Understanding and conserving the diversity of decomposers in dead-wood with a special emphasis on fungi

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LIST OF ABBREVIATIONS

Abbreviation	Definition
ASV	Amplicon Sequence Variant
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
OTU	Operational Taxonomic Unit

SUMMARY

Anthropogenic interventions have altered all ecosystems around the world. One of those ecosystems are forests, the main resource for timber. They have been strongly transformed in their structure with large consequences on forest biodiversity. Especially the decrease in dead-wood volume due to the timber extraction and alternation of natural forest structures with even-aged stands of less diverse tree species composition has put especially saproxylic, i.e., dead-wood dependent species, under threat, which comprise about 20% of all forest species. Beetles, fungi and bacteria are three functional important groups for decomposition processes but we still lack much information about their sampling and the drivers of their diversity, thus it is difficult to comprehensively protect their diversity. Saproxylic fungi are a highly diverse species group and the main drivers of dead-wood decomposition; hence they play a major role in the global carbon cycle. Due to their cryptic lifestyle, many species are still unknown, but the recent advances in environmental DNA barcoding methods (metabarcoding) shed light on the formerly underestimated diversity. Yet, this method's accuracy and suitability in detecting specific species have not been assessed so far, limiting its current usefulness for species conservation. On the other hand, these methods are a convenient tool to study highly diverse areas with high numbers of unknown species, enabling the study of global diversity and its drivers, which are unknown for saproxylic fungi, but important to assess to predict the future impacts of global change. Since nature conservation concepts are usually not applied on a global scale, the drivers of diversity must also be assessed on smaller scales. Besides understanding the drivers of diversity, to identify focus scales to create comprehensive, evidence-based conservation concepts must utilize multi-taxonomic studies since saproxylic species are differently sensitive towards environmental variables and closely interact with each other. Filling these knowledge gaps is utterly needed to protect the high saproxylic diversity and ensure the functional continuity of decomposition processes, especially regarding the global change.

To address the usefulness of metabarcoding for fungal species conservation, I compared the traditional method of fruit body sampling with metabarcoding and their efficiency in detecting threatened fungal species in the first chapter of this thesis. Both methods have advantages and disadvantages. Their ability to detect threatened saproxylic fungal species and their dependencies on detecting specific fungal groups have not been compared, albeit they are important to inform species conservation like Red Lists properly. I found metabarcoding to

generally detect more threatened fungal species than fruit body sampling with a higher frequency than fruit body sampling. Moreover, fruit body sampling detected a unique set of species, while fruit body sampling missed large parts of fungal diversity due to species-specific fruiting characteristics. Metabarcoding with high sampling intensity is thus a viable method to assess threatened saproxylic fungal diversity and inform nature conservation like Red Lists about distribution and abundances. Nevertheless, a complementary approach with fruit body sampling is indispensable for assessing all threatened fungal species.

In order to analyse the global diversity of saproxylic fungi and its drivers, I examined whether fungal species richness increases from the poles towards the equator and thus follows the latitudinal diversity gradient already found in many other species groups. I further investigated whether such an increase is caused by increasing ecological specialisation, i.e., niche partitioning, or local tree diversity, i.e., niche space. Gamma diversity per biome increased from the boreal, over the temperate to the tropics and thus confirmed the latitudinal diversity for saproxylic fungi. Contrastingly, alpha diversity at the log level did not significantly increase towards the tropics, suggesting a grain size dependency of the observed pattern and an equal niche space within dead-wood across latitudes. Ecological specialisation on the plot level was globally on a high level but did not increase significantly towards the equator. Additionally, I found local tree species richness to drive plot-based fungal diversity. Further analysis of gamma diversity against the total number of sampled tree species strengthened the assumption that tree species diversity and not increased ecological specialisation was the main driver of the latitudinal diversity gradient, as there was no significant difference between the gamma diversity of the temperate and tropical biome. Nonetheless, as the gamma diversity of the boreal biome was still significantly smaller, my results do not allow a complete neglection of the ecological specialisation hypothesis. The overall results indicate a strong dependency of saproxylic fungi diversity with host tree species diversity and that the global loss of tree species threatens saproxylic fungi with an unpredictable impact on carbon and nutrient cycling.

To support saproxylic conservation, I conducted two analyses. First, I compared the beta diversity of the three main decomposer groups (beetles, fungal fruit bodies, mycelial fungi (metabarcoding), and bacteria (metabarcoding)) across different scales to assess the impact of different environmental variables on their overall diversity. I used an experimental design to disentangle two different spatial scales, influenced by differences in macroclimate, forest microclimate and spatial distance, and two host scales, driven by differences between tree

lineages and tree species. I set these beta diversities in relation to the gamma diversity of the three main decomposer groups to identify whether a unified conservation concept could be applied to one scale to optimally protect the diversity of all three species groups. Second, I identified whether diversity and community composition of fungi and bacteria differed among climate and land use gradients. Further I explored whether specialisation and niche packing could explain the expected pattern. To do so I used an experimental design disentangling climate and land use across a large gradient in Germany. The results differed among the species groups, denying a unified conservation concept focusing on one scale. Saproxylic beetle and fruit body beta diversity was equally high on each scale, as they are more sensitive towards environmental factors like macro- and microclimate. On the other hand, mycelial fungi and bacteria beta diversity was highest on the host scale, especially the host tree scale, indicating a high host specificity of the two groups. The second study also identified tree species as the main driver of diversity and community composition of these two study groups. Specialisation of fungi was not influenced by land use or climate. Bacterial specialisation and diversity were under a strong influence of mean precipitation. Comprehensive conservation of multi-taxonomic diversity across regions thus requires the integration of several scales. Within different macroclimatic regions, forests of varying microclimates, i.e., forest management, must be implemented. In these forests, dead-wood of different tree lineages, i.e., angio- and gymnosperms and tree species, must be provided.

Taken together, I could demonstrate that metabarcoding is an efficient method to sample threatened fungal species and identify differing drivers of fungal diversity present as fruit bodies or mycelium. Its usefulness will further increase due to the ongoing improvement of sequencing databases and thus better inform conservation concepts. Using metabarcoding, I could demonstrate that high host specialisation of saproxylic fungi is not a European but a global phenomenon and identify tree species loss under global change as one major concern for saproxylic diversity. My dissertation further highlighted the importance of multi-taxonomic studies for evidence-based nature conservation, as different species groups require varying concepts. These results were especially important for saproxylic bacteria as the drivers of their diversity are still largely unknown. Howbeit, large research gaps still exist regarding the impacts of global change on species and processes. Moreover, the spatial coverage of studies is needed to confirm or neglect the generality of current research especially concerning the highly diverse tropical areas. An increased focus on the drivers of diversity in these areas is crucial to

ensure a globally comprehensive saproxylic conservation and the various ecosystem functions they control.

1 INTRODUCTION

Anthropogenic impact is altering ecosystems and, by that threatening global biodiversity (Johnson et al., 2017). Forests harbour large numbers of the world's diversity, especially in the tropics (Gibson et al., 2011; Lindenmayer, 2009). Hence changes in the abundance and structure of forests caused by deforestation and forest management are among the most severe anthropogenic impacts on diversity (Barlow et al., 2016; Betts et al., 2017). One of these major impacts is timber extraction and the subsequent reduction of dead-wood amounts (Fridman and Walheim, 2000; Morrissey et al., 2014), which primarily affects species depending on dead-wood as a resource or habitat. These species are defined as saproxylic species:

> "any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened or dead trees."
> - Stokland et al. (2012)

Approximately 20-25% of all forest-dwelling species are saproxylic (Siitonen, 2001); in some species groups, e.g. insects, the number of species is 30% (Ulyshen and Šobotník, 2018) and can reach up to 50% in the group of beetles (Köhler, 2000). Saproxylic species groups are highly diverse and not only threatened due to the decrease of dead-wood amounts but also by a decrease in heterogeneity and type and forest structural changes induced by forest management (Stokland et al., 2012).

The threat of saproxylic diversity is not only crucial due to its intrinsic values but also as they conduct various ecosystem processes, foremost the decomposition of the dead organic matter, which comprises 8% of the global forest carbon (Pan et al., 2011), thus they are important agents in carbon sequestration and nutrient cycling. Especially fungi are the main drivers of the decomposition processes in dead-wood (Boddy and Watkinson, 1995). Due to the cryptic lifestyle and high diversity of this species group, large parts of their diversity could only be detected due to the advance of eDNA barcoding methods (called metabarcoding from now on, Ovaskainen et al., 2013; Rajala et al., 2011) and their conservation has been largely neglected. This is partly due to unresolved issues in species detection by the two main sampling methods of fruit body sampling and metabarcoding. The inclusion of metabarcoding enabled for easier assessment of saproxylic fungal communities allowing the assessment of global fungal diversity and its drivers (Baldrian et al., 2022; Tedersoo et al., 2014). For saproxylic fungi and many other microorganism groups, knowledge about their global diversity is still

lacking, hindering accurate assessments of the impact of global change on their diversity and subsequent decomposition processes.

Besides fungi, insects and bacteria also take part in the decomposition process (Johnston et al., 2016; Seibold et al., 2021), and the three species groups closely interact (Johnston et al., 2019; Odriozola et al., 2021; Seibold et al., 2019). These species groups are differently sensitive to environmental variables and different factors define their diversity (Müller et al., 2020). Hence, conservation concepts should be based on multi-taxonomic studies, which are still lacking on broader spatial scales (Seibold et al., 2015). Comprehensive conservation might not be possible without such assessments and could harm neglected species groups.

This dissertation aims to fill these research gaps by comparing fungal sampling methods, analysing global saproxylic fungal diversity patterns and comparing the importance of different, particularly larger scales, for the overall diversity of several saproxylic species groups. The results should build the basis to further develop evidence-based conservation concepts for saproxylic species and help to predict better the impact of global change on the latter and the subsequent consequences on decomposition and global nutrient and carbon cycles.

1.1 ACCURATE FUNGAL SAMPLING AS BASIS OF NATURE CONSERVATION

Elaborating comprehensive nature conservation concepts requires reliable sampling data. Such data can only be obtained using appropriate sampling methods applied at spatial and temporal scales of different grain sizes and is necessary to track population dynamics and evaluate the effectiveness of nature conservation measures. Furthermore, as extensive sampling is time-consuming, nature conservation requires rapid diversity assessment.

