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

Lea Heidrich^{*1}, Soyeon Bae¹, Shaun Levick², Sebastian Seibold^{3,1}, Wolfgang Weisser³, Peter Krzystek⁴, Paul Magdon⁵, Thomas Nauss⁶, Peter Schall⁷, Alla Serebryanyk⁴, Stephan Wöllauer⁶, Christian Ammer⁷, Claus Bässler^{8,9}, Inken Doerfler^{3,10}, Markus Fischer¹¹, Martin M. Gossner¹², Marco Heurich^{8,13}, Torsten Hothorn¹⁴, Kirsten Jung¹⁵, Holger Kreft^{16,17}, Ernst-Detlef Schulze¹⁸, Nadja Simons¹⁹, Simon Thorn¹, and Jörg Müller^{1,8}

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

2) CSIRO Land and Water, PMB 44, Winnellie, 0822 NT, Australia

3) Terrestrial Ecology Research Group, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

4) Department of Geoinformatics, Munich University of Applied Sciences, Germany

5) Forest Inventory and Remote Sensing, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Büsgenweg 5, 37077 Göttingen, Germany

6) Faculty of Geography, Philipps-University Marburg, Deutschhausstr. 10, 35037 Marburg, Germany

7) Silviculture and Forest Ecology of the temperate Zones, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

8) Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany

9) Goethe University Frankfurt, Faculty of Biological Sciences, Institute for Ecology, Evolution and Diversity, D- 60438 Frankfurt am Main, Germany.

- 24 10) Institute of Biology and Environmental science, Vegetation science & Nature
 25 conservation, University of Oldenburg, Ammerländer Heerstraße 114-118, 26129
 26 Oldenburg, Germany
- 27 11) Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern,
 28 Switzerland
- 29 12) Forest Entomology, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-
 30 8903 Birmensdorf, Switzerland
- 31 13) Chair of Wildlife Ecology and Wildlife Management, University of Freiburg,
 32 Germany
- 33 14) Epidemiology, Biostatistics and Prevention Institute, University of Zurich,
 34 Hirschengraben 84, 8001 Zurich, Switzerland
- 35 15) Evolutionary Ecology and Conservation Genomics, University Ulm, Albert-Einstein-
 36 Allee 11, 89069 Ulm
- 37 16) Biodiversity, Macroecology & Biogeography, University of Goettingen, Büsgenweg
 38 1, D-37077 Göttingen, Germany
- 39 17) Centre of Biodiversity and Sustainable Land Use (CBL), University of Goettingen,
 40 Büsgenweg 1, D-37077 Göttingen, Germany
- 41 18) Max Planck Institute for Biogeochemistry, Box 100164, 07701 Jena, dschulze@bgc-
 42 jena.mpg.de
- 43 19) Ecological Networks, Technical University of Darmstadt, Schnittspahnstraße 3, 64287
 44 Darmstadt

45 * Lea Heidrich.

46 **Email:** lea.heidrich@gmx.de

47 **Abstract**

48 The *habitat-heterogeneity hypothesis* predicts that biodiversity increases with increasing
49 habitat heterogeneity due to greater niche dimensionality. However, recent studies have
50 reported that richness can decrease with high heterogeneity due to stochastic extinctions,
51 creating trade-offs between area and heterogeneity. This suggests that greater complexity in
52 heterogeneity–diversity relationships (HDRs) may exist, with potential for group-specific
53 responses to different facets of heterogeneity that may only be partitioned out by a
54 simultaneous test of HDRs of several species groups and several facets of heterogeneity.
55 Here, we systematically decompose habitat heterogeneity into six major facets on ~500
56 temperate forest plots **across Germany** and quantify biodiversity of 12 different species
57 groups, including bats, birds, arthropods, fungi, lichens and plants, representing 2600 species.
58 Heterogeneity in horizontal and vertical forest structure underpinned most HDRs, followed by
59 plant diversity, deadwood and topographic heterogeneity, but the relative importance varied
60 even within the same trophic level. Among significant HDRs, 53% increased monotonically,
61 consistent with the classical *habitat-heterogeneity hypothesis*, but 21% were humped-shaped,
62 25% had a monotonically decreasing slope and 1% showed no clear pattern. Overall, we
63 found no evidence of a single generalizable mechanism **determining HDR patterns**.

65 **Introduction**

66 The *habitat heterogeneity hypothesis* is one of the central pillars of ecological theory. It states
 67 that spatial heterogeneity in abiotic and biotic conditions increases niche dimensionality, i.e.
 68 the number of available niches, allowing different species to co-exist such that biodiversity
 69 increases (Fig. 1)¹⁻³. However, if heterogeneity increases the number of species, the amount
 70 of suitable area available for individual species decreases per area unit. According to the *area-*
 71 *heterogeneity trade-off hypothesis*³, this can result in a decrease in mean population sizes
 72 especially at high levels of habitat heterogeneity (Fig. 1). The result is an increased
 73 probability of stochastic extinctions and ultimately a decline in species richness. This
 74 mechanism, along with fragmentation effects that often accompany heterogeneity, can lead to
 75 hump-shaped heterogeneity-diversity relationships (HDRs)^{3,4} (Fig. 1).

