Disentangling the importance of space and host tree for the beta-diversity of beetles, fungi, and bacteria: lessons from a large dead-wood experiment

Abstract

Forestry in Europe changed the tree species composition and reduced dead-wood amount and heterogeneity, and therefore negatively affected saproxylic diversity. Efficient conservation requires knowledge about the importance of the relevant diversity drivers across taxa. We examined the relative importance of space vs. host for saproxylic diversity at a spatial extend of 600 km in Germany. Further, we disentangled effects of among regions, forest stands, host clades, and tree species on saproxylic diversity. This allows inferences for spatial- and host tree-related conservation strategies. Beetle, fungal sporocarp, molecular-derived fungal, and bacterial communities were studied in a large nested dead-wood experiment comprising 11 tree species. We used multiplicative diversity partitioning to assess the diversity of rare, typical, and dominant species. The beta-diversity of beetles and fungal sporocarps was equally explained by space and host, but that of molecular fungi and bacteria mainly by the host. Across taxa, beta-diversity was higher among forest stands than among regions. However, for beetles and fungal sporocarps, differences among regions were also important. Host tree clade and host tree species were important for beetle and host clade for fungal sporocarp beta-diversity. Host tree species was more important than host clade for the beta-diversity of molecular fungi and bacteria. The divergent response of different taxa to space and host calls into question the use of a simple spatially-centered or host-centered strategy. Instead, a high dead-wood tree species diversity on a broad spatial coverage at the national scale in temperate European forests is necessary to maintain rare and abundant species.

Keywords: beta-partitioning, cross-taxonomic, forest conservation, regional, saproxylic, spatial scale, tree species

1. Introduction

Formerly large forest-dominated areas in Europe have been highly fragmented with alterations in their tree species and structural composition (Jonsson et al., 2016; Rüther and Walentowski, 2008). These transformations have led to resource and habitat losses that have negatively affected forest biodiversity (Paillet et al., 2010). The silvicultural focus on only a few tree species has also reduced the tree species diversity of dead-wood (Seibold and Thorn, 2018; Jonsson et al., 2016), which, together with reduced amounts of dead-wood has negatively affected dead-wood-dependent (saproxylic) species (Lassauce et al., 2011). Saproxylic species groups, especially beetles, fungi, and bacteria, are extremely species-rich, comprising approximately one-third of the total forest biodiversity (Stokland et al., 2012). They are also of high functional importance in dead-wood decomposition and thus in nutrient cycling (Boddy and Watkinson, 1995; Johnston et al., 2016; Ulyshen, 2016). In general, variability of environmental conditions acting at different spatial scales and at different scales of host tree identity (e.g. angio- vs. gymnosperm, tree genera or tree species) structure saproxylic species communities (e.g., Müller et al., 2020). However, the relative importance of these scales differs between saproxylic species groups, thus hampering straightforward recommendations regarding dead-wood retention in managed forests (Seibold et al., 2015). In this study, we sought to identify the spatial and host scales at which conservation actions aimed at enhancing the biodiversity of the major saproxylic species groups will be most effective.

Among regions, saproxylic diversity might be influenced by variability in large scale environmental conditions like macroclimate (Olou et al. 2019), tree species composition, forest management (Müller and Gossner, 2010), but also dispersal limitation (Norros et al. 2012). However, a recent study suggested that environmental factors rather than dispersal limitation better explain the species turnover of different taxa among regions in Germany (ca. 600 km scale) (Bae et al., 2021). Within regions, forest stand structures differ, e.g., due to forest management altering the natural variability in tree species composition and the natural structural heterogeneity (Commarmot et al. 2005) at the stand level, which may further affect species diversity (Paillet et al., 2010). Previous studies showed that the sensitivity of saproxylic species groups to such alterations differs at different spatial scales. For example, beetle diversity differed strongly among regions compared to forest stand

variability within regions (Gossner et al., 2016; Müller and Gossner, 2010), while for fungal diversity the opposite was found (Blaser et al., 2013; Purahong et al., 2016). For bacteria in dead-wood, the spatial patterning across different spatial scales has not been studied.

In addition to the spatial scale, saproxylic species diversity is strongly affected by the identity of the host tree species (e.g., Gossner et al., 2016). For example, the composition of saproxylic communities differed significantly between host tree clades (broad-leaved vs. coniferous) (e.g., Müller et al., 2015; Hoppe et al., 2016; Krah et al., 2018; Purhonen et al. 2021; Shanshan et al., 2021). Yet, many studies tested host effects based on only a few host tree species, e.g., one broad-leaved- and one coniferous species (e.g., Krah et al., 2018). However, studies using many host tree species of both broad-leaved and coniferous clades have shown that host specificity is also strongly pronounced among host tree species within clades (e.g., Gossner et al. 2016; Moll et al. 2018; Olou et al. 2019; Purahong et al. 2018; Odriozola et al. 2021). The relationship between saproxylic diversity concerning different taxonomic groups and a broad set of tree species has not been tested within a unified framework.

The above findings suggest that conservation actions need to operate at different spatial and host scales. However, a joint evaluation of the relative importance of different spatial and host scales across saproxylic species groups is lacking (Seibold et al., 2015). Disentangling the spatial vs. the host scale allows answering whether a spatially-centered or a host-centered strategy should be applied to maintain diversity (Fig. 1b). If the spatial scale matters more, conservation actions across space are more effective than a pure focus on host characteristics to maintain diversity. If the host scale matters more, conservation efforts should focus mainly on preserving and promoting certain host structures to maintain diversity. Further, disentangling the spatial scale (among regions vs. among forest stands) allows specifying whether a regional or stand-based strategy is more appropriate and similarly, disentangling the host scale allows specifying whether a strategy focusing on host tree clade or host tree species is more promising to maintain diversity (Fig. 1b).

To improve conservation strategies for saproxylic taxa, we used a fully nested dead-wood experiment in three different regions along a 600 km gradient across Germany (Fig. 1a). Each region was hierarchically composed of three different levels of forest management intensity, each represented

with three plots in three forest stands. Each forest stand contained 11 dead-wood tree species from two tree clades (broad-leaved vs. coniferous). Beetles and fungal sporocarps on each dead-wood object were sampled in field inventories, with fungi and bacteria then assessed via DNA-metabarcoding. Multiplicative diversity partitioning was used to simultaneously evaluate the relative importance of space and host at different scales for saproxylic beta-diversity. At the spatial scale, beta-diversity was compared among regions and among forest stands and at the host-scale among host tree clades and host tree species. The study was designed to address three questions linked to particular conservation strategies (Fig. 1):

(1) Space vs. host strategy: Does space or host beta-diversity contribute more to gamma-diversity?

(2) Regional vs. stand strategy: Does beta-diversity among regions or among forest stands contribute more to gamma-diversity?

(3) Host tree clade vs. host tree species strategy: Does beta-diversity among host tree clades or among host tree species contribute more to gamma-diversity?

