Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S. & Kiesecker, J. (2019) Managing the middle: a shift in conservation priorities based on the global human modification gradient. *Global Change Biology*, 25(3), 811–826. Available from: https://doi.org/10.1111/gcb.14549

Kolb, A. & Diekmann, M. (2004) Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science*, 15(2), 199–208. Available from: https://doi.org/10.1111/j.1654-1103.2004.tb02255.x

Lenoir, J., Decocq, G., Spicher, F., Gallet-Moron, E., Buridant, J. & Closset-Kopp, D. (2021) Historical continuity and spatial connectivity ensure hedgerows are effective corridors for forest plants: evidence from the species–time–area relationship. *Journal of Vegetation Science*, 32(1), e12845. Available from: https://doi.org/10.1111/jvs.12845

Litza, K., Alignier, A., Closset-Kopp, D., Ernoult, A., Mony, C., Osthaus, M. et al. (2022) Hedgerows as a habitat for forest plant species in the agricultural landscape of Europe. *Agriculture, Ecosystems & Environment*, 326, 107809. Available from: https://doi.org/10.1016/j.agee.2021.107809

Loreau, M. (2000) Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters*, 3(2), 73–76. Available from: https://doi.org/10.1046/j.1461-0248.2000.00127.x

Lüdecke et al. (2021) Performance: an R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60), 3139.

Márialigeti, S., Tinya, F., Bidló, A. & Ódor, P. (2016) Environmental drivers of the composition and diversity of the herb layer in mixed temperate forests in Hungary. *Plant Ecology*, 217(5), 549–563. Available from: https://doi.org/10.1007/s11258-016-0599-4

McGuire, J.L., Lawler, J.J., McRae, B.H., Nuñez, T.A. & Theobald, D.M. (2016) Achieving climate connectivity in a fragmented landscape. *Proceedings of the National Academy of Sciences*, 113(26), 7195–7200. Available from: https://doi.org/10.1073/pnas.1602817113

Melliger, R.L., Braschler, B., Rusterholz, H.-P. & Baur, B. (2018) Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. *PLoS One*, 13(6), e0199245. Available from: https://doi.org/10.1371/journal.pone.0199245

Michalet, R., Maalouf, J.-P., Choler, P., Clément, B., Rosebery, D., Royer, J.-M. et al. (2015) Competition, facilitation and environmental severity shape the relationship between local and regional species richness in plant communities. *Ecography*, 38(4), 335–345. Available from: https://doi.org/10.1111/ecog.01106

Mölder, A., Bernhardt-Römermann, M. & Schmidt, W. (2008) Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? *Forest Ecology and Management*, 256(3), 272–281. Available from: https://doi.org/10.1016/j.foreco.2008.04.012

Pärtel, M., Szava-Kovats, R. & Zobel, M. (2013) Community completeness: linking local and dark diversity within the species pool concept. *Folia Geobotanica*, 48(3), 307–317. Available from: https://doi.org/10.1007/s12224-013-9169-x

Penn, C.J. & Camberato, J.J. (2019) A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. *Agriculture*, 9, 120. Available from: https://doi.org/10.3390/agriculture9060120

Peppler-Lisbach, C. & Kleyer, M. (2009) Patterns of species richness and turnover along the pH gradient in deciduous forests: testing the continuum hypothesis. *Journal of Vegetation Science*, 20(6), 984–995. Available from: https://doi.org/10.1111/j.1654-1103.2009.01092.x

Poschlod, P. & Braun-Reichert, R. (2017) Small natural features with large ecological roles in ancient agricultural landscapes of Central Europe - history, value, status, and conservation. *Biological Conservation*, 211, 60–68. Available from: https://doi.org/10.1016/j.biocon.2016.12.016

QGIS.org. (2012) *QGIS geographic information system*. QGIS Association. Available from: https://www.qgis.org

Raduła, M.W., Szymura, T.H. & Szymura, M. (2018) Topographic wetness index explains soil moisture better than bioindication with Ellenberg's indicator values. *Ecological Indicators*, 85, 172–179. Available from: https://doi.org/10.1016/j.ecolind.2017.10.011

Rahman, M., Lee, S.-H., Ji, H., Kabir, A., Jones, C. & Lee, K.-W. (2018) Importance of mineral nutrition for mitigating aluminum toxicity in plants on acidic soils: current status and opportunities. *International Journal of Molecular Sciences*, 19(10), 3073. Available from: https://doi.org/10.3390/ijms19103073

R Core Team (2021) *R: A Language and Environment forStatistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from: https://www.R-project.org/

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, 235(4785), 167–171.

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

Schuster, B. & Diekmann, M. (2003) Changes in species density along the soil pH gradient - evidence from German plant communities. *Folia Geobotanica*, 38(4), 367–379. Available from: https://doi.org/10.1007/BF02803245

Schuster, B. & Diekmann, M. (2005) Species density and environmental factors in deciduous forests of Northwest Germany. *Forest Ecology and Management*, 206, 197–205.

Silvertown, J., Araya, Y. & Gowing, D. (2015) Hydrological niches in terrestrial plant communities: a review. *Journal of Ecology*, 103(1), 93–108. Available from: https://doi.org/10.1111/1365-2745.12332

Small Forest. Biodiversa+ European Biodiversity Partnership. Available from: https://www.biodiversa.eu/2022/10/31/smallforest [Accessed 12 March 2024]

Szava-Kovats, R.C., Ronk, A. & Pärtel, M. (2013) Pattern without bias: local—regional richness relationship revisited. *Ecology*, 94(9), 1986–1992.

