Unravelling drivers of forest biodiversity: Contrasting effects of mean environmental conditions, environmental heterogeneity and landscape context

Abstract

1. Understanding how biodiversity varies under different environmental conditions is one of the central aims of ecology. Mean environmental conditions and heterogeneity have an effect on biodiversity. Increased heterogeneity is generally associated with increased diversity, but mean conditions tend to have a stronger influence. Conditions on site are embedded into a landscape context, which adds another layer of complexity to be considered. Due to the rarity of multi-taxon data it remains unclear if resulting patterns are similar across taxa. Most European forests are managed, and management strongly influences both mean conditions and heterogeneity. How different species groups respond to variation in these forest characteristics is therefore crucial for testing ecological theories and designing effective conservation measures for management.

2. We assessed the effects of environmental conditions on biodiversity of seven taxonomic groups in a temperate mountain forest area in Central Europe. We analysed the responses of biodiversity (species richness, Shannon diversity, and β-diversity) to three groups of environmental variables: local mean conditions, local heterogeneity, and landscape. Our objectives were to determine which group of variables is most important in explaining biodiversity variation, and whether certain environmental conditions have consistent effects on the diversity of multiple taxonomic groups.

3. We found that the effects of environmental conditions varied substantially between taxa and aspects of biodiversity. The proportion of conifers had the largest number of significant effects overall, but the direction varied between taxa. None of the three groups of variables was more relevant in explaining the variation in biodiversity. While an increase in local heterogeneity and higher values in the landscape context were associated with increased diversity, an increase in mean conditions was mainly negatively associated with diversity.

4. *Synthesis and applications.* Our results show that no single factor or group of factors affects biodiversity across different species groups in the same way. For management, this means that stand-level interventions, such as retention of old-growth elements, are likely not sufficient to promote the many aspects of biodiversity. Instead, different types of management are likely needed for objective-specific biodiversity conservation at the landscape scale.

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[1]**Corresponding Author:** Carlos M. Landivar Albis. carlos.landivar@bfw.gv.at. Department of Forest Growth, Silviculture and Genetics, Austrian Research Centre for Forests (BFW). Vienna, Austria

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Gita Benadi[1], Julian Frey[2], Carlos M. Landivar Albis[3,4], Michael Wohlwend[1], Marco Basile[5], João M. Cordeiro Pereira[1,12], Martin Denter[6], Anna-Lena Hendel[1], Marlotte Jonker[1,7], Sara Klingenfuß[8], Nolan Rappa[9], Sebastian Schwegmann[1], Ninon Meyer[1, 16], Andreea Petronela Spînu[10], Max Zibold[8,11], Nathalie Winiger[1], Jürgen Bauhus[10], Veronika Braunisch[12, 16], Carsten F. Dormann[3], Marc Hanewinkel[13], Alexandra Klein[10], Daniela Kleinschmit[15], Barbara Koch[6], Michael Staab[14], Gernot Segelbacher[1], Michael Scherer-Lorenzen[8], and Ilse Storch[1]

[1]Chair of Wildlife Ecology and Management, University of Freiburg. Freiburg, Germany

[2]Chair of Forest Growth and Dendroecology, University of Freiburg.Freiburg, Germany

[3]Chair of Biometry and Environmental System Analysis. University of Freiburg. Freiburg, Germany

[4]Department of Forest Growth, Silviculture and Genetics, Austrian Research Centre for Forests (BFW). Vienna, Austria

[5]Swiss Federal Research Institute for Forest, Snow and Landscape Research (WSL). Birmensdorf, Switzerland

[6]Chair of Remote Sensing and Landscape Information Systems, University of Freiburg. Freiburg, Germany

[7]Zoogdiervereniging (Dutch Mammal society), Nijmegen, Netherlands

[8]Chair of Geobotany, University of Freiburg. Freiburg, Germany

[9]Chair of Nature Conservation and Landscape Ecology, University of Freiburg. Freiburg, Germany

[10]Chair of Silviculture, University of Freiburg. Freiburg, Germany

[11]State Museum of Natural History Karlsruhe, Department of Biosciences, Karlsruhe, Germany

[12]Forest Research Institute Baden-Wuerttemberg (FVA). Freiburg, Germany

[13]Chair of Forestry Economics and Forest Planning, University of Freiburg. Freiburg, Germany

[14]Ecological Networks, Technical University Darmstadt. Darmstadt, Germany

[15]Department of Biology, University of Toronto. Toronto, Canada

[16]Department of Conservation Biology, Institute of Ecology and Evolution, University of Bern. Bern, Switzerland

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Author Contribution

The research setting (GRK2123 ConFoBi) was designed by Ilse Storch, Jürgen Bauhus, Veronika Braunisch, Carsten F. Dormann, Marc Hanewinkel, Alexandra Klein, Barbara Koch, Gernot Segelbacher and Michael Scherer-Lorezen. Gita Benadi, Julian Frey, Carlos Miguel Landivar and Michael Wohlwend conceived the ideas and designed methodology; Marco Basile, Joao M. Cordeiro, Martin Denter, Anna-Lena Hendel, Marlotte Jonker, Sara Klingenfuß, Nolan Rappa, Sebastian Schwegmann, Ninon Meyer, Andreea Petronela Spinu, Max Zibold and Nathalie Winiger collected the data; Gita Benadi, Carlos Miguel Landivar Albis and Julian Frey prepared and analysed the data; Gita Benadi, Carlos Miguel Landivar Albis and Michael Wohlwend led the writing of the manuscript. All authors critically contributed to the manuscript and gave their final approval for publication.

Corresponding Author

Carlos M. Landivar Albis. carlos.landivar@bfw.gv.at. Department of Forest Growth, Silviculture and Genetics, Austrian Research Centre for Forests (BFW). Vienna, Austria

Data Availability

The data supporting this study's findings will be made available on Dryad upon acceptance of the manuscript.

Conflict of interest

The authors have no conflict of interest to declare.

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Keywords

Multi-taxa biodiversity, environmental conditions, environmental heterogeneity, temperate forest, conservation management.

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2. We assessed the effects of environmental conditions on biodiversity of seven taxonomic groups in a temperate mountain forest area in Central Europe. We analysed the responses of biodiversity (species richness, Shannon diversity, and β-diversity) to three groups of environmental variables: local mean conditions, local heterogeneity, and landscape. Our objectives were to determine which group of variables is most important in explaining biodiversity variation, and whether certain environmental conditions have consistent effects on the diversity of multiple taxonomic groups.

