



Effects of heterogeneity on the ecological diversity and redundancy of forest fauna

Lea Heidrich^{a,b,x,*}, Roland Brandl^a, Christian Ammer^c, Soyeon Bae^{b,d}, Claus Bässler^{e,f,g}, Inken Doerfler^h, Markus Fischerⁱ, Martin M. Gossner^{j,k}, Marco Heurich^{l,f,m}, Christoph Heibl^f, Kirsten Jungⁿ, Peter Krzystek^o, Shaun Levick^p, Paul Magdon^q, Peter Schall^c, Ernst-Detlef Schulze^r, Sebastian Seibold^{d,s}, Nadja K. Simons^{t,u}, Simon Thorn^{v,w}, Wolfgang W. Weisser^d, Stephan Wöllauer^{q,x}, Jörg Müller^{b,f}

^a Animal Ecology, Faculty of Biology, Philipps-University of Marburg, Karl-von-Frisch-Str. 8, 35032 Marburg, Germany

^b Department of Animal Ecology and Tropical Biology, University of Würzburg, Glashüttenstr. 5, 96181 Rauhenebrach, Germany

^c Silviculture and Forest Ecology of the Temperate Zones, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Büsingenweg 1 37077 Göttingen, Germany

^d Terrestrial Ecology Research Group, Department for Life Science Systems, School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

^e Conservation Biology, Institute for Ecology, Evolution and Diversity, Faculty of Biological Sciences, Goethe University Frankfurt, Frankfurt am Main, Germany

^f Bavarian Forest National Park, Freyunger Str. 2, D-94481 Grafenau, Germany

^g Ecology of Fungi, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Germany

^h Institute of Biology and Environmental Science, Vegetation Science & Nature Conservation, University of Oldenburg, Ammerländer Heerstraße 114–118, 26129 Oldenburg, Germany

ⁱ Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

^j Forest Entomology, Research Unit Forest Health and Biotic Interactions, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

^k Institute of Terrestrial Ecosystems, Department of Environmental Systems Science, ETH Zürich, 8092 Zürich, Switzerland

^l Wildlife Ecology and Wildlife Management, University of Freiburg, Tennenbacher Straße 4, Freiburg, Germany

^m Institute for Forest and Wildlife Management, Inland Norway University of Applied Sciences, Koppang, Norway

ⁿ Evolutionary Ecology and Conservation Genomics, University Ulm, Albert-Einstein Allee 11, 89069 Ulm, Germany

^o Department of Geoinformatics, Munich University of Applied Sciences, Karlstraße 6, 80333 München, Germany

^p Ecosystem Dynamics Land and Water, CSIRO, 564 Vanderlin Drive, Berrimah NT 0828, Australia

^q Faculty of Resource Management, HAWK University of Applied Sciences and Arts, Büsingenweg 1a, 37077 Göttingen, Germany

^r Max Planck Institute for Biogeochemistry, Hans-Knöll-Straße 10, 07745 Jena, Germany

^s Forest Zoology, Technische Universität Dresden, Piener Str. 7, 01737 Tharandt, Germany

^t Ecological Networks, Technical University of Darmstadt, Schnittspahnstraße 3/1, 64287 Darmstadt, Germany

^u Applied Biodiversity Sciences, Julius-Maximilians-Universität Würzburg, John-Skilton-Straße 4a, 97974 Würzburg

^v Hessian Agency for Nature Conservation, Environment and Geology, Biodiversity Center, Europastrasse 10, Gießen 35394, Germany

^w Czech Academy of Sciences, Biology Centre, Institute of Entomology, Branišovská 1160/31, České Budějovice CZ-37005, Czech Republic

^x Faculty of Geography, Philipps-University of Marburg, Deutschhausstraße 12, 35032 Marburg, Germany

ARTICLE INFO

Keywords:

Heterogeneity
Functional traits
Assembly
Forests
Redundancy
Environmental filtering
Niches

ABSTRACT

Heterogeneity in forests might promote biodiversity not only through an increase in niche volume but also through other processes, such as an increase in resources and their spatial distribution. However, negative relationships between heterogeneity and biodiversity have also been observed, which may indicate that heterogeneity acts as a filter for some species. This study examined the effects of different facets of heterogeneity in forest stands, i.e. deadwood, plant diversity, forest stand structure, and micro-scale topography, on the ecological (functional-phylogenetic) diversity and redundancy of nine animal groups: moths, true bugs, different functional groups of beetles, spiders, birds, and bats. Overall, we found positive effects of heterogeneity on ecological diversity and redundancy. Although the effect of heterogeneity at the local scale was moderate compared with the general effect of region, greater heterogeneity could be beneficial to some species groups and lead to more resilient species communities.

* Corresponding author at: Environmental Informatics, Faculty of Geography, Philipps-University of Marburg, Deutschhausstraße 12, 35032 Marburg, Germany.
E-mail address: lea.heidrich@gmx.de (L. Heidrich).

<https://doi.org/10.1016/j.baae.2023.10.005>

Received 31 March 2022; Received in revised form 21 October 2023; Accepted 27 October 2023

Available online 30 October 2023

1439-1791/© 2023 The Authors. Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Introduction

Environmental heterogeneity may increase biodiversity via two distinct pathways. First, areas characterised by high environmental heterogeneity provide greater niche space than homogeneous areas (Stein et al., 2014). The greater niche space should be reflected in larger ecological differences between species, that is, *ecological diversity* (Stark et al., 2017) (Fig. 1A), with a parallel increase in *taxonomic diversity*. The second pathway involves processes which are independent of changes in niche space. For example, spatial partitioning across an area allows for the co-existence of ecologically similar and therefore competing species (Stein et al., 2014). The difference between taxonomic and ecological diversity, that is, *ecological redundancy*, increases (Fig. 1B). Both ecological diversity and redundancy play essential roles in ecosystem functioning and resilience (Rosenfeld, 2002). However, most studies focus solely on taxonomic diversity (e.g. Heidrich et al., 2020) and cannot disentangle whether heterogeneity affects ecological diversity, redundancy, or both.

Some of the earliest evidence of heterogeneity-diversity-relationships was documented in forest stands (MacArthur & MacArthur, 1961). Here, various facets of heterogeneity could affect single or multiple species groups that share specific ecological requirements (Heidrich et al., 2020). For example, the ecological diversity of phytophagous and saproxylic species groups is likely to be affected by the diversity of plants and deadwood, respectively (Rappa et al., 2022). However, an increase in structural complexity is likely to increase ecological diversity across species groups, as it is related to a wide range of microclimates and micro-habitats (Stein et al., 2014).