As the basis of generating analysable data, appropriate sampling methods are needed to assess most of the target species groups' diversity in a particular area. For most saproxylic species groups, these methods have been developed and used for several decades, giving reliable estimates of diversity, abundance and community composition. For example, vascular and non-vascular plant diversity and abundance are identified on each dead-wood object of interest (e.g., Dittrich et al., 2014; Staniaszek-Kik et al., 2019). Saproxylic beetles can be sampled via stem eclectors attached to the dead-wood object (e.g., Gossner et al., 2016; Seibold et al., 2023), flight interception traps placed at the sampling plot (e.g., Lachat et al., 2007; Gossner and Ammer, 2006) or reared directly from the object (e.g., Vogel et al., 2021). Bacteria are sampled via metabarcoding (e.g., Moll et al., 2018; Odriozola et al., 2021). This new method of sampling the DNA of saproxylic species in situ (Ovaskainen et al., 2013; Rajala et al., 2011)

has now challenged the standard procedure of sampling the diversity of fungi via their fruit bodies in the field, as it made apparent several limitations of this method.

Fruit body sampling is based on the morphological differentiation of the sexual reproduction organs of a fungus in the field, which requires expert mycological knowledge. These structures are highly ephemeral in space and time, as their production depends on many variables, like climate and weather (Sakamoto, 2018). Hence species display different intra- (Halme and Kotiaho, 2012; Purhonen et al., 2017) and inter-annual fruiting patterns (Moore et al., 2008; van der Linde et al., 2012). Furthermore, fruit body size varies strongly, and small species can be easily overlooked (Lõhmus, 2009), while others require long-term nutrient acquisition to form fruit bodies (Ovaskainen et al., 2013), or produce no fruit body at all (Bridge and Spooner, 2001).

Metabarcoding allows the detection of fungal species which are only present as mycelia without requiring identification skills (Fischer et al., 2012; Kubartová et al., 2012; Rajala et al., 2011) and a highly standardised sampling (Thomsen and Willerslev, 2015). But metabarcoding data can contain many low-quality sequences, which must be excluded before analysation (Lindahl et al., 2013). Also, DNA from dead organisms can remain in the substrate (Carini et al., 2016), or nonviable species can be sampled (Tuovinen et al., 2015). Compared to fruit body sampling, which usually covers the whole dead-wood object, only a small amount of substrate is sampled, neglecting species not growing in the particular sample, e.g. due to small mycelial size (Kubartová et al., 2012; Ovaskainen et al., 2013) or limitation in spatial distribution due to competition (Boddy and Hiscox, 2016). Further problematic is the quality of reference data bases for species identification, as not every species is represented therein (Hibbett et al., 2016).

The reliability of sampling data is important to monitor population dynamics to assess the threat status of other species groups for Red Lists and consequently evaluate the effectiveness of conservation measures. Ecological studies show that metabarcoding is a promising addition for sampling fungal diversity (Frøslev et al., 2019; Ovaskainen et al., 2013; Saine et al., 2020). The effectiveness of metabarcoding in detecting threatened species has only been studied for soil fungi so far, detecting slightly more species than traditional fruit body sampling (Frøslev et al., 2019). As saproxylic fungi are an additional large group of forest fungi, the main decomposers of dead-wood and a highly threatened species group, a comparison of both methods regarding their effectiveness in sampling threatened saproxylic fungal species is necessary as metabarcoding is a promising approach to improve threatened fungal species assessments and the derived Red list statuses (Runnel et al., 2015). This will hopefully increase

overall fungal conservation, which is lacking behind other species groups (Heilmann-Clausen and Vesterholt, 2008; Hochkirch et al., 2021).

1.2 GLOBAL DIVERSITY OF SAPROXYLIC FUNGI

The latitudinal diversity gradient of species richness is one of the most striking global biodiversity patterns. The species richness of almost all taxonomic groups, regardless of whether they inhabit aquatic or terrestrial ecosystems, increases from the poles towards the equator (Hillebrand, 2004). So far, no study has focused on the global diversity patterns of any saproxylic species group. Assessing global diversity patterns in important functional groups like saproxylic fungi is thus crucial to improving our overall knowledge of global carbon and nutrient cycling, especially in the face of climate change and positive feedback loops.

Albeit high in quantity, the numerous other studies have not found a consensus explanation from the vast theories trying to explain the latitudinal diversity gradient (reviewed in Mittelbach et al., 2007). In recent years studies have determined the influence of the abiotic environment, like climate and postulated biotic interactions, to play a big part in the origin and maintenance of the latitudinal diversity gradient (Mittelbach et al., 2007; Schemske et al., 2009). Since these causes are interconnected and often correlated with latitude, a combination of several and not a single one can likely explain the latitudinal diversity gradient (Fine, 2015). Nevertheless, studying the single causes is important for better understanding global diversity patterns.

One heatedly debated topic within species interactions is the role of specialisation (Dyer and Forister, 2019; Moles and Ollerton, 2016). The ecological specialisation hypothesis suggests that increased specialisation towards the equator causes increased species richness (Dobzhansky, 1950; MacArthur, 1972). Ecological specialisation and species richness are linked (Hutchinson, 1959), and an increase in specialisation allows higher numbers of species to coexist by reducing competition due to higher niche partitioning (MacArthur and Levins, 1967). Without external influences like the Connell-Janzen effects (Connell, 1971; Janzen, 1970), this results in a simultaneous increase of specialisation and species richness (Schluter, 2008; Thompson, 2005) as species diverge due to competition (Grant and Grant, 2006). Equatorial areas were ice-free for more extended periods than poleward ones, and the climate was generally more stable, thus species in these areas had more time for specialisation and speciation, while abiotic processes were less selective while facilitating the importance of biotic interactions and niche partitioning (Dobzhansky, 1950; Fischer, 1960; Schemske, 2002; Wallace, 1878). Consequently, communities in tropical areas should be more specialised and, thus, more species-rich than poleward areas. The ecological specialisation hypothesis was

studied several times in different interaction systems with differing results (approval: e.g., Dyer et al., 2007; Trøjelsgaard and Olesen, 2013; disapproval: e.g., Frank et al., 2018; Novotny et al., 2006; Zanata et al., 2017). These results caused a heated debate about its general validity (Moles and Ollerton, 2016). The conducted studies have several issues, though, which argue pro and contra a general discard of the ecological specialisation hypothesis (Dyer and Forister, 2019; Moles and Ollerton, 2016). Especially confounding effects of resource availability and resource type could not be controlled for in these field studies or meta-analyses and need experimental approaches controlling for them. Additionally, all ecological specialisation hypothesis studies were conducted on macroorganisms. In this context, dead-wood-inhabiting fungi are ideal for testing the ecological specialisation hypothesis. They co-evolved with their hosts to bypass plants' secondary metabolites (Floudas et al., 2012) and became highly host-specific (Moll et al., 2021; Lee et al., 2020) and can only occur in the respective substrate, which greatly simplifies the manipulation and control of resources.

An alternative hypothesis identified for the global diversity of host-dependent organism groups is the abundance and diversity of their hosts (Dyer et al., 2007; Zanata et al., 2017). Thus, the diversity of saproxylic fungi might also depend on the local tree species diversity, which also increases from the poles towards the tropics (Liang et al., 2022) and increases the overall resource heterogeneity (niche space), allowing more species to co-exist. This tree species diversity hypothesis could thus increase the diversity of saproxylic fungi by increasing the available niche space.

Analysing global diversity patterns of dead-wood inhabiting fungi can clarify the case of the ecological specialisation hypothesis and hence further complete our knowledge about the latitudinal diversity gradient. Moreover, it can indicate the impacts of global change on fungi and subsequent changes in decomposition and carbon cycling.

1.3 MULTI-TAXONOMIC CONSERVATION CONCEPTS

The implementation of conservation concepts usually happens on a nationwide scale. Within a country, different environmental variables impact the diversity of saproxylic species on various scales. For saproxylic species, environmental variables, like climate, resource abundance, or land use can impact diversity on a spatial scale. As they rely on dead-wood objects as a resource, different dead-wood traits (e.g., tree species, volume, type, decay class) can impact the diversity on a host scale. For conservation, it is important to identify the drivers of diversity. One way is

to analyse diversity and its drivers at different scales and then target the structures at high diversity scales through conservation concepts.

1.3.1 REGIONAL AND LOCAL SCALE

Each species group has a climatic niche, defining its distribution and range size. Depending on the size and topography, a country can contain several climatically different regions (regional scale) which harbour different species communities (Peterson, 2011). Further, as tree species also have climatic niches, climatic differences also impact the general tree species composition. Regional differences in tree communities could thus especially impact host-specialized species, like many saproxylic species are (Stokland et al., 2012), due to the provision of different resources. The specialisation of saproxylic organisms could also impact the diversity under different climates. It follows the same principle of environmental stability favouring the evolution of specialisation explained in Chapter 1.2, allowing more species rich communities in climatically favourable habitats. Additionally, to climate, the dispersal capability of species groups plays an important role in structuring communities and diversity across regions. Species groups with a generally lower dispersal capability (e.g., beetles) might display higher beta diversity between regions than species with larger dispersal capability (e.g., fungi, Komonen and Müller, 2018). For saproxylic bacteria, no study on dispersal capability has been conducted so far (Johnston et al., 2016). Dispersal capability is believed to play an important role at each scale but has an increasing influence with increasing distance, as suitable dead-wood resources are less likely to be detected or reached randomly the farther they are apart.

On a local scale, habitat structure, resource abundance, and land use impact diversity and community composition. Habitat structure, i.e. forest structure is defined by the tree species composition and age, forming a specific canopy cover with specific phenology (Juchheim et al., 2019). These structures define forest microclimate by controlling solar radiation and surpassing wind throughout the day and year (Ehbrecht et al., 2019; Richter et al., 2021; De Frenne et al., 2019). Species groups relying on warmer temperatures, like beetles, thus favour more open forests with higher radiation (Müller et al., 2015; Seibold et al., 2016; Vogel et al., 2020), while humidity-dependent ones, like fungi, favour more closed canopies (Bässler et al., 2010; Krah et al., 2018; Thorn et al., 2018). There is high variability among the tree species and their effect on canopy openness (Juchheim et al., 2019). Thus, forests dominated by different tree species harbour different saproxylic communities. Further, the tree community defines the amount and type of dead-wood within a forest and hence the resource abundances for saproxylic species.