Szava-Kovats, R.C., Zobel, M. & Pärtel, M. (2012) The local-regional species richness relationship: new perspectives on the null-hypothesis. *Oikos*, 121(3), 321–326. Available from: https://doi.org/10.1111/j.1600-0706.2011.19603.x

Szymura, T.H., Szymura, M. & Macioł, A. (2014) Bioindication with Ellenberg's indicator values: a comparison with measured parameters in central European oak forests. *Ecological Indicators*, 46, 495–503. Available from: https://doi.org/10.1016/j.ecolind.2014.07.013

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8(8), 857–874. Available from: https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tyler, G. (2003) Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behaviour—contribution to a debate. *Folia Geobotanica*, 38(4), 419–428. Available from: https://doi.org/10.1007/BF02803249

Uroy, L., Ernoult, A. & Mony, C. (2019) Effect of landscape connectivity on plant communities: a review of response patterns. *Landscape Ecology*, 34(2), 203–225. Available from: https://doi.org/10.1007/s10980-019-00771-5

Valdés, A., Lenoir, J., De Frenne, P., Andrieu, E., Brunet, J., Chabrerie, O. et al. (2020) High ecosystem service delivery potential of small woodlands in agricultural landscapes. *Journal of Applied Ecology*, 57(1), 4–16. Available from: https://doi.org/10.1111/1365-2664.13537

Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrerie, O. et al. (2015) The contribution of patch-scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forests across Europe. *Global Ecology and Biogeography*, 24(9), 1094–1105. Available from: https://doi.org/10.1111/geb.12345

Vanneste, T., Govaert, S., De Kesel, W., Van Den Berge, S., Vangansbeke, P., Meeussen, C. et al. (2020) Plant diversity in hedgerows and road verges across Europe. *Journal of Applied Ecology*, 57(7), 1244–1257. Available from: https://doi.org/10.1111/1365-2664.13620

Verheyen, K. & Hermy, M. (2001) Spatio-temporal colonization patterns of forest plant species in a mixed deciduous forest. *Journal of Vegetation Science*, 12(4), 567–578.

Vinter, T., Dinnétz, P., Danzer, U. & Lehtilä, K. (2016) The relationship between landscape configuration and plant species richness in forests is dependent on habitat preferences of species. *European Journal of Forest Research*, 135(6), 1071–1082. Available from: https://doi.org/10.1007/s10342-016-0994-3

Vockenhuber, E.A., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D. & Tscharntke, T. (2011) Tree diversity and environmental context predict herb species richness and cover in Germany's largest connected deciduous forest. *Perspectives in Plant Ecology, Evolution and Systematics*, 13(2), 111–119. Available from: https://doi.org/10.1016/j.ppees.2011.02.004

Wang, C., Fu, B., Zhang, L. & Xu, Z. (2019) Soil moisture–plant interactions: an ecohydrological review. *Journal of Soils and Sediments*, 19(1), 1–9. Available from: https://doi.org/10.1007/s11368-018-2167-0

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30(3), 279–338. Available from: https://doi.org/10.2307/1943563

Wilcox, B.A. & Murphy, D.D. (1985) Conservation strategy: the effects of fragmentation on extinction. *The American Naturalist*, 125(6), 879–887. Available from: https://doi.org/10.1086/284386

Wilson, M.C., Chen, X.Y., Corlett, R.T., Didham, R.K., Ding, P., Holt, R.D. et al. (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. *Landscape Ecology*, 31(2), 219–227. Available from: https://doi.org/10.1007/s10980-015-0312-3

Zarfos, M.R., Dovciak, M., Lawrence, G.B., McDonnell, T.C. & Sullivan, T.J. (2019) Plant richness and composition in hardwood forest understories vary along an acidic deposition and soil-chemical gradient in the northeastern United States. *Plant and Soil*, 438, 461–477. Available from: https://doi.org/10.1007/s11104-019-04031-y

Zobel, M. (2016) The species pool concept as a framework for studying patterns of plant diversity. *Journal of Vegetation Science*, 27(1), 8–18. Available from: https://doi.org/10.1111/jvs.12333

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Verlag.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Detailed information on the historical maps.

Appendix S2. Output from additional models with m*N* (soil nitrogen, Ellenberg indicator value) instead of m*R* (soil pH, Ellenberg indicator value).

Appendix S3. Collinearity of patch size and patch age with patch-scale diversity.

Appendix S4. Output from additional models with study region and forest patch as random terms (instead of study region, landscape type and forest patch).

Appendix S5. Output from plot-scale diversity and saturation models.

Appendix S6. Output from a model analyzing the difference in optimum light conditions between forest generalists and specialists.

Appendix S7. Figures visualizing the relationship between plot-scale diversity (of all species, forest specialist species and generalist species) and light availability (m*L*), soil moisture (m*F*) and soil pH (m*R*) (derived from Ellenberg indicator values) separately for all eight study regions.

How to cite this article: Paulssen, J., Brunet, J., Cousins, S.A.O., Decocq, G., De Frenne, P., De Smedt, P. et al. (2024) Patterns of local plant diversity and community saturation in deciduous forests in Europe. *Journal of Vegetation Science*, 35, e13318. Available from: https://doi.org/10.1111/jvs.13318