The effect of environmental heterogeneity on communities

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November 2020

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Dissertation zur Erlangung des

naturwissenschaftlichen Doktorgrades

der Julius-Maximilians-Universität Würzburg

vorgelegt von

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Arnsberg

Würzburg, 2020

Eingereicht am: ……..……..

<u>Mitglieder der Promotionskommission:</u>

Vorsitzender: ……..

Gutachter: ……..….

Gutachter: ……..….

Tag des Promotionskolloquiums: ……..…

Doktorurkunde ausgehändigt am: …….…….

Table of Contents

Table of Contents

Summary

How diversity of life is generated, maintained, and distributed across space and time is the central question of community ecology. Communities are shaped by three assembly processes: (I) dispersal, (II) environmental, and (III) interaction filtering. Heterogeneity in environmental conditions can alter these filtering processes, as it increases the available niche space, spatially partitions the resources, but also reduces the effective area available for individual species. Ultimately, heterogeneity thus shapes diversity. However, it is still unclear under which conditions heterogeneity has positive effects on diversity and under which conditions it has negative or no effects at all. In my thesis, I investigate how environmental heterogeneity affects the assembly and diversity of diverse species groups and whether these effects are mediated by species traits.
In Chapter II, I first examine how much functional traits might inform about environmental filtering processes. Specifically, I examine to which extent body size and colour lightness, both of which are thought to reflect the species thermal preference, shape the distribution and abundance of two moth families along elevation. The results show, that assemblages of noctuid moths are more strongly driven by abiotic filters (elevation) and thus form distinct patterns in colour lightness and body size, while geometrid moths are driven by biotic filters (habitat availability), and show no decline in body size nor colour lightness along elevation. Thus, one and the same functional trait can have quite different effects on community assembly even between closely related taxonomic groups.
In Chapter III, I elucidate how traits shift the relative importance of dispersal and environmental filtering in determining beta diversity between forests. Environmental filtering via forest heterogeneity had on average higher independent effects than dispersal filtering within and among regions, suggesting that forest heterogeneity determines species turnover even at country-wide extents. However, the relative importance of dispersal filtering increased with decreasing dispersal ability of the species group. From the aspects of forest heterogeneity covered, variations in herb or tree species composition had overall stronger influence on the turnover of species than forest physiognomy. Again, this ratio was influenced by species traits, namely trophic position, and body size, which highlights the importance of ecological properties of a taxonomic group in community assembly.
In Chapter IV, I assess whether such ecological properties ultimately determine the level of heterogeneity which maximizes species richness. Here, I considered several facets of heterogeneity in forests. Though the single facets of heterogeneity affected diverse species groups both in positive and negative ways, we could not identify any generalizable mechanism based on dispersal nor the trophic position of the species group which would dissolve these complex relationships.
In Chapter V, I examine the effect of environmental heterogeneity of the diversity of traits itself to evaluate, whether the effects of environmental heterogeneity on species richness are truly based on increases in the number of niches. The results revealed that positive effects of heterogeneity on species richness are not necessarily based on an increased number of niches alone, but proposedly also on a spatially partition of resources or sheltering effects. While ecological diversity increased overall, there were also negative trends which indicate filtering effects via heterogeneity.
In Chapter VI, I present novel methods in measuring plot-wise heterogeneity of forests across continental scales via Satellites. The study compares the performance of Sentinel-1 and LiDar-derived measurements in depicting forest structures and heterogeneity and to their predictive power in modelling diversity. Sentinel-1 could match the performance of Lidar and shows high potential to assess free yet detailed information about forest structures in temporal resolutions for modelling the diversity of species.
Overall, my thesis supports the notion that heterogeneity in environmental conditions is an important driver of beta-diversity, species richness, and ecological diversity. However, I could not identify any generalizable mechanism which direction and form this effect will have.

Zusammenfassung

Eine zentrale Frage in der Ökologie ist es, wie die Diversität von Artgemeinschaften generiert, aufrechterhalten, und über Zeit und Raum verteilt wird. Die Zusammensetzung von Artgemeinschaften wird durch drei Prozesse bestimmt, die einzelne Arten herausfiltern: (I) Ausbreitung, sowie (II) Umweltbedingungen und (III) Interaktionen mit anderen Arten. Heterogenität in Umweltbedingungen verändert das Zusammenspiel dieser Filterprozesse, da es die Anzahl verfügbarer Nischen erhöht und Ressourcen räumlich aufteilt, aber auch den für die jeweilige Art verfügbaren Raum reduziert, was schlussendlich die Diversität der Artgemeinschaft beeinflusst. Es ist jedoch immer noch unklar, wann Heterogenität die Diversität positiv und wann negativ oder sogar überhaupt nicht beeinflusst. In dieser Dissertation werde ich der Frage nachgehen, wie Heterogenität die Artzusammensetzung und Diversität verschiedenster Artengruppen beeinflusst und ob deren Reaktion auf Heterogenität durch Artmerkmale beeinflusst wird.

In Kapitel II untersuche ich zunächst inwieweit funktionale Merkmale den Einfluss von Umweltbedingungen auf Arten widerspiegeln. Dazu untersuchte ich den Einfluss von Körpergröße und Helligkeit auf die Verbreitung und Abundanz zweier Nachtfalterfamilien entlang eines Höhengradienten. Es zeigte sich, dass Noctuidae stärker von abiotischen Filterprozessen, d.h. Höhe, betroffen waren und klare Zu- bzw. Abnahmen in Körpergröße und Helligkeit entlang der Höhe aufwiesen, während Geometridae eher von biotischen Filterprozessen, d.h. der Verfügbarkeit ihres Habitats, beeinflusst wurden und keine Merkmalsmuster entlang der Höhe aufwiesen. Entsprechend kann ein- und dasselbe Merkmal selbst innerhalb nah-verwandter Artgruppen unterschiedliche Effekte auf die Zusammensetzung von Arten haben.

In Kapitel III erläutere ich, wie funktionelle Merkmale die relative Wichtigkeit von Ausbreitungs- und Umweltfiltern für beta-Diversität verschieben können. Sowohl innerhalb als auch zwischen den untersuchten Regionen beeinflusste Heterogenität in Wäldern die beta-Diversität stärker als die räumliche Distanz. Letztere wurde allerdings immer bedeutender, je schlechter die Ausbreitungsfähigkeit der jeweiligen Artengruppe war. Wenn die Heterogenität in Wäldern nach floristischen und strukturellen Aspekten aufgeteilt wird, so hatte erstere alles in allem einen stärkeren Einfluss auf Unterschiede zwischen Artgemeinschaften. Bei Artengruppen höheren trophischen Levels und größeren Körperbaus hatten die strukturellen Aspekte jedoch einen stärkeren Einfluss. Diese Ergebnisse verdeutlichen, dass die Artzusammensetzung von bestimmte Merkmale beeinflusst werden kann.

In Kapitel IV untersuche ich ob solche Merkmale das Level an Heterogenität festlegen, an welchen Artenreichtum am höchsten ist. Dazu betrachtete ich mehrere Aspekte von Heterogenität in Wäldern. Obwohl Heterogenität in diesen Aspekten sowohl positive als auch negative Einfluss auf den Artenreichtum der verschiedensten Artengruppen hatte, konnten wir diese nicht anhand der Ausbreitungsfähigkeit oder des trophischen Levels der Artengruppen ableiten.

In Kapitel V untersuche ich schließlich den Effekt von Heterogenität auf die Vielfalt von funktionalen Merkmalen. Dieser Ansatz soll helfen zu evaluieren, ob eventuelle Anstiege in der Artenzahl mit Heterogenität einem Zuwachs in der Anzahl der ökologischen Nischen zurückzuführen sind. Die Ergebnisse legen nahe, dass ein Anstieg von Artenreichtum nicht dadurch beeinflusst wird, sondern auch durch andere Mechanismen wie die räumliche Aufteilung von Ressourcen oder durch die Schaffung von Zufluchtsräumen. Obwohl Heterogenität die ökologische Diversität überwiegend positiv beeinflusste, gab es auch einige negative Reaktionen die darauf hindeuten, dass Heterogenität auch bestimmte Merkmale aus einer Artgemeinschaft herausfiltern kann.

In Kapitel VI präsentiere ich neue, Satelliten-gestützte Methoden in der Erfassung von Waldstrukturen. In dieser Studie werden die Eignung von LiDar (Lasergestützte Waldvermessungen aus der Luft) und Sentinel-1 (Satellitenscan durch Radiowellen) verglichen, Waldstrukturen und deren Heterogenität zu messen sowie verschiedene Diversitäts-indices zu modellieren. Hierbei schnitt Sentinel-1 ähnlich gut ab wie LiDar. Somit zeigt Sentinel-1 großes Potential zukünftige Biodiversitätsaufnahmen zu unterstützen, auch aufgrund der kostenfreie Verfügbarkeit von Daten, deren globalen Abdeckung und hohen zeitlichen Auflösung.

Insgesamt unterstützen die Ergebnisse meiner Arbeit die große Bedeutung von Heterogenität, insbesondere von Waldstrukturen, für beta-Diversität, Artenreichtum und funktionaler Diversität. Allerdings konnte keine generelle Regel identifiziert werden, nach der sich vorhersagen lassen würde welche genaue Richtung dieser Effekt haben wird.

Chapter 1

General Introduction

How diversity of life is generated, maintained and distributed across space and time is the central question of community ecology and of great importance for the maintenance of diversity under global change (Mittelbach & McGill, 2019). Why communities, that is "group(s) of species that occur together in space and time" (Begon *et al.*, 2005) can differ from each other is commonly thought to be based on a hierarchy of scale-dependent assembly processes (Cadotte & Tucker, 2017). Biogeography and evolutionary history shape the *regional species pool* to begin with (Mittelbach & McGill, 2019). Whether species occurring in the regional species pool are ultimately also occurring in the area of interest depends on three processes. First, a community can only draw from a set of species which can disperse to where this area is located ("neutral process", Hubbell (1997) or "dispersal filter", Cadotte & Tucker, (2017)). Second, the abiotic environmental conditions in this specific location must satisfy the specific requirement of the species ("environmental filter"; Kraft *et al.* (2015); Cadotte & Tucker, 2017)). Third, the final set of species interact with each other, so that species can competitively exclude each other ("interaction filter", Cadotte & Tucker, 2017)).

The latter two processes relate to the niche concept, which "is an important element in almost every element of ecological thinking" (Chase & Leibold, 2007). The niche concept has undergone multiple adjustments and redefinitions, from the classical "n-dimensional hyperspace" of all environmental factors acting on an organisms (Hutchinson, 1957) more mathematical formulations (Chase & Leibold, 2007). The revised niche concept of Chase and Leibold (2007) integrates both, the species demands, as well as the set of per capita impacts of the species on its environment. Taken together, a given environment can only maintain those species whose requirements fit its' specific abiotic conditions and resources, but to thrive, species in the community must require the existing resources differently to co-exist (Chase & Leibold, 2007).

Environmental heterogeneity

If a given area provides only a limited amount and range of environmental conditions and resources, it can thus only contain few species. If, however, the area is spatially heterogenous in its environmental conditions, it a) fulfils the basic requirements of a larger amount of species (increase in available niche space, Stein *et al.* (2014)) and furthermore b) spatially partitions the resources, so that otherwise competing species may coexist (Ben-Hur & Kadmon, 2020). Both mechanisms would then increase the number of species (Tews *et al.*, 2004). However, an increase in environmental heterogeneity could also reduce the average effective area available for individual species, thereby leading to lower average population sizes and ultimately increasing the risk of stochastic extinctions (Allouche *et al.*, 2012).

A matter of perspective

Though straight forward in a theoretical setting, testing the effect of environmental heterogeneity on neutral, environmental and interaction filters in real-world settings remain challenging, as the relative importance of all three filtering processes as well as the perception of heterogeneity are known to be scale- and taxon dependent (Tews *et al.*, 2004; Keil *et al.*, 2012; Schweiger & Beierkuhnlein, 2016a). For example, a red kite which migrates to southern Spain and back again will be less affected by dispersal filters in choosing its foraging ground than a vole. Likewise, a vole will notice if soil conditions vary within an area, but the red kite probably won't. It is thus not surprising, that studies focussing on different scales, taxonomic groups and environmental measures impede finding generalizable conclusions.

Functional traits

One way to tackle this issue is to move from focussing on the number and taxonomic identity of species to functional traits (Enquist *et al.*, 2015). These are "any trait which impacts fitness indirectly via it effects on growth, reproduction and survival" (Violle *et al.*, 2007) and are generally thought to be associated with dispersal, environmental and interaction filtering processes; functional traits which affect dispersal ability should ultimately also affect the neutral assembly processes (Harrison *et al.*, 1992) and those which affect the species response to changes in the abiotic environment should respond to environmental filter processes (McGill *et al.*, 2006). Lastly, traits can be associated the species-specific requirement of resources, so that species with diverge traits compete less with each other than species with similar traits, and thus inform about interaction-filter processes (Adler *et al.*, 2013).

Aim of the thesis

The work in hand aims at investigating how environmental heterogeneity affects the assembly and diversity of communities and whether these effects are mediated by species traits. Therefore, I first examine how much functional traits might inform about environmental filtering processes (Chapter II), how traits shift the relative importance of dispersal and environmental filtering in determining beta diversity between forests (Chapter III) and how they alter the response of alpha diversity to heterogeneity within forests (Chapter IV). Then I examine the effect of environmental heterogeneity of the diversity of traits itself (Chapter V). Finally, the thesis prospects novel methods in measuring plot-wise heterogeneity of forests across continental scales (Chapter VI).

Assessing the value of functional traits in informing about environmental filtering

Traits are often classified as being functional by macroecological studies which link large-scale patterns in traits to abiotic filtering processes and integrate over heterogeneity in abiotic conditions as well as biotic factors. At smaller spatial scales, however, the latter play important roles in community assembly (Schweiger & Beierkuhnlein, 2016a). Moreover, the effects of certain functional traits are often extrapolated from one taxonomical unit to the other, although those might be differently affected by the single assembly processes. Thus, the question rises, whether the trait-environment relationships observed at a macroscale can indeed contribute to predictions of the general responses of organisms to environmental change at smaller spatial and temporal scales (Law *et al.*, 2020). The study presented in Chapter II thus explores the effect of two functional traits, body size and colour lightness, on distribution and abundance of two moth families along an elevational gradient. Both traits were shown to vary along thermal gradients in macroecological studies, but are also inherently connected to life-history and reproduction (True, 2003). Assemblage-based analyses were performed using the classical community-weighted means and a fourth-corner analysis to test for variations in color and body size within communities as a function of elevation. To address the relative importance of abiotic vs. biotic filtering processes, a species-level analysis tested whether species abundance and occurrence along an elevation gradient were related to these traits, after controlling for habitat availability.

Assessing the value of functional traits in informing about the relative importance of filtering processes

The spatial context does not only affect the ratio in the relative importance of abiotic and

biotic filtering processes, but naturally also the relative importance of the regional species pool and neutral processes. As soon as study areas are drawn from different regions, the question arises whether the lack of certain species at a focal area is based on dispersal limitations alone, or rather its lack in the overall species pool. Chapter III investigates the relative importance of neutral processes and different environmental filtering processes in species turnover between communities after controlling for the effect of the regional species pool. With this control in hand we can investigate the effect of specific traits, namely dispersal ability, trophic position and body size, on the relative importance of the single assembly processes. Additionally, this chapter deals with the importance of plant composition relative to heterogeneity in forest structure, and whether this is relation can be affected by trophic position and body size. Therefore, eleven species groups were sampled in plots clustered in five different forest regions across Germany. For each of the species groups, variance partitioning was used to assess the independent effects of spatial distance and species pool, modelled using principle components of neighbour matrices, and differences in plant compositions and forest structures in species turnover. Changes in the relative importance of those components between groups were then tested against the groups rank in dispersal ability, trophic position, and body size, respectively.

Impact of environmental heterogeneity on species richness

The study presented in chapter IV "Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests", shifts the spotlight from beta- to alpha diversity and goes into full detail on the effect of heterogeneity on the number of available niches and on the effective area available for each species. The heterogeneity in forests is systematically broken down to six different facets, spanning not only aspects of structural heterogeneity and plant species composition, but also addressing heterogeneity in dead wood and microtopography. Specifically, it deals with the question which level of heterogeneity is beneficial, which might result in the loss of species, e.g. via reduced effective area (Kadmon & Allouche, 2007), and whether this turning point is altered by niche breadth and dispersal ability of each of the twelve species groups considered (Ben-Hur & Kadmon, 2020).

Impact of environmental heterogeneity on ecological diversity

After showing the effects of environmental heterogeneity on taxonomic diversity, I address its effect on ecological diversity in Chapter V. Based on the rationale, that area with a wide range of environmental conditions should support ecologically more diverse species, one would expect a higher ecological divergence in heterogenous than in homogenous areas (Stark *et al.*, 2017). However, if colonization and extinction processes are not random, but favour species with certain traits such as high dispersal ability and high niche breadth both in abiotic and biotic conditions (Allouche *et al.*, 2012), heterogeneity could rather lead to an ecologically impoverished community. Such negative effects would not necessarily be apparent number of species alone. To gain a broad picture of ecological diversity, I selected a subset of the species groups used in Chapter IV for which there was a relatively good coverage of informative, functional traits and rooted phylogenies. These were than combined using the method described in Cadotte (2013) to gain as much information about the distinctiveness of species as possible. The standardized effect size of the ecological distance of each community was then modelled against the six facets of heterogeneity as in the previous chapter, so that the responses of both, species richness and ecological diversity,

towards environmental heterogeneity could be compared.

Future assessments of diversity in forests

Although the chapters outlined above built upon assessments of multiple taxa and forest sites, they still can only a fraction of the diversity of forests and especially, single moments therein. The study presented in Chapter VI, "Radar vision in the mapping of forest biodiversity", thus evaluates the potential of Sentinel-1 in depicting forest structure, heterogeneity therein and its effect on communities. Sentinel-1 is a newly launched satellite-borne radar system, which is characterized by high spatial and -importantly- temporal resolution, covering the whole globe. Furthermore, the data can be used open-source. The performance of Sentinel-1 in depicting forest structures and heterogeneity as well as in modelling diversity of species is compared with that of airborne-laser scanning, the current (and expensive) standard in measuring forests and validated with external species assessments.

Chapter 2

Noctuid and geometrid moth assemblages show contrasting elevational gradients in body size and color lightness

with
Stefan Pinkert | Roland Brandl | Claus Bässler | Hermann Hacker | Nicolas Roth | Jörg Müller | Nicolas Frieß |

under review in Ecography (10.11.2020)

The underlying study design, establishment of the study sites and first species assessment of moths were led by Claus Bässler and Jörg Müller. The newly resampling campaign was done by me under supervision of Nicolas Friess. Mr. Hermann Hacker identified the moth species. First drafts and analyses were conducted in close collaboration of Nicolas Friess, Stefan Pinkert and me. Nicolas Roth added trait data and references. The final analysis and draft were conducted by me. Data and R-Script and receipt of submission for this chapter can be found in the digital supplement

Summary

Previous macroecological studies suggested that larger and darker insects are favored in cold environments and that the importance of body size and color for the absorption of solar radiation is not limited to diurnal insects. However, whether these effects hold true for local communities and are consistent across taxonomic groups and sampling years remains unexplored. This study examined the variations in body size and color lightness of the two major families of nocturnal moths, Geometridae and Noctuidae, along a 660-m elevational gradient in Southern Germany, using data from 262 species and 17,561 individuals collected in 2007 and 2016. An assemblage-based analysis was performed using community-weighted means and a fourth-corner analysis to test for variations in color and body size within communities as a function of elevation. This was followed by a species-level analysis to test whether species abundance and occurrence along an elevation gradient were related to these traits, after controlling for habitat availability. In both 2007 and 2016, noctuid moth assemblages became larger and darker with increasing elevation while the opposite was true for geometrids. In single species models, geometrid, but not noctuid species abundance was driven by habitat availability. In turn, the abundance of dark-colored noctuid, but not geometrid species increased with elevation. While body size and colour lightness certainly affect insect physiology and the ability to cope with harsh conditions, contrasting trait-environment relationships between both families underline that inferences from coarse scales are not necessarily transferable to finer scales. In the case of the geometrids, for example, local abundance and occurrence seems to be more strongly driven by local site factors such as habitat availability. We discuss potential explanations such as taxon-specific flight characteristics and the effect of microclimatic condition

Introduction

Macrophysiological approaches aim to understand the importance of trait variation for the distribution and abundance of species along environmental gradients (Chown & Gaston, 2016). The key assumption of this conceptional framework is that trait-environment interactions scale from individuals, over local patterns in abundance and distribution, to larger taxonomic and spatial scales—as an effect of individual advantages in terms of growth, fecundity, or survival (Gaston *et al.*, 2009). Hence large-scale patterns in the diversity of, for instance, the average traits of species assemblages should be indicative of a higher physiological performance of individuals with certain traits in a given environment (Gaston *et al.*, 2009). Such inferences provide a powerful starting point not only for a better understanding of the processes that shape diversity on Earth, but also for improving mechanistic predictions of species responses to climate change (Chown & Gaston, 2008; Violle *et al.*, 2014; Urban *et al.*, 2016). However, for the sake of identifying generalities, macroecological approaches necessarily reduce biological detail, that is they integrate over local factors that might limit the realized niche (McGill, 2019), such as habitat availability (Platts *et al.*, 2019), species interactions (Wiens, 2011), or microclimatic variation (Hof *et al.*, 2011). Thus, the question is whether the trait-environment relationships observed at a macroscale can indeed contribute to predictions of the responses of organisms to environmental change at smaller spatial and temporal scales (Law *et al.*, 2020).

For highly diverse groups such as insects, however, trait-based generalizations still offer a promising tool to overcome the taxonomic impediments in studying organismal responses to environmental changes (Wong *et al.*, 2019). Most insects are ectothermic and thus rely on external heat sources to reach

their thermal optimum. Therefore, functional traits that influence an insect's heat budget, particularly body size and color lightness, are often the focus of trait-based approaches (Chown *et al.*, 2004). Large bodies are assumed to be advantageous in colder climates because the body surface-to-volume ratio decreases with size. This means that larger species can raise their body temperature above the ambient temperature because of the slower loss of heat gained by solar radiation of the body surface ("heat conservation hypothesis;" Stone , 1993; Zamora-Camacho et al., 2014). Furthermore, ectotherms develop faster in warm regions but reach a smaller adult body size than in colder regions ("temperature size rule", Atkinson and Sibly ,1997). In addition to body size, the color lightness of a body surface influences the absorption of solar radiation. Dark organisms heat up faster than their light-colored counterparts at a given level of solar irradiance (Watt, 1968), ultimately leading to a fitness advantage in colder environments ("thermal melanism hypothesis", Clusella -Trullas et al., 2007)). Moreover, temperature dependencies in insect color lightness may be the product of pleiotropic linkages to a particular life history might also lead to temperature-dependencies in insects colour lightness (Umbers *et al.*, 2013; Clusella-Trullas & Nielsen, 2020).

Although covarying factors, such as season length and habitat availability, might have constraining impacts on both traits (Zeuss *et al.*, 2017; Pinkert *et al.*, 2020) most of the more recent macroecological studies report that insect assemblages become larger and darker in colder climates (Zeuss *et al.*, 2014; Bishop *et al.*, 2016; Pinkert *et al.*, 2016; Stelbrink *et al.*, 2019; Acquah-Lamptey *et al.*, 2020). The assemblages investigated in some of those studies were drawn from distribution maps that covered large latitudinal gradients (Zeuss *et al.*, 2014; Pinkert *et al.*, 2016; Stelbrink *et al.*, 2019) whereas in others they were derived from in-field samplings of local assemblages along large elevational gradients (Bishop *et al.*, 2016). According to Acquah-Lamptey *et al.* (2020), the color lightness and body size variations described by a continent-wide dataset of 518 local assessments of dragonfly and damselfly occurrences implied that the underlying mechanisms connecting both traits to the thermal environment scaled to local assemblages.

In diurnal insects, traits related to the uptake and storage of external heat provide a direct mechanistic link to the environmental temperature. However, their nocturnal counterparts, while not directly exposed to solar radiation during their periods of activity, nonetheless exhibit distinct patterns in both size and color. For instance, the mean color lightness of assemblages of geometrid moths was shown to decrease with increasing latitude across Europe (Heidrich *et al.*, 2018) and along elevational gradients (local assessments; Xing *et al.*, 2018). Increases in body size along elevational gradients have been found in assemblages of tropical geometrid and arctiid moths (Brehm *et al.*, 2019) and in assemblages of temperate moths in the Alps (Beck *et al.*, 2016). These repeated observations linking color lightness and body size to thermal gradients in nocturnal insects suggest that this relationship is of a more fundamental and general nature than merely serving to regulate the uptake and retention of heat gained by solar radiation (Heidrich *et al.*, 2018; Brehm *et al.*, 2019; but see the discussion in Beck *et al.*, 2016). However, moths display a variety of behavioral adaptations and differ in their flight-performance and thermal strategies (Heinrich, 2013), all of which could affect the sensitivity of a species to thermal changes and thus ultimately the relationship between its functional traits and the environment, as demonstrated in diurnal insects (Pinkert *et al.*, 2017; Stelbrink *et al.*, 2019; Bladon *et al.*, 2020; Law *et al.*, 2020).

In this study, we used standardized and spatially explicit monitoring data for the years 2007 and 2016 to investigate whether the previously reported relationships of body size and color lightness with the thermal environment hold at a local scale in two dominant moth families with distinct thermal strategies: geometrid and noctuid. Our analysis took into account the confounding effects of differences in habitat availability and tested for consistency across families and sampling years to assess the importance of physiological processes in both elevational gradients of local abundance and the habitat occupancy of moths. If a larger body and darker color are generally beneficial in colder climates, then body size should increase and color lightness decrease with increasing elevation.

Methods

Study area

The study was conducted at the Bavarian Forest National Park, in the German part of the Bohemian Forest, in southeastern Germany. 36 sampling sites established along an elevational gradient from 660 m to 1,368 m a.s.l. were sampled in 2007. These sites and an additional 15 sites located between the National Park and the Danube River and spanning an elevational gradient between 297 m a.s.l. and 1,150 m a.s.l. (Bässler *et al.*, 2015) were also sampled in 2016. The National Park is dominated by mixed mountain forests of spruce *Picea abies*, European beech *Fagus sylvatica*, and fir *Abies alba*. At elevations > 1,150 m a.s.l., spruce dominates but low proportions of mountain ash *Sorbus aucuparia* and European beech *F. sylvatica* are present as well.

Sampling

Moths were sampled monthly from June to August in 2007 and 2016, respectively, using light-traps during nights with optimal weather conditions (excluding nights with full moon or rain). The light traps consisted of 12 V, 15 W superarctinic UV-lights controlled by a twilight-sensor and operated by a 12 V, 15 Ah battery. The traps were emptied the next day and their contents were frozen until the species classification of individuals belonging to *Noctuidae*, *Geometridae*, *Arctiidae*, *Lymantriidae*, *Erebidae*, *Lasiocampidar*, *Sphingidae*, *Drepanidae*, *Notodontidae*, *Nolidae*, *Hepialidae* and *Cossidae*. The overall catch consisted of 27,823 individuals of 345 species.

Morphological traits

Recently published information on wing spans (hereafter called "body size" for simplicity) was used as a proxy for species body size (Potocký *et al.*, 2018). The color lightness of the considered species was estimated by scanning photographs of museum specimens published as colored plates in *The Macrolepidoptera of Germany* (Segerer *et al.*, 2011). The plates were scanned at 300 dpi with RGB color space. Subsequently, the images were separated and their backgrounds removed. The mean gray value of all pixels was calculated for each image. If more than one image was available per species, their mean gray values (ranging from 0 to 1; absolute black to pure white) were averaged.

Habitat availability

Variations in habitat availability were taken into account by including information on the occurrence of larval host plants into the analysis. For all species in our study region, information on the most frequent host plants is available from the literature (e.g. Pearse & Altermatt, 2013; Steiner *et al.*, 2014). At all study sites, the scale suggested by Londo (1976) was used to estimate the coverage of each plant species within a radius of 8 m around the center of the site (~200 m²) at four vertical layers (> 15 m; > 5–15 m; > 1–5 m and < 1 m), once in 2006 (used for the moths sampled in 2007) and once in 2016. The percentages of

all layers were summed per plant, site, and year and then divided by the number of layers, followed by a logit transformation to achieve normality. For each moth species and year, the coverage of all potential host plants was summed per site to obtain an estimate of habitat availability.

Statistical analysis

To investigate whether body size and colour lightness influence the community composition and abundance of species along an elevational gradient, we performed three types of analyses. Because we wanted to test whether patterns are repeated over time, we only used sites which were equally sampled three times in both years for the single analyses. From the 36 sites sampled in both years, three had to be excluded due to trap failure. The following analyses and results thus refer to the 33 equally sampled sites. A year-wise analysis covering the whole elevational gradient of 2016 can be found in Chaper 8.1.

First, to enable comparisons between our results and those of previous large-scale studies, assemblage-level patterns in body size and color lightness were investigated. For geometrid and for noctuid species, community-weighted means of body size and color lightness were calculated based on the species abundances at each site in 2007 and in 2016. The relationship between community-weighted means and elevation was assessed using linear models. The inclusion of an interaction term of both variables allowed direct comparisons of the slopes per year and per family. In addition, family was included as a fixed factor to account for general differences in body size and color lightness. In a second step, this model was repeated but with year also included as a fixed factor, which revealed whether the differences in the slopes between the two years were significant (for details, see Chapter 8.1).

One of the shortcomings of assemblage-level approaches is that only trait averages and not trait variations among co-occurring species are taken into account (Peres-Neto *et al.*, 2017). This deficit was addressed by additionally applying a fourth-corner analysis, as implemented in the *ade4* package (Dray & Dufour, 2007). The fourth-corner approach allows direct testing of the interactions between the environment and a given functional trait at the species level (Peres-Neto *et al.*, 2017). In this study, the analysis was conducted using the species-site matrices for both moth families in both years, a matrix of site-level elevations, and a matrix of species-level trait values. The fourth-corner statistic measures the link between these matrices and thus allows inferences about an unknown "fourth corner," which is the trait-environt-interaction matrix (Braak *et al.*, 2012). The link between trait and environment is determined as a Pearson correlation coefficient, with its significance assessed by bootstrapping. Here, both site and species values were permuted and the two outputs were combined, as other procedures are prone to inflated type I statistical errors (Braak *et al.*, 2012). As a third approach, the occurrence and abundance of species were modeled using generalized linear mixed models as implemented in the *glmmTMB* package (Brooks *et al.*, 2017). The 95 species that occurred in fewer than five samples were excluded. The interaction of elevation with each of the two traits as predictor variables was used to assess whether body size and color lightness influence the abundance of species along an elevational gradient.

TABLE C2.1: Results of linear regression modeling of community-weighted means of body size and color lightness against elevation for two moth families, Geometridae and Noctuidae, and the sampling years 2007 and 2016. In the linear regression, family was included as a fixed factor to account for family-based differences in body size and color lightness. Interaction terms of elevation with family (Geo = Geometridae; Noc= Noctuidae) and year (2007 and 2016) were used to calculate and compare the slopes of the relationship between the traits and elevation, both per family and per sampling year. Estimates (Est) and the corresponding standard errors (SE) indicate a response to changes per 100 m. Significant effects are shown bold, and slopes that significantly differed between the two years (same model, but with year as a fixed factor, see Chapter 8.1.2) in gray.

Variable	Body size				Color lightness			
	Est	±	SE	t-value	Est	±	SE	t-value
Noctuidae	**−9.0**	**±**	**2.6**	**−3.43 *****	0.006	±	0.021	0.265
Geo:2007:elevation	−0.22	±	0.18	−1.27	**0.004**	±	**0.001**	**2.72 ****
Geo:2016:elevation	−0.30	±	0.18	−1.70	**0.004**	±	**0.001**	**2.86 ****
Noc:2007:elevation	**1.1**	**±**	**0.18**	**6.33 *****	**−0.007**	**±**	**0.001**	**−5.11 *****
Noc:2016:elevation	**1.0**	**±**	**0.18**	**5.81 *****	**−0.006**	**±**	**0.001**	**−4.12 *****
R^2	**0.52**				**0.84**			

TABLE C2.2: Results of the fourth-corner analysis of Geometridae and Noctuidae for both 2007 and 2016. R is the Pearson correlation between single traits and elevation. The significance of the fourth-corner statistic was determined via permutations of site and species values based on 9999 permutations.

	Geometridae				Noctuidae			
	2007		2016		2007		2016	
	R	p-value	R	p-value	R	p-value	R	p-value
Elevation * body size	–0.05	0.736	–0.02	0.827	**0.32**	**0.040**	**0.32**	**0.032**
Elevation * Color lightness	0.10	0.551	0.02	0.710	**–0.37**	**0.016**	**–0.28**	**0.052**

As variations in abundance along elevational gradients can be hump- or U-shaped (Choi & An, 2013), the independent effect of elevation on species abundance was modeled using a general additive model, as implemented in the *mgcv*-package v1.8 (Wood, 2018), Chapter 8.1), while also accounting for habitat availability. This allowed a visual determination of non-linear patterns. Since no clear hump- or U-shaped pattern was evident (Fig. C8.1.2), only the linear term of elevation was included. Family and year were added as interaction terms to obtain group-wise estimates, and habitat availability was included as a fixed factor. The models also contained a random factor of the species identity nested in family and genus, to account for non-random differences between species due to phylogenetic relatedness. Prior to the analysis, all independent variables were centered. A negative-binomial error distribution (quadratic parametrization) with truncated zero inflation was used to model both the likelihood of occurrence and the effect on abundance.

Results

In 2007 and 2016, 11,144 individuals of 221 species and 10,535 individuals of 216 species, respectively, were sampled. The two families comprised 40% and 37% of the species and 53% and 28% of the individuals (Geometridae and Noctuidae, respectively). In 2007, Geometridae were represented by 5,781 individuals of 89 species and Noctuidae by 3,193 individuals of 82 species; in 2016, these two families were represented by 5,578 individuals of 89 species and 2,908 individuals of 75 species, respectively. The wing spans of the considered species ranged from 17 mm (*Chlorochlystis v-ata*, Geometridae) to 55 mm (*Eurois occulta*, Noctuidae) with a mean± standard deviation of 32.19 ± 8.21 mm. The wing spans of geometrid moth species were on average 8.4 mm shorter than those of noctuid moth species (Welch two sample t-test: t =−9.85, df = 258.06, $P < 0.001$; Fig. C2.1A). Color lightness values ranged from 0.34 (*Noctua janthina,* Noctuidae) to 0.81 (*Lomographa bimaculata,* Geometridae), with a mean of 0.55 ± 0.10. Geometrid moth species were on average 0.14 gray values lighter in color than noctuid species (t = 13.89, df = 203.69, $P <$ 0.001, Fig. C2.1B). Geometrid moth assemblages in 2007 and 2016 did not differ with respect to body size (t = −0.60) or color lightness (t = 1.11). The mean body size of noctuid assemblages did not differ between the two years size (t =1.15, p = 0.253), but these moths were on average lighter in 2016 than in 2007, (t-test, t = −3.08, p = 0.003, Fig. C2.2).

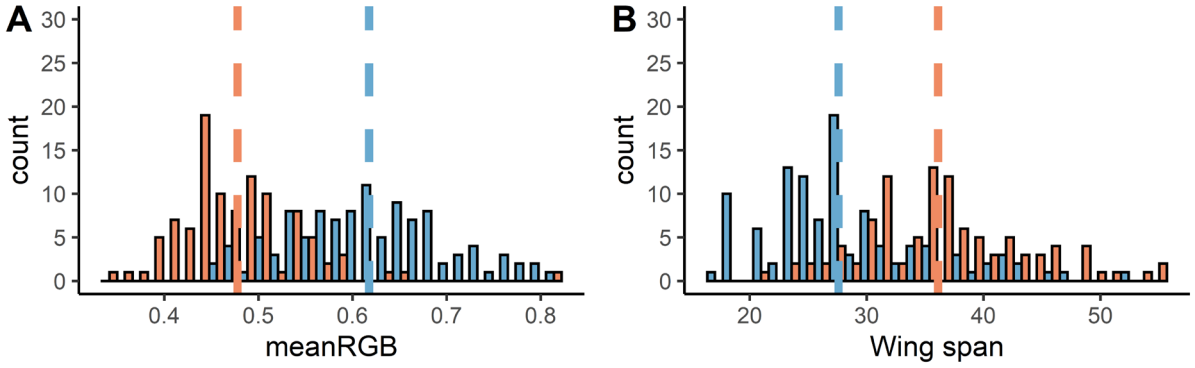

FIGURE C2.1 Histograms of (A) color lightness and (B) the wing span of moth species of the two families investigated in this study: Geometridae (blue) and Noctuidae (red). Color lightness (mean RGB) ranges from 0 (black) to 1 (white). Dashed lines represent the mean values.

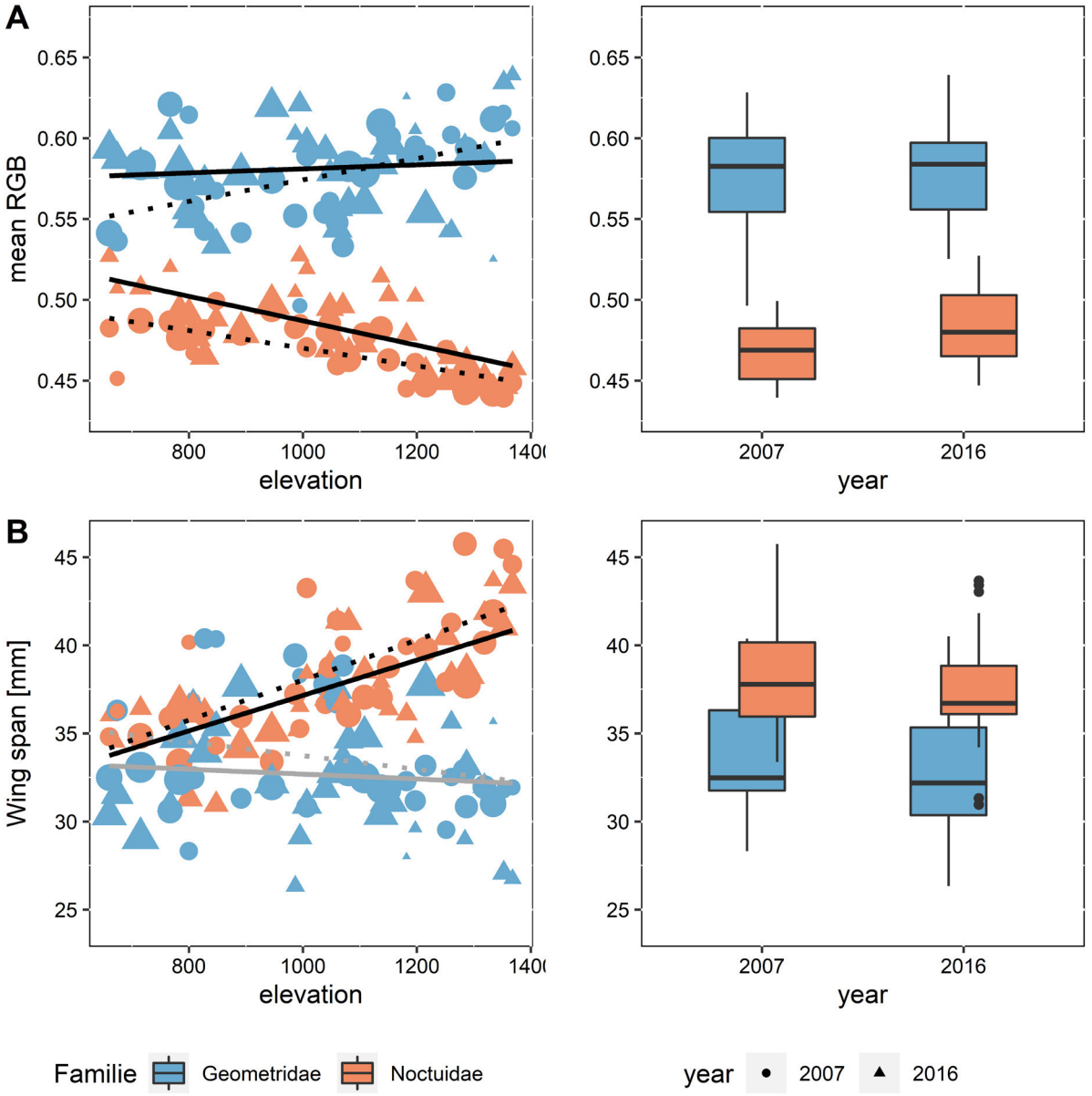

FIGURE C2.2: Scatterplots of the relationships of abundance-weighted community trait means of the (A) color lightness and (B) body size of assemblages of geometrid (blue) and noctuid (orange) species with increasing elevation above sea level. The mean values are shown in the plots on the right. Dotted regression lines and circles indicate the results for 2007, and solid regression lines and triangles the results for 2016. Species trait values in the assemblage were weighted according to species abundances. Note that for species of the family Geometridae the relationship between mean body size and elevation was non-significant in both years (gray lines). Lines refer to raw data, not the predicted values from the models.

With increasing elevation, the mean body size of geometrid assemblages did not change, but the moths became lighter colored, with a less steep slope in 2016 (Table C2.1, Chapter 8.1). By contrast, noctuid assemblages at higher elevations were on average larger and darker. These trends were consistent across the two sampling years (Table C2.1, Fig. C2.2). The results of the fourth-corner analysis were similar to those of the assemblage approach (Table C2.2) in the case of noctuid moths, as both showed an increase in body size (r =

0.32 in 2007 and 2016) and a decrease in color lightness with elevation ($r = -0.37$ in 2007, $r = -0.28$ in 2016). In geometrid moths, neither the relationship between body size and elevation nor that between color lightness and elevation was significant. Similar results were obtained in the two years of the study (Table C2.2).

Geometrid moths were more abundant and more likely to occur at sites with high habitat availability in both 2007 and 2016, whereas habitat availability promoted the occurrence (but not abundance) of noctuid moths only in 2007. In 2016, dark colored geometrid moths were less likely to occur at high elevations. In contrast, the distribution of noctuid moths along the elevation gradient was affected by color lightness in both years. Specifically, light-colored noctuid moths were less likely to occur at high elevations and had a steeper decline in abundance with increasing elevation. Large-bodied noctuid moths were more likely to occur at high elevation in 2016 (Table C2.3).

Discussion

In accordance with previous studies of several diurnal ectothermic insect taxa conducted on continental scales (body size: (Shelomi & Zeuss, 2017; Zeuss *et al.*, 2017; colour lightness: Zeuss *et al.*, 2014; Bishop *et al.*, 2016; Pinkert *et al.*, 2017; Stelbrink *et al.*, 2019) our results showed that the average body size and color lightness of moth assemblages covaried with elevation. However, inconsistencies in the strength and direction of the clines among moth families were also determined, as the predicted pattern occurred only in noctuid moths whereas in geometrid moths it was either non-existent (body size) or opposite to that documented at larger scales (color lightness). Thus, our results do not unambiguously support the assumption that the trait-environment relationships observed at large scales or gradients are applicable at local scales and across shorter gradients (Messier *et al.*, 2010).

TABLE C2.3: Species-level analysis to test the effect of habitat availability on species abundances and whether species distributions along an elevation gradient are mediated by traits. The results are reported as the t-and z-values. The model had a truncated negative-binomial error distribution. The conditional part represents the effect on abundance, and the zero-inflated part the probability of the absence of a species. The interactions of the sampling year (2007, 2016) and family (Geo= Geometridae, Noc = Noctuidae) were included to test whether the trends were consistent across taxonomic groups and repeatable between two sampling events. Significant effects are shown in bold, with "." = p < 0.1; "*" = p < 0.05; "" = p < 0.01, "***" = p < 0.001.**

		Geometridae		**Noctuidae**	
	Variable	**2007**	**2016**	**2007**	**2016**
conditional	Habitat availability	**3.22*** **	**1.96.**	0.69	-1.19
	Elevation	0.30	**-2.29***	-1.37	**-3.14****
	Elevation:wingspan	1.02	-1.51	1.83.	1.20
	Elevation:meanRGB	0.74	-0.14	**-3.03****	**-2.13***
Zero-inflated	Habitat availability	**-3.79*** **	**-4.96*** **	**-2.48***	-0.51
	Elevation	1.69	**7.10*** **	0.81	**3.00****
	Elevation:wingspan	-1.09	-1.73	-1.31	**-2.28***
	Elevation:meanRGB	0.12	**-2.11***	**2.40***	**2.31***

Inconsistencies in the relationship between traits and the thermal environment

The observed increase in color lightness of geometrid moth assemblages along the elevation gradient contrasts with the findings of large-scale studies of this family (Heidrich *et al.*, 2018; Xing *et al.*, 2018). However, the elevational shift in the community-weighted means of geometrid moths was not supported by the results of the fourth-corner-analysis in terms of statistical significance. Thus, it may be that the significance of the elevational increase in the community-weighted means of color lightness of geometrid moths was based on an underestimation of the total variance and thus an overestimation of the correlation, which is a recognized problem in approaches that rely on community-weighted means (Peres-Neto *et al.*, 2017).

Furthermore, community-weighted means do not provide information on whether species distributions along an environmental gradient are causally linked to species traits (Peres-Neto *et al.*, 2017). The results of the species-level model indicated no consistent relationships between body size or color lightness and the distribution of geometrid moths, which was instead strongly driven by habitat availability. Habitat availability has been referred to as one of those "mind-boggling details" (Lawton, 1999) that are averaged out in macroecological studies but can obscure trait patterns in local assemblages (McGill, 2019).

Potential effects of differing flight energetics

Habitat availability can have strong effects on the distribution and abundance of herbivorous insects (Friess *et al.*, 2017), and like other biotic factors its relative importance often increases with decreasing scale (Schweiger & Beierkuhnlein, 2016a). Across an elongated thermal gradient (s. Chapter 8.1)—and thus an increased probability that the ends of the climatic niche of geometrid moths will be covered—patterns in body size become more apparent and follow expectations and while patterns in color lightness, which were contrary to expectations on the small gradient, vanish. It is therefore unclear why, on a focal scale, habitat availability more strongly impacts geometrid than noctuid moths. The relative importance of habitat availability can be altered by an organism's mobility, as a low mobility is associated with a strong relationship between the host plant and organismal abundance (Curtis *et al.*, 2015). Geometrid moths have a low wing load and require no pre-flight warm-up, which reduces their energetic costs for flying (Utrio, 1995). However, this energetically cheap flight comes at the cost of a poor flight performance, such that the occurrence and abundance of geometrid moths are more likely to be driven by resource availability. Noctuid moths, however, have a significantly higher wing load and stroke frequency (Casey & Joos, 1983) and may thus be less dependent on local habitat availability. Nonetheless, they need to shiver to raise their body temperatures 15°C above the ambient temperature (Heinrich, 2013) in order to take off ("hot moths", Utrio, 1995)). This pre-flight warm up together with the high wing load is energetically costly, especially if ambient temperatures are low (Casey & Joos, 1983). Larger body sizes reduce the loss of body temperature and may therefore benefit noctuid moths. Pleiotropic linkages between body size and color lightness (Schweiger & Beierkuhnlein, 2016b) could also lead to darker noctuid moth assemblages at high elevations. The thermoregulatory propensities of large bodies should thus be even more relevant for sphingid moths, the "hottest" moth family (Heinrich, 2013). However, in their macroecological study, Beerli et al. (2019) found that the body size of sphingid moths did not show any tendency to increase in colder regions. Factors other than

temperature, e.g., longer life spans, as well as filtering towards more robust species (Beck *et al.*, 2016) may instead lead to body size clines along an elevation. These same factors could affect color lightness, given that melanin production is linked to several life history traits (Clusella-Trullas & Nielsen, 2020). The differences in the two families with respect to their life histories, with most noctuid moths overwintering in the larval stage whereas geometrid moths overwinter as pupae (Fig C8.1.3), could further add to the difference in the observed trait patterns. For now, our conclusions remain speculative and await confirmation by additional data, preferably based on sampling at multiple points in time, to gain a deeper understanding of the mechanisms underlying body size and color lightness variation in insects and the effect of those variations on species distributions (Clusella-Trullas & Nielsen, 2020).

Limitations and potential extensions of the study

While we had a lower spatial grain in comparison to macroecological studies, the taxonomic unit mostly remained unchanged, such that intraspecific variations in color lightness and body size could not be considered in our analysis. Nevertheless, it is a premise of trait-based ecological studies that trait-environment relationships can be scaled up from the individual to the ecosystem (Enquist *et al.*, 2015). Consequently, the use of mean values from the literature may lower the power of predictions, especially if turnover between species is low (Yang *et al.*, 2018). For instance, Xing *et al.* (2018) found support for the thermal melanism hypothesis at the individual level but not at the species level. Hence, future studies on smaller scales should, whenever possible, include intraspecific variations to improve the power of their predictions. Advancements in the field of digital image processing via deep learning algorithms may facilitate the generation of data from local collections (Wu *et al.*, 2019).

Moreover, the use of elevation as a proxy for a thermal gradient has its shortcomings, as not only do other environmental factors covary (see Discussion above) but the decrease in temperature along the elevation gradient is also not necessarily uniform. Sinks of cold air occurring within the mixed montane zone (800–900 m a.s.l.) can strongly favor the occurrence of cold-adapted species (Bässler *et al.*, 2010a) and in the case of geometrid moths may be responsible for the low average community-weighted means of color lightness within the respective elevational range. If cold-air sinks are at the lower border of the elevational gradient and the elevational gradient is not long enough to compensate for their presence, the result may ultimately be a change in the sign of the slope of trait-elevation clines. This again points to the importance of microclimate in assessing trait-environment relationships (Hof *et al.*, 2011). Hence, insights into the effect of color lightness and body size on the performance of species await further experimental studies that additionally control for microclimate.

Conclusion

Our study showed that colour lightness and body size affect the physiology and shape the abundance and occurrence of noctuid moths along elevation. However, the lack of such patterns in geometrid moths show that such trait-environment relationships are inconsistent and underline that coarse-scale patterns are not necessarily transferable to smaller scales, where local environmental factors such as the habitat availability can modify occurrence and abundance pattens. The strength of this modification is likely to be based on taxon-specific flight capacities, though also other factors, such as thermoregulatory propensities and life history might

play a role. Thus, one should be careful to not overestimate the effect of single functional traits on the performance of species.

Acknowledgments

NF received a scholarship from the Rudolf and Helene Glaser Foundation, part of the "Stifterverband für die deutsche Wissenschaft". We thank Klaus Thiele, Helmut Linhard and Marion Dorsch for the determinations of the plant species and the year 2016 interns of the Nationalpark Bavarian Forest for helping in the sampling of moths. The research was partly funded by the Hessen State Ministry for Higher Education, Research and the Arts, Germany, as part of the LOEWE priority project Nature 4.0 – Sensing Biodiversity.

Chapter 3

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

with

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accepted for publication in *Diversity and Distributions* (05.11.2020)

This study builds upon data from several biodiversity monitoring projects and was mainly analyzed written by Soyeon Bae, the lead author. I contributed the compilation of data of the different species groups and their respective traits and discussion thereof, as well as previous revisions of the text.

Summary

Despite increasing interest in β-diversity, i.e. the spatial and temporal turnover of species, the mechanisms underlying species turnover at different spatial scales are not fully understood, although they likely differ among different functional groups. We investigated the relative importance of dispersal limitations and the environmental filtering caused by vegetation for local, multi-taxa forest communities differing in their dispersal ability, trophic position and body size. In the inter-region analysis, the independent and shared effects of the regional spatial structure (regional species pool), landscape spatial structure (dispersal limitation) and environmental factors on species turnover were quantified with a 1-ha grain across 11 functional groups in up to 495 plots by variation partitioning. In the intra-region analysis, the relative importance of three environmental factors related to vegetation (herb and tree layer composition and forest physiognomy) and spatial structure for species turnover was determined. In the inter-region analysis, over half of the explained variation in community composition (23% of the total explained 35%) was explained by the shared effects of several factors, indicative of spatially structured environmental filtering. Among the independent effects, environmental factors were the strongest on average over 11 groups, but the importance of landscape spatial structure increased for less dispersive functional groups. In the intra-region analysis, the independent effect of plant species composition had a stronger influence on species turnover than forest physiognomy, but the relative importance of the latter increased with increasing trophic position and body size. Our study revealed that the mechanisms structuring assemblage composition are associated with the traits of functional groups. Hence, conservation frameworks targeting biodiversity of multiple groups should cover both environmental and biogeographical gradients. Within regions, forest management can enhance β-diversity particularly by diversifying tree species composition and forest physiognomy

Introduction

Since Whittaker (1960) defined β-diversity as the difference in species composition among sites, β-diversity has gained the increasing attention of ecologists. To promote overall diversity within a region (γ-diversity), either α-diversity (the within-site species diversity) or β-diversity (Müller & Goßner, 2010; Beck *et al.*, 2012) must be increased. In European beech forests for instance, ecologists have highlighted the importance of β-diversity and the need to foster a mosaic of structurally diverse habitat patches at landscape levels rather than homogeneous landscapes with high local small-grain heterogeneity (Hilmers *et al.*, 2018; Schall *et al.*, 2018). However, the processes that promote compositional differentiation between local communities (species turnover) remain under debate and differ among habitat types and species groups (Murphy *et al.*, 2015; Aisen *et al.*, 2017; Zellweger *et al.*, 2017). Four mechanisms are considered to account for the species composition of local communities (Fig. C3.1a). First, at large spatial (inter-region) scales, historical biogeography (e.g. glaciation history), long-distance dispersal and macro-scale environmental filters shape the regional species pool that constrains the composition of local assemblages (Ricklefs, 1987; Cornell & Lawton, 1992; Hubbell, 1997; Legendre *et al.*, 2005; Dobrovolski *et al.*, 2012). Second, at the intra-region scale, neutral processes linked to dispersal limitations may further determine local communities (Hubbell, 2001) and operate together with third and fourth mechanisms related to niche-based processes, including environmental filtering and biotic interactions (competition, predation, mutualism, etc.). Of the latter, environmental filtering has been studied for many years (Whittaker *et al.*,

1973). Community assembly processes occurring under extreme environmental conditions such as those of climate, lead to communities composed of species with similar response traits by environmental filtering (Cadotte & Tucker, 2017). However, the relative contributions of mechanisms operating at different spatial scales in shaping species composition are still under debate (Chase & Myers, 2011).

The relative importance of dispersal limitations on species turnover is likely to depend on the dispersal ability of the species studied. Previous studies showed that at a global scale β-diversity is more pronounced for less mobile taxa due to their limited dispersal. Qian (2009), for example, found that the β-diversity of birds and mammals was lower than that of reptiles and amphibians. However, studies at national or regional scales (extents) did not find an effect of dispersal ability on β-diversity, based on comparisons of birds, bats, non-flying mammals, reptiles and amphibians (Calderón-Patrón *et al.*, 2013) and of non-flying vs. flying groups (Harrison *et al.*, 1992).

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

In fact, spatial-scale dependency is frequently invoked to explain the inconsistent conclusions of previous studies. For example, among the determinants of community assembly at larger spatial extents, geographic distance (neutral processes) was shown to be more important than environmental factors (niche process), as demonstrated in pan-European vs. country-wide analyses (Qian *et al.*, 2005; Keil *et al.*, 2012). However, recent studies have shown regional effects with an explicit spatial clustering, such as the effects of biogeographical history on local assemblages over a continental spatial extent in Europe (Jiménez-Alfaro *et al.*, 2018; Hagge *et al.*, 2019). These observations demonstrate the importance of resolving spatial structure into multiple spatial scales in studies on species turnover. Yet, studies that separate the effects of spatial structure into those occurring at inter-regional (i.e. regional species pool) and intra-regional (i.e. dispersal limitations) scales, thus allowing investigation of their independent contributions, are lacking.

In this study, we examined the relative importance of dispersal limitations in shaping the species composition of local communities across a range of taxa (henceforth "functional groups") differing in their dispersal abilities, after controlling for the regional species pool (the result of macro-scale processes) and environmental filters (henceforth "inter-region analysis") (Fig. C3.1b). We hypothesized that the relative importance of dispersal limitations increases with decreasing dispersal ability and thus from spore-dispersal groups, to flying vertebrates, to arthropods (flying, ballooning or walking dispersers) (Fig. C3.1c).