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Introduction

Environmental conditions are the architects of biodiversity. Among these conditions, the availability of energy and limiting resources plays a pivotal role fostering greater biodiversity (Coelho et al., 2025). More energy allows for larger population sizes, which reduces extinction risk and expands the community's total niche space, ultimately enriching the regional species pool (e.g. Hawkins et al., 2003; Field et al., 2009). This relationship aligns with the "more-individuals hypothesis," which posits that higher resource availability sustains greater numbers of individuals and, consequently, more species reducing the probability of local extinctions (Srivastava and Lawton, 1998; Storch et al., 2018).

One of the most studied mechanisms of biodiversity variation under environmental conditions is the heterogeneity-diversity relationship (e.g. Stein et al., 2014, and references therein). According to thishypothesis, spatially heterogeneous environments can accommodate more species because they provide a greater variety of niches and resources (Bazzaz, 1975). However, some studies also found none or even negative effects of heterogeneity on species richness (reviewed by Tews et al., 2004; Stein et al., 2014). An explanation for such divergent patterns is a trade-off between the amount of resources or habitat types and the available area of each habitat or resource (area-heterogeneity trade-off: Kadmon and Allouche, 2007; Allouche et al., 2012). This trade-off produces a hump-shaped relationship between heterogeneity and diversity, with a decrease of biodiversity at high heterogeneity levels due to a greater risk of stochastic extinctions in increasing smaller patches with suitable conditions. Although the relationship between environmental heterogeneity and biodiversity can be more complex than initially thought (Heidrich et al., 2020), the notion that heterogeneity is generally beneficial for biodiversity is still widespread in the ecological and nature conservation literature (e.g. Benton et al., 2003; Bollmann et al., 2009; Brunet et al., 2010; Kati et al., 2010; Uhl et al., 2024; Ampoorter et al., 2020).

However, biodiversity also depend on historical and biotic conditions. Common or historically predominant environmental conditions tend to harbour larger, yet often less diverse, species pools, as these conditions favour a narrower range of ecological strategies (e.g. Taylor et al., 1990; Pärtel et al., 1996; Ewald, 2003; Zobel, 2016). Finally, the physical landscape itself acts as both a canvas and a constraint: it defines the spatial availability of habitats and their fragmentation, particularly influencing species with limited dispersal ability and strongly dependent on habitat connectivity (Fuentes-Montemayor et al., 2017). Together, these factors intricately weave the tapestry of biodiversity, highlighting the interplay between environmental mean conditions, heterogeneity, historical processes, and spatial structure.

Although the separate effects of environmental heterogeneity, mean environmental site conditions, and landscape context on biodiversity have been the subject of numerous studies, few have evaluated the relative importance of these factors for variation in species diversity. Evidence from plant communities suggests that the quantity of resources influence the richness of the species under a wider range of conditions than resource heterogeneity (Stevens and Carson, 2002; Bartels and Chen, 2010; Šímová et al., 2013). However, direct comparisons between these drivers across different taxa are still scarce. Such a comparison would improve our understanding of forest biodiversity drivers and provide valuable information to preserve and promote biodiversity in managed ecosystems, where environment heterogeneity can be influenced.

In temperate European forests, both mean environmental conditions and heterogeneity are strongly influenced by management (Menge et al., 2023). While traditionally the primary purpose of forest management has been timber production, biodiversity conservation has become an important additional goal in managed forests, as unmanaged forests dedicated for conservation are limited in size and connectivity (Bollmann and Braunisch, 2013). Traditional forest management for timber production frequently reduces structural heterogeneity at the stand level, for example, variation in tree age and height (Brunet et al., 2010; Bauhus et al., 2017), and decreases the availability of resources and habitats such as deadwood and tree cavities (e.g. Müller et al., 2007).

In order to compensate for these effects, retention forestry was recently introduced to Central Europe to promote the preservation of physical old-growth elements such as deadwood and large old trees. These could act as resources and refuges for species dependent on them. This old-growth elements also serve as stepping stones in the landscape contributing to connectivity (Gustafsson et al., 2012; Lindenmayer et al., 2012; Fedrowitz et al., 2014). Whether biodiversity in general benefits from retention forestry is still an area of active investigation (Gustafsson et al., 2020, and references therein), however this knowledge is crucial for practitioners and conservationists alike.

Previous studies on the effects of forest characteristics on biodiversity compared general management types (such as clear cut and selective cutting) (e.g. Paillet et al., 2010; Chaudhary et al., 2016; Schall et al., 2018) or focused on relationships between particular forest characteristics (e.g., tree species diversity, deadwood) and diversity of single taxonomic groups (e.g. Gil-Tena et al., 2007; Vockenhuber et al., 2011; Bouget et al., 2013). In comparison, the response of multiple taxa to variation in forest structure still remains understudied, mostly because it requires a large, concerted effort. Studies such as Penone et al. (2019); Ampoorter et al. (2020); Sabatini et al. (2019); Schall et al. (2020); Heidrich et al. (2020) and Heidrich et al. (2023) showed mixed responses for different species groups, but also clear and consistent effects of mean local conditions related, in particular, to the type of dominant tree (conifers vs. oak) and canopy cover. However, it is unclear whether their results can be transferred to other species groups or forest types, such as conifer-dominated mountain forests.

In this study, we investigate the influence of mean environmental conditions and environmental heterogeneity on the species diversity of seven taxonomic groups in a temperate mountain forest area in central Europe. Forest stands included in this study are mainly conifer-dominated or mixed conifer-broadleaved forests and managed by selective logging under continuous cover forestry with different degrees of retention of deadwood and large habitat trees. As predictors of diversity, we included structural and compositional variables largely determined by forest management and physical site conditions, which in previous studies explained a substantial part of the variation in biodiversity, especially in mountain ecosystems (Körner, 2007). In addition to local-scale heterogeneity and mean conditions, we also included variables describing the landscape in our analyses, as many organisms move and disperse over areas larger than the size of our study plots. We studied three aspects of biodiversity: I) species richness, as it is the most widely used diversity measure, higher levels of species richness are generally associated with greater ecosystem functioning, stability, and productivity, II) Shannon diversity, to account for species' relative abundances, using a good indicator of abundance and evenness, and III) β diversity, to account for the identity of species co-occurring at each site and species turnover between sites. Our main aims were to elucidate whether one of the three groups of environmental variables has a dominant effect in explaining variation in biodiversity, and to test if any of the environmental conditions has a homogeneous effect (same direction) across several taxonomic groups and aspects of biodiversity.

Concise information regarding these aspects will give a concise evaluation of the range and way in which they shape biodiversity and foster ecological theory evaluation as conservation practice alike.