All these factors are superimposed by human land use (Schall et al., 2020, 2021). Forest management alters the tree species composition and age (Schulze et al., 2016) and hence the microclimate (Juchheim et al., 2019), thereby altering the diversity and communities of forest species. Further, forest management actively structures the amount and structural heterogeneity of dead-wood. Timber production decreased dead-wood amounts in managed forests compared to unmanaged ones by extracting trees before their natural death (Verkerk et al., 2011). Additionally, dead-wood still is actively cleared from the forests as it is a assumed pest source (Stokland et al., 2012). In strong interaction with the resource amount is resource abundance, the distribution of dead-wood objects in space. Low dead-wood volumes usually condition a sparse distribution in space (Haeler et al., 2021), negatively impacting species with low dispersal capability, which cannot bridge inhabitable gaps between dead-wood objects. Nevertheless, not only the overall dead-wood amounts decreased, but also the volume of the dead-wood items themselves. Forest management is sought-after large-diameter trees due to their higher monetary value. Often only branches and stumps were left in forests, yet due to technical improvements, even those small parts are now used as fuel, and the complete removal of trees is increasingly common (Rudolphi and Gustafsson, 2005). A lower amount of resources increases competition for the remaining resources, negatively impacting especially less competitive species (species-energy theory; Wright, 1983). Thus, forests with lower dead-wood volumes harbour fewer saproxylic species and the overall decrease in dead-wood amounts is threatening many saproxylic species (Lassauce et al., 2011).

Land use can also have direct effects on diversity and can lead to a decrease with increasing intensity (Newbold et al., 2015). One explanation for this might again be the favouring of generalist species under higher environmental variability, like disturbances and habitat perturbation caused by land use (Curtis et al., 2018; Polasky et al., 2011; Tittensor et al., 2014; van Tienderen, 1991). The impact of land use, other than forest management, on saproxylic species has not been assessed yet. But following ecological hypothesis it could be assumed that their diversity would decrease with increasing land use intensity, caused by a lower abundance of specialized species.

The factors influencing the diversity of saproxylic species on regional and local scales are manifold. The sensitivity of different species groups towards these factors varies (e.g., Lee et al., 2020; Müller et al., 2020; Thorn et al., 2018), and hence do their requirements for conservation concepts. We are currently lacking diversity assessments across larger scales (among regions) and the impact of land use intensity outside of forests, preventing

comprehensive estimations on human impact on saproxylic diversity and conservation across regions.

1.3.2 HOST SCALE

Diversity in and on a dead-wood object is driven by four main aspects, the dead-wood size, dead-wood type, the decay stage and the tree species. The number of existing niches due to different combinations of these four factors is vast (Stokland et al., 2012). Some are more important for saproxylic diversity than others. Larger diameter objects contain more nutrients and can support more or specific species (Bässler et al., 2010; Heilmann-Clausen and Christensen, 2004; Jonsell et al., 2007; Lindhe et al., 2004). However, smaller dead-wood supports different communities than large dead-wood and is thus equally important for overall diversity (Brin et al., 2011; Juutilainen et al., 2017; Toivanen et al., 2012). Further, different species utilized different dead-wood types (stumps, logs, branches, snags; Uhl et al., 2022). Dead-wood decay leads to changes in water and nutrient availability and concentration (Laiho and Prescott, 2004), and dead-wood of advanced decay stages harbours the highest diversity due to higher colonisation over time and more readily available resources due to previous decomposition processes (e.g., Rajala et al., 2011; Saint-Germain et al., 2007).

Another main factor impacting saproxylic diversity is the tree species. Beetles, fungi and bacteria are known to be specialized on specific host tree species (Gossner et al., 2016; Moll et al., 2021), although beetles seem less specialized than fungi and bacteria (Müller et al., 2020). Tree species differ in physico-chemical properties which define for example pH or water holding capacity, and define the chemical defence of a tree, which saproxylic species have adapted to encompass to access the resource (Floudas et al., 2012). As these differences are especially pronounced between angio- and gymnosperms (Kahl et al., 2017), the specialisation was often found on either of the two clades (e.g., Brändle and Brandl, 2006; Hoppe et al., 2015; Krah et al., 2018). However, such studies often only focused on one tree species per clade. Recent studies covering higher tree species diversity found the tree species to be an important or the primary driver of saproxylic diversity for these three species groups (Baber et al., 2016; Gossner et al., 2016; Lee et al., 2020; Müller et al., 2020). Consequential natural or managed forests with heterogeneous tree species compositions accumulate more heterogeneous dead-wood tree species, which enhances diversity compared to forests with low tree species diversity or plantation forests.

The previous two chapters show that saproxylic diversity depends on the various niches provided by the forest stand and the dead-wood itself and are superimposed by humans. While for many saproxylic groups, the main diversity drivers and scales have already been identified

by former studies, most of these studies are single-taxonomic or small-scaled (Seibold et al., 2015). Studies focusing on multi-taxonomic saproxylic diversity are still rare (e.g., Haeler et al., 2021; Müller et al., 2020; Lee et al., 2020), but ensure a better understanding of the overall drivers of diversity. This broader coverage is crucial for comprehensive conservation as conservation concepts suited for one species group might harm others. Further, experimental approaches which manipulate specific variables allow determining the exact relative importance of different variables for each species group under standardised conditions, while field surveys cannot always disentangle influences of different variables. Currently, we still lack experimental studies simultaneously assessing the drivers of diversity on several scales of different grain size and cannot ensure evidence-based conservation concepts across regions for all targeted species groups.

2 MAIN OBJECTIVES

The overall goal of this dissertation was to deepen our understanding of saproxylic diversity with an emphasis on saproxylic fungi. I aim to fill current knowledge gaps concerning fungal sampling and conservation. Further, I attempt to analyse the first global study on saproxylic fungal diversity and its drivers. Moreover, I investigate the possibility of a unified conservation concept for the three main saproxylic decomposer groups. I want to help deepen our understanding of saproxylic diversity and conservation by targeting these three main objects specifically:

In a first step, I compared the traditional fungal sampling method of fruit body sampling with metabarcoding data in their ability to detect threatened fungal species in dead-wood on five sites in temperate Europe. These results should help improve the understanding of the advantages and limitations of both methods in species assessment and help with incorporating metabarcoding methods in nature conservation (Fig. 1a). In the second part, I analysed if saproxylic fungal diversity increases from the poles towards the equator and thus follows the latitudinal diversity gradient, as many other species groups do. I examined two possible hypotheses causing this potential pattern. The ecological specialisation hypothesis states an increase in niche partitioning towards the equator, allowing more species to co-exist. The tree species diversity hypothesis states that an increase in tree species diversity increases niche space for this highly host-specific species group, thus allowing for higher saproxylic fungal diversity in tree species-rich areas. These results should not only shed light on the unknown global diversity patterns of saproxylic fungi but also contribute to a better understanding of the latitudinal diversity gradient. In addition, these results can contribute to increasing predictions

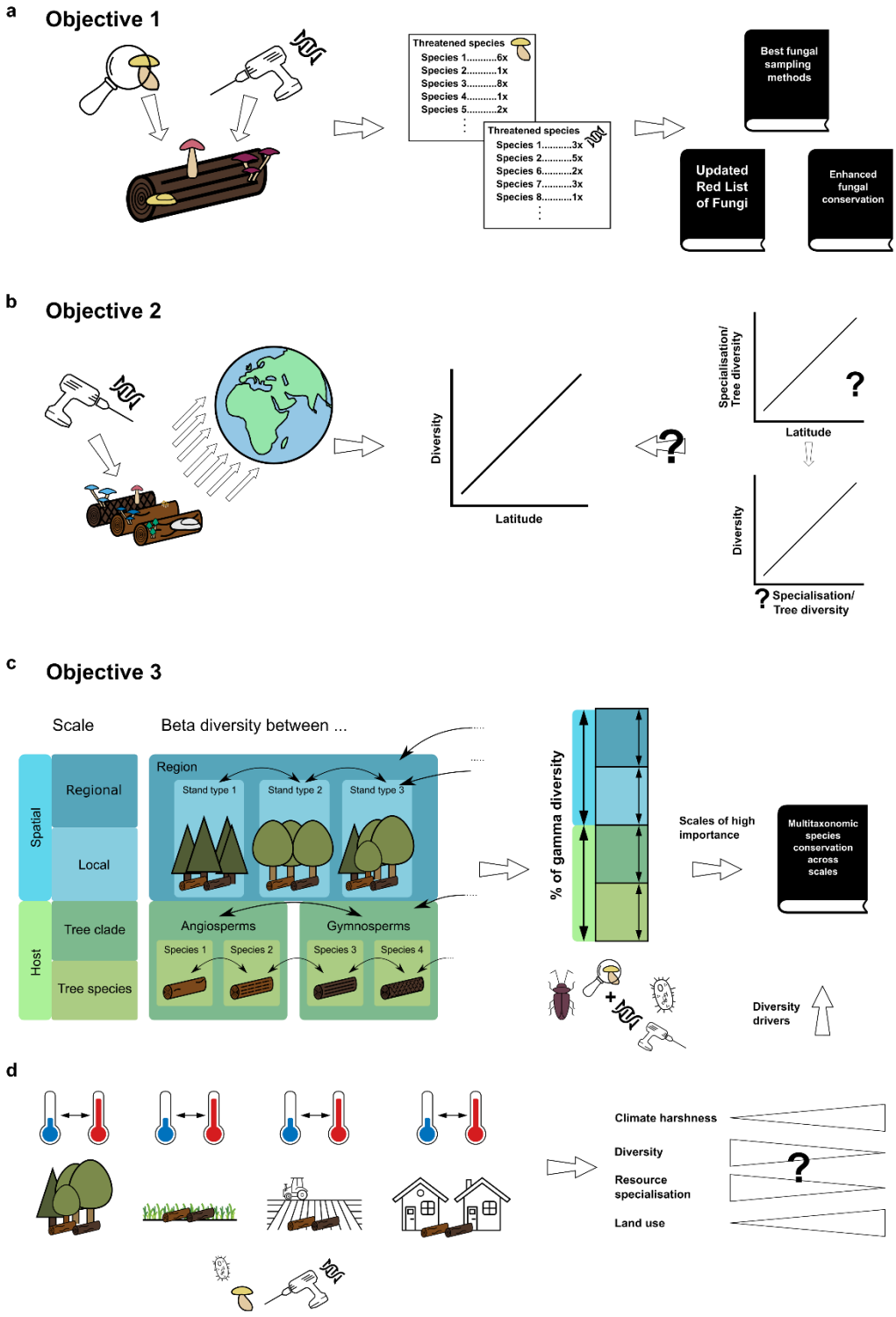

Figure 1: Conceptional figure of the three main objectives of this dissertation. ***a*** *Objective 1 is an assessment of the efficiency of the two fungal sampling methods of fruit body sampling and metabarcoding in the detection of threatened saproxylic fungal species and how this increased knowledge about the function of either method can be used for fungal conservation.* ***b*** *Objective 2 is the assessment of the latitudinal diversity gradient in saproxylic fungi and whether it is caused by an increase in specialisation or tree species diversity towards the equator.* ***c & d*** *Objective 3 is parted into two studies.* ***c*** *is a comparison of the relative importance of space and host for overall gamma diversity of three saproxylic species groups, and whether unified conservation concepts can be applied to one scale or several scales have to be the focus. In* ***d*** *the impact of land use and climate on the diversity and specialisation of mycelial fungi and bacteria is tested to identify further diversity drivers on regional and local scale.*

about the impact of global change on fungal diversity and the related decomposition processes and thus might enhance global conservation (Fig. 1b).