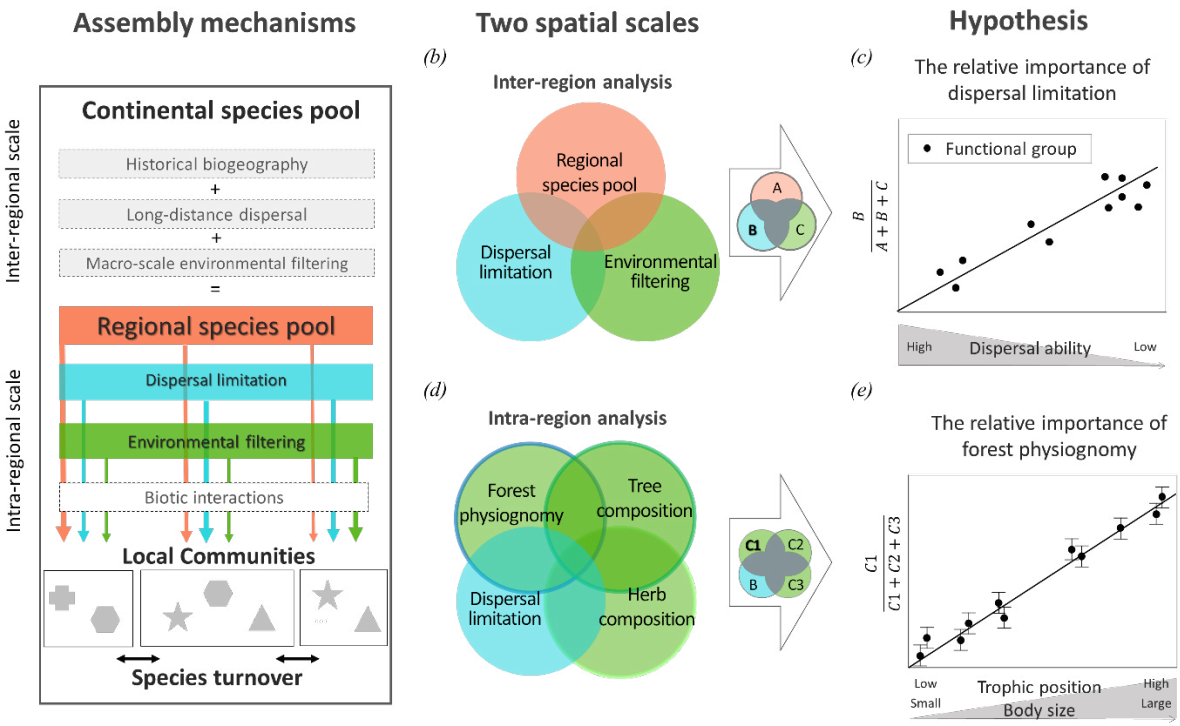


FIGURE C3.1: The framework of the inter-region and intra-region analyses. (a) Assembly mechanisms influencing the species turnover of the local community at the inter-region and intra-region scales. (b) The inter-regional variation partitioning analysis of the species composition using predictor sets of the regional species pool, dispersal limitations and environmental filtering. (c) The first hypothesis examined by the inter-region analysis that the relative importance of dispersal limitations increases with decreasing dispersal ability. (d) The intra-regional variation partitioning analysis of the species composition using the predictor sets of dispersal limitations, herb composition, tree composition and forest physiognomy. (e) The second hypothesis examined by the intra-region analysis that the relative importance of forest physiognomy vs. plant species composition increases with increasing trophic position and body size

In studies of environmental filtering, a long-standing question is the role of plant species composition vs. physiognomy in driving species turnover (Rotenberry, 1985). Both of these environmental filters are directly affected by forest management and influence the species comprising each functional group. A shift in plant species composition mainly causes changes in the amount and type of available resources or microhabitats, while a shift in forest physiognomy, such as the vertical profile and heterogeneity, changes the spatial arrangement thereof (see Penone *et al.*, 2019). While this question has been actively discussed in α-diversity studies since MacArthur and MacArthur (1961) (Schuldt *et al.*, 2018; Penone *et al.*, 2019), it has gained little attention in β-diversity studies, in which coarser variables, such as climate, topography, or land cover, have been employed over larger spatial grains and extents (Keil *et al.*, 2012; Kent *et al.*, 2014, Svenning *et al.*, 2011). A better understanding of the mechanisms underlying α-diversity and species turnover in forests, especially those mechanisms directly related to forest management, are crucial to promote α- and β-diversity. However, with the possible exception of birds, knowledge on the relative importance of plant composition and physiognomy on species turnover of local assemblages is incomplete (Rotenberry, 1985; Wiens *et al.*, 1987; Macnally, 1990; Müller *et al.*, 2010; Zellweger *et al.*, 2017). We are aware of only one study addressing diverse functional groups in grasslands: Schaffers et al. (2008) found that plant composition played a dominant role in determining arthropod assemblages.

The aim of our study was to elucidate the relative importance of plant species composition vs. forest physiognomy in shaping the

species composition of local communities, after controlling for dispersal limitations in each region (henceforth "intra-region analysis"; Fig. C3.1d). We predicted that plant species composition would be a strong driver of the species turnover in lower trophic positions, such as phytophagous beetles, because of their host plant specificity. Conversely, forest physiognomy was expected to strongly influence the species turnover in larger body-size groups (mostly in higher trophic positions), such as insectivorous birds and bats, due to their large home-range requirements and diverse foraging- or nesting-niche (habitat-structure) requirements. We therefore hypothesized that the relative importance of forest physiognomy vs. plant species composition would increase with increasing trophic position and body size (Fig. C3.1e).

Methods

Study site

The study was conducted in five forest regions in Germany along a north to south axis (N 48° 36′–53° 19′) covering a spatial extent of 199,000 km^2 and spanning core forest habitat types of Central Europe (Fig. C8.2.1). These regions were separated from each other by an average of ~320 km (roughly 120–630 km). Data from 503 plots were compiled from three projects: 150 plots from the Biodiversity Exploratories Project (50 plots per region) (Fischer *et al.*, 2010), 284 plots from the BIOKLIM Project (Bässler *et al.*, 2009), and 69 plots from the Steigerwald Project (Doerfler *et al.*, 2017). In the Biodiversity Exploratories Project, 50 plots were established in three regions: the UNESCO Biosphere Reserve Schorfheide-Chorin (SCH), the National Park Hainich and the surrounding Hainich-Dün region (HAI), and the UNESCO Biosphere Reserve, Schwäbische Alb (ALB). The BIOKLIM Project was conducted in the Bavarian Forest National Park (BAY), and the Steigerwald Project in Northern Bavaria (STE). (for details of the five regions, see Fig. C8.2.1 and Bae et al. (2019)). Not all functional groups were sampled in each plot. The number of plots investigated per functional group was as follows: 321 for bryophytes, 307 for lichens, 385 for saproxylic beetles, 495 for wood-inhabiting fungi, 386 for phytophagous beetles, 226 for moths, 383 for spiders, 383 for carabids, 386 for necrophagous beetles, 494 for birds and 247 for bats (Table C8.2.1).

Species data of 11 functional groups

All species data were assessed in 1-ha forest plots representing a larger forest management unit. Bryophytes, epiphytic and epixylic lichens, and saproxylic fungi were assessed in subplots within the 1-ha plots (the sizes of the subplots are listed in the note in Chapter 8.2). Pitfall traps, flight interception traps and light traps were used to sample arthropods. For bird surveys, repeated point counts were performed during breeding seasons. Bats were recorded using ultrasound detectors and analyzed at the species level with the appropriate software. Details of the sampling methods are given in the note in Chapter 8.5. The total number of species observed overall plots and the mean and standard deviation of the number of observed species per plot are presented in Table C8.5.

Before testing our hypotheses (Fig. C3.1c, e), we partitioned total β-diversity (multiple-site dissimilarity of the species composition) into the components species turnover and nestedness to calculate the percentage of the species turnover in the variation of community composition. The presence-absence data (bryophytes, lichens and fungi) were calculated with Sorensen dissimilarity, and the abundance-based data (other eight groups) with

Bray–Curtis dissimilarity using the R package 'betapart' (Baselga & Orme, 2012).

Hellinger transformations were applied for either species abundance data or species presence-absence data (as response variables) using the function *decostand* in the R package 'vegan' (Oksanen *et al.*, 2019). This avoided the possibility of double zeros as false indicators of similarity among plots and allowed the use of linear statistical tools such as redundancy analysis (Borcard *et al.*, 2011). A previous study compared several transformation methods and concluded that the Hellinger transformation was one of the best pre-transformations for general use (Legendre & Gallagher, 2001), including the analysis of presence-absence data. These transformed species composition data tables were used as multivariate response data in variation partitioning (see 'statistical analysis' for details on variation partitioning).

Predictor sets of environmental filters

Predictor sets of herb and tree compositions

Vascular plant species were recorded in 20 m × 20 m subplots for ALB, HAI and SCH, in a circular 200 m² plot for BAY, and in a square of 200 m² for STE. The percent coverage of single species was recorded for tree layer, shrub layer and herb layer (see Chapter 8.5 for details on plant species sampling). For tree composition, the percentage cover of each woody plant species at each height layer was summed to obtain the cumulative cover of the species. For herb composition, only presence-absence data from the herb layer were used.

A principal coordinate analysis (PCoA) was applied on Euclidean distance matrices computed on Hellinger-transformed matrices of tree and herb composition, respectively (see section 'species data of 11 functional groups' for details on Hellinger transformation). PCoA produces an ordination solution maximizing the variance of the observations using eigenvalue decomposition while preserving the dissimilarities among sites (Borcard *et al.*, 2011). The ordination axes that explained >75% of the variance of the data were selected as predictor sets related to tree and to herb composition.

Predictor set of forest physiognomy

Airborne laser scanning (ALS) data were collected to obtain forest physiognomy metrics for the 1-ha plots during the leaf-on seasons between 2007 and 2018, depending on the region (see Table C8.2.2 for details on ALS acquisitions). Similar pre-processing methods using 'LAStools' (LAStools, 2012) were employed overall five forest regions, including the classification of outliers as well as ground and non-ground returns (i.e. vegetation returns). The height of the vegetation returns was normalized to the height above ground level (a.g.l.) using a high-resolution elevation model derived from the ground returns. Forest physiognomy was described using ALS metrics describing the vertical profile, vertical heterogeneity, canopy surface roughness and the horizontal heterogeneity of the canopy. All ALS metrics were derived from the normalized point cloud (Table C3.1). For the vertical profile, the mean height of the vegetation returns was used, and the penetration ratios of the canopy layer (above 2 m) and regeneration layer (below 2 m) were determined. Penetration ratios, defined as the proportion of points filtered by a specific horizontal layer, were used to characterize the filtering within each layer and were calculated by dividing the number of returns above the respective layer by the number of returns below that layer. The standard deviation and coefficient of variation of the height of the vegetation returns and the foliage height diversity were computed to characterize the vertical heterogeneity

TABLE C3.1 Predictor sets as proxies of regional species pool, dispersal limitations and environmental filtering. Regional spatial structure, landscape spatial structure and environmental factors were included in the inter-region analysis and spatial structure, herb and tree composition and forest physiognomy in the intra-region analysis (see the framework of the two analyses in Fig. 1). The main axes were selected from the principal components analysis (PCA) or principal coordinate analysis (PCoA) and explained 75% of the cumulative proportion of the variance of the predictor sets. The significant variables in each predictor set were then selected by forward selection. See Section 2.5 for details on the principal coordinates of neighbor matrices (PCNM).

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

Canopy roughness was described by creating a gridded canopy height model (CHM) with a spatial resolution of 1 m using the highest point in each cell. The surface area of the CHM was derived using the triangulation algorithm presented in Jenness (2004). Surface roughness was then estimated using two metrics: the ratio between the planimetric and the surface area of the CHM and the standard deviation of the CHM.

Horizontal canopy heterogeneity was assessed by analyzing canopy-gap distributions. A gridded binary gap mask with a 1-m spatial resolution was created in which cells were classified as gaps if >20% of all vegetation returns had a height ≤2 m. To avoid very small or narrow gaps, only gap features >50 m² in size and thicker than a perimeter-area ratio >1.5 were selected. From the filtered gap mask the total area of the gaps, the standard deviation of the gap sizes, the mean-perimeter-area ratio, the mean fractal dimension, the total edge length and the edge density of forest gaps were calculated using the R package 'landscapemetrics' (Hesselbarth *et al.*, 2019). Finally, a principal components analysis (PCA) was applied to the forest physiognomy metrics acquired by ALS. Similar to the approach used for the tree and herb composition data, the ordination axes that explained >75% of the variance of the data were selected as predictors of forest physiognomy.

Predictor sets of regional species pool and dispersal limitations

For the inter-region analysis, the predictor sets of regional species pool and dispersal limitations were modeled using principal coordinates of neighbor matrices (PCNM) and the *dbmem* in the package 'adespatial' (Dray *et al.*, 2020) (Fig. C3.1b). The sites of the five regions are clearly clustered by the region. Therefore, if we would represent the spatial structure of our sites only by x and y coordinates (two variables), the fine-scale spatial structure within each region could be easily obscured by the primary large scale spatial structure. The PCNM analysis was developed by Borcard and Legendre (2002) to represent the fine-scale spectrum of spatial structures covering an extensive range of scales. In this study it was applied as follows: First, a geographical distance matrix between the plots of five regions was created, after which the distance matrix was truncated by the minimum distance between different forest regions. Any pair-wise distances above this minimum distance threshold ($min_{\text{inter-regional distance}}$) were thus considered as large and were set to four times of $min_{\text{inter-regional distance}}$ (see Borcard and Legendre (2002) for a detailed explanation of the use of the multiplicate "four"). Such an adjusted pair-wise distance matrix is an object-by-object matrix, thus required to be transformed into an object-by-variable matrix for regression analysis. For it, the PCNM analysis employs a principle component analysis which then results in the distance-based Moran's eigenvectors orthogonal to one another. Among the eigenvectors, only the positive eigen values represent the Euclidean components of the neighbourhood relationships. These positive eigenvectors were extracted and are called PCNM variables hereafter. Lastly, we fitted an analysis of variance model (ANOVA) to the PCNM variables using *aov* and region as the independent variable to disentangle the PCNM variables that differed significantly between regions to generate a predictor set for the regional species pool (henceforth, "regional spatial structure") and those that did not differ significantly between regions (henceforth, "landscape spatial structure") hence representing dispersal limitations within a region (see more details in Fig. C8.2.2).

For the intra-region analysis, a predictor set of dispersal limitations was also modeled using a PCNM in each region (Fig. C3.1d). A geographical distance matrix between the plots of each region was created and truncated by the maximum distance in the minimum spanning tree; the positive PCNM variables of the distance-based Moran's eigenvectors were then applied.

Statistical analyses

Variation partitioning

Variation partitioning through redundancy analysis ordination (RDA) was applied to the species composition of 11 functional groups to assess the independent and shared effects of the predictor sets on the variation between local communities for two hypotheses tests (Fig. C3.1c, e). RDA is a method of regression analysis modeling multivariate response data (species composition data tables in this study).

For the inter-region analysis, variation partitioning was conducted over the five forest regions to compare the importance of regional species pool, dispersal limitations and environmental filtering (Fig. C3.1b). To evaluate the contribution of environmental filtering, predictor sets of herb composition (PCoA axes), tree composition (PCoA axes) and forest physiognomy (PCA axes) were included. Regional spatial structures (regional PCNMs) were included as predictor sets of regional species pool, and landscape spatial structures (landscape PCNMs) as predictor sets of dispersal limitations (see section 'statistical analysis'). In total, variation partitioning for the inter-region analysis was conducted 11 times; i.e. on each of the Hellinger-transformed species composition data tables of 11 functional groups over entire plots at all regions as a response variable.

For the intra-region analysis, variation partitioning was conducted for each forest region to compare the importance of three environmental filters (the PCA axes of forest physiognomy and the PCoA axes of herb and tree composition) and dispersal limitations (spatial structure by PNCM) (Fig. C3.1d). In total, variation partitioning for the intra-region analysis was conducted 55 times; i.e. on each of the Hellinger-transformed species composition data tables of the 11 groups of the five regions, separately.

First, the function *forward.sel* in the R package 'adespatial' (Dray *et al.*, 2020) was used with 9999 permutations to forward-select the explanatory variables in each predictor set to select the variables that correlated significantly with the response variables. The function *varpart* in the R package 'vegan' (Oksanen *et al.*, 2019) was then used in variation partitioning with the predictor sets containing at least one significant variable.

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

Permutations-based independence tests

To determine whether the relative importance of landscape spatial structure as a proxy for dispersal limitations depends on dispersal ability, the results of variation partitioning obtained in the inter-region analysis were compared among the 11 functional groups (Fig. C3.1c). The ratio between the

independent variance explained by landscape spatial structure and the sum of the independent variance explained by all predictor sets was calculated for each group. Differences between the 11 functional groups in terms of their dispersal ability were identified by categorizing the 11 groups accordingly. Bryophytes, lichens and fungi that disperse via spores were classified into a spore-dispersal group with rank 1 on the ordinal scale, because these organisms rapidly disperse over tens to hundreds of kilometers (Abrego *et al.*, 2018; Komonen & Müller, 2018). Birds and bats as flying vertebrates were ranked second, based on their ability to move over several kilometers within a short time (Dietz *et al.*, 2009). Arthropods with shorter dispersal distances were ranked third (Komonen & Müller, 2018). Thus, the 11 groups were tested as ordinal predictors in permutations-based independence tests, with the alternative hypothesis being *greater*, using the function *independence_test* in the R package 'coin' (Hothorn *et al.*, 2019).

The dependency of the relative importance of forest physiognomy on trophic position and body size was examined by comparing the results of variation partitioning in the intra-region analysis for the 11 functional groups (11 mean values of five regions) for trophic position and for the eight animal groups for body size. (Fig. C3.1e). The relative importance of plant composition and forest physiognomy as proxies for environmental filtering was determined by first summing the effects of herb and tree composition to represent plant composition. The ratio of the variance independently explained by forest physiognomy to the sum of the variance independently explained by the predictor sets of plant composition and forest physiognomy was calculated for each group. Differences between the 11 functional groups with different trophic positions were identified by categorizing the 11 groups accordingly. Bryophytes and lichens were classified as autotrophs with rank 1, fungi and saproxylic beetles into first decomposers (rank 1.5), phytophagous beetles and moths into primary consumers (rank 2), spiders and carabids beetles into secondary consumer group (a) (rank 3), necrophagous beetles into secondary decomposers (rank 3.5) and birds and bats into a secondary consumer group (b) (rank 4). Although necrophagous beetles consume carcasses of primary and secondary consumers (a) as well as secondary consumers (b), both arthropods and vertebrates, it was assumed that in the study area they mostly consume arthropods (primary or secondary consumers (a)). The relative positions of primary and secondary decomposers were a half trophic level higher than those of their diets (Steffan *et al.*, 2017). Hence, the 11 groups were tested as ordinal predictors in permutations-based independence tests with the alternative hypothesis being *greater* and using the same function as described above for the first hypothesis test. The body size was measured by body length for all beetles, length of prosoma and opisthosoma for spiders, length from the thorax to the abdomen for moths, head-body length for bats and length from the tip of beak to end of tail feathers for birds (Table C8.2.3). The body size data were collected from literature and own measurements (see Table C8.2.3 for sources). The body size was tested only for the eight animal groups, as the underlying argument of this hypothesis was related to the expectation of higher importance of habitat structure shaping species turnover of larger home range size. The median body size of each functional group was taken and natural log-transformed to represent the body size of each group for permutations-based independence tests with the alternative hypothesis being *greater*.

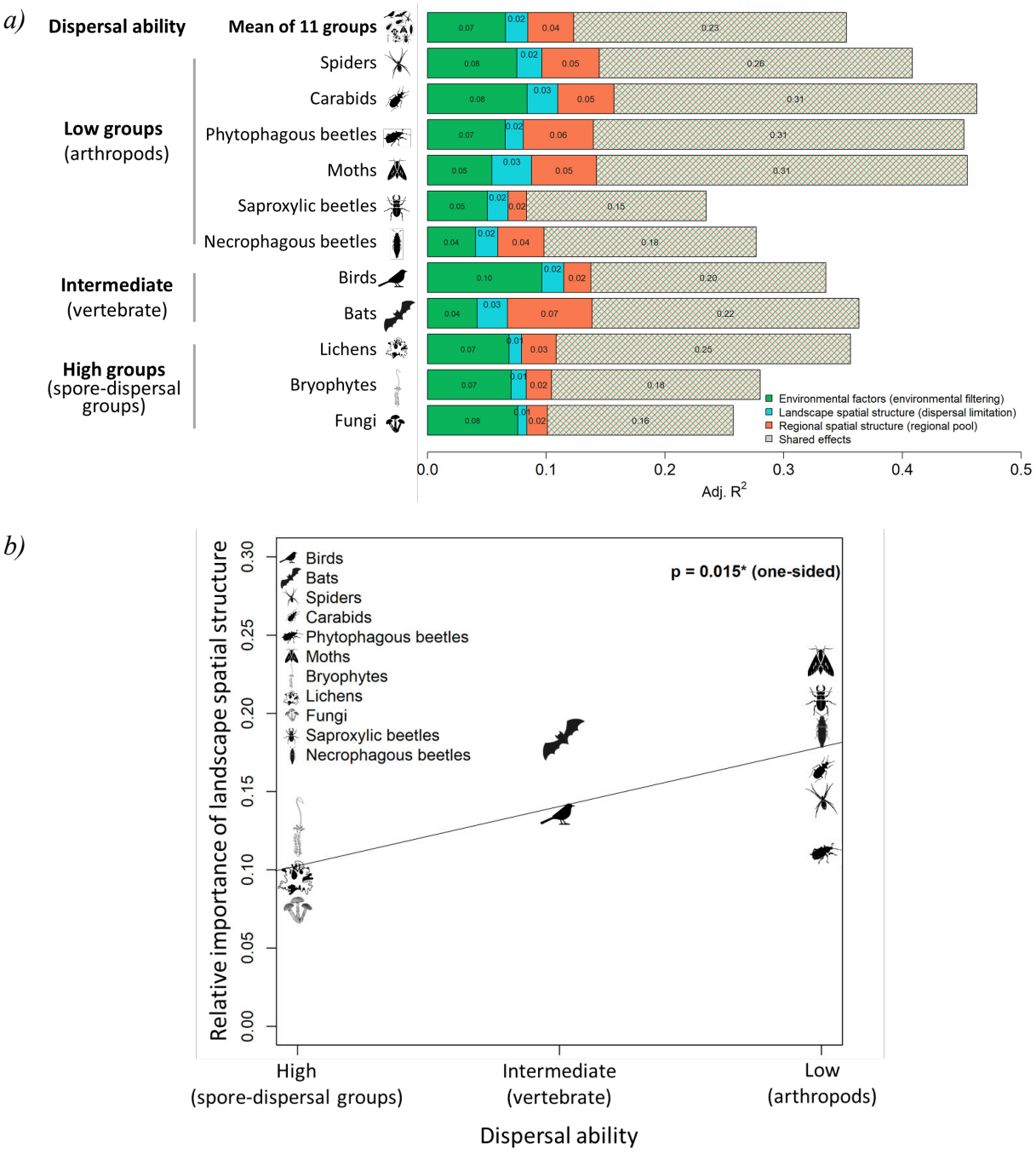


FIGURE C3.2 The relative importance of regional spatial structure, landscape spatial structure and environmental factors. (a) The variation (adjusted R^2) in the assemblage composition of 11 functional groups as explained by the three predictor sets. The environmental factors (green bars) include the effects of herb composition, tree composition and forest physiognomy. The regional spatial structure (orange bars) is represented by the principal coordinates of neighbour matrices (PCNM) variables that differed significantly between regions. The landscape spatial structure (blue bars) describes the effects of dispersal filters within regions by finer PCNM variables. Bars with shading lines represent the shared effects of at least two predictor sets. (b) The relative importance of landscape spatial structure increases significantly along groups with a decreasing dispersal ability: spore-dispersal groups, vertebrate and arthropods.

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

We also tested the robustness of our results against the addition of other environmental factors than vegetation-related factors, which was the focus of this study, especially for the intra-region analysis. We re-ran the inter-region variation partitioning and independence tests for the dispersal ability hypothesis after including climate and topographic gradients (please see details of climate and topography predictor sets in Table C8.2.4).

Results

Total β-diversity (0.990 ± 0.003) was composed of the species turnover (0.972 ± 0.025) and the species nestedness (0.018 ± 0.024) components. The species turnover, a focus of this study, accounted for 98.1% of the total β-diversity (Table C8.2.5).

In the inter-region analysis, the unique and shared effects of proxies for regional species pool (regional spatial structure), dispersal limitations (landscape spatial structure) and environmental filtering (environmental factors related to vegetation) explained 35.28% (± 8.36%) of the variation in the community composition of the 11 functional groups (Fig. C3.2a; Table C8.2.6). Over half of this variation (22.97% ± 5.95%) was explained by the shared effects of at least two predictor sets (proxies). The shared effects between regional spatial structure and environmental factors accounted for 20.77% (± 6.04%) and those between landscape spatial structure and environmental factors for 2.67% (± 1.86%) over the 11 groups (Fig. C8.2.3; Table C8.2.7). As an independent effect, environmental factors were the strongest driver of the variation in the community composition, with a unique explained proportion of the total variation of 6.56% (± 1.75%), followed by regional spatial structure and landscape spatial structure with 3.87% (± 1.88% SD) and 1.87% (± 0.74%), respectively (Fig. C3.2a; Table C8.2.7; Fig. C8.2.3). However, the order and strength of the importance of the three predictor sets varied between functional groups. The relative importance of landscape spatial structure increased significantly with decreasing dispersal ability, i.e. from the spore-dispersal groups, to vertebrates, to arthropods (Fig. C3.2b; Fig. C8.2.4a; Table C8.2.8, C8.2.9). This finding corroborated the findings of the additional data set including climate and topographic gradients (Fig. C8.2.5).

In the intra-region analysis, landscape spatial structure and the three environmental factors (tree and herb composition and forest physiognomy) together explained 19.36% (± 9.84%) of the variation in community composition for the five forest regions and 11 functional groups (Fig. C3.3a; Table C8.2.6). Half of this variation (10.34% ± 6.69%) was explained by the shared effects of at least two predictor sets, as our suites of predictor sets were associated with each other and hence simultaneously affected the response variables. The unique effect of each predictor set

was rather low, with landscape spatial structure as the most important factor as it explained 3.44% (± 4.12%) of the variation independently, followed by herb composition, forest physiognomy and tree composition with 2.86% (± 2.31%), 1.49% (± 1.88%) and 1.23% (± 1.15%), respectively (Fig.C3.3a and C3.3b; Fig. C8.2.6; Table C8.2.10).

A comparison of the importance of spatial vs. environmental factors showed that the latter had larger effects on all functional groups except moths. The comprehensive effects of the three environmental factors independent from the effect of landscape spatial structure explained a total of 11.72% (± 6.98%) (based on the mean adjusted R^2 of 55 cases) of the variation, while the landscape spatial structure independently explained 3.44% (± 4.12%) of the variation (Fig. C3.3a; Table C8.2.11).

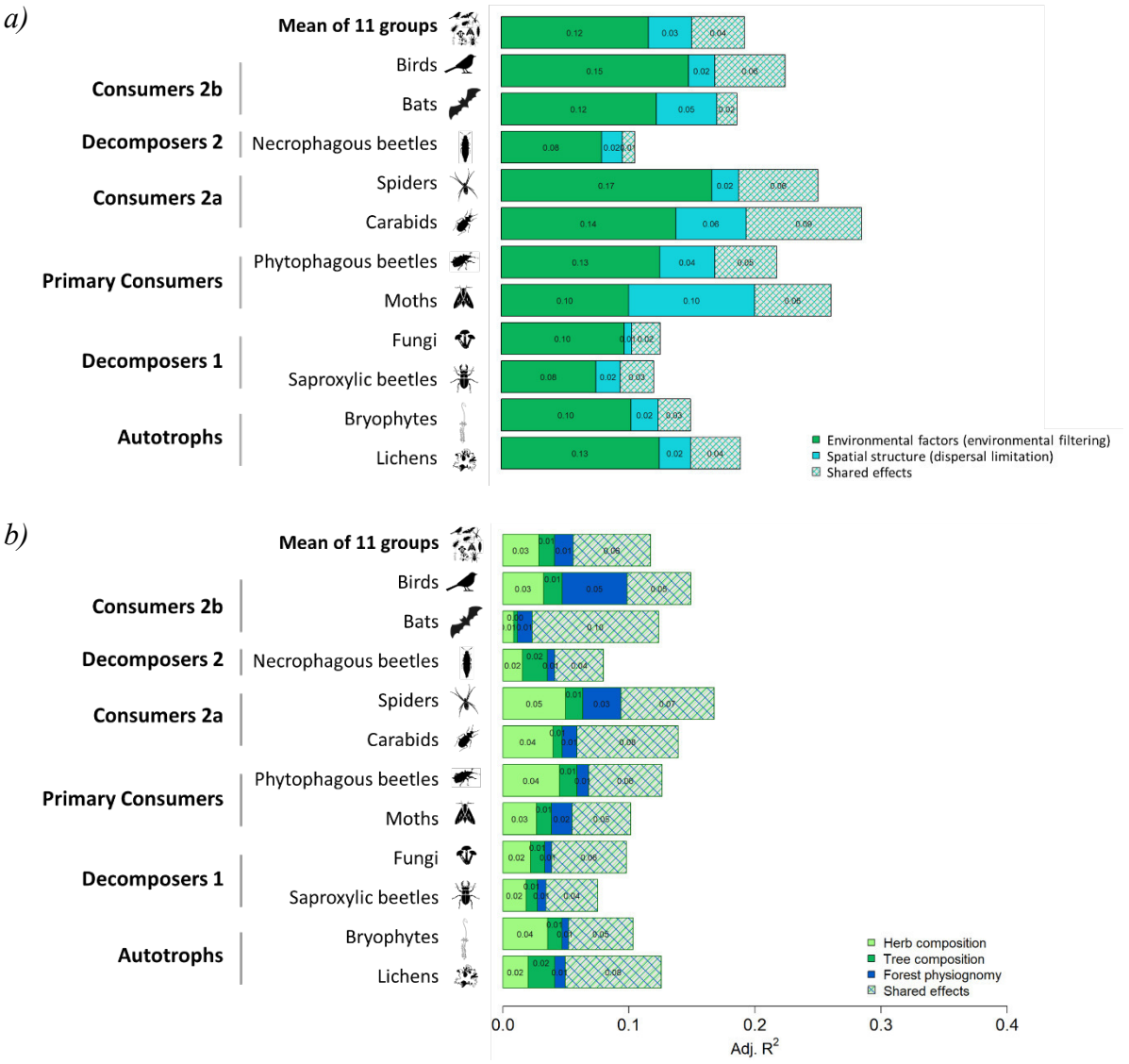
Among the environmental filtering factors, the relative importance of herb composition, tree composition and forest physiognomy differed between functional groups. For the assemblage composition of birds and bats, the highest trophic groups and the largest body size groups in our study, forest physiognomy had the most important effect on the variation in the community composition (Fig. C3.3b). For the other groups, herb or tree composition (mainly herb) was more important than forest physiognomy. The significant increase in the relative importance of forest physiognomy with increasing trophic position and body size suggested that forest physiognomy is a strong driver of the community composition of higher trophic positions and larger body size (Fig. C3.3c and C3.3d; Fig. C8.2.4b and C8.2.4c; Tables C8.2.9 and C8.2.12).

To check the robustness of our results of animals for sample completeness, we re-analyzed the data on a subset of plots with sample coverage above 70%. These findings corroborated the findings of the total data set (Tables C8.2.13–15).

Discussion

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

The aim of the inter-region analysis was to assess the relative importance of regional spatial structure, landscape spatial structure and environmental factors on species turnover. As species turnover accounted for most of the total β-diversity, we interpreted our result on the variation of community composition as species turnover henceforth. We found that environmental factors are a more important determinant of species turnover, but that the importance of landscape spatial structure increases for less dispersive species. Across the 11 functional groups, environmental factors rather than spatial structure (regional, local) were of greater importance in shaping assemblage composition across a 1-ha local grain.


a)
Mean of 11 groups
Consumers 2b
Birds
Bats
Decomposers 2
Necrophagous beetles
Consumers 2a
Spiders
Carabids
Primary Consumers
Phytophagous beetles
Moths
Decomposers 1
Fungi
Saproxylic beetles
Autotrophs
Bryophytes
Lichens
Environmental factors (environmental filtering)
Spatial structure (dispersal limitation)
Shared effects
b)
Herb composition
Tree composition
Forest physiognomy
Shared effects
0.0
0.1
0.2
0.3
0.4
Adj. R2

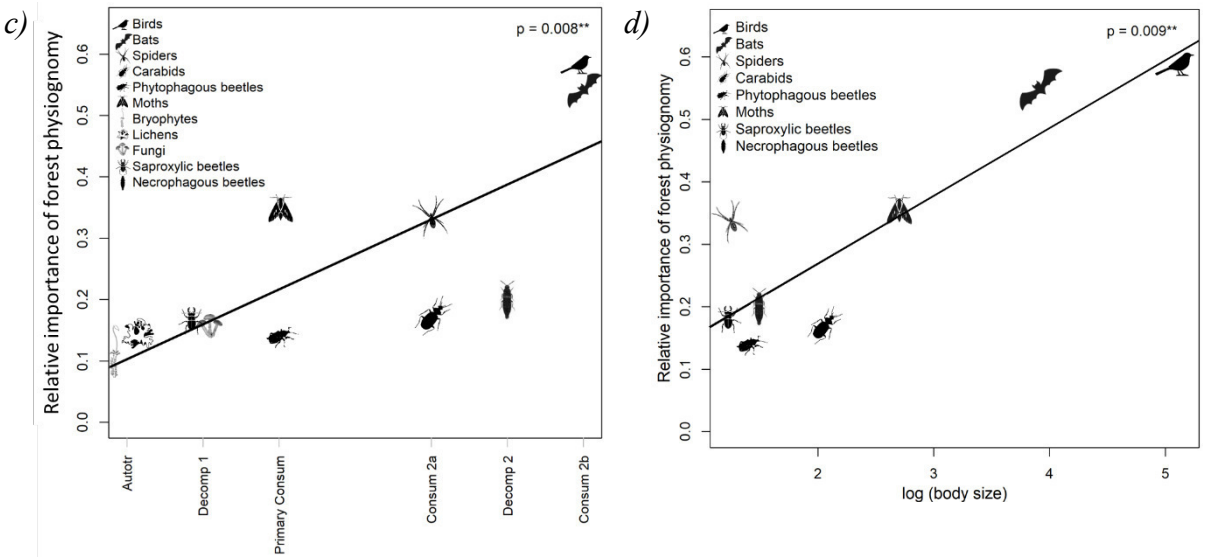

c)
Birds
Bats
Spiders
Carabids
Phytophagous beetles
Moths
Bryophytes
Lichens
Fungi
Saproxylic beetles
Necrophagous beetles
p = 0.008**
Relative importance of forest physiognomy
Autotr
Decomp 1
Primary Consum
Consum 2a
Decomp 2
Consum 2b
d)
p = 0.009**
Relative importance of forest physiognomy
log (body size)

FIGURE C.3.3 The relative importance of spatial structure vs. environmental factors and of forest physiognomy vs. plant species composition. (a) The relative importance of spatial structure vs. environmental factors. The explained variation (adjusted R^2) of the assemblage composition of 11 functional groups averaged over five regions. The environmental factors (green bars) include the effects of herb composition, tree composition and physiognomy. The spatial structure is represented by blue bars. The bars with shading lines represent the shared effects of at least two predictor sets. (b) The relative importance of forest physiognomy vs. plant species composition. The effects of herb composition (yellow green bars), tree composition (green bars) and physiognomy (blue bars) are shown together with the variation explained by the shared effects (gray bars). (c) The ratio of the effects of forest physiognomy vs. the total effects of environmental factors significantly increased with increasing trophic position. (d) The ratio of the effects of forest physiognomy vs. the total effects of environmental factors significantly increased with increasing body size. (This analysis was applied only to animals, as this hypothesis is related to the home range size.)

Previous studies showed that geographic distance is more important than environmental factors at larger spatial extents, as demonstrated for a pan-European vs. country extent (Qian *et al.*, 2005; Keil *et al.*, 2012). Therefore, spatial extent should be considered in comparisons of niche vs. neutral processes. The findings of our inter-regional analysis are in line with those of studies conducted at the same country-wide extent but with a grain coarser (0.25-400 km^2) than the 1 ha of our study. Both Keil et al. (2012) and Zellweger et al. (2017) showed that geographic distance was less important than environmental variables for plants, butterflies and birds in Europe. This suggests that environmental filtering determines species turnover even at a country-wide extent, rather than regional species pool and dispersal limitations.

However, a strong deviation from this general pattern was determined for the assemblage composition of bats in the inter-region analysis, as the effect of regional spatial structure was nearly twice as high as that of environmental factors. This result suggested a strong effect of regional species pool on the species turnover of bats and it can be explained by the different roosting behaviors and adaptations for the winter period of different species (i.e., climate filter), thus giving rise to the regional species pool currently observed for European bats (Kalda *et al.*, 2015). The addition of climate and topography predictor sets to environmental factors as a supplementary analysis (Fig. C8.2.5) reduced the unique contribution of regional spatial structure but increased the shared effects between regional spatial structure and environmental factors (i.e. effects of regionally distinguished climate and topography) in the formation of bat assemblages. The regionally clustered species pool of bats can also be attributed to land-use changes at a regional scale, which were shown to drive the regional extinction of some bat species (Safi & Kerth, 2004).

Our first dispersal ability hypothesis (Fig. C3.1c) states increasing relative importance of dispersal limitations with decreasing dispersal ability. In line with this, the relative importance of landscape spatial structure (a proxy for dispersal limitations) was shown to depend on the potential dispersal ability of the functional groups, as groups that can disperse over long distances via spores, such as fungi, lichens and bryophytes, were less affected by landscape spatial structure (as dispersal limitations) than groups with a low dispersal ability. The stronger geographical separation of less dispersive functional groups has been demonstrated for example for less mobile ground-dwelling arthropods vs. more mobile birds and vascular plants (Ferrier *et al.*, 1999) and for snails vs. birds (Steinitz *et al.*, 2006). However, our study is the first to

examine the importance of spatial structure in the species turnover of spore-dispersers vs. that of vertebrates and arthropods. This dependency on dispersal ability within a region was a consistent finding that did not change even after the addition of other environmental filters (Fig. C8.2.5), and it suggested that dispersal limitations are more important for less dispersive species.

In the debate over popular niche vs. neutral processes, ecologists have argued that species turnover explained by geographic distance (in our study, regional and landscape spatial structures) can be attributed to factors other than dispersal limitation. The relative importance of geographic distance for species turnover may vary with the environmental characteristics of the study area (e.g. latitude, land-use history, or heterogeneity) and depending on the study design (e.g. the quality of the included environmental variables and the effects of unmeasured environmental variables) (Murphy *et al.*, 2015). In our study, half of the variation explained by regional and landscape spatial structure was co-explained by environmental differences, because our predictor sets of environmental factors were highly spatially structured. It can thus be assumed that there is another, unmeasured fraction of spatially structured environmental variables, such as climate or topographic gradients, contributing to the variation uniquely explained by regional and landscape spatial structure. This can be seen in Fig. C8.2.4, which shows the increased shared effects and decreased unique effect of regional spatial structure following the addition of climate and topographic predictor sets. Disentangling the independent contributions of multiple effects, particularly those of the regional species pool, requires studies with a much larger number of regional replicates.

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

Yet, physiognomic factors were more important for the species turnover of higher trophic groups or large-bodied groups, particularly birds and bats. This finding supported our second hypothesis that the relative importance of forest physiognomy relative to plant composition increases with increasing

trophic position and body size. Our result was consistent with that reported for the species turnover of birds in a temperate forest in Central Europe (Müller *et al.*, 2010) and thus with the important role of forest physiognomy in bird diversity introduced by MacArthur and MacArthur (1961). The favored forest physiognomy (density of the shrub or tree layer) of birds depends on their diet, foraging, resting, or nesting traits (MacArthur, 1958). For bats, our results are in agreement with previous studies showing that bat species are specifically adapted to different foraging spaces such that their assemblages are strongly structured by forest physiognomy (Arlettaz *et al.*, 2001; Schnitzler & Kalko, 2001; Jung *et al.*, 2012a).

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

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

Overall, in our study the unique effects of the predictor sets and the total explained variance were low. In both cases, this may have been due to the high number of explanatory variables, reflected in the reduced adjusted R-squared values. On average, 11.02 (± 5.33 SD) predictors were used in the intra-region analysis and 38.09 (± 9.35 SD) in the inter-region analysis. The difference between R-squared and adjusted R-squared values of the total explained variance was 6.72% (± 1.79%) in the intra-region analysis and 12.98% (± 4.40%) in the inter-region analysis. A lack of important environmental information on

species turnover, such as historical or current land use and its intensity, might also account for the low total explained variance. The few unique effects of the predictor sets were due to the large proportion of their shared effects, since our chosen environmental factors were spatially structured inter- and intra-regionally.

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

Acknowledgments

This project was financed by the DFG (Deutsche Forschungsgemeinschaft), grant no. MU3621/2-1, KR 3292/2-1 and LE3316/2-1, and by Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (2020R1A6A3A03038391). This publication was supported by the Open Access Publication Fund of the University of Würzburg. We thank H. Hacker for the moth determinations, M. Blaschke for fungi sampling in the Steigerwald and P. Krzystek and T. Nauss for support with data from airborne laser scanning. We also thank the managers of the three Exploratories, K. Wells, S. Renner, F. Staub, S. Gockel, K. Wiesner, K. Lorenzen, J. Vogt, A. Hemp, M. Gorke and M. Teuscher for their work in maintaining the infrastructure of the plots and projects; C. Fischer, S. Pfeiffer and V. Grießmeier for their support through the central office; M. Owonibi, J. Nieschulze, A. Ostrowski for managing the central database and E. Linsenmair, D. Hessenmöller, D. Prati, I. Schöning, F. Buscot and the late E. Kalko for their roles in setting up the Biodiversity Exploratories project. This work was funded by the DFG Priority Program 1374, Infrastructure-Biodiversity-Exploratories. Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, Brandenburg and Bayern (see Table C8.5 for details of permits).

Chapter 4

Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests

with

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published in Nature Ecology and Evolution, 4, 2020, p. 1204 - 1212

This study builds upon data from several biodiversity monitoring projects. Measures of forest structures were compiled by the project partners. I was responsible for the compilation of data of the different species groups, the statistical analysis and was lead author in formulating the manuscript. See also electronic Supplement

Summary

The *habitat-heterogeneity hypothesis* predicts that biodiversity increases with increasing habitat heterogeneity due to greater niche dimensionality. However, recent studies have reported that richness can decrease with high heterogeneity due to stochastic extinctions, creating trade-offs between area and heterogeneity. This suggests that greater complexity in heterogeneity–diversity relationships (HDRs) may exist, with potential for group-specific responses to different facets of heterogeneity that may only be partitioned out by a simultaneous test of HDRs of several species groups and several facets of heterogeneity. Here, we systematically decompose habitat heterogeneity into six major facets on ~500 temperate forest plots across Germany and quantify biodiversity of 12 different species groups, including bats, birds, arthropods, fungi, lichens and plants, representing 2600 species. Heterogeneity in horizontal and vertical forest structure underpinned most HDRs, followed by plant diversity, deadwood and topographic heterogeneity, but the relative importance varied even within the same trophic level. Among significant HDRs, 53% increased monotonically, consistent with the classical *habitat-heterogeneity hypothesis*, but 21% were humped-shaped, 25% had a monotonically decreasing slope and 1% showed no clear pattern. Overall, we found no evidence of a single generalizable mechanism determining HDR patterns.

Introduction

The *habitat heterogeneity hypothesis* is one of the central pillars of ecological theory. It states that spatial heterogeneity in abiotic and biotic conditions increases niche dimensionality, i.e. the number of available niches, allowing different species to co-exist such that biodiversity increases (Fig. C4.1)(MacArthur & MacArthur, 1961; Davies & Asner, 2014; Stein *et al.*, 2014). The positive relationship between heterogeneity and species richness is often regarded as ubiquitous (Stein *et al.*, 2014) since its first observation in the early 1960's when MacArthur and MacArthur (1961) showed that local bird diversity strongly correlated with the vertical heterogeneity in forest stands across North America. However, if heterogeneity increases the number of species, the amount of suitable area available for individual species decreases per area unit. According to the *area-heterogeneity trade-off hypothesis* (Allouche *et al.*, 2012), this can result in a decrease in mean population sizes especially at high levels of habitat heterogeneity (Fig. C4.1). The result is an increased probability of stochastic extinctions and ultimately a decline in species richness. This mechanism, along with fragmentation effects that often accompany heterogeneity, can lead to hump-shaped heterogeneity-diversity relationships (HDRs) (Allouche *et al.*, 2012; Ben-Hur & Kadmon, 2020) (Fig. C4.1).

The *area-heterogeneity trade-off hypothesis* is a relatively recent concept and has received less scrutiny than the classical *habitat heterogeneity hypothesis*. Addressing the area-heterogeneity trade-off hypothesis requires testing for non-linear relationships between heterogeneity and biodiversity. However, such tests are poorly represented in the literature and subsequently, not included in a global meta-analysis which supported the prevalence of positive HDRs. Next to the growing evidence that HDRs can take non-linear forms (Kadmon & Allouche, 2007; Tamme *et al.*, 2010; Allouche *et al.*, 2012; Bar-Massada & Wood, 2014; Bar-Massada, 2015; Chocron *et al.*, 2015; Ben-Hur & Kadmon, 2020), it has been shown that certain ecological properties, such as niche breadth, reproduction and dispersal rates (Kadmon & Allouche, 2007; Tamme *et al.*, 2010; Bar-Massada, 2015; Ben-Hur & Kadmon, 2020), moderate the responses of species to increasing niche dimensionality,

reductions in effective area and the degree of fragmentation. Consequently, rather than investigating whether a positive or hump-shaped HDR prevail, recent theoretical approaches address the question of under which conditions HDR takes which shape(Bar-Massada & Wood, 2014; Yang *et al.*, 2015; Ben-Hur & Kadmon, 2020).

A theoretical modeling approach suggested that, despite the various ways in which environmental heterogeneity may affect species richness, HDR patterns should be predictable and robust (Ben-Hur & Kadmon, 2020). This was specifically proposed for sessile organisms, in which low niche width and high dispersal ability should decrease the level of heterogeneity which maximizes species richness. Moreover, theoretical models have shown that given a habitable surrounding, species which are limited in dispersal have positive HDRs due to fragmentation effects (Rybicki *et al.,* 2020), while those with large dispersal ranges rather have hump-shaped HDRs (Ben-Hur & Kadmon, 2020) (Figure C4.1).

A limitation of current theoretical modeling is that it is based upon strong assumptions (e.g. a lack of habitat selection; Ben-Hur & Kadmon, 2020), which are unlikely to be met in practice. Thus, the relevance of the theoretical findings to real-world settings remains to be demonstrated. At the same time, attempts to find general patterns in empirical studies of HDRs have faced several challenges. First, habitat heterogeneity can result from many different abiotic and biotic factors (Stein & Kreft, 2015), referred to in the following as facets of heterogeneity. Even within a single facet of heterogeneity, both the multitude of methods used to evaluate single facets and the varying lengths of the covered gradients have hampered comparisons of empirical results (Stein & Kreft, 2015). For example, short heterogeneity gradients are more likely to underrepresent trade-offs between area and heterogeneity than are fully covered gradients. Second, species groups differ in their ecological requirements and possibly also in their responses to different facets of heterogeneity. Thus, while a taxon may respond strongly to vertical forest structure, its response to other facets may be neutral (Tews *et al.*, 2004). A third challenge is the fact that the response of a given taxon to environmental heterogeneity might be habitat-specific. This is demonstrated by birds, which respond positively to cover-type diversity in woodlands and grasslands but not in savannas (Bar-Massada & Wood, 2014). Lastly, the shape of the HDR will also depend on the scale at which the study is conducted (Tamme *et al.*, 2010; Bar-Massada & Wood, 2014; Stein *et al.*, 2014).

Species group, habitat, heterogeneity facet and spatial scale may act together to modify the nature of the HDR. Therefore, studies focusing only on one or two of these aspects without holding the others constant are intrinsically limited. A more realistic approach would be to shift the focus from studies of single species groups to assessments of species-richness relationships of a whole habitat. This can be achieved by simultaneously testing the linear and non-linear relationships of a large number of species groups across trophic levels (Seibold *et al.*, 2018) and with respect to major facets of heterogeneity(Stein & Kreft, 2015), covering the full gradient length of a single habitat and using a constant sampling grain. This approach would provide a unique opportunity to: a) assess the degree to which the determined HDR patterns can be generalized and b) gain nuanced insights into the effects of heterogeneity and the underlying mechanisms. In the present work, we made use of the data available from three different biodiversity projects (Fig. C8.3.1),

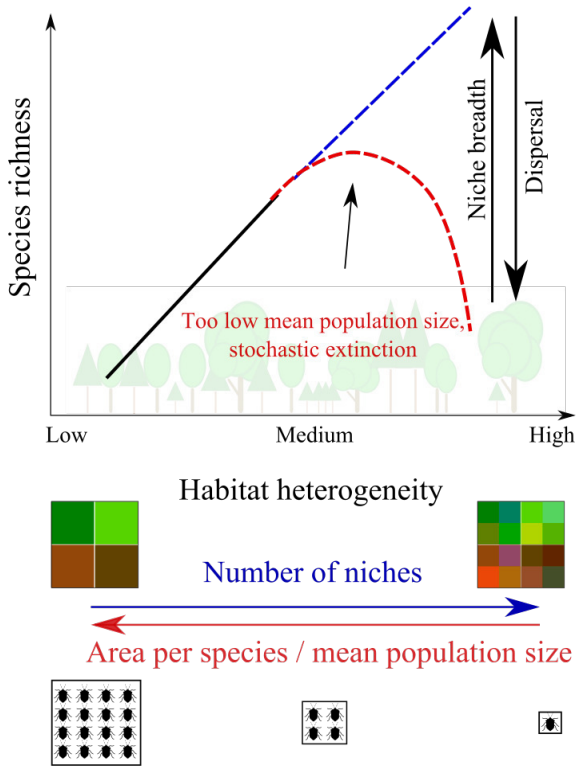


FIGURE C4.1. Conceptional framework for the relationship between habitat heterogeneity and species richness. The habitat-heterogeneity-hypothesis predicts that the number of niches, and thus species richness, increases with increasing habitat heterogeneity (blue line). The area-heterogeneity trade-off hypothesis predicts that species richness decreases at high levels of habitat heterogeneity because the amount of suitable area per species decreases as the number of niches decreases, leading to smaller mean population sizes per species and thus to stochastic extinctions (red line). These effects should be moderated by dispersal ability and niche breadth (black arrows).

comprising ~500 one-hectare forest plots containing a total of ~2600 species from 12 species groups covering a wide range of different life-histories, dispersal properties and trophic levels.

In forest ecosystems, the pronounced vertical dimension of vegetation forms a complex habitat for a broad spectrum of organisms (Davies & Asner, 2014; Seidel, 2017). Together with the heterogeneity resulting from the horizontal distribution of vegetation and the topography of the terrain, vertical heterogeneity leads to variations in light availability, microclimate and soil moisture within the forest (Davies & Asner, 2014). Another facet of heterogeneity in forests is formed by the structure and species composition of dead trees, as both impact many forest species, whether obligatorily or facultatively, during some phase of their life cycle (Ulyshen, 2018). In this study, to ensure a comprehensive assessment of forest heterogeneity, we adopted the classification system of Stein and Kreft (Stein & Kreft, 2015), which systematically divides the various facets of heterogeneity into clearly defined subject areas (Fig. C4.2a). To this *a priori* classification of independent gradients of heterogeneity within a forest stand, we added deadwood as a major subject area based on its contribution to forest-specific habitat heterogeneity. Analogous to our approach to living trees, deadwood heterogeneity was divided into structural and taxonomic richness, resulting in six statistically independent facets of heterogeneity at the scale of a forest stand: 1) the taxonomic and 2) structural richness of deadwood, 3) vascular plant diversity, 4) vertical as well as 5) horizontal structural heterogeneity and 6) micro-scale topography (Figure. C4.2a).

We assessed whether multidiversity (the scaled species richness of all recorded species (Allan *et al.*, 2014) and the species richness of each species group respond to particular facets of heterogeneity and which shape these HDRs take. We then tested whether the level of heterogeneity at which species richness is maximized increases with increasing niche breadth and decreases with increasing dispersal ability, as predicted by recent modeling approaches (Ben-Hur & Kadmon, 2020). Finally, we examined whether the response of the mean population decreases with increasing heterogeneity, as expected by stochastic extinctions and the area-trade off theory.

Results & Discussion

The species richness of all species groups, except carabids (Fig. C4.2 b, Table C4.1), responded to habitat heterogeneity. This finding supported the ubiquitous role of heterogeneity in shaping species richness across different species groups. However, as expected from the exploratory nature of the study design and the fact that species are expected to differ in their responsiveness to heterogeneity (Tews *et al.*, 2004), there was a large amount of variation in our results. Both group-specific responses to different facets of heterogeneity and the shape of responses differed among species groups.

Among 72 possible HDRs (12 species groups × 6 facets of habitat heterogeneity), 34 were significant, 17 increased monotonically, 7 were hump-shaped, 8 decreased monotonically. Two responses showed more than one pronounced change in the sign of the HDR, i.e. saproxylic beetles in response to vertical heterogeneity and spiders in response to microscale topography (Fig. C4.2 b, Table C4.1). It seems important to note that study region, next to the heterogeneity gradients, explained still an important fraction of the variance (see R^2 and ΔR^2 in Table C4.1). This underlines that heterogeneity is not the sole biological predictor of species richness across regions. Despite these variable responses of the individual species groups, multidiversity yielded hump-shaped responses only with respect to plant diversity and vertical heterogeneity. This suggested that neither the (partly) negative effects nor the positive effects of heterogeneity dominate across all species groups considered. This prompts the question whether the ecological properties of single species groups determine whether there is a relationship to a certain facet of heterogeneity, and which form this HDR will have.

In the theoretical model of Ben-Hur and Kadmon (2020), the form of the HDRs depended on fragmentation, niche breadth and dispersal ability. In our study, fragmentation effects are expected to be negligible because the surrounding matrix is habitable (Rybicki *et al.,* 2020) as all of our 1-ha plots are each embedded in larger forested matrix. Thus, we would expect strong effects of niche breath and dispersal ability; increasing niche breadth and decreasing dispersal ability should increase the level of heterogeneity which maximizes species richness, turning hump-shaped HDRs into positive ones (Ben-Hur & Kadmon, 2020). However, neither habitat niche breadth, here estimated based on trophic positions (Zalewski *et al.*, 2018) (Figure C4.3, one-sided, linear-by-linear associated test, $z=0.38$, $p=0.35$), nor dispersal abilities showed any clear response in terms of the position of the inflection points (one-sided, linear-by-linear association test, $z=0.22$, $p=0.96$, Chapter C8.3, Table C8.3.1, Fig. C8.3.2-3).

Response to single facets of heterogeneity

Not all facets of heterogeneity were expected to affect all species groups equally. In fact, ecological theory predicts that heterogeneity gradients important for some species groups will be unimportant for others, as different species use different resources (Tews *et al.*, 2004; Penone *et al.*, 2019). Indeed, single facets of heterogeneity affected different numbers of species groups. The facet affecting the largest number of groups (9 out of 12) in terms of species richness was horizontal heterogeneity, followed by vertical heterogeneity (8) and plant diversity (8). Micro-scale topography affected six groups, taxonomic richness of deadwood four and the structural richness of deadwood only one species group, namely saproxylic beetles (Fig. C4.2b, d).