Additionally, structural complexity can directly and indirectly increase ecological redundancy. Direct effects occur when structural complexity increases the number of ecologically equivalent territories (MacArthur, 1958) or acts as a buffer against adverse weather conditions, thereby securing species persistence (Kleckova & Klecka, 2016). The indirect effects of structural complexity occur through quantitative increases in resources, allowing more species to reach viable population sizes (more-individuals hypothesis; Srivastava & Lawton, 1998). For example, heterogeneity of tree heights promotes space filling (Juchheim et al., 2017), thus increasing leaf biomass. This, in turn, increases the number of phytophagous arthropods and subsequently also that of higher trophic levels (Müller et al., 2018).

Consequently, conservation-orientated forest management aims to converge monospecific, single-layered forest stands with continuous canopy cover and little deadwood, to mixed-forest, multi-layered forest

stands, with small gaps and accumulated deadwood (Asbeck et al., 2023). However, a previous study on heterogeneity-diversity relationships in forests revealed both positive and negative effects of heterogeneity on the taxonomic diversity of animals (Heidrich et al., 2020). Under intermediate resource availability, heterogeneity may increase the likelihood of the inclusion of patches with environmental extremes that allow for only a limited number of species (Yang et al., 2015). This would decrease taxonomic diversity without substantial changes in ecological diversity, i.e. decrease ecological redundancy (Fig. 1C). Ecological redundancy may also decrease with heterogeneity owing to an increased risk of stochastic extinction based on a trade-off between heterogeneity and area (Allouche et al., 2012) (Fig. 1C). The decrease in area per niche and the fragmentation of the area could also lead to the selection of highly dispersive or reproductive species, thus reducing ecological diversity (Ben-Hur & Kadmon, 2020), but not necessarily taxonomic diversity. In this scenario, ecological redundancy may even increase (Fig. 1D). For example, the heterogeneity of forests at the landscape scale has been shown to reduce the ecological diversity of moths, probably because fragmentation and forest edges hinder their dispersal (Uhl et al., 2021). Such negative effects may also occur at the stand level and generally be more widespread than previously thought, because not all changes in ecological diversity and redundancy are necessarily accompanied by significant changes in taxonomic diversity.

Here, we evaluate the mechanisms underlying the positive and negative responses of taxonomic diversity and tested whether there are diversity effects that extend beyond the response at the taxonomic level. Specifically, we examine (1) which facets of heterogeneity increase ecological diversity, (2) which facets of heterogeneity increase ecological redundancy and (3) whether there are instances in which heterogeneity selected for ecologically similar species.

Material and methods

Study system

Our analysis was based on the data in Heidrich et al. (2020), which combined information on heterogeneity in forests with species assessments of bats, birds, spiders, beetles, true bugs and moths. Beetles were further divided into carabid, necrophagous, saproxylic and phytophagous beetles. To achieve an acceptable representation of temperate forests in Central Europe, the data were assembled from three different projects across five regions of Germany. The Biodiversity Exploratories project (biodiversity-exploratories.de), which examines the effect of

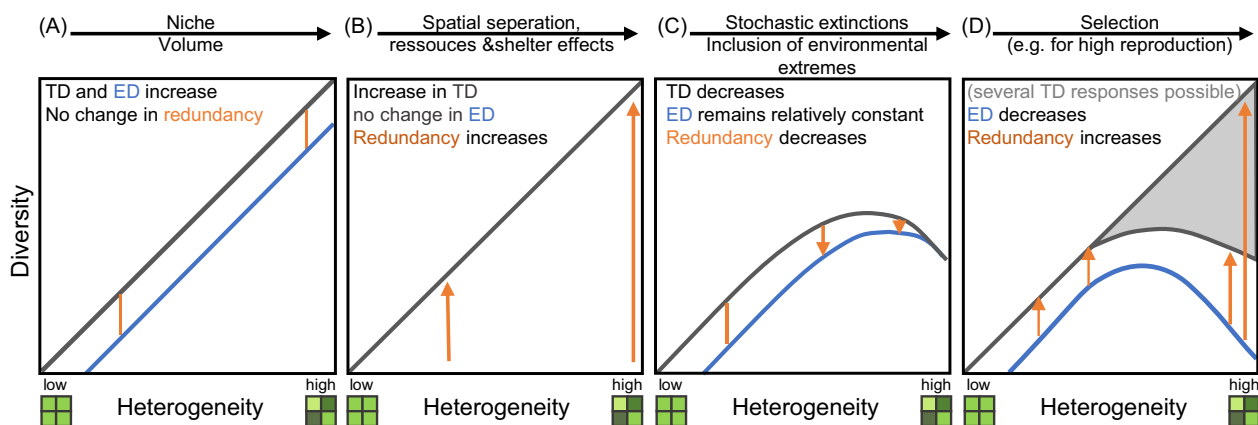


Fig. 1. Effects of environmental heterogeneity (x-axis) on diversity (y-axis). (A) high environmental heterogeneity is likely to provide a greater niche space, leading to a parallel increase of ecological diversity (ED, blue line) and taxonomic diversity (TD, black line). (B) Heterogeneity induces spatial partitioning of an area, increases resources, and provides shelter, all of which increase TD, but not ED, thus increasing ecological redundancy (orange arrow). (C) If heterogeneity selects highly dispersive and/or generalist species, ED decreases. TD and redundancy could show diverse responses. (D) Under area-heterogeneity-trade-off, or when heterogeneity includes habitat patches of environmental extremes, TD decreases at a larger rate than ED, which remains relatively constant. Thus, redundancy decreases.

land use on biodiversity (Fischer et al., 2010), provided data from (1) the Biosphere Reserve Schwäbische Alb, (50 plots), (2) the Hainich National Park and the surrounding area (50 plots) and (3) the Biosphere Reserve Schorfheide-Chorin (50 plots). The Steigerwald project examined the effects of deadwood-enrichment on biodiversity (Doerfler et al., 2017)

and provided data from (4) northern Bavaria (69 plots). Lastly, the BIOKLIM project, which examines the effect of climate on biodiversity (Bässler et al., 2009), provided data from (5) the Bavarian Forest National Park (278 plots along four elevational transects), resulting in a total of 497 plots. The study regions comprised calcareous and slate

