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

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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 2,600 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 substantial HDRs, 53% increased monotonically, consistent with the classical habitat heterogeneity hypothesis but 21% were hump-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.

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 (that is, the number of available niches), allowing different species to co-exist such that biodiversity increases (Fig. 1)[1–3]. The positive relationship between heterogeneity and species richness is often regarded as ubiquitous[2] since its first observation in the early 1960s when MacArthur and MacArthur[1] 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[4], this can result in a decrease in mean population sizes especially at high levels of habitat heterogeneity (Fig. 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)[4,5] (Fig. 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 nonlinear 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 nonlinear forms[4–10], it has been shown that certain ecological properties, such as niche breadth, reproduction and dispersal rates[5,7–9], moderate the responses of species to increasing niche dimensionality, reductions in effective area and the degree of fragmentation. Consequently, rather than investigating whether positive or hump-shaped HDRs prevail, recent theoretical approaches address the question of under which conditions HDR takes which shape[5,10,11].

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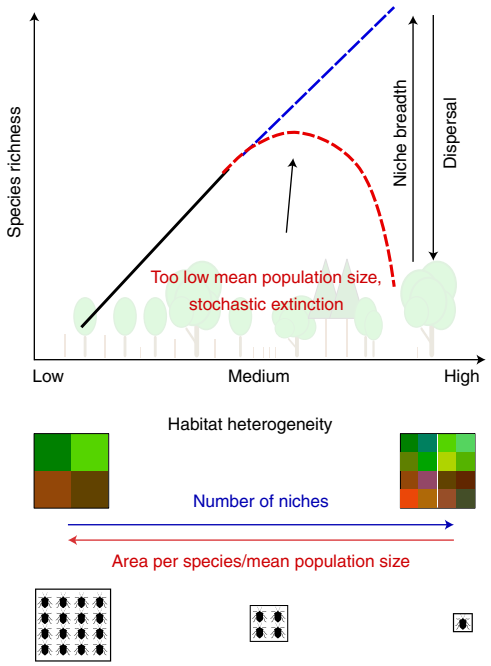

Fig. 1 | Conceptional framework for the relationship between habitat heterogeneity and species richness. The habitat heterogeneity hypothesis predicts that the number of niches, and thus species richness, increases with increasing habitat heterogeneity (blue line). The area–heterogeneity trade-off hypothesis 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).

A theoretical modelling approach suggested that, despite the various ways in which environmental heterogeneity may affect species richness, HDR patterns should be predictable and robust[5]. 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 that are limited in dispersal have positive HDRs due to fragmentation effects[12], while those with large dispersal ranges have hump-shaped HDRs[5] (Fig. 1).

A limitation of current theoretical modelling is that it is based upon strong assumptions (for example, a lack of habitat selection[5]), 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[13], 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[13]. For example, short heterogeneity gradients are more likely to under-represent 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[14]. 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[10]. Lastly, the shape of the HDR will also depend on the scale at which the study is conducted[2,8,10].

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 many species groups across trophic levels[15] and with respect to major facets of heterogeneity[13], covering the full gradient length of a single habitat and using a constant sampling grain. This approach would provide a unique opportunity to: (1) assess the degree to which the determined HDR patterns can be generalized and (2) 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 (Extended Data Fig. 1), comprising ~500 1-ha forest plots containing a total of ~2,600 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[3,16]. 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[3]. 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[17]. In this study, to ensure a comprehensive assessment of forest heterogeneity, we adopted the classification system of Stein and Kreft[13], which systematically divides the various facets of heterogeneity into clearly defined subject areas (Fig. 2a). To this a priori classification of independent gradients of heterogeneity within a forest stand, we added deadwood as a major subject area on the basis of 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) microscale topography (Fig. 2a).

We assessed whether multidiversity (the scaled species richness of all recorded species[18]) 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 modelling approaches[5]. Finally, we examined whether the response of the mean population decreases with increasing heterogeneity, as expected by stochastic extinctions and the area–heterogeneity trade-off theory.

Results and discussion

The species richness of all species groups, except carabids (Fig. 2b and Table 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[14], there was a large amount of variation in our results. Both responses to different facets of heterogeneity and the shape thereof differed among species groups.