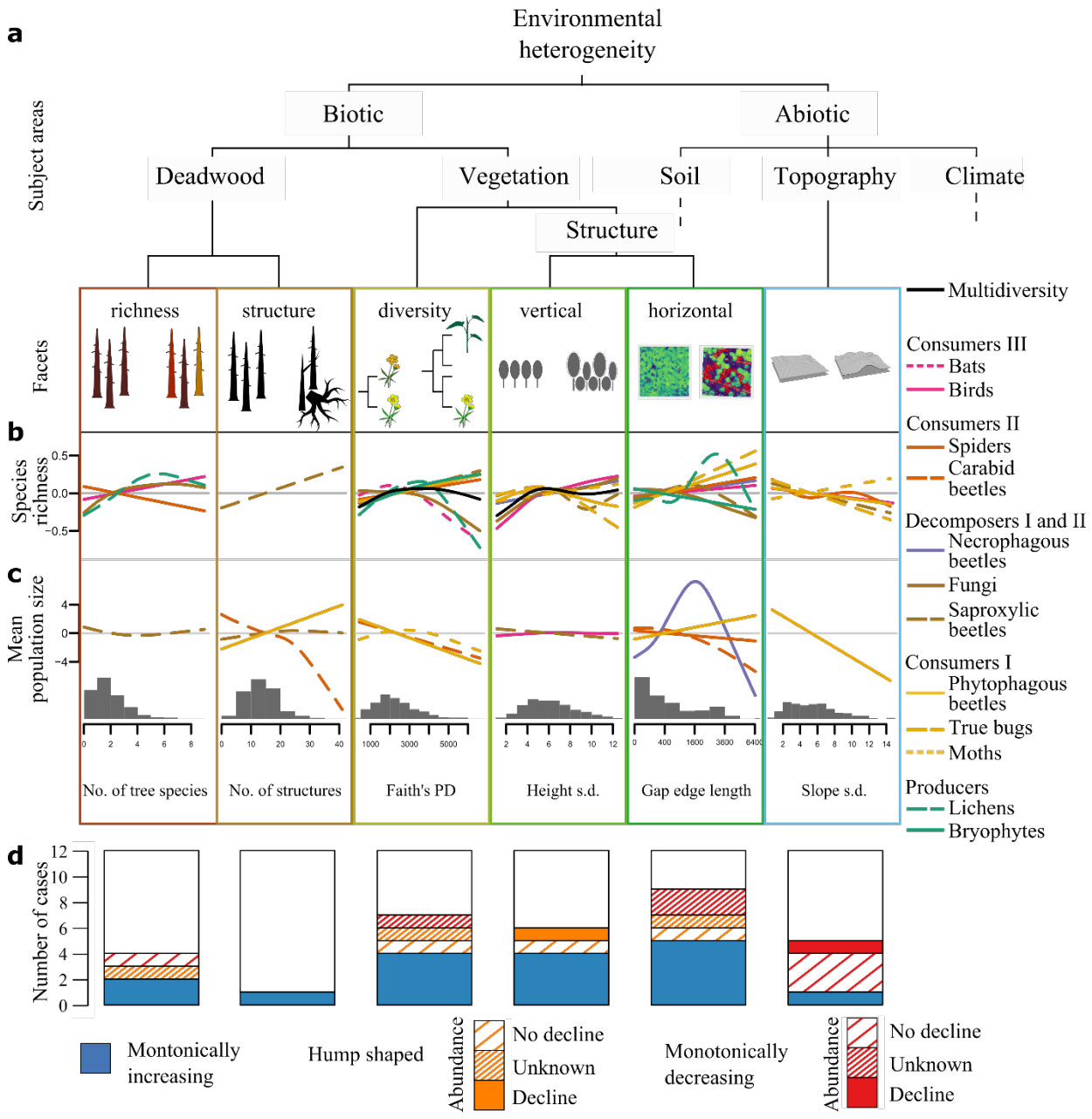


FIGURE C4.2. Summary of the relationships between the single facets of heterogeneity and species richness and mean populations size as estimated by mean abundances per species. a) Habitat heterogeneity in forests can be decomposed into the facets heterogeneity in vertical (height SD) and in horizontal structure (gap edge length), plant diversity (Faith's PD) and micro-scale topography (slope SD), expanded by the inclusion of the taxonomic and structural richness of deadwood. The partial contribution of the significant scaled and centered predictor variables in the GAMs in the modeling of b) species richness, shown for 12 species groups and for multidiversity, and c) the mean population size of the nine animal groups with available abundance data. The distribution of the predictor variables is given in the lower half of the figure. d) Bar graphs of the portion of significant effects consistent with either the habitat-heterogeneity hypothesis (blue) or the area-heterogeneity trade-off hypothesis (orange). The latter is further subdivided into the hump-shaped and negative responses of species richness and whether either one is accompanied

TABLE C4.1: Results of the generalized additive models (GAMs) of heterogeneity in the taxonomic and structural diversity of deadwood, plant diversity (Faith's phylogenetic diversity [PD]), vertical structure (height standard deviation [SD]), horizontal structure (square-rooted edge length) and micro-scale topography (slope SD) as predictor variables, and multi-diversity, species richness (upper half) and mean abundance (lower half) as dependent variables. ΔR^2 was calculated as the difference between the full models and the null models, with region as the random factor. The classification as monotonically positive (+), monotonically negative (-), hump-shaped (h) or neither (i) is shown next to the estimated degrees of freedom (edf)

	N_{Plots}	Taxonomic richness of dead wood				Structural richness of dead wood				Plant diversity				Vertical heterogeneity				Horizontal heterogeneity				Micro-scale topography				Region			R_{adj}	ΔR
		Edf		F-value		Edf		F-value		Edf		F-value		Edf		F-value		Edf		F-value		edf		F-value		edf	F-value			
Multidiversity	197	1.0		0.01	n.s	1.0		0.80	n.s	2.9	H	22.	***	3.5	H	23.	***	1.0		0.68	n.s	1.0		0.96	n.s	3.6	194.	***	0.62	0.09
Plants	497	3.1		1.5	n.s	1.0		0.32	n.s	–				1.0	+	3.9	*	3.0	h	10.	***	1.0	-	10.	**	3.9	68.	***	0.58	0.07
Bryophytes	322	1.0		0.66	n.s	1.0		1.0	n.s	1.4	+	3.4	*	1.0		0.01	n.s	1.0	-	4.9	*	1.0		1.0	n.s	3.7	13.	***	0.34	0.01
Lichens	315	2.2	H	6.3	***	1.0		0.57	n.s	3.2	H	5.3	***	1.0		3.6	n.s	4.6	h	7.4	***	1.0		1.2	n.s	3.8	33.	***	0.51	0.16
Moths	227	1.0		0.17	n.s	1.0		3.4	n.s	1.5		1.8	n.s	1.0	+	5.2	*	1.0		0.31	n.s	1.0	+	5.5	*	3.6	10.	***	0.32	0.04
True bugs	371	1.0		2.9	n.s	1.0		1.3	n.s	1.0		0.02	n.s	2.3	H	4.6	**	1.0	+	24.	***	1.0	-	6.2	*	3.7	18.	***	0.33	0.14
Phytophagous	385	1.0		0.33	n.s	1.0		1.4	n.s	1.0	+	7.6	**	2.6	H	3.4	*	1.0	+	44.	***	1.0	-	4.2	*	3.8	28.	***	0.38	0.13
Fungi	497	2.6	+	7.6	***	2.0		2.1	n.s	2.6	-	4.4	**	3.1	+	8.1	***	2.1	-	7.9	***	1.6		2.1	n.s	3.4	10.	***	0.41	0.17
Saproxylic	385	1.0		0.71	n.s	1.0	+	10.	**	1.0	+	7.9	**	3.9	I	4.3	***	2.8	h	2.6	*	1.0	-	10.	**	3.9	53.	***	0.51	0.09
Necrophagous	385	1.0		0.14	n.s	1.0		0.85	n.s	1.0		0.23	n.s	1.0	+	6.3	*	1.0	+	4.5	*	1.0		2.5	n.s	3.8	31.	***	0.35	0.02
Carabids beetles	382	1.0		0.47	n.s	1.0		1.9	n.s	1.0		1.5	n.s	1.0		0.00	n.s	1.0		3.8	n.s	1.0		2.5	n.s	3.9	93.	***	0.72	0.01
Aranea	382	1.0	-	10.	**	1.0		1.2	n.s	1.0	+	6.7	*	1.0		0.00	n.s	1.0	+	20.	***	3.6		3.7	**	3.9	101.	***	0.69	0.08
Birds	496	1.0	+	9.	**	1.0		0.00	n.s	1.0		0.49	n.s	3.3	+	19.	***	1.0	+	5.7	*	1.0	-	7.3	**	3.7	20.	***	0.26	0.14
Bats	248	1.0		0.87	n.s	1.0		0.01	n.s	2.4	H	3.3	*	1.0		1.0	n.s	1.0		0.18	n.s	1.0		3.5	n.s	3.8	26.	***	0.54	0.01
Moths	227	1.0		1.8	n.s	1.0		0.01	n.s	2.6	H	3.8	**	1.0		2.0	n.s	1.0		0.25	n.s	1.0		0.03	n.s	3.6	12.	***	0.26	0.05
True bugs	371	1.0		3.1	n.s	1.0		3.0	n.s	1.4		0.84	n.s	1.0	-	4.1	*	1.0		0.06	n.s	1.0		3.3	n.s	2.9	4.5	***	0.09	0.04
Phytophagous	385	1.0		0.32	n.s	1.0	+	5.4	*	1.0	-	7.3	**	1.0		0.09	n.s	1.0	+	5.3	*	1.0	-	31.	***	3.6	12.	***	0.28	0.1
Saproxylic	385	2.3	I	4.3	**	2.0	+	3.7	*	1.0		0.29	n.s	1.0	-	12.	***	1.0		3.6	n.s	1.0		0.61	n.s	1.9	1.6	*	0.16	0.11
Necrophagous	385	1.0		0.08	n.s	1.0		3.0	n.s	1.0		0.51	n.s	2.4		2.4	n.s	3.1	h	3.6	**	1.0		2.7	n.s	3.1	5.1	***	0.13	0.07
Carabid	382	1.0		1.2	n.s	2.6	-	4.3	**	1.0	-	5.2	*	1.0		3.0	n.s	1.9	-	5.1	**	1.0		0.86	n.s	3.9	59.	***	0.58	0.05
Aranea	382	1.0		2.5	n.s	1.0		0.73	n.s	1.0		1.9	n.s	1.0		0.32	n.s	1.0	-	5.9	*	1.0		1.8	n.s	3.4	9.	***	0.18	0.01
Birds	496	1.0		0.20	n.s	1.0		0.88	n.s	1.0		3.1	n.s	2.5	h	3.4	*	1.0		1.9	n.s	1.0		0.14	n.s	3.8	27.	***	0.25	0.02
Bats	248	1.0		0.76	n.s	1.0		0.08	n.s	1.0		2.0	n.s	1.0		0.02	n.s	1.0		0.45	n.s	1.0		0.16	n.s	3.6	17.	***	0.24	-0.01

Response to single facets of heterogeneity

Not all facets of heterogeneity were expected to affect all species groups equally. In fact, ecological theory predicts that heterogeneity gradients important for some species groups will be unimportant for others, as different species use different resources (Tews *et al.*, 2004; Penone *et al.*, 2019). Indeed, single facets of heterogeneity affected different numbers of species groups. The facet affecting the largest number of groups (9 out of 12) in terms of species richness was horizontal heterogeneity, followed by vertical heterogeneity (8) and plant diversity (8). Micro-scale topography affected six groups, taxonomic richness of deadwood four and the structural richness of deadwood only one species group, namely saproxylic beetles (Fig. C4.2b, d).

Saproxylic species and phytophagous groups are predicted to strongly react to heterogeneity in their respective resource, as deadwood and plants, respectively, provide their dietary niches. Indeed, saproxylic beetles responded to the structural richness of deadwood, i.e., the stage of decomposition and number of different dead wood objects, whereas wood-decomposing fungi were affected by its taxonomic richness (Fig. C4.2). This result provides the empirical evidence of experiments showing that fungal species richness is driven by host tree diversity (Krah *et al.*, 2018), and saproxylic beetle richness by heterogeneity related to wood physiognomy, such as diameter, decay stage and dead wood object type (Seibold *et al.*, 2016b; Andringa *et al.*, 2019). However, we also found effects of the taxonomic richness of deadwood on the species richness of birds, spiders and lichens, in accordance with experiments and observational studies showing an effect of heterogeneity in dead wood on non-saproxylic organisms (Seibold *et al.*, 2015, 2016a). While saproxylic groups responded to the heterogeneity of deadwood, phytophagous beetles were the only group among three phytophagous groups that responded to plant diversity, although further responses to plant diversity were determined in spiders, saproxylic beetles, bryophytes, lichens and bats (Fig. C4.2b). It is unclear why the number of species groups affected by the taxonomic richness of deadwood and by plant diversity exceeded the number of species groups whose diet directly depends on these two facets. It may be that some groups, such as spiders, benefit from increased plant diversity or bottom-up effects and an increased number of microstructures (Malumbres-Olarte *et al.*, 2013). It might also be the case that these facets correlate with other, covarying variables that were not directly measured.

In contrast to the direct dependence of saproxylic and phytophagous insects on their respective dietary niche, the niches provided by forest structure and micro-topography are more difficult to specify. Heterogeneity in either one can affect the heterogeneity of soil attributes and microclimatic conditions, in turn affecting autotrophic groups but also providing different nesting and foraging grounds for species of higher trophic levels, especially flying animals (Davies & Asner, 2014; Froidevaux *et al.*, 2016; Renner *et al.*, 2018). In this study, structural heterogeneity was divided into vertical and horizontal components representing canopy layering and gap distribution, respectively. The species richness of birds, fungi, necrophagous beetles, true bugs, phytophagous beetles and moths responded to vertical heterogeneity (Fig. C4.2b, Fig. C8.3.4). Thus, for birds, different vertical structures offer different niches in terms of nesting sites and foraging grounds, just as MacArthur and MacArthur (1961) predicted. However, vertical heterogeneity also provides niches for other species groups, most likely through microclimatic conditions and shelter (Baz *et al.*, 2014; Kadlec *et al.*, 2018).

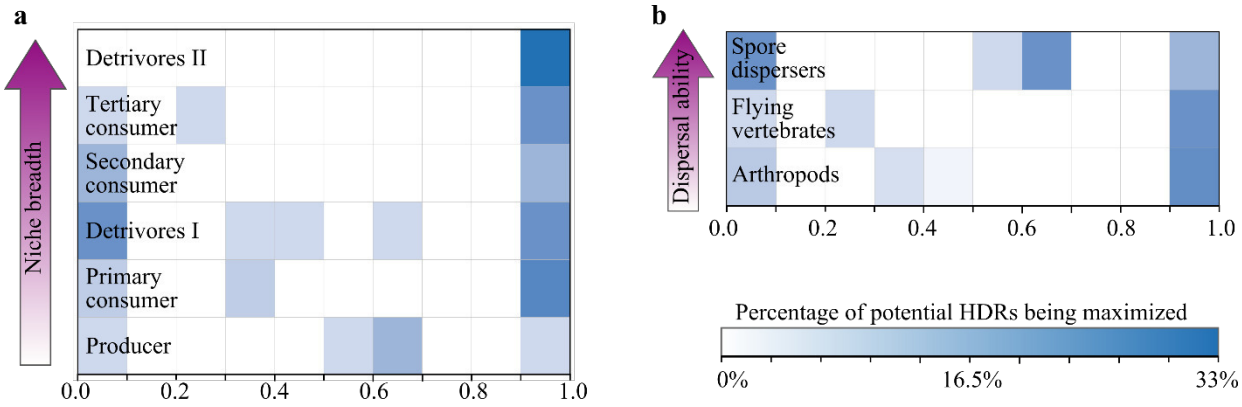


FIGURE C3.3: Inflection points, i.e., the level of heterogeneity at which species richness was highest, summarized over all six facets of heterogeneity, which were binned from 0 (lowest heterogeneity in all plots) to 1 (highest heterogeneity in all plots), and ordered along a) trophic position as a surrogate for niche breadth and b) dispersal ability

Horizontal heterogeneity determines variations in light availability and microclimatic conditions near ground (Frenne *et al.*, 2019). In our study, all species groups except moths, bats and carabid beetles responded to horizontal heterogeneity. Many arthropods are sensitive to microclimatic conditions such that forest gaps will favor communities different from those associated with stands with a closed canopy (Seibold *et al.*, 2016b,a). Birds may profit from an increased diversity of nesting sites, foraging sites and food sources. Neither vertical nor horizontal heterogeneity, however, correlated with a higher species richness of bats. For this group, differences in horizontal forest structure, due to species-specific adaptations in echolocation and flight performance, likely affect species composition rather than species richness (Jung *et al.*, 2012b; Müller *et al.*, 2012). The relationship of species richness to topographic heterogeneity, measured as the standard deviation in the slope, was significant for six species groups (Table C4.1), and affected most arthropod groups and birds, but the underlying mechanism remains unclear. Topographic heterogeneity can be seen as a surrogate for heterogeneities in microclimate and soil, which seem to influence plant richness (Table C4.1) and may have cascading effects on higher trophic levels. These two types of heterogeneity therefore require further study.

Irrespective of the mechanisms underlying the variable HDRs, the fact that species groups *did* respond to the heterogeneity facets with which they *were not* obviously connected clearly demonstrates that any *a priori* restriction of heterogeneity facets may overlook important HDRs. Conversely, the fact that species groups *did not* respond to heterogeneity facets to which they *were* obviously connected indicated that the spatial scale at which heterogeneity is perceived is highly variable. Moreover, whether a species group does or does not respond to a certain facet of heterogeneity seems to vary even within trophic levels. For example, vertical heterogeneity had different effects on the three phytophagous groups; while the species richness of true bugs and phytophagous beetles decreased at high levels of vertical heterogeneity that of the more mobile moths increased (Fig. C4.2b, C8.3.4). It may be the case that a stronger vertical stratification leads to area-heterogeneity trade-offs (at least for true bugs) within the near-ground strata, such as those where the groups were sampled and where plant suckers

are typically of low abundance (Leidinger *et al.*, 2019).

Area effects on population size

Decreases in the mean population size with increasing habitat heterogeneity support the assumptions of *area-heterogeneity trade-off hypothesis* and the results of the theoretic model of Ben-Hur and Kadmon (2020). However, habitat heterogeneity affected the mean population size only in 15 out of 54 cases (9 animal groups × 6 facets of habitat heterogeneity; note that no abundance data were available for fungi, lichens and bryophytes). In these cases, population size was almost always lowest at the highest levels of heterogeneity. In others, however, the initial or even monotonic increases in population size contradicted the theoretical modeling results (Ben-Hur & Kadmon, 2020). Also, decreases in mean populations sizes that coincided with a humped-shaped or negative HDR, as expected by an area-heterogeneity trade-off, occurred only in two cases (true bugs with vertical heterogeneity and phytophagous beetles with topographic heterogeneity, Figure C8.3.4). Our results therefore suggest that trade-offs between a suitable area available for individual species and habitat heterogeneity play only a minor role in shaping diversity patterns in the stands of temperate forests. One possible explanation is that increased vertical heterogeneity can lead to higher total leaf biomass per area (Dănescu *et al.*, 2016; Juchheim *et al.*, 2017; Schulze *et al.*, 2018), and increased horizontal heterogeneity to a larger amount of ground vegetation (Leidinger *et al.*, 2019). This mechanism may average out area-heterogeneity trade-off effects at high levels of structural heterogeneity, a scenario supported by the positive effect of high horizontal heterogeneity on phytophagous beetle and true bug richness and the positive effect of high vertical heterogeneity on moth richness (Fig. C4.2c). Positive effects of vertical heterogeneity on species richness via increased resource availability and larger population sizes have been shown for arthropods in the forest canopy (Müller *et al.*, 2018). In our study, arthropods accounted for 8 of the 12 studied species groups; their high mobility and fast reproduction rates may reduce their vulnerability to stochastic extinction (Allouche *et al.*, 2012).

Thus, overall, our study provided little support for area-heterogeneity trade-offs. Surprisingly, however, its results revealed a considerable number of hump-shaped or even negative HDRs across the studied animal groups. This was especially the case for the facet topographic heterogeneity, as all responding groups except moths were characterized by a monotonous decrease in species richness with increasing slope SD. Such monotonic declines of species richness are likely to occur when the studied scale is small (Tamme *et al.*, 2010; Stein *et al.*, 2014) or the studied species groups are highly specialized (Allouche *et al.*, 2012). While the 1-ha scale of our study was indeed smaller than the scale used in others (though comparable to the early studies of MacArthur & MacArthur, 1961 for birds) the latter condition is not met by all species groups that responded to topographic heterogeneity.

Mechanisms other than area-trade-offs might explain the hump-shaped or negative HDRs. HDR shape is influenced by the position of the community on the gradient of environmental severity (Yang *et al.*, 2015). Under highly favorable environmental conditions, any heterogeneity that reduces inter- and intraspecific competition will ultimately increase species richness. Under unfavorable conditions, heterogeneity increases the prevalence of patches which support larger species pools. However, under intermediate conditions, such as in temperate forests, heterogeneity only increases the likelihood of

patches that contain smaller species pools, thus leading to negative HDRs independent of the population size (Yang *et al.*, 2015). For example, saproxylic beetles and lichens, both of which have larger species richness in gaps (usually associated with larger amounts of deadwood) than under a closed canopy (Seibold *et al.*, 2016b; Kaufmann *et al.*, 2018), had a hump-shaped response to horizontal heterogeneity, indicating that species richness will not reach a maximum when gaps and closed canopy are equally distributed but only when the habitat type that draws from a larger species pool dominates. By contrast, the species richness of fungi and bryophytes decreased with increasing horizontal heterogeneity (Fig. C3.2b, Fig. C8.3.4). These two groups are dominated by closed-forest specialists that are sensitive to dry conditions (Nelson & Halpern, 2005; Thorn *et al.*, 2018) and may perceive the increases in solar radiation and the decreases in humidity associated with increasing horizontal heterogeneity as a constraint. Unfortunately, whether this constraint was pronounced due to smaller species pools or smaller population sizes could not be resolved with our data.

Conclusions & implications

Our study across multiple species groups and different facets of stand-level heterogeneity in temperate forests revealed a complex picture of HDRs. Habitat heterogeneity did not necessarily result in reductions in suitable areas available for individual species and area-heterogeneity trade-offs were rare. However, negative responses to heterogeneity occurred, independent of trophic niche or dispersal ability. The variable responses across species groups well demonstrated that there is no universal gradient of habitat heterogeneity within a forest. More importantly, it appears that in real world settings, HDRs are not as predictable as theoretical models would suggest. Thus, comprehensive assessments of possible HDRs considering different facets of heterogeneity as well as different species groups representing different life-histories, functional groups and trophic levels are likely to be the most promising approach to capture all the details necessary for informed forest management. Such assessments should be repeated across different scales and for different habitats.

Certain facets of habitat heterogeneity affected more species groups than others. Among the studied facets, vertical and horizontal heterogeneity (which can be easily managed in silviculture), were found to be major drivers of biodiversity in forests. Hence, forest and conservation management measures designed to increase within-stand biodiversity should enhance habitat heterogeneity by increasing vertical and, especially, horizontal stand heterogeneity, as this will have more positive than negative effects on species richness. However, we caution against a wide-ranging establishment of fine-scaled heterogeneity in forest structure. Instead, to minimize the effect of negative responses, a mosaic of stands comprising different gradients of structural heterogeneity should be provided.

Methods

Study regions. Our data are based on comprehensive assessments of biodiversity and habitat variables obtained from 497 one-hectare plots covering five regions in Germany and representing the full range of zonal temperate forests in Central Europe (Figure C8.3.1). The Biodiversity Exploratories project (biodiversity-exploratories.de, (Fischer *et al.*, 2010) comprised three forest areas, spanning from south to north: the Biosphere Reserve Schwäbische Alb in the Swabian Jura (50 Plots), Hainich National Park and the surrounding area (50 plots) and the Schorfheide-

Chorin Biosphere Reserve (50 plots). This database (Boch *et al.*, 2016; Goßner *et al.*, 2016b,c,a; Müller *et al.*, 2016; Fischer, 2017; Schäfer *et al.*, 2017; Jung & Tschapka, 2018; Tschapka *et al.*, 2018) has been supplemented with plots from the Steigerwald project (Doerfler *et al.*, 2018) in northern Bavaria (69 plots) and the BIOKLIM project (Bässler *et al.*, 2009) in the Bavarian Forest National Park (Moning *et al.*, 2009; Müller & Brandl, 2009; Müller *et al.*, 2009, 2012; Bässler *et al.*, 2010a,b; Raabe *et al.*, 2010) (278 plots).

Facets of habitat heterogeneity. To address heterogeneity in forests as comprehensively as possible, we adopted the classification system of Stein and Kreft (2015) , which systematically divides the facets of heterogeneity into five subject areas, of which four can be applied to a 1-ha plot scale: vegetation, micro-scale topography, soil and climate (Fig. C4.2a). In this study, the subject areas soil and climate were excluded, because their respective measures were not available for all plots. However, at the plot level, soil and climate would most likely strongly correlate with vegetation and topographic heterogeneity (Parker, 1982), both of which were included in our study. We also added deadwood (Bässler *et al.*, 2010b; Doerfler *et al.*, 2018; Kahl & Bauhus, 2018) as an ecosystem-specific subject area of habitat heterogeneity and further divided it into structural and taxonomic richness. The subject area vegetation was further divided into plant diversity and structural aspects, i.e., the vertical and horizontal heterogeneity of the vegetation.

Quantifying habitat heterogeneity. Based on several reviews (McElhinny *et al.*, 2005; Davies & Asner, 2014; Müller & Vierling, 2014; Stein & Kreft, 2015), we selected potential measurements *a priori* for each of the six facets (Chapter 8.3, Figures C8.3.5-11). For the final selection, we examined the statistical behaviors (distributions) of the variables and the within- and between-aspect co-linearity (Chapter 8.3, Figures C8.3.5-11), which is often an issue in LiDAR-derived measurements (Fig. C8.3.12). In our study, the *a posteriori* selection of the measurements had several advantages over statistical variable selection in terms of dealing with multicollinearity (Fig. C8.3.13) and the testing of ecological hypotheses. However, we are aware that the response of single species group will slightly vary if different measures for the same facet of heterogeneity are considered (Stein & Kreft, 2015). Thus, in group-specific studies a broader use of LiDAR metrics might be a suitable approach. However, this was not the aim of our study; rather the measures were used to capture the major heterogeneity of the whole forest stand relevant for all species groups.

Deadwood heterogeneity was quantified according to Siitonen (2001). The taxonomic richness of deadwood was calculated by counting the number of different tree species within a plot, and the structural richness of deadwood by counting the number of different deadwood types, classified according to diameter and decomposition classes as well as subtype (broken snag, lying dead tree, etc.; see also Chapter 8.3). Plant diversity was characterized by considering all vascular plants in the tree, shrub and herb layers determined as part of biodiversity assessments (Bässler *et al.*, 2010a; Schäfer *et al.*, 2017; Doerfler *et al.*, 2018) (349 in total, Chapter 8.5). However, the number of plant species alone does not necessarily reflect ecological differences relevant to herbivores (Flynn *et al.*, 2011; Cadotte *et al.*, 2013), as closely related plant species may host similar communities of insects (Ward *et al.*, 2003). Therefore, phylogenetic diversity (Faith's PD) was used as a measure of the amount of evolutionary divergence within a plant community. Faith's PD was calculated based on the phylogeny proposed by Durka and Michalski (2012), using the R

software package *picante*, version 1.7 (Kembel *et al.*, 2018). However, this approach does not necessarily reflect all functional differences between plant species (but see the Discussion in Chapter 8.3). Standardized measurements of the 3D structure of the forests were obtained using high-resolution airborne laser scanning (ALS) (Chapter 8.3), a method that provides accurate 3D measurements across large areas. The high point density of the ALS measurements allows forest structure to be characterized using salient metrics that describe the vertical and horizontal distribution of vegetation at high spatial resolution (Vierling *et al.*, 2008). For the standard deviation (SD) of all the heights from all vegetation returns as aggregates over the entire 1ha plot area. This metric is able to powerfully explain biodiversity patterns in forests (Davies & Asner, 2014) and is less sensitive to artificial classifications of layers than foliage height diversity (Chapter 8.3). To calculate horizontal heterogeneity, we classified the area within plots as gap and non-gap areas. Gap areas were defined as areas with a minimum size of 50 m^2, a perimeter/area ratio of <1.5 (thus excluding narrow linear structures such as forest aisles), a height threshold of 2 m and a penetration ratio > 80%. Since the total gap area per plot would not capture a linear increase in horizontal heterogeneity—as both extremes, i.e., 100% canopy cover as well as a 100% gap area, are homogeneous in horizontal structure —we instead calculated the total length of the gap edges to obtain a continuous measurement of horizontal heterogeneity (for details, see Chapter 8.3, Fig. C8.3.8). Both structural measures, i.e., total gap edge length and height SD, were largely independent of the tree species composition (Fig C8.3.10). Micro-scale topography was calculated as the within-plot terrain heterogeneity, determined using a high-resolution digital terrain model (DTM) with 1-m spatial resolution derived from the ALS measurements. The SD of the slope measured in the DTM across our 1-ha plots served as a measure of topographic heterogeneity, as it was better than the SD of the elevation in capturing small-scale variation (see Chapter 8.3).

Biodiversity data. The species richness of bats, birds, several arthropod taxa, fungi, lichens, bryophytes and vascular plants had been assessed in each of the three projects using standardized protocols (Moning *et al.*, 2009; Müller & Brandl, 2009; Müller *et al.*, 2009, 2016; Bässler *et al.*, 2010a,b; Raabe *et al.*, 2010; Boch *et al.*, 2016; Goßner *et al.*, 2016b,c,a; Fischer, 2017; Schäfer *et al.*, 2017; Doerfler *et al.*, 2018; Jung & Tschapka, 2018; Tschapka *et al.*, 2018). In this study, for each group only data acquired during the year closest to that of the ALS flights were chosen. In Biodiversity Exploratories, transect walks were used to record bats with a bat detector while the other two projects employed fixed autonomous batcorders (Müller *et al.*, 2012; Jung & Tschapka, 2018). Birds were monitored acoustically and visually within a fixed time span during their breeding season (Müller *et al.*, 2009; Doerfler *et al.*, 2018; Tschapka *et al.*, 2018). Arthropods were collected using pitfalls, crossed flight interception traps and low-intensity light traps (Müller & Brandl, 2009; Goßner *et al.*, 2016b,c,a; Doerfler *et al.*, 2018). Fungi, bryophytes and lichens present on deadwood objects and the plants within a fixed area were mapped (Moning *et al.*, 2009; Raabe *et al.*, 2010; Boch *et al.*, 2016; Müller *et al.*, 2016). Animal abundance (or activity) data were available for all five regions and were used to estimate the mean population size among species of a specific group at a plot (Allouche *et al.*, 2012). For species recorded repeatedly within the year, species richness and abundance data were pooled for each plot. Details on the sampling methods used in each of the projects are provided in Chapter 8.5.

Statistical analysis. This study sought answers to the following questions; (1) Does the relationship between species richness and habitat heterogeneity increase monotonically or follow a non-linear humped shape curve (Fig. C4.1)? (2) Does population size, here estimated by abundances (Allouche e. al, 2012) (or calls in the case of bats), decline with increasing heterogeneity? Species richness and abundances were modeled by generalized additive models (GAMs) allowing for unconstrained and smooth relationships. The models therefore did not relate to any particular hypothesis. Whether a particular model supported a specific hypothesis (formulated in terms of a monotonically increasing, decreasing or hump-shaped HDR) was instead decided based on the graphical representations of the results. Significant relationships between richness and the single predictors were defined as hump-shaped if the changes in the sign of the modeled slope from positive to negative could be visually detected. If the overall sign was positive (negative) and the slope intersected the horizontal line at a partial effect of zero once, it was considered monotonically increasing (decreasing) (Figure C8.3.4). This approach was chosen because formal model-specification tests (i.e., based on p-values against a specific hypothesis, such as the absence of a quadratic effect) are ill-defined in the presence of many observations (see the discussion in Chapter C8.3). Specifically, we applied two-sided GAMs, which account for an overdispersion by a quasi-Poisson estimation procedure in modeling species richness and a Gaussian distribution of the mean abundance of animals (package *mgcv*, function *gam*, version 1.8.26, Wood, 2018). 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 to improve the distribution. The smoothness term, representing the taxonomic richness of deadwood, was restricted to six degrees of freedom to achieve model convergence. The study region was considered as a random factor to account for regional effects. Model assumptions were checked visually using the model diagnostics provided by the *Mgcviz*-package version 0.1.1 (Fasiolo & Nedellec, 2018).

In a last step, multi-diversity was calculated by scaling the species richness of each of the species groups to its maximum and then averaging the resulting scaled species richness across all groups (Allan *et al.*, 2014). This procedure weighted every species group equally. However, only data from plots in which all species group had been assessed (n=197) could be used for this purpose. Here, a GAM with a β-regression estimation procedure was applied. Finally, the single species groups were ordered according to their trophic position, which was used as a surrogate for niche breadth (Zalewski *et al.*, 2018), with producers assigned the lowest rank, followed by primary consumers, detritivores on deadwood (Steffan *et al.*, 2017), secondary consumers and tertiary consumers. Necrophagous beetles were assigned the highest rank, assuming that they need to have the highest flexibility in terms of foraging grounds. To test the level of heterogeneity at which species richness is maximized against this ordered predictor, we used a simple one-sided linear-by-linear association test (*coin*-package vers. 1.3, Hothorn *et al.*, 2019) with the 0 hypothesis being "less". Therefore, heterogeneity measures of each facet were scaled to range from 0 (lowest detected heterogeneity) to 1 (highest detected heterogeneity). The same procedure was applied to three orders of dispersal abilities of the single species groups, with the 0 hypothesis being "greater". In this case, we expected that arthropods would have smaller dispersal abilities than vertebrates, while spore-dispersers were expected to have the best dispersal

ability. Other classifications and rankings led to similar results (see Fig. C8.3.3).

Note that we intentionally did not include the species richness or abundance of plants, either as a response variable or in the calculation of multi-diversity, as this would have heavily interfered with the Faith's PD of the plant community as an independent variable. However, a reduced GAM without Faith's PD was applied to the species richness of plants (see Table C4.1). All statistical analyses were carried out using the statistical software R, version 3.5.0 (R Core Team, 2018).

Data reported in this paper can be accessed from the Biodiversity Exploratories Information System (https://www.bexis.uni-jena.de), DataSetID 25126.

Acknowledgments

We dedicate this work to the memory of Kwesi Abbey Afful and Emmanuel Lartey-Williams, who were part of the moth sampling campaign.

We sincerely thank the local management teams and student helpers for their assistance in the assessment of the species data, Hermann Hacker for moth determination, 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. This work was (partly) funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" grant MU3621/2-1, KR 3292/2-1 and LE3316/2-1. Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg

Chapter 5

Effects of heterogeneity in forests on the ecological diversity of assemblages

with

Holger Kreft | Jörg Müller |

first draft in preparation for submission in *OIKOS*

This is a follow up study to the previous chapter and the phylogenetic data compiled in Chapter III. The analysis and major conclusions were contributed by me on the basis of discussions with Jörg Müller and Holger Kreft.

Summary

Heterogeneity in environmental conditions is commonly assumed to increase the number of niches. This is often accompanied by an increase in the number of species, though neutral mechanisms such as area effects or drawing of smaller species pools could ultimately lead to a random loss of species. The ecological diversity of species, however, should generally profit from heterogeneity. Here, we test whether this assumption is true. We furthermore compare the response of species richness and ecological diversity to evaluate, whether responses in terms of species richness are based on an increase in the number of available niches. Therefore, we calculated standardized functional-phylogenetic distances (MFPD) of assemblages of six species groups in study size across five regions of Germany. Responses in MFPD were mostly positive but did not always result in an increase in species richness. Likewise, increases in species richness were accompanied by increases in MFPD in less than half of the cases, suggesting that heterogeneity affects species richness in more ways than increasing the number of niches.

Introduction

That heterogeneity in environmental conditions increases the available niche space seems to be an undisputed paradigm in ecology (Allouche *et al.*, 2012; Stein *et al.*, 2014). The underlying rationale is that species have different environmental requirements, which can be reflected by differences in their traits. If a certain area offers a wide range of environmental conditions, they pose as a set of different environmental filters which select for a wider range of ecological adaptations than a homogenous area, which limits the set of species to those adapted to that specific range of environmental conditions (Stark *et al.*, 2017) (Figure C5.1 b, solid line). Whether this increase in available niche space ultimately leads to a constant increase in species diversity, as proposed by the habitat-heterogeneity-hypothesis (Figure C5.1 a, solid line), is less certain (Allouche *et al.*, 2012; Ben-Hur & Kadmon, 2019). For example, it has been suggested that partitioning the area into a mosaic of different environmental conditions reduces the effective area per niche, thus sustaining less viable populations and ultimately resulting in random extinctions (area-heterogeneity-trade-off hypothesis, (Allouche *et al.*, 2012) (Figure C5.1a, dashed line). Others point to the possibility that under intermediate severity in environmental conditions, the added niches draw from a smaller species pool (Yang *et al.*, 2018). While both these mechanisms can ultimately lead to a decrease in species diversity at high levels of heterogeneity, the basic assumption that heterogeneity adds new niches and thus favours ecologically distinct species remains untouched. Although the random loss of species and drawing from a smaller species pool might overall weaken the increase in average ecological distinctiveness, the overall trend remains positive (Figure C5.1b, dashed line). However, already Allouche et al. (2012) noted, that specific traits might affect the relationship between species richness and heterogeneity. For example, fast reproducing and highly dispersive species are less likely to be affected by a reduced effective niche area (Bar-Massada, 2015; Ben-Hur & Kadmon, 2019). Such deterministic colonization and extinction processes could not only affect the species richness of a community, but also reduce the ecological differentiation between species, hereafter called ecological diversity (Figure C5.1b).

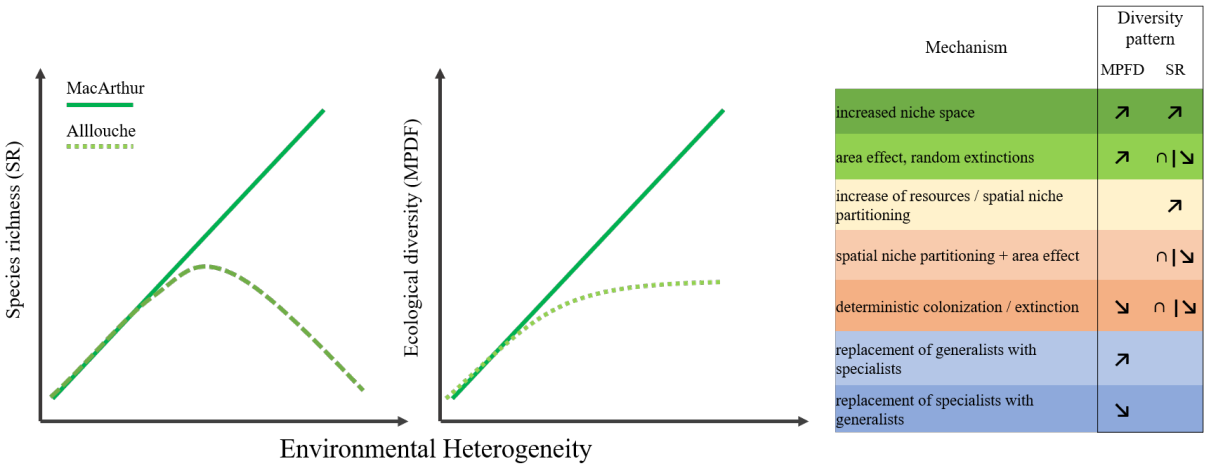


Figure C5.1: According to MacArthur&MacArthur, the creation of new niches with heterogeneity leads to an increase in species richness (a, solid line). Accordingly, also the ecological diversity between species should increase (b, solid lines). However, increase in heterogeneity might lead to a decrease in effective niche area, which then decreases mean population sizes which ultimately results in stochastic extinctions (a, dashed line). If species fall out of the system randomly, ecological differences will level of at the level of heterogeneity which has maximum level of species richness, but not decrease (b, dashed line) Other mechanisms affecting species richness and ecological diversity are given in (c).

can lead to an increase in species richness without necessarily providing new niches. First, the spatial separation of one environmental factor alone might allow otherwise competing species to co-exist (Chase & Leibold, 2007), without the patch leading to the spatial separation adding new species. Second, environmental heterogeneity can, under certain circumstances, lead rather to an increase than a decrease in effective niche area (Müller *et al.*, 2018). For example, heterogeneity in forest physiognomy often leads to a larger biomass of leaves (Müller *et al.*, 2018). Quantitative increases in such resources can have similar effects on species richness as qualitative increases thereof, as they enable more species to gain viable population sizes (*more-individuals hypothesis,* Müller *et al.*, 2018 and references therein). If not controlled for experimentally, as done in Seibold et al. (2016b), or statistically, as done in Müller et al. (2018), every change in species richness along heterogeneity gradients could be a mixture of both, increased number of niches as well as increased quantity of resources. Moreover, the diverse microhabitats with come along with heterogeneity in forests do not necessarily act as an additional niche but can be used as a refuge for species already living in the surrounding, thereby securing their persistence. Structural complex environments may make it easier to escape predators and offer a suite of microclimates which can act as a buffer against adverse weather conditions (Kleckova & Klecka, 2016; Müller *et al.*, 2018)

In a recently published study, we examined how species richness of twelve species groups related to six facets of environmental heterogeneity in forests (Heidrich *et al.*, 2020). The single facets of heterogeneity affected diverse species groups, but we could not identify any generalizable mechanism, which determines under which condition species richness shows positive, unimodal, or negative relationships with heterogeneity. To shed more light on whether the complex relationships found in Heidrich et al (2020) are based on increases in niche space or rather neutral processes such as increased amount of resources, we assessed the ecological diversity of several

species groups. Ecological diversity displays the assembly rules governing species communities (Laureto *et al.*, 2015). We evaluate the relationship between ecological diversity to increases in heterogeneity of six different forest aspects and compare those to the responses of species richness identified in Heidrich et al (2020). If heterogeneity increases niche space, which would expect that it affects species richness as well as ecological diversity, whereas neutral processes would affect species richness only. Lastly, this approach allows us to identify whether heterogeneity in forests acts indeed as an overall promotor of diversity as suggested in Heidrich et al. (2020), or whether it rather diminishes ecological diversity. To assess ecological diversity, we use the approach of Cadotte et al. (2013), which combines two complimentary measures, differences in traits and the amount of evolutionary divergence.

Methods

Our analysis is based on the same data compiled in Heidrich et al. (2020), which combined information about six facets of heterogeneity in forests and species assessments of twelve different groups across five regions of Germany. To achieve a thorough representation of temperate forests, data from three different projects were compiled; the Biodiversity Exploratories project (biodiversity-exploratories.de) with the Biosphere Reserve Schwäbische Alb in the Swabian Jura (50 plots), Hainich National Park and the surrounding area (50 plots) and the Schorfheide-Chorin Biosphere Reserve (50 plots), the Steigerwald project in northern Bavaria (69 plots) and the BIOKLIM project in the Bavarian Forest National Park (278 plots), resulting in a total of 497 plots. Each project used standardized protocols to assess the species richness of diverse species groups, which were comparable across projects. For detailed information on how the single species were recorded, see Supplementary information of Heidrich et al (2020) and Chapter 8.5. .For each of the various species groups studied in Heidrich et al (2020), data on traits was compiled from literature or own measurements. However, many of the available traits were either describing habitat preferences or had an unknown effect on performance, and thereby miss the definition of functional traits. Others covered only a fraction of the species included in the study. Thus, we restrict the analysis to five species groups for which several informative traits are available for more than 80% of the species, namely birds, bats, saprotrophic beetles, moths and plants.

Traits

Information about morphology and echolocation characteristics compiled from Dietz et al (2009), which inform about the species foraging strategy, that is, whether the species prefers open or densely vegetated foraging grounds (Denzinger & Schnitzler, 2013). However, this also leads to redundancy in the information they provide. For example, duration call average and echolocation distance are strongly correlated to wing load (Haarsma & Siepel, 2013). Here, we chose aspect ratio, start frequency and end frequency as variables which represent distinctiveness between species without being intercorrelated. Aspect ratio of the wing was measured as the ration between 5th finger and the length of the 3rd finger together with the forearm, and minimum and maximum of call frequency. As a measure for body size, we chose the condyle basal length (CBL). These traits were supplemented the time needed for weaning, gained from Haarsma & Siepel (2013), which offers a rough indication postnatal cost and is related to the the bats' migration strategy. In Heidrich et al (2020), not all recorded calls could be identified to species level. Two pairs of species, *Myotis brandtii and M. mystancius* and *Plecotus auritus* and *P. austriacus*, cannot distinguished by sound, respectively. For each of

this pair, trait information of the pair-forming was averaged.

All morphological and ecological characteristics of birds were taken from Storchova and Horak (2018), who provide a broad range of detailed information for all our 82 species. For information about life history, we multiplied the mean size of the clutch, the number of broods per year and egg mass, and divided the product by the average mass of adult females. Because this variable was only weakly correlated with life span, life span was also included in the analysis. We furthermore used bill length, corrected for body size measured as wingspan, as a variable for foraging strategy. Preferred nesting site (open arboreal, ground, or medium strata) and territoriality further inform about the species ecology. Whether the species are sessile, short distance or long-distance migrants gives information about their strategy to cope with harsh climates. Lastly, we included information about the main components of the yearly diet.

For saproxylic beetles, a large data set of morphological measurements was compiled and made available to me by Lukas Drag and Jonas Hagge. The measures include colour lightness, measured by averaging the red, green and blue colour channel of scanned images published in Dries (2015) and is related to thermoregulation and resistance against environmental stressors (True, 2003; Clusella-Trullas & Nielsen, 2020), wing load and wing aspect, both related to dispersal ability (Gibb *et al.*, 2006), roundness of the body, measured by dividing body height by body width, which is thought to be associated with microhabitat use (personal communication, L.D.), eye area, related to hunting strategy and nocturnal behaviour (Ribera *et al.*, 1999) and hairiness, i.e. the number of hairs intersecting a transect line of diverse parts of the body, as a form of protection (Suter *et al.*, 2004). Lastly, the relation of mandible length to mandible width was used as a trait for foraging and competition.

Morphological traits of moths were measured from images published in Segerer (2011), and include colour lightness and wing aspect ratio. Further data were extracted from Potocky (2018), namely the seasonal time of occurrence, the part of plant on which the larvae feed, whether they feed as adults how specialized they are on certain plant species.For plants, we decided to use the three traits spanning the trait space, namely plant height, seed mass and leaf area index, described in Venneste (2019). These traits were extracted from LEDA. Missing values were supplemented from the TRY database (Kattge *et al.*, 2011).

If there were still single trait values missing, these were estimated by taking the mean trait values of the genus of the species in question. For saproxylic beetles, there were isolated cases in which there were no other representatives of the genus. Here, mean trait values of the family were taken. In case where also no representatives of the families were found, species were excluded from the analysis.

Phylogenies

For bats we used the phylogenetic tree by Riedinger, et al (2013). and added the missing tips using the addTips function in megaptera v1.1.6 (Heibl, 2019). Phylogenetic trees for birds were compiled following the phylogeny subset methodology from www.birdtree.org and used to mine 4,000 bootstrap trees, based on the backbone provided by Hackett, et al. (2008). Those bootstrap replicates were then condensed into a fully dated consensus tree using TreeAnnotator 1.8.2 (available on http://beast.community/treeannotator). The species-level phylogeny of Chesters (2017) provided the phylogenetic information for beetles and heteroptera. The tree was pruned to the recorded species and all missing species were added via the addTip function

(megaptera v1.1.6) to their monophyletic generic clade. For moths, a phylogeny of 1355 Lepidoptera reported from Germany was constructed using megaptera. COI sequences were downloaded from GenBank, BOLD, and non-public sequences were provided by Advanced Identification Methods (AIM), Munich. Orthologous sequences were selected using the Basic Local Alignment Search Tool (BLAST). Alignment and tree search were conducted using a super-familial backbone tree based on Mitter et al (2017). Tree topology and branch lengths were modelled in a maximumlikelihood framework (RAxML v8.4.2. Stamatakis, 2014) and sequence evolution was modelled using the GTRCAT approximation for each marker gene separately on a common topology. A topological constraint was imposed on the phylogeny based on recent phylogenomic studies. More detailed information about the programs and methods used can be found in Bae et al. (2019). For pl ants, we used the phylogeny of Durka and Michalski (2012). Two species which were not included there, *Taraxacum campylodes* and *Taraxacum hamatum*, were added as replacements for the Taraxacum species for which no representative occurred in our data.

Facets of habitat heterogeneity.

In Heidrich et al (2020), heterogeneity in forest habitats was broken down to six different facets based on the classification of Stein & Kreft (2015); heterogeneity in topography, horizontal forest structures, vertical forest structures, plant diversity as well as structural and taxonomic richness of dead wood (Figure C5.2a). For the full reasoning refer to Heidrich et al (2020). *Structural and taxonomic richness of deadwood* was calculated by counting the number of different deadwood types, which were classified according to diameter and decomposition classes as well as subtype (broken snag, lying dead tree and so on; see also Supplementary Methods in Heidrich et al, 2020) and the number of tree species per plot, respectively. *Plant diversity* was characterized by calculating phylogenetic diversity (Faith's PD) based on the phylogeny of Durka & Michalski (2012) of all vascular plants in the tree, shrub and herb layers of each plot. Standardized measurements of heterogeneity in horizontal and vertical forest structure as well as topography were obtained using high-resolution airborne laser scanning. *Vertical heterogeneity* was calculated as standard deviation if the heights of the vegetation returns. The total length of gap edges per plot were used as a measure for *horizontal heterogeneity,* with gap being defined as having a minimum size of 50 m², a perimeter/area ratio of <1.5 and a penetration ratio of >80%. *Microscale topography* was calculated as the standard deviation of the slope of the digital terrain model derived from ALS. For a more detailed description, see Heidrich et al (2020).

Analysis

We followed the protocol of Cadotte et al (2013) and calculated pairwise phylogenetic functional diversity as the following:

$$FPDist = (aPDist^p + (1-a)FDist^p)^{1/p}$$

PDist is the phylogenetic distance between species. FDist is the functional distance, which was calculated as the Gower distance (Gower, 1971). Both were scaled to range between 0 and 1. The combining variant p was set to 2 to obtain Euclidean distance between the combined functional and phylogenetic distances. The weighing factor a determines how much emphasize is set on the phylogenetic information. If a is set to zero, FPDist is functional distance only, while a = 1 represents phylogenetic distance only. A priori, we selected species groups for which we should have gained enough functionally relevant traits, so that the phylogeny should add little information. However, we cannot exclude that we missed important functional traits.

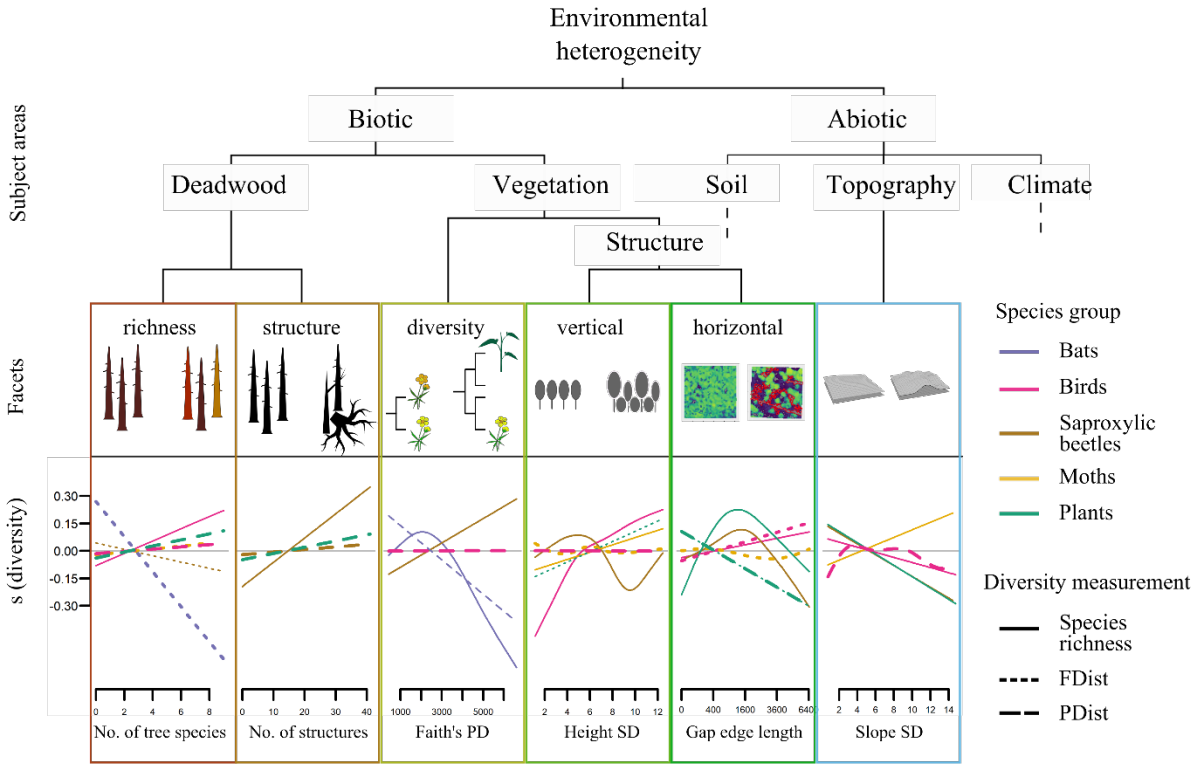


Figure C5.2: Summary of the relationships between the single facets of heterogeneity and species richness and ecological diversity, measured as standardized mean functional-phylogenetic-distance (MFPD). Habitat heterogeneity was decomposed into the facets heterogeneity in vertical (height SD) and in horizontal structure (gap edge length), plant diversity (Faith's PD) and micro-scale topography (slope SD), and taxonomic and structural richness of deadwood. The lines represent the partial contribution of the significant scaled and centered predictor variables in the GAMs (s (diversity)) in the modeling of species richness (solid lines), MFPD with a phylogenetic weight of zero, representing functional distance (point lines) and MFPD with a phylogenetic weighting of one, representing phylogenetic distance (dashed lines).

Thus, we performed the analysis described below for a sequence of *a* values ranging from 0 to 1 in 0.05 steps and compared the resulting R^2-values.

To evaluate whether the ecological diversity is higher or lower than what would be expected from their number of species, calculated the standardized effect size of the mean FPDist using the ses.mpd function. For matching of phylogeny, trait and community data as well as calculation of functional distances and Null analysis, we used the pez-package (Pearse et al., 2020). The resulting standardized mean functional-phylogenetic distances were than modelled against the six facets of heterogeneity using generalized additive models (GAMs), allowing for unconstrained and smooth relationships. We used a quasi-binomial distribution family, because the values of MPFD are constrained between 0 and 1 (package mgcv, function gam, version 1.8, Wood, 2018)). 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 to improve the distribution. The smoothness term, representing the taxonomic richness of deadwood, was restricted to six degrees of freedom to achieve model convergence. The study region was considered as a random factor to account for regional effects.

For birds, the models performed equally well across different weights of a, suggesting that the ecological differences between species are phylogenetically conserved. For bats and moths, putting weight on the phylogenetic component rather decreased the explained variance. For plants and saproxylic beetles, putting weight on the phylogenetic component rather increased the explained variance, suggesting that important traits are missing. However, the high R^2 in the model with the highest phylogenetic weighing could also result from high regional phylogenetic clustering. As R^2 was maximized at the extremes of the weighing and not at intermediate levels (Figure 2), we performed the analysis for a = 0 and a =1.

Because several species were excluded due to missing trait values, we re-ran the modelling of species richness in Heidrich et al (2020).

Results

Taxonomic dead wood richness

Only the species richness of birds increased with increasing taxonomic richness in dead wood. However, this facet of heterogeneity affected four species groups in ecological diversity. Parallel to the increase in species richness, birds became ecologically more diverse in terms of phylogenetic differences (a = 1). Also, moths and plants increased in ecological diversity, the former if functional distance (a = 0) and the latter if phylogenetic distances (a = 1) were considered. In contrast, assemblages of bats and saproxylic beetles became ecologically more clustered on plots with high taxonomic richness in dead wood in terms of functional distance (a = 0).

Structural dead wood richness

Richness in dead wood structures not only promoted species richness but also ecological diversity of saprotrophic beetles in terms of phylogenetic distance (a = 1). It furthermore increased the ecological diversity of plants, also in terms of phylogenetic distances (a = 1).

Plant diversity

Species richness of saprotrophic beetles increased with plant diversity and formed a hump-shaped shape in bats. The latter was accompanied with a decrease in ecological diversity in terms of phylogenetic distances (a = 1). Though there was a significant response in the ecological diversity of birds, it was nearly non-distinguishable (a =1), and none was apparent in saproxylic beetles.

Vertical heterogeneity

Vertical heterogeneity increased the species richness of birds and moths and had an indifferent effect on saproxylic beetles. The effect on the ecological biodiversity of these groups was either so low, that it won't be accounted for despite a significant p-value (birds, a =1), indifferent (moths, a = 0) or non-apparent (saproxylic beetles). Only ecological diversity of plants showed a positive relationship to increases in vertical heterogeneity, and only in terms of functional distance (a = 0)

Horizontal heterogeneity

Species richness and ecological diversity in respect phylogenetic as well as functional distance of birds increased with horizontal heterogeneity. Species richness of saproxylic beetles showed a hump-shaped relationship with horizontal heterogeneity but was not accompanied by a response in ecological diversity. Species richness of plants had a hump-shaped relationship with horizontal heterogeneity and decreased in ecological diversity both in terms of phylogenetic as well as functional distances.