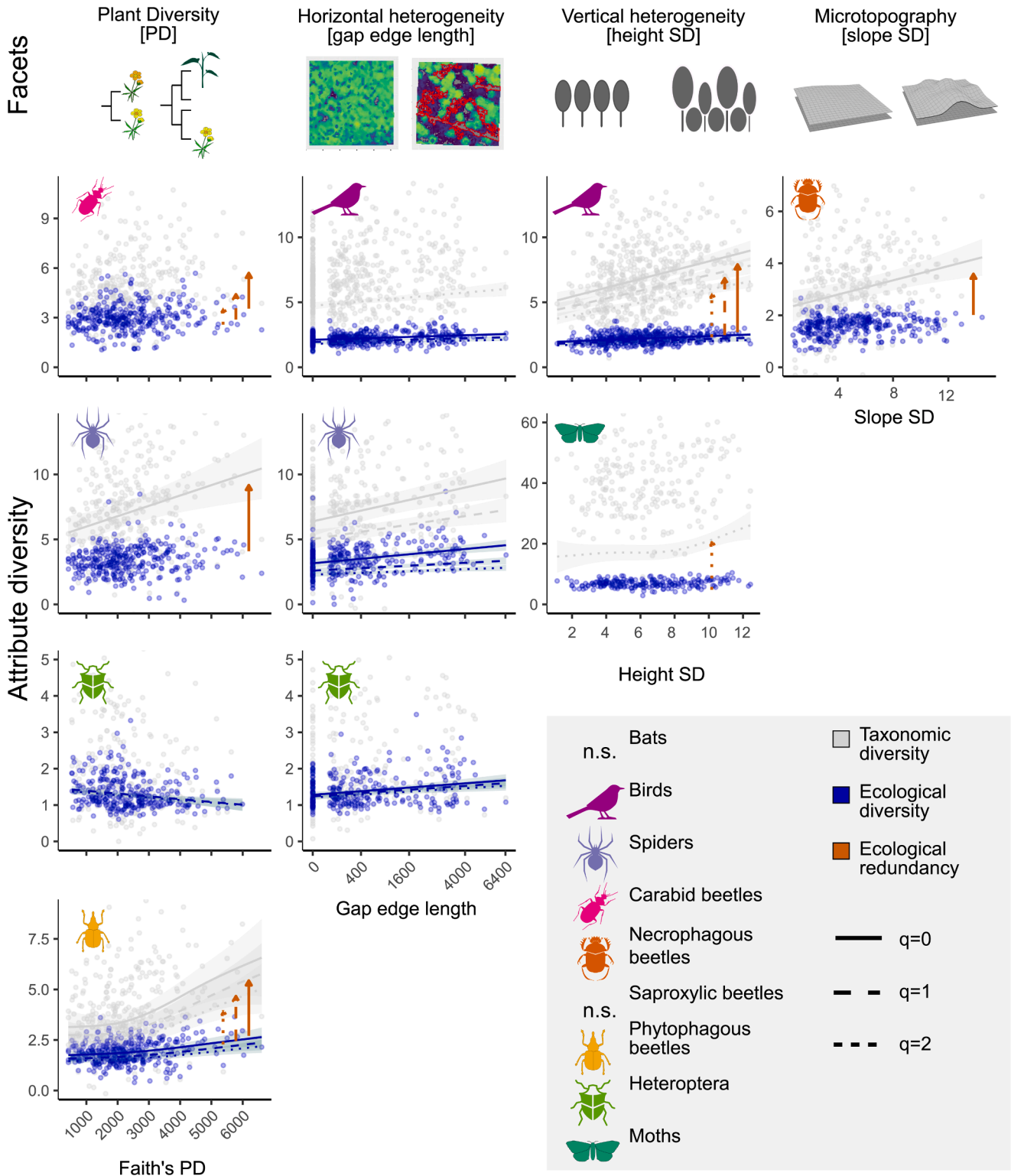


Fig. 2. Significant relationships between plant diversity, heterogeneity in vertical and horizontal structure, and micro-scale topography (upper row) and taxonomic and ecological diversity of the different species groups after accounting for the other variables. Significant increases in ecological redundancy are indicated by arrows. Solid, dashed, and dotted lines represent diversity calculations for $q = 0, 1,$ and $2,$ respectively, with residual data points for $q = 0$ (s. Appendix A: Fig. 7 for all relationships).

mountain ranges, undulating and moraine landscapes, and different bedrock. The forests were dominated by either European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*). Each plot had a dimension of 1 ha.

Measuring heterogeneity

For reasons of comparability, we divided heterogeneity in forest stands into the same facets as in Heidrich et al. (2020): the heterogeneity in vertical and horizontal forest structures, topographical heterogeneity, plant diversity (top row Fig. 2) and the structural and taxonomic richness of deadwood (Appendix A: S1). Horizontal and vertical forest structures as well as topography of each plot was assessed using high-resolution airborne laser scanning (ALS), carried-out during leaf-on conditions. The ALS-data were normalized and classified using LAStools (LAStools, 2012). Vertical heterogeneity was calculated as the standard deviation of the heights of the vegetation returns. Although this measurement is difficult to generalize (Loke & Chisholm, 2022), it correlates well with the ratio of the surface of the canopy and the ground area and allows to separate the effects of vertical and horizontal heterogeneity (Appendix A: S1). For the latter, we used the square-rooted total length of canopy gap edges of each plot. A gap was defined as an area with a minimum size of 50 m², a perimeter to area ratio under < 1.5, a height threshold of 2 m and a penetration ratio of more than 80 %. Topographical heterogeneity was calculated as the standard deviation of the slope of the digital terrain model (1 m spatial resolution). Structural richness of deadwood was calculated as the number of the combinations formed by diameter and decomposition classes (beginning, moderately, heavily and fully decayed) as well as by subtype (broken snag, lying dead tree, etc.) following Siitonen et al. (2001), but with taxonomic richness of deadwood calculated as a separate measure. Plant diversity was characterized by calculating phylogenetic diversity (Faith's PD) of all vascular plants recorded on vegetation survey areas of 400 m², 200 m² and 2000 m² squares in the Exploratories, the Steigerwald and the Bavarian Forest National Park, respectively. Faith's PD was calculated based on the phylogeny of Durka and Michalski (2012). The final set of heterogeneity measures displayed no collinearity (Appendix A:S1).

Taxonomic diversity

For each species group, only data acquired during the year closest to that of the ALS flights were selected. In the Biodiversity Exploratories, transect walks were used to record bats with a detector (2 × 48 minute walks within each plot) while the other two projects used fixed autonomous detectors (3 nights per plot in Steigerwald forest, 7 nights per plot in the BIOKLIM project). Birds were monitored acoustically and visually within a fixed time span (5, 7 and 10 min in the Biodiversity Exploratories, Steigerwald and BIOKLIM project respectively) five times during their breeding season. Arthropods were collected using pitfall traps and crossed flight interception traps. Per plot, one trap was installed throughout the vegetation period. Additionally, low-intensity light traps were installed for two nights. For detailed information on the methods used to record individual taxa, see the Supplementary information in Heidrich et al. (2020).