76 The *area-heterogeneity trade-off hypothesis* is a relatively recent concept and has received
 77 less scrutiny than the classical *habitat heterogeneity hypothesis*. Addressing the area-
 78 heterogeneity trade-off hypothesis requires testing for non-linear relationships between
 79 heterogeneity and biodiversity. However, such tests are poorly represented in the literature
 80 and subsequently, not included in a global meta-analysis which supported the prevalence of
 81 positive HDRs. Next to the growing evidence that HDRs can take non-linear forms³⁻⁹, it has
 82 been shown that certain ecological properties, such as niche breadth, reproduction and
 83 dispersal rates^{4,6-8}, moderate the responses of species to increasing niche dimensionality,
 84 reductions in effective area and the degree of fragmentation. Consequently, rather than
 85 investigating whether a positive or hump-shaped HDR prevail, recent theoretical approaches
 86 address the question of under which conditions HDR takes which shape^{4,9,10}.

87 A theoretical modeling approach suggested that, despite the various ways in which
 88 environmental heterogeneity may affect species richness, HDR patterns should be predictable
 89 and robust⁴. This was specifically proposed for sessile organisms, in which low niche width
 90 and high dispersal ability should decrease the level of heterogeneity which maximizes species
 91 richness. Moreover, theoretical models have shown that given a habitable surrounding,
 92 species which are limited in dispersal have positive HDRs due to fragmentation effects ¹¹,
 93 while those with large dispersal ranges rather have hump-shaped HDRs ⁴ (Figure 1).

94 A limitation of current theoretical modeling is that it is based upon strong assumptions (e.g. a
 95 lack of habitat selection⁴), which are unlikely to be met in practice. Thus, the relevance of the
 96 theoretical findings to real-world settings remains to be demonstrated. At the same time,
 97 attempts to find general patterns in empirical studies of HDRs have faced several challenges.
 98 First, habitat heterogeneity can result from many different abiotic and biotic factors¹², referred
 99 to in the following as facets of heterogeneity. Even within a single facet of heterogeneity, both
 100 the multitude of methods used to evaluate single facets and the varying lengths of the covered
 101 gradients have hampered comparisons of empirical results¹². For example, short heterogeneity
 102 gradients are more likely to underrepresent trade-offs between area and heterogeneity than are
 103 fully covered gradients. Second, species groups differ in their ecological requirements and
 104 possibly also in their responses to different facets of heterogeneity. Thus, while a taxon may
 105 respond strongly to vertical forest structure, its response to other facets may be neutral¹³. A
 106 third challenge is the fact that the response of a given taxon to environmental heterogeneity
 107 might be habitat-specific. This is demonstrated by birds, which respond positively to cover-
 108 type diversity in woodlands and grasslands but not in savannas⁹. Lastly, the shape of the HDR
 109 will also depend on the scale at which the study is conducted^{1,7,9}.

110 Species group, habitat, heterogeneity facet and spatial scale may act together to modify the
 111 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 levels¹⁴ and with respect to major facets of heterogeneity¹², 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 (Extended Data 1), 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^{15,16}. 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 forest¹⁵. 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 cycle¹⁷. In this study, to ensure a comprehensive assessment of forest heterogeneity, we adopted the classification system of Stein and Kreft¹², 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 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

137 independent facets of heterogeneity at the scale of a forest stand: 1) the taxonomic and 2)
138 structural richness of deadwood, 3) vascular plant diversity, 4) vertical as well as 5) horizontal
139 structural heterogeneity and 6) micro-scale topography (Fig. 2a).

140 We assessed whether multidiversity (the scaled species richness of all recorded species¹⁸) and
141 the species richness of each species group respond to particular facets of heterogeneity and
142 which shape these HDRs take. We then tested whether the level of heterogeneity at which
143 species richness is maximized increases with increasing niche breadth and decreases with
144 increasing dispersal ability, as predicted by recent modeling approaches⁴. Finally, we
145 examined whether the response of the mean population decreases with increasing
146 heterogeneity, as expected by stochastic extinctions and thus consistent with the area-trade off
147 theory.

148 Results and Discussion

149 The species richness of all species groups, except carabids (Fig. 2 b, Table 1), responded to
 150 habitat heterogeneity. This finding supported the ubiquitous role of heterogeneity in shaping
 151 species richness across different species groups. However, as expected from the exploratory
 152 nature of the study design and the fact that species are expected to differ in their
 153 responsiveness to heterogeneity¹³, there was a large amount of variation in our results. Both
 154 group-specific responses to different facets of heterogeneity and the shape of responses
 155 differed among species groups.

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

169 In the theoretical model of Ben-Hur and Kadmon⁴, the form of the HDRs depended on
 170 fragmentation, niche breadth and dispersal ability. In our study, fragmentation effects are
 171 expected to be negligible because the surrounding matrix is habitable¹¹ as all of our 1-ha plots

are [each embedded in](#) larger forested matrix. Thus, we would expect strong effects of niche breadth 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 ones⁴. However, neither habitat niche breadth, here estimated based on trophic positions¹⁹ (Figure 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, $z=0.22$, $p=0.96$, [Supplementary Methods](#), [Supplementary Table 1](#), [Supplementary Figure 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^{13,20}. 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. 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. 2). This result provides the [empirical evidence](#) of experiments showing that fungal species richness is driven by host tree diversity²¹, and saproxylic beetle richness by heterogeneity related to wood physiognomy,

such as diameter, decay stage and dead wood 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 dead wood on non-saproxyllic organisms^{24,25}. While saproxyllic 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, saproxyllic 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 microstructures²⁶. 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 saproxyllic 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^{15,27,28}. 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, [Supplementary Figure 2.1](#)). Thus, for birds, different vertical structures offer different niches in terms of nesting sites and foraging grounds, just as MacArthur and MacArthur² predicted. However, vertical heterogeneity also

220 provides niches for other species groups, most likely through microclimatic conditions and
 221 shelter^{29,30}.