2. Methods and Materials

2.1 Study area and design

Sampling was carried out within the framework of the Biodiversity Exploratories, a large-scale biodiversity project in Germany (Fischer et al., 2010). The three regions included in the project are aligned along a climatic gradient from southwest to northeast (Fig. 1a) and consist of: (1) the UNESCO Swabian Alb Biosphere Reserve (48°20′28″–48°32′02″N/9°10′49″–09°35′54″E, ~420 km² in size); the uplands of the Swabian Alb are made up of calcareous bedrock, with an altitude of 460–860 m a.s.l. and a mean annual temperature (MAT) and annual precipitation (MAP) of 6–7°C and 700–1 000 mm, respectively; (2) the Hainich-Dün region in Central Germany, including Hainich National Park, (50°56′14″-51°22′43″N/10°10′24″–10°46′45″E, ~1 560 km²), which extends over a range of hills of calcareous bedrock covered by loess and lies 285–550 m a.s.l. The MAT and MAP are 6.5–8°C and 500–800 mm; (3) the Schorfheide-Chorin UNESCO Biosphere Reserve, a young glacial moraine lowland located in north-east Germany (52°47′25″–53°13′26″N/13°23′27″–

14°08′53″E, ~1 300 km²), with an altitude of 3–140 m a.s.l., a MAT of 8–8.5°C, and a MAP of 500–600 mm. European beech (*Fagus sylvatica*) would naturally dominate the forests in all three regions. Today, only the Hainich-Dün is still dominated by beech, with only 12% conifer cover, whereas in the Swabian Alb beech forests make up 46% and Norway spruce (*Picea abies*) 24%, and the forests in Schorfheide are dominated by Scots pine (*Pinus sylvestris*) (39%), with beech accounting for only 12% of the forest cover. For our study, which is part of the BELongDead experiment (Fischer et al. 2010), nine forest stands along a forest management intensity gradient were selected in each of the three regions: three planted conifer stands, three even-aged managed beech stands, and three unmanaged (for at least 20 years) beech stands. At each forest stand in the three regions, 11 logs [4.0 ± 0.25 m length and 31 ± 5.9 cm (SD) mean diameter] were used, resulting in a total of 297 sampled logs. The logs had been placed at the stands in 2009. They consisted of four conifers (*Larix decidua*, *Picea abies*, *Pinus sylvestris*, and *Pseudotsuga menziesii*) and seven deciduous (*Betula pendula*, *Carpinus betulus*, *F. sylvatica*, *Fraxinus excelsior*, *Populus* spp., *Quercus* spp., and *Tilia* spp.) tree species. All species, including non-native *P. menziesii*, are common tree species in Central Europe.

2.2. Sampling

2.2.1. Beetles

Saproxylic beetles were sampled annually from 2010 to 2017 using closed eclector traps (Gossner et al., 2016), mounted in March, emptied monthly until the end of October, and kept open during winter. Each year and for each log, the eclectors were moved 40 cm along the log's axis to allow for insect colonization. The samples were collected in jars were filled with 50% ethylene glycol, and the insects were subsequently stored in 70% ethanol. Individuals were counted and identified to the species level. For the complete species list, see Appendix A Table A.1. Due to incomplete sampling, the data from 2010 and 2012 had to be excluded, and only logs with complete observations in May, June, and July of a year were included. Thus, 1 672 of the 1 782 samples (297 logs × 6 sampling years) were analyzed.

2.2.2. Fungal sporocarps

For the sporocarp inventory, all sporocarp data were gathered in autumn (September to October), during the peak fruiting season (see also Halme and Kotiaho, 2012), in 2012, 2015, and 2018. Abundance was estimated on a five-level scale, reflecting the percent coverage of a stem by sporocarps (0 = no sporocarps; 1 = <1% covered; 2 = 1–10% covered; 3 = 10–50% covered; 4 = > 50% covered).The fungal species selected for the study were macrofungi, easily visible to the naked eye and unambiguously identified by an experienced field worker. Fungi were determined directly in the field or with a microscope in the lab. The sample sporocarps were mainly Basidiomycetes from the subdivision Agaricomycotina (e.g., *Polyporales, Corticiales, Agaricales*) and Ascomycota from the subdivision Pezizomycotina (e.g., *Xylariales, Helotiales, Pezizales*). For the complete species list, see Appendix A Table A.2. From the 891 samples (297 logs × 3 sampling years), 866 were further analyzed.

2.2.3. Fungi and bacteria for DNA-metabarcoding

Wood samples were collected using a cordless drill (Makita BDF 451) in September 2012, May 2015, and May 2017. At the sampling location, the bark was removed, minimizing the possibility of including microorganisms occurring on the bark, and an auger was driven horizontally into the center of each log (see Purahong et al., 2018 for details). Each wood sample was homogenized into fine powder using liquid nitrogen and a swing mill (Retsch, Haan, Germany).

Sample DNA was isolated from ~0.1 g of each homogenized wood sample using the ZR soil microbe DNA MiniPrep kit (Zymo Research, Irvine, CA, USA) according to the manufacturer's protocol. The V4 region of the bacterial 16S rRNA gene was amplified in triplicate using the primers 515F/806r, as previously described (Moll et al., 2018), and the fungal ITS2 region using the primers fITS7/ITS4, also as previously described (Leonhardt et al. 2019). These amplicons were 2 × 300-bp paired-end sequenced (MiSeq Reagent kit v3) on an Illumina MiSeq system (Illumina Inc., San Diego, CA, USA).

Amplicon sequencing data were processed using DADA2 (Callahan et al., 2016) implemented in Dadasnake (Weißbecker et al., 2020). Raw reads were searched for both primer sites, and primer sequences were cut using cutadapt v1.18. The 16S forward and reverse reads were cut to a length of

170 and 130 nt and a minimum base quality of 9. Reads with a maximum expected error rate > 0.5 were discarded, and the quality-checked reads were merged with an overlap of 12 bp and 0 mismatches. For fungi, only forward and reverse reads with expected error rates < 4 and a minimum base quality of 9 were retained. The remaining reads were merged with an overlap of 20 bp and one mismatch allowed. For both groups, chimeras were removed using the consensus algorithm. Subsequently, the bacterial and fungal ASVs (amplicon sequence variants) were taxonomically assigned using the Bayesian Classifier implemented in mothur (Schloss et al., 2009) against the SILVA (SSU Ref, version 138; Quast et al., 2013) and UNITE (version 8.0; UNITE Community, 2019) databases, respectively.

For bacteria, only ASVs of 240-265 bp, assigned to the kingdoms Bacteria and Archaea and thus not identified as chloroplasts or mitochondria, were included in the analysis. Since Archaea accounted for only 0.25% of the ASV data and the results for the kingdoms did not differ (data not shown), an aggregated analysis was performed, and, for simplicity, the two kingdoms are referred to herein as bacteria. Fungal ASVs were further analyzed using the software ITSX (Bengtsson-Palme et al., 2013). ASVs not identified as fungal ITS2 were again taxonomically assigned using blastn against the NCBI 'nr' database. Only ASVs with a consistent fungal classification for both taxonomic databases and a length of 200-450 bp were finally recorded in the ASV table. Raw sequences have been deposited to the NCBI short read archive (SRA) and are accessible under BioProject accession number PRJNA756463. Since two samples were missing from the dataset, 889 of the potential 891 samples (297 logs × 3 sampling years) were analyzed. In the following, the term "species" is used for fungal and bacterial ASVs, although we are aware that ASVs are only putative species.

2.3. Data analysis

2.3.1. Data preparation

The data were prepared and analyzed in R 4.0.2 (R Core Team, 2020). The sampled data for each log were pooled across all sampling years (for the sensitivity analysis, see 2.3.2.), resulting in a community matrix for each species group. For beetles, individual counts (sum of all individuals across all years) were used, and for fungal sporocarps, the mean coverage over all years was calculated.