Ecological diversity

The correlation of taxonomic and ecological diversity complicates their comparison (Bosch et al., 2021), but “correcting” ecological diversity for taxonomic diversity poses a “chicken and egg” problem, as taxonomic diversity itself is primarily driven by ecological diversity. The iNEXT.3D-standardization (Chao et al., 2021) and the corresponding R-package (KaiHsiangHu, 2021/2021) allows for a meaningful

comparison of ecological and taxonomic diversity. This framework employs so-called attribute diversity, which expresses the changes in taxonomic diversity (TD) and functional diversity (FD) in the same units across Hill numbers (q) and allows the standardization to a common sample coverage.

The iNEXT.3D-standardization forms so-called virtual functional groups, by truncating the species-pairwise functional-distance matrix $FDist$ at a given level of distinctiveness τ , which determines the distance at which two species are considered ecologically distinct (Appendix A: Fig. 3). Analogous to species identities (“taxonomic attributes”) in the calculation of TD, these virtual functional groups (“functional attributes”) and their frequencies can then be used in the diversity calculation (see the formulas in Chao et al. (2021)). As τ can be set at any value ranging from 0 to 1, the area under the τ -profile (AUC), represents an integrated functional measure (Chao et al., 2021). In this study, we used a combined pairwise phylogenetic-functional-distance matrix ($FPDist$) instead of $FDist$ to complement information about species' differences, which are not necessarily reflected in traits (Cadotte et al., 2013). $FPDist$ is calculated as

$$FPDist = (aPDist^2 + (1 - a)FDist^2)^{\frac{1}{2}}$$

The phylogenetic distance $PDist$ is divided by the maximal pairwise distance to range between 0 and 1 to reflect the range of $FDist$, which is calculated based on the Gower distance (Gower, 1971), also ranging between 0 and 1. The weighting factor a determines the amount of emphasis assigned to the phylogenetic information. If $a = 0$, $FPDist$ reduces to $FDist$, and if $a = 1$, $FPDist$ reduces to $PDist$. $FPDist$ can be applied to the iNEXT.3D-standardization in the same manner as the original trait distance matrix, resulting in a measure of ecological diversity (ED).

Traits and phylogenies

Trait data on morphology, foraging strategies and/or seasonal occurrences were compiled from the literature or own measurements (Table 1). To avoid circular conclusions, characteristics that describe general habitat requirements were not included. To avoid collinearity, only one trait was selected from highly correlated trait pairs. Furthermore, the analysis was restricted to traits sampled for > 80 % of the species. Missing single values were estimated by taking the mean trait values of the genus of the respective species. Factor variables were converted into binary columns (one per factor level), which were proportionally weighted in analyses.

Phylogenies for bats and birds were based on consensus trees which were constructed from vertlife.org (Upham et al., 2019) and birdtree.org, respectively. The phylogeny of Chesters (2017) was used for beetles and true bugs. Missing species were added to their monophyletic generic clade via the *addTip*-function (megaptera v1.1.6, Heibl, 2016/2019). For spiders and moths, phylogenies were constructed based on DNA sequences from GenBank (Benson et al., 2013), Barcode of Life Data Systems (BOLD) repositories and, for moths only, non-public sequences provided by Advanced Identification Methods (AIM). For moths, alignment and tree search were conducted using a super-family backbone tree based on Mitter et al. (2017).

For an overview of the final trait set per species group, see Table 1 and Appendix A: S2 for more details on traits, phylogenies and tools used.

Calculating standardized attribute diversity

Differences in the survey methods used in the three projects (see above) could affect the sample completeness of the assemblages. Thus, the sample coverage was calculated using the iNEXT.3D:“coverage”-command (Appendix A: S3). To identify a reasonable minimum sample

Table 1

Overview of the used traits, their potential functions and the sources from which they were gathered.

	Trait	(Presumed) links
Bats	Length of gestation period [days] ^{A)}	Energetic costs, have negative effects of foraging efficiency
	Length of the lactation period until offspring are fully independent [days] ^{A)}	
	Average age at first reproduction [days] ^{A)}	
	Longevity, age of the oldest observed individual [years] ^{A)}	Trade-offs with reproduction (population size)
	Body size [CBL length mm] ^{B)}	Home range & population size
	Wing loading, mass per wing area [g/cm ²] ^{B)}	Dispersal, maneuverability
	Average duration of call [s] ^{B)}	Foraging strategy
Birds	Average mean call frequency [kHz] ^{B)}	
	Bandwidth of call frequency [kHz] ^{B)}	
	Mean length of the bird, unsexed [log (mm)] ^{C)}	Home range & population size
	Average age of the first breeding [years] ^{C)}	Trade-offs with reproduction (population size)
	Maximum life span recorded in wild [years] ^{C)}	
	Migration type ^{C)}	Dispersal
	Diet throughout the year ^{C)}	Habitat requirements, competition effects
Spiders	Position of nest ^{C)}	
	defense of a territory (yes or no) ^{C)}	Competition effects
	Mean size male [mm] ^{D)}	Home range & population size
	Mean size female [mm] ^{D)}	
	Seasonal occurrence [monthly] ^{D)}	Habitat requirements, competition effects
Diverse beetles	Stratum ^{E)}	
	Net type ^{E)}	foraging strategy
	Gray value [mean RGB] ^{F)}	Habitat use (temperature, UV..)
	Mean body size, mean of sexes [mm] ^{G,H)}	Home range & population size
Saproxylic beetles	Wing-class number [ranked between 0 (none) to 1 (good flyers)] ^{H)}	Dispersal
	Microhabitat (on ground, vegetation, rotting material or eurytop), depending on group ^{H)}	Habitat requirements, competition effects
	Body length [mm] ^{F)}	Home range, population size, resource use
	Gray value [mean RGB] ^{F)}	Habitat use (temperature, UV..)
	Body roundness (body height / width) ^{F)}	Microhabitat use
	Head length [mm] ^{F)}	
	Wing length [mm] ^{F)}	Dispersal
	Wing aspect (wing length/elytra width) ^{F)}	
	Wing load (mass / wing area) [mg/mm ²] ^{F)}	
	Front femur length [mm] ^{F)}	
	Antennae length [mm] ^{F)}	Temporal niche
Heteroptera	Eye length [mm] ^{F)}	Temporal niche, feeding type
	Hairiness pronotum dorsal [hairs/mm] ^{F)}	Dehydration tolerance
	Mandible aspect (width/length) ^{F)}	Feeding type
	Wing-class number [ranked from 0 (none) to 1 (good flyers)] ^{H)}	Dispersal
	Mean body size [mm] ^{H)}	Home range & population size
	Food source ^{H)}	Habitat requirements
	Specialization ^{H)}	Habitat requirements, competition effects
Moths	Preferred stratum ^{H)}	
	Forewing length [mm] ^{I)}	Dispersal
	Wing load (body length × thorax width) / wing area [mm ²] ^{I)}	Dispersal, maneuverability
	Aspect ratio (wing length/width) ^{I)}	
	Gray value [mean RGB] ^{I)}	Habitat use (temperature, UV..)
	Voltinism ^{J)}	Reproduction
	Seasonal occurrence ^{J)}	Temporal niche
Trophic range ^{J)}	Habitat requirements, competition effects	