Methods

Study area

The study area is located in the Black Forest (Schwarzwald) in Baden-Württemberg, southern Germany. Small parts of the study area to the east are outside of the bioregion of the Black Forest (Naturraum Baar) but are subsumed for simplicity. The area is dominated by granite and gneiss to the west and south, while to the east and north sandstone prevails. Limestone areas can be found on the eastern edge. The climate is temperate, but has a relatively large temperature gradient, ranging from 4°C average annual temperature in the mountains ($<$1500 m. a.s.l.) to 10.4°C in the lowlands ($>$ 120 m.a.s.l.) (Gauer and Aldinger, 2005). About 75% (3650 km^2) of the area is forested, with forest mostly consisting of Norway spruce (*Picea abies*) (42.8%) followed by silver fir (*Abies alba*) (18.5%) and beech (*Fagus sylvatica*) (15.3%). While Norway spruce is seen as naturally occurring in the region in higher elevations, it has been planted preferably in the past for economic reasons, leading to a high share of canopy cover in the landscape (Spiecker et al., 2000).

Plot selection

Our study is based on 135 one hectare forest plots located within state-owned and managed forests. The plots are above 400 and below 1500 metres m.a.s.l. and contain no bodies of water except for puddles or little brooks. None of the plots exceed an average slope of more than 35°, but plots are rarely flat. Plots were selected based on two gradients, initially estimated using remote sensing and later confirmed and adjusted on the ground. Those gradients were 1) forested area in proximity (as an indicator of connectivity) and 2) the volume of deadwood (as a proxy for the effect of different retention levels). (Storch et al., 2020)

Biodiversity data

We included data from seven groups defined by taxonomy and sampling methods in the analyses: vascular plants, wood-inhabiting fungi (hereafter: fungi), birds, bats, mammals, beetles (insect order Coleoptera) and cavity-nesting bees and wasps (order Hymenoptera). Beetles were identified at the family level, and bats were assigned to acoustic groups (some of which are single species) according to their calls. All other groups were identified at the species level. Larger, terrestrial mammals (hereafter: mammals) were recorded using camera traps. Small mammals (rodents and insectivores) were excluded because the camera setup was not optimal for their detection. Data collected during repeated visits to a study plot or at more than one location within a plot were pooled for the analyses to obtain a single abundance/activity value per species and plot. Plants, fungi, bees and wasps were sampled with equal effort in all study plots. For the remaining four groups, we quantified the sampling effort per plot according to the sampling method (e.g. number of visits for birds). We included the sampling effort as a covariate in the statistical models for all taxa. A detailed description of the sampling methods can be found in the supplementary material.

Environmental variables

We classified our predictors of species diversity into three groups: local mean conditions (LM), local heterogeneity (LH), and landscape context (LC) (Table 1). Most variables could be placed

Table 1: Overview of environmental variables included as predictors in the analyses of species richness, Shannon diversity and β diversity. Variables are categorized as local mean (LM), local heterogeneity (LH), a special category for variables that fall in both mean and heterogeneity (LM/LH) and landscape context (LC) and separated by dashed lines. Landscape variables are reported here for a circle of 10 km^2. Values for all buffer sizes can be found in the supplementary information.

Variable	**Category**	**Minimum**	**Maximum**	**Median**
Mean canopy height (m)	Local mean	4.35	32.45	16.90
Mean elevation (m a.s.l.)	Local mean	443	1334	831
Deadwood volume (m^3)	Local mean	4.91	486.01	42.14
Aspect – Northness	Local mean	-1.00	1.00	0.14
Aspect – Eastness	Local mean	-1.00	1.00	0.05
Proportion of coniferous tree cover	Local mean/local heterogeneity	0.04	1.00	0.92
Canopy gap share	Local mean/local heterogeneity	0.00	0.42	0.12
Mean slope (°)	Local mean/local heterogeneity	1	34	14
Stand structural complexity index (SSCI)	Local heterogeneity	2.01	13.28	3.59
Standard deviation of canopy height (m)	Local heterogeneity	3.26	17.92	10.15
Shannon diversity of tree species	Local heterogeneity	0.06	1.87	0.96
Deadwood diversity	Local heterogeneity	1.04	3.12	2.16
Forest cover (in a circle of 10 km^2)	Landscape	0.12	0.90	0.51
Proportion of coniferous forest (in a circle of 10 km^2)	Landscape	0.01	0.96	0.62

in a single category, but some can be interpreted as both local mean or local heterogeneity (e.g. Canopy gap share). Since we were interested in general patterns across different taxa, we chose variables potentially important for biodiversity and species composition of several taxonomic groups and excluded variables likely to affect one or two specific taxa disproportionately (e.g. soil pH). This means that our study does not raise the claim to capture the most important driver for a specific taxa, but focuses on the relative effect of drivers affecting many or all taxa in a dominant way.

For local mean and heterogeneity conditions, we included variables that describe both abiotic conditions and forest structure at each site. Where several measures were available to represent an aspect of forest structure or abiotic conditions, we selected the one that was closely correlated with the alternative measures and not too strongly correlated with other environmental conditions (Pearson's $r < 0.7$, supporting information). To characterise the landscape context around the study plots, we compiled a set of variables from publicly available data sources, including abiotic conditions, various classes of landcover, and NDVI (Normalized Difference Vegetation Index) as a measure of productivity. As many of these landscape context variables showed strong correlations either to the respective local conditions or to other landscape context variables, we decided to only include two landscape context variables in our models: forest cover and the proportion of coniferous forest (supporting information) calculated for circles of 1, 5, 10, 15 and 20 km² around plot centres. Since the strength and direction of the effects of landscape context attributes on biodiversity often vary with the spatial extent at which the landscape context variables are measured (e.g. Jackson and Fahrig, 2015), we tested both landscape context variables at five spatial scales and selected the scale with the best model performance (10 km²) . A detailed description of the data acquisition and preparation can be found in the supplementary material.

Statistical analyses

We modeled, species richness, Shannon diversity (e^H, i.e. the effective number of species) and β diversity (Bray-Curtis distance) of each of the seven taxonomic groups as a function of all environmental variables. In the following, α diversity refers to species richness and Shannon diversity, and β diversity refers to the Bray-Curtis distance. Deadwood volume and stand structural complexity index (SSCI) were log-transformed before the analyses to reduce skew in their distributions. Sampling effort was included as an additional covariate in the models of bats, birds, beetles and mammals in order to include any influence caused by it. All predictors were standardised to a mean of zero and a standard deviation of one to facilitate model convergence and comparisons of the strengths of the effects. Each model was run with the two landscape context variables (forest cover and proportion of coniferous forest) measured at each of the five spatial scales. We then selected the spatial scale with the best model performance based on AICc (Shannon diversity and species richness) or percent deviance explained (β diversity). Since we expected non-linear effects of some of the environmental variables on biodiversity, we modelled Shannon diversity and species richness using Generalized Additive Models (GAM; Wood, 2017), assuming a Gamma distribution with a logarithmic link for Shannon diversity and a Poisson distribution for species richness. We checked model assumptions using simulated residuals provided by the R package "DHARMa" (Hartig, 2022) and tested for residual spatial autocorrelation using Moran's I. As the residuals of the models of species richness of bats, beetles, birds and mammals showed underdispersion, we switched to a quasi-Poisson estimation procedure for these groups. To account for overdispersion in the models of bees and wasps and plants, we specified a negative binomial distribution. We did not a spatial autocorrelation structure in the model, since Moran's I test for residual spatial autocorrelation was only significant for the Shannon diversity of bats, and a semi-variogram of the residuals of this model showed no signs of autocorrelation. To model the β diversity of the seven species groups, we used generalized dissimilarity modelling (GDM; Ferrier et al., 2007). We modelled the matrix of Bray-Curtis distances between pairs of study plots as a function of their differences in environmental conditions and geographic distance. With the fitted model, we calculated a measure of variable importance based on the permutation of single predictors. Specifically, variable importance is the percentage change in deviance between models with the respective variable permuted and unpermuted.