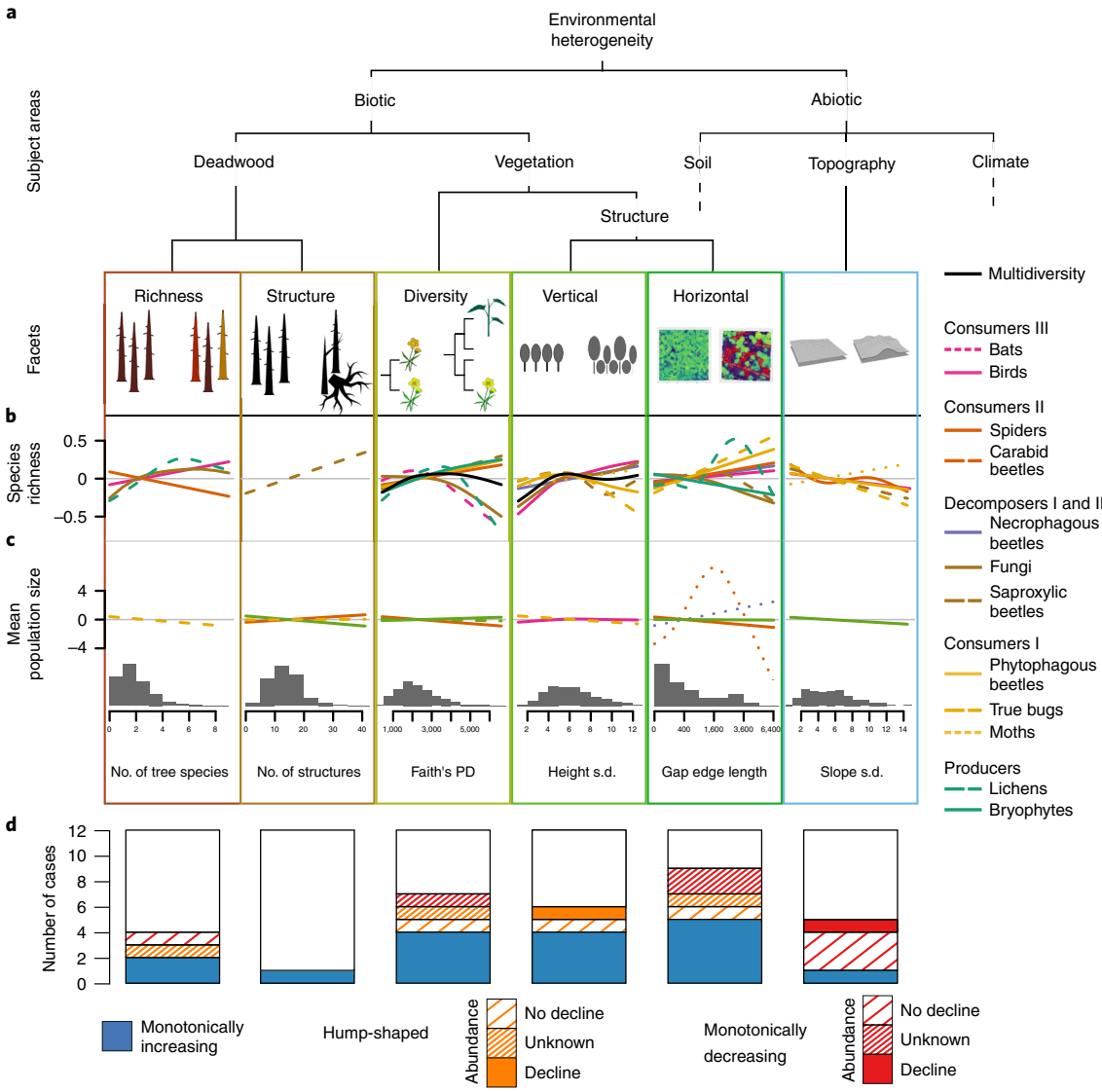

Fig. 2 | Summary of the relationships between the single facets of heterogeneity and species richness and mean populations size as estimated by mean abundances per species. a, Habitat heterogeneity in forests can be decomposed into the facets: heterogeneity in vertical (height s.d.) and in horizontal structure (gap edge length), plant diversity (Faith's PD) and microscale topography (slope s.d.), expanded by the inclusion of the taxonomic and structural richness of deadwood. **b**,**c**, The partial contribution of the scaled and centred predictor variables with $P \leq 0.05$ in the GAMs in the modelling of species richness, shown for 12 species groups and for multidiversity (**b**) and the mean population size of the nine animal groups with available abundance data (**c**). The distribution of the predictor variables is given in the lower half of the figure. **d**, Bar graphs of the portion of significant effects ($P \leq 0.05$) 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 by a decrease in mean abundance.

Among 72 possible HDRs (12 species groups × six facets of habitat heterogeneity), 34 were significant with $P \leq 0.05$, 17 increased monotonically, seven were hump-shaped and eight decreased monotonically. Two responses showed more than one pronounced change in the sign of the HDR: saproxylic beetles in response to vertical heterogeneity and spiders in response to microscale topography (Fig. 2b and Table 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 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[5], 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[12] 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[5]. However, neither habitat niche breadth, here estimated on the basis of trophic positions[19] (Fig. 3, one-sided, linear-by-linear associated test, $z = 0.38$, $P = 0.35$) nor

Table 1 | Results of the GAMs of different facets of heterogeneity as predictor variables, and multidiversity, species richness (upper half) and mean abundance (lower half) as dependent variables

	n (plots)	Taxonomic richness of deadwood			Structural richness of deadwood			Plant diversity			Vertical heterogeneity			Horizontal heterogeneity			Microscale topography			Region			R^2_{adj}	ΔR^2
		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 NS	1.0		0.80 NS	2.9	H	22. ***	3.5	H	23. ***	1.0		0.68 NS	1.0		0.96 NS	3.6	194. ***		0.62	0.09
Plants	497	3.1		1.5 NS	1.0		0.32 NS				1.0		3.9 *	3.0	H	10. ***	1.0	-	8. **	3.9	68. ***		0.58	0.07
Bryophytes	322	1.0		0.66 NS	1.0		1.0 NS	1.4	+	3.4 *	1.0		0.01 NS	1.0	–	4.9 *	1.0		1.0 NS	3.7	13. ***		0.34	0.01
Lichens	315	2.2	H	6.3 ***	1.0		0.57 NS	3.2	H	5.3 ***	1.0		3.6 NS	4.6	H	7.4 ***	1.0		1.2 NS	3.8	33. ***		0.51	0.16
Moths	227	1.0		0.17 NS	1.0		3.4 NS	1.5		1.8 NS	1.0	+	5.2 *	1.0		0.31 NS	1.0	+	5.5 *	3.6	10. ***		0.32	0.04
True bugs	371	1.0		2.9 NS	1.0		1.3 NS	1.0		0.02 NS	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 NS	1.0		1.4 NS	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 NS	2.6	–	4.4 **	3.1	+	8.1 ***	2.1	–	7.9 ***	1.6		2.1 NS	3.4	10. ***		0.41	0.17
Saproxylic	385	1.0		0.71 NS	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 NS	1.0		0.85 NS	1.0		0.23 NS	1.0	+	6.3 *	1.0	+	4.5 *	1.0		2.5 NS	3.8	31. ***		0.35	0.02
Carabids beetles	382	1.0		0.47 NS	1.0		1.9 NS	1.0		1.5 NS	1.0		0.00 NS	1.0		3.8 NS	1.0		2.5 NS	3.9	93. ***		0.72	0.01
Aranea	382	1.0	–	10. **	1.0		1.2 NS	1.0	+	6.7 *	1.0		0.00 NS	1.0	+	20. ***	3.6		3.7 **	3.9	101. ***		0.69	0.08
Birds	496	1.0	+	9. **	1.0		0.00 NS	1.0		0.49 NS	3.3	+	19. ***	1.0	+	5.7 *	1.0	–	7.3 **	3.7	20. ***		0.26	0.14
Bats	248	1.0		0.87 NS	1.0		0.01 NS	2.4	H	3.3 *	1.0		1.0 NS	1.0		0.18 NS	1.0		3.5 NS	3.8	26. ***		0.54	0.01
Moths	227	1.0		1.8 NS	1.0		0.01 NS	2.6	H	3.8 **	1.0		2.0 NS	1.0		0.25 NS	1.0		0.03 NS	3.6	12. ***		0.26	0.05
True bugs	371	1.0		3.1 NS	1.0		3.0 NS	1.4		0.84 NS	1.0	–	4.1 *	1.0		0.06 NS	1.0		3.3 NS	2.9	4.5 ***		0.09	0.04
Phytophagous	385	1.0		0.32 NS	1.0	+	5.4 *	1.0	–	7.3 **	1.0		0.09 NS	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 NS	1.0	–	12. ***	1.0		3.6 NS	1.0		0.61 NS	1.9	1.6 *		0.16	0.11
Necrophagous	385	1.0		0.08 NS	1.0		3.0 NS	1.0		0.51 NS	2.4		2.4 NS	3.1	H	3.6 **	1.0		2.7 NS	3.1	5.1 ***		0.13	0.07
Carabid	382	1.0		1.2 NS	2.6	–	4.3 **	1.0	–	5.2 *	1.0		3.0 NS	1.9	–	5.1 **	1.0		0.86 NS	3.9	59. ***		0.58	0.05
Aranea	382	1.0		2.5 NS	1.0		0.73 NS	1.0		1.9 NS	1.0		0.32 NS	1.0	–	5.9 *	1.0		1.8 NS	3.4	9. ***		0.18	0.01
Birds	496	1.0		0.20 NS	1.0		0.88 NS	1.0		3.1 NS	2.5	H	3.4 *	1.0		1.9 NS	1.0		0.14 NS	3.8	27. ***		0.25	0.02
Bats	248	1.0		0.76 NS	1.0		0.08 NS	1.0		2.0 NS	1.0		0.02 NS	1.0		0.45 NS	1.0		0.16 NS	3.6	17. ***		0.24	−0.01