Singletons (cells with a read entry of 1) were excluded from the fungal molecular and bacterial matrices. These are typically PCR and sequencing errors that can lead to an overestimation of rare ASVs, thus inflating diversity estimates (Brown et al., 2015; Kunin et al., 2010). The matrices were rarefied to the lowest number of sequences in all samples, resulting in 6,926 sequence reads per sample for fungal ITS and 1,879 sequence reads per sample for bacterial 16S (function *rrarefy*, R package *vegan*, Oksanen et al., 2019). This threshold excluded the same samples in the two datasets whose reads were considerably lower than the others. Rarefaction was conducted to account for differences in sampling effort (McKnight et al., 2019).

2.3.2. Statistical analysis

Adequate sampling coverage for the three species groups was confirmed by calculating sample-based rarefaction/interpolation curves using the R package *iNEXT* (Hsieh et al., 2016). These analyses demonstrated high sample completeness (89.3–99.6%; Appendix B Fig. B.1). The three study questions were addressed using multiplicative diversity partitioning (Whittaker, 1960), as suggested by Chao et al. (2012). This method reflects the variability of the diversity at a given scale appropriately, and allows reliable comparison of beta-diversity across studies (e.g. Wilsey, 2010; Gossner et al., 2013; Müller et al., 2013).

In this analytical framework, the overall gamma-diversity of the three species groups across all regions was partitioned into beta-diversity levels at the spatial and host scales. A high beta-diversity at a given scale indicated a large contribution to gamma-diversity and thus its potential importance to maintaining diversity within a conservation context (Jost et al., 2010). Multiplicative diversity partitioning was performed using the function *multipart* in the *vegan* package (Oksanen et al., 2019). Considering different facets of diversity, e.g., focusing on rare, typical, and dominant species, has been recommended (Gaston et al., 2008). Therefore, we calculated the number-equivalents of three diversity indices, i.e., the Hill numbers (Hill, 1973) of species richness, Shannon entropy (exponential of Shannon entropy), and Simpson diversity (inverse Simpson concentration). Within the *multipart* function, number-equivalents weight species according to their abundance based on an exponent q. Species richness ($q = 0$) weights all species equally and thus emphasizes rare species (hereafter "rare

222 species"), Shannon entropy (q = 1) reflects the species' sampled abundance, without favoring rare or
223 dominant species (hereafter "typical species", after Gotelli and Chao (2013)), while Simpson diversity
224 (q = 2) assigns most weight to dominant species (hereafter "dominant species") (Jost, 2007). Each
225 observed beta-diversity value calculated was compared to a null model with 1,000 randomizations,
226 based on complete randomizations at all levels but keeping species frequencies and species richness
227 constant (function *r2dtable*). Null modeling indicated whether the observed beta-diversity at a given
228 scale was larger or smaller than expected or not different from random.
229 The overall gamma-diversity of each species group was partitioned simultaneously into spatial and
230 host scales, resulting in four levels (Fig. 1): spatial scale was partitioned into β_1, representing the beta-
231 diversity among regions, and β_2, the beta-diversity among forests stands; host scale was partitioned
232 into β_3, among host tree clades and β_4, among host tree species. This output addresses the first study
233 question (space vs. host), with β_1 and β_2 summed into the overall space component and β_3 and β_4 into
234 the overall host component, scaled to 100%.
235 The imbalance resulting from the inclusion of seven broad-leaved vs. four conifer host tree species
236 was taken into account by analyzing subsets of the data containing only four broad-leaved species each
237 time together with all four conifer host trees. Accordingly, 35 matrices covering all possible
238 combinations of four broad-leaved and the four conifer tree species were created. For each matrix, the
239 beta-diversity and respective null models were calculated for each group and diversity index as
240 described above. Mean beta-diversity and variance for each beta-diversity scale were then calculated
241 and the results of each of the 35 null models recorded. This was followed by a calculation for each
242 beta-diversity scale of the percentage of observed values larger or smaller than or not different from
243 random (Appendix B Table B.1). It should be noted that: (i) we are aware that reads do not necessarily
244 represent the actual abundance of ASVs (Lamb et al., 2019). However, using sample-based relative
245 abundance in our analysis did not change the inferences (data not shown). Furthermore, incidence data
246 were accounted for in the analysis of species richness (q = 0, see 2.3.2.). Possible sequence errors
247 (Modin et al., 2020) were accounted for by excluding singletons, through the rarefaction of the data,
248 and by comparison with null models. (ii) Separate analyses of the data for 2012 (2011 for beetles),
249 2015, and 2017 (2018 for fungal sporocarps) did not reveal differences in the main results compared to

pooling the data across years, thereby representing the early to middle stage of succession (Appendix B Table B.2). This also demonstrated the absence of a confounding effect based on slight differences in sampling time among taxa (see 2.2.1., 2.2.2., 2.2.3.); for the complete community matrices, see Appendix C Tables C.1 – C.6.

3. Results

Sampling using eclector traps resulted in a total of 438 beetle species (Appendix B Table B.3, Appendix C Table C.1), and sporocarp sampling 368 fungal species (Appendix B Table B.3, Appendix C Table C.2). From the rarefied ASV tables, 5 690 putative fungal (Appendix B Table B.3, Appendix C Table C.3) and 39 977 putative bacterial species (Appendix B Table B.3, Appendix C Table C.4 - C.6) were further identified (after singletons excluded). Note that in the following the results are reported as the observed contribution of beta-diversity to gamma-diversity, scaled to 100%. All observed beta-diversity values were larger than expected for the clear majority of the runs (in most cases 100%, in the worst-case >70%) at each scale, based on the 35 matrices (all possible combinations of the four broad-leaved tree species with the four conifer tree species, see 2.3.2.; Appendix B Table B.1). Only for fungal sporocarps, the scale among host tree species (β_4) was significantly smaller than expected.

3.1. Importance of space vs. host

For beetles, beta-diversity among space and host contributed equally (~50%) to gamma-diversity across all diversity indices (Appendix B Table B.4). For rare species of fungal sporocarps, the beta-diversity among space (53.0%) was slightly more important than among host. For typical and dominant fungal sporocarp species, the beta-diversity among hosts was slightly more important than beta-diversity among space (54.8% and 57.8% respectively, Appendix B Table B.4). For molecular fungi, the beta-diversity among hosts explained 86.7% of the gamma-diversity of rare species and contributed substantially to that of typical (84.0%) and dominant (80.7%) species (Appendix B Table B.4). For bacteria, the beta-diversity among hosts explained 84.2%, 74.6%, and 68.3% of the gamma-diversity in rare, typical, and dominant species, respectively (Appendix B Table B.4).

3.2. Importance of among regions vs. among forest stands

Beta-diversity among forest stands contributed more to gamma-diversity than beta-diversity among regions for all studied species groups (Fig. 2). Beta-diversity among forest stands increased from rare to typical to dominant species in all species groups, except fungal sporocarps, which showed the opposite pattern (Appendix A Table A.1). In typical and dominant beetle species, beta-diversity among regions contributed 25.9% and 26.2% to total gamma diversity. For fungal sporocarps, the contribution of beta-diversity among forest stands to gamma-diversity was 34.8%, 27.7%, and 23.8% for rare, typical, and dominant species, while for molecular fungi, it was 11.0%, 11.9%, and 13.1%, and for bacteria 12.6%, 16.2%, and 18.2%, respectively.