TABLE C5.1: Results of the generalized additive models (GAMs) of heterogeneity in the taxonomic and structural diversity of deadwood, plant diversity (Faith's phylogenetic diversity [PD]), vertical structure (height standard deviation [SD]), horizontal structure (square-rooted edge length) and micro-scale topography (slope SD) as predictor variables, and multi-diversity, species richness (upper half) and mean abundance (lower half) as dependent variables. ΔR^2 was calculated as the difference between the full models and the null models, with region as the random factor. The classification as monotonically positive (+), monotonically negative (-), hump-shaped (h) or neither (i) is shown next to the estimated degrees of freedom (edf)

Diversity measurement	*Species group*	N_{Plots}	Taxonomic richness of dead wood				Structural richness of dead wood				Plant diversity				Vertical heterogeneity				Horizontal heterogeneity				Micro-scale topography				Region		
			Edf		F-value		Edf		F-value		Edf		F-value		Edf		F-value		Edf		F-value		edf		F-value		edf	F-value	
Species richness	Bats	248	1		0.87	n.s.	1		0.01	n.s.	**2.4**	**H**	**3.3**	*	1		1	n.s.	1		0.18	n.s.	1		3.5	n.s.	3.78	26	***
	Birds	496	**1**	**+**	**9.19**	**	1		0	n.s.	1		0.49	n.s.	**3.29**	**+**	**19**	***	**1**	**+**	**5.7**	*	1	-	**7.3**	**	3.74	20	***
	Moths	227	1		0.15	n.s.	1		3.4	n.s.	1.45		1.6	n.s.	**1**	**+**	**5.2**	*	1		0.42	n.s.	1	**+**	**6.2**	*	3.55	10	***
	Plants	497	3.2		1.5	n.s.	1		0.41	n.s.					1		4	n.s.	**3.01**	**H**	**10**	***	1	-	**8.1**	***	3.93	67	***
	Saproxylic beetles	385	1		0.54	n.s.	**1**	**+**	**10**	**	**1**	**+**	**7.1**	**	**3.98**	**i**	**4.6**	***	**2.78**	**H**	**2.7**	*	1	-	**11**	**	3.9	54	***
Fdist (a = 0)	Bats	248	**1**	**-**	**7.4**	**	1		0.05	n.s.	1		3.1	n.s.	1		0.05	n.s.	1		0.11	n.s.	1		0.01	n.s.	3.31	10	***
	Birds	496	1		0.84	n.s.	1		0.66	n.s.	1		0.01	n.s.	1		0.01	n.s.	**1**	**+**	**39**	***	**4.87**	**i**	**3.3**	**	0	0	n.s.
	Moths	385	**1**	**+**	**10**	**	1		0.46	n.s.	1		0.03	n.s.	5.66		3.1	**	**3.72**	**i**	**4.5**	***	1		0	n.s.	2.19	1.7	*
	Plants	227	1		1.01	n.s.	1		0.67	n.s.					1	i	9.5	***	**1**	**-**	**20**	***	1		1.2	n.s.	3.81	26	***
	Saproxylic	497	**1**	**-**	**6.8**	**	1		0.74	n.s.	1		0.67	n.s.	1	+	3.2	n.s.	1		0.01	n.n	1		0.05	n.s.	2.63	2.6	**
Pdist (a= 1)	Bats	248	1		0.57	n.s.	1		2	n.s.	**1**	-	**3.1**	*	1		0.52	n.s.	1		0.16	n.s.	1		0.15	n.s.	2.01	1.5	*
	Birds	496	**1**	**+**	**11**	***	1		1.01	n.s.	*1*	*+*	*4.4*	*	4.67	-	3.1	**	**1**		3.6	n.s.	2.02	**i**	**5.1**	**	2.25	2.4	**
	Moths	385	1		0.01	n.s.	1		0.01	n.s.	1		0	n.s.	1		3.4	n.s.	1		1.5	n.s.	1		0.34	n.s.	3.39	6.1	***
	Plants	227	**1**	**+**	**7.8**	*	**1**	**+**	**13**	***	NA		NA	NA	1		0	n.s.	**1**	**-**	**34**	***	1		0	n.s.	3.91	97	***
	Saproxylic	497	1		2.8	n.s.	1	**+**	**4.5**	*	1		0.09	n.s.	1		1.8	n.s.	1		1.8	n.s.	1		1.5	n.s.	3.74	27	***

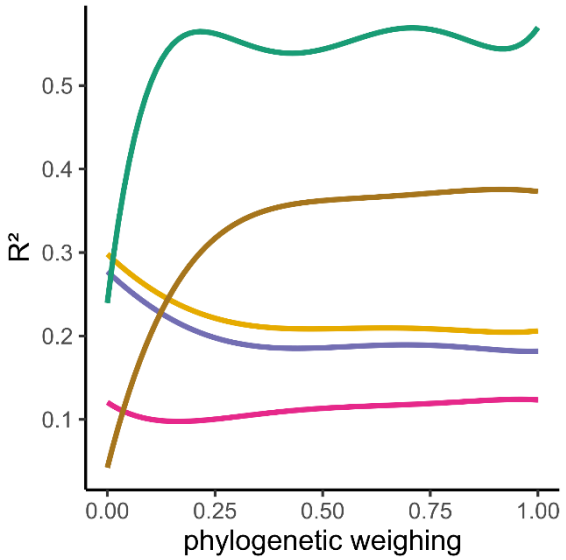


Figure C5.3: Explained variance of the GAM model per species group depending on the phylogenetic weighing variable a. For color-coding, refer to Figure C5.2

Microscale heterogeneity

Heterogeneity in topographic heterogeneity was accompanied by decreases in the species richness of birds, saproxylic beetles and plants, whereas moths had higher species richness. None of these HDRs was reflected by directed changes in ecological diversity.

In total, from 13 changes in species richness across all facets of heterogeneity, only five were accompanied by an explicit and directed change in ecological diversity in either phylogenetic or functional distance. Vice versa, changes in ecological diversity were not accompanied by significant changes in species richness in six cases (Table C5.2).

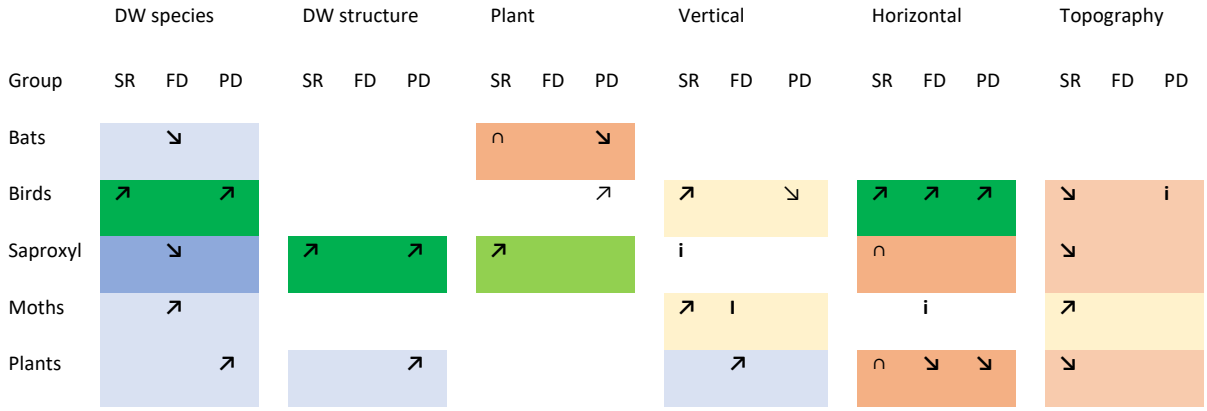
Discussion

Positive and hump-shaped relationships between species richness and heterogeneity are commonly thought to be based on increases in the number of niches. Surprisingly, increases in species richness were accompanied by increases in ecological diversity in less than half of the cases. Even vertical heterogeneity, which was the base variable leading to the formulation of the habitat-heterogeneity-hypothesis (MacArthur & MacArthur, 1961), did show only a minimal effect on ecological diversity – and even in an opposite direction to the expectation. If ecological diversity is representative for niche differentiation, as suggested in Stark (2017), these results suggest that the addition of new niches via heterogeneity in environmental conditions occurs more seldomly than expected.

In the case of birds, it has been noted that bird assemblages in temperate forests are often functionally saturated (Oliveira *et al.*, 2019). If most of the species have the functional trait equipment to forage in multiple layers of the forest, increased vertical layering must not necessarily inflate the trait space. Rather, the spatial separation as well as the added space of foraging grounds would allow more functionally similar species to co-exist.

Other neutral mechanisms have led to the increase in species richness moths with vertical heterogeneity. Here, increased vertical heterogeneity is associated higher leaf volume, which, according to the more-individuals-hypothesis, could then lead to an increase in species numbers despite niche overlap. However, in Heidrich et al (2020), we found no increase in the mean population size of moths with vertical heterogeneity which could support this hypothesis. Changes in species richness without changes in ecological diversity could also occur if environmental heterogeneity affects the probability to record species. Increased leaf volume, for example, might have affected the attractancy of the light trap. Variation in canopy structure also leads to different micro-climates (Frenne *et al.*, 2019), which then provide shelter from unsuitable abiotic conditions (Kleckova & Klecka, 2016) and the increased volume of leaves exclude predators (Müller *et al.*, 2012).

Table C5.2: Comparison of the form of the diversity-heterogeneity relationship for species richness (SR), functional diversity (phylogenetic weighing parameter a set to 0) and phylogenetic diversity (a set to 1) and the six facets of heterogeneity. FD or PD were shaded grey, if it resulted in a lower R^2 of the total model compared to the R^2 of the highest and lowest a value, respectively. Arrows pointed upwards represent overall positive, arrows pointed downwards overall negative trends. Hump-shaped relationships are indicated by the sign ∩. Indifferent relationship, i.e. relationships with more than one sign change, are indicated by "I". Colour coding reflects the mechanisms presented in Figure 1.



Reasons for other species richness relationships which are not mirrored by any change in ecological diversity remain unclear.

Interestingly, there are also occasions, in which ecological diversity, but not species richness is affected, for example the increase of ecological diversity of plants and moths and the decrease of bats with taxonomic richness of dead wood. Here, certain structures could lead to the inclusion or exclusion of few, but ecologically very distinct species. This would lead to drastic changes in the pairwise difference between species but have little weight in species richness.

Lastly, there is also two occasions in which heterogeneity appears to filter specific traits, thereby reducing not only ecological diversity, but ultimately also species richness. Horizontal heterogeneity seems to filter plant species with specific traits. In plots with a high number of small gaps, light conditions are likely to become diffuse. Thus, plants adapted to full shade or full sun are likely to be replaced by light generalist species. The response of ecological diversity and species richness of bats towards increasing plant diversity might be explained by an indirect effect of this relationship. If plant diversity (and cover) are highest at intermediate levels of horizontal heterogeneity, they are potentially in areas with few but relatively large connected gaps. Such areas offer hunting grounds for all feeding guilds, including open-space foragers (Jung *et al.*, 2012) and thus provide a higher number of niches.

The results of this study display a multitude of effects of heterogeneity on species diversity, both in terms of species richness as well as ecological diversity. Most importantly, they suggest that heterogeneity can increase species richness in several ways, by increasing but also by partitioning the present niche space or increasing the effective area thereof. Note, that also mean environmental conditions can affect ecological diversity. According to the "environmental means hypothesis" (Stark *et al.*, 2017), areas lying at the extreme of a climate gradient naturally have more clustered trait sets, independent of heterogeneity. Though the inclusion of region as a random factor should already have accounted for most of the variation explained by

environmental means, future studies should be refined to also include intra-regional variation therein.

Further increases in ecological distinctiveness highlight the positive effects of heterogeneity on diversity in forests. However, as shown in the response of diversity in plants towards horizontal heterogeneity, there are also filtering effects which should be accounted for in management in forests. It should be also kept in mind, that the species groups which responded most negatively to heterogeneity in Heidrich et al (2020), namely fungi, bryophytes and lichens, were not considered in this analysis, as we included only six species groups for which we had a comprehensive and informative set of traits at hand. The lack of meaningful functional traits was one of the reasonings of Cadotte (2013) to combine functional and phylogenetic information. However, adding phylogenetic distances decreased the variance explained by our models in four species groups. For the other two, namely saproxylic beetles and plants, replacing functional by phylogenetic distances may result in higher total R^2-values. Yet, that increase seemed to be rather a result of spatial shifts in lineages than to be a result of better represented ecological diversity, as indicated by the high F-values of the regional random effect and the low difference of the model R^2 to the Null-model only including regional random effects. For a deeper understanding of the effect of heterogeneity on colonization and extinction processes in forests, trait data bases such as TRY or LEDA need to be also available for other taxonomic groups.

Chapter 6

Radar vision in the mapping of forest biodiversity from space

with

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published in *Nature Communications* 10:4757 (2019), https://doi.org/10.1038/s41467-019-12737-x

This study builds upon data from several biodiversity monitoring projects and was mainly analyzed written by Soyeon Bae, the lead author. I contributed the compilation of data of the different species groups as well as previous revisions of the text.

Summary

Recent progress in remote sensing provides much-needed, large-scale spatio-temporal information on habitat structures important for biodiversity conservation. Here we examine the potential of a newly launched satellite-borne radar system (Sentinel-1) to map the biodiversity of twelve taxa across five temperate forest regions. We show that the sensitivity of radar to habitat structure is similar to that of airborne laser scanning (ALS), the current gold standard in the measurement of forest structure. Our models of different facets of biodiversity reveal that radar performs as well as ALS; median R^2 over twelve taxa by ALS and radar are 0.51 and 0.57 respectively for the first non-metric multidimensional scaling axes representing assemblage composition. We further demonstrate the promising predictive ability of radar-derived data with external validation based on the species composition of birds and saproxylic beetles. Establishing new area-wide biodiversity monitoring by remote sensing will require the coupling of radar data to stratified and standardized collected local species data.

Introduction

The impact of humans on the planet has progressively escalated to the extent that the current geological age is referred to as the Anthropocene, in recognition of the geological dimensions of the human footprint (Crutzen, 2002). Its characteristics include declines in non-human populations and the extinction of species, due most prominently to anthropogenically mediated habitat degradation (Sala *et al.*, 2000; Barnosky *et al.*, 2011). The resulting loss of biodiversity is evident at local and landscape scales, but attempts to measure habitat loss for diverse species over large areas have been frustrated by the high cost and the considerable effort involved. The unsolved challenge here is to monitor the area-wide diversity within and between habitats (α-diversity and β-diversity, respectively) across large areas, which impedes estimates of total diversity (γ- diversity) of landscapes. However, over the last decade, advances in remote sensing have led to an exponential increase in the use of these technologies, including in ecological investigations (Schmeller *et al.*, 2017; Rocchini *et al.*, 2018), and a recognition of their potential in obtaining reliable and frequent updates on the spatial information required to monitor biodiversity over larger areas, information that is essential for conservationists. Skidmore et al (2015) called upon ecologists and space agencies throughout the world to forge a global monitoring strategy that includes a definitive set of biodiversity variables and a plan for tracking them from space. Despite the theoretical progress that has been made under the umbrella of Group on Earth Observation Biodiversity Observation Network (GEOBON), quantitative evidence of how well different essential biodiversity variables (Pereira *et al.*, 2013) can be mapped and monitored from space is lacking, and the relationship of these variables to different facets of biodiversity remains poorly understood (Hardisty *et al.*, 2019).

With its ability to characterise the complex three-dimensional (3-D) structure of terrain and vegetation, airborne laser scanning (ALS) has been particularly successful in biodiversity monitoring (Lefsky *et al.*, 2002). Objective remote measurements can now be conducted with ALS and the acquired data used to model vegetation metrics (e.g. canopy cover, height, layering, and basal area) that traditionally were estimated based on laborious fieldwork. The 3-D data acquired with ALS has provided the basis for a number of advances in animal ecology and biodiversity

conservation (Müller & Brandl, 2009; Davies & Asner, 2014). Although large-area mapping by space-borne laser scanning has thus far been limited in scope, progress towards this long-term goal is being made by programs such as Global Ecosystem Dynamics Investigator (GEDI) (Qi & Dubayah, 2016) and ICESat-2 (Ice, Cloud, and land Elevation Satellite-2) (Narine *et al.*, 2019), in which spot measurements of canopy height and profile layering are obtained within the laser beam footprint (~22 m and 90 m respectively). Both missions are expected to supply critical information in support of the mapping of structural essential biodiversity variables. While current and future space-borne laser-scanning systems provide only patchy information, space-borne synthetic aperture radar (SAR) systems are also sensitive to the geometric properties of the Earth's surface, such as forest canopy structure, and capable of complete coverage of the entire globe. Hence, SAR data could be an alternative source for ecologically meaningful information on vegetation structure from regional to global scales. SAR is similar to ALS as both remote sensing techniques actively emit electromagnetic radiation and measure the returned signal. A major advantage of SAR is its ability to penetrate clouds, making it a suitable technique also for regions with nearly constant cloud coverage, such as the tropics or mountain areas. Depending on the wavelength used (e.g. C-band), SAR backscatter signals can be interpreted to derive ecologically meaningful structural information from terrain and vegetation. SAR has already had a significant impact on ecological research, and both C- and L-band sensors have been used extensively in the mapping of biomass within boreal (Thurner *et al.*, 2014) and tropical forest regions (Saatchi *et al.*, 2011; Avitabile *et al.*, 2016).

The launch of the Sentinel-1 mission, a constellation of two C-band SAR satellites, by the European Space Agency in 2014 and 2016 revolutionised SAR remote sensing, due to Sentinel 1's unprecedented combination of high spatial resolution (5–20 m), high revisit frequencies (5–10 days), complete geographic coverage and the ESA's open-access policy regarding the availability of the collected data. C-band SAR has a wavelength of 5.6 cm, which means it is sensitive to vegetation structures and is likely to be scattered from elements within the tree canopy. However, the formation of SAR backscatter signals is complex, as factors other than canopy structure, such as scan angle, direction, soil moisture and plant water content, also exert considerable influence on backscatter properties. Some of these confounding influences can be mediated by making use of multi-date acquisitions, as was the case in this study.

Using the open-access, dense time-series data obtained by the Sentinel-1 mission, we conduct the first evaluation of Sentinel-1's potential in biodiversity mapping. Our study begins with a comparison of the ecological application of radar (henceforth, "Sentinel-1" is referred to as "radar") metrics vs. the well-established ALS metrics in providing a better understanding of habitat structure in forest ecosystems. A suite of ground-truth taxonomic and phylogenetic biodiversity measures covering within forest stand (α-) and among forest stand (β-) diversity from a broad range of trophic levels and taxa (henceforth "functional groups") is then modelled using either ALS data or time-series radar data to explore the extent to which rich time-series radar data can be used to represent ecologically meaningful gradients of habitat conditions in temperate forests. Thus, we quantify the predictive power of radar in modelling different aspects of biodiversity, including species composition and richness and phylogenetic diversity, and compare the results to those obtained using very high density (8-40 pulses/m² in this study) ALS data.

For this purpose, we make use of a distributed ground-based network of 463 biodiversity monitoring plots spanning five Central European temperate forest regions and capturing biodiversity data for 12 functional groups. Finally, to test their suitability for biodiversity mapping and monitoring, the radar models for two taxa are validated using independent external data collected from areas outside the five training areas.

Our analysis shows the close association of the structural attributes of forests as described by radar and ALS data, which also similarly reflect gradients of forest maturity and structural heterogeneity. As predictors of biodiversity, the two remote sensing techniques are similar in their power, albeit with radar data being superior for species composition and ALS for species richness. Global biodiversity monitoring requires both a consistent method of satellite image acquisition and open access to those images. Our study demonstrates the potential of such data for monitoring biodiversity of forests and thus of other large-scale habitats as well.

Results

The ecological relevance of radar-derived structural variables

Canonical correlation analysis (CCoA) showed a strong correlation between the habitat metrics derived from the ALS and radar sensors. The ecological relevance of the latter with respect to 3-D forest structure and resident animal diversity was established in prior studies (Davies & Asner, 2014). Among the 13 canonical axes from the two remote sensing data sets, nine statistically significant pairs ($p<0.05$ with Pearson's correlation test), explaining 96.30% of the variance of the datasets (Table C8.4.4), were identified. The first and second axes showed the highest canonical correlation coefficients (for the pairs of canonical axes from the two datasets): 0.92 and 0.75 respectively (Fig. C6.1).

The first canonical axes represented a gradient of decreasing forest maturity, as the first ALS axis correlated negatively with both the penetration ratio of the canopy layer and the vegetation height and positively with the gap area described by the ALS metrics (Fig. C6.2 and Table C8.4.5). The correlation of the first radar axis with yearly and winter radar backscatter was highly negative (Fig. C6.2 and Table C8.4.6). The second canonical axes represented the variability in height, as the second ALS axis had a strong correlation with the standard deviations of vegetation height and canopy surface height. Similarly, the second radar axis correlated with the standard deviation of the yearly and summer backscatter, which we calculated to represent structural heterogeneity indices. The third and fourth canonical axes represented gradients of structural heterogeneity, as the third ALS axis strongly correlated with the penetration of the regeneration layer and the edge length of forest gaps and the fourth ALS axis with foliage height diversity. The third radar axis showed strong correlations with texture measures (contrast and orderliness, quantifying spatial heterogeneity) and the fourth radar axis with the ratio between the two descriptors of polarisation, VV (vertically-sent, vertically-received radar pulses) and VH (vertically sent, horizontally-received radar pulses).

The drivers of different components of diversity

Boosted generalised additive models (GAMs), i.e. fixed effects models, were employed with five-fold cross-validation for the internal validation of all response variables: the main axes of species assemblage composition based on non-metric multidimensional

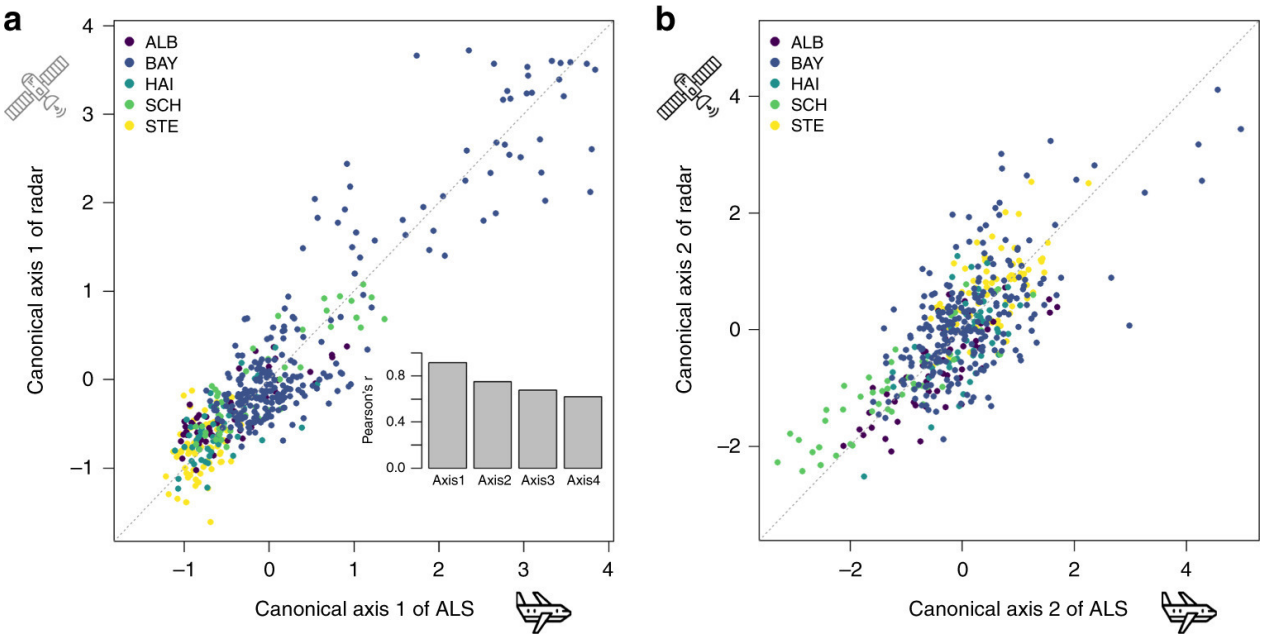

FIGURE C6.1: Correlations between the metrics from the two sensors. Correlations between the (a) first (forest maturity) and (b) second (structural heterogeneity) axes of a canonical correlation analysis, extracted to maximise the correlation between the data sets of the radar- and airborne laser scanning (ALS)-derived variables. The inset in (a) shows the Pearson's correlation coefficients for the first four axes of the two data sets with the significance level $p < 0.001$.

scaling (NMDS) ordination scores, log-transformed species richness and phylogenetic diversity, with the latter calculated as the standardised effect size to ensure independence from species richness. Overall, the performances of the radar and ALS metrics were similar. In addition, for both sensors, with the use of metrics related to forest maturity the assemblage composition was better predicted than were diversity indices. This was indicated by the cross-validated R^2 (coefficient of determination) and root mean square error (RMSE) values for the first NMDS axes representing assemblage composition (median R^2 values over 12 functional groups by ALS and radar: 0.51 and 0.57 respectively) and the second NMDS axes representing assemblage composition (0.30 and 0.27), species richness (0.21 and 0.11) and phylogenetic diversity (0.19 and 0.16) (Fig. C6.3 and Table C8.4.7; additional RMSE results are shown in Table C8.4.8). The first axes of assemblage composition (NMDS1) were distinctively better predicted by radar than by ALS, with the exception of the assemblage composition of bats, but the second axes of assemblage composition (NMDS2) were better predicted by ALS, with the exceptions of the assemblage composition of lichens and phytophagous beetles. However, for species richness and phylogenetic diversity, the predictive performances of the two sensors were comparable. To check the robustness of our results of arthropods for sample size we reanalysed the data on a subset of plots with sufficient sample completeness. These findings corroborated the findings of the total data set (Fig. C8.4.22).

To take into account repeated measures within the five forest regions, we additionally fitted mixed effects models in which region was a random factor (see the "Methods" section for details). Overall, this reduced the explained variance in the ALS and radar models, but the results between taxa were highly variable.

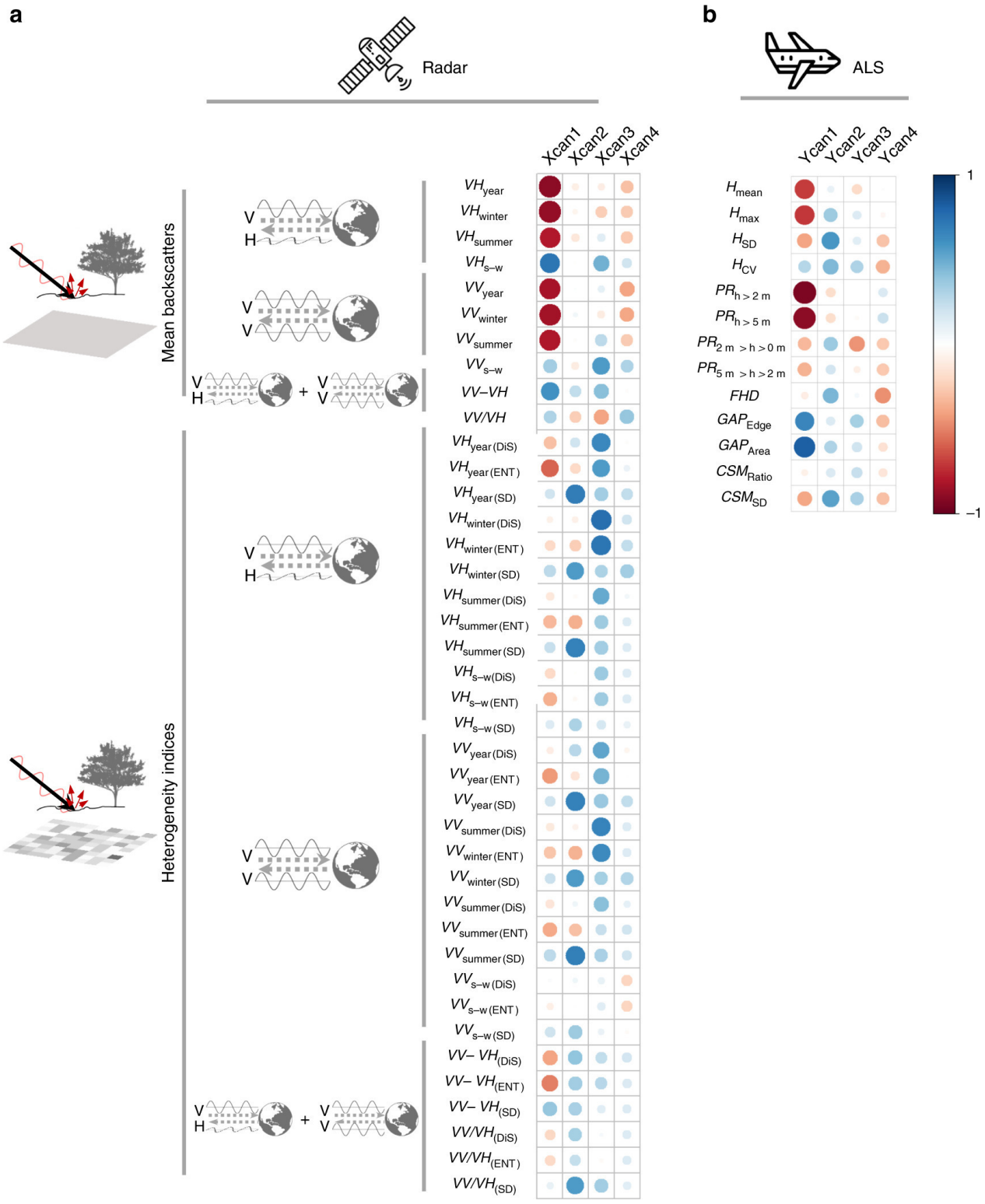

FIGURE C6.2 Ecological relevance of the metrics from the two sensors. Pearson's correlation matrix a between the first four main canonical axes (Xcan1–4) and the radar metrics and (b between the first four main canonical axes (Ycan1–4) and the ALS metrics at the significance level $p < 0.05$. The first canonical axes represent a gradient of decreasing forest maturity, and the second, third, and fourth canonical axes gradients of structural heterogeneity. Positive correlations are displayed in blue and negative correlations in red colour. Colour intensity and the size of the circle are proportional to the correlation coefficients. See Tables C8.4.4 and C8.4.5 for details

The decrease in the explained variance was strongest in ground-living spiders and carabids, although a decrease in that of bats was obtained as well. The loss of explained variance by a region effect in the mixed effects models was stronger in the ALS models (0.14, a median of 48 response variables) than in the radar models (0.10) (Tables C8.4.9 and C8.4.10). This tendency of the superiority of one sensor over the other in the mixed effects models was mostly consistent with the tendency in the fixed effects models, except in the cases of 4 of 48 response variables.

The most important variables in the predictions of the NMDS axes representing assemblage composition were the penetration ratio of the canopy-understorey ($PR_{\mathrm{h>2m}}$) in the ALS model and the winter VH (VH_{winter}) in the radar model. This was determined consistently across 12 functional groups (Fig. C8.4.6-17). In the ALS models, $PR_{\mathrm{h>2m}}$ was the most important predictor of the first and second NMDS axes of 11 of the 12 functional groups, with the exception being the assemblage composition of necrophagous beetles. Using the same approach for the radar models, VH_{winter} was the most important predictor of 10 of the 12 groups, with the exceptions being the assemblage compositions of carabid beetles and bats. Nevertheless, among the exceptional groups, $PR_{\mathrm{h>2m}}$ and VH_{winter} ranked second among the list of dominant factors in the ALS models of necrophagous beetles and in the radar models of bats, respectively.

The most critical predictors of species richness varied across the different functional groups. The predictors related to structural heterogeneity as identified by ALS, such as the coefficient of variation of vegetation height (H_{CV}), the standard deviation of canopy surface height (CSM_{SD}) and the edge length of forest gaps (Gap_{Edge}), actively contributed to the construction of the species richness models. Likewise, in the species richness models derived from radar data, horizontal heterogeneity predictors, such as standard deviation, dissimilarity and the entropy of radar backscatters, was of greater importance than in the corresponding assemblage composition models. In contrast to the species richness models, the phylogenetic diversity models derived from ALS and radar were strongly driven by measures sensitive to forest maturity, such as $PR_{\mathrm{h>2m}}$ and $PR_{2m>h>0m}$ and VH_{winter} respectively.

External validation of the assemblage composition models of two selected groups, birds (n=72) and saproxylic beetles (n=91), using data from outside the five forest regions further demonstrated the substantial predictive power of the models (coefficients of determination: 0.26 and 0.22 respectively) (Fig. C6.4). However, some of the validation plots featured very different bird species composition than those from the training space, such as those of the Rhön region (Fig. C6.4a and Fig. C8.4.19a), and, as is to be expected, could not be predicted well in terms of NMDS1.

Discussion

Our results showed a strong correlation between pairs of canonical axes from radar and ALS data describing gradients of forest maturity and structural heterogeneity in forest ecosystems on a 1-ha scale. In biodiversity models of 12 functional groups, radar and ALS performed equally well. While the model performance of radar was better than that of ALS in predicting species composition, ALS was better in predicting species richness and phylogenetic diversity. The results obtained with both sensors showed the closer association of species composition and phylogenetic diversity with gradients of forest maturity,

and that of species richness with structural heterogeneity. However, the models of the diversity indices were inferior to those of assemblage composition.

The prediction accuracy of ALS for the structural attributes of forests and consequently for attributes of the associated communities, such as taxonomic diversity, has been well established over the last two decades (Davies & Asner, 2014). Previous studies comparing ALS and radar in terms of the accuracy of forest attribute estimation for variables such as canopy height, stem volume and biomass revealed the superiority of ALS over radar at the local scale (Yu *et al.*, 2015; Naesset *et al.*, 2016). ALS was also shown to be better for high-accuracy characterisations of understorey layering and the structural complexity at local scales (Martinuzzi *et al.*, 2009; Kane *et al.*, 2010). These findings are not surprising, given the small footprint and the available high-energy sources of airborne platforms, compared with the challenges of interpreting the longer wavelengths and larger footprints of space-borne C-band SAR (Bergen *et al.*, 2009). Nonetheless, while at the scale of individual trees radar may not be able to provide the same level of height accuracy provided by ALS, this does not preclude the possibility that backscatter properties recorded from space can suitably capture the broader structural properties relevant to forest-dwelling organisms.

Using a similar CCoA methodology, field inventory data were previously compared with ALS data to determine the ability of the latter to predict critical forest stand structure and animal communities (Lefsky *et al.*, 2005; Müller & Brandl, 2009). In their CCoA analysis of ALS and forest field inventory data, Lesfky et al. (2005) found that forest structure could be characterised by three main factors: aboveground biomass (related to height), canopy cover (or openness) and structural heterogeneity (related to height variability).

Our CCoA analysis of radar and ALS metrics showed that two main factors, forest maturity and structural heterogeneity, comprehensively captured forest structure. The first pair of axes was directly related to forest maturity, which was represented by canopy cover (or openness) and canopy height. The fusion of these axes was likely due to the lower penetration depth of C-band SAR, which is limited to the very upper layers of the canopy, than of L- and P-band systems using longer wavelengths. The relatively short wavelengths of C-band SAR account for its poor ability in separating canopy height or biomass from canopy cover. A weak correlation between aboveground biomass and the backscatter of C-band SAR in dense forest has been reported and is generally associated with the early saturation of backscatter intensities for high aboveground biomass (Kellndorfer *et al.*, 2003; Huang *et al.*, 2018). The remaining significant axes from CCoA mostly reflected the structural heterogeneity of the forest stand, which is in line with the third main characteristic of forest structure identified by Lefsky et al (2005). The ALS and radar metrics approximating vertical and horizontal heterogeneity were associated with those structural heterogeneity axes. Image texture was employed in previous studies to improve land cover classification (Balzter *et al.*, 2015) but it had not been used to characterise the structural heterogeneity of a forest. Our study demonstrated that, by using image texture, the structural heterogeneity of a forest at a 1-ha spatial level and a resolution of 10 m can be captured by C-band radar, despite its limited penetration of the canopy.

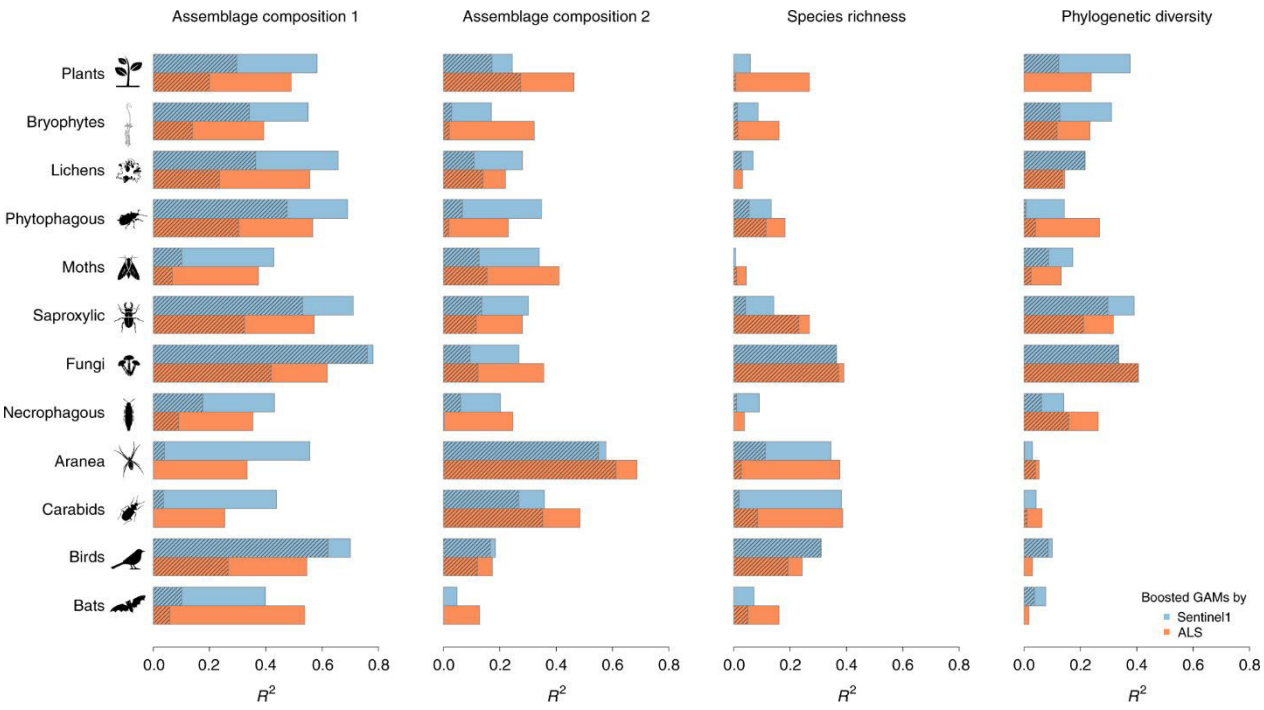

FIGURE C6.3: Predictive power of radar and ALS in modelling different aspects of biodiversity. Cross-validated performance (R^2, coefficient of determination) of assemblage habitat models (boosted generalised additive models), i.e. fixed effects models, using the ALS (orange bars) and radar (blue bars) data sets. The shaded bars represent R^2 derived from the mixed effects models. For mixed effects models, R^2 was calculated using only the fixed factors to predict the response variables, in order to exclude the variance explained by region

The CCoA also demonstrated that, for biodiversity modelling, multi-temporal radar data can substitute for a large proportion of the information available from ALS. Moreover, compared to readily interpretable ALS metrics, we were able to derive an ecological interpretation from numerous radar metrics, which was a prerequisite for the later biodiversity modelling.

Both the changes in openness as a consequence of forest succession and the accompanying changes in microclimatic conditions heavily structure species composition (Moning & Mueller, 2008; Leutner *et al.*, 2012; Seibold *et al.*, 2016b; Thorn *et al.*, 2016; Hilmers *et al.*, 2018). These accumulated effects associated with forest maturity were well reflected in the radar as well as the ALS models, as both showed the strong effects of forest maturity on the species composition of most of the 12 functional groups, even after controlling for repeated measurements in a specific region. Interestingly, the model performance of radar in predicting species composition was better than that of ALS. Although radar cannot provide the highly detailed information on forest structure that is generated by ALS, its measurements still allow a sufficiently fine-scale description of forest maturity. Moreover, multi-temporal radar data had a better discriminatory ability with respect to the composition of dominant tree species than did ALS data on single leaf-on acquisition (see Fig. 8.4.21 for additional models predicting the conifer tree ratio). The split between conifers and broadleaved trees greatly affects the composition not only of herbivores but also of fungi (Brändle & Brandl, 2006) and may cascade to higher trophic levels (Schuldt *et al.*, 2018; Penone *et al.*, 2019). Similarly, Schaffers et al. (2008) found that plant composition is a more powerful predictor of the communities of

predators and herbivores than is the physical habitat structure of grasslands. Therefore, radar data combine two important determinants of forest assemblage composition: maturity and conifer proportion. The drop in predictive power regarding the assemblage composition of carabids, spiders and bats after accounting for regions may reflect the geographical patterns or unmeasured environmental determinants of these groups. In the case of bats, the number of species found in Germany is highly regionally restricted (see Fig. C8.4.5). For ground-dwelling carabids and spiders, climate and soil conditions, mostly related to regional differences, likely override the structural patterns derived from remote sensing data. However, within a specific region, remote sensing data well predicted both ground-dwelling beetles and spiders (Müller & Brandl, 2009; Vierling *et al.*, 2011).

Overall, the models of species richness and phylogenetic diversity were inferior to those of assemblage composition. This was not surprising, as species richness does not consider the taxonomic identity of species and ignores species turnover. For example, two forest patches with different environmental conditions, such as open vs. closed forests, might exhibit the same species richness but harbour assemblages that differ completely in their composition. This was previously shown for saproxylic beetles, in which large numbers of conifer specialists were present in open forests whereas broadleaf specialists predominated in forests characterised by a closed canopy (Mueller *et al.*, 2010). Hence, in predictions of species richness and assemblage composition based on environmental information, that is, on remote sensing data, the relationship between predictor and response is much weaker for the former than for the latter. This was also suggested by Leutner et al (2012), who found that plant assemblage composition, but not species richness, could be successfully modelled with ALS and hyperspectral data. Along the same lines, a recent study reported an overall weak and highly variable relationship between species richness and carbon stock at the stand scale in the temperate forests of Europe, presumably because of trade-offs between species (Sabatini *et al.*, 2019).

However, we showed that various structural heterogeneity indices in both the ALS and radar metrics strengthened the respective species richness models. The structural heterogeneity metrics of ALS were important for the species richness of most groups (Figs. C8.4.5–16). This is consistent with the habitat-heterogeneity hypothesis, which assumes increasing species richness with the increase in niche availability arising from habitat heterogeneity (MacArthur & MacArthur, 1961). Support for this assumption comes from previous ALS studies in which the strong effects of 3-D structural heterogeneity on species richness were described (Davies & Asner, 2014). In our approach, radar-derived data were used to derive heterogeneity metrics in forests that were then applied successfully in biodiversity modelling. These metrics appeared to have been those representing the most important drivers in the species richness models of several taxonomic groups. Hence, our study well demonstrates the high explanatory and predictive power of coarse, spaceborne, radar-derived data in ecological studies at local scales.

Forest attributes not only differentiate between communities, but they also can be used to recognise the phylogenetic diversity within communities. For example, forest succession has been shown to shift communities in terms of their phylogeny, from closely related species in early-stage forests to more remotely related species in mature forest stands (Letcher *et al.*, 2012). This finding was supported by our study, which showed the

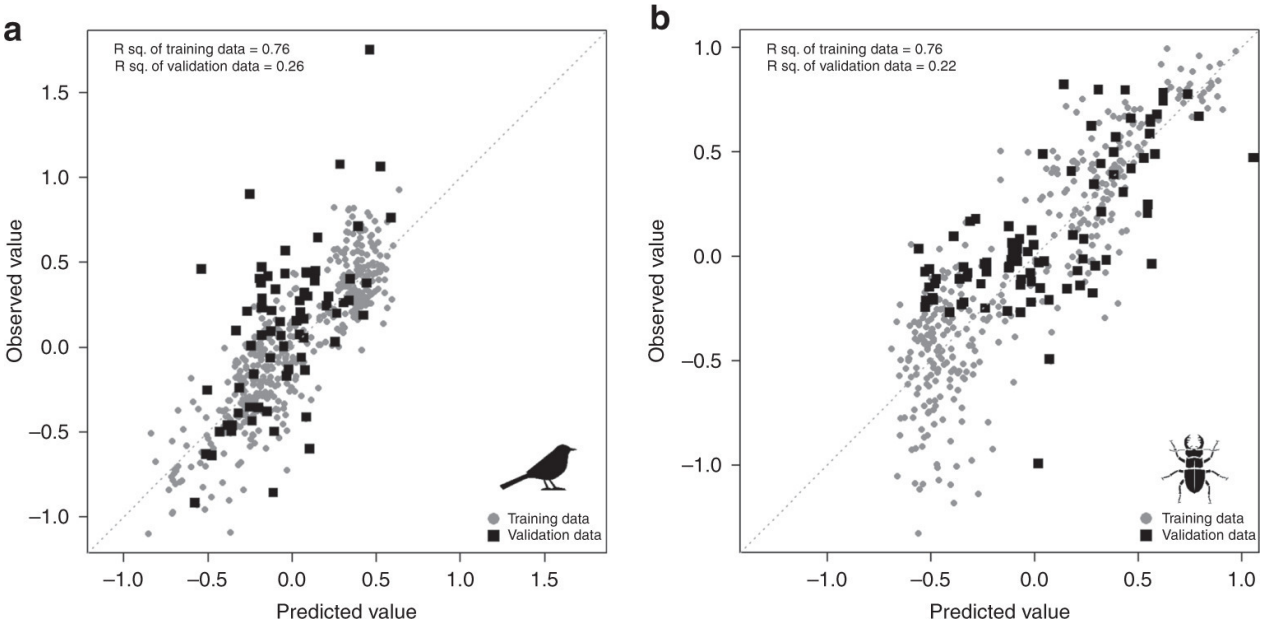

FIGURE C6.4: External validation of the assemblage composition models. Scatter plots of the first axis of the NMDS of a birds and b saproxylic beetles, between the observed and predicted value of the training data (grey circles) and the validation data (black squares). The R^2 (the coefficient of determination) of training data and validation data are shown..

dominance of forest maturity in the phylogenetic models whose performance for several groups was moderate, such as bryophytes, saproxylic beetles and fungi. However, the phylogenetic diversity of higher trophic groups was not well predicted, as the determinants of those models were associated with the density of the understorey (Figs. C8.4.6–17). Species richness and phylogenetic diversity patterns in forests may follow very different and at times even opposite patterns (Bässler *et al.*, 2016; Bae *et al.*, 2018). Hence phylogenetic diversity is not a surrogate but a complementary biodiversity measure that provides additional information on local diversity. However, the high R^2 of the coefficient of determination determined using the radar-based models for both the phylogenetic diversity of some groups, such as plants and saproxylic beetles, and the species composition support the global monitoring of phylogenetic diversity from space, and not only for plants (Jetz *et al.*, 2016).

The results of our studies of five forest regions in Central Europe demonstrate the potential of open-access space-borne radar data in predicting different components of biodiversity. Importantly, the correlation between radar and ALS gradients indicated the substantial cost-effectiveness of Sentinel-1 approach when applied to large-area mapping. As evidenced by the attributes of Sentinel-1 backscatters in their representation of forest maturity and tree composition, two of the main drivers of local species turnover, and by the various measures of structural heterogeneity, open-access Sentinel-1 clearly offers an alternative method to model the biodiversity of different functional groups. Furthermore, as gamma diversity could be estimated as a product of alpha and beta diversity, Sentinel-1 can be applied to estimate gamma diversity even for large landscapes where ground estimations will stay impossible.

The shortcoming of Sentinel-1 data that we uncovered was in the prediction of species richness and phylogenetic diversity for groups that were more strongly driven by the development of the understorey. Weak permeability through overstorey layers is unavoidable with space-borne C-band SAR

systems, due to their short wavelengths (Bergen *et al.*, 2009), whereas L- and P-band systems make use of longer wavelengths. Nonetheless, Sentinel-1 performed as well as ALS with respect to the biodiversity models of groups driven by forest maturity or specific indices of structural heterogeneity. In the near future, L-band and S-band SAR data will become increasingly availability (e.g. NASA-ISRO synthetic aperture radar (NISAR), a dual-frequency SAR carried on an Earth observation satellite). Used in conjunction with Sentinel-1's C-band, they may allow a better characterisation of the understory and of the different-sized elements of forest structure. Although our study covered five forested regions, these were representative only of the major temperate forest ecosystems of Central Europe. Nonetheless, given that radar data for the Earth's forested regions are ubiquitously available, there is more than ample opportunity to test the generality of our findings in essentially all forests. The major barrier to the larger-scale application of our methodology is the lack of availability of georeferenced and well-stratified (both spatially and ecologically) biodiversity data that span multiple taxa. Datasets such as those from the Biodiversity Exploratories (Fischer *et al.*, 2010) together with those generated in well-established long-term biodiversity monitoring, such as undertaken at the Steigerwald (Doerfler *et al.*, 2018) and in the Bavarian Forest National Park (Bässler *et al.*, 2009) at the scale of the individual forest, provide excellent test-dataset allowing the broader application of the approach described herein. However, at larger scale such as at the country level or within the EU as a whole, standardised monitoring systems with high resolution are currently available only for a few taxa, for example, bird surveys by the Umbrella Organization of German Avifaunists (Dachverband Deutscher Avifaunisten, DDA). Until governments compile or generate data from the well-stratified, consistent sampling of a larger number of taxonomic and trophic levels, the immediate application of Sentinel-1 data will be restricted to existing data, such as the DDA's bird data. For forests, Sentinel-1 data may well be highly suitable for the mapping of environmental gradients at national scales, which in turn can facilitate the stratified random selection of appropriate locations for field-based biodiversity calibration and validation sites, e.g. selected sites from national forest inventories. For generations, biodiversity data have been collected according to a bottom-up approach. However, the tools to complement this information, by analyses conducted on top-down-collected data, are now available. Their use will ensure that a broad spectrum of biodiversity is covered. Our research has shown a way forward in the mapping of structural indicators of biodiversity as determined from space. Yet, the question remains: how well can changes in biodiversity be monitored? Since radar provides multi-temporal measurements needed to detect trends, it has the potential to provide a basis for future research. Furthermore, thresholds for the detection of alterations in habitat conditions that trigger positive and negative biodiversity outcomes, the time delay in extinction after the habitat degradation and synergistic process with other threats such as climate change must still be defined.

Methods

The study was conducted at up to 463 plots in five forest regions distributed from north to south in Germany and representative of forest habitat types in Central Europe (Fig. C8.4.1). The data were compiled from three different projects: Biodiversity Exploratories (Fischer *et al.*, 2010), the BIOKLIM Project (Bässler *et al.*, 2009) and the Steigerwald Project (Doerfler *et al.*, 2017, 2018). Data were collected from 150 experimental plots of the Biodiversity Exploratories study site. These

had been established in three regions: (1) 50 plots in the UNESCO Biosphere Reserve Schorfheide-Chorin, (2) 50 plots in the National Park Hainich and its neighbouring areas and (3) 50 plots in the UNESCO Biosphere Reserve, Schwäbische Alb. From the BIOKLIM Project, conducted in the Bavarian Forest National Park, 244 plots among the 293 sampling plots were selected; the 49 excluded plots were those in which the change in canopy cover between 2007 (year of ALS acquisition) and 2016 (year of radar acquisition) exceeded 20% due to disturbances such as bark beetle infestation and wind-throw (Lehnert *et al.*, 2013). From the Steigerwald Project, located in the Steigerwald forests in Bavaria, 69 plots were included. For the analysis of each functional group, plots for which observations of the corresponding group were available were selected. The number of investigated plots per group was 454 for plants, 298 for bryophytes, 290 for lichens, 362 for phytophagous beetles, 219 for moths, 361 for saproxylic beetles, 458 for fungi, 361 for spiders, 347 for carabids, 334 for necrophagous beetles, 456 for birds and 201 for bats.

The Schorfheide-Chorin region (SCH) is located in the lowlands (80–140 m above sea level, a.s.l) of north-eastern Germany (N 52° 86′–53° 19′; E 13° 63′–14° 00′). It is a glacially formed landscape with many wetlands. The Hainich region (HAI) is located in the hilly areas (330–550 m a.s.l) of central Germany (N 51° 05′–51° 37′; E 10° 21′–10° 53′). The Schwäbische Alb (ALB) region is located in the low mountain areas (740–870 m a.s.l) of south-western Germany (N 48° 36′–48° 50′; E 9° 20′–9° 50′). The three regions of the Biodiversity Exploratories cover different forest management intensities: unmanaged old-growth forests, managed uneven-aged forests and managed age-class forests including natural broad-leaved tree species, mainly European beech *Fagus sylvatica*, and non-natural conifer plantations, *i.e.* Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. The Steigerwald region (STE) is located in a hilly area (400–520 m a.s.l.) in central Germany (N 49° 80′–49° 94′; E 10° 45′–10° 62′) with a large gradient of broadleaf forest use intensity. It is dominated by *F. sylvatica.* The Bavarian Forest National Park region (BAY) is located in a mountainous area (710–1530 m a.s.l.) (N 48° 91′–49° 20′; E 13° 19′–13° 45′). The dominant tree species are *P. abies* and *F. sylvatica.* Half of the area, at the time of data sampling, was dominated by common production forests, while the other half was covered by strictly protected area with intensive natural disturbances or old-growth stands. Thus, the 463 plots included a long gradient of forest management intensity on the stand scale ranging from unmanaged old-growth forests to intensively managed forests.

Radar data

C-band synthetic aperture radar (C-SAR) data acquired by the Sentinel-1 mission throughout Germany, including in our sampling areas, were used in this study. The C-SAR data were acquired in the interferometric wide mode in two polarisations, VV (vertically transmitted, vertically received radar pulse) and VH (vertically transmitted, horizontally received radar pulse), during both ascending and descending orbits. The ground-range-detected high-resolution product (GRDH), with a pixel spacing of 10 m, was downloaded from the ESA Scientific Hub. The Sentinel Application Platforms (SNAP) Sentinel-1 Toolbox software (http://step.esa.int) was used in the further processing of the GRDH product to generate γ^0, defined as the backscatter coefficient normalised by the cosine of the incidence angle. Processing followed the typical pre-processing steps, involving precise orbit determination, removal of thermal and border noise, radiometric

calibration to β^0, defined as the radar brightness coefficient, and radiometric terrain flattening to γ^0 based on the digital elevation model (DEM) of the Shuttle Radar Topography Mission (SRTM v.4.1), with 1-arc-second resolution. Lastly, a range-Doppler terrain correction was performed, generating γ^0 with a 10 × 10 m pixel spacing also based on the SRTM DEM (see the Chapter 8.4 for further details and the batch processing graph at https://github.com/So-YeonBae/Sentinel1-Biodiversity and Supplementary Software).

Multiple pixel-wise summary statistics were then calculated over these pre-processed conditions (Table C8.4.1). The limitation of the short wavelength of Sentinel-1 was overcome by the application of multi-temporal approaches. First, the median values of VV and VH backscatter in a year, during summer and during winter were determined since backscatter varies with the seasonal changes in canopy structure. The difference between the median winter and summer values was then computed to detect the seasonal difference in backscatter. The difference and the ratio between the yearly median values of VV and VH were computed as well, since they are related to the seasonal canopy development cycle (Frison *et al.*, 2018). The mean and standard deviation were extracted to characterise the spatial heterogeneity, within a 9 × 9 pixel neighbourhood. Further textural variables were then derived by means of the grey-level co-occurrence matrix (GLCM), which specifically considers the spatial arrangement of different neighbourhood pixels (Haralick *et al.*, 1973). In a GLCM analysis, the contrast group measures the contrast between adjacent pixels, and the orderliness group the orderliness of the neighbourhood pixel values. Both the dissimilarity index in the contrast group and the entropy index in the orderliness group were calculated using window sizes of 9 × 9 pixels (Hall-Beyer, 2017). All metrics-calculations were performed in R, version 3.4.0 (R Core Team, 2018), using the package *glcm* (Zvoleff, 2016) with a common discretisation of 32 grey levels (see Note in Chapter C8.4 for details and R script at https://github.com/So-YeonBae/Sentinel1-Biodiversity).

ALS data

ALS data were acquired during leaf-on periods between 2007 and 2018, depending on the region (see Table C8.4.2). The same pre-processing and metrics-calculation methods were applied over the ALS datasets of all five forest regions. *LAStools* (http://lastools.org) was used in pre-processing, coordinate transformation, outlier filtering, the classification of the returns into ground and non-ground and the normalisation of the height of the vegetation returns to the height above ground level.

Based on the normalised height, metrics characterising the three-dimensional forest structure were calculated (Table C8.4.3). The mean and maximum height of the vegetation returns were determined as information on forest maturity, and the standard deviation and coefficient of variation to characterise the vertical variability of the vegetation distribution. Canopy cover as well as the average and variability of the vegetation height are among the most significant predictors of animal species diversity (Davies & Asner, 2014). To characterise the development of canopy sub-layers, the penetration ratios were calculated by dividing the number of returns blocked (or captured) by each sub-layer by the number of returns that reached the layer. Penetration ratios were calculated for three sub-layers: canopy (above 5 m), understory (2–5 m) and regeneration layers (below 2 m). Foliage height diversity was then derived using the Shannon entropy index and the penetration ratios of the three sub-layers. The canopy cover was

also determined based on the penetration ratio of the canopy and the understorey layer (above 2 m).

Spatial heterogeneity composed of forest gaps were considered by calculating the square-root-transformed total edge length of gap and gap area. Both were determined based on a gap mask raster obtained by mapping pixels with a penetration ratio of the canopy-understory layer <20% and aggregating neighbouring gap pixels into gap features. Gap features smaller than 50 m^2 or narrower than a perimeter-area-ratio <1.5 were excluded. Lastly, a canopy surface height model (CHM) with a spatial resolution of 1 m was developed according to Khosravipour et al. (2014) and using the *lid*R package (Roussel, 2018). Based on the CHM, the ratio of the canopy surface area to the flat area and the standard deviation of the CHM were calculated.

