BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Dispersal ability, trophic position and body size mediate species turnover processes: Insights from a multi-taxa and multi-scale approach

Soyeon Bae[1] | Lea Heidrich[1] | Shaun R. Levick[2] | Martin M. Gossner[3,4] | Sebastian Seibold[5,6] | Wolfgang W. Weisser[5] | Paul Magdon[7] | Alla Serebryanyk[8] | Claus Bässler[9,10] | Deborah Schäfer[11] | Ernst-Detlef Schulze[12] | Inken Doerfler[13,14] | Jörg Müller[15,16] | Kirsten Jung[17] | Marco Heurich[9,18] | Markus Fischer[19,20] | Nicolas Roth[1,21,3] | Peter Schall[22] | Steffen Boch[23] | Stephan Wöllauer[24] | Swen C. Renner[25] | Jörg Müller[1,9]

[1]Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg, Germany

[2]CSIRO Land and Water, Winnellie, Northern Territory, Australia

[3]Forest Entomology, WSL Swiss Federal Research Institute, Birmensdorf, Switzerland

[4]Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland

[5]Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Technical University of Munich, Freising, Germany

[6]Ecosystem Dynamics and Forest Management Group, Technical University of Munich, Freising and Berchtesgaden National Park, Berchtesgaden, Germany

[7]Forest Inventory and Remote Sensing, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

[8]Department of Geoinformatics, Munich University of Applied Sciences, München, Germany

[9]Bavarian Forest National Park, Grafenau, Germany

[10]Faculty of Biological Sciences, Institute for Ecology, Evolution and Diversity, Goethe University, Frankfurt, Frankfurt am Main, Germany

[11]Botanical Garden of the University of Bern, Bern, Switzerland

[12]Max Planck Institute for Biogeochemistry, Jena, Germany

[13]Plant Biodiversity Research Group, Department of Ecology & Ecosystem Management, Technical University of Munich, Freising, Germany

[14]Institute of Biology and Environmental Science, Vegetation Science & Nature Conservation, University of Oldenburg, Oldenburg, Germany

[15]Department of Nature Conservation, Heinz Sielmann Foundation, Wustermark, Germany

[16]Institute of Biology and Biochemistry, University of Potsdam, Potsdam, Germany

[17]Evolutionary Ecology and Conservation Genomics, University Ulm, Ulm, Germany

[18]Chair of Wildlife Ecology and Wildlife Management, University of Freiburg, Freiburg im Breisgau, Germany

[19]Institute of Plant Sciences, University of Bern, Bern, Switzerland

[20]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany

[21]School of Agricultural Forest and Food Sciences, Bern University of Applied Sciences, Zollikofen, Switzerland

[22]Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Göttingen, Germany

[23]Research Unit Biodiversity & Conservation Biology, WSL Swiss Federal Research Institute, Birmensdorf, Switzerland

[24]Faculty of Geography, Philipps-University Marburg, Marburg, Germany

[25]Head of Ornithology, Natural History Museum Vienna, Vienna, Austria

Correspondence
Jörg Müller, Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg, Germany.
Email: joerg.mueller@uni-wuerzburg.de

Abstract

Aim: Despite increasing interest in β-diversity, that is the spatial and temporal turnover of species, the mechanisms underlying species turnover at different spatial scales are not fully understood, although they likely differ among different functional groups. We investigated the relative importance of dispersal limitations and the environmental filtering caused by vegetation for local, multi-taxa forest communities differing in their dispersal ability, trophic position and body size.

Location: Temperate forests in five regions across Germany.

Methods: In the inter-region analysis, the independent and shared effects of the regional spatial structure (regional species pool), landscape spatial structure (dispersal limitation) and environmental factors on species turnover were quantified with a 1-ha grain across 11 functional groups in up to 495 plots by variation partitioning. In the intra-region analysis, the relative importance of three environmental factors related to vegetation (herb and tree layer composition and forest physiognomy) and spatial structure for species turnover was determined.

Results: In the inter-region analysis, over half of the explained variation in community composition (23% of the total explained 35%) was explained by the shared effects of several factors, indicative of spatially structured environmental filtering. Among the independent effects, environmental factors were the strongest on average over 11 groups, but the importance of landscape spatial structure increased for less dispersive functional groups. In the intra-region analysis, the independent effect of plant species composition had a stronger influence on species turnover than forest physiognomy, but the relative importance of the latter increased with increasing trophic position and body size.

Main conclusions: Our study revealed that the mechanisms structuring assemblage composition are associated with the traits of functional groups. Hence, conservation frameworks targeting biodiversity of multiple groups should cover both environmental and biogeographical gradients. Within regions, forest management can enhance β-diversity particularly by diversifying tree species composition and forest physiognomy.

KEYWORDS
body size, dispersal ability, environmental filtering, forest physiognomy, neutral processes, plant composition, regional species pool, species turnover, trophic position, β-diversity

1 | INTRODUCTION

Since Whittaker (1960) defined β-diversity as the difference in species composition among sites, β-diversity has gained the increasing attention of ecologists. To promote overall diversity within a region (γ-diversity), either α-diversity (the within-site species diversity) or β-diversity (Beck et al., 2012; Müller & Goßner, 2010) must be increased. In European beech forests for instance, ecologists have highlighted the importance of β-diversity and the need to foster a mosaic of structurally diverse habitat patches at landscape levels rather than homogeneous landscapes with high local small-grain heterogeneity (Hilmers et al., 2018; Schall et al., 2018).

However, the processes that promote compositional differentiation between local communities (species turnover) remain under debate and differ among habitat types and species groups (Aisen et al., 2017; Murphy et al., 2015; Zellweger et al., 2017). Four mechanisms are considered to account for the species composition of local communities (Figure 1a). First, at large spatial (inter-region) scales, historical biogeography (e.g. glaciation history), long-distance dispersal and macro-scale environmental filters shape the regional species pool that constrains the composition of local
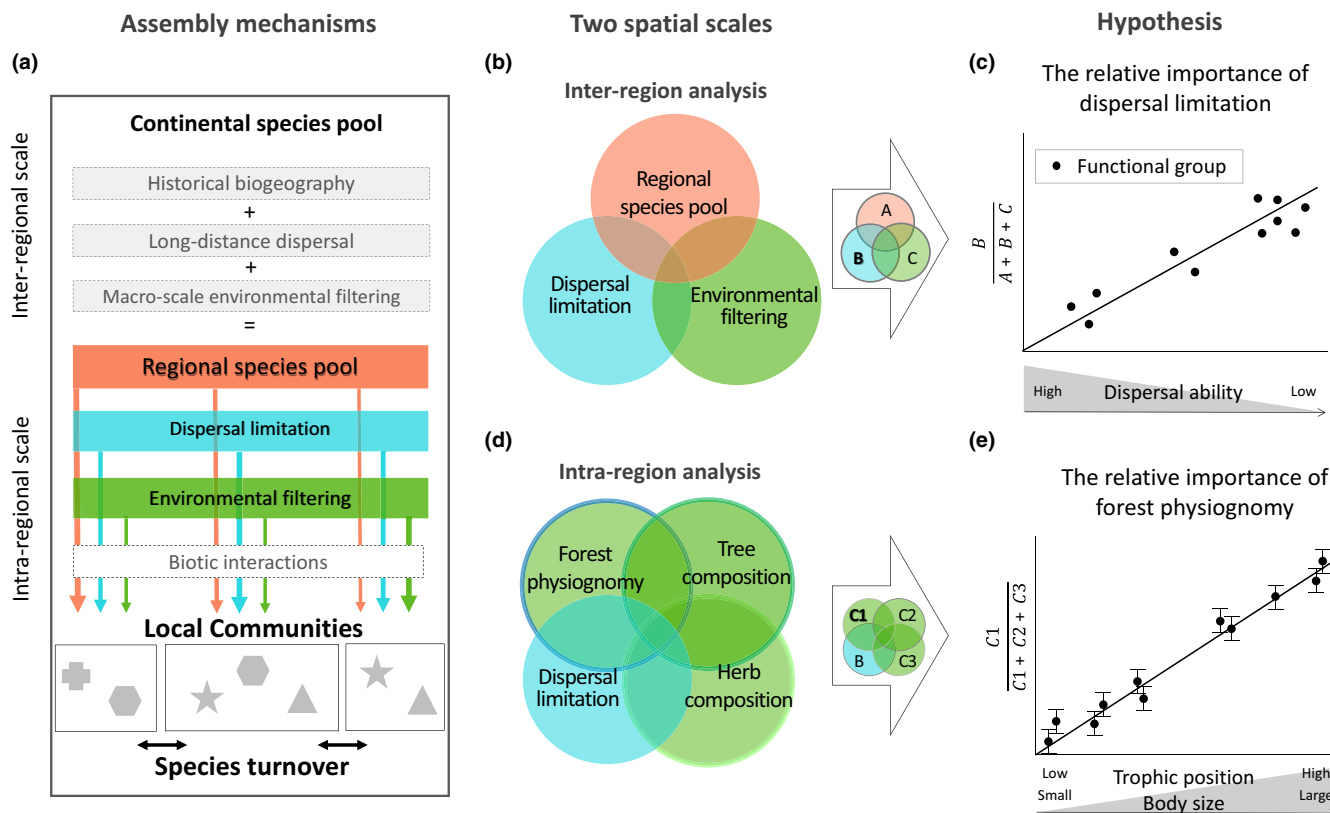
FIGURE 1 The framework of the inter-region and intra-region analyses. (a) Assembly mechanisms influencing the species turnover of the local community at the inter-region and intra-region scales. (b) The inter-regional variation partitioning analysis of the species composition using predictor sets of the regional species pool, dispersal limitations and environmental filtering. (c) The first hypothesis examined by the inter-region analysis that the relative importance of dispersal limitations increases with decreasing dispersal ability. (d) The intra-regional variation partitioning analysis of the species composition using the predictor sets of dispersal limitations, herb composition, tree composition and forest physiognomy. (e) The second hypothesis examined by the intra-region analysis that the relative importance of forest physiognomy vs. plant species composition increases with increasing trophic position and body size