3.3. Importance of host tree clade vs. host tree species

Beta-diversity among host tree species explained large parts of the gamma-diversity of most species groups and diversity indices (Fig. 2). The relative importance of the host tree clade was more pronounced for beetles and fungal sporocarps than for molecular fungi and bacteria. Additionally, beta-diversity among host tree species of fungal sporocarps was smaller than expected. The importance of the host tree clade increased from rare to typical to dominant species diversity for all groups (Table A.1). For beetles, beta-diversity among host tree species explained 30.9% (rare), 28.3% (typical), and 25.7% (dominant), whereas, for fungal sporocarps, it explained 26.7% for rare, 30.5% for typical and 32.02% for dominant species. For molecular fungi, beta-diversity among tree species explained 66.5% (rare), 62.4% (typical), and 58.0% (dominant) of the gamma-diversity, and for bacteria, 62.8%, 51.3%, and 44.0%, respectively.

4. Discussion

4.1. Importance of space vs. host for saproxylic diversity

Our focus on the relative importance of space and host as drivers of saproxylic beta-diversity was aimed at determining whether a spatially-centered or a host-centered strategy can be recommended to maintain overall saproxylic diversity. Our results showed that the response of beta-diversity to space

and host variability is dichotomous. While both space and host variability were important for the beta-diversity of beetles and fungal sporocarps, host variability better explained the beta-diversity of molecular fungi and bacteria. We were surprised by the contradicting results between fungal sporocarps and molecular fungi. We assumed both methods reflect the same ecological inferences (Saine et al., 2020, see discussion section 4.3). This suggests that neither a purely spatially centered nor a host-centered strategy is sufficient to maintain overall saproxylic diversity; instead, a combined approach is needed.

4.2. Importance of among regions vs. among forest stands for saproxylic diversity

The among forest stand scale contributed more than the among regions scale to the gamma-diversity of the studied taxa. Assuming no dispersal limitation for any of the taxa among forest stands within regions (Müller et al., 2020), this finding can be explained by the structural variability among forest stands resulting from forest management. The forest management gradient in our study area is characterized by a tree species composition gradient ranging from spruce and pine plantation to forest stands characterized by natural broad-leaved tree species, particularly European beech (Fischer et al., 2010). Forest stand structural variables potentially affecting the beta-diversity of saproxylic groups include the microclimate caused by differences in tree species composition. A relatively dense canopy characterizes beech forest stands, in contrast to the more open canopies of spruce and especially pine forest stands (Boch et al., 2013). Previous studies from other regions on landscape scale demonstrated an effect of forest stand microclimate on the community composition of wood-inhabiting fungal sporocarps and beetles, with stronger effects on the latter (Abrego and Salcedo, 2014; Krah et al., 2018; Müller et al., 2020). The variability in beta-diversity among forest stands observed in our study might also be attributed to the variability in the amount of surrounding dead-wood since, in our case, a larger amount of dead-wood is present in less intensively managed stands (Schall et al., 2018). However, the effects of surrounding dead-wood on saproxylic diversity are inconsistent. For example, Krah et al. (2018) found no influence of either the amount or the heterogeneity of immediate surrounding dead-wood (0.1 ha) on the diversity of fungal sporocarps per dead-wood object. In contrast, Edman et al. (2004) found that fungal sporocarp species richness was higher if the dead-

334 wood amount in the 9 000 m² plot was higher. This was also supported by Abrego and Salcedo (2014),
335 who studied the influence of forest management on fungal sporocarp diversity at the plot scale of 100
336 m². For saproxylic beetles, an increased dead-wood amount in a 40m radius around the plot had a
337 positive effect on the species richness (Seibold et al., 2017). Although further studies are needed, our
338 results clearly underline the importance of among-stand environmental variability for saproxylic
339 diversity.
340 While the among forest stand scale seems to be more important than the among regions scale
341 across taxa, the variability of environmental conditions among regions explained a considerable
342 amount of the beta-diversity of beetles and fungal sporocarps. Additional evidence is needed, but
343 dispersal limitation is unlikely to be the reason for this finding. In fact, in a previous study, the beta-
344 diversity of beetles at a scale similar to that used in our study was better explained by environmental
345 conditions than by spatial structure, with the latter serving as a surrogate for dispersal limitation (Bae
346 et al., 2021). Müller and Gossner (2010) also concluded that dispersal limitation is not the primary
347 reason for beetle diversity at scales around 240 km. In their analysis, the scale between forest sites,
348 likewise separated by non-forest land, was of minor importance. These arguments for beetles should
349 also apply to fungi since, at the regional scale, they are less dispersal-limited than beetles (Komonen
350 and Müller, 2018; Bae et al., 2021).
351 The spatial pattern determined for bacterial beta-diversity was between that of fungal sporocarps
352 and that of molecular fungi. To the best of our knowledge, bacterial beta-diversity across these spatial
353 scales has not been analyzed previously in this context. Our study demonstrated that the beta-diversity
354 caused by spatial variation contributed more to the gamma-diversity of bacteria than to that of
355 molecular fungi (Fig. 2c). If bacteria are also assumed to have no dispersal limitation at the examined
356 spatial scale, spatial environmental variability would also be the most plausible explanation of their
357 high beta-diversity (Van der Gucht et al., 2007; Barberán et al., 2014). This would also point to
358 bacterial communities' stronger sensitivity than fungal molecular communities to environmental
359 variability across space.
360 The importance of the among regions scale for beetles, fungal sporocarp, and bacteria (dominant
361 species) can be explained by: (i) macroclimatic differences, given that the variability in the MAT and

MAP greatly differs among regions (from the south, where the MAP and MAT are 700–1 000 mm and 6–7°C, to the north where the MAP and MAT are 500–600 mm and 8–8.5°C; see 2.1.). And (ii) the fact that all of the studied regions have been modified by forest management aimed at more productive coniferous tree species and the removal of old trees and dead-wood (McGrath et al., 2015; Lassauce et al., 2011). Within the study area, warm and dry regions have been enriched by pine and colder and more humid landscapes by spruce (see 2.1.). Hence, differences in tree species may also in part explain the importance of the among regions scale for the beta-diversity of beetles, fungal sporocarp, and dominant bacteria. Given that beta-diversity is considerable among regions and that macroclimate might play a pivotal role, the maintenance of the diversity of these groups will require the country-level coordination of conservation strategies. Furthermore, the particular importance of the among regions scale for the dominant species across the studied taxa highlights the need for conservation efforts across all regions since the numerically-dominant species are critical for maintaining ecosystem processes, such as wood decomposition (Winfree et al., 2015). This can be achieved by setting up protected areas and/or by implementing dead-wood enrichment strategies across regions.

4.3. Importance of host tree clade vs. host tree species for saproxylic diversity

By comparing the beta-diversity among two host tree clades and among host tree species within tree clades, we contribute to unifying existing knowledge and raise further questions about saproxylic diversity-host relationships: (i) Previous studies showed that the relationship between saproxylic communities and host identity is more closely correlated for fungi and bacteria than for beetles (Wende et al., 2017; Thorn et al., 2018; Müller et al., 2020; Moll et al., 2021; Odriozola et al. 2021). However, our study only partly confirmed those findings. It showed the stronger host specificity of fungi than of beetles only in the case of molecular fungal communities, not fungal sporocarp communities. Possible reasons for this discrepancy include the greater environmental exposure of sporocarps than the fungal assemblage occurring within the substrate. Likewise, beetles spend the mature part of their life cycle outside the substrate (Ulyshen, 2018), where environmental effects are likely to be more pronounced. We also cannot exclude that the difference in response to host identity between the two fungal measures simply reflected differences in the number of species, as the host