Lastly, I analysed the drivers of multi-taxonomic saproxylic diversity at different spatial scales within Germany using two set ups. In the first approach, I compared the relative importance of beta diversity at spatial and host scales to the overall gamma diversity of saproxylic beetles, fungi and bacteria (Fig. 1c). In a second approach I analysed the specialisation and diversity of saproxylic fungi and bacteria under different climate and land use types to deepen our understanding on the diversity drivers on regional and local scale (Fig. 1d). The aim was to identify if one specific scale can be targeted by nature conservation to protect saproxylic diversity or if each species group requires different concepts. Using experimental approaches, I could simultaneously address several problems of recent saproxylic studies. First experiments detect the influence of manipulated conditions and thus deliver more reliable results on the relative importance of diversity drivers than field surveys. Second, multi-taxonomic studies are still scarce, although they allow for a more precise evaluation of the relative importance of different drivers on diversity to estimate the effects of conservation measurements on several species groups. Third, large-scale studies are still lacking, examining several scales at once (Seibold et al., 2015).

The specific objectives of the dissertation were:

1. How to rapidly assess threatened fungal diversity?
2. Is there a latitudinal diversity gradient in global wood-inhabiting fungal diversity, and can it either be explained by increased specialisation or tree species diversity?
3. At which scale do conservation concepts need to be implemented to conserve the diversity of multi-taxonomic saproxylic communities?

3 MATERIALS AND METHODS

3.1 OBJECTIVE 1: HOW TO RAPIDLY ASSESS THREATENED FUNGAL DIVERSITY?

The following is a shortened methodological overview, and a more in-depth description can be found in Annex A.1. The location of the sites is displayed in Figure 2a.

3.1.1 STUDY SYSTEMS

3.1.1.1 BAVARIAN FOREST EXPERIMENT

The Bavarian Forest National Park, in south-east Germany, is a mountain range at elevations between 650 to 1450 m a.s.l. Mean annual temperature (MAT) ranges from 3.5 to 7.0°C (1972-2001), and the total annual precipitation (MAP) ranges from 1,300 to 1,900 mm (Bässler, 2004). In the high elevations, upwards of 1,100 m high montane forest stands, dominated by Norway spruce (*Picea abies*) with a low amount of European beech (*Fagus sylvatica*) and Mountain ash (*Sorbus aucuparia*). Below stand mixed montane forests, dominated by spruce, beech and European silver fir (*Abies alba*, Walentowski et al., 2020). In the management zone of the national park, 67 plots (0.1 ha) were installed in 2011. In one half of the plots, all standing trees were cleared. One log (diameter: 33 ± 6.5 cm, length: 5 m) of *F. sylvatica* and *A. alba* were freshly cut and placed on each plot.

3.1.1.2 ZOFIN NATIONAL PARK

The study area was located in the Novohradske Hory mountains, specifically in the 25 ha Zofin ForestGEO® Dynamics Plot (www.forestgeo.si.edu), in the core zone of the Zofínský prales National Nature Reserve in the Czech Republic. The elevation ranges between 735 to 830 m a.s.l. with a slight NW slope. MAP is 866 mm and MAT is 6.2°C (Anderson-Teixeira et al., 2015). At present, the reserve is covered by a mixed forest. *F. sylvatica* predominates (51.5%), followed by *P. abies* (42.8%) and *A. alba* (4.8%). In total, 111 logs (diameter: 30 - 100 cm) were chosen, with the following distributions among tree species: 37 *F. sylvatica,* 44 *P. abies* and 36 *A. alba*.

3.1.1.3 BELONGDEAD EXPERIMENT

The BELongDead Experiment is a dead-wood experiment within the Biodiversity Exploratories in Germany (Fischer et al., 2010). The experimental plots are located in three areas but will be handled as different sampling sites for this analysis: (1) the UNESCO Swabian Alb Biosphere Reserve, on an altitude of 460–860 m a.s.l. with 6–7°C (MAT) and 700–1000 mm (MAP),

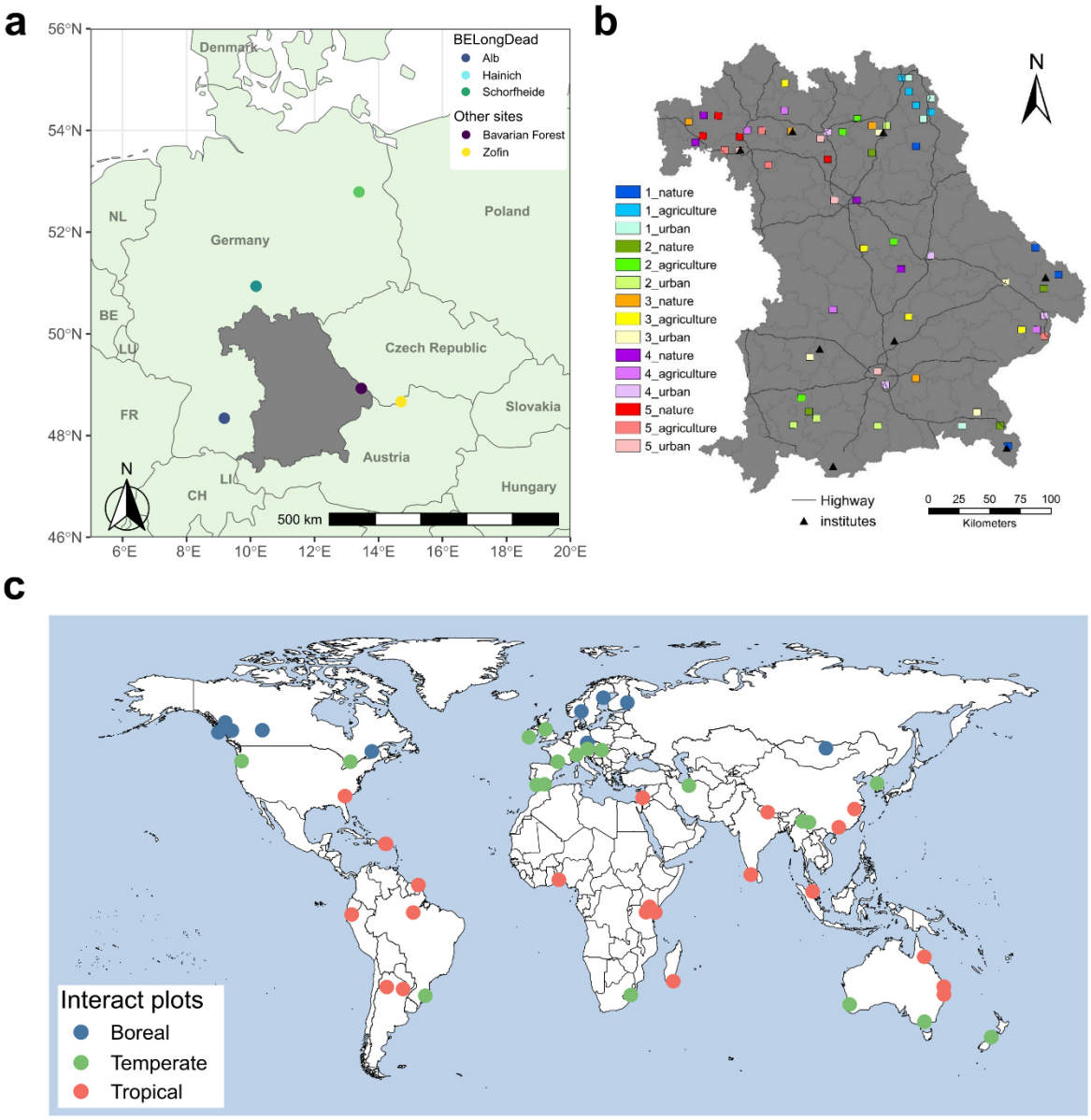

Figure 2: Overview of the sampling sites used in this dissertation. ***a*** *Locations of the sampling sites for Objective 1 and Objective 3 (BELongDead only) in Germany and the Czech Republic. The sites Alb, Hainich, Schorfheide and Bavarian Forest contain several sampling plots across different forests, while Zofin is one consecutive forest patch. The gray shaded area resembles the extent of the distribution of the plots in the LandKlif project in map* ***b****. Numbers represent climate zones (1: cold, 5: warm) followed by the landscape (nature, agriculture, and urban).* ***c*** *Distribution of the plots in the Interact experiment in the three different biomes boreal (blue), temperate (green) and tropical (red) for Objective 2.*

dominated by *Fagus sylvatica*, *Picea abies* makes up to 24% of the forest cover; (2) the Hainich-Dün region in Central Germany, including Hainich National Park, on an altitude of 285–550 m a.s.l. with 6.5–8°C MAT and 500–800 mm MAP, dominated by *F. sylvatica* and a conifer cover of only 12%; (3) the Schorfheide-Chorin UNESCO Biosphere Reserve, on an altitude of 3–140 m a.s.l. with 8–8.5°C (MAT) and 500–600 mm (MAP), dominated by Scots pine (*Pinus sylvestris*) (39%), and only 12% beech cover. Nine plots were established in forests of different management types in each region; three each in planted conifer stands, even-aged managed

beech stands, and unmanaged (for at least 20 years) beech stands. With selective cutting, Hainich-Dün has an additional forest management type and, thus additional three plots, adding up to a total of 30 plots. On each plot, 13 logs (4.0 ± 0.25 m length and 31 ± 5.9 cm (SD) mean diameter) were placed in 2009, resulting in a total of 390 logs. The logs consisted of four conifers (*Larix decidua*, *Picea abies*, *Pinus sylvestris*, and *Pseudotsuga menziesii*) and nine deciduous (*Acer spp.*, *Betula pendula*, *Carpinus betulus, Fagus sylvatica*, *Fraxinus excelsior*, *Populus spp*., *Prunus avium*, *Quercus spp*., and *Tilia spp*.) tree species. All species, including non-native *P. menziesii*, are common tree species in Central Europe.