assemblages (Cornell & Lawton, 1992; Dobrovolski et al., 2012; Hubbell, 1997; Ricklefs, 1987). Second, at the intra-region scale, neutral processes linked to dispersal limitations may further determine local communities (Hubbell, 2001) and operate together with third and fourth mechanisms related to niche-based processes, including environmental filtering and biotic interactions (competition, predation, mutualism, etc.). Of the latter, environmental filtering has been studied for many years (Whittaker et al., 1973). Community assembly processes occurring under extreme environmental conditions such as those of climate lead to communities composed of species with similar response traits by environmental filtering (Cadotte & Tucker, 2017). However, the relative contributions of mechanisms operating at different spatial scales in shaping species composition are still under debate (Chase & Myers, 2011).

The relative importance of dispersal limitations on species turnover is likely to depend on the dispersal ability of the species studied. Previous studies showed that at a global scale β-diversity is more pronounced for less mobile taxa due to their limited dispersal. Qian (2009), for example, found that the β-diversity of birds and mammals was lower than that of reptiles and amphibians. However, studies at national or regional scales (extents) did not find an effect of dispersal

ability on β-diversity, based on comparisons of birds, bats, non-flying mammals, reptiles and amphibians (Calderón-Patrón et al., 2013) and of non-flying vs. flying groups (Harrison et al., 1992).

The importance of dispersal limitations relative to environmental filters in explaining species turnover across several functional groups is unclear. Ferrier et al. (1999) found that dispersal limitation was stronger for ground-dwelling arthropods than for vertebrates and vascular plants in a region of Australia (~76,000 km^2). Similar results were obtained by Steinitz et al. (2006) for snails vs. birds across Israel (~22,000 km^2). By contrast, Jiménez-Valverde et al. (2010) did not find stronger dispersal limitations in less mobile groups of spiders in a region of Spain (~8,000 km^2). This contradiction may reflect differences in the studied taxa or the failure to account for assembly mechanisms acting at different spatial scales.

In fact, spatial scale dependency is frequently invoked to explain the inconsistent conclusions of previous studies. For example, among the determinants of community assembly at larger spatial extents, geographical distance (neutral processes) was shown to be more important than environmental factors (niche process), as demonstrated in pan-European vs. country-wide analyses (Keil et al., 2012; Qian et al., 2005). However, recent studies have shown regional effects

with an explicit spatial clustering, such as the effects of biogeographical history on local assemblages over a continental spatial extent in Europe (Hagge et al., 2019; Jiménez-Alfaro et al., 2018). These observations demonstrate the importance of resolving spatial structure into multiple spatial scales in studies on species turnover. Yet, studies that separate the effects of spatial structure into those occurring at inter-regional (i.e. regional species pool) and intra-regional (i.e. dispersal limitations) scales, thus allowing investigation of their independent contributions, are lacking.

In this study, we examined the relative importance of dispersal limitations in shaping the species composition of local communities across a range of taxa (henceforth "functional groups") differing in their dispersal abilities, after controlling for the regional species pool (the result of macro-scale processes) and environmental filters (henceforth "inter-region analysis") (Figure 1b). We hypothesized that the relative importance of dispersal limitations increases with decreasing dispersal ability and thus from spore-dispersal groups, to flying vertebrates, to arthropods (flying, ballooning or walking dispersers) (Figure 1c).

In studies of environmental filtering, a long-standing question is the role of plant species composition vs. physiognomy in driving species turnover (Rotenberry, 1985). Both of these environmental filters are directly affected by forest management and influence the species comprising each functional group. A shift in plant species composition mainly causes changes in the amount and type of available resources or microhabitats, while a shift in forest physiognomy, such as the vertical profile and heterogeneity, changes the spatial arrangement thereof (see Penone et al. (2019)). While this question has been actively discussed in α-diversity studies since MacArthur and MacArthur (1961) (Penone et al., 2019; Schuldt et al., 2019), it has gained little attention in β-diversity studies, in which coarser variables, such as climate, topography or land cover, have been employed over larger spatial grains and extents (Keil et al., 2012; Kent et al., 2014; Svenning et al., 2011). A better understanding of the mechanisms underlying α-diversity and species turnover in forests, especially those mechanisms directly related to forest management, is crucial to promoting α- and β-diversity. However, with the possible exception of birds, knowledge on the relative importance of plant composition and physiognomy on species turnover of local assemblages is incomplete (Mac Nally, 1990; Müller et al., 2010; Rotenberry, 1985; Wiens et al., 1987; Zellweger et al., 2017). We are aware of only one study addressing diverse functional groups in grasslands: Schaffers et al. (2008) found that plant composition played a dominant role in determining arthropod assemblages.

The aim of our study was to elucidate the relative importance of plant species composition vs. forest physiognomy in shaping the species composition of local communities, after controlling for dispersal limitations in each region (henceforth "intra-region analysis"; Figure 1d). We predicted that plant species composition would be a strong driver of the species turnover in lower trophic positions, such as phytophagous beetles, because of their host plant specificity. Conversely, forest physiognomy was expected to strongly influence the species turnover in larger body size groups (mostly in

higher trophic positions), such as insectivorous birds and bats, due to their large home-range requirements and diverse foraging- or nesting-niche (habitat structure) requirements. We therefore hypothesized that the relative importance of forest physiognomy vs. plant species composition would increase with increasing trophic position and body size (Figure 1e).

2 | METHODS

2.1 | Study site

The study was conducted in five forest regions in Germany along a north to south axis (N 48° 36′–53° 19′) covering a spatial extent of 199,000 km^2 and spanning core forest habitat types of Central Europe (Figure S1). These regions were separated from each other by an average of ~ 320 km (roughly 120–630 km). Data from 503 plots were compiled from three projects: 150 plots from the Biodiversity Exploratories Project (50 plots per region) (Fischer et al., 2010), 284 plots from the BIOKLIM Project (Bässler et al., 2009) and 69 plots from the Steigerwald Project (Doerfler et al., 2017). In the Biodiversity Exploratories Project, 50 plots were established in three regions: the UNESCO Biosphere Reserve Schorfheide-Chorin (SCH), the National Park Hainich and the surrounding Hainich-Dün region (HAI), and the UNESCO Biosphere Reserve, Schwäbische Alb (ALB). The BIOKLIM Project was conducted in the Bavarian Forest National Park (BAY) and the Steigerwald Project in Northern Bavaria (STE) (for details of the five regions, see Figure S1 and Bae et al. (2019)). Not all functional groups were sampled in each plot. The number of plots investigated per functional group was as follows: 321 for bryophytes, 307 for lichens, 385 for saproxylic beetles, 495 for wood-inhabiting fungi, 386 for phytophagous beetles, 226 for moths, 383 for spiders, 383 for carabids, 386 for necrophagous beetles, 494 for birds and 247 for bats (Table S1).

2.2 | Species data of 11 functional groups

All species data were assessed in 1-ha forest plots representing a larger forest management unit. Bryophytes, epiphytic and epixylic lichens, and saproxylic fungi were assessed in subplots within the 1-ha plots (the sizes of the subplots are listed in Supporting information S1.2). Pitfall traps, flight interception traps and light traps were used to sample arthropods. For bird surveys, repeated point counts were performed during breeding seasons. Bats were recorded using ultrasound detectors and analysed at the species level with the appropriate software. Details of the sampling methods are given in Supporting information S1.2. Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, Brandenburg and Bayern (see Table S2 for details of permits). The total number of species observed overall plots and the mean and standard deviation of the number of observed species per plot are presented in Table S1.