Species data sampling

Bats were recorded using ultrasound detectors or bat-call recorders and analysed with the corresponding software to the species level (see Chapter 8.5). Repeated point counts were conducted for bird surveys during the breeding seasons. Arthropods were sampled using pitfall traps, flight interception traps and light traps. Vascular plants, bryophytes, lichens and fungi were recorded in spatial subsets of the 1-ha plots. However, the species sampling methods slightly differed between Biodiversity-Exploratories, the Steigerwald Project and the BioKlim-Project in terms of sampling periods, duration and grain size. Hence, the species data were refined to achieve comparability among projects (Chapter 8.5). We complied with all relevant ethical regulations for animal research. All the records of species, except for arthropods, were conducted by sightings or sound recordings in the field. The methods used in this study to assess arthropod diversity were legally mandated by the field work permits listed in the acknowledgement section and in Table C8.5.

Calculation of biodiversity variables

Among the various aspects of biodiversity, alpha diversity measures the diversity of species within each plot and beta diversity the difference of species composition among these plots. Gamma diversity is a measure of the overall diversity within a region, a product of the alpha diversity for all the plots within a region and the beta diversity among them, thus often called as regional diversity (Whittaker, 1972). At our 1-ha local scale, species richness and phylogenetic diversity, as alpha diversity, and species composition, the base of calculating beta diversity, were investigated. Functional groups were separated based on taxonomy, and the assemblage composition per functional group by NMDS (non-metric multidimensional scaling) was derived using presence-absence data. The goodness of NMDS for 1–5 dimensions was tested based on the stress value using the function *dimcheckMDS* in the R package *goeveg* (Goral &Schellenberg, 2018). The smallest dimension with a stress value <0.2 was chosen, as done in Clarke (1993). The chosen dimensionality was 2 for plants, lichens, moths, carabid beetles and bats and 3 for all others. NMDS was performed using the function *metaMDS* in the R package *vegan* (Oksanen *et al.*, 2019); the Bray-Curtis dissimilarity index and 30 maximum numbers of random starts were used to identify a stable solution.

The number of observed species in each plot was counted and the value log-transformed to calculate species richness. The standardised effect size of the mean phylogenetic distance was determined as phylogenetic diversity which has become influential for an understanding of ecosystem functioning in association with assemblage communities and has

been used as a proxy for functional diversity (Webb *et al.*, 2002; Cadotte, 2015). Accordingly, data on published and newly created phylogenies were merged with our community data using the *ses.mpd* function in *picante* (Kembel *et al.*, 2018)(see Chaper 8.4). The null-model approach was applied to correct for species richness, by comparing the diversity value of the observed assemblage per plot with the values of 999 random artificial assemblages containing the same number of species. The species in the 999 assemblages were randomly selected from within each species pool corresponding to that of our five forest regions.

Canonical correlation analysis

A CCoA was applied to two datasets, the metrics derived from radar and from ALS. The CCoA represents the observations along new canonical axes that maximise the correlation between two datasets (Borcard *et al.*, 2011). It was employed in this study to explore the correlation of the radar metrics with the ALS metrics, as the ecological relevance of the latter with respect to 3-D structure and resident animal species diversity has already been investigated. The function *cancor* in the R package *candisc* (Friendly & Fox, 2016) was used in the analysis and all variables in the analysis were standardised. The F-approximations of Wilks' lambda statistic and its significance, the canonical correlations between axes pairs and the RDA-adjusted R^2 values were checked to determine whether the canonical axes extracted a considerable variation.

Modelling biodiversity variables

Boosted GAMs were applied to all response variables (NMDS axes, log-transformed species richness, and standardised effect size of phylogenetic diversity) with Gaussian error distributions using the function *gamboost* in the package *mboost* (Hothorn et al 2016). Boosted GAMs are suitable for ecological modelling characterised by non-linearity and high collinearity among predictors, which are very common in metrics derived from remote sensing (Hothorn et al., 2011). The predictors chosen in this study had high collinearity; for example, the yearly, summer and winter backscatter of VH showed strong mutual correlations in the radar metrics and the same was determined for the mean and maximum vegetation height in the ALS metrics. Boosted GAMs were chosen because they are suitable for disentangling the effects of variables with collinearity (Hothorn, 2011) and assumed to be non-linear (Bae *et al.*, 2018). The boosted GAMs were implemented with component-wise gradient boosting techniques to optimise parameter estimations and variable selection.

Five-fold cross-validations were performed using the *kfold* function in the R package *dismo* (Hijmans et al 2017); for each one, regions served as the sub-group, achieved by separating the training and test datasets by region and then combining the respective datasets to obtain total training and total test datasets for the five forest regions. To make use of the full range of environmental spaces and species pools covering all the gradients of the five regions, training and test data were extracted from all five regions. For each cross-validation, two models were constructed, one using the radar metrics and the other the ALS metrics. The 40 metrics derived from the radar data and the 13 metrics from the ALS data were used as predictors. Additionally, to account for possible spatial-autocorrelations of plots in the same region and the slightly different sampling years and methods, mixed effects models including the region as a random factor were fitted to determine the comparability with the fixed effects models. However, since the aim of this study was to explore the potential of remote sensing data in predicting biodiversity over a large area including our external validation area, and not to test a

specific ecological hypothesis, we focused on constructing fixed effects models and adjunctively included mixed effects models.

In each model in each cross-validation, to find the appropriate number of boosting iterations (*mstop*) as a hyper-parameterisation, the *mstop* was increased from 10 to 500 and the corresponding cross-validated estimates of the empirical risk were then checked using the function *cvrisk*; 25 bootstraps were applied in the sampling cross-validation using the function *cv*. Each model was constructed from a training dataset and a hyper-parameter of *mstop* using the function *gamboost* and then applied to a test dataset to examine its predictive performance, using the function *prediction*. The coefficient of determination (R^2) between observed values of a test dataset and the predicted values were calculated together with the RMSE. Finally, both the R^2 and the RMSE of the five-fold cross-validations were averaged to compare the performances of the different models. For the mixed effects models, in the calculation of R^2 and RMSE, only the fixed factors were used to predict the response variables, thereby excluding the variance explained by region (a random factor). Previous studies have shown that the R^2 of biodiversity measures increase with sampling size in arthropod samples collected by flight interception and pitfall traps up to a sample size of sufficient individuals (Müller & Brandl, 2009). Chao and Jost (2012) introduced the sample completeness to standardize the comparability of diversity among communities. Therefore, to check the robustness of our results for arthropods against the sampling completeness we re-ran the richness and community composition analyses using a subset of plots with sample coverage more than 90%, 80% and 70%.

As external validations, the first axes of the assemblage composition for birds (n=72) and saproxylic beetles (n=91) outside the five study regions were predicted using radar metrics and fixed effects models, and R^2 and RMSE again calculated. In the last step, the assemblage compositions for birds and saproxylic beetles were mapped based on the first NMDS scores across the Bavarian Forest National Park (Fig. C8.4.20).

Acknowledgments

This project was financed by the Deutsche Forschungsgemeinschaft (DFG), grant no. MU3621/2–1, KR 3292/2-1 and LE3316/2-1. We thank Hermann Hacker for the determination of moths, Markus Blaschke for lichen sampling in the Steigerwald, and Maria-Barbara Winter for bird sampling in Berchtesgaden. We also thank the managers of the three Exploratories, K. Wells, S. Renner, S. Gockel, K. Wiesner, K. Lorenzen, J. Vogt, A. Hemp and M. Gorke, for their work in maintaining the plots and project infrastructure; C. Fischer and S. Pfeiffer for their support through the central office; M. Owonibi and J. Nieschulze for managing the central database and E. Linsenmair, D. Hessenmöller, D. Prati, I. Schöning, F. Buscot, E.-D. Schulze and the late E. Kalko for their roles in setting up the Biodiversity Exploratories project. This work was funded by the DFG Priority Programme 1374 'Infrastructure-Biodiversity-Exploratories'. Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, Brandenburg and Bayern (see Table C8.5 for details of permits)

Chapter 7

Conclusion

In the previous chapters, I tried to shed light on how environmental heterogeneity affects the assembly and diversity of communities and whether these effects are mediated by species traits. Approaching this topic through the lens of somebody who delt with straightforward macroecology before, I hoped to find trait-based explanations for the different responses of species to heterogeneity. At single community level, however, assembly mechanisms remain frustratingly complex.

Chapter II

In chapter II, I examined to which extent body size and colour lightness shape the distribution and abundance of two moth families along elevation. The occurrence and abundance of noctuid moth communities interacted with body size and colour lightness, leading to larger and darker noctuid moth assemblages at high elevations. In contrast, the occurrence and abundance of geometrid moths was driven by habitat availability, not by their traits. These interdependencies to habitat availability could have even led to assemblages of geometrid moths becoming lighter coloured along elevation, which contrasts the results of macroecological studies using explicitly this moth family as a study organism (Heidrich *et al.*, 2018; Xing *et al.*, 2018). It can be concluded that the relative importance of abiotic filters (elevation) and biotic filters (habitat availability) differ between both families. Potential reasons for the different weighing of both processes are potentially grounded in the flight-capacities of the species. Geometrid moths are have low flying capabilities in comparison to noctuid moths (Casey & Joos, 1983) and are thus more dependent on habitat availability. Taken together, one and the same functional trait can have quite different effects on community assembly even between closely related taxonomic groups.

Chapter III

Chapter two outlined the effect of traits on the assembly processes on two levels, on an inter-regional level and on an intra-regional level. In the former, environmental filtering via forest heterogeneity had on average higher independent effects than dispersal filtering within the region and among regions, suggesting that environmental filtering via forest heterogeneity determines species turnover even at country-wide extents. However, the relative importance of the latter increased with decreasing dispersal ability of the species group. These results extent the observation of geographic separation in less dispersive groups in, e.g. (Ferrier *et al.*, 1999 and Steinitz *et al.*, 2006) over a wide array of different taxonomical groups. In both analyses the unique effects of the predictor sets and the total explained variance were low, potential due to the high number of explanatory variables in the analyses. In the intra-regional study, variations in herb or tree species composition had a stronger influence on the turnover of species than forest physiognomy. However, the relative importance of plant species composition versus forest physiognomy was shaped by species trophic position and body size, as it is to be expected for groups which move within the whole 3D-space of a forest (Davies & Asner, 2014). Both results underlined that the relative importance of single mechanisms structuring community composition between and withing different regions are altered by the species groups functional traits.

Chapter IV

While changes in community composition along plant composition and heterogeneity in vertical structures were clearly altered by trophic position, the response of species richness to heterogeneity was less predictable. The single facets of heterogeneity affected diverse species groups. However, species

groups which were thought to be clearly associated with one facet or the other, due to the facet being connected the species groups resource, did not always respond to heterogeneity therein. These results suggest, that any a priori selection of facets of heterogeneity might overlook important responses. Likewise, species groups which show no clear association with a certain facet of heterogeneity were nevertheless affected by heterogeneity therein. These results suggest that the spatial scale at which heterogeneity is perceived is highly variable.

In contrast to beta diversity (Chapter III), more species groups responded to heterogeneity in forest structures than in plant composition. However, this responsiveness seemed not to be associated with trophic position or body size, given that birds did respond heterogeneity in forest structures while bats did not. Also, small-bodied groups of low trophic position responded strongly to heterogeneity in structures. Moreover, the shape of the response could neither be predicted by dispersal ability nor by the niche breadth of the species groups studied. While we could not identify any generalizable mechanism, which determines under which condition species richness shows positive, unimodal, or negative relationships with heterogeneity, some important conclusions emerged. First, heterogeneity in one facet or the other affected all species groups except carabid beetles. Second, area – heterogeneity trade-offs as described in Allouche et al. (Allouche *et al.*, 2012) are quite rare in temperate forest stands as we only found few occasions in which a hump-shaped or negative response in species richness towards heterogeneity was associated with a decrease in mean abundance. Third, vertical and horizontal heterogeneity are the major facets of heterogeneity in forests and affect species groups from all guilds. Although both increased species richness of the majority of groups, some responded negatively, which cautions against a wide-ranging establishment of fine-scaled heterogeneity in forest structures as already noted in Schall et al. (2018).

Chapter V

The more detailed evaluation of assembly mechanisms in Chapter V revealed that positive effects of heterogeneity are not necessarily based on increasing the niche space, but often either spatially partition it or increase its effective area. Further increases in ecological distinctiveness highlight the positive effects of heterogeneity on diversity in forests. However, as shown in the response of diversity in plants towards horizontal heterogeneity, there are also filtering effects which should be accounted for in management in forests.

Chapter VI

The last chapter explored the potential of a newly launched satellite-borne radar system in depicting structure and heterogeneity in comparison to the current, yet expensive, gold-standard in measuring larger areas of forests. Although it is not able to depict structural changes in the same resolution as LiDar, the main axes of forest structure were good enough represented to model the diversity of the forests. It was slightly worse in modelling alpha and phylogenetic diversity but was better in modelling species turnover. The successful validation with external data further underlines its great potential of radar as a tool in predicting biodiversity across space and time.

Summary and outlook

Taken together, this thesis leads to two statements. First, I found more support against than for general assembly rules. Although the results of Chapter III outline some general effects of dispersal activity, trophic position, and body size on the relative importance if

the three filter processes driving beta-diversity, the overall explained variance was low. Moreover, the traits were assigned group-wise. As outlined in Chapter II, the relative effect of environmental filters on even well-known functional traits varies even within closely related groups. This underlines that trait-based tests of assembly mechanisms often fail to differentiate the filter processes, as the mechanistic links between functional traits, the environment, the heterogeneity therein and biotic interactions are often poorly understood (Adler *et al.*, 2013). The applicability of functional traits in disentangling assembly processes is further hindered by the lack of big trait databases, which are only available for a handful of species groups. Though the underlying assembly mechanisms could not be disentangled, it does not change the fact that heterogeneity in environmental conditions is an important driver of beta-diversity, species richness, and ecological diversity. If we focus on heterogeneity in forest structures, we find mostly positive effects on the latter. Yet, before urging stakeholders to universally apply management strategies aimed at promoting structural heterogeneity within single forest stands, one should keep in mind, that these positive effects were observed at the level of alpha diversity. As outlined in Schall et al. (2018), increasing small-scale heterogeneity over broader spatial scales leads to an overall homogenization of structures and ultimately reduce beta – and gamma diversity within a regaion. Given, that environmental filtering via forest heterogeneity has higher independent effects on beta diversity than dispersal filtering not only within the region but also among regions (Chapter III), forest management must thus coordinate across large areas. Unfortunately, it was beyond the scope of Chapter V to assess the effect of heterogeneity in ecological diversity between sites. Here, it would be interesting to know whether heterogeneity has similar effects to the ones described in Schall et al (2018). Altogether, I could not identify any generality in community responses to heterogeneity. Though standardized monitoring of species and measurements of their traits are urgently needed for a wide range of species groups, at least the environmental basis to conduct further studies on heterogeneity across space and time is covered by the newly launched Sentinel-1 system.

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Chapter 8.1

Appendix chapter 2

Noctuid and geometrid moth assemblages show contrasting elevational gradients in body size and color lightness

with
Stefan Pinkert | Roland Brandl | Claus Bässler | Hermann Hacker | Nicolas Roth | Jörg Müller | Nicolas Frieß |

under review in Ecography (10.11.2020)

Year-wise analysis

In the main analysis, we wanted to test whether patterns are repeated over time and included year as an interaction term. To have balanced data, we had to exclude plots which were only sampled in 2016. Here, we performed the analyses separately for each year to include the full available elevational gradient sampled in 2016. Like in the main analyses, Family was included kept as an interaction term for the assemblage-level model and the species-level model. Inclusion of the lower plots changed the signs in the relationship between community weighted means of both traits and elevation in Geometrid moth. For noctuid moth, signs did not change but the effect of elevation on average color lightness became non-significant (Table C8.1.1, Figure C8.1.1). These trends were also apparent in the fourth-corner analysis. Again, signs of the relationships between traits and elevation changed in geometrid moths, though the effect was not significant, whereas in noctuid moths trends became non-significant (Table C8.1.2). Still, small and light colored noctuid moth species were less likely to occur at high elevations (Table C8.1.3). The sudden insignificance of the assemblage-based analyses and the fourth-corner analysis might be a result of the increased strength in the relationship between abundance and habitat-avaiability, which might occur if the inclusion of new plots now adds either new species with a stronger host-plant-association, or plots which had stronger correlations between host plants and abundances to the equation.

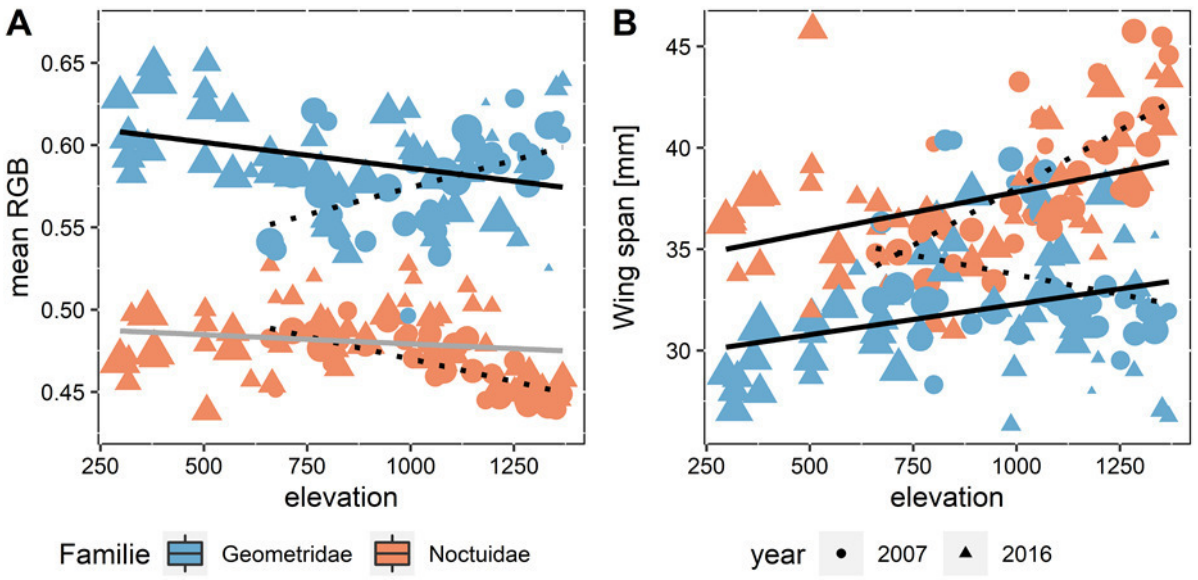

FIGURE C8.1.1: Scatterplots of the relationships of abundance weighted community trait means of (A) the color lightness and (B) the body size of assemblages of geometrid (blue) and noctuid (orange) species with elevation above sea level, including the full gradient sampled in 2016. Dotted regression lines and circles indicate results for the year 2007 and solid regression lines and triangle the results for the year 2016. Species' trait values in the assemblage were weighted according to species' abundances. Lines refer to raw data, not the predicted values from the models.

TABLE C8.1.1: Results of linear regression. Modelling community weighted means of body size and color lightness against elevation for both moth families, separately for each year. In the linear regression, family was included as a fixed factor to account for family-based differences in body size and color lightness. Interaction terms of elevation with family (Geo = Geometridae; Noc= Noctuidae) are used to calculate and compare the slopes of the relationship between the traits and elevation per family. Estimates (EST) and the corresponding standard errors (SE) shown here respond to changes per 100m. Significant effects are printed bold.

		Body size				Color lightness			
	Variable	Est	±	SE	t-value	Est	±	SE	t-value
2007	Noctuidae	**-10.**	**±**	**3.61**	**-3.03 *****	0.017	±	0.027	0.63
	Geo:elevation	-0.39	±	0.24	-1.61 .	**0.007**	**±**	**0.002**	**3.74 *****
	Noc: elevation	**1.1**	**±**	**0.24**	**4.71 *****	**-0.005**	**±**	**0.002**	**-3.09 ****
	R^2			0.54				0.88	
2016	Noctuidae	**4.53**		**1.72**	**2.63 ****	**-0.127**		**0.015**	**-8.59*****
	Geo:elevation	**0.30**		**0.13**	**2.27 ***	**-0.003**		**0.001**	**-2.75****
	Noc: elevation	**0.40**		**0.13**	**3.02 ****	-0.001		0.001	-0.99
	R^2			0.49				0.83	

TABLE: C8.1.2 Results from the fourth corner analysis for Geometridae and Noctuidae of all plots sampled in 2016. Columns "R" are referring to the observed Pearson value between the single traits and the elevation. Significance of the fourth corner statistic determined via permutation of site and species values based on 9999 permutations.

	Geometridae		Noctuidae	
	R	p-value	R	p-value
Elevation * color lightness	0.02	0.701	–0.28	0.06
Elevation * body size	–0.02	0.821	0.32	0.03

TABLE C8.1.3: T-and z-values of species-level analysis separately for each year. The model had a has a truncated negative-binomial error distribution. The conditional part represents the effect on abundance, the zero-inflated part the probability of the absence of a species. Family (Geo= Geometridae, Noc = Noctuidae) was included in form of an interaction to see whether trends are consistent across taxonomic groups and repeatable between two sampling events. Significant effects are printed in bold.

		Geometridae		Noctuidae	
	Variable	2007	2016	2007	2016
conditional	Habitat availability	**3.95*** **	**2.68** **	1.95	−1.32
	Elevation	0.42	1.01	−1.83	−0.84
	Elevation:wingspan	0.19	**2.21***	**2.40** *	−0.30
	Elevation:meanRGB	0.13	0.95	**−3.64*** **	−1.53
Zero-inflated	Habitat availability	**−3.26*** **	**−8.53*** **	−1.84	**−3.22** **
	Elevation	1.93	**6.08*** **	0.76	**3.35** **
	Elevation:wingspan	−1.34	−1.78	−1.76	**−4.57** *
	Elevation:meanRGB	0.14	−0.88	**2.09** *	0.36

Year-wise differences in slopes of the assemblage-level model

To analyse whether the slopes of the assemblage level model differed between both years, we repeated the linear model with family and year as interaction term, but also included year as a fixed factor.

TABLE C8.1.4: Assemblage-level-Model with year as fixed factor.

	Body size				Color lightness			
Variable	Est	±	SE	t-value	Est	±	SE	t-value
Noctuidae	-8.94	±	2.61	-3.43 ***	-0.006	±	0.020	-0.27 ***
2016	-1.54	±	2.61	-0.59	0.049	±	0.020	2.41 *
Geo:elevation	-0.29	±	0.21	-1.38	0.006	±	0.002	3.64 ***
Noc:elevation	1.04	±	0.21	4.89 ***	-0.005	±	0.002	-2.95 **
Geo:2016:elevation	0.07	±	0.25	0.26	-0.004	±	0.002	-2.21 *
Noc:2016:elevation	0.05	±	0.25	0.20	-0.003	±	0.002	-1.60
R^2			0.52				0.85	

Abundance along elevation

We modelled the independent effect of elevation on species abundance while accounting for habitat availability using a general additive model implemented in the *mgcv*-package vers 1.8 (Wood, 2018) to visually check for non-linear patterns. Species was included as random factor. Shown are the predicted values against elevation in 100 m steps.

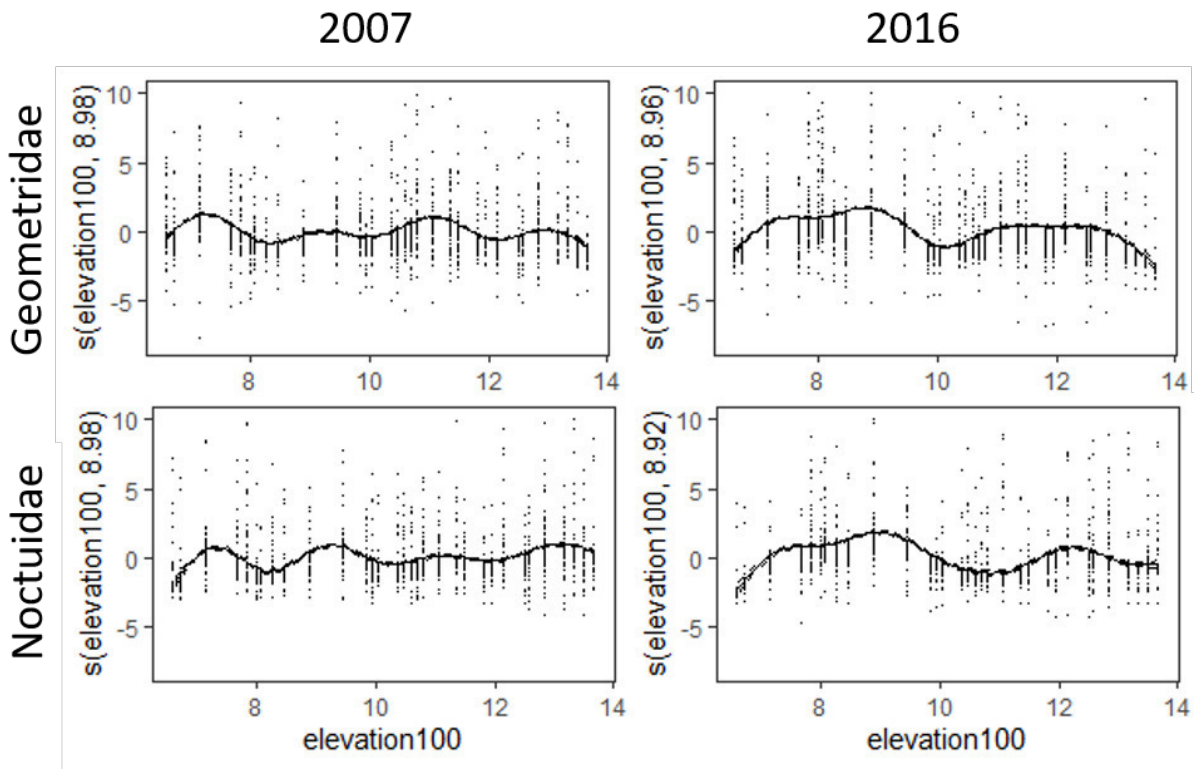

FIGURE C8.1.2: Abundance along elevation, modelled by GAMs

Differences between families

Information about life-history was taken from Potocky (2018). Noctuid moths had a higher proportion of univoltine species (69%) than Geometrid moths (51 %) (Kruskal-Wallis rank sum test, $Chi^2 = 6.99$, p-value=0.008). They also had a higher proportion of species overwintering as larvae than Geometrid moths (62% vs 30%), whose majority (56%) overwinters as pupae (Kruskal-Wallis rank sum test, $Chi^2 = 11.60$, p-value < 0.001).

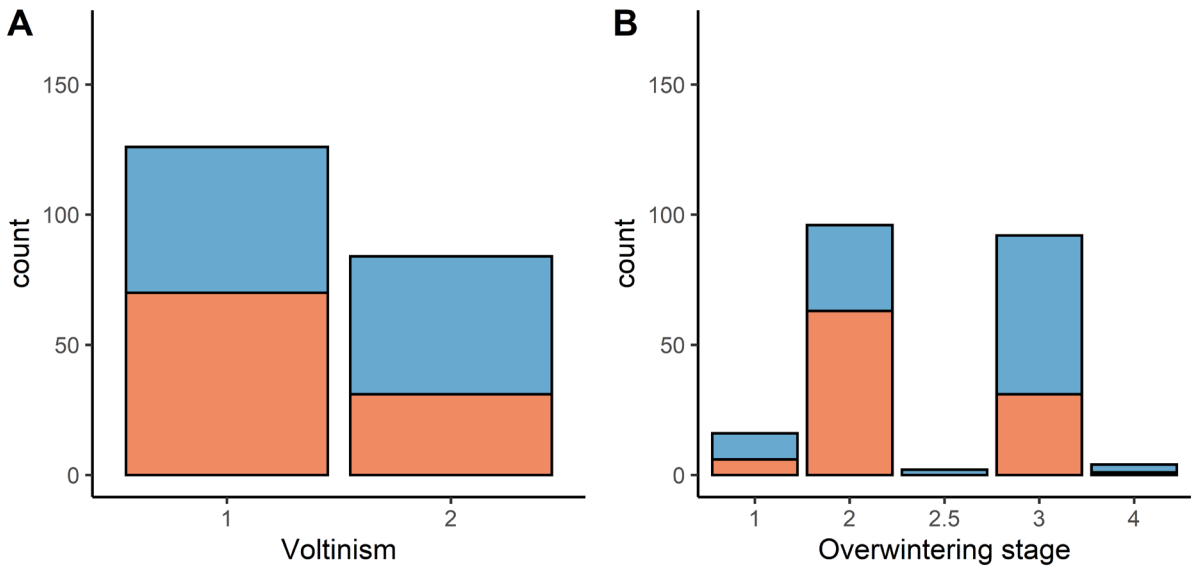

FIGURE C8.1.3: Comparison of A) numbers of species being uni- (1) or bi-voltine (2) and B) numbers of species overwintering as egg (1), larvae (2), larvae or pupae (2.5), pupae (3) or adult (4) between geometrid moths (blue) and noctuid moths (red).

Chapter 8.2

Appendix chapter 3

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

with

Soyeon Bae | Shaun R, Levick | Martin M. Gossner | Sebastain Seibold | Wolfgang W. Weisser | Paul Magdon | Alla Serebryanyk | Claus Bässler | Deborah Schäfer | Ernst-Detlef Schulze| Inken Doerfler | Jörg Müller | Kirsten Jung |Marco Heurich | Markus Fischer| Nicolas Roth | Peter Schall | Steffen Boch | Stephan Wöllauer | Swen C. Renner | Jörg Müller |

accepted for publication in *Diversity and Distributions* (05.11.2020)

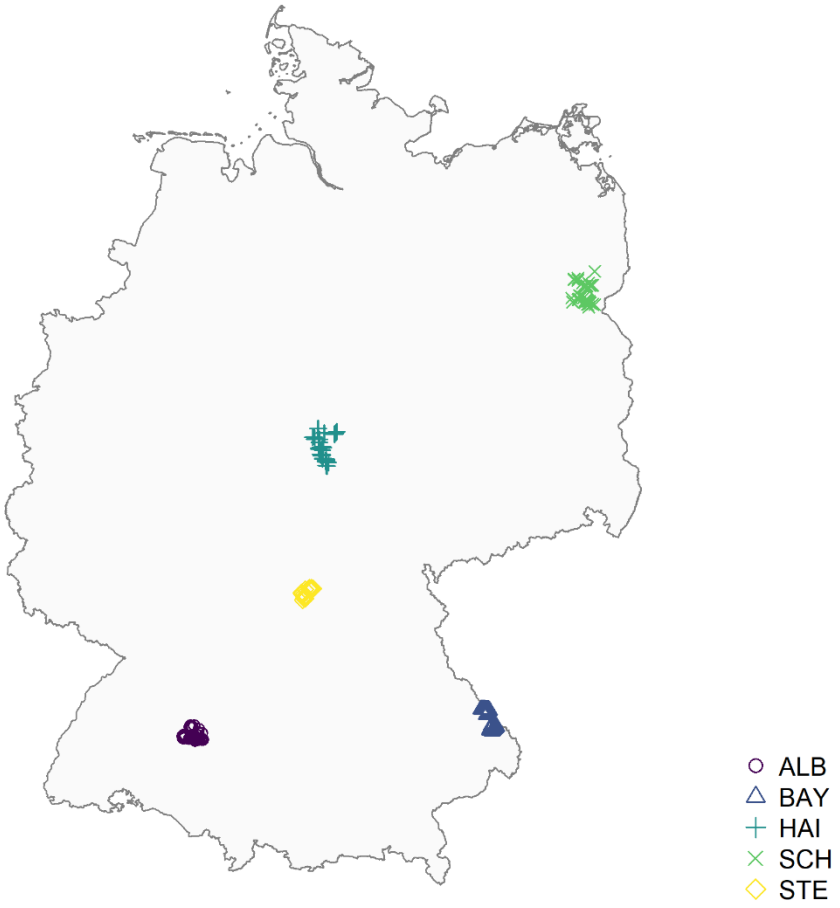

FIGURE C8.2.1 Distribution map of the plots. The study was conducted in five forest regions in Germany: the UNESCO Biosphere Reserve, Schwäbische Alb (N 48° 36′–48° 50′; E 9° 20′–9° 50′; 740–870 m a.s.l; ALB), the Bavarian Forest National Park (N 48° 91′–49° 20′; E 13° 19′–13° 45′; 710–1530 m a.s.l.; BAY), the National Park Hainich and the surrounding Hainich-Dün region (N 51° 05′–51° 37′; E 10° 21′–10° 53′; 330–550 m a.s.l; HAI), the UNESCO Biosphere Reserve Schorfheide-Chorin (N 52° 86′–53° 19′; E 13° 63′–14° 00′; 80–140 m above sea level (a.s.l); SCH) and the Steigerwald (N 49° 80′–49° 94′; E 10° 45′–10° 62′; 400–520 m a.s.l.; STE).

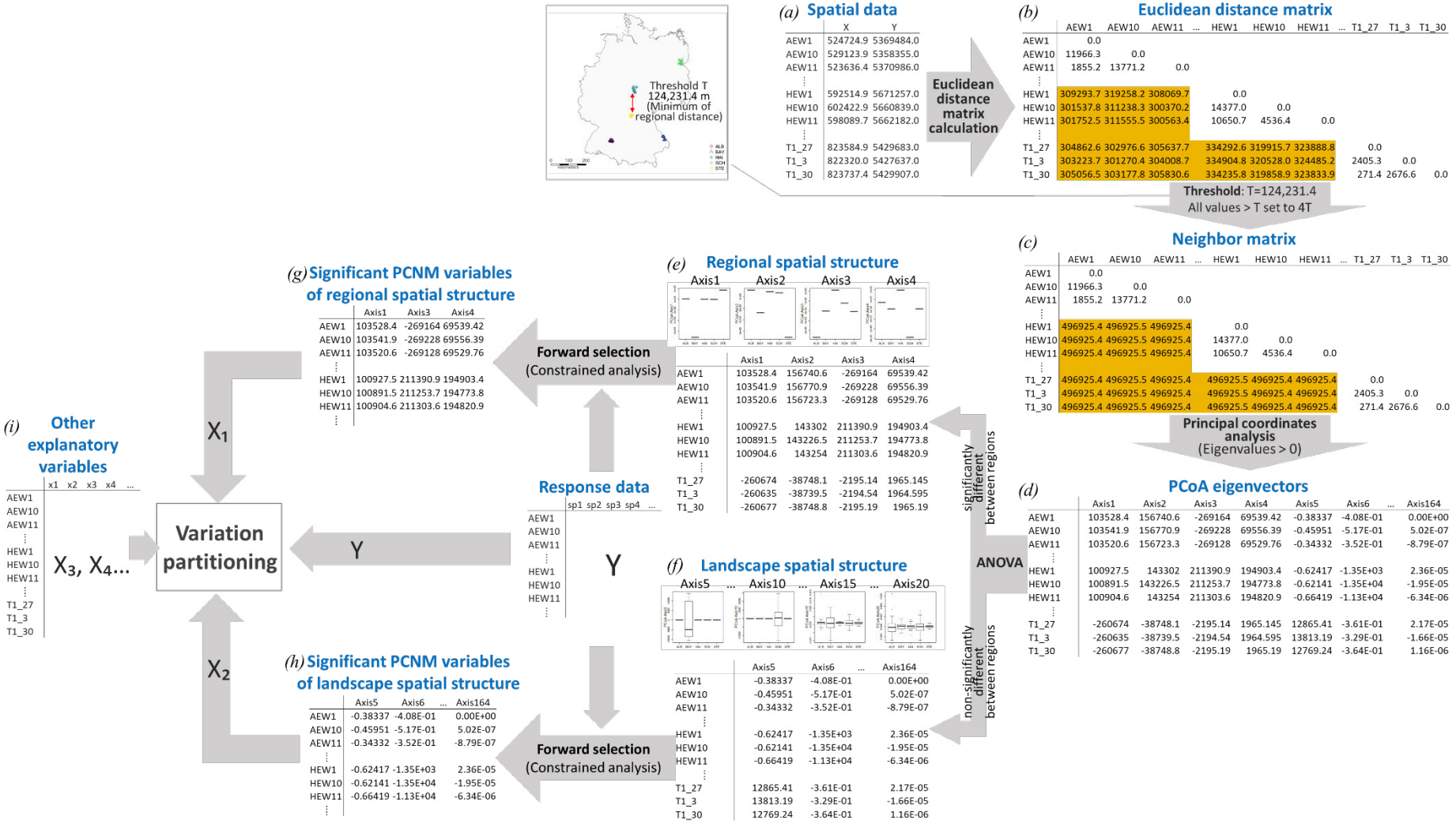

FIGURE C8.2.2 Principal coordinates of neighbor matrices (PCNM) used for making the predictor sets of regional species pool and dispersal limitations for the inter-region analysis.

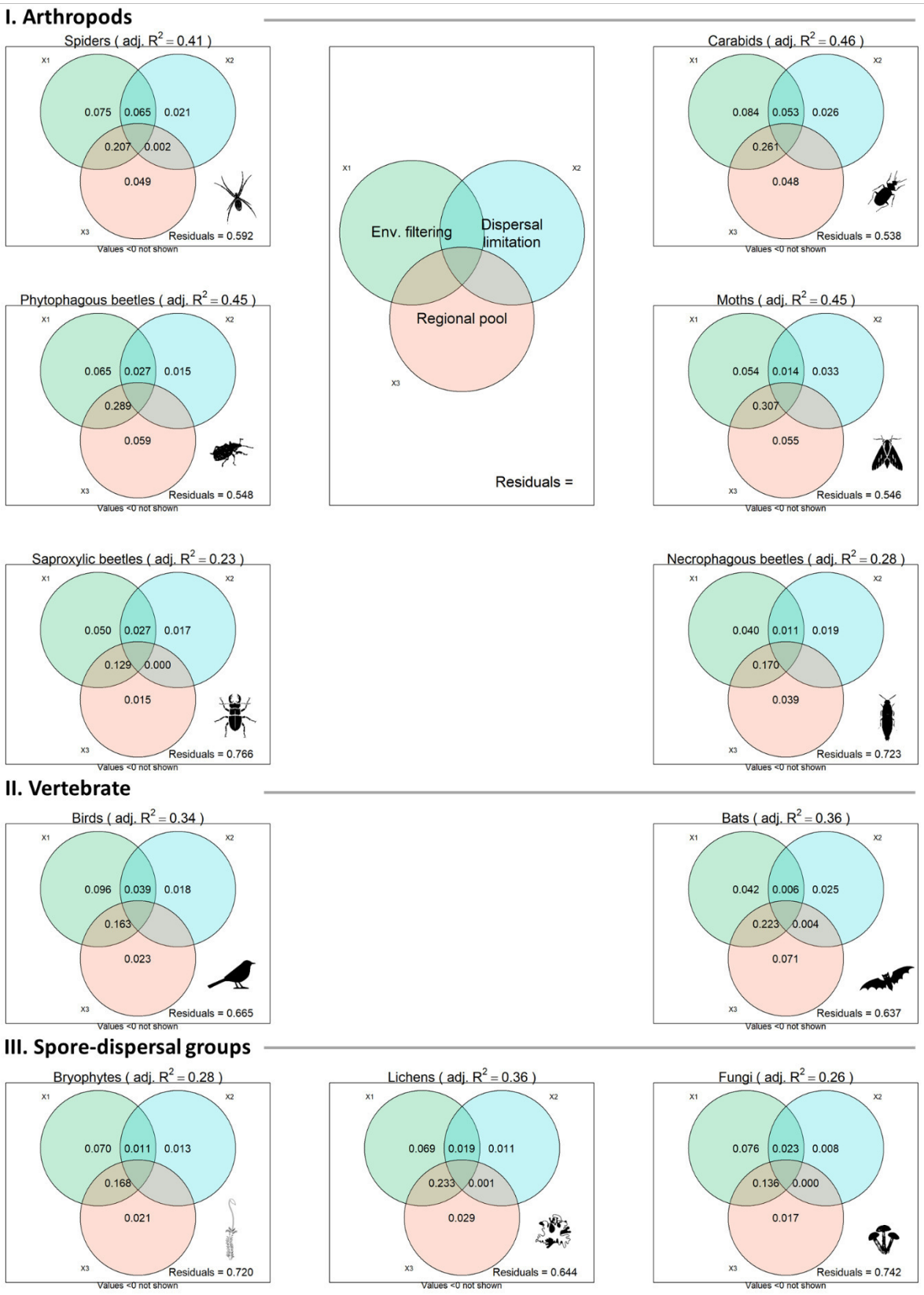

FIGURE C8.2.3 Venn diagrams of the effects of regional spatial structure (proxy of regional species pool), landscape spatial structure (proxy of dispersal limitations) and environmental factors (proxy of environmental filtering) on the species turnover within 11 functional groups. The independent effects of regional spatial structure, landscape spatial structure and environmental factors are shown in orange, sky blue and green, respectively.

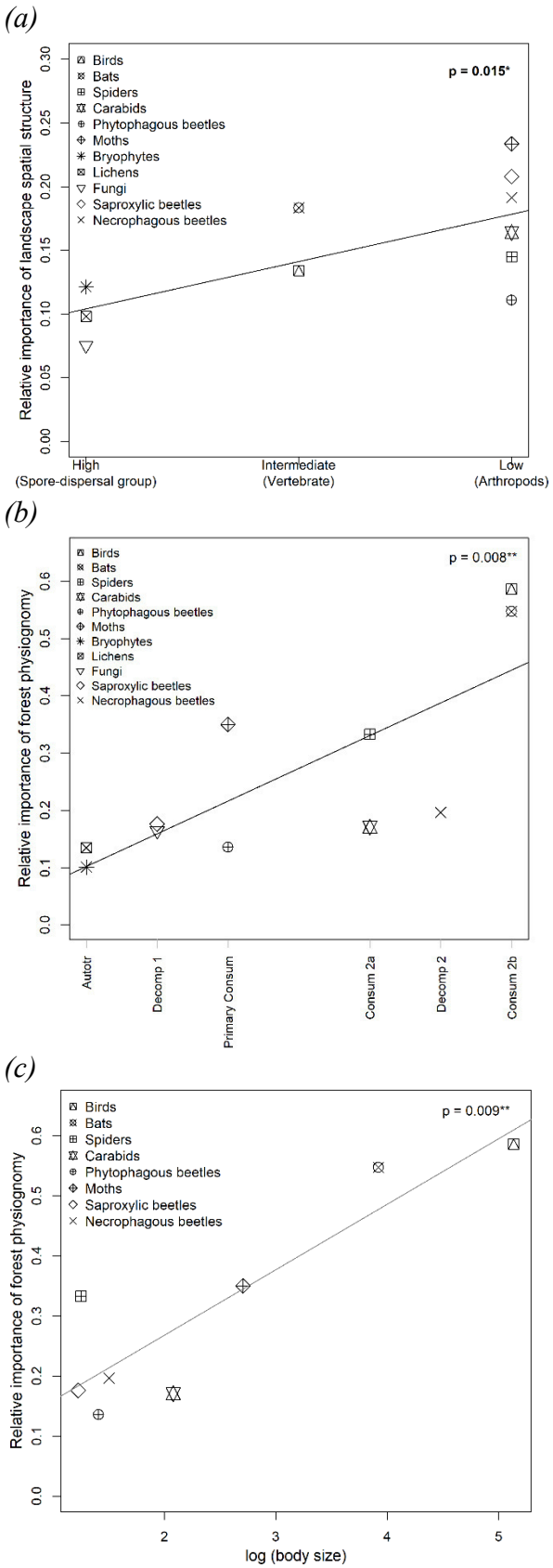

FIGURE C8.2.4 The original figures of (a) Figure C3.2b, (b) Figure C3.3c and (c) Figure C3.3d.

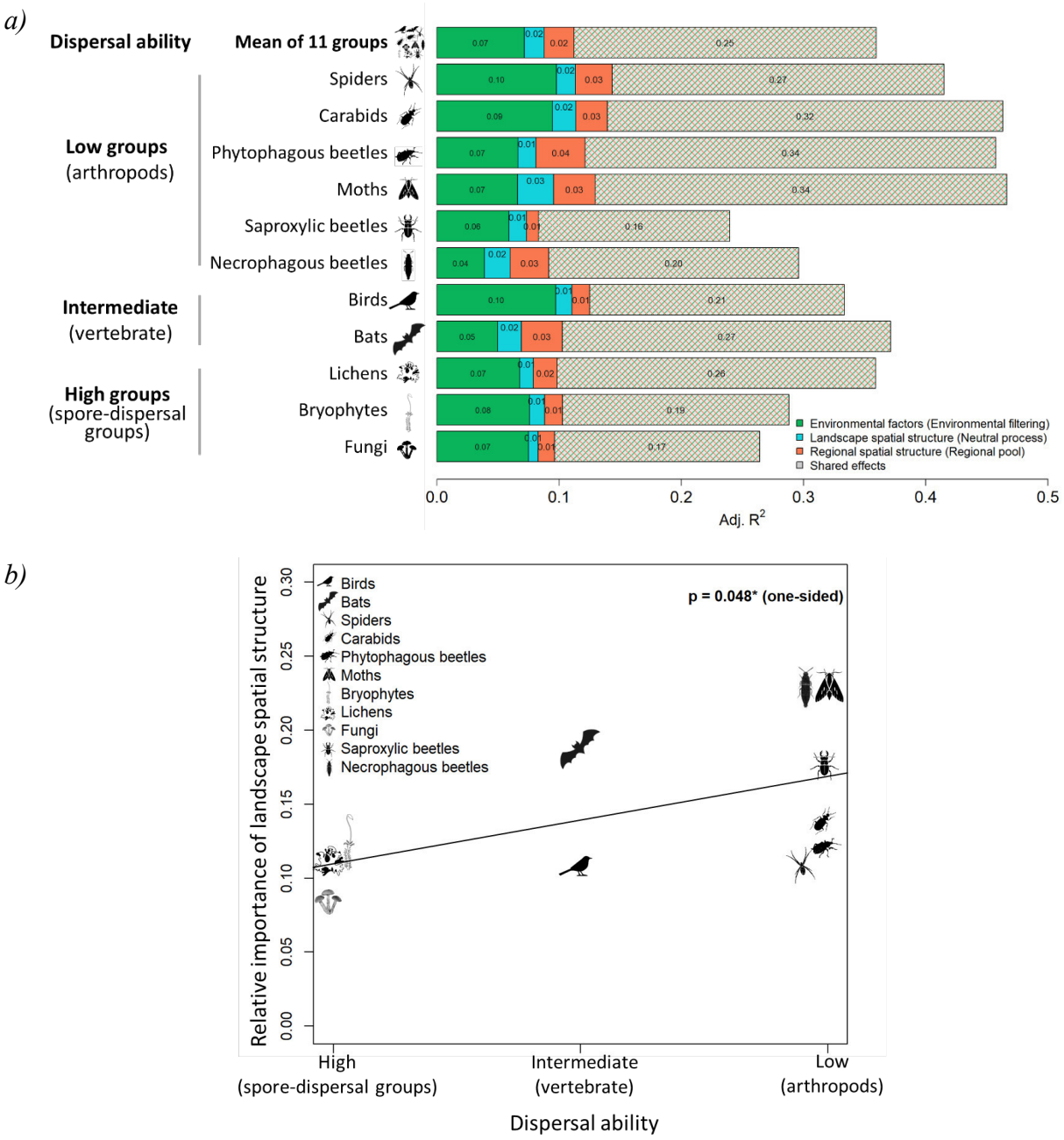

FIGURE C8.2.5 The relative importance of regional spatial structure (regional species pool), landscape spatial structure (dispersal limitations) and environmental factors (environmental filtering) when climate and topography predictor sets are added (see Table S10 for the climate and topography predictor sets). (a) The variation (adjusted R2) in the assemblage composition of the 11 functional groups explained by the three predictor sets. Environmental factors (green bar) include the effects of herb composition, tree composition, forest physiognomy, climate and topography. The regional spatial structure (orange bars) is represented by the principal coordinates of neighbor matrices (PCNM) variables that differed significantly among regions. The landscape spatial structure (sky blue bars) describes the effects of dispersal filters within regions by finer PCNM variables. Bars with shading lines represent the shared effects of at least two predictor sets. (b) The relative importance of landscape spatial structure increases significantly along groups with decreasing dispersal ability: spore-dispersal groups, vertebrate and arthropods.

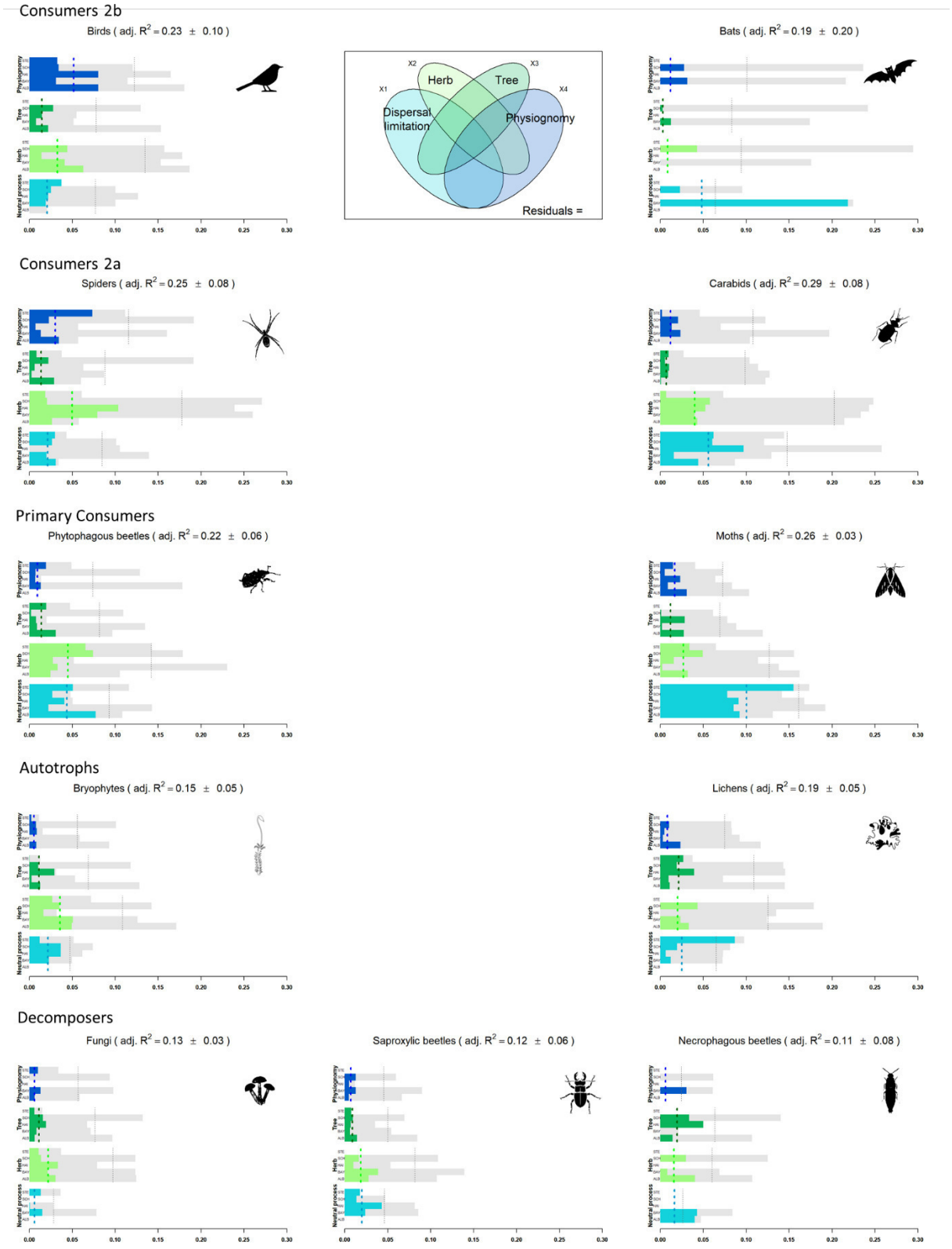

FIGURE C8.2.6 Independent and comprehensive effects of spatial structure (proxy of dispersal limitations), herb composition, tree composition and forest physiognomy on species turnover. Independent effects of spatial structure, herb composition, tree composition and forest physiognomy are shown in sky blue, yellow green, green and blue, respectively. Comprehensive effects are shown in gray. Non-significant effects are not shown. The mean of each of the four independent effects in the five regions is indicated by a dashed line with the corresponding color.

TABLE C8.2.1: Summary of the observed species comprising 11 functional groups over all plots and per plot.

Functional group	No. of plots	Total number of species across all plots	Mean number of species per plot	Standard deviation of number of species per plot
Bryophytes	321	197	11.69	6.88
Lichens	307	196	9.44	7.11
Phytophagous beetles	386	293	9.90	4.15
Moths	226	468	65.50	22.07
Saproxylic beetles	385	517	19.39	10.04
Fungi	495	210	13.43	4.98
Spiders	383	267	14.86	7.47
Carabids	383	105	9.72	5.38
Necrophagous beetles	386	40	5.76	3.01
Birds	494	81	11.84	3.57
Bats	247	15	4.02	2.49

TABLE C8.2.2: Airborne laser scanning (ALS) data sources

Region	Sensor	Year	Month	Flight height (m, agl)	Pulse density* (pls/m²)	Data provider
HAI	Riegl Q560	2008	August	400–600	8.2	Max-Planck-Institute for Biogeochemistry, Jena
ALB	Riegl Q560	2010	July	400–600	21.09	
SCH	Riegl Q560	2009	September	400–600	27.03	
STE	Riegl Q560/ VQ780i	2015 / 2018	September /May	650–700	40.07	Munich University of Applied Sciences
BAY	Riegl Q560	2007	May	350	33.25	Bavarian Forest National Park

* The pulse density was derived from the clipped point cloud per plot and aggregated as a median value for each region.

TABLE C8.2.3 Median body sizes, their natural logarithm transformation and their source of eight animal groups.

Functional group	Measurement	Body size (mm)	Log (body size)	Source
Saproxylic beetles	Body length	3.415	1.228	Seibold et al. (2015)
Phytophagous beetles	Body length	4.100	1.411	Gossner et al. (2013)
Necrophagous beetles	Body length	4.500	1.504	further information based on Freude, Harde, and Lohse (1964-83)
Carabids	Body length	8.000	2.079	
Spiders	Length of prosoma and opisthosoma	3.500	1.253	Nentwig et al. (2020)
Moths	Length from the thorax to the abdomen	15.000	2.708	Measured from specimens depicted in Segerer, Hausmann, Behounek, Speidel, and Witt (2011)
Bats	Head-body length	50.500	3.922	Richarz (2012)
Birds	Length from the tip of beak to end of tail feathers	170.000	5.136	Svensson, Mullarney, and Zetterström (2011)

TABLE C8.2.4: Topography and climate predictor sets used in the supplementary analysis. Principal components analysis (PCA) was applied to both predictor sets. The first ordination axes that together explained > 75% of the variance of the data were selected for the final predictor sets.

Variable	Description
Topography	
$Elevation_{\text{mean}}$	Mean of ground a.s.l. (based on DTM raster pixels)
$Elevation_{SD}$	Standard deviation of ground a.s.l.
DTM_{ratio}	Ratio between the values of the ground surface and flat areas
TIS	Total potential incoming solar radiation (TIS) over May–August (kwh)
TWI	Topographic wetness index (TWI)
Climate	
bio01	Annual mean temperature
bio02	Mean diurnal range
bio03	Isothermality
bio04	Temperature seasonality
bio05	Max temperature of warmest month
bio06	Min temperature of coldest month
bio07	Temperature annual range
bio08	Mean temperature of wettest quarter
bio09	Mean temperature of driest quarter
bio10	Mean temperature of warmest quarter
bio11	Mean temperature of coldest quarter

bio12	Annual precipitation
bio13	Precipitation of wettest period
bio14	Precipitation of driest period
bio15	Precipitation seasonality
bio16	Precipitation of wettest quarter
bio17	Precipitation of driest quarter
bio18	Precipitation of warmest quarter
bio19	Precipitation of coldest quarter

TABLE C8.2.4 Total beta diversity and its two components, species turnover and nestedness, of 11 functional groups.

Functional group	Turnover	Nestedness	Total	Ratio of turnover in total beta diversity
Birds	0.985	0.005	0.990	0.995
Bats	0.899	0.089	0.988	0.910
Spiders	0.982	0.010	0.991	0.990
Carabids	0.969	0.022	0.991	0.978
Phytophagous beetles	0.983	0.009	0.992	0.991
Moths	0.974	0.011	0.985	0.988
Bryophytes	0.979	0.009	0.988	0.991
Lichens	0.977	0.011	0.988	0.989
Fungi	0.990	0.003	0.992	0.997
Saproxylic beetles	0.987	0.006	0.993	0.994
Necrophagous beetles	0.966	0.026	0.992	0.974
Mean of 11 functional groups	0.972	0.018	0.990	0.981

TABLE C8.2.6: Adjusted R^2 values of the inter-region and intra-region analyses covering 11 functional groups

Functional group	Adjusted R^2 in the inter-region analysis	Mean adjusted R^2 over 5 forest regions in the intra-region analysis
Birds	0.3354	0.2260
Bats	0.3634	0.1875
Spiders	0.4084	0.2522
Carabids	0.4625	0.2869
Phytophagous beetles	0.4518	0.2193
Moths	0.4545	0.2626
Bryophytes	0.2801	0.1508
Lichens	0.3562	0.1906
Fungi	0.2576	0.1264
Saproxylic beetles	0.2345	0.1214
Necrophagous beetles	0.2766	0.1062
Mean of 11 functional groups	0.3528	0.1936

TABLE C8.2.5 The unique and shared effects of regional spatial structure (regional species pool), landscape spatial structure (dispersal limitations) and environmental (Env) factors (environmental filtering) on the species turnover within the 11 functional groups in the inter-region analysis.