3.1.2 DATA SAMPLING

3.1.2.1 FRUIT BODY

For the fruit body inventory, all fungal fruiting bodies were identified in the field or later in the laboratory during the peak fruiting seasons (see also Halme and Kotiaho, 2012) in the years 2012, 2013 and 2015 in the Bavarian forest, 2013 in Zofin and 2012, 2015, and 2018 in the sites of the Alb, Hainich and Schorfheide.

3.1.2.2 BARCODING DATA

In all sites, wood samples for DNA metabarcoding were collected as drilling dust using a cordless drill. In the Bavarian Forest and Zofin, four samples were collected per dead-wood log at 1/8, 3/8, 5/8 and 7/8 of the length of the log. In the three BELongDead sites, only one sample was collected in each sampling campaign, consisting of two points facing each other, 45° degrees from the vertical centre of the log. In the first year, the sample was collected 50cm from the log basis and moved by 30 cm upwards each campaign. Before drilling, the bark was removed at each sampling location, and the auger was sterilised between drillings by rinsing with ethanol and burning with a Bunsen burner. Samples were then frozen within a few hours after drilling. Each wood sample was homogenised into a fine powder using liquid nitrogen and a swing mill (Retsch, Haan, Germany). Samples were then sent to the laboratory and kept frozen at -20°C. Before processing, the samples from the Bavarian Forest and Zofin were coarsely shredded with an electric drill and then freeze-dried; samples from all sites were milled and homogenised using a swing mill and liquid nitrogen (Retsch, Germany).

The DNA from the homogenised samples of the Bavarian Forest and Zofin were isolated using 200 mg of the material and the NucleoSpin Soil Kit (Macherey-Nagel, Germany), samples of the BELongDead using 100 mg and the ZR soil microbe DNA MiniPrep kit (Zymo Research, Irvine, CA, USA). In both cases, the fungal ITS2 region was amplified using the

fITS7 and ITS4 primers (Ihrmark et al., 2012) and sequenced on Illumina MiSeq (Illumina Inc., San Diego, CA, United States). In the Bavarian Forest and Zofin sequence, raw data were processed using the pipeline SEED 1.2.1 (Větrovský and Baldrian, 2013). Within the pipeline, chimeras were removed with Usearch 7.0.1090 (Edgar, 2010) and the remaining sequences were clustered into operational taxonomic units (OTUs) at 97% similarity using UPARSE within Usearch (Edgar, 2013). In the BELongDead experiment sequence, raw data were processed using the pipeline Dadasnake (Weißbecker et al., 2020). Within the pipeline, DADA2 (Callahan et al., 2016) was used to calculate fungal ASVs (amplicon sequence variants). The consensus algorithm was used to remove chimeras, and the remaining reads were merged with an overlap of 20 base pairs and one mismatch allowed amplicon sequence variants (ASVs). Taxonomy assignment for all sequences was performed in PipeCraft 2 bioinformatics platform (Anslan et al., 2017; pipecraft2-manual.readthedocs.io/en/stable) using blastn algorithm (BLAST v2.11.0+; Camacho et al., 2009) against UNITE v8.3 all eukaryotes database (Abarenkov et al., 2010). Blastn settings were strands=both, e-value=0.001, word size=7, reward=1, penalty=-1, gapopen=1, gapextend=2. To improve readability, the term "species" will be used for OTUs and ASVs, albeit I am aware that OTUs and ASVs are only putative species concepts. Twelve fungal species detected via fruit body sampling but lacking reference sequences were excluded in the following analysis.

3.1.3 DATA PREPARATION

All preparations and analyses were conducted using R 4.2.2 (R Core Team, 2022).

Prior to the final analyses, local singletons from the metabarcoding community matrix were excluded (i.e. cells with a value of 1 were set to 0), as these are likely PCR and sequencing errors (Brown et al., 2015). The OTU and ASV community matrices were then aggregated on the species level, and the presence-absence of each species on each log was used in the further analysis.

For better comparability between the sites, the Red List of threatened Fungi of Germany (Dämmrich et al., 2016) and the Czech Republic (Holec and Antonín, 2006) were combined into one regional Red List. Species listed as "not evaluated", "least concern", or "data deficient" were excluded from further analysis. The nomenclatures of each data set and our combined Red List were unified using the "Current name" stated in MycoBank (Crous et al., 2004, accessed: 24.03.2022).

3.1.4 DATA ANALYSIS

All Euler plots were created with https://eulerr.co/.

For the methodological comparison, I first split metabarcoding data into samples of low (BELongDead) and high sampling intensity (Bavarian Forest/Zofin), depending on the number of drilling cores collected. For each of the following assessments, I compared the results of low sampling intensity metabarcoding and high sampling intensity metabarcoding with respective fruit body sampling data.

In order to assess the overall efficiency of each method in sampling red-listed species (from now on "threatened species"), I compared the number of threatened species detected uniquely or shared between the methods. To test which method was more efficient in detecting threatened species on the log level, I calculated generalized linear mixed effect models for the negative-binomial family using the function g*lmer.nb* (package *lme4*, Bates et al., 2015). I used the number of threatened species detected per log as a response and the sampling method as an explanatory variable, with "log ID" as a random factor.

Subsequently, I assessed the simultaneous detection of species on the same log by both methods in the same sampling year in relation to the number of occupied logs in the respective year.

I then compared the overall and log level performance of both methods in regard to dead-wood traits, namely decay stages and whether the host tree was angiosperm or gymnosperm. Again, I used negative-binomial generalized linear mixed-effects models (*glmer.nb*) with the number of threatened species detected on each log as a response and method as an explanatory variable, "log ID" was again the random effect.

Last, I calculated the overall total number of logs occupied by threatened species by each method. On the log level, I used generalized linear mixed effects models (family = binomial) with the function g*lmer* (package *lme4*), using a binomial code of 1 (threatened species detected) or 0 (threatened species not detected) for each log as a response variable. The sampling method was the explanatory variable, and "log ID" was again the random effect.

3.2 OBJECTIVE 2: IS THERE A LATITUDINAL DIVERSITY GRADIENT IN GLOBAL WOOD-INHABITING FUNGAL DIVERSITY, AND CAN IT EITHER BE EXPLAINED BY INCREASED SPECIALISATION OR TREE SPECIES DIVERSITY?

The following is a shortened methodological overview, and a more in-depth description can be found in Annex A.2. The location of the sites is displayed in Figure 2c.

3.2.1 STUDY SYSTEM

The Interact experiment is an established global network of 52 experimental forest sites across boreal, temperate and tropical biomes. Within biomes, the variability in temperature and precipitation was considered in the site design (Fig. 1, see Seibold et al., 2021 for more details). Site installation took place between March 2015 and July 2016, depending on seasonality (see Seibold et al., 2021). At each site, branches or stems of young trees (~3 cm in diameter, 50 cm in length) from the three of the most common tree species were freshly cut from trees without signs of insect or fungal damage. Three logs per tree species (9 objects altogether) were placed next to each other on the forest floor after removing the topmost layer of leaf litter to ensure that all logs had full soil contact. Alongside with these logs, three dried and barkless broomsticks of *Fagus sylvatica* (termed standardised logs in the following) were exposed. This standardised resource accounts for alternations in specialisation along latitude caused by changes in host phylogeny. Altogether 468 natural logs representing 131 different tree species and 156 standardised logs got exposed. Due to disturbance or lab problems, samples were lost, reducing the number of analysed logs to 426 natural and 105 standardised logs.

3.2.2 DATA SAMPLING

Logs were collected after two years; due to high decomposition rates and lost samples, some got collected after one or three years. Logs were dried at 40°C, and a 5 cm long sample was cut and stored frozen (-20°C). These samples were drilled lengthwise horizontally; the collected drilling dust was milled and homogenised (Retsch, Germany). Fungal genomic DNA was extracted from 200 mg of the sample with the Quick-DNA Fecal/Soil Microbe MiniPrep Kit (Zymo Research, Freiburg, Germany). The fungal ITS2 region was amplified during PCR with the primers gITS7 and ITS4 (Ihrmark et al., 2012). Amplicons were sequenced using the pipeline SEED 2 (Větrovský et al., 2018) and sequences clustered to OTUs at 97% similarity using UPARSE within Usearch (Edgar, 2013) or DADA 2 (Callahan et al., 2016). Species were assigned using BLASTn against UNITE (Version 9, Kõljalg et al., 2013) and GenBank. Lifestyles were assigned with FungalTraits (Põlme et al., 2020). To improve readability, the term “species” will be used for OTUs, albeit I am aware that OTUs are only putative species concepts.

3.2.3 DATA PREPARATION

All data preparation and analyses were performed in R 4.0.2 (R Core Team, 2022).

I excluded local singletons (setting cells in the community matrix with a value of 1 to 0), as these are likely PCR and sequencing errors that lead to an overestimation of rare species and overestimations of diversity estimates (Brown et al., 2015; Kunin et al., 2010). Besides an analysis of all saproxylic fungal species, I additionally analysed a subset of "wood saprotrophic" fungi based on the primary lifestyle by Põlme et al. (2020) as their relationship to the host should be stronger due to close co-evolution (see Chapter 1.2).

3.2.4 DATA ANALYSIS

First, I assessed whether the diversity of saproxylic fungi follows the latitudinal diversity gradient by calculating the gamma diversity of the boreal, temperate and tropical biome as sample-based rarefaction/interpolation curves (package *iNEXT*, Hsieh et al., 2016). Further, I calculated alpha diversity per log as species richness per log and tested it with a negative binomial linear mixed effect model against absolute latitude using the function *glmer.nb* (*lme4*, Bates et al., 2015). To account for repeated sampling at the plot level, I used plot ID as a random effect. If the latitudinal diversity gradient is present in saproxylic fungal diversity, both diversity indices should be lowest near the poles and highest near the equator.

To evaluate whether ecological specialisation is the possible cause of the expected latitudinal diversity gradient, I calculated the standardised two-dimensional Shannon entropy H_2' (hereafter "network specialisation", Blüthgen et al., 2006) for each fungi-host network per plot with the function *h2fun* (*bipartite*, Dormann et al., 2009). To do so, I created networks for each combination of natural logs of different tree species and the respective fungal species occupying these logs. H_2' is defined as the complementary specialisation of a given network (referred to as network specialisation) and ranges from 0 (complete generalism = all species use all resources) to 1 (complete specialisation = each species uses only one resource; Blüthgen, 2010). This and the fact that it is independent of network size and sampling effort makes it a good index to compare large or various data sets (Blüthgen et al., 2006). For the standardised logs, I calculated the standardised Kullback-Leibler distance d' (hereafter "resource specialisation", Blüthgen et al., 2006) with the function *specieslevel* (*bipartite*, Dormann et al., 2009). It has the same properties as the H_2', except that it calculates the specialisation on a specific partner within a given network. A d' of 0 would thus mean only generalist interactions; that is, all species interact with this partner, and all fungi inhabit this log. And a d' of 1 would thus mean specialist

interactions; fungal species only interact with this partner. I calculated d' for each standardised log put in each network created as described above. I calculated beta regression models for both indices against absolute latitude using the function *gam* (*mgcv*, Wood et al., 2016) using plot ID as a random effect in both models and log ID as an additional random effect for d'. If specialisation caused the latitudinal diversity gradient, I expect both indices to display a negative linear relationship with absolute latitude.