All statistical analyses were performed using R version 4.2.2 (R Core Team, 2022).

Results

Effects of environmental conditions varied both between taxonomic groups (Table 2 and 3, Fig. 1 and 2). The predictors included in the models of α diversity explained on average 31% of variation in species/group richness and 23% of variation in Shannon diversity between sites. However, this proportion was much lower for plants (7% and 5%, respectively). Across all taxonomic groups, 18 of 102 combinations of predictor and response variable were significant for species/group richness and Shannon diversity. The number of significant variables was lowest in plant and mammal α diversity models. Most significant variables had monotonously increasing or decreasing effects on α diversity, which were often approximately linear (Supplementary material). Few relationships were hump-shaped or even more strongly non-linear. In models of β diversity, the average proportion of deviance explained was markedly lower (15.2%) than in models of Shannon diversity (34%) and species richness (41%). This proportion was highest for the β diversity of beetle families (34%) and lowest for plants (1%).

All three groups of variables (local mean conditions, local heterogeneity, landscape context) were equally important across taxa or aspects of biodiversity. While local higher levels of mean environmental conditions had mostly negative effects on α diversity, significant effects of local heterogeneity were generally positive, except for a negative relationship between stand structural complexity (SSCI) and Shannon diversity of beetle families (Fig. 1). At the local scale, both abiotic conditions and forest structure and composition explained some of the variation in biodiversity between study plots, but most variables only had significant effects on one or two of the seven taxonomic groups. For example, only mean canopy height had a significant effect on Shannon diversity of bats, while only canopy gap share affected the species richness of bees and wasps. Deadwood volume and diversity had no significant effect on any taxonomic group's richness or Shannon diversity, except for a slight positive effect of deadwood diversity on bat Shannon diversity. However, the two deadwood-related variables had an effect on the β diversity of several groups. Elevation was the most important abiotic factor, having a negative effect on richness of bees and wasps and Shannon diversity of bats, bees and wasps. The proportion of conifers (either at the local plot scale or in the surrounding landscape) was important for richness, Shannon diversity and β diversity of several taxonomic groups, but the direction of its effect on α diversity varied between taxa. For instance, both local and landscape scale proportion of conifers had negative effects on species richness of fungi, whereas landscape scale coniferous share was positively related to Shannon diversity of beetle families, birds and bees and wasps.

Model performance comparisons indicated that the most relevant spatial scale of the two landscape context variables differed between the seven taxonomic groups (Table 2 and 3) and between α and β diversity (supporting information). In models of α diversity, the smallest scale (1 km^2) was selected for Shannon diversity of plants and fungi and species richness of mammals, plants, and fungi, while the best models for bees and wasps had the largest extent tested (20 km^2), and the remaining groups were at an intermediate scale (5-15 km^2). For β diversity, the proportion of deviance explained by the model was highest at the largest spatial scale for four groups (plants, fungi, bees and wasps, mammals), at a slightly smaller scale for beetle families (15 km^2) and a much smaller scale for bats and birds (1 km^2).

For the four taxonomic groups with varying sampling efforts, sampling effort was of greater importance for richness and β diversity and less important for Shannon diversity (Fig. 1, 2). In models of β diversity, geographic distance did not play a major role for any taxonomic group (Fig. 2). Thus, communities closer together were not markedly more or less similar than communities farther away.

Table 2: Results of Generalized Additive Models (GAM) of species richness as a function of all environmental variables. Dashed lines separate variable groups: local mean (LM), local heterogeneity (LH), mean and heterogeneity (LM/LH), landscape context (LC), and sampling effort (in this order from top to bottom). For each taxonomic group, the landscape context scale with the lowest model AICc was chosen.

	Plants		Fungi		Beetles		Bees/wasps		Birds		Bats		Mammals	
	Edf	F value	Edf	F value	Edf	F value	Edf	F value	Edf	F value	Edf	F value	Edf	F value
Mean canopy height (m)	1.0	0.1	1.0	0.3	1.0	0.2	1.0	2.8	1.0	0.4	2.5	3.2*	2.2	1.3
Elevation (m)	1.0	0.8	1.3	1.1	2.5	0.9	1.0	34.8***	1.0	1.7	1.0	0.1	1.4	0.3
log(Deadwood volume (m^3))	1.0	0.2	1.0	1.7	1.0	0.4	2.0	5.7	2.3	1.9	1.0	1.1	1.0	0.0
Northness	1.1	0.0	1.0	0.1	1.0	2.0	1.0	2.3	1.0	0.6	1.5	0.7	1.0	0.1
Eastness	1.0	0.3	1.0	1.3	1.6	0.5	1.0	1.7	1.0	2.4	1.0	0.3	1.0	7.1**
Proportion of conifers	1.0	0.5	1.0	29.7***	1.5	1.5	1.0	0.0	1.0	0.3	1.0	0.0	1.0	0.4
Canopy gap share	1.0	0.2	1.8	1.7	1.0	0.6	1.0	5.0*	1.0	0.2	1.0	2.3	1.0	0.0
Mean slope	1.0	0.9	2.7	6.9	2.2	2.1	1.0	1.2	2.0	2.0	1.0	3.5	1.0	1.6
log(SSCI)	1.0	1.1	3.2	10.9*	1.7	2.6	1.0	8.3**	1.0	0.4	1.0	2.6	1.3	0.1
S.d. of canopy height (m)	1.0	0.8	1.0	2.0	1.0	0.0	1.7	4.8	1.3	0.1	1.0	8.6**	1.3	1.0
Tree Shannon diversity	1.4	0.2	1.2	9.4**	1.0	1.8	1.3	0.2	1.0	1.2	1.0	0.1	1.0	0.1
Deadwood diversity	1.0	0.3	1.0	0.1	1.0	1.3	1.0	1.5	1.0	0.3	1.0	1.6	1.0	0.8
Forest cover (1 km^2)	1.7	1.0	1.0	2.1									1.0	0.2
Coniferous forest share (1 km^2)	3.5	10.1*	1.0	5.0*									2.2	1.7
Forest cover (5 km^2)					1.0	9.5**								
Coniferous forest share (5 km^2)					2.2	0.8								
Forest cover (10 km^2)											1.0	2.8		
Coniferous forest share (10 km^2)											2.2	1.3		
Forest cover (15 km^2)									1.0	3.4				
Coniferous forest share (15 km^2)									1.0	4.3*				
Forest cover (20 km^2)							1.0	1.8						
Coniferous forest share (20 km^2)							1.1	6.0*						
Sampling effort					1.4	18.8***			1.0	65.1***	2.1	12.3***	3.0	5.2**
Deviance explained	0.18		0.45		0.44		0.49		0.56		0.44		0.30	
R^2	0.07		0.35		0.33		0.37		0.50		0.36		0.19	
Num. obs.	133		135		135		134		135		135		135	