relationship of fungal molecular communities, with their high number of species, is probably stronger. (ii) The simultaneous consideration of both fungal measures yielded additional insights, including that certain environmental conditions are crucial for the production of fruit bodies (Sakamoto, 2018) but not necessarily for (vegetative) mycelium, as indicated by the response of the fungal molecular community. If dispersal is not a limitation, as discussed above, fungal diversity can be maintained by applying a host-centered strategy at the scale of our study. Under this dispersal capability scenario, fungal species would produce fruit bodies wherever possible (suitable environmental conditions) and colonize dead-wood objects throughout the country. However, if dispersal is a limiting factor, then inferences drawn only from the molecular diversity response might be erroneous if sexual reproduction is crucial for maintaining fungal populations. An alternative explanation could be that different environmental (e.g., macro- and microclimate) conditions at the scale of our study cause differences in decomposition processes (A'Bear et al., 2014). Ovaskainen et al. (2013) showed that some rare species produce fruit bodies very late during succession while being prevalent as mycelia during earlier successional stages. Therefore, differences in successional stages of the dead-wood objects between the regions could cause differences in communities sampled via fruit bodies. Consequently, this could also explain a higher beta diversity based on fruit bodies compared to the beta diversity based on the molecular derived fungal community. The fact that particularly beta-diversity based on rare fruiting fungi shows a strong response to the spatial variation supports this view. However, we used data that integrate across 10 years of succession (late-mid-stage of decay), which increases the probability of detecting rare species that fruit later during succession. Nevertheless, further studies are needed to examine which fungal species present in dead-wood produce sporocarps under different environmental and successional conditions and the relevancy of sexual reproduction in population maintenance. (iii) Earlier studies reported a high host specificity of bacterial assemblages (Hoppe et al., 2015; Moll et al., 2021; Odriozola et al., 2021), but they also showed that host specialization was more pronounced for fungi than for bacteria based on metabarcoding data (Moll et al., 2021). This has been partly explained because the fungal community composition strongly influences the bacteria community (Odriozola et al., 2021). Our results support the former results, although the difference between bacterial and molecular fungal beta-diversity was

not strongly pronounced. (iv) The differences observed in previous studies of host specificity were attributed to the angiosperm (broad-leaved) and gymnosperm (coniferous) split due to considerable differences in the chemical and physical properties of the wood from the respective trees (Hoppe et al., 2015; Kahl et al., 2017; Wende et al., 2017; Moll et al., 2018; Krah et al., 2018). It has been suggested that fungi and bacteria involved in the enzymatic decay of wood are more host-specific than beetles (Boddy and Watkinson, 1995; Baldrian, 2017; Thorn et al., 2018; Müller et al., 2020). Thus, one might expect that for fungi and bacteria, but not for beetles, the beta-diversity among host tree clades would be higher than the beta-diversity among host tree species. However, in our study, beta-diversity among host tree clades was only important for fungal sporocarps, not molecular fungi. Moreover, a higher beta-diversity among host tree clades than among host tree species was also found for beetles. The higher beta-diversity of host tree species than of host tree clade for molecular fungi and bacteria indicates further strong host specificity also within angio- and gymnosperm hosts. The discrepancy in the response between the two fungal measures (sporocarp vs. metabarcoding) and the similarity of the fungal sporocarp response to that of beetle communities deserve further attention.

4.4. *Response of rare, typical, and dominant species*

Threatened and rare species are of particular conservation concern. Therefore, analyses across Hill numbers in our study contribute to our knowledge to maintain rare species. Even though not a focus of our study, a first rough assessment revealed that rare beetle and fungi species within our dataset include species which assigned a threat category based on red-lists or are defined as old-growth indicators (Appendix A, Table A.1 - A.3). Our results of rare species might therefore be cautionary interpreted in the context of threatened species. However, red-lists do not exist for the majority of bacteria groups, and red-lists for fungi are based only on fruit body inventories and hence might be biased. However, besides rare and threatened species, a focus on typical and dominant species in conservation biology has been recommended (e.g., Gaston et al., 2008). One reason for this is that typical and dominant species are linked to important ecosystem processes and the resilience of forest ecosystems (e.g., Winfree et al., 2015). Interestingly, we found only minor differences of the beta-diversity response to space and host based on Hill numbers. This indicates that conservation

recommendations can be generalized across rare, typical and dominant species. However, some differences occurred, which allow further interpretation: (i) The importance of the host increased from dominant to typical to rare species. This indicates that rare species are more driven by host-related processes than environmental variability (Nordén et al. 2013; Abrego et al., 2017). One exception are the fungal fruiting species, which showed the opposite pattern. Although speculative, this supports the view that fungal fruiting communities might be particularly sensitive to environmental variability, as discussed above. Finally, it is important to note that differences in the effects between host tree clade vs. host tree species seem not very pronounced among rare, typical and dominant species (see discussion above). (ii) The importance of among regions on beta-diversity increased from rare to typical to dominant species. Particularly for bacteria and to some extent for molecular fungi, the among regions scale became important for dominant species. This underpins the importance of large scale environmental variability, explaining the beta-diversity of dominant species supporting earlier findings (Jiao et al., 2017). An alternative explanation could be that dominant species are dispersal limited. However, this would contradict current knowledge about rare species which has been shown to be stronger dispersal limited than dominant ones (e.g., Norros et al., 2012; Baur 2014).

5. Management implications

Our results showed that the response of beta-diversity to space and host differs between saproxylic taxa in temperate European forests. Accordingly, neither a spatially-centered nor a host-centered strategy would be sufficient to maintain the diversity of saproxylic beetles, fungi, and bacteria, the main actors of wood decay. Our results demonstrate the possible errors of conservation recommendations derived from single-taxon studies, with potentially negative effects on other species groups if they respond very differently than the focus-group. The goal of conservation strategies in a country includes the protection of overall saproxylic diversity, including rare, typical, and dominant species. To achieve this goal, we recommend a strategy based on a diverse tree species composition made up of species from different tree clades and implemented in forests under different management types across ecoregions.

Data Accessibility Statement

Molecular data is available at:
https://dataview.ncbi.nlm.nih.gov/object/PRJNA756463?reviewer=csfdp5h8htnmrqq37qs5l7qj88

References

A'Bear, A. D., Jones, T. H., Kandeler, E., Boddy, L. 2014. Interactive effects of temperature and soil moisture on fungal-mediated wood decomposition and extracellular enzyme activity. Soil Biology and Biochemistry 70:151–158.

Abrego, N., Salcedo, I., 2014. Response of wood-inhabiting fungal community to fragmentation in a beech forest landscape. Fungal Ecology 8:18–27.

Abrego, N., Dunson, D., Halme, P., Salcedo I., Ovaskainen, O., 2017. Wood-inhabiting fungi with tight associations with other species have declined as a response to forest management. Oikos 126.

Bae, S., Heidrich, L., Levick, S.R., Gossner, M.M., Seibold, S., Weisser, W.W., Magdon, P., Serebryanyk, A., Bässler, C., Schäfer, D., Schulze, E.-D., Doerfler, I., Müller, J., Jung, K., Heurich, M., Fischer, M., Roth, N., Schall, P., Boch, S., Wöllauer, S., Renner, S.C., 2021. Dispersal ability, trophic position and body size mediate species turnover processes: Insights from a multi-taxa and multi-scale approach. Divers Distrib 27, 439–453.

Baldrian, P., 2017. Forest microbiome: diversity, complexity and dynamics. FEMS microbiology reviews 41, 109–130.

Barberán, A., Casamayor, E.O., Fierer, N., 2014. The microbial contribution to macroecology. Frontiers in microbiology 5, 203.