To illuminate tree diversity as an alternative cause of the saproxylic fungal latitudinal diversity gradient, I calculated the species richness per plot at an interpolated or extrapolated sample coverage of 75% (*iNEXT*, Hsieh et al., 2016) across all natural logs at a plot (hereafter "alpha diversity at plot"). I extracted local tree diversity from Liang et al. (2022) either at the plot location or, if not available, with a nearest neighbor approach with the *extract* (*raster*, Hijmans and van Etten, 2022). I calculated a negative binomial generalized linear model for expected species richness against tree diversity using *glm.nb* (*MASS*, Venables and Ripley, 2002). If tree diversity causes the latitudinal diversity gradient, I expect a positive relationship between expected species richness and tree diversity. Additionally, I again calculated gamma diversity per biome, yet against the number of unique tree species and not unique logs. If all curves share the same slope and the curves of boreal and temperate biomes stop earlier, this is another hint for tree diversity being the main driver of the latitudinal diversity gradient in saproxylic fungi. If the slope of the boreal biome curve is lowest and of the tropical curve highest, this hints towards specialisation as a cause.

3.3 OBJECTIVE 3: AT WHICH SCALE DO CONSERVATION CONCEPTS NEED TO BE IMPLEMENTED TO CONSERVE THE DIVERSITY OF MULTI-TAXONOMIC SAPROXYLIC COMMUNITIES?

This objective is structured in two approaches. First the assessment of relative importance of different scales for overall diversity using the BELongDead experiment, with a more in-depth description in Annex A.3. And second, the impact of land use on the specialisation and diversity of saproxylic species using the LandKlif experiment, in-depth described in Annex A.4. The location of the sites is displayed in Figure 2a & b.

3.3.1 STUDY SYSTEM

3.3.1.1 THE BELONGDEAD EXPERIMENT

For the first part of this objective, I again used data from the BELongDead experiment described in Chapter 3.1.1.3. To improve standardisation for the following analysis, logs of *Acer spp.* and *P. avium* were excluded, as they were infrequently distributed across the plots due to supply shortage during installation, resulting in a total of 297 analysed logs.

3.3.1.2 THE LANDKLIF EXPERIMENT

The LandKlif experiment was installed in April 2019. Deadwood was placed along a climate and land-use gradient in Bavaria, Germany, across an area of 300 x 300 km and on an 1000 m elevational gradient (Redlich et al., 2022). To do so, five climate zones (mean annual temperature from 1981 to 2010: < 7.5° C, 7.5–8° C, 8–8.5° C, 8.5–9° C, > 9° C; Deutscher Wetterdienst, 2020) and three land-use categories (near-natural, agricultural; urban) were defined and combined in 60 study regions, representing all 15 possible combinations of climate and land-use categories with four replicates each. Within each study region, three study plots (3 x 30 m) were created representing the three dominant habitat types (out of forest, grassland, arable fields, and settlements). As one region only included two plots 175 study plots were created Plots were standardised by using open areas with herbaceous vegetation (forest clearings, meadows, crop field margins, green spaces within settlements or cities). On each plot one dead-wood log (branches of length 50 cm and a diameter of 10 cm) of the four, locally dominant, tree genera were chosen: *Fagus sylvatica*, *Quercus* sp., *Picea abies*, and *Pinus sylvestris*. To exclude variations in dead-wood traits and "homefield advantage" for colonizers (Gholz et al., 2000)all deadwood branches originated from one area, the Steigerwald Forest in northern Bavaria. Branches were positioned vertically on a pole, with direct soil contact.

3.3.2 DATA SAMPLING

3.3.2.1 BELONGDEAD

3.3.2.1.1 BEETLES

Sampling took place annually from 2010 to 2017, using emergence traps (Gossner et al., 2016), mounted on each log 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 colonisation. The samples were collected in jars filled with 50% ethylene glycol, and

the insects were subsequently stored in 70% ethanol. Individuals were counted and identified to the species level.

3.3.2.1.2 FUNGAL FRUIT BODIES

The same fruit body data as described in 3.1.2.1 was used in this experiment. Fruit body abundance was estimated on a five-level scale, reflecting the percent coverage of a stem by fruit bodies (0 = no fruit body; 1 = <1% covered; 2 = 1–10% covered; 3 = 10–50% covered; 4 = >50% covered).

3.3.2.1.3 FUNGAL AND BACTERIAL METABARCODING

Sampling and sample processing was the same as described in Chapter 3.1.2.2. sequencing of fungal DNA (referred to as "mycelial fungi") also followed therein depicted steps. Bacteria and Archaea DNA was isolated from the same samples. For the PCR, the V4 region of the bacterial 16S rRNA gene was amplified using the primers 515F and 806r and sequenced on Illumina MiSeq. Raw data were processed using DADA2 (Callahan et al., 2016) implemented in the pipeline Dadasnake (Weißbecker et al., 2020) to calculate ASVs. The consensus algorithm was used to remove chimeras. As Archaea only accounted for 0.25% of the ASVs and sensitivity analysis for each kingdom resulted in similar results, both kingdoms are further referred to as bacteria.

3.3.2.2 LANDKLIF

3.3.2.2.1 ENVIRONMENTAL DATA

For each plot MAT was calculated as long-term mean from 1991 to 2020, provided by the German Meteorological Service (DWD) and described in Kaspar et al. (2013). Local temperature for each plot was measured in the shade at 1.1 m height as average day and night temperature (April – September 2019) with iButton thermologgers (type DS1923, Hygrochron iButton, Whitewater, WI, USA) on each study plot (average day and night temperature from April to September 2019). Furthermore, MAP was used as a co-variate to account for offset effects and assessed analogous to MAT. As land use types the four habitat types (forest, grassland, arable field, settlements) embedded within near-natural, agricultural, or urban landscapes were considered.

3.3.2.2.2 FUNGAL AND BACTERIAL METABARCODING

In all sites, wood samples for DNA metabarcoding were collected as drilling dust using a cordless drill. In September 2019, three holes (0.5 cm diameter) were drilled horizontally into the middle of each log, after bark was removed with a sterilized knife. Sampling material was

sterilized by flaming (Bunsen burner) and 99% ethanol. All samples per log were pooled and 5 g were pulverized using a swing mill and liquid nitrogen (MM400, Retsch, Haan, Germany). The DNA from the homogenised samples were isolated using 250 mg of the Quick-DNA Fecal/ Soil Microbe Miniprep kit (D6010) (Zymoresearch, Irvine, CA, USA) following the manufacturer's instructions. Fungal ITS2 region was amplified using the fITS7 and ITS4 primers (Ihrmark et al., 2012), including no template control samples and sequenced on Illumina MiSeq (Illumina Inc., San Diego, CA, United States). Bacterial V4 region (16S gene) was amplified likewise using 515F amd 806R pimers modified by (Caporaso et al., 2011; Caporaso et al., 2012). Chimeras were removed and OTUs were clusterd at 97% similarity using Mothur (Schloss et al., 2009). For taxonomy assignment of all fungal sequences the database UNITE ver. 6 (Nilsson et al., 2019) was used, using a blastn search (NCBI BLAST+ ver. 2.10.0, $E \leq 0.1$, percent identity $\geq 90\%$). For bacterial taxonomy the ribosomal database project release 11.4 (Cole et al., 2014) was used in the same way.

3.3.3 DATA PREPARATION

All data preparation and analyses were performed in R 4.0.2 (R Core Team, 2022).

I excluded local singletons from the metabarcoding data (setting cells in the community matrix with a value of 1 to 0), as these are likely PCR and sequencing errors that lead to an overestimation of rare species and overestimations of diversity estimates (Brown et al., 2015; Kunin et al., 2010). To improve readability, the term "species" will be used for OTUs and ASVs, albeit I am aware these are only putative species concepts.

3.3.3.1 BELONGDEAD

I accounted for sampling effort, which is varying sequencing depth, in fungal and bacterial metabarcoding data by rarefying (function *rrarefy*, package *vegan*, Oksanen et al., 2022) to the lowest number of reads. I then pooled the data for each species group across all sampling years, as handling each year individually did not yield different results (Annex A3).

3.3.3.2 LANDKLIF

Prior analyses, both species groups' community matrices were rarefied (function *rrarefy*, package *vegan*, Oksanen et al., 2022). Rarefaction depth was chosen for each species group individually (fungi: 1 345, bacteria: 373), based on histograms to identify samples with relatively low read sums, indicating low sequence quality. That way, 92% of all logs for the fungal analysis and 86% for the bacterial analysis were retained. These data were used for log-level analyses.

For analyses on plot level, I aggregated the rarefied community matrices per plot and excluded plots from further analyses which did not have logs of all four tree species (lost due to rarefaction). That way, 81% of the plots for fungi and 67% of the plots for bacteria were kept for further analyses.

3.3.4 DATA ANALYSIS

3.3.4.1 BELONGDEAD

In this setup, I used multiplicative beta diversity partitioning, which helps to disentangle the relative importance of beta diversity at differing scales to overall gamma diversity in a single approach (e.g., Gossner et al., 2013; Müller et al., 2013; Wilsey, 2010). In addition, it allows to consider different diversity indices and thus allows the comparison of rare, common and dominant species, which is helpful when deriving differently purposed conservation concepts (Gaston and Fuller, 2008). This can be done by the use of number equivalents of common diversity indices, so-called Hill numbers (Hill, 1973). They allow for the comparison of otherwise differently scaled diversity indices such as species richness (rare species), Shannon entropy (common species) and Simpson diversity (dominant species; Gotelli and Chao, 2013; Jost, 2007). Multiplicative diversity partitioning was performed using the function *multipart* in the *vegan* package (Oksanen et al., 2022). I partitioned the overall gamma diversity of each species group into two spatial scales, either comparing the beta diversity among the three sampling regions or the different forest stands and two host scales, either comparing the beta diversity among logs of different lineages (angio- and gymnosperms) or the eleven different tree species. Overall, I aimed to elaborate on whether space- or host-scale contributed more to the overall gamma diversity of each species group. Further, I determined which of the two scales within the respective spatial or host scale was more important for each scale. From that, I wanted to derive large-scale information on the important scales for nature conservation and whether a unified conservation concept can be applied to conserve all three species groups or whether different scales have to be targeted. Results were compared against the results of 1 000 null model calculations (*r2dtable*) to ensure significant differentiation from random assemblage.