Predictor variables are taxonomic and structural diversity of deadwood, plant diversity (Faith's PD), vertical structure (height s.d.), horizontal structure (square-rooted edge length) and microscale topography (slope s.d.). 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). NS, not significant.
$^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

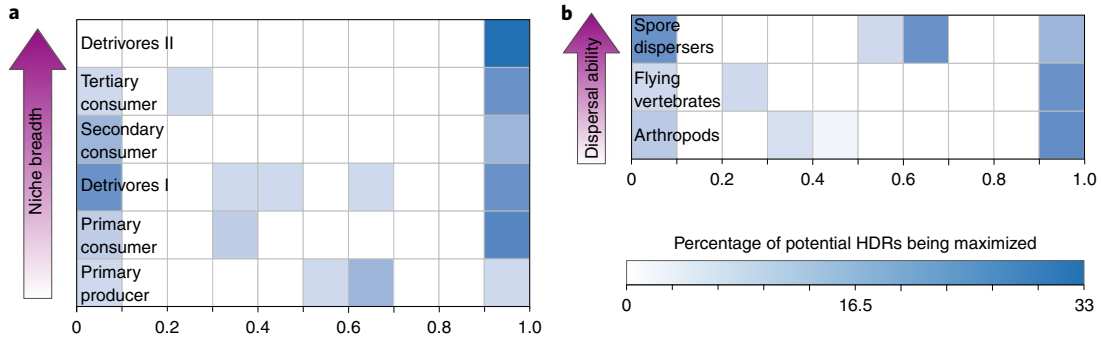

Fig. 3 | The level of heterogeneity which maximizes species richness summarized over all six facets of heterogeneity and ordered along trophic position and dispersal ability of the species groups. a,**b**, Heterogeneity was binned from 0 (lowest heterogeneity in all plots) to 1 (highest heterogeneity in all plots). Blue shading refers to the percentage of potential HDRs (calculated as number of species groups within a certain trophic position (**a**) or dispersal ability class (**b**) times six facets of heterogeneity) which are maximized at a certain bin.

dispersal abilities showed any clear response in terms of the position of the inflection points (one-sided, linear-by-linear association test, $z=0.22$, $P=0.96$; Supplementary Methods, Supplementary Table 1 and Supplementary Fig. 1).

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[14,20]. Indeed, single facets of heterogeneity affected different numbers of species groups. The facet affecting the largest number of groups (nine out of 12) in terms of species richness was horizontal heterogeneity, followed by vertical heterogeneity (eight) and plant diversity (eight). Microscale topography affected six groups, taxonomic richness of deadwood affected four and the structural richness of deadwood affected only one species group, namely saproxylic beetles (Fig. 2b,d).

Saproxylic species and phytophagous groups are predicted to react strongly 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 (that is, the stage of decomposition and number of different deadwood objects) whereas wood-decomposing fungi were affected by its taxonomic richness (Fig. 2). This result provides the empirical evidence of experiments showing that fungal species richness is driven by host tree diversity[21] and saproxylic beetle richness by heterogeneity related to wood physiognomy, such as diameter, decay stage and deadwood object type[22,23]. 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 deadwood on non-saproxylic organisms[24,25]. 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. 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[26]. 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 microtopography 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[3,27,28]. 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. 2b and Supplementary Fig. 2). Thus, for birds, different vertical structures offer different niches in terms of nesting sites and foraging grounds, just as MacArthur and MacArthur[1] predicted. However, vertical heterogeneity also provides niches for other species groups, most likely through microclimatic conditions and shelter[29,30].

Horizontal heterogeneity determines variations in light availability and microclimatic conditions near ground[31]. 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 favour communities different from those associated with stands with a closed canopy[22,24]. 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, probably affect species composition rather than species richness[32,33]. The relationship of species richness to topographic heterogeneity, measured as the standard deviation in the slope, was significant ($P \leq 0.05$) for six species groups (Table 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 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. 2b and Supplementary Fig. 2). 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[34].

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[5]. However, habitat heterogeneity affected the mean population size only in 15 out of 54 cases (nine animal groups × six 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 modelling results[5]. Also, decreases in mean populations sizes that coincided with a hump-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; Supplementary Fig. 2). 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[35–37] and increased horizontal heterogeneity to a larger amount of ground vegetation[34]. 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. 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[38]. In our study, arthropods accounted for eight of the 12 studied species groups; their fast reproduction rates may reduce their vulnerability to stochastic extinction[4].

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 s.d. Such monotonic declines of species richness are likely to occur when the studied scale is small[2,8] or the studied species groups are highly specialized[4]. 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 and MacArthur[1] for birds) the latter condition is not met by all species groups that responded to topographic heterogeneity.

Mechanisms other than area–heterogeneity 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[11]. Under highly favourable environmental conditions, any heterogeneity that reduces interspecific and intraspecific competition will ultimately increase species richness. Under unfavourable conditions, heterogeneity increases the prevalence of patches that 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[11]. 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[22,39], 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. 2b and Supplementary Fig. 2). These two groups are dominated by closed-forest specialists that are sensitive to dry conditions[40,41] 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 and 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 demonstrated well 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 capturing 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 facets studied, vertical and horizontal heterogeneity (which can easily be 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 1-ha plots covering five regions in Germany and representing the full range of zonal temperate forests in Central Europe (see Extended Data Fig. 1). The Biodiversity Exploratories project (biodiversity-exploratories.de[42]) 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[43–51] has been supplemented with plots from the Steigerwald project[52] in northern Bavaria (69 plots) and the BIOKLIM project[53] in the Bavarian Forest National Park[32,54–59] (278 plots).

Facets of habitat heterogeneity. To address heterogeneity in forests as comprehensively as possible, we adopted the classification system of Stein and Kreft[13], which systematically divides the facets of heterogeneity into five subject areas, of which four can be applied to a 1-ha plot scale: vegetation, microscale topography, soil and climate (Fig. 2a). In this study, the soil and climate of the subject areas 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[60] both of which were included in our study. We also added deadwood[52,55,61] 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 (that is, the vertical and horizontal heterogeneity of the vegetation).