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Table 3: Results of Generalised Additive Models (GAM) of Shannon diversity as a function of all environmental variables. Dashed lines separate variable groups: local mean (LM), local heterogeneity (LH), mean and heterogeneity (LM/LH), landscape context (LC), and sampling effort (in this order from top to bottom). For each taxonomic group, the landscape scale with the lowest model AICc was chosen.

	Plants		Fungi		Beetles		Bees/wasps		Birds		Bats		Mammals	
	Edf	F value	Edf	F value	Edf	F value	Edf	F value	Edf	F value	Edf	F value	Edf	F value
Mean canopy height (m)	1.0	1.1	1.0	0.5	1.0	0.0	2.3	1.7	1.0	0.2	1.0	10.4^{**}	2.8	2.1
Elevation (m)	1.0	0.8	1.3	2.4	3.3	2.6^{*}	1.2	25.4^{***}	1.0	1.1	1.0	4.2^{*}	1.0	0.1
log(Deadwood volume (m^3))	1.0	0.0	1.0	0.0	1.1	0.1	2.2	1.5	1.9	0.8	1.8	1.3	1.0	0.0
Northness	1.0	0.0	1.0	0.1	2.3	3.6^{*}	1.0	4.9^{*}	1.0	0.0	1.0	0.3	1.0	0.0
Eastness	1.0	0.0	1.0	0.3	1.0	0.1	1.0	4.1^{*}	1.0	2.7	1.0	0.3	1.0	0.3
Proportion of conifers	1.0	1.4	1.0	19.2^{***}	1.0	3.0	1.0	0.0	1.0	1.3	1.0	3.5	1.0	0.4
Canopy gap share	1.0	0.0	1.3	0.3	1.0	1.4	2.1	1.5	1.0	0.1	1.7	0.5	1.0	0.2
Mean slope	1.0	0.7	2.5	2.5	1.0	2.6	1.0	0.0	2.3	2.9^{*}	1.0	1.5	1.0	2.2
log(SSCI)	1.0	2.2	1.0	0.2	1.0	10.7^{**}	1.0	6.4^{*}	1.0	2.2	1.0	0.0	2.0	0.8
S.d. of canopy height (m)	1.0	0.9	1.0	1.5	1.0	1.9	1.7	0.7	1.1	0.9	1.0	0.1	1.0	2.4
Tree Shannon diversity	1.4	0.2	1.0	11.6^{***}	1.0	1.7	1.0	0.0	1.0	2.2	1.0	0.0	1.0	0.2
Deadwood diversity	1.0	0.1	1.0	0.0	1.0	0.3	1.0	1.2	1.0	0.2	1.0	7.5^{**}	1.0	0.2
Forest cover (1 km^2)	1.0	0.5	1.0	2.1										
Coniferous forest share (1 km^2)	3.4	2.8^{*}	1.0	3.6										
Forest cover (10 km^2)					1.0	1.8			1.0	2.4	1.6	1.7	1.5	2.8
Coniferous forest share (10 km^2)					2.1	5.6^{**}			1.0	5.8^{*}	1.0	2.2	1.0	0.2
Forest cover (20 km^2)							1.0	1.6						
Coniferous forest share (20 km^2)							1.0	9.1^{**}						
Sampling effort					1.0	0.2			1.0	27.4^{***}	1.4	0.9	2.0	2.9
Deviance explained	0.15		0.36		0.40		0.47		0.47		0.30		0.27	
R^2	0.05		0.27		0.30		0.27		0.40		0.18		0.16	
Num. obs.	133		135		135		134		135		135		135	