3.3.4.2 LANDKLIF

Species richness was calculated on log- and plot level for each species group. To assess the effect of MAT, local temperature and land use a negative binomial generalized linear mixed effects model was calculated for each species group on each level with the function *glmer.nb*

(package *lme4*, Bates et al., 2015). MAT, local temperature, habitat type and landscape type were used as explanatory variables. For analysis on plot level, study region was used as a random effect. On log level the random effect was study plot nested within study region as random effect. MAP was used as a covariable. To further illuminate the effects of host tree species, habitat and landscape type, post hoc-test were calculated using function *glht* (package *multcomp*, Hothorn et al., 2008).

The effect of host tree species, MAT, local temperature and land use on community composition was analysed using Bray-Curtis dissimilarity matrices (function *vegdist*, package *vegan*, Oksanen et al. 2022) within a permutational multivariate analysis of variance (permanova, function *adonis2*, package *vegan*).

To identify whether specialisation decreases with increased land use intensity, network specialisation (H_2') was calculated on the rarefied community matrices at each plot using again the function *h2fun* (package *bipartite,* Dormann et al., 2009). Generalized linear mixed models (*glmmTMB*, package *glmmTMB*, Brooks et al., 2017) were calculated using MAT, local temperature and land use as explanatory variables, MAP as covariate and study plot as random effect.

4 MAIN RESULTS AND DISCUSSION

4.1 OBJECTIVE 1: HOW TO RAPIDLY ASSESS THREATENED FUNGAL DIVERSITY?

I compared the methods of fungal fruit body sampling and metabarcoding of different sampling intensities in their efficiency to detect endangered saproxylic fungal species (Annex A.1). Metabarcoding of low and high sampling intensity detected overall and per log more threatened fungi than fruit body sampling. Only about 10% of all species were exclusively detected by fruit body sampling – and 20% of all threatened species were detected by both methods (Fig. 3). These species were rarely detected simultaneously by both methods on the same dead-wood log. Thus, each method detected a unique set of species, and the method-specific detection prevalence appears to be species-specific. Furthermore, metabarcoding of both sampling intensities detected overall more threatened fungal species regardless of decay stage and whether the log was from an angio- or gymnosperm tree species. When compared to low-intensity metabarcoding, fungal fruit body sampling detected its highest numbers of threatened species in decay stages one and two, or two and three when compared with high-intensity metabarcoding (Fig. 4). These results also translated to the log level for metabarcoding of high sampling intensity. However, metabarcoding of low sampling intensity did not detect

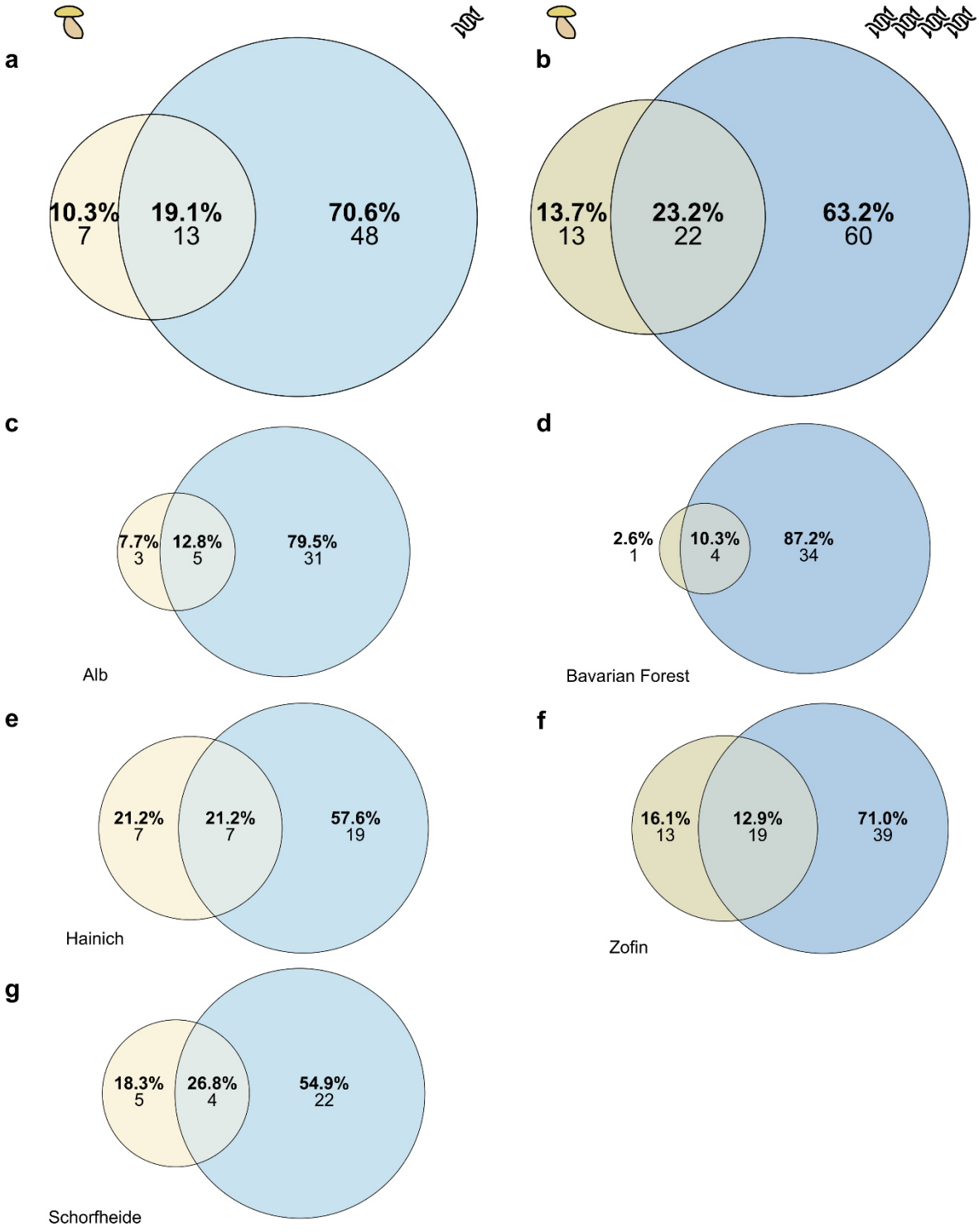

*Figure 3: Relative and absolute numbers of threatened species detected by fruit body sampling or metabarcoding with low (**a, c, e, h**) or high sampling intensity (**b, d, f**). Figure **a** and **b** display the overall comparison of fruit body sampling and metabarcoding of the respective sampling intensity. Figure **c – g** display the site-specific comparisons.*

significantly more fungal species than fruit body sampling on logs of decay stages two and three. Overall and per site, I found metabarcoding of both sampling intensities detected

threatened species on more log than fruit body sampling (Fig. 5). Compared with low-intensity metabarcoding, fruit body sampling detected more logs uniquely as when compared with high-intensity metabarcoding (Fig. 5).

Efficiency in detecting threatened species

Overall and among logs, I detected more threatened fungal species using metabarcoding data than fruit body data. This result indicates that metabarcoding is a viable option in detecting threatened fungal species and is in line with field studies that found a higher fungal diversity present as mycelium than present as fruit bodies (e.g., Frøslev et al., 2019; Ovaskainen et al., 2013; Saine et al., 2020; Blaschke et al., 2023). Currently, only one study directly compared the efficiency of both methods in detecting threatened species in soil. Frøslev et al. (2019) found only a slightly higher number of threatened fungi with metabarcoding than fruit body sampling, but no difference regarding their abundance. Differences in sampling intensity are likely not the cause of the greater differences in my study, as Frøslev et al. (2019) sampled 0.01% of the plot surface and took only 4 g out of 5 to 20 kg of soil to assess the mycelial fungal communities. In my study, even the high-intensity metabarcoding probably covered less than 0.01% of the surface of a log. Thus, this cannot explain the higher number of threatened species by metabarcoding. More likely are updated reference databases. As species detection in metabarcoding studies relies on correct assignments via databases like UNITE (Põlme et al., 2020), increases in the accuracy of such have a large impact on the study outcome. Frøslev et al. (2019) used UNITE v8.0 while I used UNITE v8.3. Hence, a higher taxonomic resolution can partly explain the contradicting results. Frøslev et al. also pointed out that a large part of their species detected uniquely via fruit body sampling had no reference sequence. This indicates that the regular updates of databases will enhance the usefulness of metabarcoding techniques for species conservation. Finally, I cannot rule out the possibility that the detection probability of methods within the different substrates of soil and dead-wood could differ, but I currently lack a compelling explanation for the potential variations in fructification patterns (such as frequency) or the quantity and distribution of mycelia in soil or dead-wood, which could impact detection probability.

Low share of species

I found the overall share of species numbers between the two methods to be relatively low at ~20 %; further, both methods rarely detected these species simultaneously on the same log. There appear several reasons for the observed patterns.

i) Detectability with a specific method might be related to species traits. For example, some fungal species inhabit the dead-woods' surface or bark. As bark or parts of the surface are removed prior to sampling to minimalize the contamination by nonviable species' DNA the detectability of surface related species might be lower for metabarcoding. This was not true in this study, as I detected more corticioid fungi with metabarcoding than via fruit body sampling. Further, the detectability of fungal species with small mycelia is lower, as the sample volume for metabarcoding is small. On the other hand does fruit body sampling miss species with small or inconspicuous fruit bodies more easily (Lõhmus, 2009). In conclusion, the detectability differences between the two methods may indicate trait-specific biases. The fact that each species seems to display specific detection prevalence for one method further supports this. In-depth analyses of these differences are necessary to elaborate on the differences in sampling efficiency of specific species or fungal groups between the two methods.

ii) Inappropriate sampling time might lower the number of fungal species detected via fruit body sampling, further enlarging the discrepancies between the both methods. Fructification depends on many intrinsic and extrinsic factors (Moore et al., 2008); species are thus missed if sampling time and unfavourable environmental conditions overlap. Moreover, species with fruiting phenologies outside of the main fruiting season or irregular fruiting patterns (Halme and Kotiaho, 2012) are also missed.

iii) Lastly, functional groups like mycorrhiza utilize dead-wood but do rarely fructify, and if, mainly in late decay stages (Mäkipää et al., 2017; Rajala et al., 2011; Tedersoo et al., 2003). Thus their detectability with fruit body sampling should be lower. Albeit I found several threatened fungal species assigned as mycorrhiza fructifying in all decay stages, metabarcoding detected much more.