Baur, B., 2014. Dispersal-limited species – A challenge for ecological restoration. Basic and Applied Ecology 15, 559-564.

Bengtsson-Palme, J., Ryberg, M., Hartmann, M., Branco, S., Wang, Z., Godhe, A., Wit, P. de, Sánchez-García, M., Ebersberger, I., Sousa, F. de, Amend, A.S., Jumpponen, A., Unterseher, M., Kristiansson, E., Abarenkov, K., Bertrand, Y.J.K., Sanli, K., Eriksson, K.M., Vik, U., Veldre, V., Nilsson, R.H., 2013. Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods Ecol Evol 4, 914-919.

Blaser, S., Prati, D., Senn-Irlet, B., Fischer, M., 2013. Effects of forest management on the diversity of deadwood-inhabiting fungi in Central European forests. Forest Ecology and Management 304, 42–48.

Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E.K., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.-D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic and Applied Ecology 14, 496–505.

Boddy, L., Watkinson, S.C., 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Can. J. Bot. 73, 1377–1383.

Brown, S.P., Veach, A.M., Rigdon-Huss, A.R., Grond, K., Lickteig, S.K., Lothamer, K., Oliver, A.K., Jumpponen, A., 2015. Scraping the bottom of the barrel: are rare high throughput sequences artifacts? Fungal Ecology 13, 221–225.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nat Methods 13, 581–583.

Chao, A., Chiu, C.-H., Hsieh, T. C., 2012. Proposing a resolution to debates on diversity partitioning. Ecology 93 (9), 2037–2051.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R., Zingg, A., 2005. Structure of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. Forest Snow and Landscape Research, 79 (1-2), 45-56.

Edman, M., Kruys, N., Jonsson, B.G., 2004. Local dispersal sources strongly affect colonisation patterns of wood-decaying fungi on experimental logs. Ecological Applications 14, 893–901.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K., Linsenmair, K.E., Schulze, E.-D., Weisser, W.W., 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology 11, 473–485.

Gaston, K.J., Fuller, R.A., 2008. Commonness, population depletion and conservation biology, Trends in Ecology & Evolution, 23

Gossner, M. M., Getzin, S., Lange, M., Pašalić, E., Türke, M., Wiegand, K., Weisser, W. W., 2013. The importance of heterogeneity revisited from a multiscale and multitaxa approach. Biological Conservation 166:212–220

Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan-Dewenter, I., Schulze, E.-D., Weisser, W.W., 2016. Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity? Biological Conservation 201, 92–102.

Gotelli, N., Chao, A., 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: S.A. Levin (Ed.), The Encyclopedia of Biodiversity. 195-211.

Halme, P., Kotiaho, J.S., 2012. The importance of timing and number of surveys in fungal biodiversity research. Biodivers Conserv 21, 205–219.

Hill, M. O., 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology, 54(2), 427-432.

Hoppe, B., Krüger, D., Kahl, T., Arnstadt, T., Buscot, F., Bauhus, J., Wubet, T., 2015. A pyrosequencing insight into sprawling bacterial diversity and community dynamics in decaying deadwood logs of Fagus sylvatica and Picea abies. Scientific reports 5, 9456.

Hoppe, B., Purahong, W., Wubet, T., Kahl, T., Bauhus, J., Arnstadt, T., Hofrichter, M., Buscot, F., Krüger, D., 2016. Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. Fungal Diversity 77, 367–379.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Methods Ecol Evol 7, 1451–1456.

Johnston, S.R., Boddy, L., Weightman, A.J., 2016. Bacteria in decomposing wood and their interactions with wood-decay fungi. FEMS microbiology ecology 92, fiw179.

Jonsson, B.G., Ekström, M., Esseen, P.-A., Grafström, A., Ståhl, G., Westerlund, B., 2016. Dead wood availability in managed Swedish forests – Policy outcomes and implications for biodiversity. Forest Ecology and Management 376, 174–182.

Jiao, S., Chen, W., Wei, G., 2017: Biogeography and ecological diversity patterns of rare and abundant bacteria in oil-contaminated soils. Mol. Ecol. 26(19):5305-5317.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427–2439.

Jost, L., DeVries, P., Walla, T., Greeney, H., Chao, A., Ricotta, C., 2010. Partitioning diversity for conservation analyses. Divers Distrib 16, 65–76.

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K.E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., Schulze, E.-D., Wende, B., Weisser, W.W., Gossner, M.M., 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. Forest Ecology and Management 391, 86–95.

Komonen, A., Müller, J., 2018. Dispersal ecology of deadwood organisms and connectivity conservation. Conservation Biology 32, 535–545.

Krah, F.-S., Seibold, S., Brandl, R., Baldrian, P., Müller, J., Bässler, C., 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. J Ecol 106, 1428–1442.

Kunin, V., Engelbrektson, A., Ochman, H., Hugenholtz, P., 2010. Wrinkles in the rare biosphere: pyrosequencing errors can lead to artificial inflation of diversity estimates. Environmental microbiology 12, 118–123.

Lamb, P.D., Hunter, E., Pinnegar, J.K., Creer, S., Davies, R.G., Taylor, M.I., 2019. How quantitative is metabarcoding: A meta-analytical approach. Molecular ecology 28, 420–430.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11, 1027–1039.
Leonhardt, S., Hoppe, B., Stengel, E., Noll, L., Moll, J., Bässler, C., Dahl, A., Buscot, F., Hofrichter, M., Kellner, H., 2019. Molecular fungal community and its decomposition activity in sapwood and heartwood of 13 temperate European tree species. PloS one 14, e0212120.
McGrath, M.J., Luyssaert, S., Meyfroidt, P., Kaplan, J.O., Bürgi, M., Chen, Y., Erb, K., Gimmi, U., McInerney, D., Naudts, K., Otto, J., Pasztor, F., Ryder, J., Schelhaas, M.-J., Valade, A., 2015. Reconstructing European forest management from 1600 to 2010. Biogeosciences 12, 4291–4316.
McKnight, D.T., Huerlimann, R., Bower, D.S., Schwarzkopf, L., Alford, R.A., Zenger, K.R., 2019. Methods for normalizing microbiome data: An ecological perspective. Methods Ecol Evol 10, 389–400.
Modin, O., Liébana, R., Saheb-Alam, S., Wilén, B.-M., Suarez, C., Hermansson, M., Persson, F., 2020. Hill-based dissimilarity indices and null models for analysis of microbial community assembly. Microbiome 8, 132.
Moll, J., Kellner, H., Leonhardt, S., Stengel, E., Dahl, A., Bässler, C., Buscot, F., Hofrichter, M., Hoppe, B., 2018. Bacteria inhabiting deadwood of 13 tree species are heterogeneously distributed between sapwood and heartwood. Environmental microbiology 20, 3744–3756.
Moll, J., Heintz-Buschart, A., Bässler, C., Hofrichter, M., Kellner, H., Buscot, F., Hoppe, B., 2021. Amplicon Sequencing-Based Bipartite Network Analysis Confirms a High Degree of Specialization and Modularity for Fungi and Prokaryotes in Deadwood. mSphere 6.
Müller, J., Gossner, M.M., 2010. Three-dimensional partitioning of diversity informs state-wide strategies for the conservation of saproxylic beetles. Biological Conservation 143, 625–633.
Müller, J., Brunet, J., Brin, A., Bouget, C., Brustel, H., Bussler, H., Förster, B., Isacsson, G., Köhler, F., Lachat, T., Goßner, M. M., 2013. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. Insect Conservation and Diversity 6:162–169.
Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K.E., Weisser, W.W., Gossner, M.M., 2015. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. J Appl Ecol 52, 753–762.
Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiß, I., Baldrian, P., Tláskal, V., Thorn, S., 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. Oikos 129, 1579–1588.
Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J Ecol 101 (3), 701–712.
Norros, V., Penttilä, R., Suominen, M., Ovaskainen, O., 2012. Dispersal may limit the occurrence of specialist wood decay fungi already at small spatial scales. Oikos 121:961–974.
Odriozola, I., Abrego, N., Tláskal, V., Zrůstová, P., Morais, D., Větrovský, T., Ovaskainen, O., Baldrian, P. 2021. Fungal Communities Are Important Determinants of Bacterial Community Composition in Deadwood. mSystems 6.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package.
Olou, B. A., Yorou, N. S., Striegel, M., Bässler, C., Krah, F.-S., 2019. Effects of macroclimate and resource on the diversity of tropical wood-inhabiting fungi. Forest Ecology and Management 436, 79–87.
Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., Nordén, J., 2013. Combining high-throughput sequencing with fruit body surveys reveals contrasting life-history strategies in fungi. ISME J 7 (9), 1696–1709.
Paillet, Y., Bergès, L., Hjältén, J., Odor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., Bruyn, L. de, Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation Biology 24, 101–112.