A) Haarsma and Siepel (2013) B) Dietz et al. (2016) C) Storchová and Hořák (2018) D) <https://araneae.nmbe.ch>; E) Information by Ingmar Weiss F) Hagge et al. (2021) (2021) G) Seibold et al. (2015); H) Gossner et al. (2015) I) extracted from Behounek et al. (2011) J) Potocký et al. (2018).

coverage to which data can be standardized without losing too much information, the lower quantiles of coverage were extracted region-wise and the minimum of these five values then set as the cut-off criterion (C_{\min}). Assemblages with a coverage value below this minimum were excluded (between 4.8 % and 17 % of plots removed, Appendix A: Fig. 4).

Species data, trait data, and phylogenies were aligned using the *comparative.comm*-command of the *pez*-package (Pearse et al., 2021). *FPDist* matrices were calculated with α -values ranging from 0 to 1 in 0.1-unit steps. Standardized TD and ED were calculated for three orders of q : 0, 1, and 2 and standardized by rarefaction to C_{\min} .

Modeling relationships between diversity and environmental heterogeneity

The observed and standardized TD and ED values were then regressed to the six facets of heterogeneity using generalized additive mixed models (GAMMs) with a Gaussian distribution family, allowing for smooth relationships using the *mgcv*-package (Wood, 2020). All

predictors were standardized prior to the analysis by scaling to a zero mean and unit variance to account for large differences in scales. Prior to the standardization, the total gap-edge length was square-rooted. The smoothness term representing the taxonomic richness of deadwood was restricted to six degrees of freedom. The study region was included as a random factor to account for regional effects. Following the suggestion in Cadotte et al. (2013), the α -value that resulted in the highest R^2_{adj} of all ED models was chosen as the ratio of phylogenetic and functional differences, because it should depict ecological attributes relevant on the scale considered (Appendix A: Fig. 5).

After standardization, ED should increase 1:1 with TD if all species are equally distinct. Ecological redundancy was thus calculated as the difference between TD and ED and applied as a response variable in the same model structure as described above. Due to repeated testing, the level of significance was adjusted to 0.00185 (Bonferroni correction: $0.05/(\text{number of species groups (9)} \times \text{measurements (3)})$). The effect of the facets of heterogeneity on TD, ED and redundancy was estimated by calculating the difference between the R^2_{adj} of the full model and that of

a model in which only the region was included as a random factor (ΔR^2).

All statistical analyses were carried out using the statistical software R, v.4.1.2 (R Core Team, 2022).

Results

Average sample coverage ranged from 100 % (bats) to 70% (saproxylid beetles). For the latter as well as true bugs, large variations in sample coverage led to a very low cut-off criterion (C_{\min}) of 40 % and 39 %, respectively (see Appendix A: Fig. 4).

If all functional-phylogenetic attributes were weighted equally ($q = 0$), moths reached the highest ED per plot ($ED = 7 \pm 2$ mean \pm SD) and true bugs the lowest ($ED = 1 \pm 1$ at $q = 0$). At the level of $q = 0$, horizontal heterogeneity increased the ecological diversity of birds, spiders and true bugs, vertical heterogeneity increased the ecological diversity of birds and plant diversity increased the ecological diversity of phytophagous beetles (Table 2, Fig. 2). These increases were also observed after abundance was included in the diversity calculation (higher orders of q). Moreover, at $q = 1$ and $q = 2$, there was a decrease in ecological diversity of true bugs in response to increasing plant diversity, which was only observed when abundances were included in the calculation (Fig. 2, Appendix B).

Vertical heterogeneity had positive effects on ecological diversity and redundancy of birds for all levels of q (Fig. 2, Appendix B). At $q = 2$, there was also an increase in ecological redundancy of moth communities. Plant diversity increased the ecological redundancy of spiders, carabid beetles and phytophagous beetles at the level of $q = 0$ (Table 2, Fig. 2). While the increase in ecological redundancy with plant diversity was also observed for both beetle groups at higher orders of q , this was not the case for spiders. Here, ecological redundancy increased only when abundances were not accounted for (Table 2, Fig. 2). Likewise, ecological redundancy of necrophagous beetles increased with topographic heterogeneity, but only at the level of $q = 0$.

Most often, increases in ecological diversity or redundancy were paralleled by a significant increase in taxonomic diversity. When this

was not the case, the relationship between heterogeneity and taxonomic diversity was significant prior to the adjustment of the significance level to $p < 0.00185$ (Appendix A: S4 & Fig. 6).

The explained variance was generally low after subtracting the regional effect. Only birds and, at higher orders of q , also moths, had ΔR^2 values of more than 10 % (Appendix B).

Discussion

Heterogeneity has been considered an important driver and stabilizer of diversity in forest stands. In our study, we found some support for this hypothesis; ecological diversity, redundancy, or both increased with heterogeneity in several species groups.

Most of the observed increases in ecological diversity were restricted to horizontal and vertical heterogeneity or plant diversity. Horizontal heterogeneity increases the range in light and moisture conditions, which represent fundamental niche axes for spiders and other arthropods (Perry et al., 2018). Thus, an increase in the ecological diversity of these groups due to increasing niche space was expected. Additionally, horizontal and vertical heterogeneity allow for new nesting and foraging opportunities, thereby increasing the ecological diversity of birds (Sitters et al., 2016). Lastly, the observed relationship between plant diversity and the ecological diversity of phytophagous beetles was expected because of their co-evolutionary history (Schaffers et al., 2008). However, we found no evidence of similar patterns in moths, for which plant diversity is known to affect functional diversity (Uhl et al., 2021).