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

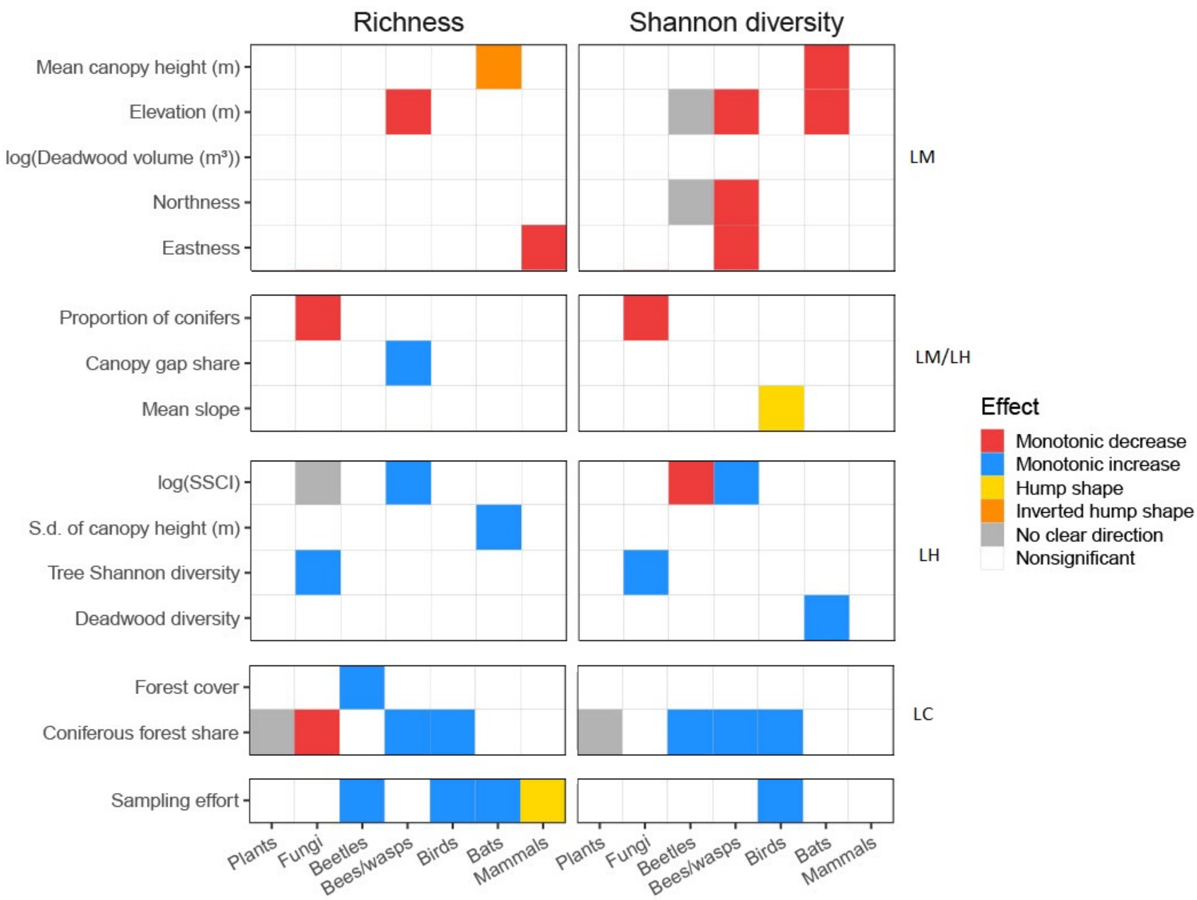

Figure 1: Effects of environmental conditions and sampling effort on Shannon diversity and species/group richness of all seven taxonomic groups. Environmental conditions are separated into groups: local mean (LM), local heterogeneity (LH), local mean or heterogeneity (LM/LH) and landscape context (LC). The results shown are based on Generalized Additive models (GAM) of the response variable modeled as a function of all predictors. Significant effects were assigned to one of five categories based on visual inspection of the fitted relationship (supporting information).

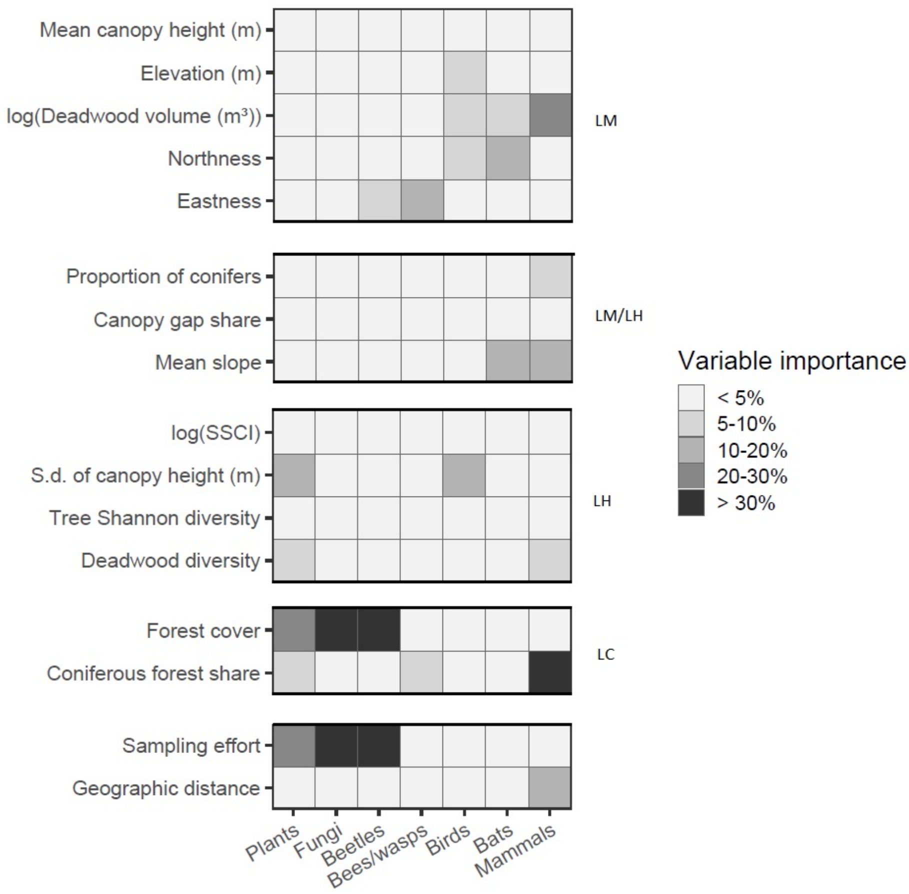

Figure 2: Importance of environmental variables, sampling effort and geographic distance for β diversity (Bray-Curtis distance between pairs of study plots) of all seven taxonomic groups. Environmental conditions are separated into groups: local mean (LM), local heterogeneity (LH), local mean or heterogeneity (LM/LH) and landscape context (LC). Variable importance was quantified as the per cent change in deviance between Generalized Dissimilarity Models (GDM) with the respective variable permuted and unpermuted.

Discussion

Our results highlight the variation of environmental predictor´s effect between different taxa diversity. Neither of the three groups of variables was more important than the other two in explaining the variation of biodiversity. However, the effect of local heterogeneity (when significant effect was found) was generally positive, suggesting that heterogeneity trade-offs do only play a minor role at the investigated spatial scales. The results of our study contributes to the growing evidence that each aspect of diversity is shaped by specific factors.

Relative importance of mean conditions, heterogeneity and landscape context for biodiversity

Among the environmental variables that were related to the diversity of more than one taxonomic group in this study, measures of mean conditions were not more or less important than those of heterogeneity. Although most studies comparing the effects of resource quantity (a mean condition) and resource heterogeneity on plant species richness found that quantity is the most important factor (e.g. Stevens and Carson, 2002; Bartels and Chen, 2010; Dormann et al., 2020), there is a lack of comparable studies on other groups of organisms. In a global meta-analysis, Field et al. (2009) found that variables related to climate or productivity explained significantly more of the difference in species richness of several taxa than other explanatory variables, including environmental heterogeneity. This difference was similar for plants and animals. However, the relative importance of climate and productivity diminished with decreasing spatial grain or extent of the study. At spatial scales comparable to our study, all groups of variables showed similar performance. In addition, Jorba et al. (2025) found that macro-climatic means (temperature and moisture) and vegetation-structure heterogeneity contributed almost equally to taxonomic, functional and phylogenetic diversity. Our results therefore outline the importance of mean conditions as well as heterogeneity for biodiversity. In fact, they demonstrate that different aspects of biodiversity in different species groups are highly diversely impacted by a multitude of factors and reductive approaches are unable to capture the complexity of forest ecosystems.