222 Horizontal heterogeneity determines variations in light availability and microclimatic
 223 conditions near ground³¹. In our study, all species groups except moths, bats and carabid
 224 beetles responded to horizontal heterogeneity. Many arthropods are sensitive to microclimatic
 225 conditions such that forest gaps will favor communities different from those associated with
 226 stands with a closed canopy^{22,24}. Birds may profit from an increased diversity of nesting sites,
 227 foraging sites and food sources. Neither vertical nor horizontal heterogeneity, however,
 228 correlated with a higher species richness of bats. For this group, differences in horizontal
 229 forest structure, due to species-specific adaptations in echolocation and flight performance,
 230 likely affect species composition rather than species richness^{32,33}. The relationship of species
 231 richness to topographic heterogeneity, measured as the standard deviation in the slope, was
 232 significant for six species groups (Table 1), and affected most arthropod groups and birds, but
 233 the underlying mechanism remains unclear. Topographic heterogeneity can be seen as a
 234 surrogate for heterogeneities in microclimate and soil, which seem to influence plant richness
 235 (Table 1) and may have cascading effects on higher trophic levels. These two types of
 236 heterogeneity therefore require further study.

237 Irrespective of the mechanisms underlying the variable HDRs, the fact that species groups *did*
 238 respond to the heterogeneity facets with which they *were not* obviously connected clearly
 239 demonstrates that any *a priori* restriction of heterogeneity facets may overlook important
 240 HDRs. Conversely, the fact that species groups *did not* respond to heterogeneity facets to
 241 which they *were* obviously connected indicated that the spatial scale at which heterogeneity is
 242 perceived is highly variable. Moreover, whether a species group does or does not respond to a
 243 certain facet of heterogeneity seems to vary even within trophic levels. For example, vertical
 244 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, [Supplementary Figure 2.1](#)). 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 abundance³⁴.

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 & Kadmon⁴. However, habitat heterogeneity affected the mean population size only in 15 out of 54 cases (9 animal groups $\times$ 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 results⁴. 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). 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 vegetation³⁴. 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 canopy³⁸. 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 extinction³.

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^{1,7} or the studied species groups are highly specialized³. While the 1-ha scale of our study was indeed smaller than the scale used in others (though comparable to the early studies of Robert MacArthur 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 severity¹⁰. 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 size¹⁰. 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

295 bryophytes decreased with increasing horizontal heterogeneity (Fig. 2b, [Supplementary](#)
 296 [Figure 2.1](#)). These two groups are dominated by closed-forest specialists that are sensitive to
 297 dry conditions ^{40,41} and may perceive the increases in solar radiation and the decreases in
 298 humidity associated with increasing horizontal heterogeneity as a constraint. Unfortunately,
 299 whether this constraint was pronounced due to smaller species pools or smaller population
 300 sizes could not be resolved with our data.

301 *Conclusions & implications*

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

314 Certain facets of habitat heterogeneity affected more species groups than others. Among the
 315 studied facets, vertical and horizontal heterogeneity ([which can be easily managed in](#)
 316 [silviculture](#)), were found to be major drivers of biodiversity in forests. Hence, forest and
 317 conservation management measures designed to increase within-stand biodiversity should
 318 enhance habitat heterogeneity by increasing vertical and, especially, horizontal stand

319 heterogeneity, as this will have more positive than negative effects on species richness.
320 However, we caution against a wide-ranging establishment of fine-scaled heterogeneity in
321 forest structure. Instead, to minimize the effect of negative responses, a mosaic of stands
322 comprising different gradients of structural heterogeneity should be provided.

323 **Methods**

324 **Study regions.** Our data are based on comprehensive assessments of biodiversity and habitat
 325 variables obtained from 497 one-hectare plots covering five regions in Germany and
 326 representing the full range of zonal temperate forests in Central Europe (see [Extended Data](#)
 327 [1](#)). The Biodiversity Exploratories project (biodiversity-exploratories.de⁴²) comprised three
 328 forest areas, spanning from south to north: the Biosphere Reserve Schwäbische Alb in the
 329 Swabian Jura (50 Plots), Hainich National Park and the surrounding area (50 plots) and the
 330 Schorfheide-Chorin Biosphere Reserve (50 plots). This database^{43–51} has been supplemented
 331 with plots from the Steigerwald project⁵² in northern Bavaria (69 plots) and the BIOKLIM
 332 project⁵³ in the Bavarian Forest National Park^{32,54–57} (278 plots).

333 **Facets of habitat heterogeneity.** To address heterogeneity in forests as comprehensively as
 334 possible, we adopted the classification system of Stein and Kreft¹², which systematically
 335 divides the facets of heterogeneity into five subject areas, of which four can be applied to a 1-
 336 ha plot scale: vegetation, micro-scale topography, soil and climate (Fig. 2a). In this study, the
 337 subject areas soil and climate were excluded, because their respective measures were not
 338 available for all plots. However, at the plot level, soil and climate would most likely strongly
 339 correlate with vegetation and topographic heterogeneity⁵⁸, both of which were included in our
 340 study. We also added deadwood^{52,59,60} as an ecosystem-specific subject area of habitat
 341 heterogeneity and further divided it into structural and taxonomic richness. The subject area
 342 vegetation was further divided into plant diversity and structural aspects, i.e., the vertical and
 343 horizontal heterogeneity of the vegetation.