TABLE 1 Predictor sets as proxies of regional species pool, dispersal limitations and environmental filtering

Mechanism	Predictor set	Description	Data	
Regional species pool	Regional spatial structure	PCNM differing significantly between regions		Geographical distance matrix from coordinates of X and Y
Dispersal limitation	(Landscape) spatial structure[a]	PCNM not differing significantly between regions		Geographical distance matrix from coordinates of X and Y
Environmental filtering	Herb composition	Main axes of the PCoA of Hellinger-transformed herb species		The presence–absence of vascular plant species in herb layer
	Tree composition	Main axes of the PCoA of Hellinger-transformed tree species		The percentage cover of tree species from all height layers
	Forest physiognomy	Main axes of the PCA of forest physiognomy metrics derived from airborne laser scanning	Vertical profile	Mean height of vegetation returns
				Penetration ratio of the regeneration layer (<2 m)
				Penetration ratio of the canopy layer (>2 m)
			Vertical heterogeneity	Standard deviation of the height of vegetation returns
				Coefficient of variation of the height of vegetation returns
				Foliage height diversity[b]
			Canopy surface heterogeneity	Ratio of the values of the canopy surface areas to flat areas
				Standard deviation of the canopy surface height
			Horizontal heterogeneity	Total gap area
				Standard deviation of gap area
				Mean perimeter–area ratio of gaps
				Mean fractal dimension of gaps
				Total edge length of gaps
				Edge density of gaps

Note: Regional spatial structure, landscape spatial structure and environmental factors were included in the inter-region analysis and spatial structure, herb and tree composition and forest physiognomy in the intra-region analysis (see the framework of the two analyses in Figure 1). The main axes were selected from the principal component analysis (PCA) or principal coordinate analysis (PCoA) and explained 75% of the cumulative proportion of the variance of the predictor sets. The significant variables in each predictor set were then selected by forward selection. See Section 2.4 for details on the principal coordinates of neighbour matrices (PCNM).

[a]In the intra-region analysis, a PCNM was determined for each region separately; it was not necessary to divide the spatial structure into regional and landscape structures. The result is referred to as "spatial structure."

[b]Foliage height (h) diversity was calculated for the canopy (h > 5 m), understorey (5 m > h>2 m) and regeneration layers (2 m > h>0 m).

Before testing our hypotheses (Figure 1c,e), we partitioned total β-diversity (multiple-site dissimilarity of the species composition) into the components species turnover and nestedness to calculate the percentage of the species turnover in the variation of community composition. The presence–absence data (bryophytes, lichens and fungi) were calculated with Sorensen dissimilarity and the abundance-based data (other eight groups) with Bray–Curtis dissimilarity using the R package "betapart" (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2018).

Hellinger transformations were applied for either species abundance data or species presence–absence data (as response variables) using the function *decostand* in the R package "vegan" (Jari Oksanen et al., 2017). This avoided the possibility of double zeros as false indicators of similarity among plots and allowed the use of linear statistical tools such as redundancy analysis (Borcard et al., 2011). A previous study compared several transformation methods and concluded that the Hellinger transformation was one of the best pre-transformations for general use (Legendre & Gallagher, 2001), including the analysis of presence–absence data. These transformed species composition data tables were used as multivariate response data in variation partitioning (see section 2.5 for details on variation partitioning).

2.3 | Predictor sets of environmental filters

2.3.1 | Predictor sets of herb and tree compositions

Vascular plant species were recorded in 20 m × 20 m subplots for ALB, HAI and SCH, in a circular 200 m² plot for BAY, and in a square of 200 m² for STE. The per cent coverage of single species was recorded for tree layer, shrub layer and herb layer (see Supporting information S1.2 for details on plant species sampling). For tree composition, the percentage cover of each woody plant species at each height layer was summed to obtain the cumulative cover of the species. For herb composition, only presence–absence data from the herb layer were used.

A principal coordinate analysis (PCoA) was applied on Euclidean distance matrices computed on Hellinger-transformed matrices of tree and herb composition, respectively (see Section 2.2 for details on Hellinger transformation). PCoA produces an ordination solution maximizing the variance of the observations using eigenvalue decomposition while preserving the dissimilarities among sites (Borcard et al., 2011). The ordination axes that explained >75% of the variance of the data were selected as predictor sets related to tree and to herb composition.

2.3.2 | Predictor set of forest physiognomy

Airborne laser scanning (ALS) data were collected to obtain forest physiognomy metrics for the 1-ha plots during the leaf-on seasons between 2007 and 2018, depending on the region (see Table S3 for details on ALS acquisitions). Similar pre-processing methods using

"LAStools" (Isenburg, 2018) were employed overall five forest regions, including the classification of outliers as well as ground and non-ground returns (i.e. vegetation returns). The height of the vegetation returns was normalized to the height above ground level (a.g.l.) using a high-resolution elevation model derived from the ground returns. Forest physiognomy was described using ALS metrics describing the vertical profile, vertical heterogeneity, canopy surface roughness and the horizontal heterogeneity of the canopy. All ALS metrics were derived from the normalized point cloud (Table 1). For the vertical profile, the mean height of the vegetation returns was used, and the penetration ratios of the canopy layer (above 2 m) and regeneration layer (below 2 m) were determined. Penetration ratios, defined as the proportion of points filtered by a specific horizontal layer, were used to characterize the filtering within each layer and were calculated by dividing the number of returns above the respective layer by the number of returns below that layer. The standard deviation and coefficient of variation of the height of the vegetation returns and the foliage height diversity were computed to characterize the vertical heterogeneity. Canopy roughness was described by creating a gridded canopy height model (CHM) with a spatial resolution of 1 m using the highest point in each cell. The surface area of the CHM was derived using the triangulation algorithm presented in Jenness (2004). Surface roughness was then estimated using two metrics: the ratio between the planimetric and the surface area of the CHM and the standard deviation of the CHM. Horizontal canopy heterogeneity was assessed by analysing canopy-gap distributions. A gridded binary gap mask with a 1-m spatial resolution was created in which cells were classified as gaps if >20% of all vegetation returns had a height ≤2 m. To avoid very small or narrow gaps, only gap features >50 m² in size and thicker than a perimeter–area ratio >1.5 were selected. From the filtered gap mask the total area of the gaps, the standard deviation of the gap sizes, the mean perimeter–area ratio, the mean fractal dimension, the total edge length and the edge density of forest gaps were calculated using the R package "landscapemetrics" (Hesselbarth et al., 2019). Finally, a principal component analysis (PCA) was applied to the forest physiognomy metrics acquired by ALS. Similar to the approach used for the tree and herb composition data, the ordination axes that explained >75% of the variance of the data were selected as predictors of forest physiognomy.

2.4 | Predictor sets of regional species pool and dispersal limitations

For the inter-region analysis, the predictor sets of regional species pool and dispersal limitations were modelled using principal coordinates of neighbour matrices (PCNM) and the *dbmem* in the package "adespatial" (Stéphane Dray et al., 2017) (Figure 1b). The sites of the five regions are clearly clustered by the region. Therefore, if we would represent the spatial structure of our sites only by x and y coordinates (two variables), the fine-scale spatial structure within each region could be easily obscured by the primary large-scale

spatial structure. The PCNM analysis was developed by Borcard and Legendre (2002) to represent the fine-scale spectrum of spatial structures covering an extensive range of scales. In this study, it was applied as follows: First, a geographical distance matrix between the plots of five regions was created, after which the distance matrix was truncated by the minimum distance between different forest regions. Any pair-wise distances above this minimum distance threshold ($\text{min}_{\text{inter-regional distance}}$) were thus considered as large and were set to four times of $\text{min}_{\text{inter-regional distance}}$ (see Borcard and Legendre (2002) for a detailed explanation of the use of the multiplicate "four"). Such an adjusted pair-wise distance matrix is an object-by-object matrix, thus required to be transformed into an object-by-variable matrix for regression analysis. For it, the PCNM analysis employs a principle component analysis which then results in the distance-based Moran's eigenvectors orthogonal to one another. Among the eigenvectors, only the positive eigenvalues represent the Euclidean components of the neighbourhood relationships. These positive eigenvectors were extracted and are called PCNM variables hereafter. Lastly, we fitted an analysis of variance model (ANOVA) to the PCNM variables using *aov* and region as the independent variable to disentangle the PCNM variables that differed significantly between regions to generate a predictor set for the regional species pool (henceforth, "regional spatial structure") and those that did not differ significantly between regions (henceforth, "landscape spatial structure") hence representing dispersal limitations within a region (see more details in Figure S2).

For the intra-region analysis, a predictor set of dispersal limitations was also modelled using a PCNM in each region (Figure 1d). A geographical distance matrix between the plots of each region was created and truncated by the maximum distance in the minimum spanning tree; the positive PCNM variables of the distance-based Moran's eigenvectors were then applied.

2.5 | Statistical analyses

2.5.1 | Variation partitioning

Variation partitioning through redundancy analysis (RDA) ordination was applied to the species composition of 11 functional groups to assess the independent and shared effects of the predictor sets on the variation between local communities for two hypotheses tests (Figure 1c,e). RDA is a method of regression analysis modelling multivariate response data (species composition data tables in this study).

For the inter-region analysis, variation partitioning was conducted over the five forest regions to compare the importance of regional species pool, dispersal limitations and environmental filtering (Figure 1b). To evaluate the contribution of environmental filtering, predictor sets of herb composition (PCoA axes), tree composition (PCoA axes) and forest physiognomy (PCA axes) were included. Regional spatial structures (regional PCNMs) were included as predictor sets of regional species pool and landscape spatial structures (landscape PCNMs) as predictor sets of dispersal limitations

(see Section 2.4 for details). In total, variation partitioning for the inter-region analysis was conducted 11 times, that is on each of the Hellinger-transformed species composition data tables of 11 functional groups over entire plots at all regions as a response variable.