Quantifying habitat heterogeneity. On the basis of several reviews[3,13,62,63], we selected potential measurements a priori for each of the six facets (Supplementary Methods and Extended Data Fig. 2). For the final selection, we examined

the statistical behaviours (distributions) of the variables and the within- and between-aspect collinearity (Supplementary Figs. 3–7), which is often an issue in LiDAR-derived measurements (Extended Data Fig. 3). In our study, the a posteriori selection of the measurements had several advantages over statistical variable selection in terms of dealing with collinearity (Extended Data Fig. 4) and the testing of ecological hypotheses. However, we are aware that the response of a single species group will slightly vary if different measures for the same facet of heterogeneity are considered[13]. 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[64]. 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 and so on; see also Supplementary Methods). Plant diversity was characterized by considering all vascular plants in the tree, shrub and herb layers determined as part of biodiversity assessments[51,52,54] (349 in total; Supplementary Methods). However, the number of plant species alone does not necessarily reflect ecological differences relevant to herbivores[65,66], as closely related plant species may host similar communities of insects[67]. 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 on the basis of the phylogeny proposed by Durka and Michalski[68], using the R software package picante, v.1.7[69]. However, this approach does not necessarily reflect all functional differences between plant species (but see Supplementary Methods). Standardized measurements of the three-dimensional structure of the forests were obtained using high-resolution airborne laser scanning (ALS) (Supplementary Methods), a method that provides accurate three-dimensional 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[70]. To calculate vertical heterogeneity, we used the standard deviation (s.d.) of the heights of vegetation returns over the entire 1-ha plot area. This metric is able to powerfully explain biodiversity patterns in forests[3] and is less sensitive to artificial classifications of layers than foliage height diversity (Supplementary Methods). 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 of >80%. Since the total gap area per plot would not capture a linear increase in horizontal heterogeneity—as both extremes (that is, 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 Supplementary Methods and Extended Data Fig. 2). Both structural measures (total gap edge length and height s.d.) were largely independent of the tree species composition (Extended Data Fig. 5). Microscale topography was calculated as the within-plot terrain heterogeneity, determined using a high-resolution digital terrain model with 1-m spatial resolution derived from the ALS measurements. The s.d. of the slope measured in the digital terrain model across our 1-ha plots served as a measure of topographic heterogeneity, as it was better than the s.d. of the elevation in capturing small-scale variation (see Supplementary Methods).

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[43–52,54–59]. 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 used fixed autonomous batcorders[32,43]. Birds were monitored acoustically and visually within a fixed time span during their breeding season[44,52,58]. Arthropods were collected using pitfalls, crossed flight interception traps and low-intensity light traps[45–47,52,57]. Fungi, bryophytes and lichens present on deadwood objects and the plants within a fixed area were mapped[49,50,56,59]. 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[4]. 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 Supplementary Methods and Supplementary Table 3.

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 nonlinear hump-shaped curve (Fig. 1)? (2) Does population size, here estimated by abundances[4] (or calls in the case of bats), decline with increasing heterogeneity? Species richness and abundances were modelled 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 on the basis of the graphical representations of the results. Significant relationships (with $P \leq 0.05$) between richness and the single predictors were defined as hump-shaped if the changes in the sign of the modelled 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) (Supplementary Fig. 2). This approach was chosen because formal model-specification tests (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 Supplementary Methods). Specifically, we applied two-sided GAMs, which account for an overdispersion by a quasi-Poisson estimation procedure in modelling species richness and a Gaussian distribution of the mean abundance of animals (R package mgcv, function gam, v.1.8.26; ref. [71]). All predictors were standardized before the analysis by scaling to a zero mean and unit variance to account for large differences in scales. Before 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 R package mgcViz, v.0.1.1 (ref. [72]).

In a last step, multidiversity 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[18]. This procedure weighted every species group equally. However, only data from plots in which all species groups 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[19], with producers assigned the lowest rank, followed by primary consumers, detritivores on deadwood[73], 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 (R package coin, v.1.3, ref. [74]) 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 Supplementary Methods and Extended Data Fig. 6).

Note that we intentionally did not include the species richness or abundance of plants, either as a response variable or in the calculation of multidiversity, 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 1). All statistical analyses were carried out using the statistical software R, v.3.5.0 (ref. [75]).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data reported in this paper can be accessed from the Biodiversity Exploratories Information System (https://www.bexis.uni-jena.de), DataSetID 25126. All data used in this manuscript is publicly available at https://doi.org/10.25829/bexis.25126-1.

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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, H. Hacker for moth determination, A. Ostrowski for managing the central database and M. Fischer, E. Linsenmair, D. Hessenmöller, D. Prati, I. Schöning, F. Buscot, E.-D. Schulze, W. W. Weisser and the late E. 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 nos 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.

Author contributions

L.H., J.M., S.B. and S.L. conceived the manuscript. J.M. designed the study. L.H., J.M., P.M., S.B., K.J., M.M.G., M.F., C.B., N.S., S.W., W.W., I.D., M.H., P.K., T.N., A.S. and P.S. acquired and processed the data. L.H., J.M., S.L., P.M., M.M.G., S.S. and W.W. drafted the manuscript. L.H., S.B., S.L., S.S., W.W., P.K., P.M., T.N., P.S., A.S., S.W., C.A., C.B., I.D., M.F., M.M.G., M.H., T.H., K.J., H.K., E.-D.S., N.S., S.T. and J.M. participated in analysing and interpreting the data and contributed critically to the revisions.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-020-1245-z.

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-020-1245-z.

Correspondence and requests for materials should be addressed to L.H.