344 **Quantifying habitat heterogeneity.** Based on several reviews^{12,15,61,62}, we selected potential
 345 measurements *a priori* for each of the six facets ([Supplementary Methods, Extended Data 2](#)).
 346 For the final selection, we examined the statistical behaviors (distributions) of the variables

and the within- and between-aspect co-linearity ([Supplementary Figures 3-7](#)), which is often an issue in LiDAR-derived measurements ([Extended Data 3](#)). In our study, the *a posteriori* selection of the measurements had several advantages over statistical variable selection in terms of dealing with multi-collinearity ([Extended Data 4](#)) 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 considered¹². 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 Siitonen⁶³. 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 [Supplementary Methods](#)). Plant diversity was characterized by considering all vascular plants in the tree, shrub and herb layers determined as part of biodiversity assessments (349 in total, [Supplementary Methods](#)). However, the number of plant species alone does not necessarily reflect ecological differences relevant to herbivores^{64,65}, as closely related plant species may host similar communities of insects⁶⁶.

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 Michalski⁶⁷, using the R software package *picante*, version 1.7⁶⁸ (Kembel *et al.* 2018). However, this approach does not necessarily reflect all functional differences between plant species (but see the Discussion in [Supplementary Methods](#)).

Standardized measurements of the 3D structure of the forests were obtained using high-resolution airborne laser scanning (ALS) ([Supplementary Methods](#)), a method that provides

372 accurate 3D measurements across large areas. The high point density of the ALS
 373 measurements allows forest structure to be characterized using salient metrics that describe
 374 the vertical and horizontal distribution of vegetation at high spatial resolution⁶⁹. For the
 375 standard deviation (SD) of all the heights from all vegetation returns as aggregates over the
 376 entire 1ha plot area. This metric is able to powerfully explain biodiversity patterns in forests³
 377 and is less sensitive to artificial classifications of layers than foliage height diversity
 378 ([Supplementary Methods](#)). To calculate horizontal heterogeneity, we classified the area within
 379 plots as gap and non-gap areas. Gap areas were defined as areas with a minimum size of 50
 380 m², a perimeter/area ratio of <1.5 (thus excluding narrow linear structures such as forest
 381 aisles), a height threshold of 2 m and a penetration ratio > 80%. Since the total gap area per
 382 plot would not capture a linear increase in horizontal heterogeneity—as both extremes, i.e.,
 383 100% canopy cover as well as a 100% gap area, are homogeneous in horizontal structure —
 384 we instead calculated the total length of the gap edges to obtain a continuous measurement of
 385 horizontal heterogeneity (for details, see [Supplementary Methods, Extended Data 2](#)). Both
 386 structural measures, i.e., total gap edge length and height SD, were largely independent of the
 387 tree species composition ([Extended Data 5](#)). Micro-scale topography was calculated as the
 388 within-plot terrain heterogeneity, determined using a high-resolution digital terrain model
 389 (DTM) with 1-m spatial resolution derived from the ALS measurements. The SD of the slope
 390 measured in the DTM across our 1-ha plots served as a measure of topographic heterogeneity,
 391 as it was better than the SD of the elevation in capturing small-scale variation (see
 392 [Supplementary Methods](#)).

393 **Biodiversity data.** The species richness of bats, birds, several arthropod taxa, fungi, lichens,
 394 bryophytes and vascular plants had been assessed in each of the three projects using
 395 standardized protocols^{43–52,54–57,60,70}. In this study, for each group only data acquired during the
 396 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. Birds were monitored acoustically and visually within a fixed time span during their breeding season. Arthropods were collected using pitfalls, crossed flight interception traps and low-intensity light traps. Fungi, bryophytes and lichens present on deadwood objects and the plants within a fixed area were mapped. 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 plot⁴. 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 non-linear humped shape curve (Fig. 1)? (2) Does population size, here estimated by abundances⁴ (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) ([Supplementary Figure 2](#)). 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 [Supplementary Methods](#)). 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 1.8.26⁷¹). 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 0.1.1⁷².

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 groups¹⁸. 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 breadth¹⁹, with producers assigned the lowest rank, followed by primary consumers, detritivores on deadwood⁷³, 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. 1.3⁷⁴) 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”.

447 In this case, we expected that arthropods would have smaller dispersal abilities than
448 vertebrates, while spore-dispersers were expected to have the best dispersal ability. Other
449 classifications and rankings led to similar results (see [Supplementary Methods, Extended](#)
450 [Figure 6](#)).

451 Note that we intentionally did not include the species richness or abundance of plants, either
452 as a response variable or in the calculation of multi-diversity, as this would have heavily
453 interfered with the Faith's PD of the plant community as an independent variable. However, a
454 reduced GAM without Faith's PD was applied to the species richness of plants (see Table 1).
455 All statistical analyses were carried out using the statistical software R, version 3.5.0⁷⁵.
456 Data reported in this paper can be accessed from the Biodiversity Exploratories Information
457 System (<https://www.bexis.uni-jena.de>), DataSetID 25126.

458 **Acknowledgements**

459 We dedicate this work to the memory of Kwesi Abbey Afful and Emmanuel Larrey-Williams,
 460 who were part of the moth sampling campaign. We sincerely thank the local management
 461 teams and student helpers for their assistance in the assessment of the species data, Hermann
 462 Hacker for moth determination, Andreas Ostrowski for managing the central database and
 463 Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Prati, Ingo Schöning,
 464 François Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser and the late Elisabeth Kalko,
 465 for their role in setting up the Biodiversity Exploratories project. This work was (partly)
 466 funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" grant
 467 MU3621/2-1, KR 3292/2-1 and LE3316/2-1. Field work permits were issued by the
 468 responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg.