For the intra-region analysis, variation partitioning was conducted for each forest region to compare the importance of three environmental filters (the PCA axes of forest physiognomy and the PCoA axes of herb and tree composition) and dispersal limitations (spatial structure by PNCM) (Figure 1d). In total, variation partitioning for the intra-region analysis was conducted 55 times, that is on each of the Hellinger-transformed species composition data tables of the 11 groups of the five regions, separately.

First, the function *forward.sel* in the R package "adespatial" (Stéphane Dray et al., 2017) was used with 9,999 permutations to forward-select the explanatory variables in each predictor set to select the variables that correlated significantly with the response variables. The function *varpart* in the R package "vegan" (Jari Oksanen et al., 2017) was then used in variation partitioning with the predictor sets containing at least one significant variable.

The variation explained by each independent and shared effect for each functional group was quantified by calculating an adjusted R^2 following the method of Peres-Neto et al. (2006). In the inter-region analysis, the total variation explained was assessed by calculating an adjusted R^2 for each functional group. In the intra-region analysis, the mean of the adjusted R^2 of the five forest regions for each functional group was used. In calculations of the mean values over regions, if an effect on a forest region was insignificant, the adjusted R^2 was defined as 0.

2.5.2 | Permutation-based independence tests

To determine whether the relative importance of landscape spatial structure as a proxy for dispersal limitations depends on dispersal ability, the results of variation partitioning obtained in the inter-region analysis were compared among the 11 functional groups (Figure 1c). The ratio between the independent variance explained by landscape spatial structure and the sum of the independent variance explained by all predictor sets was calculated for each group. Differences between the 11 functional groups in terms of their dispersal ability were identified by categorizing the 11 groups accordingly. Bryophytes, lichens and fungi that disperse via spores were classified into a spore-dispersal group with rank 1 on the ordinal scale, because these organisms rapidly disperse over tens to hundreds of kilometres (Abrego et al., 2018; Komonen & Müller, 2018). Birds and bats as flying vertebrates were ranked second, based on their ability to move over several kilometres within a short time (Dietz et al., 2009). Arthropods with shorter dispersal distances were ranked third (Komonen & Müller, 2018). Thus, the 11 groups were tested as ordinal predictors in permutation-based independence tests, with the alternative hypothesis being *greater*, using the function *indepence_test* in the R package "coin" (Hothorn et al., 2008).

The dependency of the relative importance of forest physiognomy on trophic position and body size was examined by comparing the results of variation partitioning in the intra-region analysis for the 11 functional groups (11 mean values of five regions) for the trophic position and for the eight animal groups for body size (Figure 1e). The relative importance of plant composition and forest physiognomy as proxies for environmental filtering was determined by first summing the effects of herb and tree composition to represent plant composition. The ratio of the variance independently explained by forest physiognomy to the sum of the variance independently explained by the predictor sets of plant composition and forest physiognomy was calculated for each group. Differences between the 11 functional groups with different trophic positions were identified by categorizing the 11 groups accordingly. Bryophytes and lichens were classified as autotrophs with rank 1, fungi and saproxylic beetles into first decomposers (rank 1.5), phytophagous beetles and moths into primary consumers (rank 2), spiders and carabids beetles into secondary consumer group (a) (rank 3), necrophagous beetles into secondary decomposers (rank 3.5) and birds and bats into a secondary consumer group (b) (rank 4). Although necrophagous beetles consume carcasses of primary and secondary consumers (a) as well as secondary consumers (b), both arthropods and vertebrates, it was assumed that in the study area they mostly consume arthropods (primary or secondary consumers (a)). The relative positions of primary and secondary decomposers were a half trophic level higher than those of their diets (Steffan et al., 2017). Hence, the 11 groups were tested as ordinal predictors in permutation-based independence tests with the alternative hypothesis being *greater* and using the same function as described above for the first hypothesis test. The body size was measured by body length for all beetles, length of prosoma and opisthosoma for spiders, length from the thorax to the abdomen for moths, head-body length for bats and length from the tip of beak to end of tail feathers for birds (Table S4). The body size data were collected from literature and own measurements (see Table S4 for sources). The body size was tested only for the eight animal groups, as the underlying argument of this hypothesis was related to the expectation of higher importance of habitat structure shaping species turnover of larger home-range size. The median body size of each functional group was taken and natural log-transformed to represent the body size of each group for permutation-based independence tests with the alternative hypothesis being *greater*.

Chao and Jost (2012) introduced the coverage-based sample completeness to standardize the comparability of species data of different communities. Therefore, to check the robustness of our results for animal groups (eight groups with the abundance-based data) against the sampling completeness, we re-ran the inter-region and intra-region variation partitioning using a subset of plots with sample coverage over 70%. Although sample coverages of bryophytes, fungi and lichens could not be calculated by plot due to its data type (the presence–absence data), sample completeness of the three groups was expected to be more stable than animal groups due to their static characteristics. When re-analysing independence

tests using a subset of plots with sample coverage over 70%, the relative importance of bryophytes, fungi and lichens was fixed with their values of the total data set.

We also tested the robustness of our results against the addition of other environmental factors than vegetation-related factors, which was the focus of this study, especially for the intra-region analysis. We re-ran the inter-region variation partitioning and independence tests for the dispersal ability hypothesis after including climate and topographic gradients (please see details of climate and topography predictor sets in Table S5).

3 | RESULTS

Total β-diversity (0.990 ± 0.003) was composed of the species turnover (0.972 ± 0.025) and the species nestedness (0.018 ± 0.024) components. The species turnover, a focus of this study, accounted for 98.1% of the total β-diversity (Table S6).

In the inter-region analysis, the unique and shared effects of proxies for regional species pool (regional spatial structure), dispersal limitations (landscape spatial structure) and environmental filtering (environmental factors related to vegetation) explained 35.28% (± 8.36%) of the variation in the community composition of the 11 functional groups (Figure 2a; Table S7). Over half of this variation (22.97% ± 5.95%) was explained by the shared effects of at least two predictor sets (proxies). The shared effects between regional spatial structure and environmental factors accounted for 20.77% (± 6.04%) and those between landscape spatial structure and environmental factors for 2.67% (± 1.86%) over the 11 groups (Figure S3; Table S8). As an independent effect, environmental factors were the strongest driver of the variation in the community composition, with a unique explained proportion of the total variation of 6.56% (± 1.75%), followed by regional spatial structure and landscape spatial structure with 3.87% (± 1.88% *SD*) and 1.87% (± 0.74%), respectively (Figure 2a; Table S8; Figure S3). However, the order and strength of the importance of the three predictor sets varied between functional groups. The relative importance of landscape spatial structure increased significantly with decreasing dispersal ability, that is from the spore-dispersal groups, to vertebrates, to arthropods (Figure 2b; Figure S4a; Tables S9, S10). This finding corroborated the findings of the additional data set including climate and topographic gradients (Figure S5).

In the intra-region analysis, landscape spatial structure and the three environmental factors (tree and herb composition and forest physiognomy) together explained 19.36% (± 9.84%) of the variation in community composition for the five forest regions and 11 functional groups (Figure 3a; Table S7). Half of this variation (10.34% ± 6.69%) was explained by the shared effects of at least two predictor sets, as our suites of predictor sets were associated with each other and hence simultaneously affected the response variables. The unique effect of each predictor set was rather low, with landscape spatial structure as the most important factor as it explained 3.44% (± 4.12%) of the variation independently, followed by herb composition, forest physiognomy