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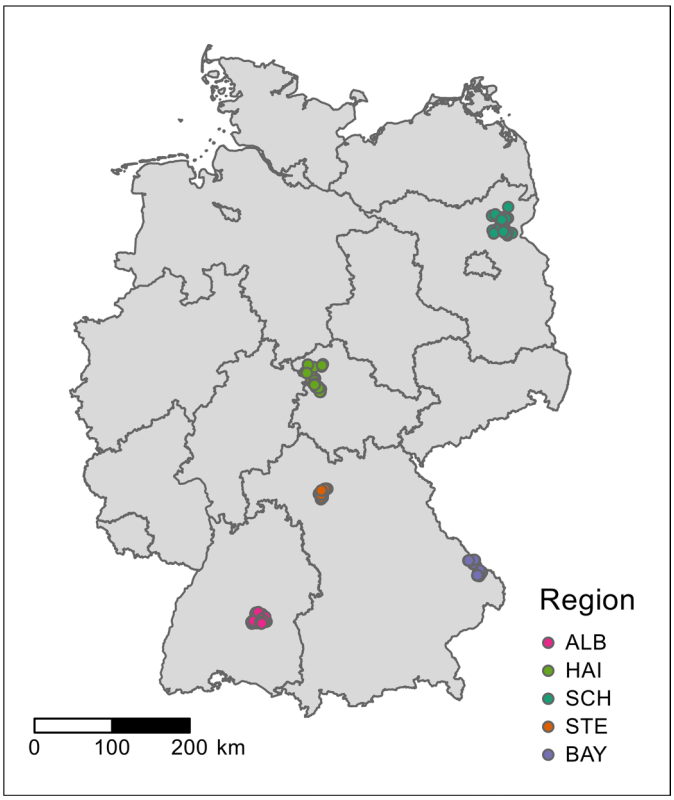
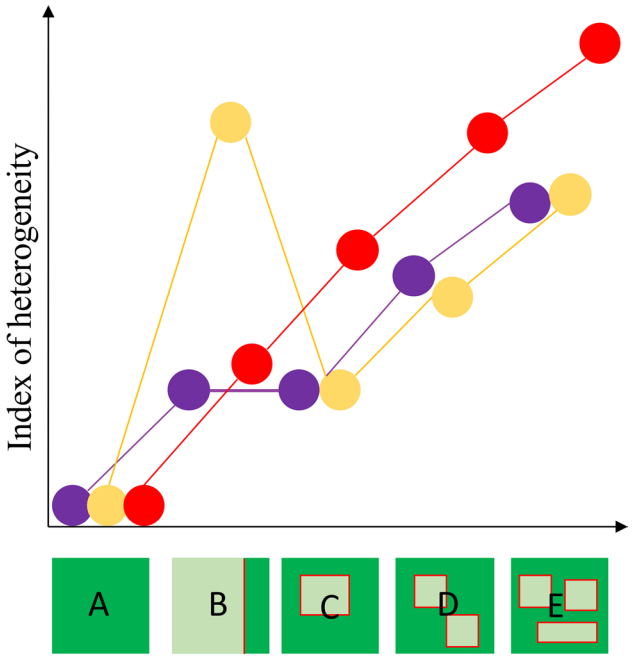
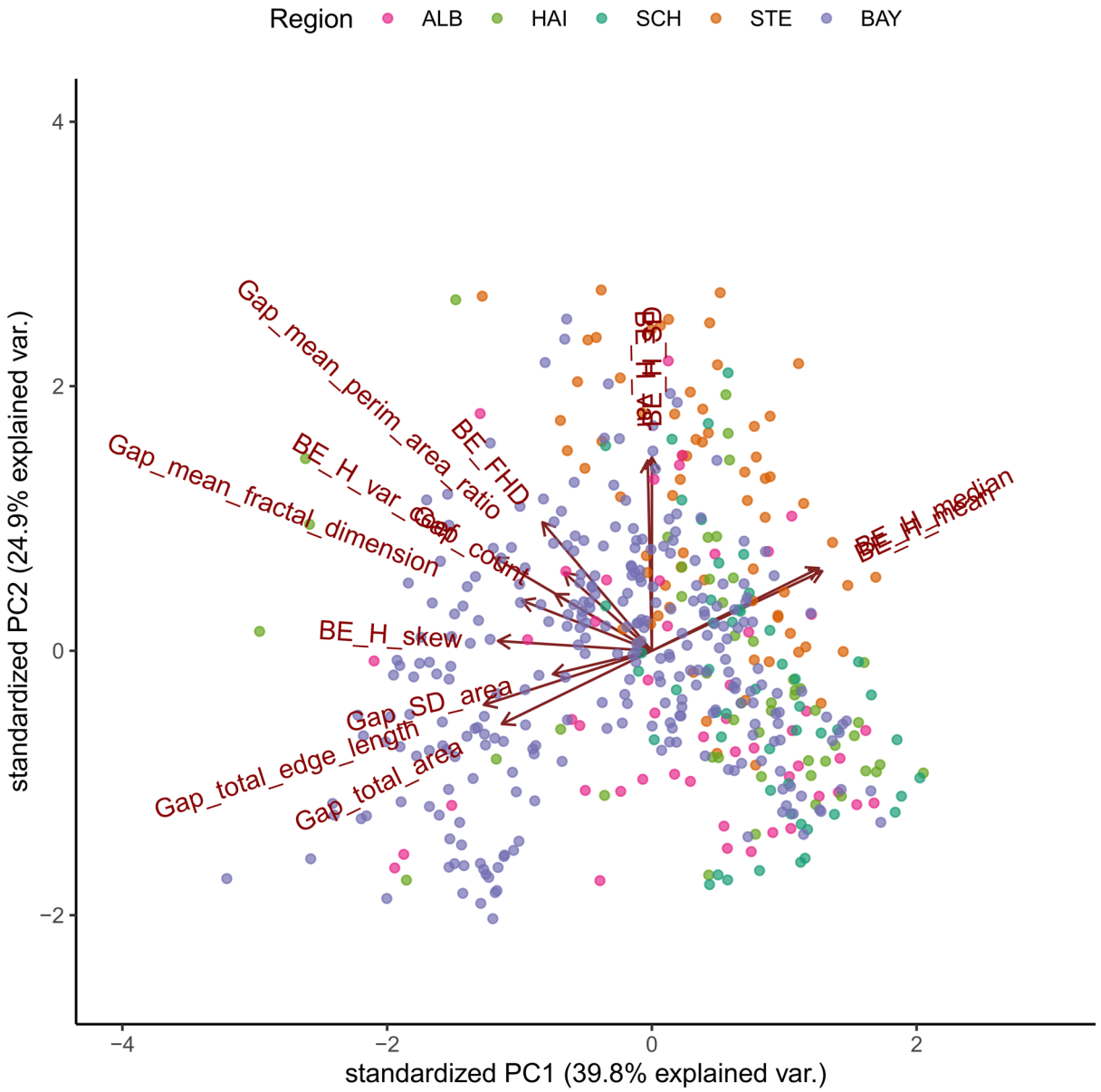


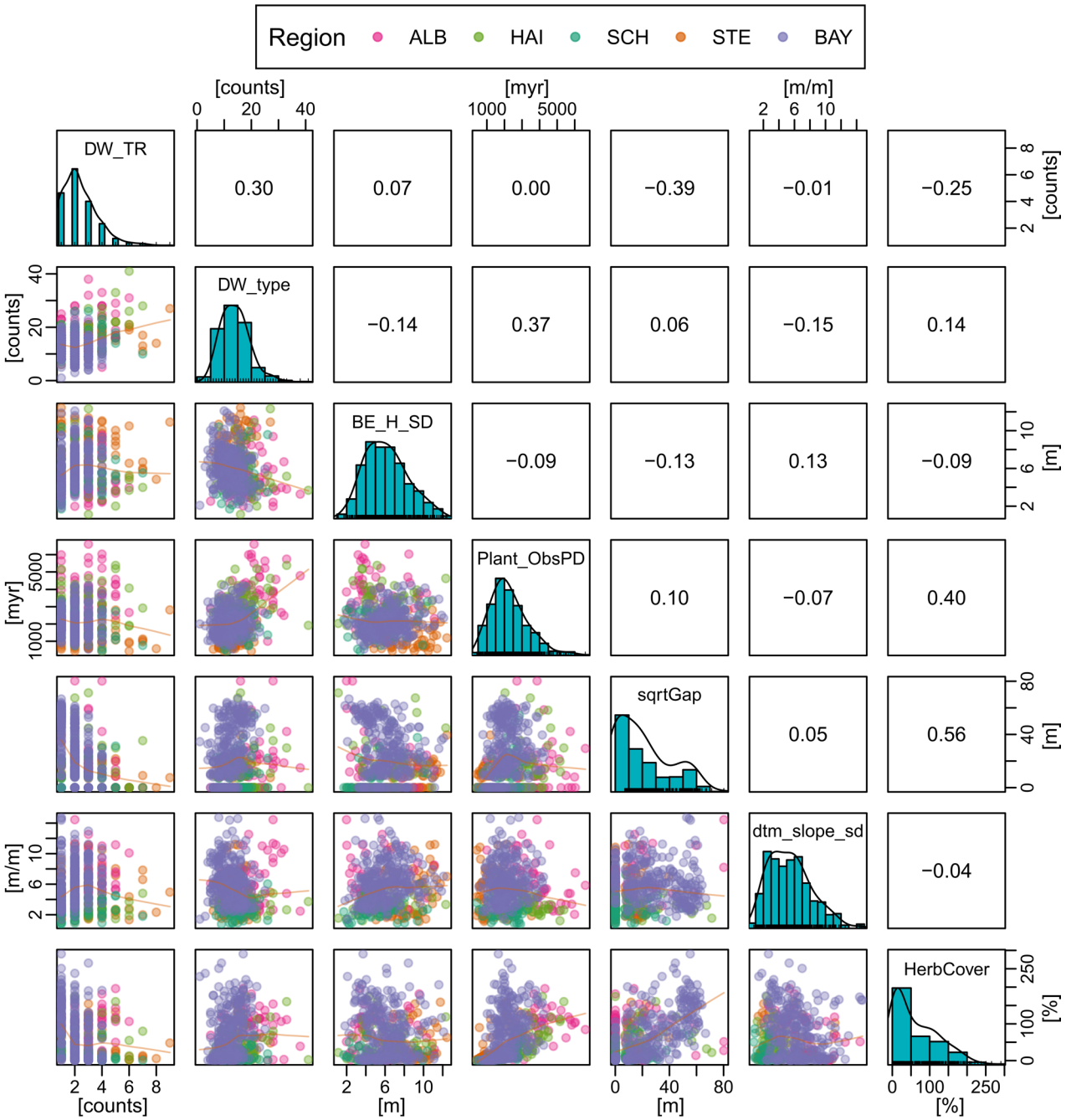
Extended Data Fig. 1 | Locations of the single regions from which data was derived. The Biodiversity Exploratories project (biodiversity-exploratories.de), comprised three forest areas spanning from south to north: the Biosphere Reserve Schwäbische Alb in the Swabian Jura (ALB, 50 Plots), Hainich National Park and the surrounding area (HAI, 50 plots) and the Schorfheide-Chorin Biosphere Reserve (SCH, 50 plots). This database is supplemented with plots from the Steigerwald project in northern Bavaria (STE, 69 plots) and the BIOKLIM project in the Bavarian Forest National Park (BAY, 278 plots). In all three projects diverse environmental variables and species were monitored in a comparable fashion.