469 **Author Contributions**

470 L.H., J.M., S.B., S.L conceived the manuscript; J.M. designed the study; L.H., J.M., P.M,
 471 S.B., K.J., M.G., M.F., C.B, J.B., S.W., W.W., I.D., M.H. acquired and processed the data.
 472 All authors participated in analyzing and interpreting the data; L.H., J.M., S.L., P.M., S.S. ,
 473 W. W. drafted the manuscript; all authors contributed critically to the revisions.

474 **Data Availability statement**

475 All data used in this manuscript is publicly available at DOI [XXX](#).

476 **Competing Interests statement:**

477 The authors have no competing interests to declare.

478

479 References

- 480 1. Stein, A., Gerstner, K. & Kreft, H. Environmental heterogeneity as a universal driver of species
481 richness across taxa, biomes and spatial scales. *Ecol. Lett.* **17**, 866–880 (2014).
- 482 2. MacArthur, R. H. & MacArthur, J. W. On Bird Species Diversity. *Ecology* **42**, 594–598 (1961).
- 483 3. Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M. & Kadmon, R. Area–heterogeneity
484 tradeoff and the diversity of ecological communities. *Proc. Natl. Acad. Sci.* **109**, 17495–17500
485 (2012).
- 486 4. Ben-Hur, E. & Kadmon, R. Heterogeneity–diversity relationships in sessile organisms: a unified
487 framework. *Ecol. Lett.* **23**, 193–207 (2020).
- 488 5. Chocron, R., Flather, C. H. & Kadmon, R. Bird diversity and environmental heterogeneity in North
489 America: a test of the area–heterogeneity trade-off. *Glob. Ecol. Biogeogr.* **24**, 1225–1235 (2015).
- 490 6. Kadmon, R. & Allouche, O. Integrating the effects of area, isolation, and habitat heterogeneity on
491 species diversity: a unification of island biogeography and niche theory. *Am. Nat.* **170**, 443–454
492 (2007).
- 493 7. Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R. & Pärtel, M. Environmental heterogeneity,
494 species diversity and co-existence at different spatial scales. *J. Veg. Sci.* **21**, 796–801 (2010).
- 495 8. Bar-Massada, A. Complex relationships between species niches and environmental
496 heterogeneity affect species co-occurrence patterns in modelled and real communities. *Proc. R.*
497 *Soc. B Biol. Sci.* **282**, 20150927 (2015).
- 498 9. Bar-Massada, A. & Wood, E. M. The richness–heterogeneity relationship differs between
499 heterogeneity measures within and among habitats. *Ecography* **37**, 528–535 (2014).
- 500 10. Yang, Z. *et al.* The effect of environmental heterogeneity on species richness depends on
501 community position along the environmental gradient. *Sci. Rep.* **5**, 15723 (2015).
- 502 11. Rybicki, J., Abrego, N. & Ovaskainen, O. Habitat fragmentation and species diversity in
503 competitive communities. *Ecol. Lett.* **n/a**,.

- 504 12. Stein, A. & Kreft, H. Terminology and quantification of environmental heterogeneity in species-
505 richness research. *Biol. Rev.* **90**, 815–836 (2015).
- 506 13. Tews, J. *et al.* Animal species diversity driven by habitat heterogeneity/diversity: the importance
507 of keystone structures. *J. Biogeogr.* **31**, 79–92 (2004).
- 508 14. Seibold, S., Cadotte, M. W., MacIvor, J. S., Thorn, S. & Müller, J. The Necessity of Multitrophic
509 Approaches in Community Ecology. *Trends Ecol. Evol.* **33**, 754–764 (2018).
- 510 15. Davies, A. B. & Asner, G. P. Advances in animal ecology from 3D-LiDAR ecosystem mapping.
511 *Trends Ecol. Evol.* **29**, 681–691 (2014).
- 512 16. Seidel, D. A holistic approach to determine tree structural complexity based on laser scanning
513 data and fractal analysis. *Ecol. Evol.* **8**, 128–134 (2017).
- 514 17. *Saproxyllic Insects: Diversity, Ecology and Conservation*. (Springer International Publishing, 2018).
- 515 18. Allan, E. *et al.* Interannual variation in land-use intensity enhances grassland multidiversity. *Proc.*
516 *Natl. Acad. Sci.* **111**, 308–313 (2014).
- 517 19. Zalewski, M. *et al.* β -diversity decreases with increasing trophic rank in plant – arthropod food
518 chains on lake islands. *Sci. Rep.* **8**, 1–8 (2018).
- 519 20. Penone, C. *et al.* Specialisation and diversity of multiple trophic groups are promoted by different
520 forest features. *Ecol. Lett.* **22**, 170–180 (2019).
- 521 21. Krah, F.-S. *et al.* Independent effects of host and environment on the diversity of wood-
522 inhabiting fungi. *J. Ecol.* **106**, 1428–1442 (2018).
- 523 22. Seibold, S. *et al.* Microclimate and habitat heterogeneity as the major drivers of beetle diversity
524 in dead wood. *J. Appl. Ecol.* **53**, 934–943 (2016).
- 525 23. Andringa, J. I. *et al.* Combining tree species and decay stages to increase invertebrate diversity in
526 dead wood. *For. Ecol. Manag.* **441**, 80–88 (2019).
- 527 24. Seibold, S. *et al.* Dead-wood addition promotes non-saproxyllic epigeal arthropods but effects are
528 mediated by canopy openness. *Biol. Conserv.* **204**, 181–188 (2016).