The increase in ecological redundancy of spiders with plant diversity may be due to the separation of individuals through different plant structures (Pinzon et al., 2011), although the indirect effect of higher prey abundance is presumably more decisive (Müller et al., 2022). Notably, an increase in the ecological redundancy of spiders with plant diversity was only observed at $q = 0$, that is, when abundances were not considered. This suggests that while resources like foraging grounds and prey are being added, they do not lead to an even spatial distribution of

Table 2

F-values, R^2 -values of the GAMM models and the added variance (ΔR^2) to a model including only region as a random factor. Shown are taxonomic diversity (TD), ecological diversity (ED), and redundancy at the level of $q = 0$. Weightings of the phylogenetic component in the calculation of ED are given in parentheses. Number of plots is given per species group in parentheses (raw/after standardization). Significant values ($p < 0.0019$) are indicated in bold. See Appendix B for $q = 1, q = 2$, and p -values.

		No. of tree species	No. of structures	Faith's PD	Height PD.	Gap edge length	Slope SD.	Region	R^2	ΔR^2
Bats ($N = 248$ 224)	ED ($\alpha = 0.1$)	7.64	1.77	0.11	0.10	0.45	2.34	27.7	0.49	0.02
	Redundancy	0.56	0.35	1.53	2.31	0.13	4.15	35.3	0.52	0.00
	TD	3.00	1.13	1.03	0.93	0.02	3.49	33.0	0.52	0.01
Birds ($N = 496$ 472)	ED ($\alpha = 0$)	5.82	1.51	0.03	30.4	25.2	2.63	1.93	0.11	0.11
	Redundancy	7.53	0.34	0.00	40.6	5.42	2.26	2.21	0.10	0.10
	TD	7.44	0.49	0.00	39.9	7.89	2.39	2.21	0.10	0.10
Spiders ($N = 385$ 322)	ED ($\alpha = 1$)	0.47	0.62	3.14	0.07	21.1	0.25	12.2	0.30	0.07
	Redundancy	0.06	0.08	13.2	3.34	6.28	0.86	14.1	0.35	0.07
	TD	0.13	0.00	10.6	2.68	10.6	0.71	15.1	0.36	0.08
Carabid beetles ($N = 385$ 333)	ED ($\alpha = 1$)	2.26	0.06	2.12	0.27	0.63	1.39	29.0	0.33	0.01
	Redundancy	0.33	0.26	13.8	1.08	0.35	2.87	7.34	0.29	0.02
	TD	0.99	0.07	7.96	0.76	0.49	2.63	12.7	0.28	0.01
Necrophagous beetles ($N = 385$ 316)	ED ($\alpha = 0$)	2.57	0.02	0.02	0.40	0.98	5.18	21.7	0.36	0.03
	Redundancy	0.24	0.23	0.01	2.48	0.43	11.8	26.2	0.37	0.03
	TD	0.66	0.10	0.00	2.16	0.57	11.8	26.4	0.38	0.03
Saproxylid beetles ($N = 385$ 336)	ED ($\alpha = 0.9$)	3.43	0.79	1.99	0.71	2.27	2.10	19.0	0.36	0.06
	Redundancy	0.45	0.19	1.86	0.00	2.50	1.67	13.1	0.22	0.03
	TD	1.94	0.40	2.02	0.00	2.34	1.58	16.7	0.27	0.04
Phytophagous beetles ($N = 385$ 357)	ED ($\alpha = 0.2$)	0.47	1.28	7.14	0.18	3.10	6.01	25.6	0.39	0.03
	Redundancy	0.05	2.00	6.02	0.01	1.73	2.78	27.8	0.37	0.03
	TD	0.13	1.87	6.47	0.00	2.15	3.67	27.7	0.38	0.03
True bugs ($N = 385$ 277)	ED ($\alpha = 0$)	0.32	2.88	9.44	0.01	13.2	6.36	0.00	0.08	0.05
	Redundancy	1.76	0.21	4.33	0.34	6.85	3.90	0.00	0.03	0.01
	TD	1.27	0.75	6.01	0.20	9.06	4.85	0.00	0.04	0.02
Moths ($N = 227$ 209)	ED ($\alpha = 0$)	1.48	4.00	1.16	3.57	0.72	5.65	15.4	0.35	0.06
	Redundancy	2.11	4.32	0.91	3.47	0.74	6.07	8.34	0.29	0.08
	TD	2.04	4.29	0.95	3.40	0.74	6.04	9.02	0.30	0.08

all species and individuals. Furthermore, these additional resources do not necessitate ecological adaptations beyond those already present. The increase in the redundancy of birds in response to vertical heterogeneity is likely based on the spatial partitioning of foraging grounds between ecologically similar species, which enables their co-existence (Sitters et al., 2016). This line of thought is supported by a more even distribution of individuals, as seen by the increases in redundancy along all orders of q . However, the indirect positive effects of vertical heterogeneity on resources could also be a determining factor (Bae et al., 2018). Interestingly, vertical heterogeneity did not affect the ecological redundancy of true bugs or phytophagous beetles. It only led to a more even distribution of moth individuals. This contrasts with observations by Müller et al. (2018), where vertical heterogeneity indirectly increased the species richness of phytophagous insects by increasing leaf mass and thus population size.

We speculated that the negative effects of heterogeneity on ecological diversity were responsible for the declines in the taxonomic richness of some arthropod species groups, as observed by Heidrich et al. (2020). However, we did not find corresponding declines in ecological diversity. Moreover, the negative responses in taxonomic richness of these arthropod species groups (e.g. in response to topographic heterogeneity) disappeared after standardization to a common sample coverage, suggesting that these were the product of the influence of heterogeneity on trap efficiency itself (trappability effect, Melbourne, 1999) rather than a selection of ecologically similar species. To account for potential trappability effects when sampling species in forests with various degrees of heterogeneity – be it in forest structure or topography – one should either standardize diversity measures to shared sample coverage or compensate for potential bias through greater sampling effort.

Furthermore, we found no decrease in ecological redundancy, and only one significant decline in the ecological diversity, which was not reflected by changes in taxonomic diversity. However, the low sampling coverage of the group in which it was observed (i.e. the response of true bugs to plant diversity at $q = 2$) makes it difficult to interpret this decline. Importantly, if there were any filtering-effects, they were neither strong enough to reduce the number of ecological groups (ED at $q = 0$) nor to reduce taxonomic richness. Yet it should be noted that there might be a stronger impact on sessile species groups such as lichens, bryophytes and fungi, which could not be included in this study.