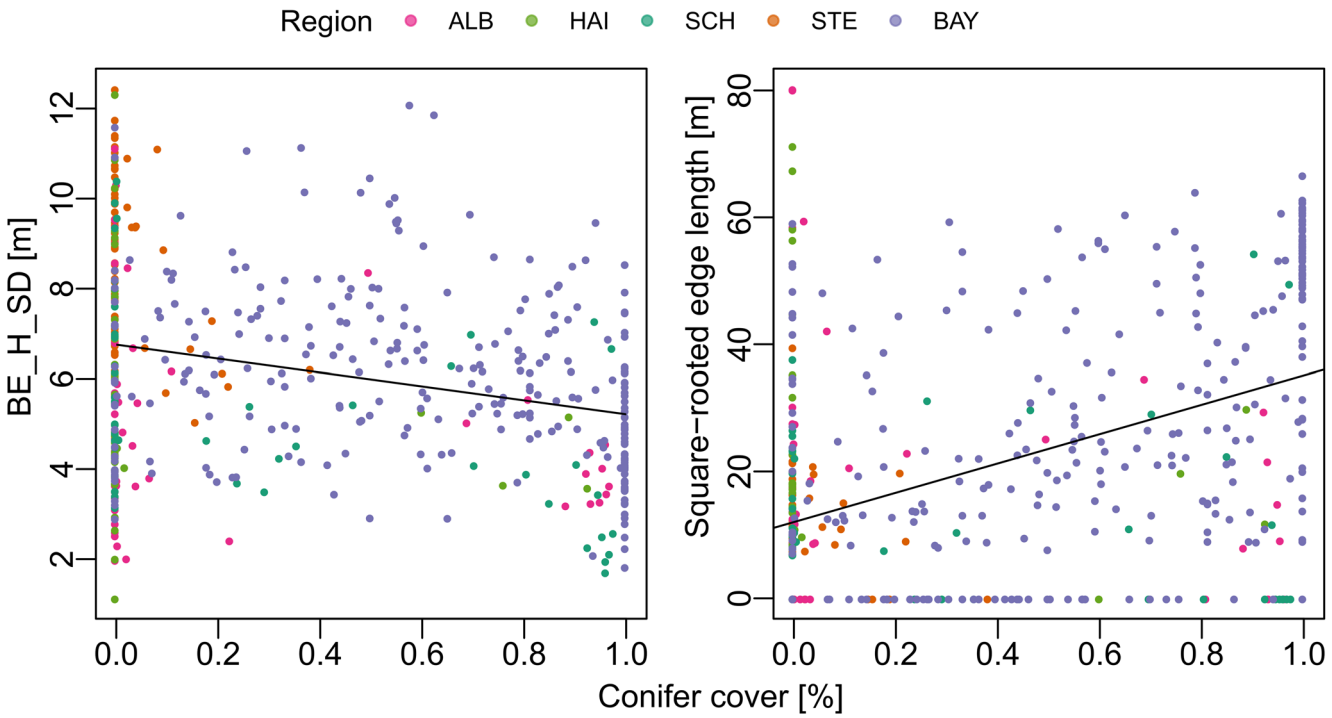
Extended Data Fig. 2 | Conceptual considerations of three potential measurements used to describe horizontal heterogeneity of five (A-E) different forest stands. The number of gaps (lilac line) is a measure which would ignore differences in gap areas (B,C). Gap area (orange line) overestimates heterogeneity 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.



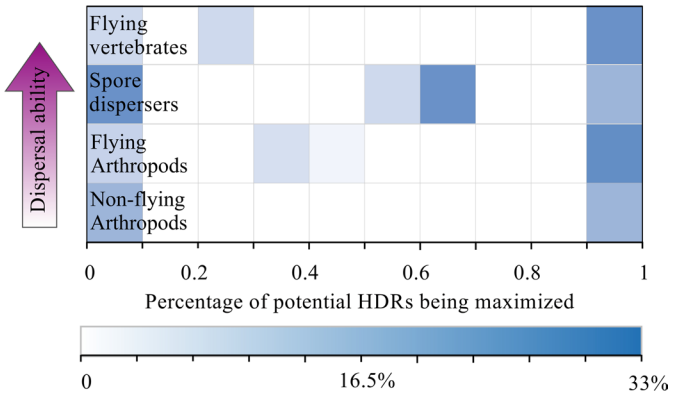
Extended Data Fig. 3 | PCA of structural parameters. Potential structural parameters, which could have been used to describe either vertical or horizontal heterogeneity, depicted via Principle Component Analysis. Many measures capture not the main axes and represent a mixture of both. The variables which were chosen in our analysis (BE_H_SD and Gap_total_edge length) represent the variation without inferring with each other. Colour-coding referring to the five regions: the Biosphere Reserve Schwäbische Alb (ALB), Hainich National Park and the surrounding area (HAI), the Schorfheide-Chorin Biosphere Reserve (SCH), the Steigerwald project (STE) and the BIOKLIM project in the Bavarian Forest National Park (BAY).