Purahong, W., Arnstadt, T., Kahl, T., Bauhus, J., Kellner, H., Hofrichter, M., Krüger, D., Buscot, F., Hoppe, B., 2016. Are correlations between deadwood fungal community structure, wood physico-chemical properties and lignin-modifying enzymes stable across different geographical regions? Fungal Ecology 22, 98–105.

Purahong, W., Wubet, T., Lentendu, G., Hoppe, B., Jariyavidyanont, K., Arnstadt, T., Baber, K., Otto, P., Kellner, H., Hofrichter, M., Bauhus, J., Weisser, W.W., Krüger, D., Schulze, E.-D., Kahl, T., Buscot, F., 2018. Determinants of Deadwood-Inhabiting Fungal Communities in Temperate Forests: Molecular Evidence From a Large Scale Deadwood Decomposition Experiment. Frontiers in microbiology 9, 2120.

Purhonen, J., Abrego, N., Komonen, A., Huhtinen, S., Kotiranta, H., Læssøe, T., Halme, P., 2021. Wood-inhabiting fungal responses to forest naturalness vary among morpho-groups. Scientific reports 11, 14585.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, FO., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucl. Acids Res. 41 (D1): D590-D596.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for for Statistical Computing, Vienna.

Rüther, C., Walentowski, H., 2008. Tree species composition and historic changes of the Central European oak/beech region. In: Floren, A., Schmidl, J. (Eds.), Canopy arthropod research in Europe. Basic and applied studies from the high frontier. bioform entomology, Nürnberg.

Saine, S., Ovaskainen, O., Somervuo, P., Abrego, N., 2020. Data collected by fruit bodyand DNA-based survey methods yield consistent species-to-species association networks in wood-inhabiting fungal communities. Oikos 129, 1833–1843.

Sakamoto, Y. (2018). Influences of environmental factors on fruiting body induction, development and maturation in mushroom-forming fungi. Fungal Biology Reviews 32, 236–248.

Schall, P., Schulze, E.-D., Fischer, M., Ayasse, M., Ammer, C., 2018. Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology 32, 39–52.

Schloss, P.D., Westcott, S.L., Ryabin, T., Hall, J.R., Hartmann, M., Hollister, E.B., Lesniewski, R.A., Oakley, B.B., Parks, D.H., Robinson, C.J., Sahl, J.W., Stres, B., Thallinger, G.G., van Horn, D.J., Weber, C.F., 2009. Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. Applied and environmental microbiology 75, 7537–7541.

Seibold, S., Bässler, C., Brandl, R., Gossner, M.M., Thorn, S., Ulyshen, M.D., Müller, J., 2015. Experimental studies of dead-wood biodiversity — A review identifying global gaps in knowledge. Biological Conservation 191, 139–149.

Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl, F., Thorn, S. and Müller, J., 2017. An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology, 98: 1613-1622.

Seibold, S., Thorn, S., 2018. The Importance of Dead-Wood Amount for Saproxylic Insects and How It Interacts with Dead-Wood Diversity and Other Habitat Factors. In: Ulyshen, M.D. (Ed.), Saproxylic Insects. Springer International Publishing, Cham. 607–637.

Shanshan, Y., Limpens, J., Sterck, F.J., Sass-Klaassen, U., Cornelissen, J.H.C., Hefting, M., van Logtestijn, R.S.P., Goudzwaard, L., Dam, N., Dam, M., Veerkamp, M.T., van den Berg, B., Brouwer, E., Chang, C., Poorter, L., 2021. Dead wood diversity promotes fungal diversity. Oikos 130:2202–2216.

Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge u.a.

Thorn, S., Förster, B., Heibl, C., Müller, J., Bässler, C., 2018. Influence of macroclimate and local conservation measures on taxonomic, functional, and phylogenetic diversities of saproxylic beetles and wood-inhabiting fungi. Biodivers Conserv 27, 3119–3135.

Ulyshen, M.D., 2016. Wood decomposition as influenced by invertebrates. Biological reviews of the Cambridge Philosophical Society 91, 70–85.

Ulyshen, M.D. (Ed.), 2018. Saproxylic Insects. Springer International Publishing, Cham.

UNITE Community, 2019: UNITE mothur release for Fungi 2. Version 18.11.2018. UNITE Community.

Van der Gucht, K., Cottenie, K., Muylaert, K., Vloemans, N.,Cousin, S., Declerck, S., Jeppsen, E., Conde-Porcuna, J.-M., Schwenk, K., Zwart, G., Degans, H., Vyvermann, W., De Meester, K., 2007. The power of species sorting: local factors drive bacterial community composition over a wide range of spatial scales. Proc Nat Acad Sci USA51:20404–20409.

Weißbecker, C., Schnabel, B., Heintz-Buschart, A., 2020. Dadasnake, a Snakemake implementation of DADA2 to process amplicon sequencing data for microbial ecology. GigaScience 9, giaa135.

Wende, B., Gossner, M.M., Grass, I., Arnstadt, T., Hofrichter, M., Floren, A., Linsenmair, K.E., Weisser, W.W., Steffan-Dewenter, I., 2017. Trophic level, successional age and trait matching determine specialization of deadwood-based interaction networks of saproxylic beetles. Proceedings. Biological sciences 284.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs, 30(3), 279-338. Ecological Monographs 30, 279–338.

Wilsey, B. J., 2010. An empirical comparison of beta diversity indices in establishing prairies. Ecology 91:1984–198

Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R., Cariveau, D.P., 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecol Letters 18, 626–635.