Functional group	Unique effects			Shared effects			
	Environmental factors	Landscape structure	Regional structure	Env + Landscape	Landscape + Regional	Env + Regional	Env + Regional + Landscape
Birds	0.0961	0.0184	0.0229	0.0385	0.0000	0.1629	0.0000
Bats	0.0418	0.0254	0.0714	0.0056	0.0038	0.2233	0.0000
Spiders	0.0751	0.0210	0.0486	0.0653	0.0023	0.2073	0.0000
Carabids	0.0837	0.0257	0.0476	0.0527	0.0000	0.2608	0.0000
Phytophagous beetles	0.0653	0.0155	0.0587	0.0267	0.0000	0.2887	0.0000
Moths	0.0542	0.0332	0.0548	0.0143	0.0000	0.3068	0.0000
Bryophytes	0.0703	0.0126	0.0214	0.0111	0.0000	0.1680	0.0000
Lichens	0.0685	0.0106	0.0291	0.0189	0.0012	0.2329	0.0000
Fungi	0.0760	0.0076	0.0173	0.0228	0.0001	0.1356	0.0000
Saproxylic beetles	0.0505	0.0173	0.0154	0.0271	0.0003	0.1292	0.0000
Necrophagous beetles	0.0403	0.0188	0.0390	0.0108	0.0000	0.1696	0.0000
Mean of 11 functional groups	0.0656	0.0187	0.0387	0.0267	0.0007	0.2077	0.0000

TABLE C8.2.6: The ratios of the unique effects of landscape spatial structure (proxy of dispersal limitations) to the total independent effects of the three predictor sets.

Dispersal-ability group	Functional group	Ratio
Spore dispersal	Bryophytes	0.121
Spore dispersal	Lichens	0.098
Spore dispersal	Fungi	0.075
Vertebrate	Birds	0.134
Vertebrate	Bats	0.183
Arthropods	Spiders	0.145
Arthropods	Carabids	0.164
Arthropods	Phytophagous beetles	0.111
Arthropods	Moths	0.234
Arthropods	Saproxylic beetles	0.208
Arthropods	Necrophagous beetles	0.191
	Mean of 11 functional groups	0.151

TABLE C8.2.7: The results of asymptotic general independence tests comparing the relative importance of landscape spatial structure (proxy of dispersal limitations) according to dispersal ability and the relative importance of forest physiognomy according to trophic position and body size.

Independence test	z value	p-value
Inter-region analysis		
Relative importance of landscape spatial structure according to dispersal ability	2.157	0.015
Intra-region analysis		
Relative importance of forest physiognomy according to trophic level	2.078	0.019
Relative importance of forest physiognomy according to body size	2.366	0.009

TABLE C8.2.8: Independent effects of spatial structure (proxy of dispersal limitations), herb composition, tree composition and forest physiognomy on species turnover in the intra-region analysis. Non-significant effects were excluded from the analyses.

Functional group	Region	Spatial structure	Herb composition	Tree composition	Physiognomy
Birds	ALB	0.000	0.063	0.022	0.080
	BAY	0.019	0.041	0.008	0.031
	HAI	0.022	0.014	0.015	0.080
	SCH	0.025	0.044	0.028	0.034
	STE	0.038	-	-	0.033
Bats	ALB	-	-	-	-
	BAY	0.218	0.000	0.012	0.031
	HAI	-	-	-	-
	SCH	0.023	0.043	0.003	0.028
	STE	-	-	-	-
Spiders	ALB	0.031	0.027	0.029	0.034
	BAY	0.020	0.079	0.003	0.013
	HAI	0.000	0.104	0.006	0.007
	SCH	0.027	0.021	0.022	0.023
	STE	0.030	0.018	0.008	0.073
Carabids	ALB	0.044	0.043	0.001	0.000
	BAY	0.016	0.040	0.009	0.024
	HAI	0.097	0.052	0.010	0.013
	SCH	0.061	0.058	0.005	0.021
	STE	0.062	0.007	0.010	0.002
Phytophagous beetles	ALB	0.077	0.025	0.031	-
	BAY	0.022	0.033	0.009	0.013
	HAI	0.041	0.028	0.008	0.007
	SCH	0.027	0.074	0.002	0.007
	STE	0.051	0.065	0.020	0.020
Moths	ALB	0.092	0.032	0.027	0.031
	BAY	0.085	0.002	0.002	0.009
	HAI	0.091	0.016	0.028	0.023
	SCH	0.078	0.050	0.001	0.005
	STE	0.155	0.034	-	0.015
Bryophytes	ALB	-	0.049	0.013	0.008
	BAY	0.023	0.051	0.003	0.000
	HAI	0.036	0.016	0.029	0.009
	SCH	0.036	0.035	0.010	0.008
	STE	0.012	0.027	0.001	0.002
Lichens	ALB	-	0.033	0.011	0.023
	BAY	0.012	0.023	0.010	0.003
	HAI	0.006	0.000	0.039	0.005
	SCH	0.020	0.043	0.019	0.010
	STE	0.087	-	0.027	-
Fungi	ALB	-	0.030	0.006	0.006

	BAY	0.015	0.021	0.008	0.013
	HAI	0.001	0.033	0.019	-
	SCH	-	0.014	0.016	0.000
	STE	0.013	0.011	0.006	0.010
Saproxylic beetles	ALB	-	0.028	0.014	0.005
	BAY	0.024	0.039	0.006	0.013
	HAI	0.043	0.010	0.007	0.005
	SCH	0.014	0.016	0.009	0.013
	STE	0.018	-	0.007	-
Necrophagous beetles	ALB	0.040	0.040	0.014	-
	BAY	0.043	0.008	0.000	0.030
	HAI	-	-	0.050	-
	SCH	-	0.030	0.033	0.000
	STE	-	-	-	-
Mean of 11 functional groups and 5 regions		0.034	0.029	0.012	0.015

TABLE C8.2.9: Independent effects of spatial structure (dispersal limitations) vs. environmental factors (environmental filtering) on species turnover. Averaged values were calculated across the five forest regions. The effect of environmental factors comprise the effects of herb composition, tree composition and forest physiognomy.

Functional group	Spatial structure	Environmental factors
Birds	0.0207	0.1491
Bats	0.0482	0.1235
Spiders	0.0214	0.1676
Carabids	0.0560	0.1391
Phytophagous beetles	0.0436	0.1263
Moths	0.1004	0.1014
Bryophytes	0.0215	0.1034
Lichens	0.0249	0.1257
Fungi	0.0058	0.0980
Saproxylic beetles	0.0196	0.0753
Necrophagous beetles	0.0165	0.0799
Mean of 11 functional groups	0.0344	0.1172

TABLE C8.2.10 :The ratios of the independent effects of forest physiognomy to the total independent effects of the environmental factors.

Trophic position	Functional group	Importance of physiognomy
Consumers 2b	Birds	0.586
Consumers 2b	Bats	0.547
Consumers 2a	Spiders	0.333
Consumers 2a	Carabids	0.171
Primary consumers	Phytophagous beetles	0.136
Primary consumers	Moths	0.350
Autotrophs	Bryophytes	0.101
Autotrophs	Lichens	0.135
Decomposers 1	Fungi	0.164
Decomposers 1	Saproxylic beetles	0.176
Decomposers 2	Necrophagous beetles	0.196

TABLE C8.2.11: Mean sample coverage of eight animal groups (of the abundance-based data) and five regions. As bryophytes, fungi and lichens were presence-absence data, sample coverages were not calculated. However, the species lists of these sessile groups were recorded in a comprehensive manner across projects.

Data type	Functional group	ALB	BAY	HAI	SCH	STE	**Mean**
Abundance data	Phytophagous beetles	0.849	0.893	0.743	0.931	0.952	**0.874**
	Moths	0.948	0.912	0.921	0.852	0.910	**0.909**
	Saproxylic beetles	0.600	0.717	0.572	0.735	0.502	**0.625**
	Spiders	0.901	0.825	0.896	0.931	0.867	**0.884**
	Carabids	0.986	0.876	0.975	0.977	0.957	**0.954**
	Necrophagous beetles	0.956	0.951	0.965	0.971	0.921	**0.953**
	Birds	0.849	0.810	0.863	0.663	0.801	**0.797**
	Bats	1.000	0.986	1.000	1.000	0.990	**0.995**

TABLE C8.2.12: The numbers of a subset of plots with sample coverage above 70% of eight animal groups and five regions.

Functional groups	Sample coverage > 70%						Total number of samples					
	ALB	BAY	HAI	SCH	STE	**Total**	ALB	BAY	HAI	SCH	STE	**Total**
Phytophagous beetles	44	158	38	50	68	**358**	50	169	49	50	68	**386**
Spiders	50	144	49	50	62	**355**	50	166	49	50	68	**383**
Moths	42	32	44	43	60	**221**	42	32	44	47	61	**226**
Saproxylic beetles	18	100	14	33	9	**174**	50	168	49	50	68	**385**
Carabids	50	137	49	50	65	**351**	50	166	49	50	68	**383**
Necrophagous beetles	49	129	48	48	62	**336**	50	169	49	50	68	**386**
Birds	46	245	50	21	60	**422**	50	276	50	50	68	**494**
Bats	28	29	40	50	58	**205**	50	29	50	50	68	**247**

TABLE C8.2.13 :The results of asymptotic general independence tests comparing the relative importance of landscape spatial structure (proxy of dispersal limitations) according to dispersal ability and the relative importance of forest physiognomy according to trophic position and body size using a subset of plots with sample coverage above 70%. When analyzing independence tests using a subset of plots with sample coverage above 70%, the relative importance of bryophytes, fungi and lichens was fixed with their values of the total data set.

Independence test	z value	p-value
Inter-region analysis		
Relative importance of landscape spatial structure according to dispersal ability	1.964	0.025
Intra-region analysis		
Relative importance of forest physiognomy according to trophic level	2.183	0.015
Relative importance of forest physiognomy according to body size	1.599	0.055

Chapter 8.3

Appendix chapter 4

Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests

with

Soyeon Bae | Shaun Levick | Sebastian Seibold | Wolfgang Weisser | Peter Krzystek | Paul Magdon | Thomas Nauss | Peter Schall | Alla Serebryanyk | Stephan Wöllauer | Christian Ammer | Claus Bässler | Inken Doerfler | Markus Fischer | Martin M. Gossner | Marco Heurich | Torsten Hothorn | Kirsten Jung | Holger Kreft | Ernst-Detlef Schulze | Nadja Simons | Simon Thorn | Jörg Müller |

published in Nature Ecology and Evolution, 4, 2020, p. 1204 - 1212

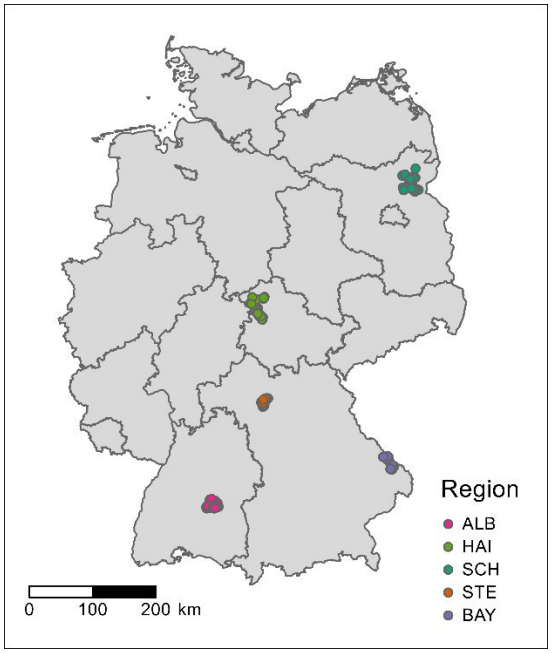

FIGURE C8.3.1: Locations of the single regions from which data was derived

Linear-by-linear association test

To test, whether ecological properties of species groups change the infliction point of heterogeneity (Figure C8.3.2), we assigned the species groups to a rough order. Hereby, their trophic level was used as a surrogate for niche breadth, and dispersal range.

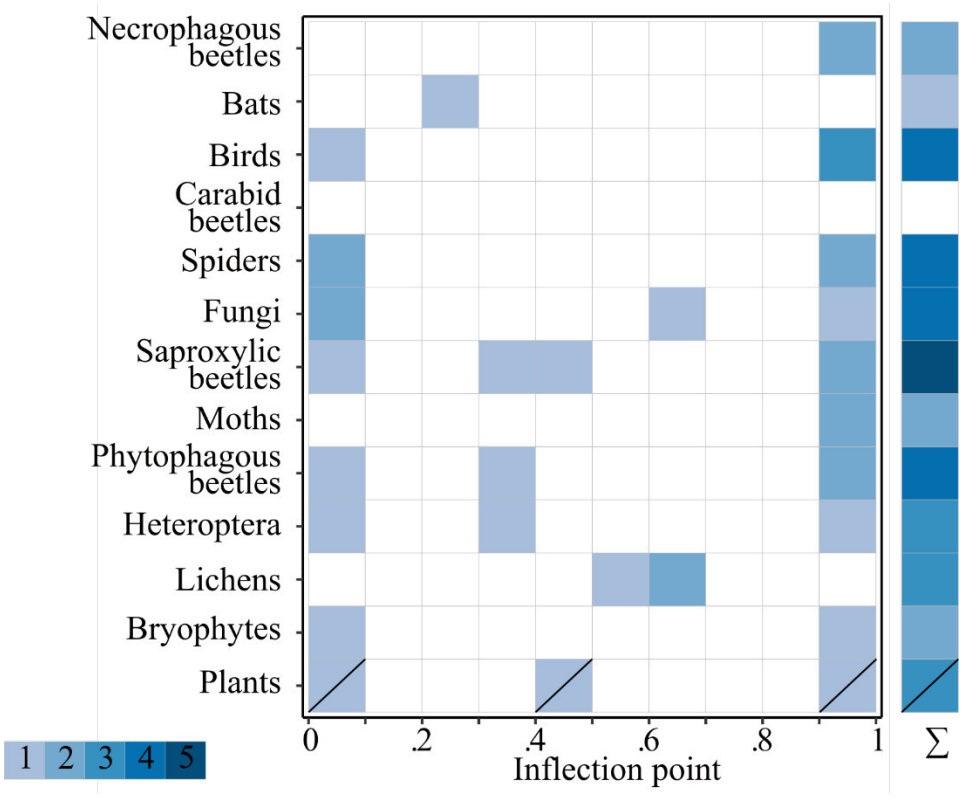

FIGURE C8.3.2: Inflection points per species groups, summarized and scaled over the six facets of heterogeneity. The shade of blue refers to the number of occurrences.

TABLE C8.3.1: List of the trophic levels and dispersal groups which have been assigned to each species group

Species Group	Trophic level	Dispersal group
Necrophagous beetles	Decomposers II	(flying) Arthropods
Bats	Consumer III	Vertebrates
Birds	Consumer III	Vertebrates
Carabid beetles	Consumer II	(non-flying) Arthropods
Aranea	Consumer II	(non-flying) Arthropods
Fungi	Decomposers I	Spore disperser
Saproxylic beetles	Decomposers I	(flying) Arthropods
Phytophagous beetles	Consumer I	(flying) Arthropods
True bugs	Consumer I	(flying) Arthropods
Moths	Consumer I	(flying) Arthropods
Bryophytes	Producer	Spore disperser
Lichens	Producer	Spore disperser

We assumed the following ranking, from small to large niche breadth:

Producer < Consumer I < Decomposer I < Consumer II < Consumer III < Decomposer II

For dispersal ability, we assumed the following ranking:

Arthropods < Vertebrates < Spore dispersers.

There are, to our knowledge, no comparable measures of dispersal ability between species groups.

Thus, we also tested another classification system, with the following ranking:

Non-flying Arthropods < flying Arthropods < Spore disperser < Vertebrates

However, both classification and ranking systems did not show any relationship to the infliction point.

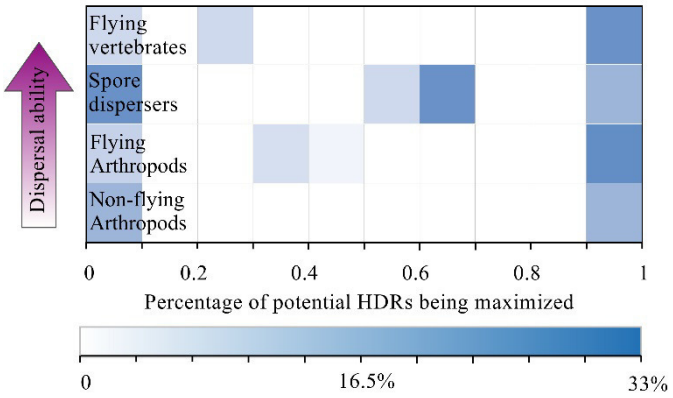

FIGURE 8.3.3: Infliction points under different ranking. Asymptotic General Independence Test, alternative "greater", Z=0.38, p-value=0.35.

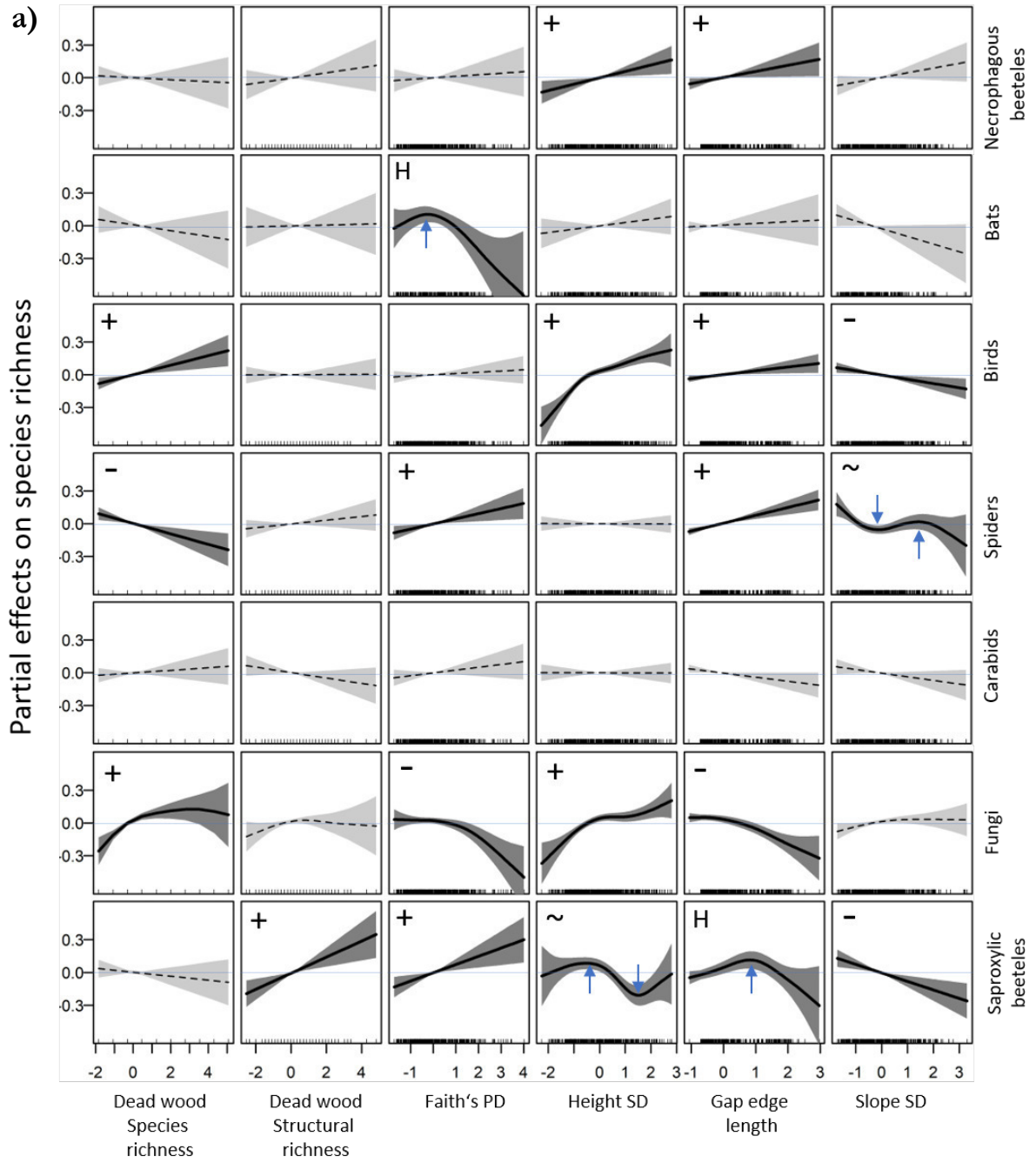

FIGURE C8.3.4: Detailed GAMM plots of partial effects on a) species richness and b) mean abundance. Smooth terms of partial effects of GAMMs with species richness as dependent variable and region as random factor, a quasipoisson error distribution for species richness, and gaussian error distribution for mean abundance, fitted by Maximum Likelihood. Blue arrows point out to changes in sign which led us to the classification as positive (+), humpshaped (H), negative (-) or erratic (~)

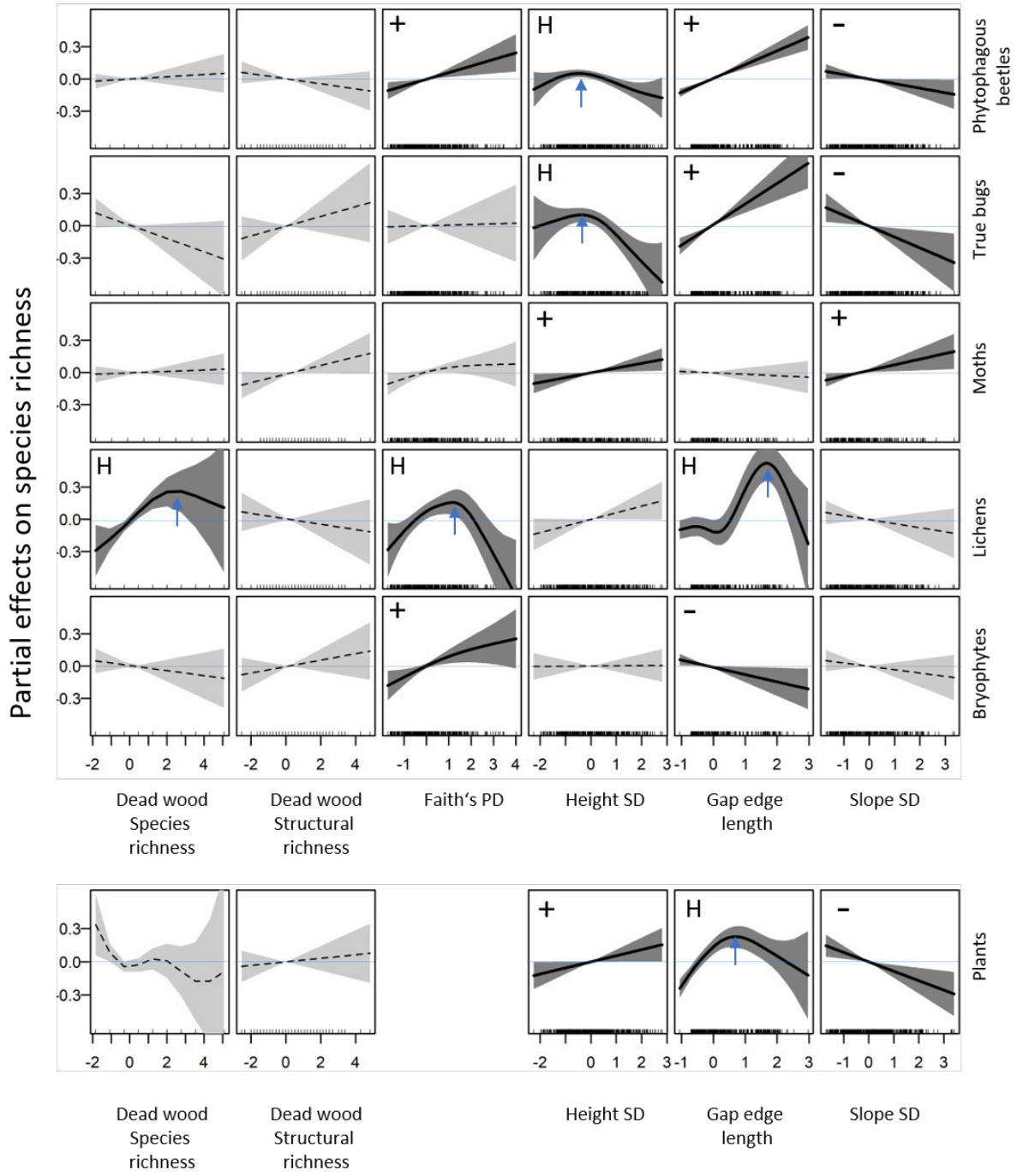

FIGURE C8.3.4 ***(continued)***

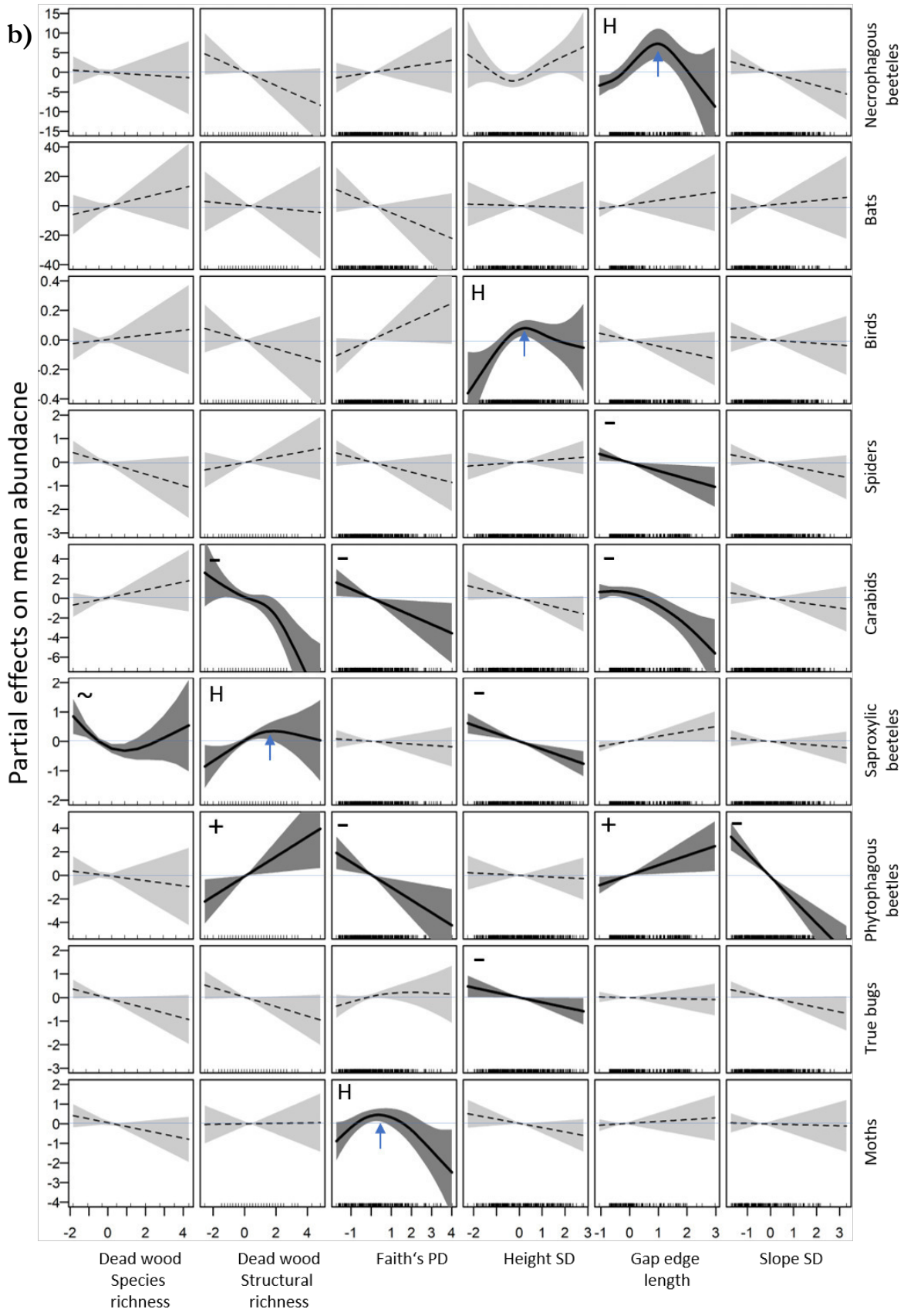

FIGURE C8.3.4: ***(continued)***

Supplementary Methods: Assessing habitat heterogeneity

Dead wood

In the Biodiversity Exploratories project, all dead-wood logs with a diameter larger than 7 cm lying within a line-transects on both diagonals of a plot and all stumps larger than 7 cm 1m left and right to that line-transect were measured. Additionally, all downed and standing dead wood objects larger than 25 cm diameter were measured on the total one-hectare plot area. Dead wood objects were classified into nine types (entire standing tree, stump, entire downed tree, root, stem, crown, branch, forest residue and dead wood piece) and five decay classes (undecayed, beginning decay, moderately decayed, heavily decayed and fully decayed) and determined to species level if possible, otherwise into coniferous or deciduous. Data source: Kahl, Tiemo; Bauhus, Jürgen (2018) Dead wood inventory 2012, v.1.0.0 Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/ . DatasetId=15386.

In the Steigerwald project, all dead wood objects larger than 12 cm diameter were recorded within 13 meter radius around the plot midpoint. They were classified into ten types (broken snags, complete standing snags, complete lying dead trees, logs, cut-stumps from harvest, scattered fwd (fine woody debris), naturally developed stumps, piled fwd, root plate and logs originated from tree crowns) and into five decay classes and determined if possible. It was determined whether the wood originated from coniferous wood, oak or any other deciduous tree species. For more information see (Doerfler *et al.*, 2017)

In the BioKlim project, all dead wood objects within an 8 m radius were recorded. Species were determined if possible or, whenever not possible, more roughly classified into either broadleaf or coniferous species. The objects were classified into nine types (standing tree, lying dead trees, large branch or trunk, cut stumps, scattered fwd, snags, crown, root plate and piled fwd) and in the same four decay classes as the Steigerwald project.

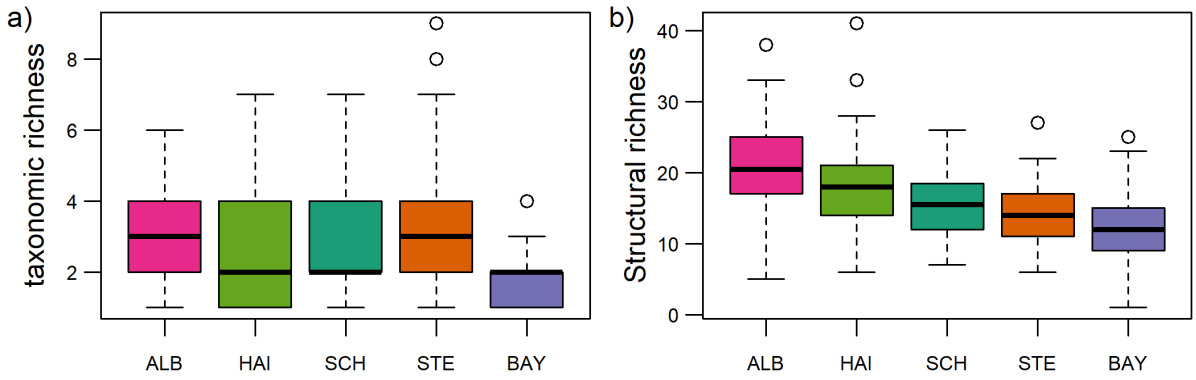

FIGURE C8.3.5: Distribution of taxonomic and type richness of dead wood objects per region

All the dead wood objects were divided into four diameter classes: below 10 cm, 10-20 cm, 20-50cm and more than 50 cm diameter. Root plates, crowns and residues could not be assigned to the diameter classes.

The final dead wood type was then defined as the combination of type, decay classes (with the exclusion of the "undecayed" stages) and diameter classes. The structural richness of dead wood was then calculated as the number of different dead wood type per plot, whereas the taxonomic richness of dead wood was the number of tree species contributing to dead wood objects.

Plant diversity

Vegetation has been recorded twice per year (spring and summer) since 2009 on 20 m x 20 m quadrats in the Exploratories. For the ALB, species records from 2010 were chosen, for HAI and SCH those of 2009. Percentage cover of the single vascular plant species was estimated separately for two tree layers (5-10 m and >10 m), the shrub layer (including all woody species older than one year and within the height of 0-5 m), and the herb layer (including phanerophyte seedlings). From the spring and summer records, always the higher record is chosen. In the Steigerwald, vegetation was mapped on a 200m² square in April and June 2014. Here, the herb layer included all plants below 1.5 m, and the shrub layer all plants from 1.5 – 5 m. Species cover was assessed according to Braun-Blanquet scale, which is not prone to overestimation of high covers. In the Bavarian Forest National park, vegetation was recorded on a circular 0.2 ha plot according to the Londo scale in summer 2006. Here, the herb layer was defined as everything below 1 m. In contrast to the other projects, only one mapping round was conducted. Here, vernal geophytes are supposed to be negligible due to the short growing season and the absence of rich soils (Bässler *et al.*, 2010a).

The number of plant species alone does not necessarily reflect their ecological differences relevant for herbivores (Flynn *et al.*, 2011; Cadotte *et al.*, 2013). Alternative metrics which better reflect ecological differences were phylogenetic diversity or functional dissimilarity. The latter measures distances between species' attributes. However, the calculation of ecologically meaningful functional dissimilarity relies on a set of informative traits (Cadotte *et al.*, 2013). Unfortunately, only few traits were available which covered a larger fraction of the 349 assessed plant species. Thus, we think that phylogenetic distances better represent ecological differences better than the limited number of measured traits. *Taraxacum campylodes* and *Taraxacum hamatum* could not be matched with the phylogeny of Durka & Michalski (2012) and were added by replacing Taraxacum sections for which no representative occurred in our data.

Phylogenetic tree of Durka & Michalski (5), renamed and pruned to the species of our communities:

((Huperzia_selago:351,(Lycopodium_clavatum:76,Lycopodium_annotinum:76)Lycopodium:275)Lycopodiales:74.5,((Equisetum_sylvaticum:359.6,(Pteridium_aquilinum:144.5,((((Cystopteris_fragilis:28.7,Cystopteris_fragilis:28.7)Cystopteris_fragilis_agg.:57.4,Gymnocarpium_dryopteris:86.1)N140:8.4,((Oreopteris_limbosperma:57.56,Phegopteris_connectilis:57.56)Thelypteridaceae:28.78,(Blechnum_spicant:78.18,Athyrium_alpestre:78.18)N195:8.16)N184:8.16)Eupolypods_II:10.2,(Dryopteris_dilatata:9,Dryopteris_carthusiana:9)N216:95.7)Eupolypods:39.8)N123:215.1)N48:53.5,(((((Pinus_sylvestris:5,Pinus_mugo:5)N272:151,Picea_abies:156)N257:20,(Larix_decidua:93,Pseudotsuga_menziesii:93)N287:83)N256:25,Abies_alba:201)Pinaceae:85,(Juniperus_communis:4.9,Juniperus_communis:4.9)N322:281.1)Pinales:69,(Asarum_europaeum:150.1,((Arum_maculatum:131,(((Paris_quadrifolia:106,Colchicum_autumnale:106)N579:4,(Lilium_martagon:58.5,Streptopus_amplexifolius:58.5)Liliaceae:51.5)N578:13,((((Platanthera_bifolia:13.5,Dactylorhiza_fuchsii:13.5)N654:50.5,((Cephalanthera_rubra:23.33,Cephalanthera_damasonium:23.33)Cephalanthera:11.67,((Epipactis_helleborine:10.8,(Epipactis_helleborine:5.4,Epipactis_helleborine:5.4)N770:5.4)Epipactis_helleborine_agg.:16.2,Neottia_ovata:27)N761:8)N755:29)N644:54,(Allium_ursinum:89,(Convallaria_majalis:16.4,(Maianthemum_bifolium:9.6,(Polygonatum_verticillatum:5,Polygonatum_multiflorum:5)Polygonatum:4.6)N1019:6.8)Nolinoideae_:72.6)N870:29)Asparagales:4,((((Luzula_luzuloides:37.12,Luzula_pilosa:37.12,(Luzula_sylvatica:18.56,Luzula_sylvatica:18.56)Luzula_sylvatica_agg.:18.56,Luzula_multiflora:37.12)Luzula:12.38,(Juncus_bulbosus:44,((Juncus_effusus:11,Juncus_conglomeratus:11)N1137:11,(Juncus_filiformis:16.5,Juncus_tenuis:16.5)N1141:5.5)N1136:22)Juncus:5.5)N1068:24.02,((Carex_pulicaris:36.5,((Carex_leporina:26.69,((Carex_echinata:19.06,Carex_muricata:19.06)N1206:3.812,(Carex_remota:15.25,Carex_canescens:15.25,Carex_brizoides:15.25)N1231:7.625)N1205:3.812)N1190:6.812,(Carex_flacca:12.1,((Carex_montana:10,Carex_pilulifera:10)N1281:1.6,(Carex_digitata:11.1,(Carex_pallescens:10.2,((Carex_hirta:8.4,Carex_nigra:8.4)N1327:1.04,(Carex_sylvatica:5.3,Carex_flava:5.3)N1379:4.14)N1326:0.76)N1313:0.9)N1290:0.5)N1280:0.5)N1266:21.4)N1185:3)Carex:7,((Eriophorum_vaginatum:6,Eriophorum_angustifolium:6)N1406:3,Scirpus_sylvaticus:9)N1405:34.5)N1164:30.02)N1063:7.475,(((Molinia_caerulea:7.25,Molinia_caerulea:7.25)Molinia:28.67,Danthonia_decumbens:35.92)N1554:18.68,(Nardus_stricta:46,(((Glyceria_fluitans:5,Glyceria_notata:5)N1643:10,(Melica_uniflora:5,Melica_nutans:5)Melica:10)Meliceae:19.5,((Brachypodium_pinnatum:18.67,(Brachypodium_pinnatum:9.333,Brachypodium_sylvaticum:9.333)N1666:9.333)Brachypodium:9.333,((Bromus_ramosus:12.5,(Hordelymus_europaeus:9.85,((Elymus_repens:4.15,Elymus_repens:4.15)N1725:4.15,Elymus_caninus:8.3)N1721:1.55)Triticeae:2.65)Triticeae+Bromeae:12.5,(((((Calamagrostis_villosa:5,Calamagrostis_epigejos:5)Calamagrostis.subgen.:1.667,Calamagrostis_arundinacea:6.667)Calamagrostis:1.667,((Agrostis_canina:1.667,Agrostis_stolonifera:1.667)N1790:3.333,Agrostis_capillaris:5)Agrostis:3.333)N1767:1.667,((Anthoxanthum_odoratum:3.111,Anthoxanthum_odoratum:3.111)Anthoxanthum_odoratum_agg.:6.222,(Trisetum_flavescens:8.667,Arrhenatherum_elatius:8.667)N1813:0.6667)N1807:0.6667)N1756:7.2,(((Poa_annua:9.688,((Poa_trivialis:5.167,(Poa_compressa:2.583,Poa_nemoralis:2.583)N1876:2.583)N1874:2.583,(Poa_chaixii:5.812,Poa_pratensis:5.812)N1883:1.938)N1873:1.938)Poa:1.938,(Milium_effusum:9.3,Phleum_pratense:9.3)N1894:2.325)N1858:3.875,Deschampsia_flexuosa:15.5,((Deschampsia_cespitosa:2.76,Deschampsia_cespitosa:2.76,Deschampsia_cespitosa:2.76)N1962:11.04,((Holcus_mollis:6.75,Holcus_lanatus:6.75)Holcus:6.75,((Festuca_altissima:10.05,(Festuca_pratensis:1.4,Festuca_gigantea:1.4)N1983:8.65)N1974:2.85,(Festuca_rubra:1.25,Festu

ca_pratensis:1.25,Festuca_rubra:1.25)Festuca_rubra_agg.:11.65)Loliinae:0.6)N1967:0.3,(Dactylis_glomerata:3.68,Dactylis_glomerata:3.68)Dactylis:10.12)N1954:1.7)N1856:1.7)Poeae+Aveneae:7.8)N1669:3)N1663:6.5)N1640:11.5)N1619:8.6)N1499:26.4)N1054:41)N636:1)N573:8)N401:16.8,(((Hepatica_nobilis:22.19,(Anemone_ranunculoides:4.598,Anemone_nemorosa:4.598)N2205:17.59)N2181:24.41,(Ficaria_verna:30.95,(Ranunculus_platanifolius:20.65,Ranunculus_auricomus:20.65,((Ranunculus_acris:3.775,Ranunculus_lanuginosus:3.775)N2326:7.55,Ranunculus_repens:11.33)N2322:9.325)Ranunculus_core_clade:10.3)Ranunculeae:15.65)N2171:7.1,(Aconitum_napellus:41.7,((Caltha_palustris:25.02,Helleborus_foetidus:25.02)Helleboreae:8.34,Actaea_spicata:33.36)N2389:8.34)Helleboroideae:12)N2170:81.3,(((Ribes_alpinum:74,(Chrysosplenium_oppositifolium:21.75,Chrysosplenium_alternifolium:21.75)Chrysosplenium:52.25)N2586:42.73,(((Euonymus_europaeus:101.4,(Oxalis_acetosella:99.6,(((Viola_palustris:16.87,(Viola_riviniana:5.3,Viola_reichenbachiana:5.3)N2775:11.57)N2751:72.13,((Populus_tremula:2.25,Populus_alba:2.25)N2823:52.75,(Salix_caprea:13.33,(Salix_cinerea:6.667,Salix_aurita:6.667)N2852:6.667)N2847:41.67)Salicaceae:34)N2745:8.5,(((Hypericum_maculatum:1.333,Hypericum_maculatum:1.333)Hypericum_maculatum_agg.:1.333,Hypericum_perforatum:2.667)N2933:2.333,Hypericum_hirsutum:5)N2928:92.5,((Euphorbia_amygdaloides:8.857,Euphorbia_cyparissias:8.857)N3001:60.64,Mercurialis_perennis:69.5)Euphorbiaceae:28)Malpighiales:2.1)N2710:1.8)N2699:1.7,((Cytisus_scoparius:56.6,((Robinia_pseudoacacia:34,(Lotus_corniculatus:18.4,Ornithopus_perpusillus:18.41)N3150:15.59)Robinioids:16.6,(((Trifolium_medium:7.909,Trifolium_pratense:7.909)N3307:15.82,(Trifolium_hybridum:19.77,(Trifolium_montanum:15.82,(Trifolium_repens:7.909,Trifolium_repens:7.909)N3327:7.909)Trifoliastrum:3.955)N3316:3.955)N3285:6.348,(((Vicia_sylvatica:10.45,Vicia_cracca:10.45)N3355:7.837,Vicia_sepium:18.29)Vicia:6.033,(Lathyrus_pratensis:16.67,(Lathyrus_vernus:13.46,Lathyrus_linifolius:13.46)N3420:3.21)N3416:7.65)Vicieae:5.755)N3268:20.52)Hologalegina:6)N3075:41.1,((((Filipendula_ulmaria:54,((Rubus_idaeus:27.3,(Rubus_vestitus:23.4,Rubus_vestitus:23.4)N3471:3.9)N3463:11.7,(Geum_urbanum:38,(Rosa_canina:33.3,(((Potentilla_sterilis:20.65,(Potentilla_anglica:4.9,Potentilla_erecta:4.9,Potentilla_reptans:4.9)N3888:15.75)N3880:12.3,Fragaria_vesca:32.95)Potentilleae:0.175,Sanguisorba_officinalis:33.13)N3876:0.175)N3820:4.7)N3808:1)N3458:15)Rosoideae:18.5,((Prunus_spinosa:31.75,(Prunus_avium:25.4,(Prunus_serotina:19.05,Prunus_padus:19.05)N4069:6.35)N4061:6.35)Amygdaleae:12.7,(Aruncus_dioicus:44,(((Sorbus_torminalis:27,Sorbus_aria:27)N4129:15,Malus_domestica:42)N4124:1.625,Sorbus_aucuparia:43.62)N4122:0.375)N4086:0.45)N4041:28.05)Rosaceae:8.95,(Frangula_alnus:67,((Ulmus_laevis:41.25,Ulmus_glabra:41.25)Ulmaceae:13.75,Urtica_dioica:55)N4240:12)N4215:14.45)Rosales:13.55,((Fagus_sylvatica:66.5,(Quercus_rubra:17,(Quercus_robur:5.667,Quercus_petraea:5.667)N4323:11.33)Quercus:49.5)Fagaceae:9.25,(((Alnus_incana:7.9,Alnus_glutinosa:7.9)N4346:19.84,(Betula_pendula:8.775,Betula_pubescens:8.775)N4351:18.97)Betuloideae:2.42,(Corylus_avellana:20.11,Carpinus_betulus:20.11)Coryloideae:10.05)Betulaceae:45.59)N4309:19.25)N3451:2.7)N3065:5.4)N2698:5.9,(((Geranium_robertianum:14.5,Geranium_molle:14.5)Geranium:92.8,((Circaea_lutetiana:8.02,Circaea_alpina:8.02)Circaea:54.48,(Epilobium_angustifolium:15,(Epilobium_montanum:12,(Epilobium_palustre:9,(Epilobium_tetragonum:3,Epilobium_tetragonum:3)Epilobium_tetragonum_agg.:6)N4447:3)N4439:3)Epilobium:47.5)N4425:44.8)N4363:0.85,(((Acer_pseudoplatanus:46,(Acer_platanoides:4,Acer_campestre:4)N4582:42)Acer:3.25,Aesculus_hippocastanum:49.25)N4577:49.85,((Daphne_mezereum:53,(Tilia_platyphyllos:14.5,Tilia_cordata:14.5)Tilia:38.5)N4607:38.4,(((Cardamine_impatiens:3.666,Cardamine_bulbifera:3.666)N4792:7.331,(Cardamine_hirsuta:7.855,((Cardamine_flexuosa:3.142,Cardamine_amara:3.142)N4802:3.142,(Cardamine_pratensis:2.357,Cardamine_pratensis:2.357,Cardamine_pratensis:2.357,Cardamine_pratensis:2.357,Cardamine_pratensis:2.357)Cardamine_

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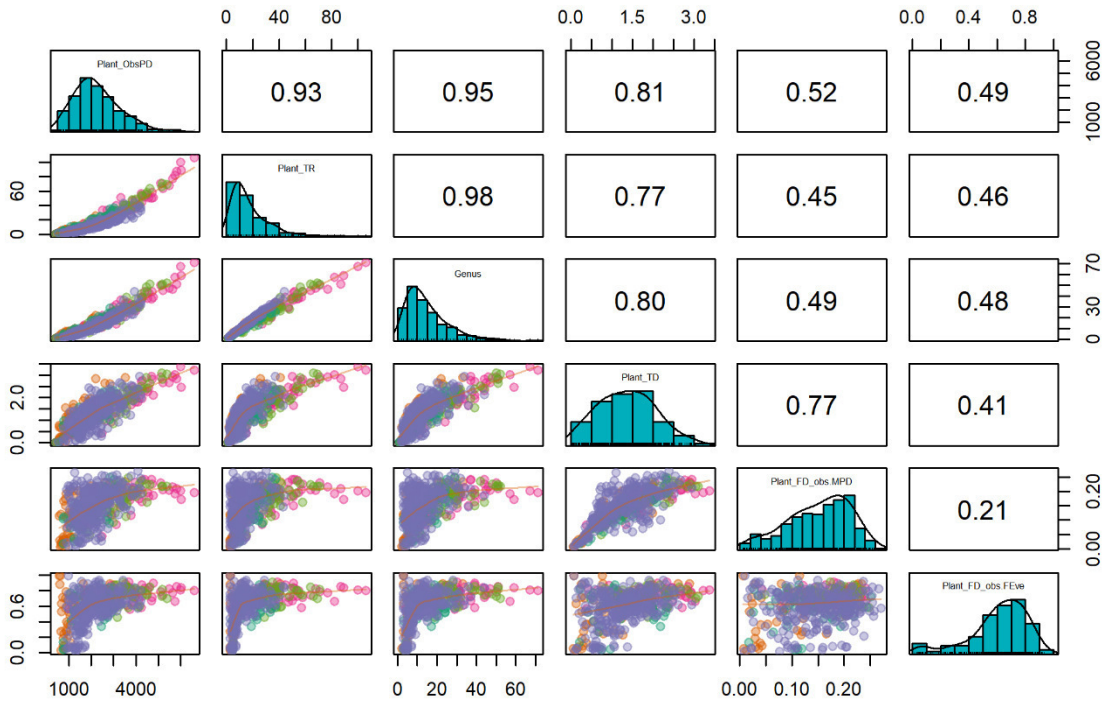

FIGURE C8.3.6: Pearson correlation between the available metrices for plant diversity Faith's PD (Plant_ObsPD), species richness (Plant_TR), number of genera per plot (Genus), plant diversity (Plant_TD), functional mean pairwise distances (Plant_FD_obs.MPD) and functional eveness (Plant_FD_obs.FEve).

Structural parameters

Airborne laserscanning (ALS) represents an active remote sensing technique, as the sensor emits short-duration light pulses illuminating the target structure. Based on the time difference between the emitted light pulse and the recorded reflection, the position, orientation of the sensor, and the scan angle, points are generated in a three-dimensional space. Therefore, ALS based metrics can quantify 3D forest structure, e.g. with information on canopy cover, height, vertical distribution or horizontal structure of the vegetation. Furthermore, detailed digital terrain models (DTM) can be filtered based on the classified ALS ground returns to characterise the topography.

ALS datasets were recorded under leaf-on conditions on forest EPs in the Exploratories (HAI, SCH, ALB) under the coordination of the Max-Planck-Institute for Biogeochemistry, Jena. Moreover, the Bavarian Forest National Park and the Munich University of Applied Sciences provided two additional ALS datasets for the regions NPBW and STE, respectively. For details see Supplementary Table 2.

TABLE C8.3.2 Basic characteristics of the ALS data. The pulse density is derived from the clipped point cloud per plot and aggregated as median value for each region. All flights happened on full leaf on conditions.

Region	Sensor	Year	Month	Flight Height (m, agl)	Pulse Density (pls/m²)
HAI	Riegl Q560	2008	August	400-600	8.2
ALB	Riegl Q560	2010	July	400-600	21.09
SCH	Riegl Q560	2009	September	400-600	27.03
STE	Riegl Q560/ VQ780i	2015 / 2018	September /Mai	650-700	40.07
NPBW	Riegl Q560	2007	Mai	350	33.25

The ALS datasets from the five regions were pre-processed and the metrics derived using the same methods for all datasets. The pre-processing was performed using LAStools (LAStools, 2012). This included transformation of the raw data into LAZ file format *(txt2las, las2las*), coordinate transformations into a unified coordinate reference system, removal of isolated returns (*lasnoise)* and retiling of the point cloud into 500 x 500m tiles (*lastile*). Classification of returns into ground, vegetation and buildings was done using *lasground* and *lasclassify*. The elevation of points was normalized w.r.t. above ground level (AGL) using *lasheight*. From the ground returns, a DTM with 1m spatial resolution was generated using the *blast2dem* function. For the gap analysis, pit free canopy height models (CHM) with a spatial resolution of 1m were created following the concept of Khosravipour et al. (2014) which was implemented in the lidR R-package (Roussel., 2018).

Based on the normalized point cloud, the DTM and the CHM we calculated a set of metrics describing the vertical and horizontal heterogeneity of the forest as well as the topographic variations. For the vertical heterogeneity, we calculated the mean, variance (VAR), standard deviation (SD) and coefficient of variation (COV) of all the heights from the vegetation returns as aggregates over the entire 1ha plot area. The Foliage Height Diversity (FHD) index, as used by McArthur & McArthur (1961), was calculated considering three fixed horizontal layers (Canopy: $5m < Z \leq max(Z)$; Understory: $2m < Z \leq 5m$; Regeneration: $0m < Z \leq 2m$).

The horizontal heterogeneity of the plots was analysed based on canopy gap masks. Gap masks were created from the normalized point cloud by calculating the penetration rate from the top of the canopy down to 2m for 1x1m raster cells. Here, penetration rate is the ratio of all returns with Z>2m to all returns <=2m. Cells with a penetration ratio > 80% were classified as gap cells. Using connected component labelling we grouped connected gap cells to gap objects and calculated area, edge length, area perimeter ratio for each gap using the *landscapemetrics* R-package (Hesselbarth *et al.*, 2019). To remove very small or narrow gaps (e.g. skidding trails) we deleted all gaps with an area < 50m² or a perimeter-area-ratio <1.5 from the gap maps before we calculated the aggregated statistics on the plot level.

Topographic variation was described based on the DTM by calculating the mean, min, max and SD of the elevation and slope values. Surface roughness was calculated based on the method of Jenness, J. (2004).

Vertical heterogeneity

Available metrics for vertical heterogeneity were *Foliage Height Diversity (BE_FHD)*, *Standard Deviation of Canopy Height (BE_H_SD)* and *Coefficient of Variation of Canopy Height (BE_H_VAR_COEF).* Because the latter is corrected by the mean vegetation height, it might describe well the vertical shape of the forest stand whether the canopy is evenly distributed but does not contain information about the absolute differences in height.- *Foliage Height Diversity*, the Shannon diversity index of the proportions of the foliage amount in pre-defined different horizontal layers, is the classic measurement used by MacArthur & MacArthur (1961) but relies on a pre-classification of the layers. Thus, we chose to stick with the raw data, leaving *Standard Deviation of Canopy Height* as measurement for heterogeneity in vertical structure.

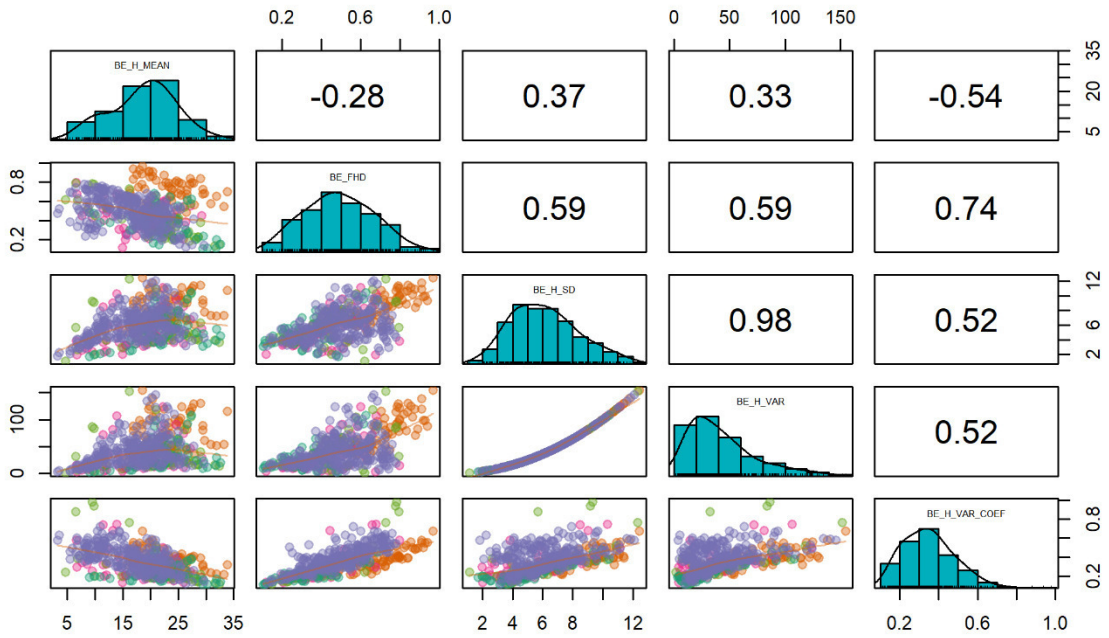

FIGURE C8.3.7: Correlation of variables describing vertical heterogeneity, i.e. Foliage Height Diversity (BE_FHD), Standard Deviation of Canopy Height (BE_H_SD), Variance of Canopy Height (BE_H_VAR) and Coefficient of Variation of Canopy Height (BE_H_VAR_COEF). Additionally, given is the Mean Canopy Height (BE_H_MEAN). In the diagonal panel, frequency distributions are shown, in the upper panel the Pearson correlation coefficient is given.