Extended Data Fig. 4 | Correlation between selected variables. Shown are Pearson Correlation Coefficients between the selected variables used in the GAMs, that is taxonomic (DW_TR) and type richness (DW_type) of deadwood, vertical heterogeneity measured as standard deviation of height from vegetation returns (BE_H_SD), vegetation diversity measured as Faith's PD (in millions of years) of the plant communities (Plant_ObsPD), horizontal heterogeneity measured as the (square-rooted) total gap edge length (sqrtGap), topographic heterogeneity measured as the standard deviation of the slope of the digital terrain model (dtm_slope_sd) as well as the cover of herbs sampled within the plots (HerbCover). All variables have a R of less than 0.6, indicating no problems with multicollinearity. Colour-coding referring to the five regions: the Biosphere Reserve Schwäbische Alb (ALB), Hainich National Park and the surrounding area (HAI), the Schorfheide-Chorin Biosphere Reserve (SCH), the Steigerwald project (STE) and the BIOKLIM project in the Bavarian Forest National Park (BAY).



Extended Data Fig. 5 | Correlation between height SD (left) and gap edge length (right) and the proportion of conifers in a forest stand. 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). 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. Colour-coding referring to the five regions: the Biosphere Reserve Schwäbische Alb (ALB), Hainich National Park and the surrounding area (HAI), the Schorfheide-Chorin Biosphere Reserve (SCH), the Steigerwald project (STE) and the BIOKLIM project in the Bavarian Forest National Park (BAY).



Extended Data Fig. 6 | Infliction points under different ranking. Inflection points, that is, 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), ordered along dispersal ability. In contrast to Fig. 3, we further subdivided into flying and non-flying arthropods and ranked spore-disperses higher than flying vertebrates in terms of dispersal ability. However, both classification and ranking systems did not show any relationship to the infliction point (Asymptotic General Independence Test, alternative "greater", Z=0.38, p-value=0.35).

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection
Data analysis	For all analyses we used R v3.5.0 via the R-Studio interface and the packages picante, version 1.7, mgcv version 1.8.26 and Mgcviz-package version 0.1.1. and coin-package vers. 1.3 Vector graphics have been edited with functions of Inkscape v0.92.3.

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Data reported in this paper can be assessed from the Biodiversity Exploratories Information System (https://www.bexis.uni-jena.de), DataSetID 25126. The DOI (https://doi.org/10.25829/bexis.25126-1.1.25) will be activated upon publication

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Ecological, evolutionary & environmental sciences study design

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Study description

Here, we test whether habitat heterogeneity has generally positive effects on species richness, as predicted by the habitat heterogeneity hypothesis, or whether heterogeneity leads to a reduced amount of suitable area available for individual species and thus a decrease in mean population size and ultimately to hump-shaped or even negative relationships (area-heterogeneity-trade-off hypothesis).
Therefore, we assessed species richness of twelve species groups spanning diverse trophic levels on up to 497 1 ha forest plots across temperate forests of Germany. For each plot, we measured six facets of heterogeneity including the subject areas forest structure, plant diversity, deadwood and micro-scale topography. This was done either by field assessments or with the help of Airborne Laser Scanning. For each species group, we modelled the relationship between species richness and all six facets using a generalized additive modelling (GAM) framework, without any a priori assumptions about the nature of the above-described relationship and accounting for overdispersion by a quasi-Poisson estimation procedure. The study region was considered as a random factor to account for regional effects. To determine whether our data supported the habitat-heterogeneity hypothesis, the area–heterogeneity-trade-off hypothesis, or neither, we considered the modelled relationships between the richness of the species groups and the single predictor variables as "supporting the habitat-heterogeneity hypothesis" (monotonous increase in species richness), "supporting the area–heterogeneity-trade-off hypothesis" (changes in sign of slope from positive to negative in species richness) or "supporting neither.". To test whether heterogeneity affects the mean population size of each animal group (note that no abundance data were available fungi, lichens and bryophytes), we also applied GAMs with a Gaussian error distribution with mean abundance or, in case of bats, calls per species, as dependent and the six facets of heterogeneity as independent variable.

Research sample

Our data are based on three projects, in which comprehensive assessments of biodiversity and habitat variables have been conducted. The Biodiversity Exploratories project (biodiversity-exploratories.de), 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 is supplemented with plots from the Steigerwald project in northern Bavaria (69 plots) and the BIOKLIM project in the Bavarian Forest National Park (278 plots). For each of the plots, several species groups have been assessed.
We sampled a broad range of trophic levels and taxa, namely bats, birds, spiders, carabid, saproxylic, necrophagous and phytophagous beetles, true bugs, moths, fungi and lichens on dead wood and bryophytes and calculated their species richness and, for the animal groups, mean abundance. A sample hereby refers to the species richness, or, if available, mean population size, per species group and plot.

Datasets used:
Exploratories Project
Jung, Kirsten; Marco Tschapka (2018): Bat activity in all Exploratories, summer 2008, using acoustic monitoring . v1.1.4. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=19848
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
Goßner, Martin; Markus Lange; Manfred Türke; Esther Pasalic; Wolfgang Weisser (2016): Window and ground traps on forest EPs in 2008 subset Hemiptera. v1.1.4. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=16867
Goßner, Martin; Manfred Türke; Markus Lange; Esther Pasalic; Wolfgang Weisser (2016): Window and ground traps on forest EPs in 2008 subset Araneae. v1.1.3. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=16868
Fischer, Markus (2017): Deadwood inhabiting fungi presence absence (2010, all forest EPs). v1.2.2. Biodiversity Exploratories Information System. Dataset. https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=18547
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 which have been provided by Jörg Müller

BIOKLIM-Project

Bässler, C., Müller, J. & Dziock, F. (2010). Detection of Climate-Sensitive Zones and Identification of Climate Change Indicators: A Case Study from the Bavarian Forest National Park. Folia Geobot., 45, 163–182.
Bässler, C., Müller, J., Dziock, F. & Brandl, R. (2010). Effects of resource availability and climate on the diversity of wood-decaying fungi. J. Ecol., 98, 822–832.
Moning, C., Werth, S., Dziock, F., Bässler, C., Bradtka, J., Hothorn, T., et al. (2009). Lichen diversity in temperate montane forests is influenced by forest structure more than climate. For. Ecol. Manag., 258, 745–751.
Müller, J. & Brandl, R. (2009). Assessing biodiversity by remote sensing in mountainous terrain: the potential of LiDAR to predict forest beetle assemblages. J. Appl. Ecol., 46, 897–905.
Müller, J., Mehr, M., Bässler, C., Fenton, M.B., Hothorn, T., Pretzsch, H., et al. (2012). Aggregative response in bats: prey abundance versus habitat. Oecologia, 169, 673–684.
Müller, J., Moning, C., Bässler, C., Heurich, M. & Brandl, R. (2009). Using airborne laser scanning to model potential abundance and assemblages of forest passerines. Basic Appl. Ecol., 10, 671–681.
Raabe, S., Müller, J., Manthey, M., Dürhammer, O., Teuber, U., Göttlein, A., et al. (2010). Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. For. Ecol. Manag., 260, 1956–1964.