FIGURE 2 The relative importance of regional spatial structure, landscape spatial structure and environmental factors. (a) The variation (adjusted R^2) in the assemblage composition of 11 functional groups as explained by the three predictor sets. The environmental factors (green bars) include the effects of herb composition, tree composition and forest physiognomy. The regional spatial structure (orange bars) is represented by the principal coordinates of neighbour matrices (PCNM) variables that differed significantly between regions. The landscape spatial structure (blue bars) describes the effects of dispersal filters within regions by finer PCNM variables. Bars with shading lines represent the shared effects of at least two predictor sets. (b) The relative importance of landscape spatial structure increases significantly along groups with a decreasing dispersal ability: spore-dispersal groups, vertebrate and arthropods
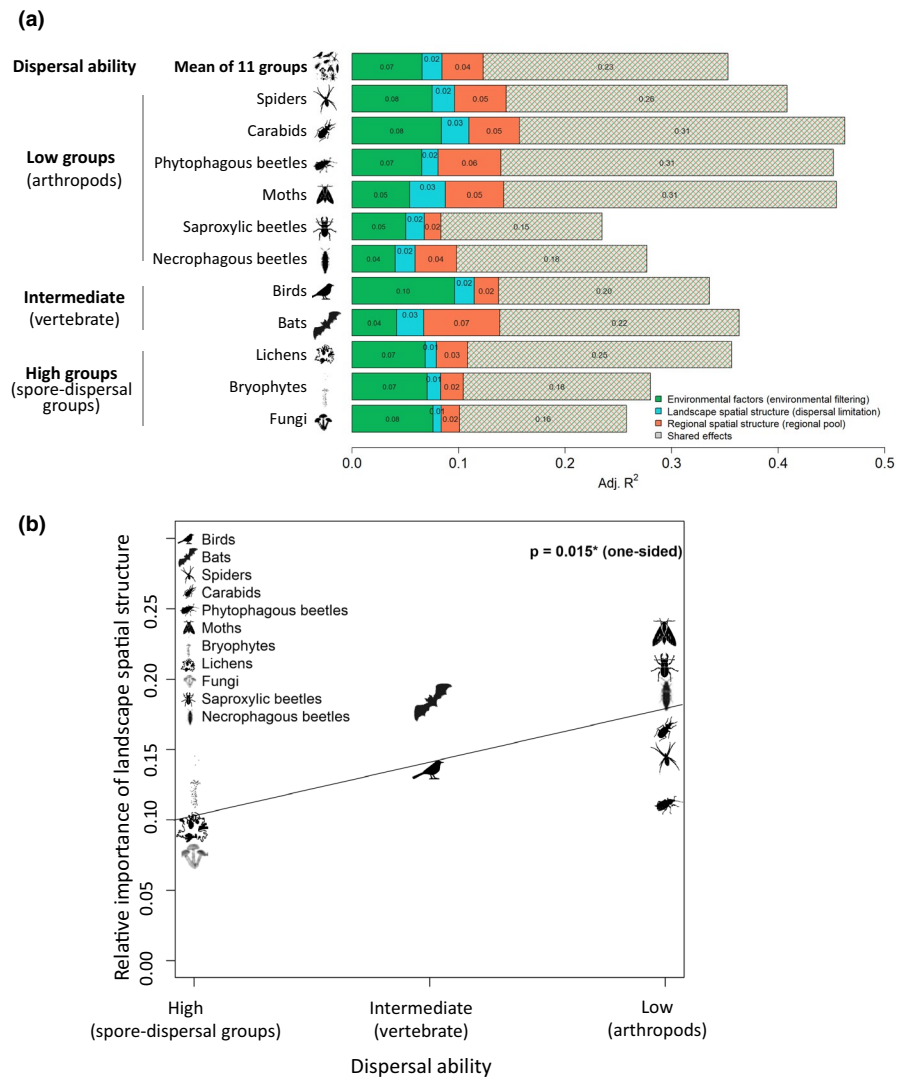
and tree composition with 2.86% (± 2.31%), 1.49% (± 1.88%) and 1.23% (± 1.15%), respectively (Figure 3a and 3b; Figure S6; Table S11).

A comparison of the importance of spatial vs. environmental factors showed that the latter had larger effects on all functional groups except moths. The comprehensive effects of the three environmental factors independent from the effect of landscape spatial structure explained a total of 11.72% (± 6.98%) (based on the mean adjusted R² of 55 cases) of the variation, while the landscape spatial structure independently explained 3.44% (± 4.12%) of the variation (Figure 3a; Table S12).

Among the environmental filtering factors, the relative importance of herb composition, tree composition and forest physiognomy differed between functional groups. For the assemblage composition of birds and bats, the highest trophic groups and the largest body size groups in our study, forest physiognomy had the most important effect on the variation in the community composition (Figure 3b). For the other groups, herb or tree composition (mainly herb) was more important than forest physiognomy. The significant increase in the relative importance of forest physiognomy with increasing trophic position and body size suggested that forest physiognomy is a strong driver of the community composition

of higher trophic positions and larger body size (Figure 3c and 3d; Figure S4b and S4c; Tables S10 and S13).

To check the robustness of our results of animals for sample completeness, we re-analysed the data on a subset of plots with sample coverage above 70%. These findings corroborated the findings of the total data set (Tables S14–S16).

4 | DISCUSSION

In the years since its introduction (Whittaker, 1972), interest in β-diversity has increased, especially following the development of statistical tools allowing its assessment (Legendre et al., 2005). However, few studies have focused on the mechanisms structuring the species composition of local communities across a wide range of taxonomic-functional groups. Our study showed that the relative contributions of the various mechanisms differ depending on the dispersal ability, trophic position or body size of the group of interest, in line with our hypotheses.

The aim of the inter-region analysis was to assess the relative importance of regional spatial structure, landscape spatial structure
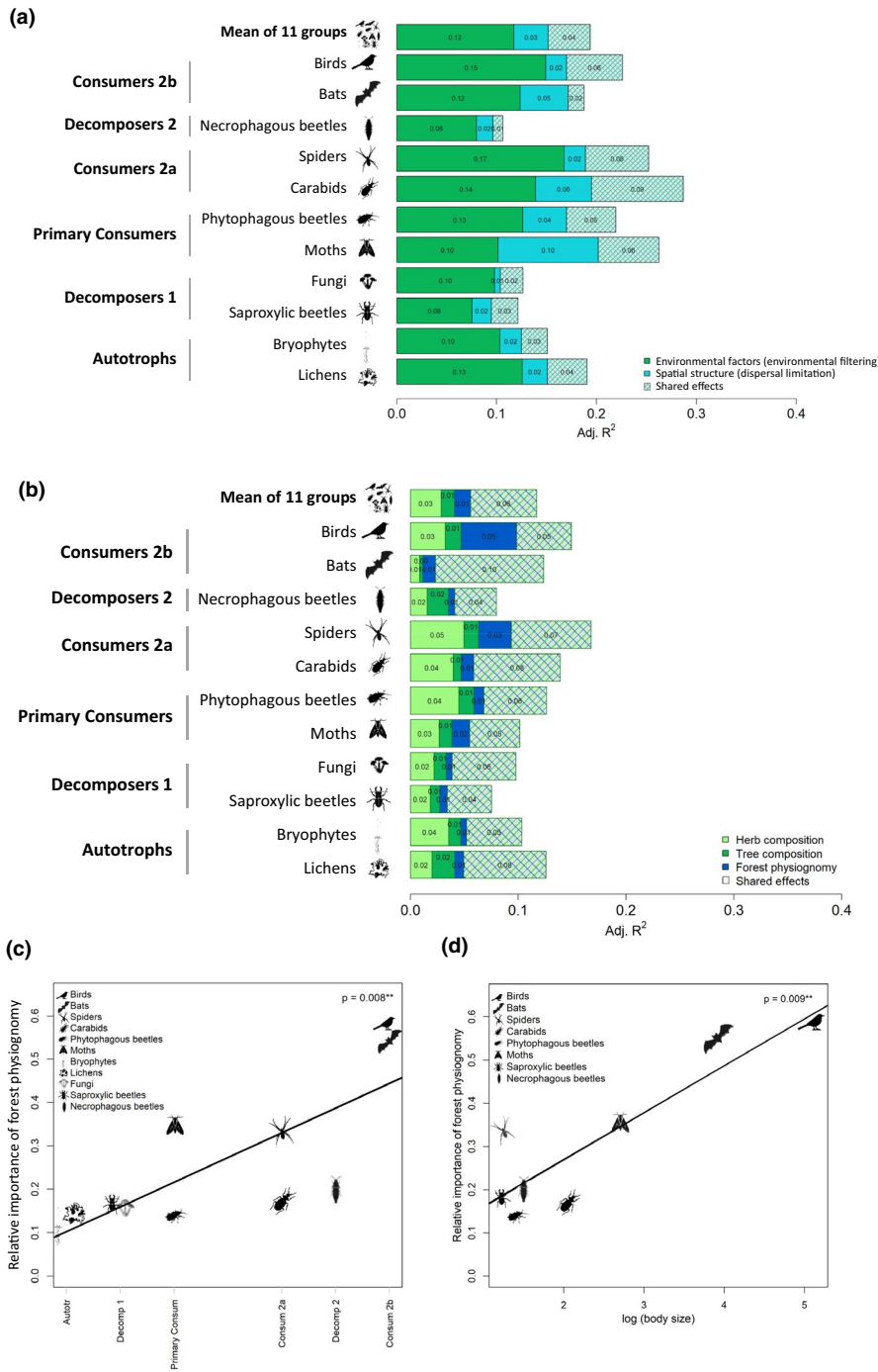
FIGURE 3 The relative importance of spatial structure vs. environmental factors and of forest physiognomy vs. plant species composition. (a) The relative importance of spatial structure vs. environmental factors. The explained variation (adjusted R^2) of the assemblage composition of 11 functional groups averaged over five regions. The environmental factors (green bars) include the effects of herb composition, tree composition and physiognomy. The spatial structure is represented by blue bars. The bars with shading lines represent the shared effects of at least two predictor sets. (b) The relative importance of forest physiognomy vs. plant species composition. The effects of herb composition (yellow green bars), tree composition (green bars) and physiognomy (blue bars) are shown together with the variation explained by the shared effects (grey bars). (c) The ratio of the effects of forest physiognomy vs. the total effects of environmental factors significantly increased with increasing trophic position. (d) The ratio of the effects of forest physiognomy vs. the total effects of environmental factors significantly increased with increasing body size. (This analysis was applied only to animals, as this hypothesis is related to the home-range size.)

and environmental factors on species turnover. As species turnover accounted for most of the total β-diversity, we interpreted our result on the variation of community composition as species turnover henceforth. We found that environmental factors are a more important determinant of species turnover, but that the importance of landscape spatial structure increases for less dispersive species. Across the 11 functional groups, environmental factors rather than spatial structure (regional, local) were of greater importance in shaping assemblage composition across a 1-ha local grain. Previous studies showed that geographical distance is more important than environmental factors at larger spatial extents, as demonstrated for a

pan-European vs. country extent (Keil et al., 2012; Qian et al., 2005). Therefore, spatial extent should be considered in comparisons of niche vs. neutral processes. The findings of our inter-regional analysis are in line with those of studies conducted at the same country-wide extent but with a grain coarser (0.25–400 km²) than the 1 ha of our study. Both Keil et al. (2012) and Zellweger et al. (2017) showed that geographical distance was less important than environmental variables for plants, butterflies and birds in Europe. This suggests that environmental filtering determines species turnover even at a country-wide extent, rather than regional species pool and dispersal limitations.