In this study, most of the significant effects of variables that indicate local heterogeneity on species richness or Shannon diversity exhibited a consistent positive trend, aligning with the habitat heterogeneity hypothesis (Stein et al., 2014, and references therein). We found barely any indication of trade-offs between area and heterogeneity. These differences in our findings compared to the most similar studies in the field, Heidrich et al. (2020) and Heidrich et al. (2023)

could potentially be attributed to variation in the selection of taxonomic groups and measures of heterogeneity. For example, the finer resolution of arthropod taxa and the inclusion of plant diversity as a predictor in their studies may explain these disparities. Therefore, results need to be re-evaluated depending on the specific taxonomic groups (e.g. higher/lower degree of aggregation) as well as the measure of heterogeneity applied and additionally the spatial scales investigated.

Our study raises a significant point: neither mean conditions nor heterogeneity emerge as predominant determinants of biodiversity variation at small spatial scales across taxa. If corroborated by further research, this represents additional proof for the complex species requirements at a fine scale.

Our investigation of landscape context variables revealed an interesting distinction. Although the share of coniferous forests exhibited strong and significant relationships with the α and β diversity of some taxonomic groups, the forest cover appeared less influential. Similar results were reprted by Li et al. (2025), where increasing the proportion of broadleaf trees doubled understory plant richness and stabilised soil-microbial β-diversity, whereas total forest cover in the buffer failed to predict any diversity metric. There is also evidence that tree-species composition and stand structure consistently outperform simple percent forest cover in explaining α- and β-diversity across arthropods, birds and fungi (Uhl et al., 2024) Thus, we cannot conclude that the landscape context was generally more or less important for biodiversity than local conditions, but rather that the type of available landscape context may play a role.

Theory posits that the scale at which environmental conditions impact species, known as the “scale of effect” should depend on species mobility (both local movements and dispersal: Miguet et al., 2016). Empirical tests, however, do not consistently support this prediction (Arroyo-Rodríguez et al., 2023). Despite the common assertion that larger animals should exhibit a larger scale of effect due to their longer dispersal distances (Jenkins et al., 2007), our findings did not align with this hypothesis. In our study system, the largest spatial scale tested (20 km^2) to α diversity for bees and wasps, but not mammals. Gengler et al. (2024) described how the spatial extent at which landscape variables shape biodiversity is influenced less by body size than by the type of metric of biodiversity, but also by life-stage-specific behaviour. This suggests that in our study, the maximum dispersal distance may not be the primary factor that determines the differences on the "scale of effect"

Effects of environmental variables across taxa

Our statistical models had relatively low proportions of explained variation, many non-significant effects and considerable variation between taxonomic group responses. These results show similarity to those of Penone et al. (2019), Heidrich et al. (2020) and Uhl et al. (2024), who studied the effects of forest attributes and environmental heterogeneity, respectively, on biodiversity of multiple taxa across temperate forests. Similarly, joint species-distribution models of 11 taxa showed that forest structure and edaphic conditions exerted highly divergent effects among groups (Kepfer-Rojas et al., 2024). One plausible explanation for the weak relationships between forest structure and biodiversity is the heterogeneous response of sub-groups and even individual species within each taxonomic group. These responses are most likely based on factors such as habitat preference, mobility, and dietary requirements. Our results suggest that the best predictors of occurrence and abundance may be species-specific, which could account for the unexplained variability in our models. For instance, Rappa et al. (2022) identified divergent effects of forest structural variables on the abundance of beetle families based on their feeding guilds. In the case of bees and wasps, forest structure exhibited significantly greater effects on biodiversity for forest specialists compared to non-forest specialists (Rappa et al., 2023). Likewise, in similar studies of subsets of the bird species and bat acoustic groups included in our analyses, Basile et al. (2021) and Hendel et al. (2023) reported that the importance of forest attributes such as mean tree size and deadwood amount varied considerably between species or groups.

Light availability is a key limiting resource for understory plants (Dormann et al., 2020, and references therein) and can affect higher trophic levels directly through its influence on microclimate (e.g. von Arx et al., 2013) or indirectly via its effects on plant abundance and community composition (e.g. Gao et al., 2015; Rappa et al., 2023). In their study of 13 trophic groups, Penone et al. (2019) found that of all stand structural variables tested, canopy cover (a measure of light availability) had the strongest and most consistent effects on biodiversity, but even so its effect on species richness was only statistically significant for four of the 13 groups (vascular plants, lichens, arthropod herbivores, arthropod carnivores). By contrast, in our analyses canopy gap share ($1 - $ canopy cover) only had substantial effects on species richness and β diversity of bees and wasps (see also Rappa et al., 2023). The limited influence on other groups could potentially be attributed to the relatively narrow range of canopy gap share in our study sites (ranging from 0 to 0.42, with a median of 0.12; Table 1), reflecting typical conditions in Central European mountain forests managed according to close-to-nature forestry principles (Bauhus et al., 2013). While the absence of plots with higher light availability may have precluded the detection of effects on other taxonomic groups, such effects at extreme light conditions may not be relevant in undisturbed central European forests. For vascular plants, the relatively coarse spatial scale of our analyses and the absence of statistical interactions between environmental variables likely prevented us from detecting an effect of light availability. In their analysis of the same plant diversity data, Helbach et al. (2022) identified a significant relationship between understory plant richness and light heterogeneity at the scale of 25 m^2 subplots, but only when soil resource heterogeneity was also high.

Despite the general consensus on the importance of large, old trees for biodiversity conservation in forests (e.g. Bauhus et al., 2009; Brunet et al., 2010; Gustafsson et al., 2020), our study revealed that mean canopy height exerted only a modest influence on α or β diversity across taxonomic groups, except for a negative hump-shaped effect on α diversity in bats. This mirrors the limited impact of mean diameter at breast height (DBH) found by Penone et al. (2019). It is conceivable that the age of stands, often associated with larger trees, may not be the primary driver of biodiversity increases, contradicting Spake et al. (2015); instead, specific structural elements more abundant in older forests may be better predictors than average tree size (Bauhus et al., 2009; Penone et al., 2019). In addition, our data set did not include some of the taxonomic groups that are typically associated with the presence of large trees (e.g. epiphytic bryophytes and lichens) (Ódor et al., 2013) and our sampling did not focused on species that depend on the specific conditions and habitats provided by large trees (e.g. Storch et al., 2023; Asbeck et al., 2021).

While canopy height may influence multiple taxonomic groups, we only found significant effects on bats. In line with previous findings (Jung et al., 2012; Froidevaux et al., 2016; Heidrich et al., 2020), bat α diversity increased with the heterogeneity of the canopy height. Forests with diverse canopies provide foraging habitats for bats with different adaptations to vegetation (Schnitzler and Denzinger, 2011) while also offering shelter and facilitating commuting flights of bats (Schaub and Schnitzler, 2007). Interestingly, the relationship between α diversity and the canopy height itself suggests that species richness is highest at low and high canopy heights, while the Shannon diversity of bats declined with increasing canopy height. Hendel et al. (2023) found that forest height played a minor role in the habitat suitability of most bat groups, and positive associations of bat occurrence and activity with canopy height have been described (Jung et al., 2012; Froidevaux et al., 2016).