and further, unpublished data which have been provided by Jörg Müller

Sampling strategy

The study was conducted at up to 497 plots in five forest regions distributed from north to south in Germany and representative of forest habitat types in Central Europe. Sample size was based on the maximum of available data with both direct assessments of diversity and ALS data. The number of investigated plots per group was 248 for bats, 496 for birds, 385 for all arthropods but moths, 227 for moths, 597 for dead wood fungi, 315 for lichens and 322 for bryophytes.
The phylogeny used in the study was taken from Durka and Michalski (Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. Ecology 93, 2297–2297; 2012)

Data collection

Biodiversity data:
For each species 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 in the other two projects fixed autonomous batcorders were used. Birds were monitored acoustically and visually within a fixed time span during their breeding season. Arthropods were collected using pitfall, crossed flight interception traps and low-intensity light traps. Fungi and lichens present on dead-wood objects within a fixed area were mapped. Bryophytes and plants were mapped within a fixed area

Environmental data: The taxonomic richness of dead wood was calculated by counting the number of different tree species within a plot. Structural richness of dead wood was calculated by counting the number of different deadwood types, classified according to diameter and decomposition classes as well as type. Plant diversity was measured as phylogenetic diversity (Faith's PD, based on a published phylogeny) of all vascular plants recorded in the tree, shrub and herb layers.
Standardized measurements of the 3D structure of the forests as well as microscale topography were obtained using high-resolution airborne laser scanning (ALS). Vertical heterogeneity was quantified as the standard deviation (SD) of the vegetation height returns. To calculate horizontal heterogeneity, the plots were classified into 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%. Then, we calculated the total length of the gap edges to obtain a continuous measurement of horizontal heterogeneity. Micro-scale topography was calculated as within-plot terrain heterogeneity, using a high-resolution digital terrain model derived from the ALS measurements. The SD of the slope based on a grain size of 1 m × 1 m across our one-hectare plots was used as a measure of topographic heterogeneity.

Further details are provided in the Supplementary information.

Timing and spatial scale

All plots were 1ha in size. Sampling of biodoversity data was conducted within the vegetation period. The sampling was conducted between 2007 and 2018, depending on the region and taxon.

Dead wood was recorded within 1m left and right along line-transects on both diagonals of a plot in the Exploratories, within a 13 m radius around the midpoint in the Steigerwald-project and within a 8 m radius in the BioKlim Project.

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. In the Steigerwald, vegetation was mapped on a 200m^2 square in April and June 2014. From the spring and summer records, always the higher record is chosen. In the Bavarian Forest National park, vegetation was recorded on a circular 0.2 ha plot in summer 2006.

Airborne laserscanning was recorded under leaf-on connditions covering the whole plot in 2007 (Bavarian Forest), 2008 (Hainich), 2009 (Schorfheide-Chorin), 2010 (Swabian Alb), and 2015 and for some plots, 2018 (Steigerwald).

Bats were recorded from 2008 – 2010 in the Exploratories with a combination of transect- and point stop detector walks.The survey time per edge was 6 minutes, same as the time spent at each corner, resulting in 48 minutes per plot. Here, detector walks were conducted twice per summer. In the BioKlim Project and the Steigerwald, autonomous bat call recorders were placed as near to the middle of the plot in three rounds from April to August 2017 in Steigerwald and in seven rounds from May to August 2009 in the BioKlim Project.

Birds were monitored during the breeding seasons from five times between March and June 2008 to 2010 in the Exploratories. All bird hearings or sightings were recorded within 5 minutes and a 50 m radius from plot midpoint. 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 (Steigerwald) and 10 minutes

in 2009 (Bavarian Forest).

In the Exploratories, the pitfall-traps and flight-interception traps were placed at three random corners of the plots from May to October in 2008. From these three, two were randomly chosen for species determination ("Priority 1" and "Priority 2"). In the Steigerwald and BioKlim Projects, only one trap was established per plot. Here, the traps 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. Light traps were installed near the midpoint of all plots for two nights per plot between the end of May and mid of August (the phenological peak of moth occurrence) on all plots. Thereby, the weeks of full moon were avoided.

For dead-wood fungi, eleven dead wood objects located within the 1 ha plot were examined in 2010 in the exploratories. 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.

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. 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.

Data exclusions

The methods, grain size and time frame for species sampling, although standardised within each project, differ between projects, albeit to varying extents. To obtained comparable estimates of diversity, the data had to be similarly cropped while in each case retaining as much information as possible. If data on certain taxonomic groups were collected for several years, as was the case in Biodiversity Exploratories, for each region only the data of the year closest to the ALS flights were chosen. For our analysis, we always selected only data from "priority 1" pitfall and ground window traps from the Exploratories to gain equal sampling sizes in comparison to the Steigerwald and Bayerwald projects. 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.

Reproducibility

Not applicable to our study. We did not conduct any experiments.

Randomization

The sampled plots were geographically clustered and used, depending on the project (see above), slightly different methods to assess biodiversity. In order to gain comparable estimates of diversity, raw data gained from the projects was cropped to a comparable extent. Furthermore, we added region as a random factor in the GAMs to account for both the geographical effect and differences in methods.

Blinding

Our data is drawn from several projects, in which species and environmental variables were obtained with standardized protocols (see above). Within each project, the sampling was the same. After cropping the data to a comparable extent (see above) all further processing steps were equally conducted.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions

Animals, plants, lichens, bryophytes and fungi were recorded throughout the vegetation period of several years. Recordings of bats, birds and moths were only conducted under suitable weather conditions and, for the latter, under respect of the moon phase. Other arthropods were sampled automatically every day.

Location

Sampling locations can be found in the data set.

Access and import/export

obtained permits:

55-8/8848.02-07 Regierungspräsidium Tübingen
13.4 64233/11-07SDH Thüringer Landesverwaltungsamt
R07/SOB-0907 Landesumweltamt Brandenburg
63.2-15.02.00.17-38-2018 UNB Eisenach;
LFU-N1- 47 43 /128+5#69 122/2018 Landesamt für Umwelt Brandenburg;
55.1-8642.10-N 25 Regierung von Niederbayern
55.1-8622 Regierung von Oberfranken

Disturbance

Mapping of birds, bats, plants, bryophytes, lichens, fungi and dead wood was done without disturbance except from walking within the plots. Disturbance was caused only by the withdrawal of arthropods for specification, though this disturbance is negligible given the high reproduction rates of arthropods.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	the study did not involve laboratory animals
Wild animals	Bats and birds were recorded using acoustic monitoring and, for the latter, sightings. Plants, bryophytes, fungi and lichens were mapped in the field. For quantitative and qualitative recordings of Arthropods, we used flight-interception traps and pitfall traps with sulphate solution as trapping and killing liquid. Moths were caught by of 12 V and 15 Watt super actinic UV lighttraps, with chloroform as killing medium.
Field-collected samples	The sampled arthropods were preserved in alcohol of frozen until they could be determined by specialists.
Ethics oversight	Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, Brandenburg and Bavaria.

Note that full information on the approval of the study protocol must also be provided in the manuscript.