- 529 25. Seibold, S. *et al.* Experimental studies of dead-wood biodiversity — A review identifying global
530 gaps in knowledge. *Biol. Conserv.* **191**, 139–149 (2015).
- 531 26. Malumbres-Olarte, J., Vink, C. J., Ross, J. G., Cruickshank, R. H. & Paterson, A. M. The role of
532 habitat complexity on spider communities in native alpine grasslands of New Zealand. *Insect*
533 *Conserv. Divers.* **6**, 124–134 (2013).
- 534 27. Renner, S. C. *et al.* Divergent response to forest structure of two mobile vertebrate groups. *For.*
535 *Ecol. Manag.* **415–416**, 129–138 (2018).
- 536 28. Froidevaux, J. S. P., Zellweger, F., Bollmann, K., Jones, G. & Obrist, M. K. From field surveys to
537 LiDAR: Shining a light on how bats respond to forest structure. *Remote Sens. Environ.* **175**, 242–
538 250 (2016).
- 539 29. Kadlec, T., Strobl, M., Hanzelka, J., Hejda, M. & Reif, J. Differences in the community composition
540 of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure.
541 *Biodivers. Conserv.* **27**, 2661–2680 (2018).
- 542 30. Baz, A., Cifrián, B. & Martín-Vega, D. Patterns of diversity and abundance of carrion insect
543 assemblages in the Natural Park ‘Hoces del Río Riaza’ (central Spain). *J. Insect Sci. Online* **14**, 162
544 (2014).
- 545 31. Frenne, P. D. *et al.* Global buffering of temperatures under forest canopies. *Nat. Ecol. Evol.* **3**,
546 744–749 (2019).
- 547 32. Müller, J. *et al.* Aggregative response in bats: prey abundance versus habitat. *Oecologia* **169**,
548 673–684 (2012).
- 549 33. Jung, K., Kaiser, S., Böhm, S., Nieschulze, J. & Kalko, E. K. V. Moving in three dimensions: effects
550 of structural complexity on occurrence and activity of insectivorous bats in managed forest
551 stands. *J. Appl. Ecol.* **49**, 523–531 (2012).
- 552 34. Leidinger, J. *et al.* Effects of forest management on herbivorous insects in temperate Europe. *For.*
553 *Ecol. Manag.* **437**, 232–245 (2019).

- 554 35. Dănescu, A., Albrecht, A. T. & Bauhus, J. Structural diversity promotes productivity of mixed,
 555 uneven-aged forests in southwestern Germany. *Oecologia* **182**, 319–333 (2016).
- 556 36. Juchheim, J., Ammer, C., Schall, P. & Seidel, D. Canopy space filling rather than conventional
 557 measures of structural diversity explains productivity of beech stands. *For. Ecol. Manag.* **C**, 19–26
 558 (2017).
- 559 37. Schulze, E. D. *et al.* Management breaks the natural productivity-biodiversity relationship in
 560 forests and grassland: an opinion. *For. Ecosyst.* **5**, 3 (2018).
- 561 38. Müller, J. *et al.* LiDAR-derived canopy structure supports the more-individuals hypothesis for
 562 arthropod diversity in temperate forests. *Oikos* **127**, 814–824 (2018).
- 563 39. Kaufmann, S., Hauck, M. & Leuschner, C. Effects of natural forest dynamics on vascular plant,
 564 bryophyte, and lichen diversity in primeval *Fagus sylvatica* forests and comparison with
 565 production forests. *J. Ecol.* **106**, 2421–2434 (2018).
- 566 40. Nelson, C. R. & Halpern, C. B. Short-term effects of timber harvest and forest edges on ground-
 567 layer mosses and liverworts. *Can. J. Bot.* **83**, 610–620 (2005).
- 568 41. Thorn, S., Förster, B., Heibl, C., Müller, J. & Bässler, C. Influence of macroclimate and local
 569 conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic
 570 beetles and wood-inhabiting fungi. *Biodivers. Conserv.* **27**, 3119–3135 (2018).
- 571 42. Fischer, M. *et al.* Implementing large-scale and long-term functional biodiversity research: The
 572 Biodiversity Exploratories. *Basic Appl. Ecol.* **11**, 473–485 (2010).
- 573 43. Jung, K. & Tschapka, M. Bat activity in all Exploratories, summer 2008, using acoustic
 574 monitoring . v1.1.4 [https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=19848)
 575 [DatasetId=19848](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=19848). (2018).
- 576 44. Tschapka, M., Renner, S. & Jung, K. Bird survey data 2008. v3.1.4. [https://www.bexis.uni-](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=21446)
 577 [jena.de/PublicData/PublicData.aspx?DatasetId=21446](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=21446). (2018).