Although positive, the effects of heterogeneity on ecological diversity and redundancy were more moderate than expected. Bats and saproxylic beetles showed no significant response in ecological diversity or redundancy to any facet of heterogeneity. One potential reason for this could be that factors other than heterogeneity determine occurrence at the local scale, such as the richness of tree-related microhabitats (Drag et al., 2023; Asbeck et al., 2023). Further, the large proportion of the variance that was covered by the random factor “region” in all species groups but birds suggests that local ecological diversity is determined by the regional species pool (Drag et al., 2023). Similarly, ecological redundancy has been shown to be heavily influenced by the composition of the landscape (Uhl et al., 2020). The relatively small extent to which local heterogeneity affects animal groups underlines the fact that conservation requires both local and regional perspectives. This is especially true because the widespread promotion of local heterogeneity, for example by creating multi-layered stands through single tree removal, can result in decreased compositional variability between stands on the landscape scale. This, in turn, leads to the homogenization of forests at the regional level (Müller et al., 2023) and the loss of habitat specialists, which require certain amounts of e.g. open canopies or specific developmental stages. Ultimately, this process can result in a reduction in biodiversity at the regional level (Schall et al., 2018).

However, the positive effects of local heterogeneity on ecological diversity and redundancy may be even greater given the potential increase in extreme weather events, which may alter the structure and communities of temperate forests (De Frenne et al., 2021). Furthermore, the role of ecological redundancy in promoting the resilience of the

system might even be greater than previously thought because traits currently unrelated to environmental heterogeneity may become important in future conditions (c.f. exaptations; Gould & Vrba, 1982), or because one might view species as definitely dissimilar by definition. However, with snapshots such as those analysed in this study, one can only speculate how decisive the effect of local heterogeneity might become in relation to regional effects. To truly understand the importance of heterogeneity in the face of environmental change, future studies should consider longer time periods.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the student helpers for their assistance and H. Hacker for moth determination. We thank the managers of the three Exploratories, Kirsten Reichel-Jung and Florian Staub, Miriam Teuscher, Christiane Fischer and all former managers for their work in maintaining the plot and project infrastructure; Christiane Fischer and Victoria Grießmeier for giving support through the central office, Andreas Ostrowski for managing the central database, and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. We thank the administration of the Hainich national park, the UNESCO Biosphere Reserve Swabian Alb and the UNESCO Biosphere Reserve Schorfheide-Chorin as well as all land owners for the excellent collaboration.

The work has been (partly) funded by the DFG Priority Program 1374 “Biodiversity-Exploratories” (MU3621/2–1, KR3292/2–1 and LE3316/2–1). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg. Open Access funding was provided by the Open Access Publishing Fund of Philipps-Universität Marburg.

Data availability

This work is based on data elaborated by the TreeScape-project of the Biodiversity Exploratories program (DFG Priority Program 1374). Datasets and R-script, including a list of used R-packages, are publicly available in the Biodiversity Exploratories Information System (<http://doi.org/10.17616/R32P9Q>), IDs 31591 - 31610.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baec.2023.10.005](https://doi.org/10.1016/j.baec.2023.10.005).

References

- Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., & Kadmon, R. (2012). Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*, 109(43), 17495–17500.
- Asbeck, T., Benneter, A., Huber, A., Margaritis, D., Buse, J., Popa, F., et al. (2023). Enhancing structural complexity: An experiment conducted in the Black Forest National Park, Germany. *Ecology and Evolution*, 13(1), e9732.
- Bae, S., Mueller, J., Lee, D., Vierling, K. T., Vogeler, J. C., Vierling, L. A., et al. (2018). Taxonomic, functional, and phylogenetic diversity of bird assemblages are oppositely associated to productivity and heterogeneity in temperate forests. *Remote Sensing of Environment*, 215, 145–156.
- 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), 21–34.