Horizontal heterogeneity

We defined areas which had a minimum size of 50 m², a perimeter/area ratio under < 1.5 (thus excluding narrow linear structures as forest aisles), a height threshold of 2 m and a penetration ratio of more than 80% as gaps. Several potential measurements could reflect horizontal heterogeneity: Heterogeneity would increase with the *number of gaps*. However, this measure would ignore differences in gap areas. Using only *gap area*, however, would overestimate heterogeneity when single gaps areas reach thresholds of more than 50% of the plot size. Here, the gap becomes the dominant habitat which makes the forest stand actually more homogeneous.
Hence, the total gap area per plot would not depict a linear increase in horizontal heterogeneity because both extremes, 100% canopy cover as well as 100% gap area are homogenous in structure (see also Figure C8.3.8); Variables such as *mean gap perimeter to area ratio* or *mean fractal dimension* loose information due to averaging across gaps. Ultimately, we chose to use the *total gap edge length*

as a measurement, which steadily increases with horizontal heterogeneity (C8.3.8) and which incorporates both composition and configuration, thereby covering the most important information in one variable.

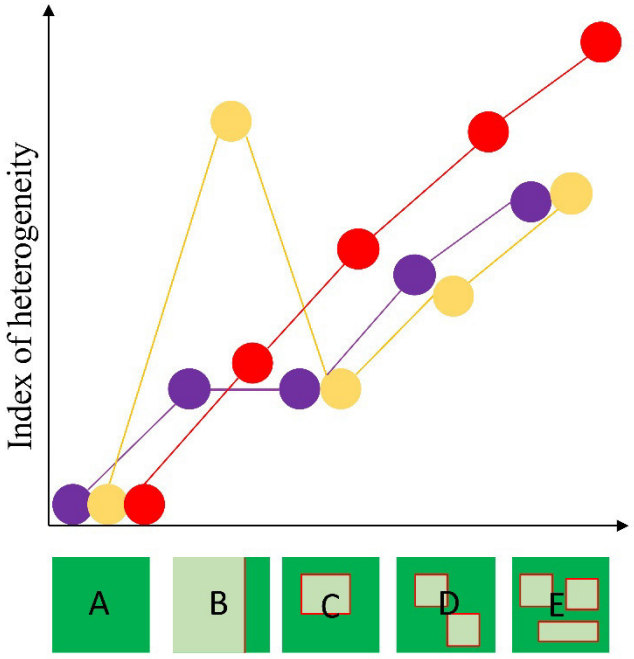

FIGURE C8.3.8: Conceptual considerations of three potential measurements used to describe horizontal heterogeneity of five (A-E) different forest stands. The number of gaps (lilac line) is a measure which would ignore differences in gap areas (B,C). Gap area (orange line) overestimates heterogeneity when single gaps areas reach thresholds of more than 50% of the plot size (B). Here, the gap becomes the dominant habitat which makes the forest stand actually more homogeneous. Hence, the total gap area per plot would not depict a linear increase in horizontal heterogeneity because both extremes, 100% canopy cover as well as 100% gap area are homogenous in structure. Total gap edge length (red line) steadily increases with horizontal heterogeneity and incorporates both composition and configuration, thereby covering the most important information in one variable.

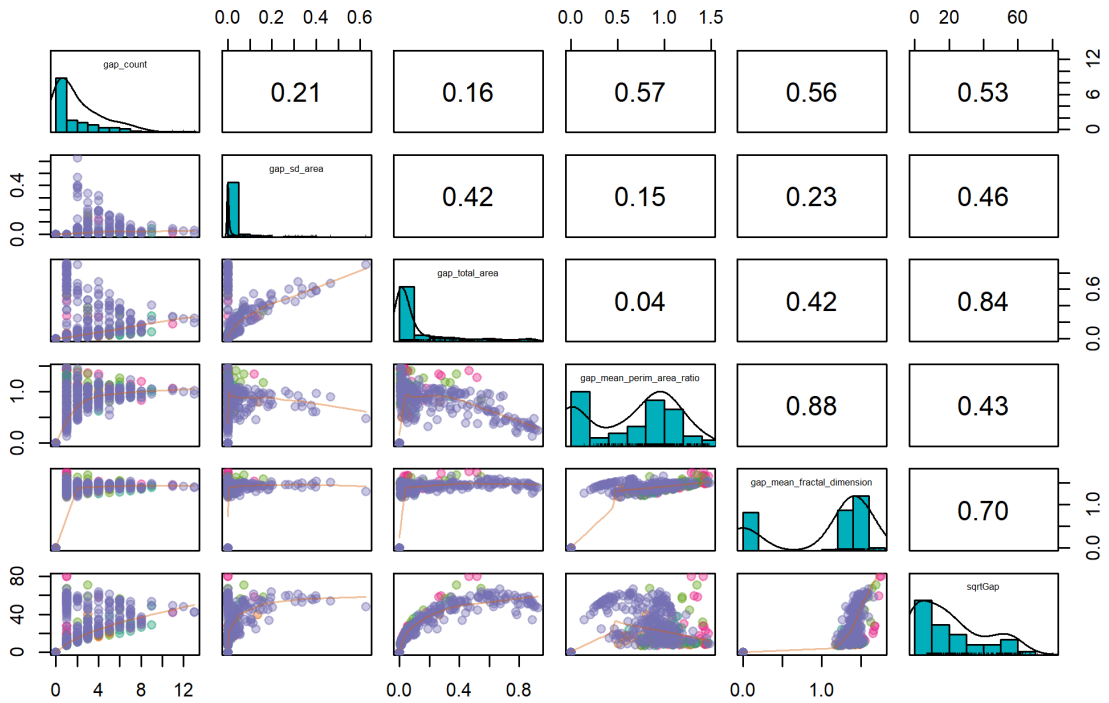

FIGURE C8.3.9: Correlation between single variables describing horizontal heterogeneity, i.e. the number of gaps (gap_count), the Standard Deviation of the area (gap_sd_area) the total gap area (gap_total_area), the mean gap area-perimeter-ratio (mean_perim_area_ratio) the mean fractal dimension (gap_mean_fractal_dimension) and the square-root-transformed total gap edge length (sqrtGapEdge)

To test, whether the selected variables are influenced by tree species composition, we summed the coverage of the single tree species over all layers except for the herb layer. Then, we calculated the proportion of coniferous species on the total cover. This value was then used as an independent variable in a simple linear models with height SD and square rooted gap perim length as response variables.

Height SD decreased with increasing proportion of coniferous trees, but the correlation was relatively weak ($F_{1,495}$=39.64, t-value = -6.29***, R^2=0.07). Horizontal heterogeneity increased with increasing proportion of coniferous trees ($F_{1,495}$=131.2, t-value = 11.45***, R^2=0.21, C8.3.10). However, this is likely due to the fact that in the Bavarian Forest, many spruce stands at higher elevations have been infected by bark beetles, which lead to many gaps.

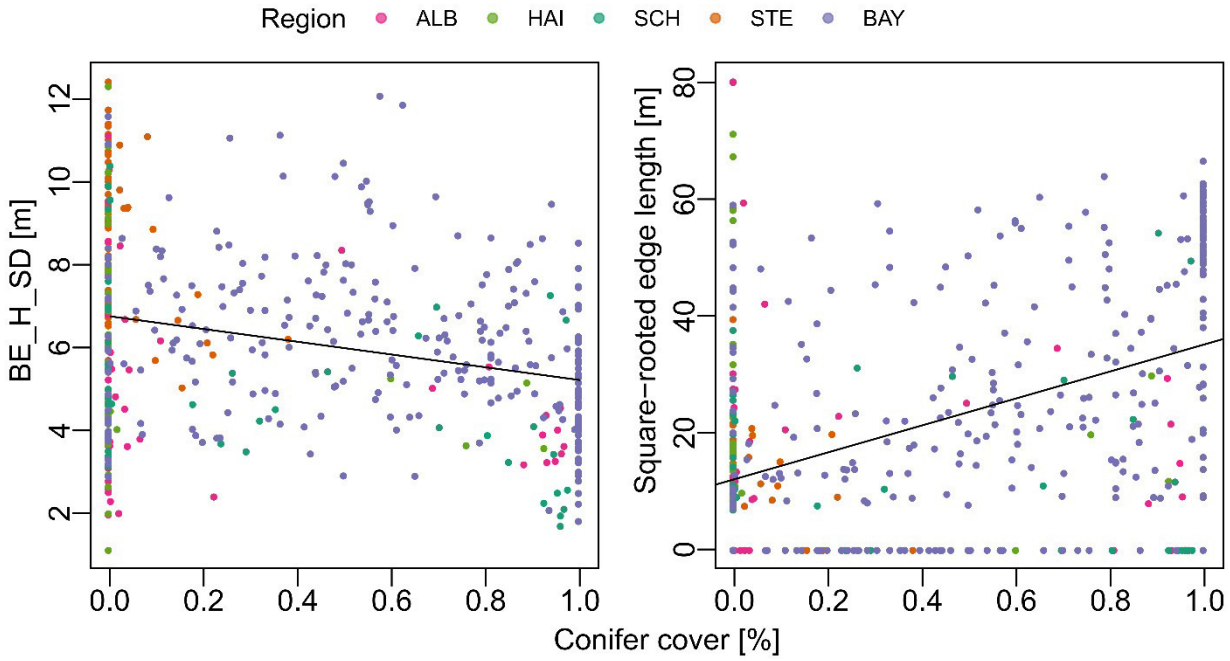

FIGURE 8.3.10: Correlation between height SD (left) and gap edge length (right) and the proportion of conifers in a forest stand.

Topographic heterogeneity

Several measurements were available to describe topographic heterogeneity: the standard deviation of the elevation or the slope as well as the ratio of the total surface to one hectare. All are relatively high correlated (Supplementary Figure 2). However, the standard deviation of the slope should better capture subtle changes in topography than the standard deviation of elevation, as it is better distributed.

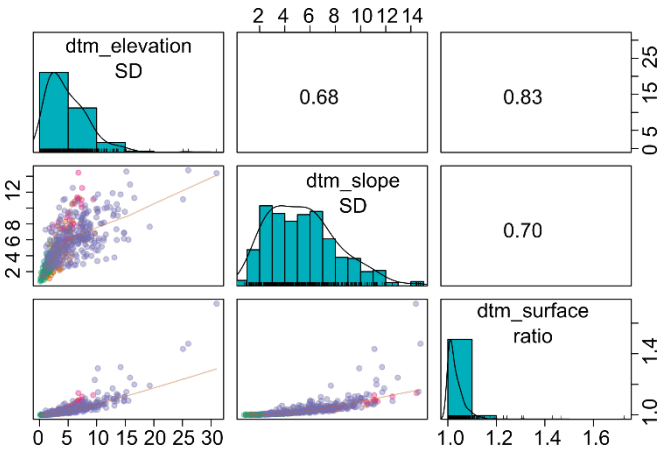

FIGURE C8.3.11: Correlation between single variables describing topographic heterogeneity, i.e. the standard deviation of elevation (dtm_elevation_sd), and of the slope (dtm_slope_sd) and the surface to area ratio (dtm_surface_ratio)

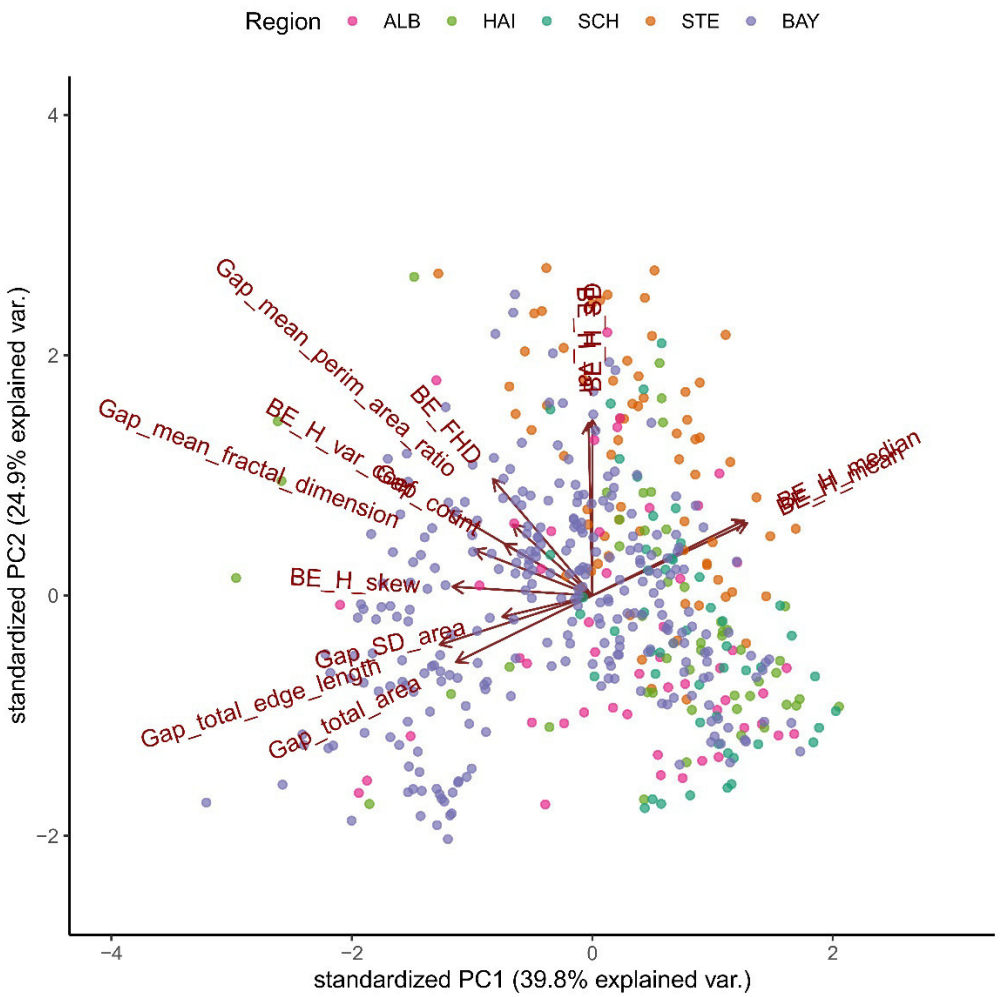

FIGURE C8.3.12: PCA of structural parameters.

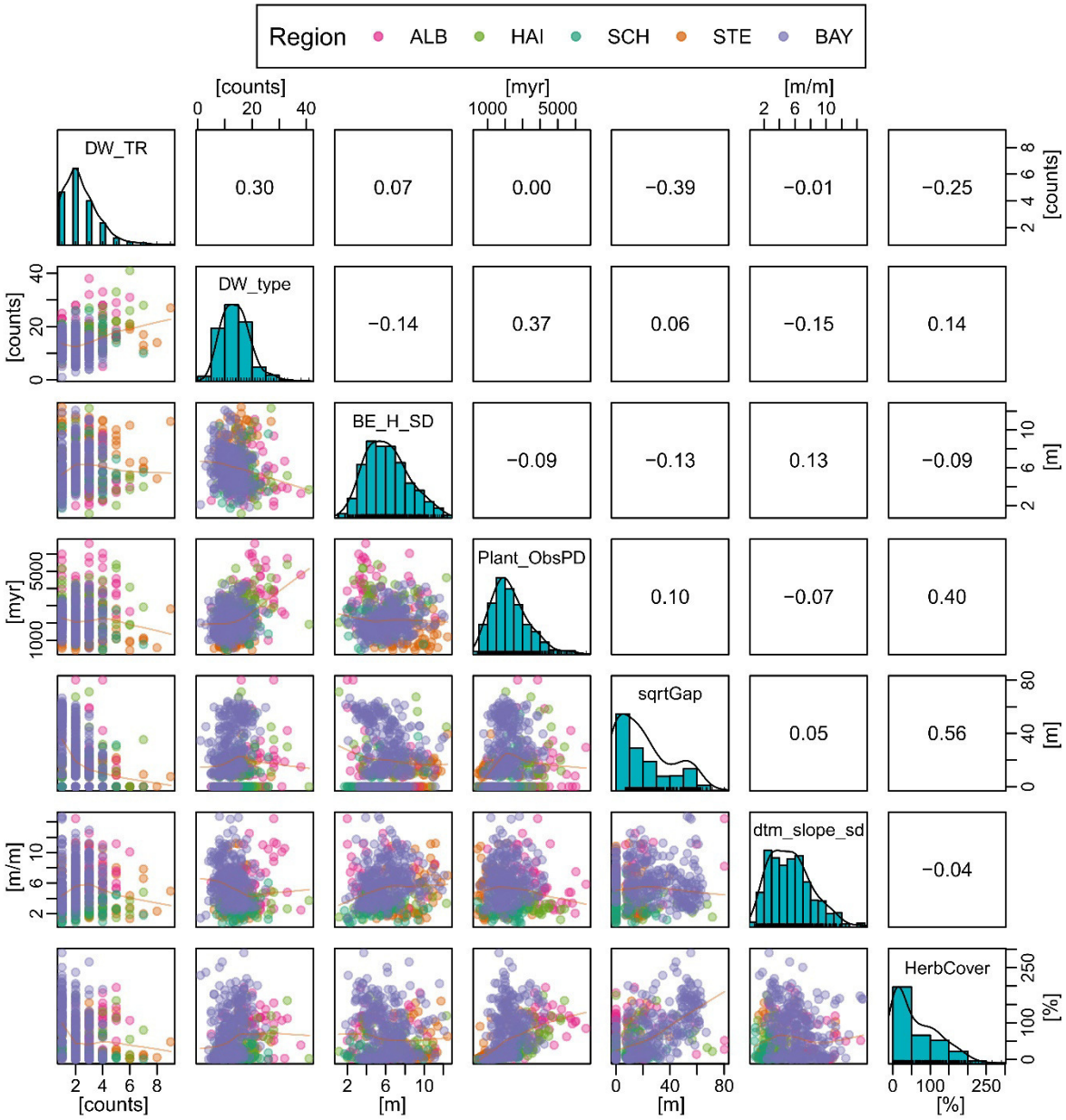

FIGURE C8.3.13: Correlation between selected variables

Supplementary notes: comments on the analyses

A formal assessment of model specification framed in terms of hypothesis testing necessarily compares the alternative hypothesis that the model is correct, or in line with a specific ecological theory, to the omnibus null hypothesis consisting of all remaining (in fact, infinitively many) models. Unlike in other testing situations, where the aim is to reject a simple model corresponding to the null hypothesis (for example, the equality of two treatments with respect to some measure of treatment success) with high power, one seeks to reject all null models in favour of a simple alternative one in this situation.

The technical difficulties with this setup often motivate data analysts to reverse the testing problem by associating the simple model (the one in line with a specific theory) to the null hypothesis and all remaining models to the alternative. Doing so has catastrophic consequences. With high power, for example very large sample sizes, as in our study with almost 500 observations, it will always be possible to find enough deviations from a simple model (because it is a model, after all) to justify a rejection of this model and thus the null hypothesis. Because the incentive for the data analyst is to 'accept' the simple model (and thus the null hypothesis), it is convenient to avoid high power, for example by looking at small sample sizes only. In this situation, there is only a very small probability of rejecting the null and thus a high probability that the simple model is declared 'acceptable'.

Consider the simple example of 'testing linearity'. Of course, a linear model is always preferred owing to its straightforward interpretability. One could, for example, add a quadratic term to the model and drop this term if the corresponding p-value is smaller than some threshold. However, given enough observations, this p-value will become very small even if the true model is close to linearity. To the contrary, the p-value will be relatively large in small samples indicating a linear relationship even if a plot of the data raises suspicions. An assessment of the effect size of the quadratic term, regardless of its p-value, is much more informative in this regard. The only way out of this dilemma is to accept that model choice is a subjective task which is impossible to cast into a (seemingly) objective procedure such as hypothesis testing. The estimation of functional forms, with or without subject-matter constraints such as monotonicity or convexity, is easily possible, for example in the generalised additive modelling framework. A graphical assessment of correspondingly estimated functions and their associated sampling variability (confidence bands, for example), are helpful tools guiding selection and interpretation of appropriate models. Hence, our approach using rigorously generalized additive models, combined with a graphical interpretation, does not suffer from the pathological situation described above and does not claim any error control (which is, theoretically, impossible to obtain in this situation).

Chapter 8.4

Radar vision in the mapping of forest biodiversity from space

with

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published in *Nature Communications* 10:4757 (2019), https://doi.org/10.1038/s41467-019-12737-x

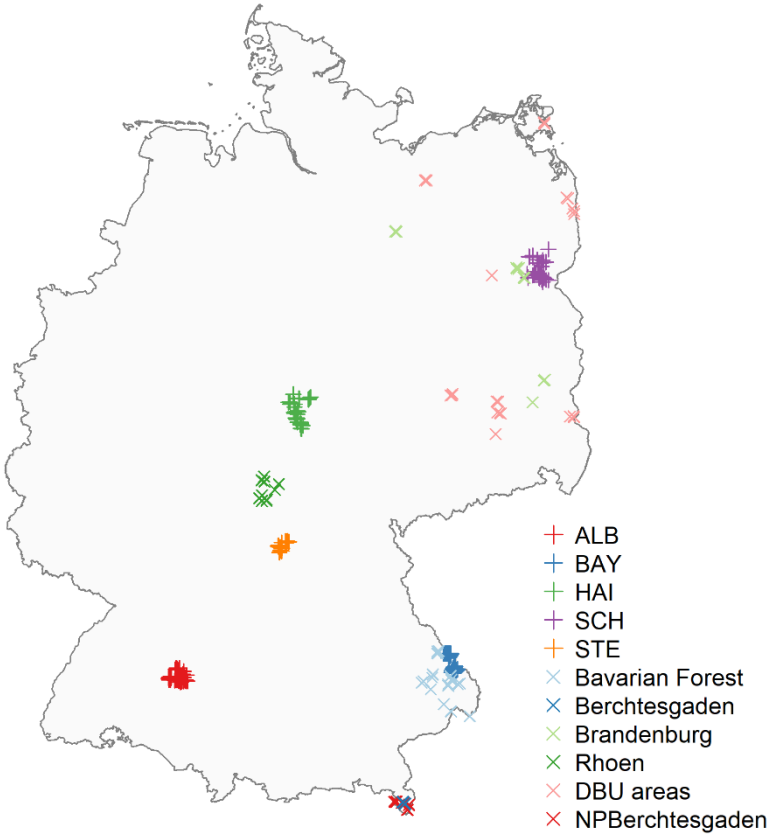

FIGURE C8.4.7 Distribution map of the plots. The first five regions are training regions; the remainder are the regions located outside the training regions and used in external validation.

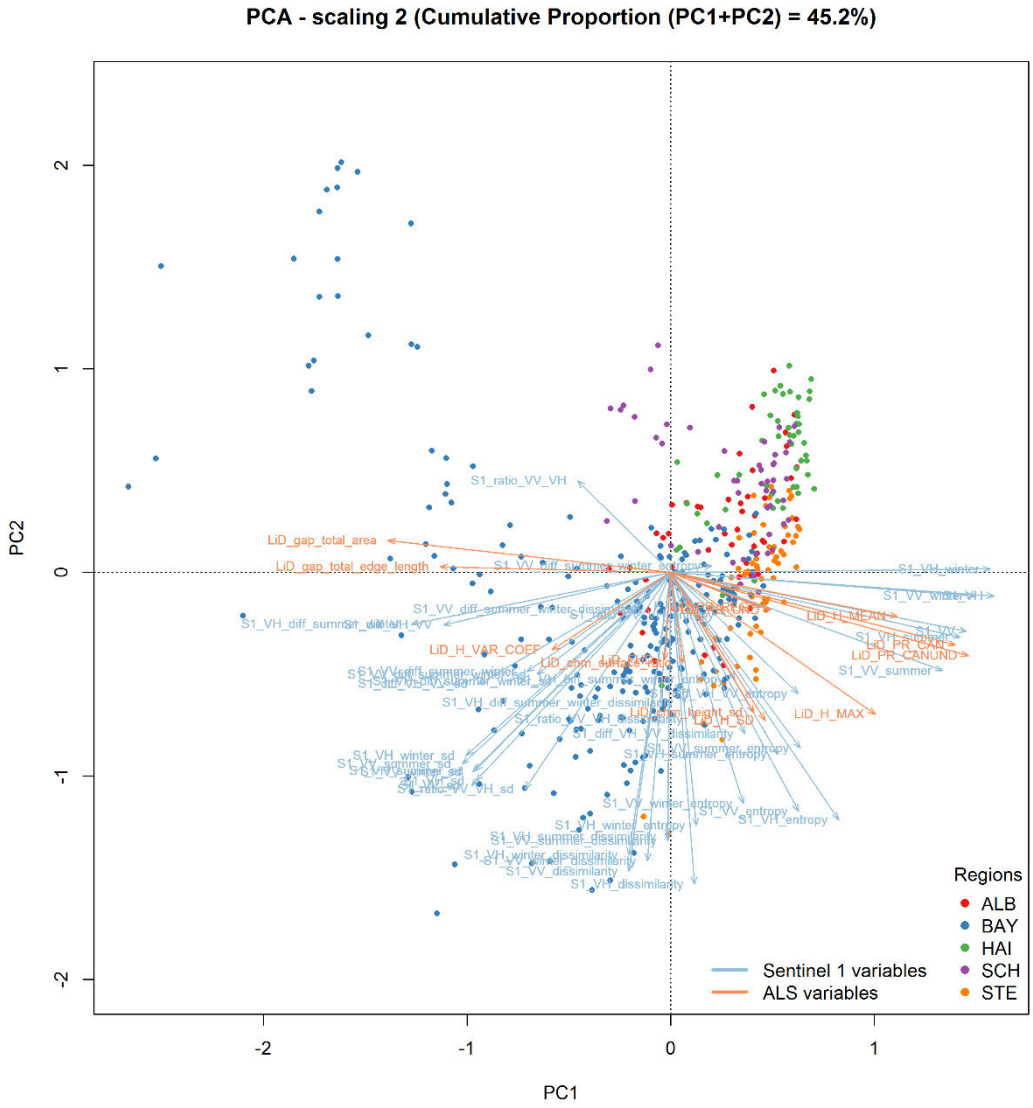

FIGURE C8.4.8 Principal components analysis of the metrics derived from the airborne laser scanning (ALS) and radar data sets. The first axis explained 24.40% of the variation in the 53 variables, 40 from radar and 13 from ALS, and was associated with forest maturity, e.g. the penetration ratio of canopy-understorey layers ($PR_{>2m}$) and the total area of forest gaps (Gap_{Area}), determined from the ALS data and the winter median of the vertically-sent, horizontally-received radar pulses (VH_{winter}) and of the vertically-sent, vertically-received radar pulses (VV_{winter}). The second axis explained 20.92% of the variation and was associated with structural heterogeneity: e.g. the standard deviation of the vegetation height (H_{SD}) and of the canopy surface height (CSH_{SD}) from the ALS data and the dissimilarity of VH and VV with respect to neighbouring pixels ($VH_{Diss}$and VV_{Diss}). Among the radar metrics, the standard deviation and image texture (i.e., dissimilarity and entropy) of the backscatters were closely related to the structural heterogeneity axes. The standard deviation of the vegetation returns (H_{SD}) and of the canopy surface height (CSH_{SD}) as well as the foliage height diversity (FHD) in the ALS metrics and the image texture of the backscatters in the radar metrics composed the second principle component.

Winter VH of the Schorfheide-Chorin area	Corine Land Cover Map of the Schorfheide-Chorin area

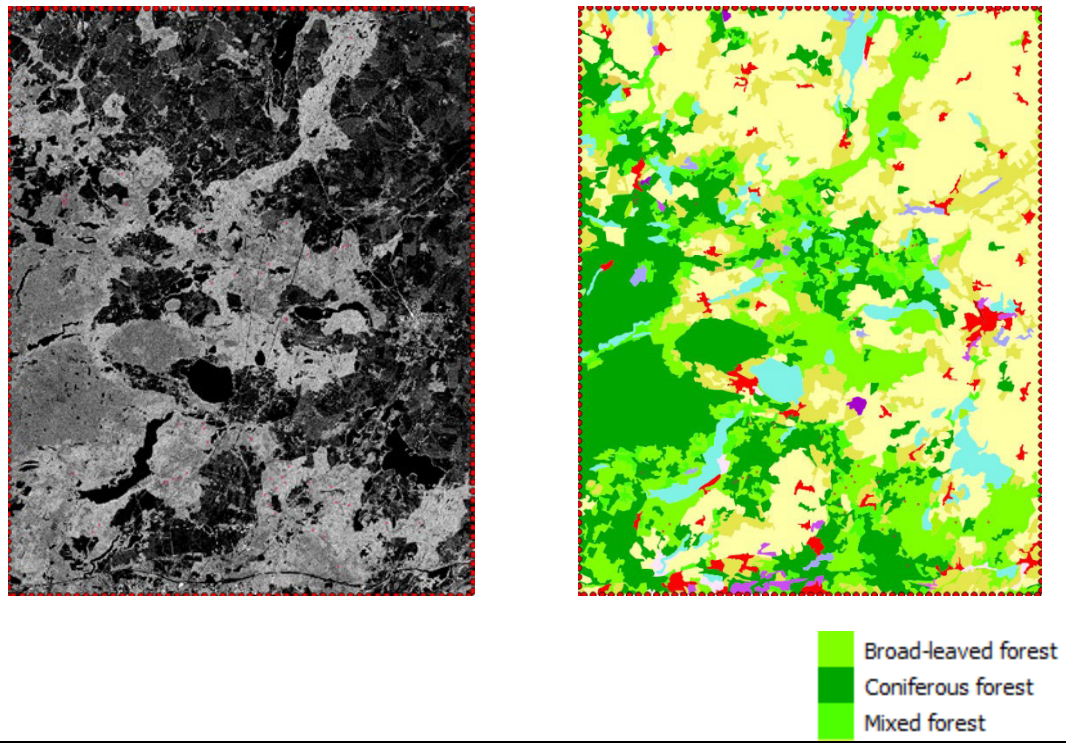

FIGURE C8.4.9 Visual comparison of the winter VH and the Corine Land Cover Map of the Schorfheide-Chorin area. Among the 40 explored metrics of the radar data, the yearly and winter VH (VH_{year} and VH_{winter}) best described forest maturity, consistent with previous studies showing the better discriminatory ability of VH for forest areas and biomass[1,2]. The ability of both variables to describe the forest area was also determined in a visual comparison of backscatter intensity and the Corine Land Cover map.

FIGURE C8.4.4: Non-metric multidimensional scaling (NMDS) of 12 functional groups

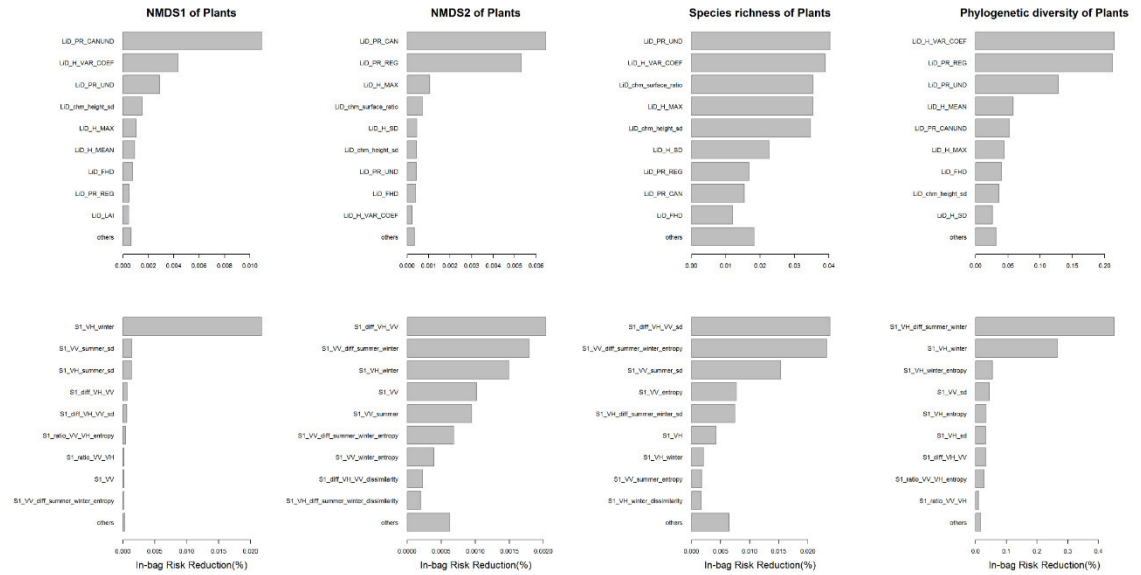

FIGURE C8.4.10: Importance of the variables in the assemblage habitat models (boosted generalised additive models, GAMs) of plants according to the ALS (first row) and radar (second row) data sets

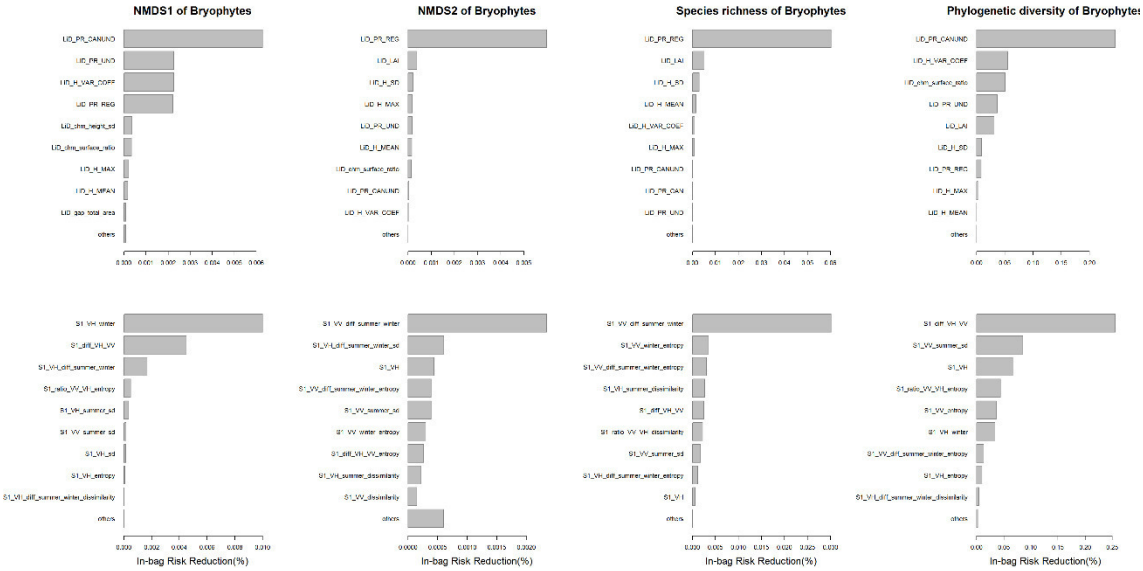

FIGURE C8.4.11: Importance of the variables in the assemblage habitat models (boosted GAMs) of bryophytes according to the ALS (first row) and radar (second row) data sets

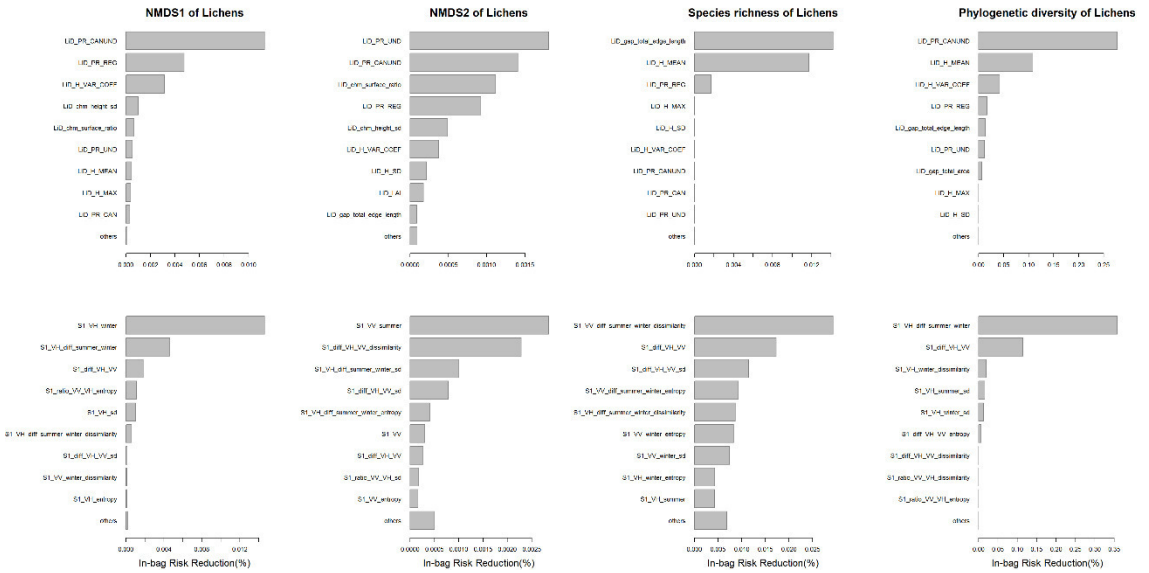

FIGURE C8.4.7: Importance of the variables in the assemblage habitat models (boosted GAMs) of lichens according to the ALS (first row) and radar (second row) data sets

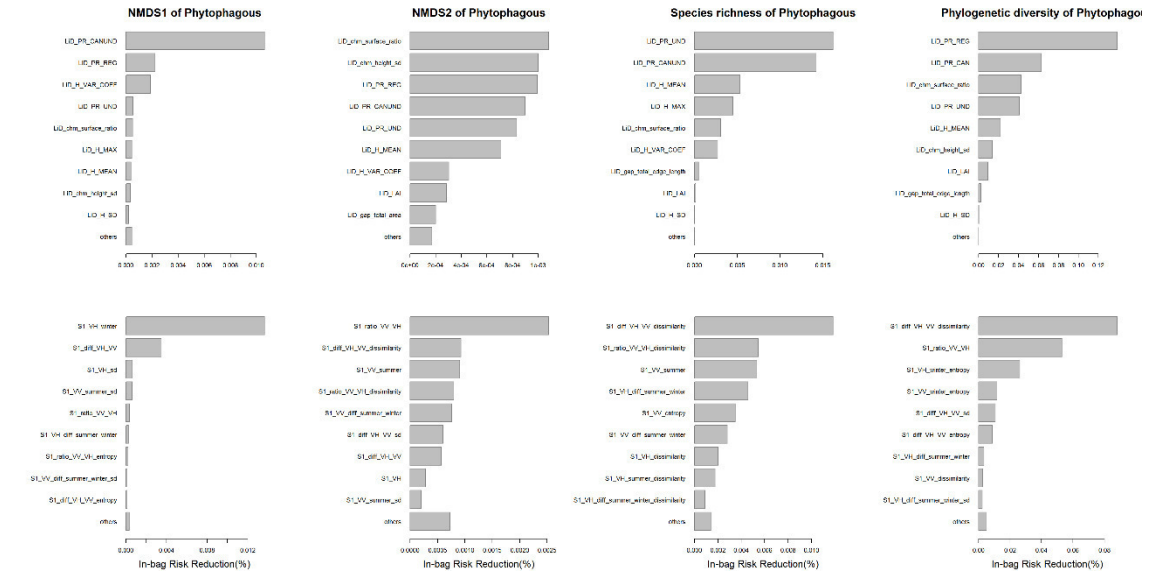

FIGURE C8.4.12: Importance of the variables in the assemblage habitat models (boosted GAMs) of phytophagous beetles according to the ALS (first row) and radar (second row) data sets

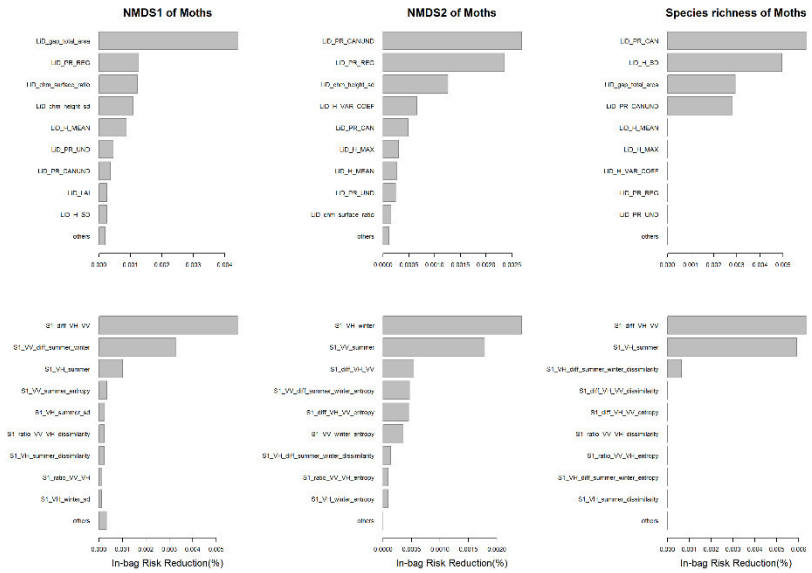

FIGURE C8.4.13: Importance of the variables in the assemblage habitat models (boosted GAMs) of moths according to the ALS (first row) and radar (second row) data sets

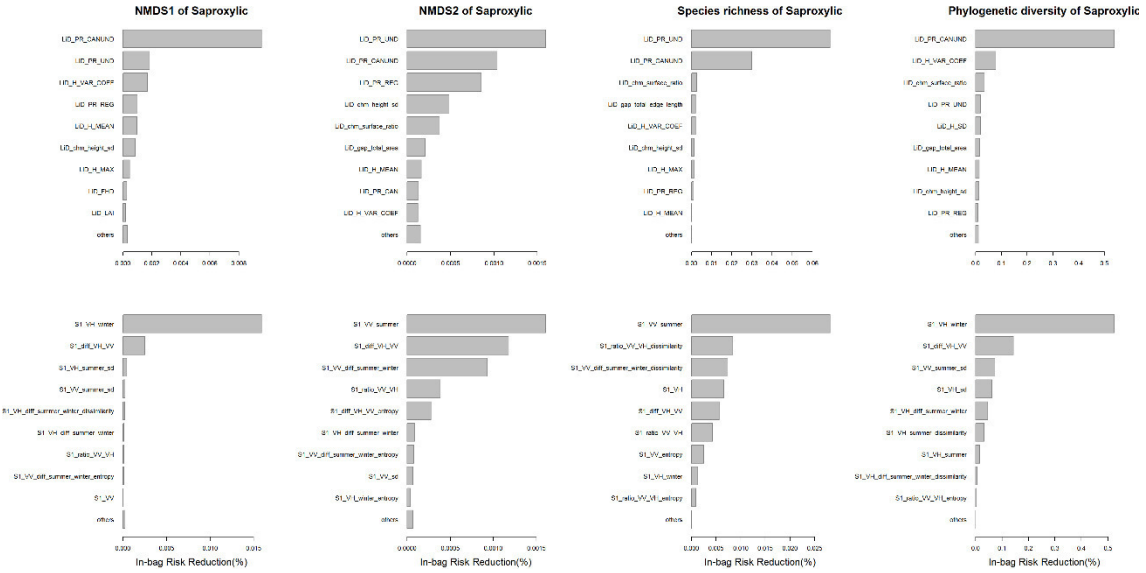

FIGURE C8.4.14 Importance of the variables in the assemblage habitat models (boosted GAMs) of saproxylic beetles according to the ALS (first row) and radar (second row) data sets

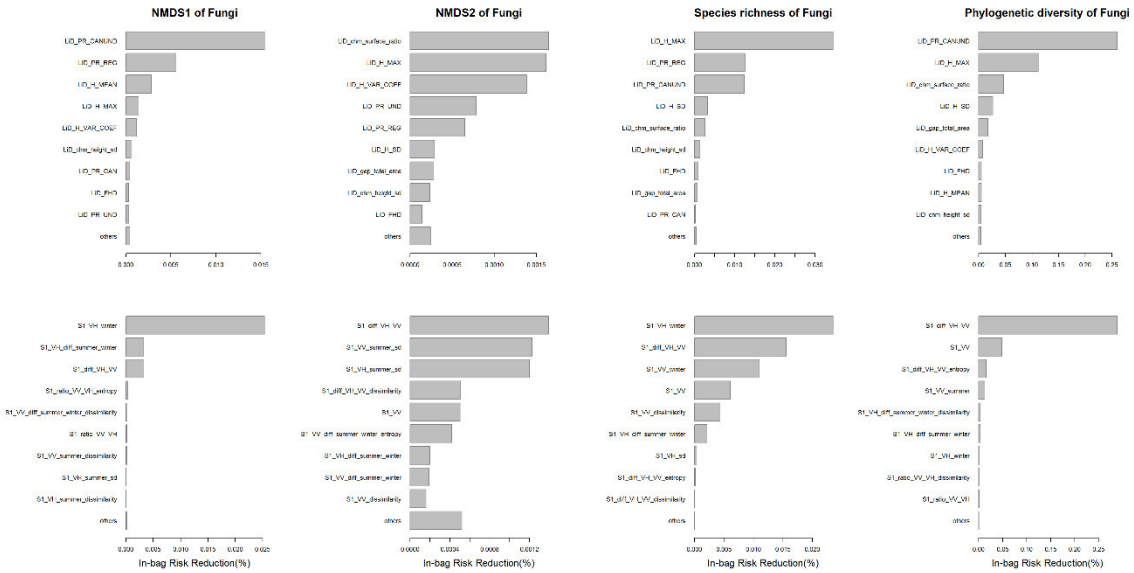

FIGURE C8.4.15: Importance of the variables in the assemblage habitat models (boosted GAMs) of fungi according to the ALS (first row) and radar (second row) data sets

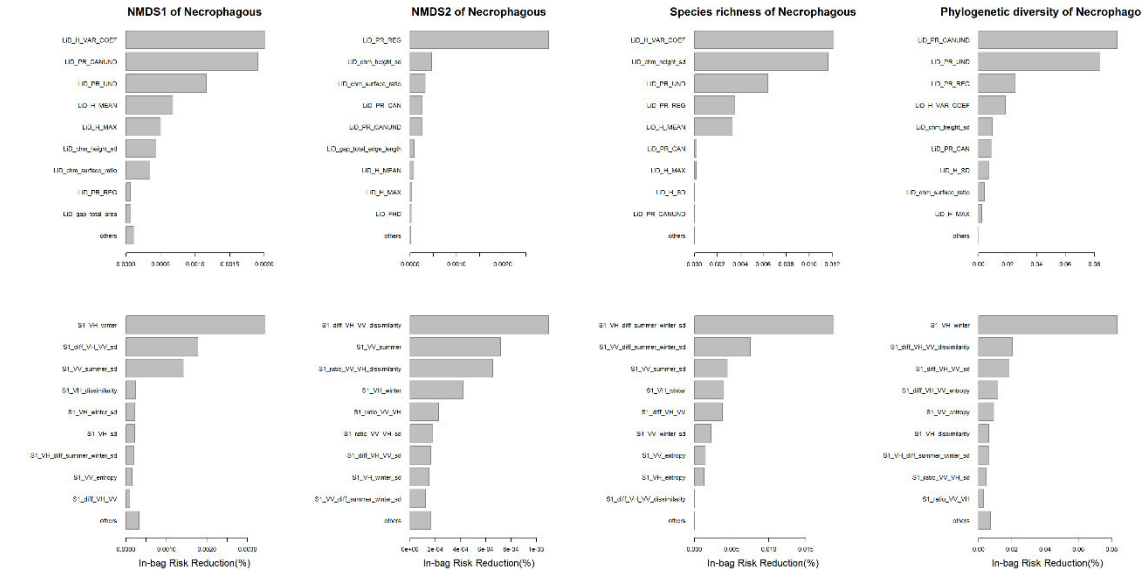

FIGURE C8.4.16: Importance of the variables in the assemblage habitat models (boosted GAMs) of necrophagous beetles according to the ALS (first row) and radar (second row) data sets

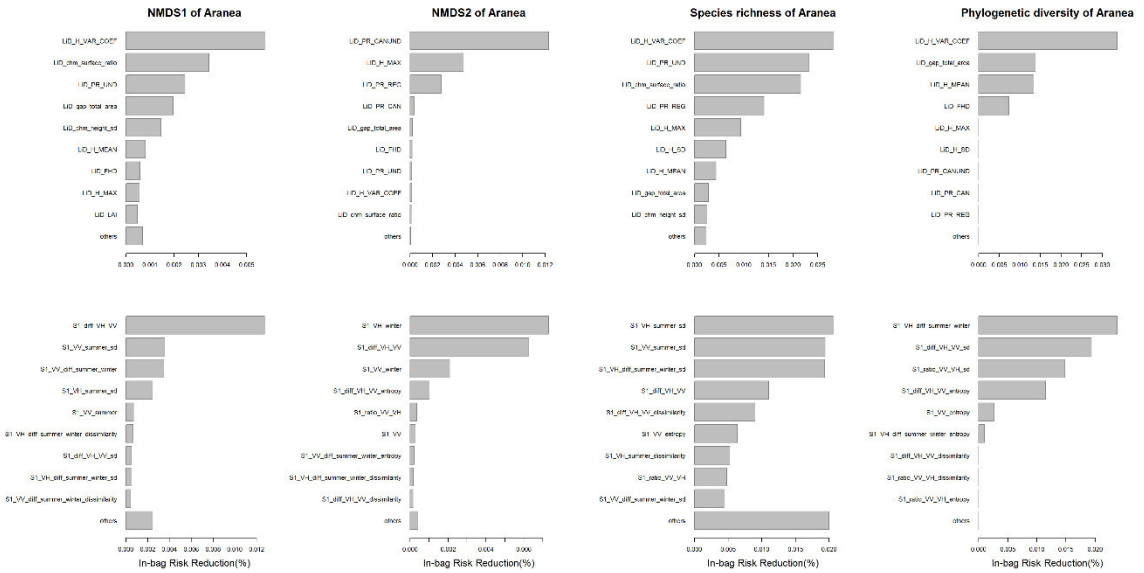

FIGURE C8.4.17: Importance of the variables in the assemblage habitat models (boosted GAMs) of spiders according to the ALS (first row) and radar (second row) data sets

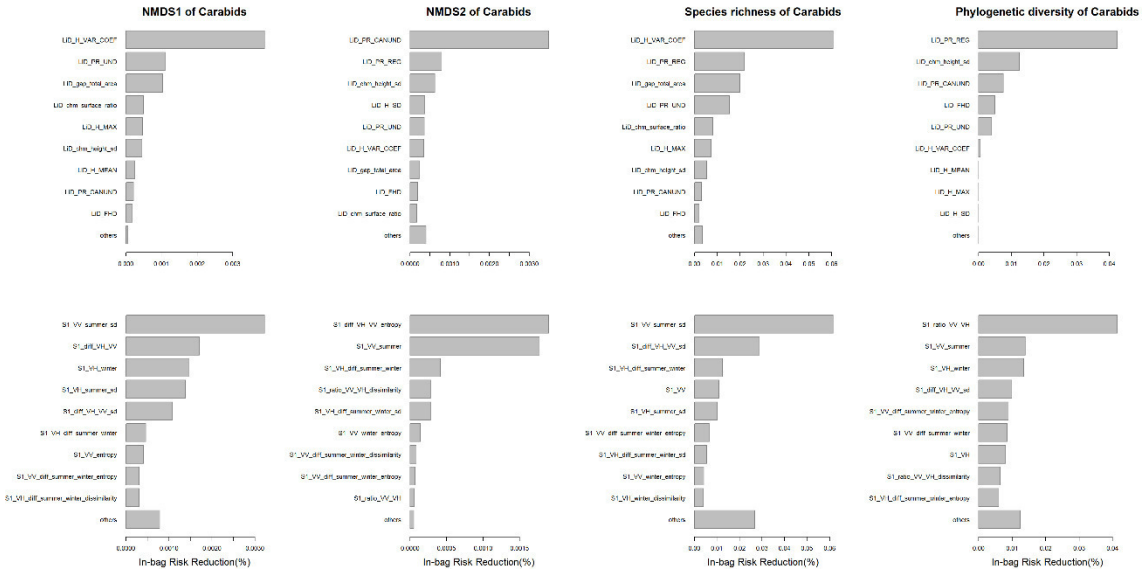

FIGURE C8.4.18: Importance of the variables in the assemblage habitat models (boosted GAMs) of carabid beetles according to the ALS (first row) and radar (second row) data sets

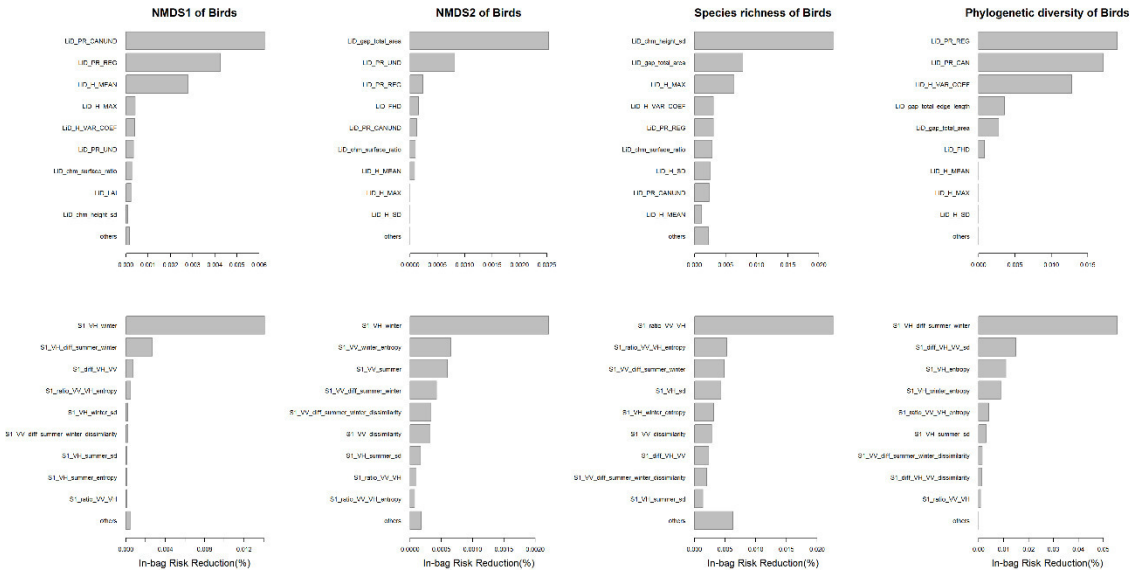

FIGURE C8.4.19: Importance of the variables in the assemblage habitat models (boosted GAMs) of birds according to the ALS (first row) and radar (second row) data sets

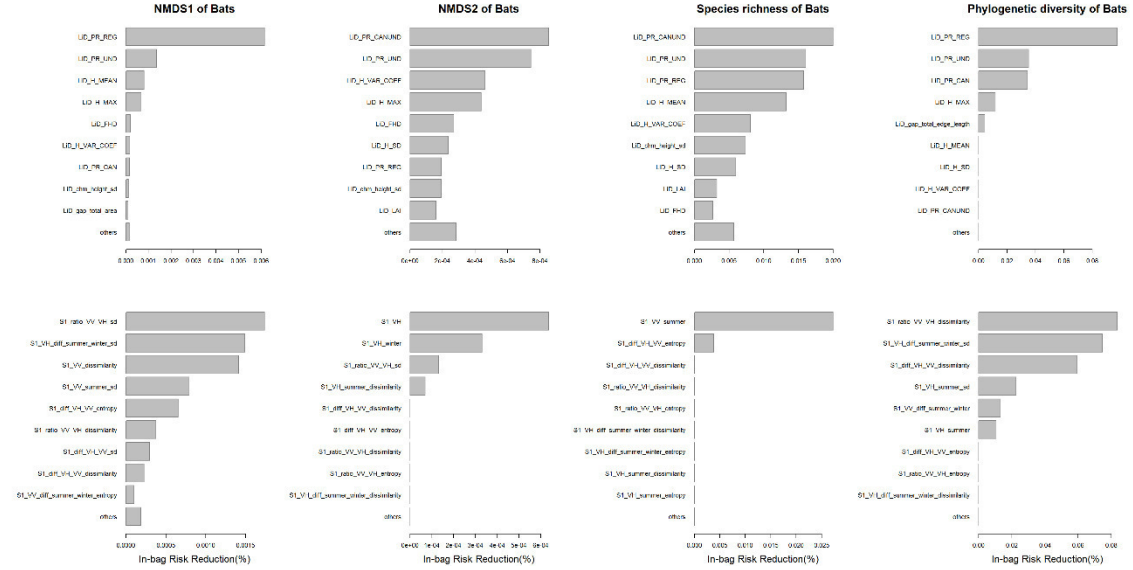

FIGURE C8.4.20: Importance of the variables in the assemblage habitat models (boosted GAMs) of bats according to the ALS (first row) and radar (second row) data sets

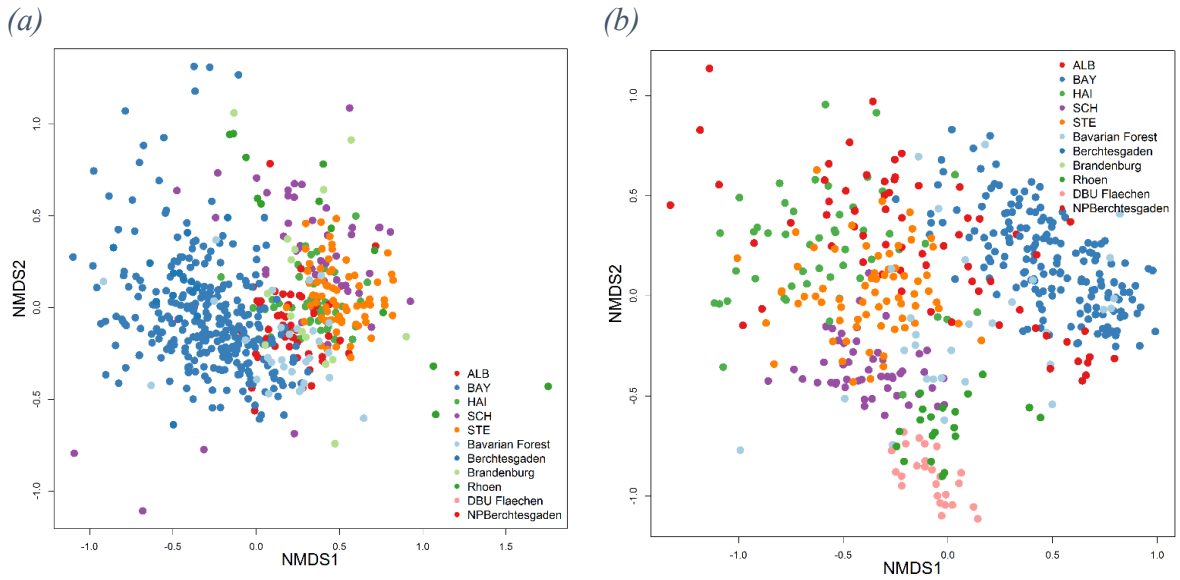

FIGURE C8.4.21: The assemblage composition of (a) birds and (b) saproxylic beetles in the different sampling regions as evaluated by NMDS. The first five regions were training regions, and the remainder external validating regions, located outside the training regions.