Apart from the presence of large, old trees and related structural elements, deadwood is conventionally regarded as a pivotal factor explaining the high biodiversity in old-growth forests compared to intensively managed production forests (Bauhus et al., 2009; Paillet et al., 2010; Doerfler et al., 2018). Consequently, retention forestry strives to augment the quantity and diversity of deadwood (logs and snags) in timber production forests (Vítková et al., 2018; Gustafsson et al., 2020). Surprisingly, our analyses showed that both deadwood volume and deadwood diversity scarcely influenced the α diversity of any taxonomic group, with the exception of a minor effect of deadwood diversity on bat Shannon diversity. Rousseau et al. (2025) found similar results, But they reported how deadwood had en effect on community composition rather than α diversity. Moreover, it is plausible that deadwood exerts limited influence on the overall species count among animal taxa, as only a subset of species within each taxonomic group rely on deadwood for sustenance or refuge. For example, beetles, which we identified on family level, have some species within each family that are known to depend on deadwood to different degrees.

Our results are also in contrast with previous reports of positive effects of deadwood diversity (Abrego and Salcedo, 2013; Penone et al., 2019; Heidrich et al., 2020; Tomao et al., 2020; Yamanaka et al., 2025) and deadwood volume (Lassauce et al., 2011; Gao et al., 2015) on associated fungal species richness. A possible reason for this discrepancy could be that in our study, deadwood assessments only included objects with a diameter of more than 7 cm, as it is also done in commercial forestry. In contrast, data on fungal fruiting bodies were collected without minimum deadwood diameter, resulting in deadwood objects with a median diameter of 5.4 cm (Zibold et al., 2024). This study found a hump-shaped effect of deadwood diversity on fungal species diversity, but it also pointed out that the strong correlation between deadwood amount and deadwood diversity measures may obscure this. This indicates a mismatch between how deadwood is generally evaluated and how it is utilized by fungal species in managed forests (Juutilainen et al., 2011). Species composition for some groups can be affected by deadwood disposition rather than just volume (Zumr et al., 2024). In addition, deadwood volumes in mature forest are reported to be higher than on most of our sites (von Oheimb et al., 2007), there are also limited diversity of deadwood sizes and decay stages, limiting the applicability in these ranges. However, all of these points reflect the reality of commercially used forests.

Among the environmental variables investigated in our study, the proportion of conifers at the local or landscape scale emerged as the most influential among taxonomic groups and facets of biodiversity. Beetle, bees and wasps, and bird richness and Shannon diversity were positively associated with the coniferous forest share in the surrounding landscape, while fungal species diversity declined with increasing conifer proportion. Our findings do not suggest that mixed coniferous and broadleafed tree stands harbor more species than conifer-dominated stands, indicating that the conifer proportion can be considered a measure of mean environmental conditions rather than heterogeneity. These results concur (where applicable) with those of Penone et al. (2019), despite their data originating from broadleaf-dominated forests, while most of our study plots and the surrounding landscape predominantly featured coniferous species, particularly spruce and fir. On the other hand, the weakly positive effect of coniferous share in the surrounding landscape on bird diversity is in contrast to the results of a previous publication (Basile et al., 2021) and a large-scale study of tree composition effects on bird diversity across Europe (Charbonnier et al., 2016). This may be due to the lower sampling effort in the first and the much larger range of tree compositions in the second study, which underlines the importance of putting our findings in perspective with similar studies on specific taxa.

The higher α diversity of some taxonomic groups in coniferous forests may be associated with the size of the regional species pool. The presence of tree resins as nesting material for trap-nesting bees and wasps and large aphid colonies as food resources on conifers may also contribute to this effect (Eckerter et al., 2022). In contrast, the adverse effect of conifers on alpha diversity of wood-dwelling fungi aligns with earlier observations and may be attributed to the higher lignin and lower nutrient content in conifer wood (Yang et al., 2021).

Management implications

Our study reports heterogeneous effects of the environment (in terms of mean conditions, heterogeneity and landscape context) on biodiversity that can not be generalized across taxonomic groups. However, our results can be used to generalize the effect of a given structure over specific taxa, without any focus on dominant species or species of high conservation value. We suggest that forest managers acknowledge the specific effects of forest elements on specific potential biodiversity targets (e.g. endangered species, forest specialists, native species or species with an important role in the ecosystem) at specific spatial scales. Diversifying forest management and considering the specific taxon requirements to provide a wide range of habitats would provide a wide range of structural elements capable of promoting suitable conditions for conservation and/or management goals. Local interventions such as planting specific combinations of tree species, thinning, selective harvesting, or deadwood conservation have a direct and specific impact in some of the variables we studied and on different aspects of biodiversity. As there is no clear main driver of biodiversity, we suggest dividing the forest landscape into a mosaic of specific target-oriented areas and applying specific interventions for conservation at the local scale.

We found that environmental variables such as elevation or exposure had a (negative) impact on some groups. Although management cannot change the abiotic circumstances in a meaningful way, it is important to consider the limitations that those variables might impose while setting conservation goals. The changes in bee/wasp and mammal β diversity with elevation indicate that even when the environmental conditions are generally associated with lower richness and Shannon diversity, those sites can still be an important habitat for specific taxa.

We highlight the importance of tree species composition and stand structure for each taxon over deadwood volume, stand age or tree species richness. The composition of tree species (proportion of conifers, tree diversity) and stand structure (Stand structure complexity index (SSCI), canopy height, deadwood diversity) can offer practitioners numerous ways of potential interventions to cause a positive effect on biodiversity.

Conclusions

This study demonstrates that local mean conditions, heterogeneity, and landscape context characteristics influence biodiversity in taxon-specific ways. We did not identify a single driver or a set of dominant drivers of biodiversity.

Our findings underscore the absence of a uniform impact of forest management on biodiversity, indicating that most taxa are only weekly affected by particular forest structures or show contrasting responses. These results are consistent with recent studies that examined multiple species groups, but contradict some studies that focused on individual taxonomic groups or species of conservation interest. Therefore, specific variables and scales should be considered for the conservation of particular targeted species, while a multifaceted landscape approach may be necessary for the overall conservation of biodiversity. This study provides a comprehensive and comparable overview of the drivers relevant for the diversity of different taxa.

Based on our findings, we recommend stakeholders establish and apply taxon-specific conservation targets. Each taxon is dependent on certain elements within the forest. Here, the diversity of forest structure at landscape level is key to meet the needs of all taxa. The creation or conservation of such a landscape can be guided by the relationships between biodiversity, forest mean conditions, heterogeneity, and landscape context we identified.

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