- 578 45. Goßner, M., Lange, M., Türke, M., Pašalić, E. & Weisser, W. Window and ground traps on forest
579 EPs in 2008 subset Coleoptera. v1.1.3. Biodiversity Exploratories Information System. Dataset.
580 <https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=16866>. (2016).
- 581 46. Goßner, M., Lange, M., Türke, M., Pašalić, E. & Weisser, W. Window and ground traps on forest
582 EPs in 2008 subset Hemiptera. v1.1.4. Biodiversity Exploratories Information System. Dataset.
583 <https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=16867>. (2016).
- 584 47. Goßner, M., Lange, M., Türke, M., Pašalić, E. & Weisser, W. Window and ground traps on forest
585 EPs in 2008 subset Araneae. v1.1.3. Biodiversity Exploratories Information System. Dataset.
586 <https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=16868>. (2016).
- 587 48. Fischer, M. Deadwood inhabiting fungi presence absence (2010, all forest EPs). v1.2.2.
588 Biodiversity Exploratories Information System. Dataset.
589 <https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=18547>. (2017).
- 590 49. Müller, J., Boch, S. & Fischer, M. Bryophyte diversity in forests. v1.6.8. Biodiversity Exploratories
591 Information System. Dataset. [https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=4141)
592 [DatasetId=4141](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=4141). (2016).
- 593 50. Boch, S., Prati, D. & Fischer, M. Lichen diversity in forests. v1.11.14. Biodiversity Exploratories
594 Information System. Dataset. [https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=4460)
595 [DatasetId=4460](https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=4460). (2016).
- 596 51. Schäfer, D., Boch, S. & Fischer, M. Vegetation Records for Forest EPs, 2009 - 2016. v1.4.5.
597 Biodiversity Exploratories Information System. Dataset.
598 <https://www.bexis.uni-jena.de/PublicData/PublicData.aspx?DatasetId=20366>. (2017).
- 599 52. Doerfler, I., Gossner, M. M., Müller, J., Seibold, S. & Weisser, W. W. Deadwood enrichment
600 combining integrative and segregative conservation elements enhances biodiversity of multiple
601 taxa in managed forests. *Biol. Conserv.* **228**, 70–78 (2018).

53. Bässler, C., Förster, B., Moning, C. & Müller, J. The BIOKLIM Project : Biodiversity Research between Climate Change and Wilding in a temperate montane forest – The conceptual framework. in (2009).
54. Bässler, C., Müller, J. & Dziöck, F. 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 (2010).
55. Moning, C. *et al.* Lichen diversity in temperate montane forests is influenced by forest structure more than climate. *For. Ecol. Manag.* **258**, 745–751 (2009).
56. Müller, J., Moning, C., Bässler, C., Heurich, M. & Brandl, R. Using airborne laser scanning to model potential abundance and assemblages of forest passerines. *Basic Appl. Ecol.* **10**, 671–681 (2009).
57. Raabe, S. *et al.* Drivers of bryophyte diversity allow implications for forest management with a focus on climate change. *For. Ecol. Manag.* **260**, 1956–1964 (2010).
58. Parker, A. J. The Topographic Relative Moisture Index: An Approach to Soil-Moisture Assessment in Mountain Terrain. *Phys. Geogr.* **3**, 160–168 (1982).
59. Kahl, T. & Bauhus, J. Dead wood inventory 2012, v.1.0.0 Biodiversity Exploratories Information System. Dataset. <https://www.bexis.uni-jena.de/> . DatasetId=15386. (2018).
60. Bässler, C., Müller, J., Dziöck, F. & Brandl, R. Effects of resource availability and climate on the diversity of wood-decaying fungi. *J. Ecol.* **98**, 822–832 (2010).
61. McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. Forest and woodland stand structural complexity: Its definition and measurement. *For. Ecol. Manag.* **218**, 1–24 (2005).
62. Müller, J. & Vierling, K. Assessing Biodiversity by Airborne Laser Scanning. in *Forestry Applications of Airborne Laser Scanning: Concepts and Case Studies* (eds. Maltamo, M., Næsset, E. & Vauhkonen, J.) 357–374 (Springer Netherlands, 2014). doi:10.1007/978-94-017-8663-8_18.
63. Siitonen, J. Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. *Ecol. Bull.* 11–41 (2001).

- 628 64. Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I. & Naeem, S. Functional and phylogenetic
629 diversity as predictors of biodiversity--ecosystem-function relationships. *Ecology* **92**, 1573–1581
630 (2011).
- 631 65. Cadotte, M., Albert, C. H. & Walker, S. C. The ecology of differences: assessing community
632 assembly with trait and evolutionary distances. *Ecol. Lett.* **16**, 1234–1244 (2013).
- 633 66. Ward, L. K., Hackshaw, A. & Clarke, R. T. Do food-plant preferences of modern families of
634 phytophagous insects and mites reflect past evolution with plants? *Biol. J. Linn. Soc.* **78**, 51–83
635 (2003).
- 636 67. Durka, W. & Michalski, S. G. Daphne: a dated phylogeny of a large European flora for
637 phylogenetically informed ecological analyses. *Ecology* **93**, 2297–2297 (2012).
- 638 68. Kembel, S. W. *et al. picante: Integrating Phylogenies and Ecology*. (2018).
- 639 69. Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S. & Clawges, R. M. Lidar: shedding new
640 light on habitat characterization and modeling. *Front. Ecol. Environ.* **6**, 90–98 (2008).
- 641 70. Müller, J. & Brandl, R. Assessing biodiversity by remote sensing in mountainous terrain: the
642 potential of LiDAR to predict forest beetle assemblages. *J. Appl. Ecol.* **46**, 897–905 (2009).
- 643 71. Wood, S. *mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation*. (2018).
- 644 72. Fasiolo, M. & Nedellec, R. *mgcViz: Visualisations for Generalized Additive Models*. (2018).
- 645 73. Steffan, S. A. *et al.* Unpacking brown food-webs: Animal trophic identity reflects rampant
646 microbivory. *Ecol. Evol.* **7**, 3532–3541 (2017).
- 647 74. Hothorn, T., Winell, H., Hornik, K., Wiel, M. A. van de & Zeileis, A. *coin: Conditional Inference*
648 *Procedures in a Permutation Test Framework*. (2019).
- 649 75. R Core Team. *R: A Language and Environment for Statistical Computing*. (R Foundation for
650 Statistical Computing, 2018).
- 651

Figure 1. Conceptual 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).