However, a strong deviation from this general pattern was determined for the assemblage composition of bats in the inter-region analysis, as the effect of regional spatial structure was nearly twice as high as that of environmental factors. This result suggested a strong effect of regional species pool on the species turnover of bats and it can be explained by the different roosting behaviours and adaptations for the winter period of different species (i.e. climate filter), thus giving rise to the regional species pool currently observed for European bats (Kalda et al., 2015). The addition of climate and topography predictor sets to environmental factors as a supplementary analysis (Figure S5) reduced the unique contribution of regional spatial structure but increased the shared effects between regional spatial structure and environmental factors (i.e. effects of regionally distinguished climate and topography) in the formation of bat assemblages. The regionally clustered species pool of bats can also be attributed to land use changes at a regional scale, which were shown to drive the regional extinction of some bat species (Safi & Kerth, 2004).

Our first dispersal ability hypothesis (Figure 1c) states increasing relative importance of dispersal limitations with decreasing dispersal ability. In line with this, the relative importance of landscape spatial structure (a proxy for dispersal limitations) was shown to depend on the potential dispersal ability of the functional groups, as groups that can disperse over long distances via spores, such as fungi, lichens and bryophytes, were less affected by landscape spatial structure (as dispersal limitations) than groups with a low dispersal ability. The stronger geographical separation of less dispersive functional groups has been demonstrated, for example, for less mobile ground-dwelling arthropods vs. more mobile birds and vascular plants (Ferrier et al., 1999) and for snails vs. birds (Steinitz et al., 2006). However, our study is the first to examine the importance of spatial structure in the species turnover of spore-dispersers vs. that of vertebrates and arthropods. This dependency on dispersal ability within a region was a consistent finding that did not change even after the addition of other environmental filters (Figure S5), and it suggested that dispersal limitations are more important for less dispersive species.

In the debate over popular niche vs. neutral processes, ecologists have argued that species turnover explained by geographical distance (in our study, regional and landscape spatial structures) can be attributed to factors other than dispersal limitation. The relative importance of geographical distance for species turnover may vary with the environmental characteristics of the study area (e.g. latitude, land use history or heterogeneity) and depending on the study design (e.g. the quality of the included environmental variables and the effects of unmeasured environmental variables) (Murphy et al., 2015). In our study, half of the variation explained by regional and landscape spatial structure was co-explained by environmental differences, because our predictor sets of environmental factors were highly spatially structured. It can thus be assumed that there is another, unmeasured fraction of spatially structured environmental variables, such as climate or topographic gradients, contributing to the variation uniquely explained by regional and landscape spatial structure. This can be seen in Figure S4, which shows the increased

shared effects and decreased unique effect of regional spatial structure following the addition of climate and topographic predictor sets. Disentangling the independent contributions of multiple effects, particularly those of the regional species pool, requires studies with a much larger number of regional replicates.

The intra-region analysis compared the importance of plant species composition and forest physiognomy on species turnover, after correcting for spatial structure. The results showed the increasing importance of forest physiognomy with increasing trophic position and body size, although the importance of plant composition was stronger on average. For the 11 functional groups in the forests, most could be sorted primarily according to the difference in plant composition, not in forest physiognomy. These results are similar to those of Schaffers et al. (2008), who found that plant composition in meadows consistently outperformed forest physiognomy and abiotic factors in predicting the variation in the composition of seven arthropod groups, even though those groups differed in their trophic positions, ranging from phytophagous to predators. The effects of plant composition on the species turnover of diverse functional groups can be attributed to the trophic associations between producers and consumers, which reflect the ability of different plant species to provide different food resources for herbivores. In addition to this direct effect, bottom-up effects across trophic positions towards carnivores and decomposers may play an indirect role (Scherber et al., 2010; Schuldt et al., 2019). Additionally, plant composition is likely to represent other factors, such as soil characteristics and local land use effects on species composition (Murphy et al., 2015), which were not measured in our study. Thus, plant composition might be the best predictor, as it not only reflects direct effects but also compensates for lack of important ecological information (Penone et al., 2019; Schaffers et al., 2008; Zellweger et al., 2017).

Yet, physiognomic factors were more important for the species turnover of higher trophic groups or large-bodied groups, particularly birds and bats. This finding supported our second hypothesis that the relative importance of forest physiognomy relative to plant composition increases with increasing trophic position and body size. Our result was consistent with that reported for the species turnover of birds in a temperate forest in Central Europe (Müller et al., 2010) and thus with the important role of forest physiognomy in bird diversity introduced by MacArthur and MacArthur (1961). The favoured forest physiognomy (density of the shrub or tree layer) of birds depends on their diet, foraging, resting or nesting traits (MacArthur, 1958). For bats, our results are in agreement with previous studies showing that bat species are specifically adapted to different foraging spaces such that their assemblages are strongly structured by forest physiognomy (Arlettaz et al., 2001; Jung et al., 2012; Schnitzler & Kalko, 2001).

Carnivorous arthropods (spiders, carabid beetles) were more strongly affected by forest physiognomy than by the species composition of the tree layer, whereas communities of producers, herbivorous insects and decomposers were structured more strongly by the tree layer composition than by forest physiognomy. For

closed forests, the major elements of their physiognomy reflect the physical structure of the tree rather than the herb layer. For carabid beetles, forest physiognomy features, such as canopy cover, were shown to separate assemblage of forest species from those of open habitat species, due to different microclimate sensitivities (Fuller et al., 2008; Lange et al., 2014). Penone et al. (2019) also noted the large effect of canopy cover across 13 trophic groups of a forest community, including carnivorous arthropods, a finding attributed to the change in light availability and therefore in temperature and moisture as well. Forest physiognomy also plays a role in the habitat selection of spiders. For example, many species respond to microclimate, such as by avoiding extreme temperatures, and build their webs using the physical structure of the habitat (Uetz, 1991). For European spiders, continental-wide niche quantification identified shading as the most important gradient shaping their niches (Entling et al., 2007).

The relative importance of plant composition vs. forest physiognomy on species turnover varies with the spatial scale and with landscape compositions that differ in the diversity of their habitat types. Early studies conducted in grass- and shrublands, in which scale dependency was explored in terms of the relative contribution of plant composition vs. forest physiognomy on bird species turnover, showed the greater importance of forest physiognomy on a large scale and plant composition on a small scale (Rotenberry, 1985; Wiens et al., 1987). In addition to scale dependency, their relative contributions on species turnover are determined by landscape composition, with forest physiognomy overriding the effects of plant composition in landscapes with more diverse habitat types (Mac Nally, 1990). Our study contributes to this discussion by showing that the relative importance of plant composition and forest physiognomy in driving species turnover varies according to the trophic position and body size of the species. Thus, our study underlines the need for studies that span multiple trophic levels and taxa of widely varying body sizes (Seibold et al., 2018).

Overall, in our study, the unique effects of the predictor sets and the total explained variance were low. In both cases, this may have been due to the high number of explanatory variables, reflected in the reduced adjusted R^2 values. On average, 11.02 ($\pm$ 5.33 SD) predictors were used in the intra-region analysis and 38.09 ($\pm$ 9.35 SD) in the inter-region analysis. The difference between R^2 and adjusted R^2 values of the total explained variance was 6.72% ($\pm$ 1.79%) in the intra-region analysis and 12.98% ($\pm$ 4.40%) in the inter-region analysis. A lack of important environmental information on species turnover, such as historical or current land use and its intensity, might also account for the low total explained variance. The few unique effects of the predictor sets were due to the large proportion of their shared effects, since our chosen environmental factors were spatially structured inter- and intra-regionally.

Our work contributes to a better understanding of the mechanisms underlying species turnover between local forest communities from a multi-taxa and multi-scale approach. It identified environmental filtering rather than the regional species pool or dispersal limitations as the most important mechanism driving species turnover on a country-wide extent. In terms of environmental filtering related to vegetation, plant composition was shown to be more important than forest physiognomy for the multi-taxa species turnover within a forest region. However, the relative importance of the mechanisms depends on the dispersal ability, trophic position and body size of the considered functional groups, consistent with our hypotheses. Dispersal limitations had a stronger influence on the species turnover of less dispersive functional groups, and forest physiognomy on that of higher trophic groups and species groups with larger body size. These results can serve as the basis for conservation planning at two scales. At the inter-regional scale, the effects of environmental filtering and regional species pools on the species turnover of forest communities call for conservation strategies establishing the systematic distribution of protected areas that cover a wide range of environmental and biogeographical gradients, such as the framework of Natura 2000 (Ostermann, 1998). For forest management within regions, our study showed that the protection of a high β-diversity requires a focus on plant species composition and forest physiognomy. Active forest management can thus control the β-diversity of different functional groups, by diversifying tree species composition and forest physiognomy.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13204.