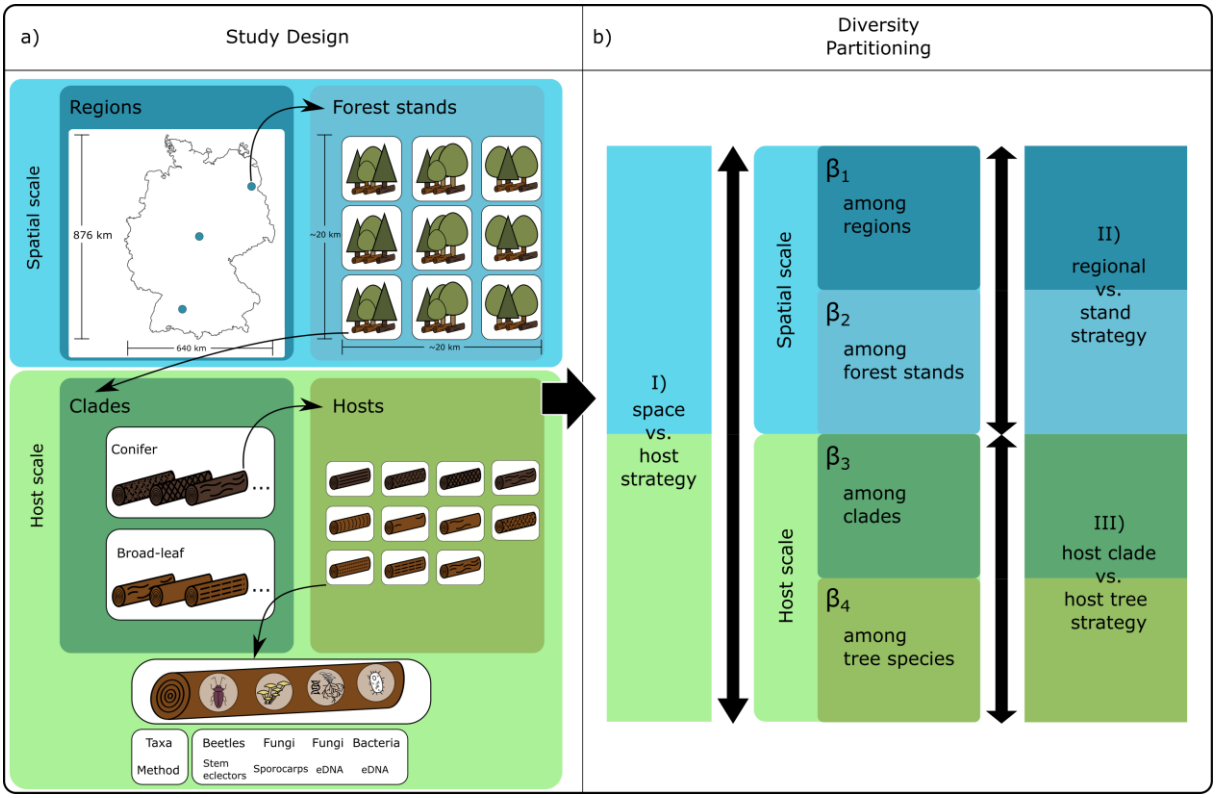
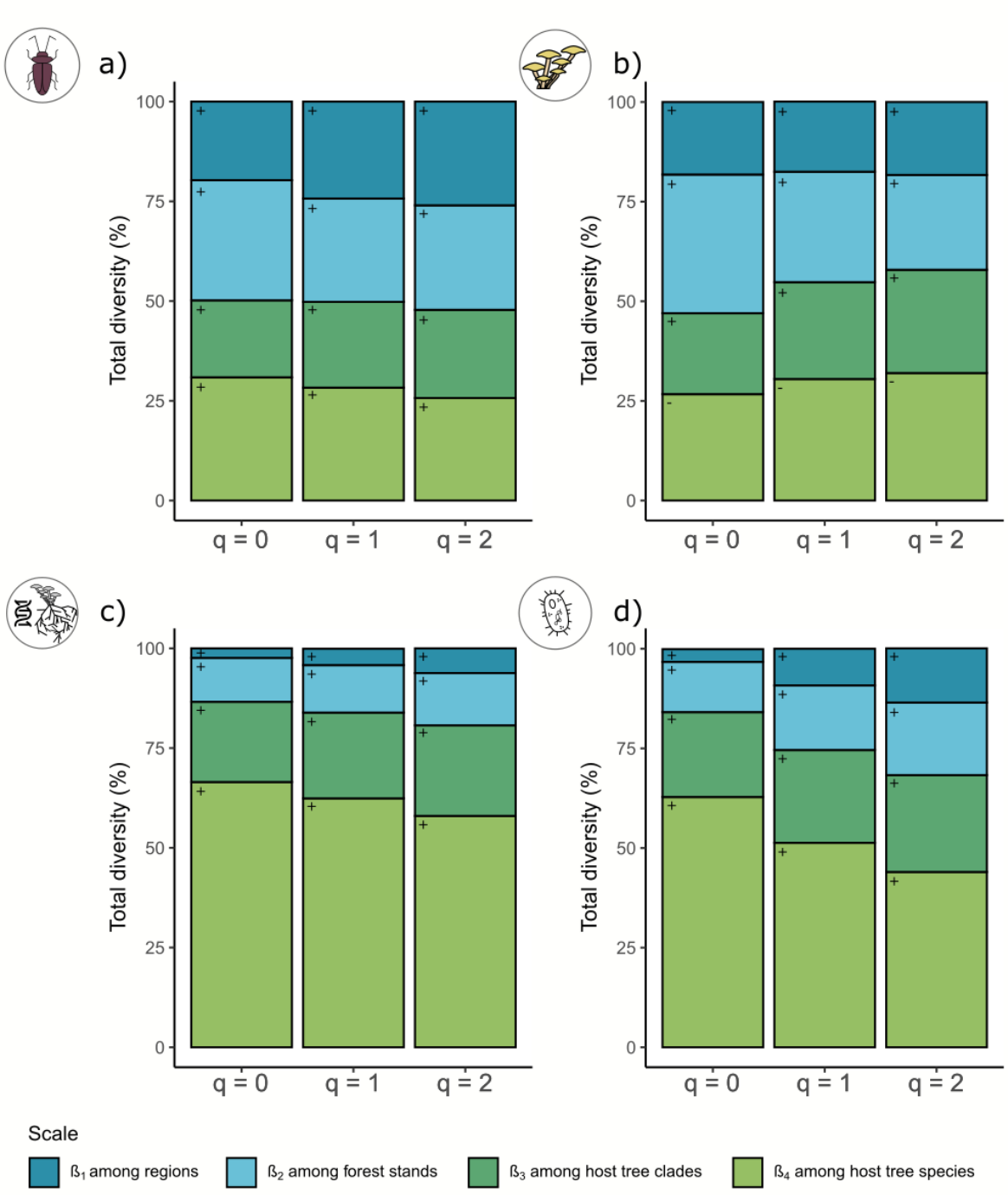


Fig. 1. Sampling design, methods, and conservation strategies. a) Sampling design: Over 7 years, the diversity of saproxylic beetles, fungal sporocarps, microbial fungi, and bacteria was studied at different scales: in three regions of Germany (regional scale) and in 27 forest stands, with 11 logs of two tree clades of 11 tree species (host tree scale, 297 logs in total). b) The beta-diversity of each scale was assessed using multiplicative diversity partitioning and compared via its relative importance for the total gamma diversity. Scales encompassing a high diversity are of particular interest for conservation, and conservation strategies can be adapted to them. Map source: freepik.com



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721 **Fig. 2**. Stacked bar plots of multiplicative diversity partitioning comparing the relative importance of the beta diversity on
722 different scales for the total diversity of saproxylic beetles (a), fungal sporocarps (b), microbial fungi (c), and bacteria (d).
723 Presented are the number-equivalents of species richness (rare species, $q = 0$), Shannon entropy (typical species, $q = 1$), and
724 Simpson diversity (dominant species, $q = 2$).Note that all observed beta-diversity values are significantly larger (+) or smaller
725 (-)expected based on null modeling (see Appendix B Table B.1).