Figure 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 by a decrease in mean abundance

Figure 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

678 Table 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		f	F-value		
Multidiversity	197	1.0	0.0	n.s.	1.0	0.8	n.s.	2.9	22.1	**	3.5	23.1	**	1.0	0.6	n.s.	1.0	0.9	n.s.	194	**	0.62	0.09
Plants	497	3.1	1.5	n.s.	1.0	0.3	n.s.	-			1.0	3.9	*	3.0	10.1	*	1.0	10.1	**	3.9	68.1	0.58	0.07
Bryophytes	322	1.0	0.6	n.s.	1.0	1.0	n.s.	4.0	3.4	*	1.0	0.0	n.s.	1.0	4.9	*	1.0	1.0	n.s.	3.7	13.1	0.34	0.01
Lichens	315	2.0	6.3	*	1.0	0.5	n.s.	3.0	5.3	*	1.0	3.6	n.s.	4.0	7.4	*	1.0	1.2	n.s.	3.8	33.1	0.51	0.16
Moths	227	1.0	0.1	n.s.	1.0	3.4	n.s.	1.0	1.8	n.s.	1.0	5.2	*	1.0	0.3	n.s.	1.0	5.5	*	3.6	10.1	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.	2.0	4.6	**	1.0	1.0	n.s.	1.0	6.2	*	3.7	18.1	0.33	0.14
Phytophagous	385	1.0	0.3	n.s.	1.0	1.4	n.s.	0.0	7.6	**	2.0	3.4	*	1.0	44.1	*	1.0	4.2	*	3.8	28.1	0.38	0.13
Fungi	497	2.0	7.6	*	2.0	2.1	n.s.	2.0	4.4	**	3.0	8.1	*	2.0	7.9	*	1.0	2.1	n.s.	3.4	10.1	0.41	0.17
Saproxylis	385	1.0	0.7	n.s.	1.0	10.1	**	0.0	7.9	**	3.0	4.3	*	2.0	2.6	*	1.0	10.1	**	3.9	53.1	0.51	0.09
Necrophagous	385	1.0	0.1	n.s.	1.0	0.8	n.s.	1.0	0.23	n.s.	1.0	6.3	*	1.0	4.5	*	1.0	2.5	n.s.	3.8	31.1	0.35	0.02
Carabids	382	1.0	0.4	n.s.	1.0	1.9	n.s.	1.0	1.5	n.s.	1.0	0.0	n.s.	1.0	3.8	n.s.	1.0	2.5	n.s.	3.9	93.1	0.72	0.01
beetles	382	1.0	7.0	n.s.	1.0	1.2	n.s.	1.0	6.7	*	1.0	0.0	n.s.	1.0	20.1	*	3.0	3.7	**	3.9	101.1	0.69	0.08
Aranea	382	0.0	10.1	**	0.0	1.2	n.s.	0.0	6.7	*	0.0	0.0	n.s.	0.0	20.1	*	6.0	3.7	**	3.9	101.1	0.69	0.08
Birds	496	1.0	9.0	**	1.0	0.0	n.s.	0.0	0.49	n.s.	3.0	19.1	*	0.0	5.7	*	1.0	7.3	**	3.7	20.1	0.26	0.14
Bats	248	1.0	0.8	n.s.	1.0	0.0	n.s.	2.0	3.3	*	1.0	0.1	n.s.	1.0	0.1	n.s.	1.0	3.5	n.s.	3.8	26.1	0.54	0.01
		0.0	7.0	n.s.	0.0	1.0	n.s.	4.0	3.3	*	0.0	1.0	n.s.	0.0	8.0	n.s.	0.0	3.5	n.s.	3.8	26.1	0.54	0.01
Moths	227	1.0	1.8	n.s.	1.0	0.0	n.s.	6.0	3.8	**	1.0	2.0	n.s.	1.0	5.0	n.s.	1.0	3.0	n.s.	3.6	12.1	0.26	0.05
True bugs	371	1.0	3.1	n.s.	1.0	3.0	n.s.	4.0	0.84	n.s.	1.0	4.1	*	0.0	6.0	n.s.	1.0	3.3	n.s.	2.9	4.5	0.09	0.04
Phytophagous	385	1.0	0.3	n.s.	1.0	5.4	*	0.0	7.3	**	1.0	0.0	n.s.	1.0	5.3	*	1.0	31.1	*	3.6	12.1	0.28	0.1

Saproxylic	385	2.3	4.3	**	2.0	+	3.7	*	1.0	0.29	n.s	1.0	-	12.	**	1.0	3.6	n.s	1.0	0.6	1	n.s	1.9	1.6	*	0.16	0.11
Necrophagous	385	1.0	0.0		1.0		3.0	n.s	1.0	0.51	n.s	2.0		2.4	n.s	3.0	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	0.8	n.s	3.9	59.	*	0.58	0.05
Aranea	382	1.0	2.5	n.s	1.0		3	n.s	1.0	1.9	n.s	2.0		2	n.s	0	-	5.9	*	1.0	1.8	n.s	3.4	9.	*	0.18	0.01
Birds	496	1.0	0.2		1.0		0.8		1.0			2.0		3.4	*	1.0		1.9	n.s	1.0	0.1	n.s	3.8	27.	*	0.25	0.02
Bats	248	1.0	0.7		1.0		0.0		1.0			1.0		0.0		1.0		0.4		1.0	0.1	n.s	3.6	17.	*	0.24	-0.01