ORCID

Soyeon Bae https://orcid.org/0000-0003-1961-1226
Lea Heidrich https://orcid.org/0000-0002-3229-4758
Shaun R. Levick https://orcid.org/0000-0003-4437-9174
Martin M. Gossner https://orcid.org/0000-0003-1516-6364
Sebastian Seibold https://orcid.org/0000-0002-7968-4489
Wolfgang W. Weisser https://orcid.org/0000-0002-2757-8959
Paul Magdon https://orcid.org/0000-0003-3777-5478
Claus Bässler https://orcid.org/0000-0001-8177-8997
Deborah Schäfer https://orcid.org/0000-0001-9591-841X
Ernst-Detlef Schulze https://orcid.org/0000-0001-6188-9219
Inken Doerfler https://orcid.org/0000-0001-9624-1922
Kirsten Jung https://orcid.org/0000-0002-9449-2215
Marco Heurich https://orcid.org/0000-0003-0051-2930
Nicolas Roth https://orcid.org/0000-0002-8423-7288
Peter Schall https://orcid.org/0000-0003-4808-818X
Steffen Boch https://orcid.org/0000-0003-2814-5343
Stephan Wöllauer https://orcid.org/0000-0002-3623-8294
Swen C. Renner https://orcid.org/0000-0002-6893-4219
Jörg Müller https://orcid.org/0000-0002-1409-1586

REFERENCES

Abrego, N., Norros, V., Halme, P., Somervuo, P., Ali-Kovero, H., & Ovaskainen, O. (2018). Give me a sample of air and I will tell which species are found from your region: Molecular identification of fungi from airborne spore samples. *Molecular Ecology Resources*, *18*(3), 511–524. https://doi.org/10.1111/1755-0998.12755

Aisen, S., Werenkraut, V., Márquez, M. E. G., Ramírez, M. J., & Ruggiero, A. (2017). Environmental heterogeneity, not distance, structures montane epigaeic spider assemblages in north-western Patagonia (Argentina). *Journal of Insect Conservation*, *21*(5), 951–962. https://doi.org/10.1007/s10841-017-0034-8

Arlettaz, R., Jones, G., & Racey, P. A. (2001). Effect of acoustic clutter on prey detection by bats. *Nature*, *414*(6865), 742–745. https://doi.org/10.1038/414742a

Bae, S., Levick, S. R., Heidrich, L., Magdon, P., Leutner, B. F., Wöllauer, S., & Müller, J. (2019). Radar vision in the mapping of forest biodiversity from space. *Nature Communications*, *10*(1), 4757. https://doi.org/10.1038/s41467-019-12737-x

Baselga, A., Orme, C. D. L., Villeger, S., De Bortoli, J., & Leprieur, F. (2018). *betapart: Partitioning Beta Diversity into Turnover and Nestedness*.

Bässler, C., Förster, B., Moning, C., & Müller, J. (2009). The BIOKLIM project: Biodiversity research between climate change and wilding in a temperate montane forest: The conceptual framework. *Waldökologie, Landschaftsforschung Und Naturschutz*, *7*(7), 21–34.

Beck, J., Holloway, J. D., Khen, C. V., Kitching, I. J. Associate Editor: Mathew, A. L., & Editor: Mark, A. M. (2012). Diversity partitioning confirms the importance of beta components in tropical rainforest lepidoptera. *The American Naturalist*, *180*(3), E64–E74. https://doi.org/10.1086/666982

Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical Ecology with R*, Vol. 17.

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, *153*(1), 51–68. https://doi.org/10.1016/S0304-3800(01)00501-4

Components. *R package version 1.5.1*. Retrieved from https://CRAN.R-project.org/package=betapart

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology and Evolution*, *32*(6), 429–437. https://doi.org/10.1016/j.tree.2017.03.004

Calderón-Patrón, J. M., Moreno, C. E., Pineda-López, R., Sánchez-Rojas, G., & Zuria, I. (2013). Vertebrate dissimilarity due to turnover and richness differences in a highly beta-diverse region: the role of spatial grain size. Dispersal ability and distance. *Plos One*, *8*(12), e82905. https://doi.org/10.1371/journal.pone.0082905

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, *93*(12), 2533–2547. https://doi.org/10.1890/11-1952.1

Chase, J. M., & Myers, J. A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1576), 2351–2363. https://doi.org/10.1098/rstb.2011.0063

Cornell, H. V., & Lawton, J. H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *Journal of Animal Ecology*, *61*(1), 1–12. https://doi.org/10.2307/5503

Dietz, C., von Helversen, O., & Nill, D. (2009). *Bats of Britain, Europe and Northwest Africa*. A & C Black Publishers Ltd.

Dobrovolski, R., Melo, A. S., Cassemiro, F. A. S., & Diniz-Filho, J. A. F. (2012). Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *21*(2), 191–197. https://doi.org/10.1111/j.1466-8238.2011.00671.x

Doerfler, I., Müller, J., Gossner, M. M., Hofner, B., & Weisser, W. W. (2017). Success of a deadwood enrichment strategy in production forests depends on stand type and management intensity. *Forest Ecology and Management*, *400*, 607–620. https://doi.org/10.1016/j.foreco.2017.06.013

Dray, S., Blanchet, G., Borcard, D., Guenard, G., Thibaut, J., Guillaume, L., & Wagner, H. H. (Eds.) (2017). *adespatial: Multivariate Multiscale Spatial Analysis*. R package version 0.0-8. Retrieved from https://CRAN.R-project.org/package=adespatial

Entling, W., Schmidt, M. H., Bacher, S., Brandl, R., & Nentwig, W. (2007). Niche properties of Central European spiders: Shading, moisture and the evolution of the habitat niche. *Global Ecology and Biogeography*, *16*(4), 440–448. https://doi.org/10.1111/j.1466-8238.2006.00305.x

Ferrier, S., Gray, M. R., Cassis, G. A., & Wilkie, L. (1999). Spatial turnover in species composition of ground-dwelling arthropods, vertebrates and vascular plants in north-east New South Wales: Implications for selection of forest reserves. In *The other 99%: The conservation and biodiversity of invertebrates* (pp. 68–76). Sydney, NSW: Royal Zoological Society of New South Wales.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E. K. V., Linsenmair, K. E., Schulze, E.-D., & Weisser, W. W. (2010). Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology*, *11*(6), 473–485. https://doi.org/10.1016/j.baae.2010.07.009

Fuller, R. J., Oliver, T. H., & Leather, S. R. (2008). Forest management effects on carabid beetle communities in coniferous and broadleaved forests: Implications for conservation. *Insect Conservation and Diversity*, *1*(4), 242–252. https://doi.org/10.1111/j.1752-4598.2008.00032.x

Hagge, J., Abrego, N., Bässler, C., Bouget, C., Brin, A., Brustel, H., Christensen, M., Gossner, M. M., Heilmann-Clausen, J., Horák,

J., Gruppe, A., Isacsson, G., Köhler, F., Lachat, T., Larrieu, L., Schlaghamersky, J., Thorn, S., Zapponi, L., & Müller, J. (2019). Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. *Journal of Biogeography*, 46(5), 1054–1065. https://doi.org/10.1111/jbi.13556

Harrison, S., Ross, S. J., & Lawton, J. H. (1992). Beta Diversity on Geographic Gradients in Britain. *Journal of Animal Ecology*, 61(1), 151–158. https://doi.org/10.2307/5518

Hesselbarth, M. H. K., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography*, 42(10), 1648–1657. https://doi.org/10.1111/ecog.04617

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018). Biodiversity along temperate forest succession. *Journal of Applied Ecology*, 55(6), 2756–2766. https://doi.org/10.1111/1365-2664.13238

Hothorn, T., Hornik, K., Van De Wiel, M. A., & Zeileis, A. (2008). Implementing a class of permutation pests: The coin package. *Journal of Statistical Software*, 28(8), 1–23.

Hubbell, S. P. (1997). A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, 16(1), S9–S21. https://doi.org/10.1007/s003380050237

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography (MPB-32)*. :Princeton University Press.