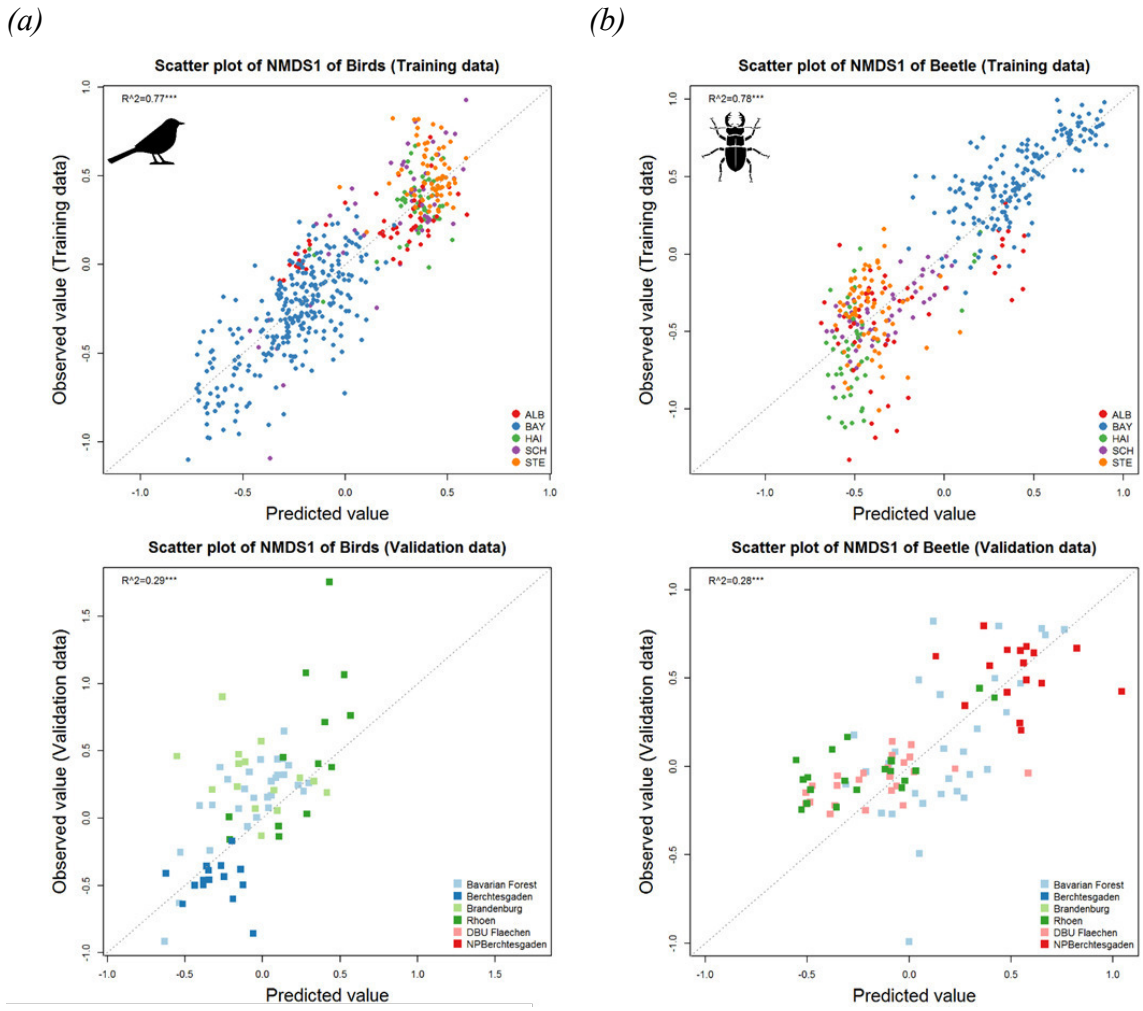

FIGURE C8.4.22: Scatter plots of the observed vs. the predicted values from the training and validation data of (a) birds and (b) saproxylic beetles.

(a) *(b)*

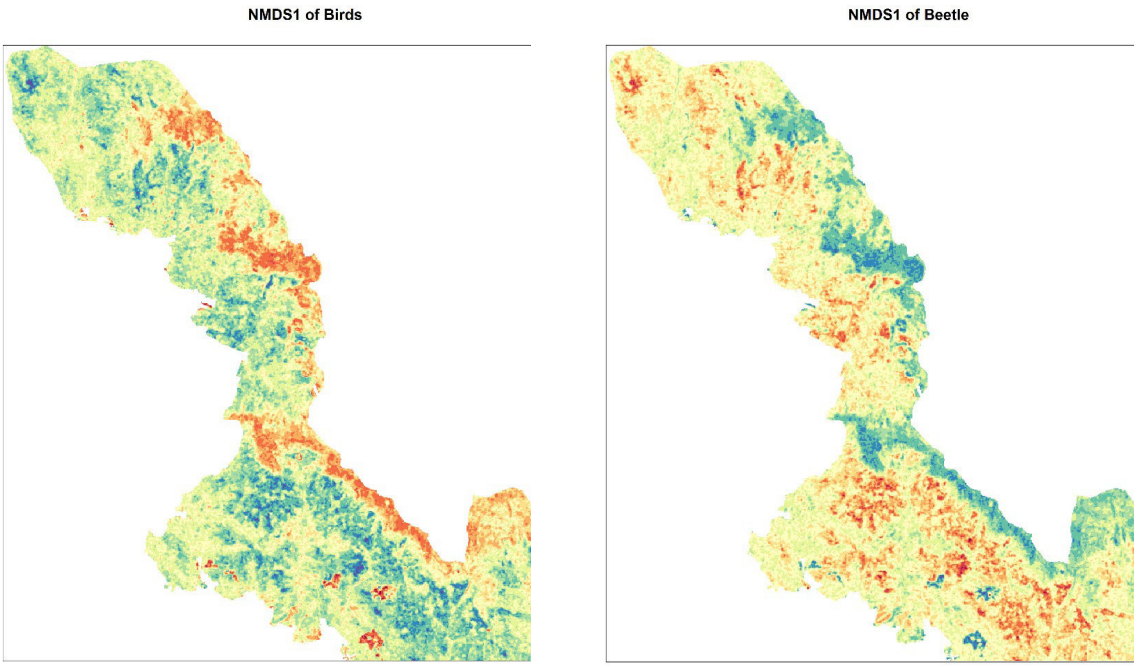

FIGURE C8.4.23: Predicted maps of the Bavarian Forest National Park.

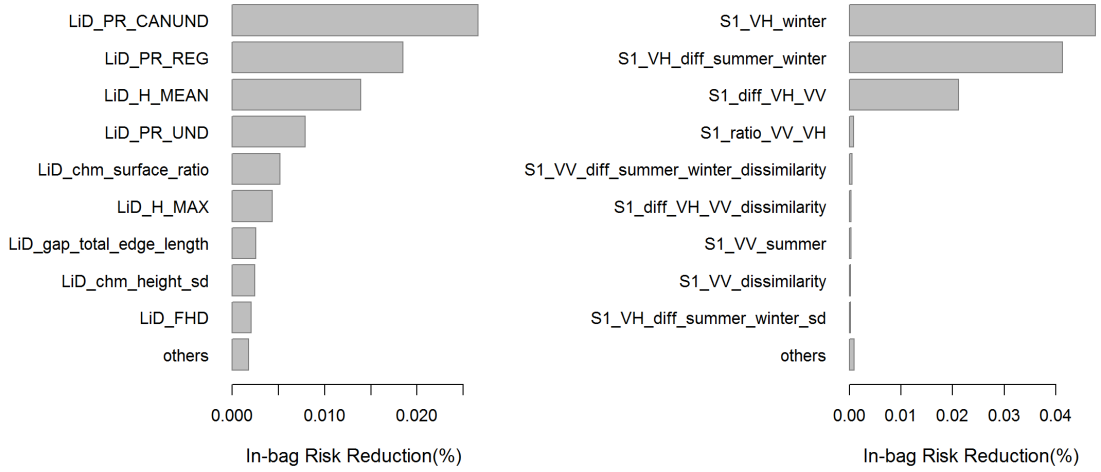

FIGURE C8.4.24: Importance of the variables in the coniferous ratio models (boosted GAMs) according to the ALS (first row) and radar (second row) data sets. In a supplementary analysis, the penetration ratio of the canopy-understorey layers ($PR_{>2m}$) and the winter VH (VH_{winter}) also dominated in terms of their importance in the ALS- and radar-based models, respectively, predicting the conifer tree ratio. However, the performance of the radar-based model (Pearson's r^2 of the observed vs. the predicted conifer ratio = 0.88, $p < 0.001$) was better than that of the ALS-based model (0.66, $p < 0.001$). Despite the demonstrated potential of multi-temporal ALS in the classification of tree species, the high costs and efforts required for multiple ALS acquisitions and data processing limit the availability of multi-temporal ALS data[44]. However, given the accessibility and attributes of radar backscatters reflecting both forest maturity and tree composition, two of the main drivers of local species turnover, and heterogeneity, the use of open-access, radar-based remote sensing data offers a promising approach to modelling the biodiversity of different functional and taxonomic groups.

TABLE C8.4.14 Radar metrics

	Variables	Description
*Median backscatter**		
VH	VH_{year}	Yearly median of VH polarisation
	VH_{winter}	Winter median of VH polarisation
	VH_{summer}	Summer median of VH polarisation
	$VH_{\text{s-w}}$	Difference between VH_{winter} and VH_{summer}
VV	VV_{year}	Yearly median of VV polarisation
	VV_{winter}	Winter median of VV polarisation
	VV_{summer}	Summer median of VV polarisation
	$VV_{\text{s-w}}$	Difference between VV_{winter} and VV_{summer}
VH and VV	$VH - VV$	Difference between VH_{year} and VV_{year}
	VV/VH	Ratio of VH_{year} and VV_{year}
*Heterogeneity indices**		
VH	$VH_{\text{year(DiS)}}$	Dissimilarity of VH_{year} with neighbourhood pixels
	$VH_{\text{year(ENT)}}$	Entropy of VH_{year} with neighbourhood pixels
	$VH_{\text{year(SD)}}$	Standard deviation of VH_{year} in a 1-ha plot
	$VH_{\text{winter(DiS)}}$	Dissimilarity of VH_{winter} with neighbourhood pixels
	$VH_{\text{winter(ENT)}}$	Entropy of VH_{winter} with neighbourhood pixels

	$VH_{\text{winter(SD)}}$	Standard deviation of VH_{winter} in a 1-ha plot
	$VH_{\text{summer(DiS)}}$	Dissimilarity of VH_{summer} with neighbourhood pixels
	$VH_{\text{summer(ENT)}}$	Entropy of VH_{summer} with neighbourhood pixels
	$VH_{\text{summer(SD)}}$	Standard deviation of VH_{summer} in a 1-ha plot
	$VH_{\text{s-w(DiS)}}$	Dissimilarity of $VH_{\text{s-w}}$ with neighbourhood pixels
	$VH_{\text{s-w(ENT)}}$	Entropy of $VH_{\text{s-w}}$ with neighbourhood pixels
	$VH_{\text{s-w(SD)}}$	Standard deviation of $VH_{\text{s-w}}$ in a 1-ha plot
VV	$VV_{\text{year(DiS)}}$	Dissimilarity of VV_{year} with neighbourhood pixels
	$VV_{\text{year(ENT)}}$	Entropy of VV_{year} with neighbourhood pixels
	$VV_{\text{year(SD)}}$	Standard deviation of VV_{year} in a 1-ha plot
	$VV_{\text{winter(DiS)}}$	Dissimilarity of VV_{winter} with neighbourhood pixels
	$VV_{\text{winter(ENT)}}$	Entropy of VV_{winter} with neighbourhood pixels
	$VV_{\text{winter(SD)}}$	Standard deviation of VV_{winter} in a 1-ha plot
	$VV_{\text{summer(DiS)}}$	Dissimilarity of VV_{summer} with neighbourhood pixels
	$VV_{\text{summer(ENT)}}$	Entropy of VV_{summer} with neighbourhood pixels
	$VV_{\text{summer(SD)}}$	Standard deviation of VV_{summer} in a 1-ha plot
	$VV_{\text{s-w(DiS)}}$	Dissimilarity of $VV_{\text{s-w}}$ with neighbourhood pixels
	$VV_{\text{s-w(ENT)}}$	Entropy of $VV_{\text{s-w}}$ with neighbourhood pixels
	$VV_{\text{s-w(SD)}}$	Standard deviation of $VV_{\text{s-w}}$ in a 1 ha plot
VH and VV	$VH - VV_{\text{(DiS)}}$	Dissimilarity of *VH-VV* with neighbourhood pixels
	$VH - VV_{\text{(ENT)}}$	Entropy of *VH-VV* with neighbourhood pixels
	$VH - VV_{\text{(SD)}}$	Standard deviation of *VH-VV* in a 1-ha plot
	$VV/VH_{\text{(DiS)}}$	Dissimilarity of *VV/VH* with neighbourhood pixels
	$VV/VH_{\text{(ENT)}}$	Entropy of *VV/VH* with neighbourhood pixels
	$VV/VH_{\text{(SD)}}$	Standard deviation of *VV/VH* in a 1-ha plot

* Median values are based on the averages within the 1-ha plots.** Dissimilarity and entropy were calculated based on a window size of 9 × 9 pixels, i.e. 0.81 ha, to consider the contrast and orderliness of the corresponding metrics within each plot

TABLE C8.4.15: ALS data sources

Region	Sensor	Year	Month	Flight height (m, agl)	Pulse density* (pls/m²)	Data provider
HAI	Riegl Q560	2008	August	400–600	8.2	Max-Planck-Institute for Biogeochemistry, Jena
ALB	Riegl Q560	2010	July	400–600	21.09	
SCH	Riegl Q560	2009	September	400–600	27.03	
STE	Riegl Q560/ VQ780i	2015 / 2018	September /Mai	650–700	40.07	Munich University of Applied Sciences
BAY	Riegl Q560	2007	Mai	350	33.25	Bavarian Forest National Park

* The pulse density was derived from the clipped point cloud per plot and aggregated as a median value for each region.

TABLE C8.4.16: ALS metrics

Variable	Description
H_{mean}	Mean height of vegetation returns
H_{max}	Maximum height of vegetation returns
H_{SD}	Standard deviation of the height of vegetation returns
H_{CV}	Coefficient of variation of the height of vegetation returns
$PR_{>5m}$	Penetration ratio of canopy layer (>5 m above ground)
$PR_{5m>h>2m}$	Penetration ratio of the understorey (2–5 m)
$PR_{2m>h>0m}$	Penetration ratio of the regeneration layer (below 2 m)

$PR_{>2m}$	Penetration ratio of the canopy-understorey layers (above 2 m)
FHD	Foliage height diversity*
Gap_{Edge}	Total edge length of gaps (square-root-transformed)
Gap_{Area}	Total area of gaps (square-root-transformed)
CSM_{Ratio}	Ratio between the values of the canopy surface and flat areas
CSM_{SD}	Standard deviation of the canopy surface height

* Foliage height diversity was calculated for the canopy, understorey and regeneration layers.

TABLE C8.4.17: Summary of the results of the canonical correlation analysis. The first and secondaxes showed the highest canonical correlation coefficients (the correlation between the pairs of canonical axes from the two datasets), 0.92 and 0.75, and explained 54.01% and 13.18% of the variance respectively. The canonical correlation coefficients of the third and fourth axes were also high, 0.68 and 0.62 respectively, and explained 8.64% and 6.41% of the variance, with the cumulative variance of the first four axes accounting for 82.24% of the total variance.

Canonical correlation pair	Canonical correlation	Eigenvalue	Variance (%)	Cumulative variance (%)	Statistic value	*F* value	Num *df*	Den *df*	*p* value
1	0.92	5.30	54.01	54.01	0.00489	5.29	520	5126.7	< 0.0001
2	0.75	1.29	13.18	67.19	0.03085	3.60	468	4763.6	< 0.0001
3	0.68	0.85	8.64	75.83	0.07077	2.99	418	4395.6	<0.0001
4	0.62	0.63	6.41	82.24	0.13082	2.54	370	4022.4	< 0.0001
5	0.57	0.48	4.89	87.14	0.21322	2.17	324	3643.9	< 0.0001
6	0.48	0.30	3.09	90.23	0.31562	1.85	280	3260	< 0.0001
7	0.44	0.25	2.51	92.73	0.41144	1.66	238	2870.5	< 0.0001
8	0.40	0.19	1.90	94.64	0.51272	1.49	198	2475.5	< 0.0001
9	0.38	0.16	1.67	96.30	0.60856	1.37	160	2074.9	< 0.001
10	0.35	0.14	1.43	97.74	0.70812	1.22	124	1668.9	0.0555
11	0.31	0.11	1.11	98.84	0.80781	1.03	90	1257.8	0.3988
12	0.24	0.06	0.64	99.48	0.89549	0.82	58	842	0.8226
13	0.22	0.05	0.52	100	0.95167	0.77	28	422	0.8021

TABLE C8.4.18: Pearson's correlation coefficient for the ALS metrics vs. axes 1–9 of the canonical correlation analysis (Ycan1–9)

	Ycan1	Ycan2	Ycan3	Ycan4	Ycan5	Ycan6	Ycan7	Ycan8	Ycan9
H_{mean}	−0.70	0.09	−0.19	0.01	−0.08	0.14	**−0.63**	0.05	0.04
H_{max}	−0.71	0.35	0.14	−0.05	0.19	−0.01	−0.47	−0.17	−0.04
H_{SD}	−0.40	**0.58**	0.13	−0.29	**0.43**	−0.04	−0.19	−0.16	0.03
H_{CV}	0.28	0.44	0.30	**−0.35**	0.30	**−0.20**	0.41	−0.16	**−0.19**
$PR_{h>2m}$	**−0.94**	−0.18	0.00	0.16	0.03	−0.03	−0.07	−0.13	0.07
$PR_{h>5m}$	**−0.89**	−0.18	−0.03	0.21	0.03	0.02	−0.22	−0.12	0.04
$PR_{2m>h>0m}$	−0.33	0.36	**−0.45**	−0.27	**0.54**	−0.07	0.04	0.25	**−0.19**
$PR_{5m>h>2m}$	−0.35	0.18	−0.09	−0.27	0.13	**−0.37**	**0.55**	**−0.39**	**0.23**
FHD	−0.10	**0.45**	0.04	**−0.46**	**0.46**	0.13	**0.51**	0.00	0.01
Gap_{Edge}	0.65	0.15	**0.33**	**−0.31**	−0.04	**−0.23**	0.22	**0.33**	0.07
Gap_{Area}	**0.81**	0.30	0.19	−0.16	−0.08	−0.16	0.15	**0.28**	0.02
CSM_{Ratio}	−0.08	0.16	0.22	−0.14	0.29	0.18	−0.36	−0.12	−0.07
CSM_{SD}	−0.39	**0.53**	**0.32**	−0.30	0.00	0.06	−0.32	−0.11	−0.10

We indicated the top 25th percentile of correlation coefficients per canonical axis with bold numbers

TABLE C8.4.19: Pearson's correlation coefficient for the radar metrics vs. axes 1–9 of the canonical correlation analysis (Xcan 1–9)

	Xcan 1	Xcan 2	Xcan 3	Xcan 4	Xcan 5	Xcan 6	Xcan 7	Xcan 8	Xcan 9
VH_{year}	**−0.89**	−0.09	−0.10	**−0.30**	−0.02	−0.02	0.13	−0.11	0.04
VH_{winter}	**−0.88**	−0.06	−0.25	**−0.26**	−0.04	−0.06	0.13	−0.02	0.01
VH_{summer}	**−0.79**	−0.13	0.13	**−0.27**	0.04	0.11	0.06	**−0.24**	0.00
$VH_{\text{s−w}}$	**0.72**	−0.01	0.47	0.19	0.09	**0.17**	−0.15	−0.15	−0.02
VV_{year}	**−0.83**	0.01	0.10	**−0.40**	−0.10	−0.08	**0.17**	−0.11	−0.06
VV_{winter}	**−0.84**	0.05	−0.11	**−0.39**	−0.07	−0.06	**0.16**	−0.02	−0.08
VV_{summer}	**−0.80**	−0.02	0.26	**−0.26**	−0.13	−0.02	0.15	−0.19	−0.05
$VV_{\text{s−w}}$	0.34	−0.11	**0.56**	0.30	−0.06	0.08	−0.07	**−0.24**	0.07
$VH - VV$	**0.60**	0.24	0.41	−0.02	−0.12	−0.11	0.01	0.06	**−0.20**
VV/VH	0.30	−0.25	−0.40	**0.38**	0.22	0.16	**−0.17**	0.06	**0.20**
$VH_{\text{year(DiS)}}$	−0.30	0.19	**0.64**	−0.02	**0.38**	0.10	−0.01	0.11	0.07
$VH_{\text{year(ENT)}}$	**−0.59**	−0.20	**0.57**	0.08	0.18	0.12	0.15	0.02	−0.11
$VH_{\text{year(SD)}}$	0.19	**0.69**	0.34	0.24	0.08	0.05	−0.05	**0.21**	0.13
$VH_{\text{winter(DiS)}}$	−0.08	−0.08	**0.75**	0.19	0.25	**0.17**	0.00	0.18	0.09
$VH_{\text{winter(ENT)}}$	−0.20	−0.25	**0.72**	0.24	0.15	**0.19**	0.09	0.11	0.06
$VH_{\text{winter(SD)}}$	0.26	0.57	0.31	**0.34**	0.08	0.07	0.05	**0.25**	0.09
$VH_{\text{summer(DiS)}}$	−0.13	−0.03	**0.50**	0.05	**0.33**	0.02	−0.01	0.19	−0.01
$VH_{\text{summer(ENT)}}$	−0.33	**−0.36**	0.35	0.14	0.21	0.03	0.09	0.08	**−0.14**
$VH_{\text{summer(SD)}}$	0.22	**0.67**	0.34	0.15	0.12	0.04	0.00	**0.26**	0.07
$VH_{\text{s−w(DiS)}}$	−0.20	−0.01	0.36	0.14	0.07	**0.25**	−0.14	−0.03	**0.34**
$VH_{\text{s−w(ENT)}}$	−0.36	−0.04	0.35	0.14	−0.10	**0.28**	**−0.17**	0.02	**0.29**
$VH_{\text{s−w(SD)}}$	0.15	0.31	0.17	0.09	**0.30**	0.01	**0.25**	0.11	−0.07
$VV_{\text{year(DiS)}}$	−0.10	0.27	**0.52**	−0.06	**0.44**	0.08	−0.02	0.12	−0.05
$VV_{\text{year(ENT)}}$	−0.43	−0.15	0.46	−0.01	0.29	0.10	0.13	−0.02	**−0.19**
$VV_{\text{year(SD)}}$	0.20	**0.67**	0.37	0.24	0.10	0.08	−0.05	**0.23**	0.13
$VV_{\text{winter(DiS)}}$	−0.12	−0.07	**0.66**	0.14	**0.37**	−0.02	0.10	0.02	−0.05
$VV_{\text{winter(ENT)}}$	−0.28	−0.35	**0.63**	0.14	0.18	0.03	**0.20**	0.05	−0.11
$VV_{\text{winter(SD)}}$	0.21	**0.56**	0.33	**0.29**	0.12	0.06	0.00	**0.22**	0.10
$VV_{\text{summer(DiS)}}$	−0.14	0.06	0.41	0.10	**0.49**	−0.07	−0.03	0.20	−0.02
$VV_{\text{summer(ENT)}}$	−0.38	−0.30	0.22	0.19	**0.41**	−0.07	0.05	0.07	−0.08
$VV_{\text{summer(SD)}}$	0.26	**0.68**	0.32	0.19	0.10	0.11	0.02	**0.24**	**0.17**
$VV_{\text{s−w(DiS)}}$	0.02	0.06	0.09	−0.22	−0.14	−0.11	**0.23**	−0.08	**0.47**
$VV_{\text{s−w(ENT)}}$	−0.09	−0.01	0.12	−0.22	**−0.33**	0.01	0.09	−0.04	**0.30**
$VV_{\text{s−w(SD)}}$	0.20	0.35	0.08	−0.03	0.21	−0.04	0.06	**0.21**	0.05
$VH - VV_{\text{(DiS)}}$	−0.40	**0.39**	0.24	0.18	0.23	**−0.23**	−0.02	0.00	0.06
$VH - VV_{\text{(ENT)}}$	**−0.51**	0.34	0.27	0.16	−0.03	**−0.40**	−0.02	0.01	−0.01
$VH - VV_{\text{(SD)}}$	0.38	0.32	0.13	0.15	**0.35**	0.01	0.22	0.20	−0.05
$VV/VH_{\text{(DiS)}}$	−0.21	0.33	0.03	0.14	**0.34**	**−0.39**	**−0.16**	0.05	−0.12
$VV/VH_{\text{(ENT)}}$	−0.20	0.23	−0.03	0.14	0.02	**−0.62**	**−0.22**	−0.05	**−0.19**
$VV/VH_{\text{(SD)}}$	0.09	**0.57**	0.34	0.12	0.26	0.08	0.05	**0.27**	0.12

TABLE C8.4.6 continued; *We indicated the top 25th percentile of correlation coefficients per canonical axis with bold numbers.*

TABLE C8.4.20: Cross-validated performance (R^2, coefficient of determination) of the assemblage habitat models (boosted generalised additive models, GAMs) in the fixed effects models using the ALS and radar data sets.

	ALS models					Radar models				
	NMDS1	NMDS2	NMDS3	Species richness	Phylogenetic diversity	NMDS1	NMDS2	NMDS3	Species richness	Phylogenetic diversity
Plants	0.49	0.46	-	0.27	0.24	0.58	0.24	-	0.06	0.38
Bryophytes	0.39	0.32	0.08	0.16	0.23	0.55	0.17	0.17	0.09	0.31
Lichens	0.56	0.22	-	0.03	0.14	0.66	0.28	-	0.07	0.22
Phytophagous	0.57	0.23	0.28	0.18	0.27	0.69	0.35	0.16	0.13	0.14
Moths	0.37	0.41	-	0.04	0.13	0.43	0.34	-	0.01	0.12
Saproxylic	0.57	0.28	0.48	0.27	0.32	0.71	0.30	0.24	0.14	0.39
Fungi	0.62	0.36	0.11	0.39	0.41	0.78	0.27	0.05	0.36	0.34
Necrophagous	0.35	0.25	0.06	0.04	0.26	0.43	0.20	0.06	0.09	0.14
Spiders	0.33	0.69	0.37	0.38	0.05	0.56	0.58	0.14	0.34	0.03
Carabids	0.25	0.48	-	0.39	0.06	0.44	0.36	-	0.38	0.04
Birds	0.55	0.17	0.38	0.24	0.03	0.70	0.18	0.20	0.31	0.10
Bats	0.54	0.13	-	0.16	0.02	0.40	0.05	-	0.07	0.08
Median of 12 taxa	0.51	0.30	0.28	0.21	0.21	0.57	0.27	0.16	0.11	0.14

TABLE C8.4.21: Cross-validated performance (root mean square error) of the assemblage habitat models (boosted GAMs) in the fixed effects models using the ALS and radar data sets.

	ALS models					Radar models				
	NMDS1	NMDS2	NMDS3	Spe-cies rich-ness	Phylogenetic diversity	NMDS1	NMDS2	NMDS3	Species rich-ness	Phylogenetic diversity
Plants	0.48	0.41	-	0.72	1.32	0.44	0.48	-	0.82	1.19
Bryophytes	0.39	0.33	0.34	0.50	1.02	0.34	0.36	0.32	0.52	0.97
Lichens	0.46	0.45	-	0.66	1.17	0.41	0.43	-	0.65	1.12
Phytophagous	0.37	0.42	0.37	0.38	0.81	0.31	0.38	0.40	0.39	0.87
Moths	0.34	0.28	-	0.35	0.76	0.33	0.30	-	0.35	0.74
Saproxylic	0.30	0.28	0.23	0.48	1.16	0.25	0.27	0.28	0.52	1.10
Fungi	0.37	0.31	0.33	0.31	0.76	0.28	0.33	0.34	0.31	0.80
Necrophagous	0.35	0.33	0.32	0.43	0.71	0.33	0.34	0.32	0.42	0.77
Spiders	0.45	0.25	0.29	0.38	0.78	0.37	0.29	0.34	0.39	0.79
Carabids	0.47	0.36	-	0.43	0.72	0.41	0.41	-	0.43	0.73
Birds	0.27	0.29	0.23	0.31	0.73	0.22	0.28	0.26	0.30	0.70
Bats	0.36	0.38	-	0.46	1.22	0.41	0.40	-	0.49	1.18
Median of 12 taxa	0.37	0.33	0.32	0.43	0.81	0.33	0.35	0.32	0.43	0.86

TABLE C8.4.22: Cross-validated performance (R^2) of the assemblage habitat models (boosted GAMs) in the mixed effects models using the ALS and radar data sets. The construction of the mixed effects models included the effect of region as a random factor. R^2 was calculated based only on fixed factors, to exclude the region effect (random factor), denoted as Fixed (F), and only on a random factor, denoted as Random (R). F+R denote the aggregated R^2 based on both the F and the R factors.

		ALS models					Radar models				
		NMDS1	NMDS2	NMDS3	Species richness	Phylogenetic diversity	NMDS1	NMDS2	NMDS3	Species richness	Phylogenetic diversity
Plants	F+R	0.78	0.56	-	0.53	0.51	0.77	0.45	-	0.42	0.51
	Fixed	0.20	0.27	-	0.01	0.00	0.30	0.17	-	−0.05	0.12
	Random	0.70	0.28	-	0.40	0.51	0.67	0.28	-	0.41	0.48
Bryophytes	F+R	0.72	0.55	0.33	0.30	0.51	0.75	0.55	0.37	0.31	0.50
	Fixed	0.14	0.02	−0.02	0.01	0.12	0.34	0.03	0.03	0.01	0.13
	Random	0.68	0.55	0.37	0.31	0.48	0.63	0.55	0.35	0.31	0.47
Lichens	F+R	0.82	0.45	-	0.35	0.21	0.80	0.51	-	0.33	0.21
	Fixed	0.24	0.14	-	−0.01	0.14	0.36	0.11	-	0.03	0.21
	Random	0.75	0.36	-	0.32	0.07	0.69	0.37	-	0.30	−0.04
Phytophagous	F+R	0.82	0.65	0.48	0.34	0.50	0.82	0.65	0.46	0.20	0.48
	Fixed	0.30	0.02	0.14	0.11	0.04	0.48	0.07	0.10	0.05	0.01
	Random	0.72	0.65	0.32	0.19	0.48	0.66	0.64	0.33	0.17	0.47
Moths	F+R	0.78	0.74	-	0.21	0.23	0.78	0.72	-	0.19	0.29
	Fixed	0.07	0.15	-	0.01	0.12	0.10	0.13	-	-0.01	0.08
	Random	0.77	0.70	-	0.19	0.19	0.76	0.69	-	0.19	0.22
Saproxylic	F+R	0.80	0.60	0.56	0.44	0.48	0.80	0.52	0.51	0.34	0.47
	Fixed	0.32	0.12	0.07	0.23	0.21	0.53	0.14	0.05	0.04	0.30
	Random	0.67	0.40	0.49	0.30	0.38	0.56	0.41	0.48	0.31	0.32
Fungi	F+R	0.76	0.52	0.22	0.40	0.41	0.79	0.54	0.12	0.41	0.33
	Fixed	0.42	0.12	0.09	0.37	0.40	0.76	0.09	0.06	0.36	0.33
	Random	0.51	0.46	0.07	0.08	0.01	0.20	0.46	0.07	0.07	−0.01
Necrophagous	F+R	0.61	0.43	0.26	0.22	0.36	0.61	0.44	0.22	0.22	0.30
	Fixed	0.09	0.00	0.03	−0.04	0.16	0.18	0.06	0.00	0.01	0.06
	Random	0.58	0.44	0.23	0.22	0.27	0.56	0.41	0.22	0.20	0.28
Spiders	F+R	0.86	0.72	0.43	0.63	0.08	0.85	0.65	0.40	0.61	0.05
	Fixed	−0.04	0.61	0.00	0.03	0.04	0.04	0.55	0.02	0.11	0.00
	Random	0.85	0.25	0.35	0.57	0.04	0.84	0.21	0.35	0.57	0.04
Carabids	F+R	0.75	0.67	-	0.69	0.31	0.73	0.62	-	0.66	0.29
	Fixed	−0.02	0.35	-	0.08	0.01	0.04	0.27	-	0.02	−0.02
	Random	0.74	0.48	-	0.67	0.30	0.73	0.48	-	0.67	0.30
Birds	F+R	0.71	0.28	0.41	0.32	0.11	0.75	0.28	0.24	0.33	0.13
	Fixed	0.27	0.12	0.34	0.19	−0.02	0.62	0.17	0.20	0.31	0.08
	Random	0.59	0.10	0.04	0.11	0.10	0.40	0.11	0.05	0.04	0.06
Bats	F+R	0.69	0.43	-	0.48	0.12	0.65	0.42	-	0.44	0.13
	Fixed	0.06	0.00	-	0.05	−0.02	0.10	−0.05	-	−0.05	0.04
	Random	0.67	0.43	-	0.43	0.13	0.65	0.43	-	0.43	0.11

TABLE C8.4.23 Loss of R^2 in the assemblage habitat models by region. The R^2 of the mixed effects models was subtracted, leaving only the fixed factors to predict the response variables, to exclude the explained variance by region (a random factor) from the R^2 of the fixed effects models.

	ALS models					Radar models				
	NMDS1	NMDS2	NMDS3	Species richness	Phylogenetic diversity	NMDS1	NMDS2	NMDS3	Species richness	Phylogenetic diversity
Plants	0.29	0.19	-	0.26	0.24	0.29	0.07	-	0.11	0.25
Bryophytes	0.25	0.30	0.09	0.15	0.12	0.21	0.14	0.14	0.07	0.18
Lichens	0.32	0.08	-	0.04	0.01	0.29	0.17	-	0.04	0.00
Phytophagous	0.26	0.21	0.14	0.07	0.23	0.21	0.28	0.06	0.08	0.14
Moths	0.31	0.26	-	0.03	0.07	0.33	0.21	-	0.01	0.04
Saproxylic	0.25	0.16	0.41	0.04	0.11	0.18	0.17	0.19	0.10	0.09
Fungi	0.20	0.23	0.02	0.02	0.00	0.02	0.17	−0.01	0.00	0.00
Necrophagous	0.26	0.24	0.03	0.08	0.10	0.25	0.14	0.05	0.08	0.08
Spiders	0.38	0.07	0.37	0.35	0.01	0.52	0.03	0.13	0.23	0.03
Carabids	0.27	0.13	-	0.30	0.05	0.40	0.09	-	0.36	0.06
Birds	0.28	0.05	0.03	0.05	0.04	0.08	0.02	0.00	0.00	0.01
Bats	0.48	0.13	-	0.11	0.03	0.30	0.10	-	0.12	0.04
Median of 48 responses					0.14					0.10

Chapter 8.5

Biodiversity assessments used in chapter 3 - 6

Detailed description of species data sampling

Description of the sampling protocols of the Exploratories (Schwäbische Alb: ALB, Hainich: HAI, Schorfheide-Chorin: SCH), the Steigerwald Project (STE) and the BioKlim-Project of the Bavaraian Forest NP (BAY).

Methods, grain and timeframe for species sampling - although standardized within the projects - differs between projects, though in various extent. In order to gain comparable estimates of diversity, data had to be of cropped to a comparable extent. Within this process, we always preferred to keep as much information as possible. Yet, if data on certain taxonomic groups was sampled for several years as it was the case for the Biodiversity Exploratories, for each region only the data of year closest to the LiDar-Flights was chosen. If, however, the sampling campaigns covered different time span within that year, we did not subsample to the months which were equally covered by all projects, as that might result in losing the peak of species occurrence. An exception to this were the moths (see below).

Bats

Bats were recorded from 2008 – 2010 in the Exploratories with a combination of transect- and point stop detector walks with a Pettersson D 1000x ultrasound detector (Pettersson Electronic AG, Uppsala, Sweden). The 100 m x 100 m plots were walked from corner to corner in a straight line. The survey time per edge was 6 minutes, same as the time spent at each corner, resulting in 48 minutes per plot. Detector walks were conducted twice per summer and analysed to species level or to Sonotype using the software Avisoft SAS Lab Pro, Version 5.0.24 and onward (Raimund Specht, Avisoft Bioacoustics, Berlin Germany). Counts were defined as a minimum of two consecutive echolocation calls and successive passes within one minute were discriminated if the time interval between calls was larger than three times the regular pulse interval of the respective species. For more detailed information on sampling see Jung *et al.* (2012). In the BioKlim Project and the Steigerwald, autonomous bat call recorders (Batcorder 2.0; ecoObs GmbH, www.ecoobs.com) were placed as near to the middle of the plot as possible at a height of ca 2 m (STE) and 2.70m (BAY). The batcorder should cover a radius of ca 20m, though the detectability differs between species. Bat sonotype and species were processed using the software bcAdmin1.11 (www.ecoobs.com), and species were identified using the software bcDiscriminator1.14 (www.ecoobs.com). Counts were defined as the number of 1-min intervals per night in which a species was recorded. Bats were recorded in three rounds from April to August 2017 in Steigerwald and in seven rounds from May to August 2009 in the BioKlim Project. For more detailed information for BAY see (Müller *et al.*, 2012). Not all bat species can be unambiguously identified to

species level based on their echolocation calls and thus are combined into sonotypes. The combination into sonotypes differs between regions. In the analysis, only species which could be identified to species level were included. An exception to this are the sonotypes "Myotis brandtii_mystacinus" and "Plecotus", which cannot be tracked down to a single species in any of the two used softwares. Here, the sonotype is used as a species surrogate. Note, that although different bat detection systems were used, regional differences were much larger than differences between the projects.

Birds

In the Exploratories, birds were monitored during the breeding seasons from five times between March and June 2008 to 2010. All bird hearings or sightings were recorded within 5 minutes and a 50 m radius from plot midpoint. For more detailed information see Wells *et al.* (2011) and Wells *et al.* (2012). In the Steigerwald forest and BioKlim Project, a similar procedure was conducted, only that it was on 1 ha and for 7 minutes in 2014 (STE, Doerfler *et al.* 2018) and 10 minutes in 2009 (BAY, Müller *et al.* 2009)

In the regions used in the external validations (Bavarian Forest, Berchtesgaden, Brandenburg), similar point-counts sampling within a fixed radius of 50 m was conducted five times during the breeding season. In the UNESCO-Biosphere reserve Rhön, another of the external validation regions, breeding birds were recorded by territory mapping following the methods of Fischer, et al. [7]. In short, all bird hearings and sightings were mapped, and territorial behaviour was recorded within several forested areas up to 25 ha in size. Sample areas were monitored seven times within the 2016–2018 breeding seasons (March–June), during which time data on territory status and breeding behaviour were also collected.

Arthropods

Ground-dwelling arthropods were sampled with pitfall – traps. In the Exploratories, the pitfall-traps consisted of funnels with a diameter of 15 cm and were placed at three random corners of the plots from May to October in 2008 (note, that in parts, pitfall – traps were already installed in April, but not on all plots. Therefore, all records from April were excluded). From these three, two were randomly chosen for species determination ("Priority 1" and "Priority 2"). Note, that whether a trap was chosen to be "Priority 1" or "Priority 2" could differ between the months. In the Steigerwald and BioKlim Projects, only one trap was established per plot. Here, plastic cups with a diameter of c.a. 8 cm were placed near the midpoint of the plot. In Steigerwald, the traps were

operated from March to October 2016, in the Bavarian Forest Nationalpark from April to October 2007. In addition to each pitfall trap, a flight interception traps was installed at ca 1.5m height in close distance. Just like the procedure for the pitfall traps, only two out of three traps were chosen each month for determination and the records from April were excluded in the Exploratories. The flight interception traps of the projects were the same in size and type. However, the Exploratories had two sampling units, one at the bottom and one at the top of the traps, whereas in Steigerwald and Bayerwald the traps had one sampling unit at the bottom. In both trap systems and across all projects, copper sulphate solution was used as trapping liquid with a drop of detergent to reduce surface tension and sampling vials were replaced once a month. Moths were collected using the same trapping technique in all projects. Here, light traps consisting of 12 V and 15 Watt super actinic UV-lights linked to a twilight-sensor and were powered by a 12 V, 15 AH Battery. Light traps were installed for two nights per plot between the end of May and mid of August (the phenological peak of moth occurrence). Thereby, the weeks of full moon were avoided. The catch was collected the next day and subsequently frozen before determination to the species level by Hermann Hacker. For more information see for example Lange *et al.* (2014), Schall et al (2018) (both EXP), Doerfler *et al.* (2018), Roth *et al.* (2019) (both STE) and Müller & Brandl (2009) for BAY.

For our analysis, we always selected only data from "priority 1" sample and ground window traps from the Exploratories to gain equal sampling sizes in comparison to the Steigerwald and Bayerwald projects. If there was no "priority 1" sample available for a certain month, "priority 2" was taken instead. Names of spiders were synchronized using the current names given in *wiki.arages (https://wiki.arages.de/, 30.09.2018)*, beetle and heteroptera names were based on Entomofauna Germanica. Because Coleoptera are a hyper – diverse group which compiles several ecological functions, we selected four subgroups. First, all beetles known to be saproxylic (based on Seibold *et al.* 2015) were compiled. The rest was divided into species belonging to the family of Carabidae, species known to be necrophagous and those known to be phytophagous (based on (Koch, 1999; Böhme, 2001). For moths, the families macrolepidoptera as well as Cossidae, Hepialidae and Limacodidae, were chosen

In the UNESCO-Biosphere Rhön, which served as an external validation region for Chapter 6, beetles were
obtained using flight interception traps and by hand collection. Two flight interception traps with sampling units at their bottom were installed at each study site at a height of ~1.5 m. The traps were operated from the end of April to October 2018. During this sampling period, beetles were also hand collected three times at each site, with special focus on deadwood structures, bark cracks

etc. All samples were stored in ethanol until their determination. In DBU Natural Heritage areas, a flight interception trap was installed in the crown of a suitable tree, if possible close to deadwood and with optimal light exposure, in the centre of each forest stand. Samples from the trap were collected five times per year from May 2015 to October 2016. In other external validation regions (Bavarian Forest, NPBBerchtesgaden), saproxylic beetles were collected using traps of the same type (flight interception traps and pitfall traps) as described for the training data regions

Fungi

In the Exploratories, eleven dead wood objects located within the 1 ha plot were examined in 2010. Thereby nine of the objects were randomly chosen while the other two were the biggest objects on the plot. In the Steigerwald, a smaller, circular area of 0.1 ha was examined. Here, all deadwood objects as well as the soil were examined for 45 minutes in spring, summer and autumn of 2014. In the Bavarian Forest Nationalpark, an area of 0.1 ha was examined for 2 h in a single survey from August to October 2006. In the process, a minimum of 15 most common dead wood objects were searched, and as much of the remaining objects as possible for the rest of the 2 hours. For more information see Bässler et al (2010b) and (Roth *et al.*, 2019)

Because the fungal communities showed extreme differences between the projects, which was unlikely to be based on regional differences alone but rather an effect of the determinability of cryptic species, data cropped to a list of species which are equally determinable according to a specialist (CB). For instance, crustean species were not included. Species names were harmonized based on *index fungorum* (http://www.indexfungorum.org/names/names.asp, 07.11.2018). Because the number of objects searched for fungi differed between the projects, a comparison of object-wise abundance data was not possible.

Lichens

In the Exploratories, lichens were recorded for four different substrates (bark, further divided into the tree species, rocks, dead wood and soil) on 20m x 20 m quadrats in one round from 2007 to 2008 (Boch *et al.*, 2013). Lichens were recorded in one round on all trees and dead wood stems and logs (hereafter referred to as stems), within a 14 m × 14 m plot in 2017 in the Steigerwald forest and within an 8-m radius from August to November 2007 in the Bavarian Forest National Park, respectively. In the Bavarian Forest National Park, 1–10 stems (average: 5 stems per plot) were examined, depending on stem availability. For a detailed description see (Moning *et al.*, 2009). Species names were harmonized based on http://www.indexfungorum.org/. Because the number of objects searched for lichens differed between the projects, a comparison of object-wise abundance

data was not possible. Because lichens growing on soil or rock were only recorded on the Exploratories plots, they were excluded from further analysis.

Bryophytes

In the Exploratories, all bryophytes within the core area (20m x 20m) of the plot were recorded and their abundance per substrate (soil, dead wood, bark and rock) estimated. In the Steigerwald, bryophytes were mapped on an area of 14m x 14m in April 2014. In the Bavarian forest NP, all bryophytes within an 0.02 ha circular plot were recorded in the summer of 2007. For bryophytes growing on the soil, the abundance was estimated as percentage of cover. Bryophytes growing on dead wood were counted object wise (see (Raabe *et al.*, 2010). Due to differing techniques for the estimation of abundance, we only used presence absence data. Species names were harmonized based on plantlist.org.

Permits received for fieldwork

Offices granting permits	Permit number
Regierungspräsidium Tübingen	55-8/8848.02-07; 55-3/8852.15
Thüringer Landesverwaltungsamt	13.4 64233/11-07SDH; 13.4 64233/08-08SDH
Landesumweltamt Brandenburg	R07/SOB-0907; LFU-N1- 47 43 /128+5#69 122/2018
UNB Eisenach	63.2-15.02.00.17-38-2018
Umweltamt Eichsfelde	001-04-18/6-85/uni-München/BiodivExploratorien
Umweltamt Kyffhäuserkreis	III.3.3-364.53.1/2018-06-01_BiodivExplo_Ergänzung_Arthropoden; III.3.3-364.53.1/2018-08-01_Biodiv Expl_Hummeln
Landkreis Nordhausen	60.1.55.400.622/0239-18
Landratsamt Unstrut-Hainich-Kreis	10491-18-301
Regierung von Oberbayern	55.1-8646-32-2013
Regierung von Niederbayern	55.1-8642.10-N 25
Regierung von Oberfranken	55.1-8622
Regierung von Unterfranken	RUF-55. 1.2 -8622.147-2-14-3

Data sources

Exploratories

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Tschapka, Marco; Swen Renner; Kirsten Jung (2018): Bird survey data 2008. v3.1.4. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=21446

Goßner, Martin; Markus Lange; Manfred Türke; Esther Pasalic; Wolfgang Weisser (2016): Window and ground traps on forest EPs in 2008 subset Coleoptera. v1.1.3. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=16866

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Müller, Jörg; Steffen Boch; Markus Fischer (2016): Bryophyte diversity in forests. v1.6.8. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=4141

Boch, Steffen; Daniel Prati; Markus Fischer (2016): Lichen diversity in forests. v1.11.14. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=4460

Schäfer, Deborah; Steffen Boch; Markus Fischer (2017): Vegetation Records for Forest EPs, 2009 - 2016. v1.4.5. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=20366

Steigerwald-Project

Doerfler, I., Gossner, M.M., Müller, J., Seibold, S. & Weisser, W.W. (2018). Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. *Biol. Conserv.*, 228, 70–78.

and further, unpublished data provided by Jörg Müller (joerg.mueller@npv-bw.bayern.de)

BIOKLIM-Project

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and further, unpublished data provided by Jörg Müller (joerg.mueller@npv-bw.bayern.de)

Overview

Species group	∑ Plots	Region	No. Plots	Year	Data source*	Method	Reference	
Bats (N=15)	**248**	ALB	50	2010	Jung & Tschapka (2018)	Transact-point-detector-walk	Jung *et al. (2012)*	activity as surrogate for abundance
		HAI	50	2008				
		SCH	50	2009				
		STE	69	2017	Data provided by Jörg Müller	fixed-batcord-ers	unpublished	
		BAY	29	2009	Müller *et al.* (2012)	fixed-batcord-ers	Müller *et al.* (2012)	
Birds (N=81)	**496**	ALB	50	2010	Tschapka, Renner & Jung (2018)	5 min point counts	Wells *et al.* (2011)	
		HAI	50	2008				
		SCH	50	2009				
		STE	69	2014	Doerfler *et al.* (2018)	7 min point counts	Doerfler *et al.* (2018)	
		BAY	277	2007	Müller *et al.* (2009)	10 min point counts	Müller *et al.* (2009)	
Spiders (N= 267) Carabid beetles (N=103) Saproxylic beetles (N=515) Necrophag. beetles (N=40) Phytophag. beetles (N=293) True bugs (N=171)	**385**	ALB	50	2008	Goßner et al. (2016 a,b,c)	Flight + pitfall traps	Lange *et al.* (2014)	
		HAI	49					
		SCH	50					
		STE	69	2016	Doerfler *et al.* (2018)	Flight + pitfall traps	Doerfler *et al.* (2018)	
		BAY	167	2007	Müller & Brandl (2009)	Flight + pitfall traps	Müller & Brandl (2009)	
Moths (N=468)	**227**	ALB	42	2018	Data provided by Wolfgang Weisser	light traps	unpublished	
		HAI	44					
		SCH	47					
		STE	62	2017	Data provided by Jörg Müller			
		BAY	32	2007				
Fungi on deadwood (N=213)	**497**	ALB	50	2010	Fischer (2017)	object based examination	unpublished	abundance data not comparable across studies, thus not included in analysis
		HAI	50					
		SCH	50					
		STE	69	2014	Doerfler *et al.* (2018)	standardized search time	Doerfler *et al.* (2018)	
		BAY	278	2006	Bässler *et al.* (2010)	standardized search time	Bässler *et al.* (2010)	
Lichens on dead-wood (N=196)	**315**	ALB	50	2007/2008	Boch et *al.* (2013)	mapping	Boch *et al.* (2013)	
		HAI	44					
		SCH	46					
		STE	69	2017	Jörg Müller	mapping	unpublished	
		BAY	106	2007	Moning *et al.* (2009)	mapping (1-10 stems)	Moning *et al.* (2009)	
Bryophytes (N=197)	**322**	ALB	50	2007/2008	Müller, Boch & Fischer (2016)	mapping	Müller *et al. (2019)*	
		HAI	49					
		SCH	48					
		STE	69	2014	Data provided by Jörg Müller	mapping	unpublished	
		BAY	106	2007	Raabe *et al.* (2010)	mapping	Raabe *et al.* (2010)	
Plants (N=351)	**497**	ALB	50	2010	Schäfer *et al.* (2017)	mapping	Boch *et al.* (2013 b)	
		HAI	50	2009				
		SCH	50	2009				
		STE	69	2014	Doerfler *et al.* (2018)	mapping	Doerfler *et al.* (2018)	
		BAY	278	2006	Bässler *et al.* (2010)	mapping	Bässler *et al.* (2010)	

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Acknowledgements

Now it's to thank those people who accompanied and supported me throughout these last three years. Jörg, you believed in my abilities when I did not myself. Furthermore, you showed me what I can accomplish if I push my limits. Sometimes, we might have argued about that, but I'm grateful that you never fled from such a discussion, and that I could be open about my problems. Second, I want to warmly thank Roland Brandl for his continuing support and for lending me an ear and also tissues if I needed. Special thanks go out to Hermann Hacker, who took me under his wing and showed me the beauty of moths, and to my favourite foresters, Sven Finnberg and Hans Stark.

Mr. Nicolas Frieß, thank you so much for helping me out and calming me in the pre-submission-panick. I owe you something, and I am looking forward for more relaxed science-discussion in the future. Stefan Pinkert, thanks for your support and for being my advocate.

Then, the dear people of Fabrikschleichach; Hermine, Roland and Hildegard, thank you for providing help with documents, equipment and provisioning me with cake and coffee. Simon, thank you for your help with R and for giving me an opportunity to ping-pong sarcastic jokes. The "senior" crew, Nico, Mareike, Sebastian, Elisa, Janina and Kosta thank you for giving me a warm welcome and valuable advises. The "junior" crew, Jana (JJ), Johannes, Sophia, Ruth, Peter, Dominik and Steffi and Annika (phd-student in spirit), thank you for your enthusiasm and energy. You make life and work at the station enjoyable. With you guys it's easy to have a good laugh, even after a whole day of light-trapping and a whole night of fogging. A well-deserved hat tip towards the Czech invasion, Lucka, Michal and Pavel, who brought some breadth of fresh air to the station. Special thanks to the latter, for long discussions about science, beauty of nature and meaning of life.

A big thanks goes out to "my" students and student helpers, Felix, Marcel, Sarah, Philip, Gabby, Nadja, Janina, Hanna, Erkan, Denise, Ruth (again), Vanessa, Lilli and Lucy, who probably taught me more about life than vice versa. Also, thanks to my non-student helpers Jana (again) for helping me out just because – in several ways, Marco and Jasmin as well as the local management teams of the exploratories – you are awesome! Without you lot, the campaigns in the Exploratories, the University forest and Bad Windsheim would have never been doable.

I also want to express our gratitude for having the opportunity to spend some time with two fine, young men, who worked without complaining, always being polite yet also a lot of fun to be around. Emmanuel and Abbey, I miss you.

Lastly, I would like to thank my family for their everlasting support, and of course my ~~boyfriend~~ ~~fiancé~~ husband, Seb. I know it was not easy, and you often had to make sacrifices for me to finish my dissertation, but you did them without hesitating. Without you, I probably wouldn't have made it. I love you.

Erklärung

Eidesstattliche Erklärungen nach §7 Abs. 2 Satz 3, 4, 5 der Promotionsordnung der Fakultät für Biologie

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation: „ **Einfluss von Heterogenität in Umwelteinflüssen auf Artgemeinschaften**“, eigenständig, d. h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

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Affidavit

I hereby declare that my thesis entitled: „ **The effect of environmental heterogeneity on communities**” is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore I verify that the thesis has not been submitted as part of another examination process neither in identical nor in similar form.

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Signature PhD-student

List of publications used in this thesis

Chapter 2

Heidrich, L., S. Pinkert, R. Brandl, R. Hacker, N. Roth, J. Müller and N. Frieß. Noctuid and geometrid moth assemblages show contrasting elevational gradients in body size and color lightness. **Under review** in *Ecography*

Chapter 3

Bae, S., **L. Heidrich**, S. R. Levick, M. M. Gossner, S. Seibold, W. W. Weisser, P. Magdon, A. Serebryanyk, C. Bässler, D. Schäfer, E.-D. Schulz, I. Doerfler, J. Müller, K. Jung, M. Heurich, M. Fischer, N. Roth, P. Schall, S. Boch , S Wöllauer, S. C. Renner and J. Müller. Dispersal ability, trophic position and body size mediate species turnover processes: insights from a multi-taxa and multi-scale approach. Accepted for publication in *Diversity and Distributions* (DDI-2020-0189.R2).

Chapter 4

Heidrich, L., Bae, S., Levick, S., Seibold, S., Weisser, W., Krzystek, P., Magdon, P., Nauss, T., Schall, P., Serebryanyk, A., Wöllauer, S., Ammer, C., Bässler, C., Doerfler, I., Fischer, M., Gossner, M.M., Heurich, M., Hothorn, T., Jung, K., Kreft, H., Schulze, E.-D., Simons, N., Thorn, S. & Müller, J. (2020) Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. *Nature Ecology & Evolution*, 4, 1204–1212.

Chapter 5

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Chapter 6

Bae, S., Levick, S.R., **Heidrich, L.**, Magdon, P., Leutner, B.F., Wöllauer, S., Serebryanyk, A., Nauss, T., Krzystek, P., Gossner, M.M., Schall, P., Heibl, C., Bässler, C., Doerfler, I., Schulze, E.-D., Krah, F.-S., Culmsee, H., Jung, K., Heurich, M., Fischer, M., Seibold, S., Thorn, S., Gerlach, T., Hothorn, T., Weisser, W.W. & Müller, J. (2019) Radar vision in the mapping of forest biodiversity from space. *Nature Communications*, 10, 4757.