- Behounek, G., Speidel, W., & Witt, T.J. (2011). *The Macrolepidoptera of Germany, 2011* (A. H. Seegerer & A. Hausmann, Eds.). Heterocera Press.
- Ben-Hur, E., & Kadmon, R. (2020). Heterogeneity–diversity relationships in sessile organisms: A unified framework. *Ecology Letters*, 23(1), 193–207.
- Benson, D. A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, I., Lipman, D. J., Ostell, J., et al. (2013). GenBank. *Nucleic Acids Research*, 41(D1), D36–D42.
- Bosch, N. E., Wernberg, T., Langlois, T. J., Smale, D. A., Moore, P. J., Franco, J. N., et al. (2021). Niche and neutral assembly mechanisms contribute to latitudinal diversity gradients in reef fishes. *Journal of Biogeography*, 48(11), 2683–2698.
- Cadotte, M., Albert, C. H., & Walker, S. C. (2013). The ecology of differences: Assessing community assembly with trait and evolutionary distances. *Ecology Letters*, 16(10), 1234–1244.
- Chao, A., Henderson, P. A., Chiu, C. H., Moyes, F., Hu, K. H., Dornelas, M., et al. (2021). Measuring temporal change in alpha diversity: A framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization. *Methods in Ecology and Evolution*, 12(10), 1926–1940.
- Chesters, D. (2017). Construction of a species-level Tree of Life for the insects and utility in Taxonomic Profiling. *Systematic Biology*, 66(3), 426–439.
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B. R., Zellweger, F., Aalto, J., et al. (2021). Forest microclimates and climate change: Importance, drivers and future research agenda. *Global Change Biology*, 27(11), 2279–2297.
- Dietz, C., Nill, D., & Kiefer, A. (2016). *Handbuch fledermäuse europas und nordwestafrikas* (2nd ed.). Franckh Kosmos Verlag.
- 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.
- Drag, L., Burner, R. C., Stephan, J. G., Birkemoe, T., Doerfler, I., Gossner, M. M., et al. (2023). High-resolution 3D forest structure explains ecomorphological trait variation in assemblages of saproxylic beetles. *Functional Ecology*, 37(1), 150–161.
- Durka, W., & Michalski, S. G. (2012). Daphne: A dated phylogeny of a large European flora for phylogenetically informed ecological analyses. *Ecology*, 93(10), 2297–2297.
- Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., et al. (2010). Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology*, 11(6), 473–485.
- Gossner, M. M., Simons, N. K., Achtziger, R., Blick, T., Dorow, W. H. O., Dziock, F., et al. (2023). A summary of eight traits of Coleoptera, Hemiptera, Orthoptera and Araneae, occurring in grasslands in Germany. *Scientific Data*, 2(1), Article 150013.
- Gould, S. J., & Vrba, E. S. (1982). Exaptation—A Missing Term in the Science of Form. *Paleobiology*, 8(1), 4–15.
- Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, 27(4), 857–871.
- Haarsma, A. J., & Stépél, H. (2013). Macro-evolutionary trade-offs as the basis for the distribution of European bats. *Animal Biology*, 63(4), 451–471.
- Hagge, J., Müller, J., Birkemoe, T., Buse, J., Christensen, R. H. B., Gossner, M. M., et al. (2021). What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. *The Journal of Animal Ecology*, 90(8), 1934–1947.
- Heibl, C. (2019). **Megaptera** [R]. <https://github.com/heibl/megaptera>.
- Heidrich, L., Bae, S., Levick, S., Seibold, S., Weisser, W., Krzystek, P., et al. (2020). Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. *Nature Ecology & Evolution*, 4(9), 9.
- Juchheim, J., Ammer, C., Schall, P., & Seidel, D. (2017). Canopy space filling rather than conventional measures of structural diversity explains productivity of beech stands. *Forest Ecology and Management*, (395), 19–26. C.
- Kai Hsiang Hu. (2021). **KaiHsiangHu/iNEXT.3D** [R]. <https://github.com/KaiHsiangHu/iNEXT.3D> ((Original work published 2021)).
- Kleckova, I., & Klecka, J. (2016). Facing the heat: Thermoregulation and behaviour of lowland species of a cold-dwelling butterfly genus, *Erebia*. *PLoS One*, 11(3), Article e0150393.
- LAStools. (2012). “Efficient LiDAR Processing Software” (version 181119, academic), obtained from <http://rapidlasso.com/LAStools> Rapidlasso GmbH.
- Loke, L. H. L., & Chisholm, R. A. (2022). Measuring habitat complexity and spatial heterogeneity in ecology. *Ecology Letters*, 25(10), 2269–2288.
- MacArthur, R. H. (1958). Population ecology of some warblers of Northeastern coniferous forests. *Ecology*, 39(4), 599–619.
- MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42(3), 594–598.
- Melbourne, B. A. (1999). Bias in the effect of habitat structure on pitfall traps: An experimental evaluation. *Australian Journal of Ecology*, 24(3), 228–239.
- Mitter, C., Davis, D. R., & Cummings, M. P. (2017). Phylogeny and evolution of Lepidoptera. *Annual Review of Entomology*, 62(1), 265–283.
- Müller, J., Brandl, R., Brändle, M., Förster, B., Araujo, B. C. de, Gossner, M. M., et al. (2018). LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. *Oikos (Copenhagen, Denmark)*, 127(6), 814–824.
- Müller, J., Brandl, R., Cadotte, M. W., Heibl, C., Bässler, C., Weiß, I., et al. (2022). A replicated study on the response of spider assemblages to regional and local processes. *Ecological Monographs*, 92(3), e1511.
- Müller, J., Mitter, O., Cadotte, M. W., van der Plas, F., Mori, A. S., Ammer, C., et al. (2023). Enhancing the structural diversity between forest patches—A concept and real-world experiment to study biodiversity, multifunctionality and forest resilience across spatial scales. *Global Change Biology*, 29(6), 1437–1450.
- Pearse, W. D., Cadotte, M. W., Cavender-Bares, J., Ives, A. R., Tucker, C., Walker, S. C., et al. (2021). **pez: Phylogenetics for the Environmental Sciences (1.2-3)**. <https://CRAN.R-project.org/package=pez>.
- Perry, K. I., Wallin, K. F., Wenzel, J. W., & Herms, D. A. (2018). Forest disturbance and arthropods: Small-scale canopy gaps drive invertebrate community structure and composition. *Ecosphere (Washington, D.C)*, 9(10), e02463.
- Pinzon, J., Spence, J. R., & Langor, D. W. (2011). Spider assemblages in the overstory, understory, and ground layers of managed stands in the Western Boreal mixedwood forest of Canada. *Environmental Entomology*, 40(4), 797–808.
- Potocký, P., Bartoňová, A., Beneš, J., Zapletal, M., & Konvička, M. (2018). Life-history traits of Central European moths: Gradients of variation and their association with rarity and threats. *Insect Conservation and Diversity*, 11(5), 493–505.
- R. Core Team. (2021). **R: The R Project for Statistical Computing**. <https://www.r-project.org/>.
- Rappa, N. J., Staab, M., Frey, J., Winiger, N., & Klein, A. M. (2022). *Multiple forest structural elements are needed to promote beetle biomass, diversity and abundance*, 9. Forest Ecosystems, Article 100056.
- Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos (Copenhagen, Denmark)*, 98(1), 156–162.
- Schaffers, A. P., Raemakers, I. P., Sykora, K. V., & Ter Braak, C. J. F. (2008). Arthropod assemblages are best predicted by plant species composition. *Ecology*, 89(3), 782–794.
- Schall, P., Gossner, M. M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., et al. (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.
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmid, J., Thorn, S., et al. (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29(2), 382–390.
- Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49, 11–41.
- Sitters, H., York, A., Swan, M., Christie, F., & Stefano, J. D. (2016). Opposing responses of bird functional diversity to vegetation structural diversity in wet and dry forest. *PLoS One*, 11(10), Article e0164917. h.
- Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *American Naturalist*, 152(4), 510–529.
- Stark, J., Lehman, R., Crawford, L., Enquist, B. J., & Blonder, B. (2017). Does environmental heterogeneity drive functional trait variation? A test in montane and alpine meadows. *Oikos (Copenhagen, Denmark)*, 126(11), 1650–1659.
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866–880.
- Storchová, L., & Horák, D. (2018). Life-history characteristics of European birds. *Global Ecology and Biogeography*, 27(4), 400–406.
- Uhl, B., Wölfling, M., & Fiedler, K. (2021). Qualitative and quantitative loss of habitat at different spatial scales affects functional moth diversity. *Frontiers in Ecology and Evolution*, 9.
- Upham, N. S., Esselstyn, J. A., & Jetz, W. (2019). Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLOS Biology*, 17(12), Article e3000494.
- Wood, S. (2020). **mgcv: Mixed GAM computation vehicle with automatic smoothness Estimation (1.8-33)**. <https://CRAN.R-project.org/package=mgcv>.
- Yang, Z., Liu, X., Zhou, M., Ai, D., Wang, G., Wang, Y., et al. (2015). The effect of environmental heterogeneity on species richness depends on community position along the environmental gradient. *Scientific Reports*, 5(1), 15723.