Isenburg, M. (2018). *LAStools*. Retrieved from http://lastools.org

Jari Oksanen, F., G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, & H. Wagner (Eds.) (2017). *vegan: Community Ecology Package. R package version 2.4-3*. Retrieved from https://CRAN.R-project.org/package=vegan

Jenness, J. S. (2004). Calculating landscape surface area from digital elevation models. *Wildlife Society Bulletin*, 32(3), 829–839. https://doi.org/10.2193/0091-7648(2004)032[0829:CLSAFD]2.0.CO;2

Jiménez-Alfaro, B., Girardello, M., Chytrý, M., Svenning, J.-C., Willner, W., Gégout, J.-C., Agrillo, E., Campos, J. A., Jandt, U., Kącki, Z., Šilc, U., Slezák, M., Tichý, L., Tsiripidis, I., Turtureanu, P. D., Ujházyová, M., & Wohlgemuth, T. (2018). History and environment shape species pools and community diversity in European beech forests. *Nature Ecology & Evolution*, 2(3), 483–490. https://doi.org/10.1038/s41559-017-0462-6

Jiménez-Valverde, A., Baselga, A., Melic, A., & Txasko, N. (2010). Climate and regional beta-diversity gradients in spiders: Dispersal capacity has nothing to say? *Insect Conservation and Diversity*, 3(1), 51–60. https://doi.org/10.1111/j.1752-4598.2009.00067.x

Jung, K., Kaiser, S., Böhm, S., Nieschulze, J., & Kalko, E. K. V. (2012). Moving in three dimensions: Effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *Journal of Applied Ecology*, 49(2), 523–531. https://doi.org/10.1111/j.1365-2664.2012.02116.x

Kalda, R., Kalda, O., Lõhmus, K., & Liira, J. (2015). Multi-scale ecology of woodland bat the role of species pool, landscape complexity and stand structure. *Biodiversity and Conservation*, 24(2), 337–353. https://doi.org/10.1007/s10531-014-0811-6

Keil, P., Schweiger, O., Kühn, I., Kunin, W. E., Kuussaari, M., Settele, J., Henle, K., Brotons, L., Pe'er, G., Lengyel, S., Moustakas, A., Steinicke, H., & Storch, D. (2012). Patterns of beta diversity in Europe: The role of climate, land cover and distance across scales. *Journal of Biogeography*, 39(8), 1473–1486. https://doi.org/10.1111/j.1365-2699.2012.02701.x

Kent, R., Bar-Massada, A., & Carmel, Y. (2014). Bird and mammal species composition in distinct geographic regions and their relationships with environmental factors across multiple spatial scales. *Ecology and Evolution*, 4(10), 1963–1971. https://doi.org/10.1002/ece3.1072

Komonen, A., & Müller, J. (2018). Dispersal ecology of deadwood organisms and connectivity conservation. *Conservation Biology*, 32(3), 535–545. https://doi.org/10.1111/cobi.13087

Lange, M., Türke, M., Pašalić, E., Boch, S., Hessenmöller, D., Müller, J., Prati, D., Socher, S. A., Fischer, M., Weisser, W. W., & Gossner, M. M. (2014). Effects of forest management on ground-dwelling beetles (Coleoptera; Carabidae, Staphylinidae) in Central Europe are mainly mediated by changes in forest structure. *Forest Ecology and Management*, 329, 166–176. https://doi.org/10.1016/j.foreco.2014.06.012

Legendre, P., Borcard, D., & Peres-Neto, P. R. (2005). Analyzing beta diversity: Partitioning the spatial variation of community composition data. *Ecological Monographs*, 75(4), 435–450. https://doi.org/10.1890/05-0549

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2), 271–280. https://doi.org/10.1007/s004420100716

Mac Nally, R. C. (1990). The roles of floristics and physiognomy in avian community composition. *Australian Journal of Ecology*, 15(3), 321–327. https://doi.org/10.1111/j.1442-9993.1990.tb01036.x

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39(4), 599–619. https://doi.org/10.2307/1931600

MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42(3), 594–598. https://doi.org/10.2307/1932254

Müller, J., & Goßner, M. M. (2010). Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. *Biological Conservation*, 143(3), 625–633. https://doi.org/10.1016/j.biocon.2009.11.027

Müller, J., Stadler, J., & Brandl, R. (2010). Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of lidar. *Remote Sensing of Environment*, 114(3), 490–495. https://doi.org/10.1016/j.rse.2009.10.006

Murphy, S. J., Audino, L. D., Whitacre, J., Eck, J. L., Wenzel, J. W., Queenborough, S. A., & Comita, L. S. (2015). Species associations structured by environment and land-use history promote beta-diversity in a temperate forest. *Ecology*, 96(3), 705–715. https://doi.org/10.1890/14-0695.1

Ostermann, O. P. (1998). The need for management of nature conservation sites designated under Natura 2000. *Journal of Applied Ecology*, 35(6), 968–973. https://doi.org/10.1111/j.1365-2664.1998.tb00016.x

Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M. R., Gossner, M. M., Seibold, S., Simons, N. K., Schall, P., Plas, F., Manning, P., Manzanedo, R. D., Boch, S., Prati, D., Ammer, C., Bauhus, J., Buscot, F., Ehbrecht, M., Goldmann, K., Jung, K., … Fischer, M. (2019). Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecology Letters*, 22(1), 170–180. https://doi.org/10.1111/ele.13182

Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, 87(10), 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:vposdm]2.0.co;2

Qian, H. (2009). Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. *Journal of Systematics and Evolution*, 47(5), 509–514. https://doi.org/10.1111/j.1759-6831.2009.00043.x

Qian, H., Ricklefs, R. E., & White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, 8(1), 15–22. https://doi.org/10.1111/j.1461-0248.2004.00682.x

Ricklefs, R. E. (1987). Community diversity: Relative roles of local and regional processes. *Science*, 235(4785), 167–171. https://doi.org/10.1126/science.235.4785.167

Rotenberry, J. T. (1985). The role of habitat in avian community composition: Physiognomy or floristics? *Oecologia*, 67(2), 213–217. https://doi.org/10.1007/bf00384286

Safi, K., & Kerth, G. (2004). A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conservation Biology*, 18(5), 1293–1303. https://doi.org/10.1111/j.1523-1739.2004.00155.x

Schaffers, A. P., Raemakers, I. P., Sýkora, K. V., & ter Braak, C. J. F. (2008). Arthropod assemblages are best predicted by plant species composition. *Ecology*, 89(3), 782–794. https://doi.org/10.1890/07-0361.1

Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S. C., … Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, 55(1), 267–278. https://doi.org/10.1111/1365-2664.12950

Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D., Roscher, C., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N., Buscot, F., Clement, L. W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., … Tscharntke, T. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468(7323), 553–556. https://doi.org/10.1038/nature09492

Schnitzler, H.-U., & Kalko, E. K. V. (2001). Echolocation by Insect-Eating Bats: We define four distinct functional groups of bats and find differences in signal structure that correlate with the typical echolocation tasks faced by each group. *BioScience*, 51(7), 557–569. https://doi.org/10.1641/0006-3568(2001)051[0557:ebieb]2.0.co;2

Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N., Durka, W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L. R., Klein, A.-M., Roscher, C., Schaller, J., von Oheimb, G., Weigelt, A., Weisser, W., Wirth, C., … Eisenhauer, N. (2019). Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications*, 10(1), 1460. https://doi.org/10.1038/s41467-019-09448-8

Seibold, S., Cadotte, M. W., MacIvor, J. S., Thorn, S., & Müller, J. (2018). The necessity of multitrophic approaches in community ecology. *Trends in Ecology & Evolution*, 33(10), 754–764. https://doi.org/10.1016/j.tree.2018.07.001

Steffan, S. A., Chikaraishi, Y., Dharampal, P. S., Pauli, J. N., Guédot, C., & Ohkouchi, N. (2017). Unpacking brown food-webs: Animal trophic identity reflects rampant microbivory. *Ecology and Evolution*, 7(10), 3532–3541. https://doi.org/10.1002/ece3.2951

Steinitz, O., Heller, J., Tsoar, A., Rotem, D., & Kadmon, R. (2006). Environment, dispersal and patterns of species similarity. *Journal of Biogeography*, 33(6), 1044–1054. https://doi.org/10.1111/j.1365-2699.2006.01473.x

Svenning, J.-C., Fløjgaard, C., & Baselga, A. (2011). Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction. *Journal of Animal Ecology*, 80(2), 393–402. https://doi.org/10.1111/j.1365-2656.2010.01771.x

Uetz, G. W. (1991). Habitat structure and spider foraging. In S. S. Bell, E. D. McCoy, & H. R. Mushinsky (Eds.), *Habitat structure: The physical arrangement of objects in space* (pp. 325–348). Springer, Netherlands.

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

Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, 21(2/3), 213–251. https://doi.org/10.2307/1218190

Whittaker, R. H., Levin, S. A., & Root, R. B. (1973). Niche, habitat, and ecotope. *The American Naturalist*, 107(955), 321–338. https://doi.org/10.1086/282837

Wiens, J. A., Rotenberry, J. T., & Van Horne, B. (1987). Habitat occupancy patterns of north american shrubsteppe birds: The effects of spatial scale. *Oikos*, 48(2), 132–147. https://doi.org/10.2307/3565849

Zellweger, F., Roth, T., Bugmann, H., & Bollmann, K. (2017). Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. *Global Ecology and Biogeography*, 26(8), 898–906. https://doi.org/10.1111/geb.12598

BIOSKETCH

Soyeon Bae is a postdoctoral researcher at the University of Würzburg, Germany. Her research concerns habitat heterogeneity and biodiversity, especially the application of remote sensing in ecology. Her current project investigates the main drivers of biodiversity in temperate forests and the main mechanisms behind species loss. The broader aim of this work is to establish a general framework for managing the three-dimensional structures and biodiversity of forests at different scales.

Author contributions: S.B. (the first one) and J.M. (the last one) conceived the idea of the study and wrote the first manuscript draft. S.B. (the first one), J.M. (the last one), L.H., M.M.G., S.S., W.W.W. and P.M. contributed to developing the study. All authors collected or processed data and contributed to revisions of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.