Further, twelve fungal species had to be excluded prior analysis due to missing reference sequences. This indicates, that metabarcoding does currently underestimate fungal diversity and its efficiency will likely increase with updated data bases. However, as conservation requires accurate sampling a combined approach of both methods is still recommended to cover all occurring fungal species.

The impact of decay stage and tree lineage

Overall, metabarcoding of both sampling intensities was more efficient in detecting threatened fungal species in any decay stage. For metabarcoding of high sampling intensity these results translated to the log level. Metabarcoding of low sampling intensity and fruit body sampling

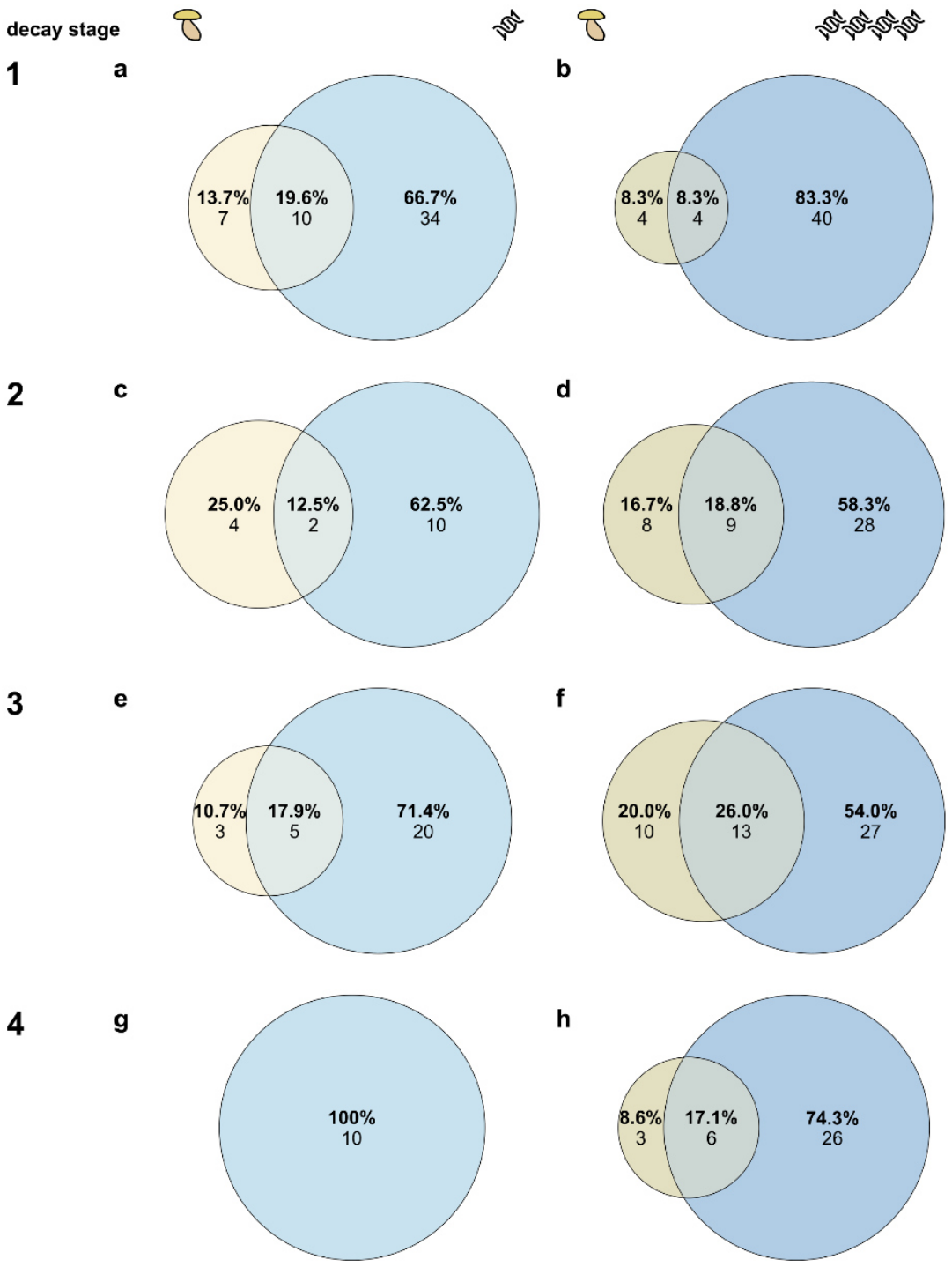

*Figure 4: Relative and absolute number of threatened species detected by fruit body or metabarcoding with low (**a, c, e, g**) or high sampling intensity (**b, d, f, h**) per decay stage.*

performed similar in decay stage two and three. Here two detectability patterns might intertwine and explain the differing results. As fungal species need time to acquire enough nutrients for fructification (Moore et al., 2008), the fructification frequency will increase with ongoing decay, resulting in higher detectability by fruit body sampling. In addition, with ongoing decay

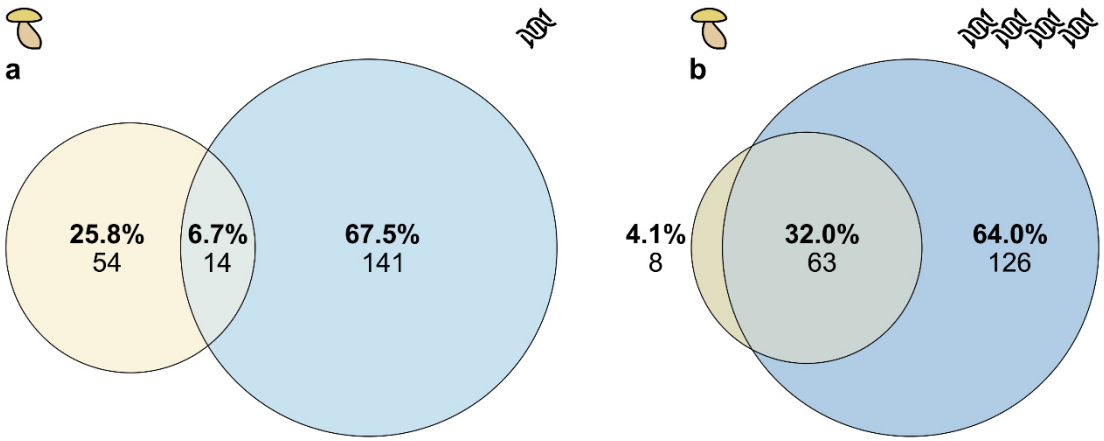

Figure 5: Number of unique and shared dead-wood logs inhabited by threatened fungi species detected by fruit body sampling or metabarcoding.

more mycelial fungi colonize the dead-wood log (Mäkipää et al., 2017; Rajala et al., 2011), this higher diversity might be undersampled due to small spatial coverage of low-intensity metabarcoding.

Metabarcoding detected more overall more species in angio- and gymnosperm dead-wood. Moreover, high-intensity metabarcoding detected similar numbers in both dead-wood types, while low-intensity metabarcoding detected less species in gymnosperms than in angiosperms. On the log level no such differences were apparent.

I conclude that metabarcoding of high sampling intensity is more reliable in detecting threatened fungal species in dead-wood and unaffected by dead-wood traits, than metabarcoding of low sampling intensity. Thus, it should be the preferred option fungal conservation.

The detected number of occupied logs

I detected threatened species on more dead-wood logs using metabarcoding of any intensity than fruit body sampling. The possibility of detecting threatened fungal species is thus higher when sampling random dead-wood logs. This higher detection probability of metabarcoding allows for more efficient sampling on a specific number of dead-wood objects, especially as resources in conservation metabarcoding allows for a rapid assessment of species diversity and abundance.

Implications for fungal Red Lists

The threat status of a species is noted in Red Lists, based on its population dynamics (IUCN, 2012). Usually, they are used to guide prioritisation of conservation guidelines, however for

fungi they are rather new (Mueller et al., 2022). Moreover, the depicted threat status of many fungi might not be accurate, as these are assessed via fruit body sampling. Fungal Red Lists might benefit from the overall good suitability of metabarcoding in detecting fungal species present as mycelia (Blaschke et al., 2023; Frøslev et al., 2019).

Metabarcoding can detect fungal species not producing conspicuous fruit bodies, whose threat status can then be evaluated and included in Red Lists, ultimately leading to a more comprehensive fungal conservation. Moreover, metabarcoding gives additional information on abundance and distribution of fungal species. Current fungal Red Lists are biased, as fruit body formation is weather dependent (Sakamoto, 2018). Further it is arguable whether the threat status of a species be assessed only by sexual reproduction events (fruit body formation), while the main part of the fungus, the mycelium, spreads through the substrate, competes over and acquires nutrients, and plays a more pivotal role in the local survival of the fungi (Boddy et al., 2008). Metabarcoding would be less biased towards environmental factors and could give additional information on ranges and distributions of fungi (van der Linde et al., 2009).

This is not to say that metabarcoding should completely replace fruit body sampling, as it is not without flaws and introduces new problems, but again be used complementary. While many mycelial fungi can be found fructifying in close proximity (Runnel et al., 2015), it is not known how often fungi need to sexually reproduce in order to keep vital populations or whether mycelial spread to other suitable habitats and enduring unfavourable climatic conditions as mycelia (Treseder and Lennon, 2015) is enough to sustain vital populations. The lower sensitivity of mycelial fungi to environmental factors (Chapter 4.3) could result in the case of, poor environmental conditions preventing fruiting body formation and necessary sexual reproduction, while metabarcoding still detects these species, which would ultimately result in an extinction debt (Tilman et al., 1994).

Implications for conservation

Metabarcoding, especially of high sampling intensity, has been proven to be an efficient and reliable technique to detect threatened saproxylic fungi. With further increase of reference databases, its accuracy and efficiency in species detection will increase further. Metabarcoding improves abundance estimates, allowing further information on species distributions. Consequently, this approach appears to be a valuable asset in advancing fungal Red Lists. Firstly, it allows for the inclusion of previously overlooked species with inconspicuous sexual characteristics or no fruit bodies through fruit body assessments. Secondly, it facilitates the revaluation of species abundances that were previously assessed solely based on fruit bodies.

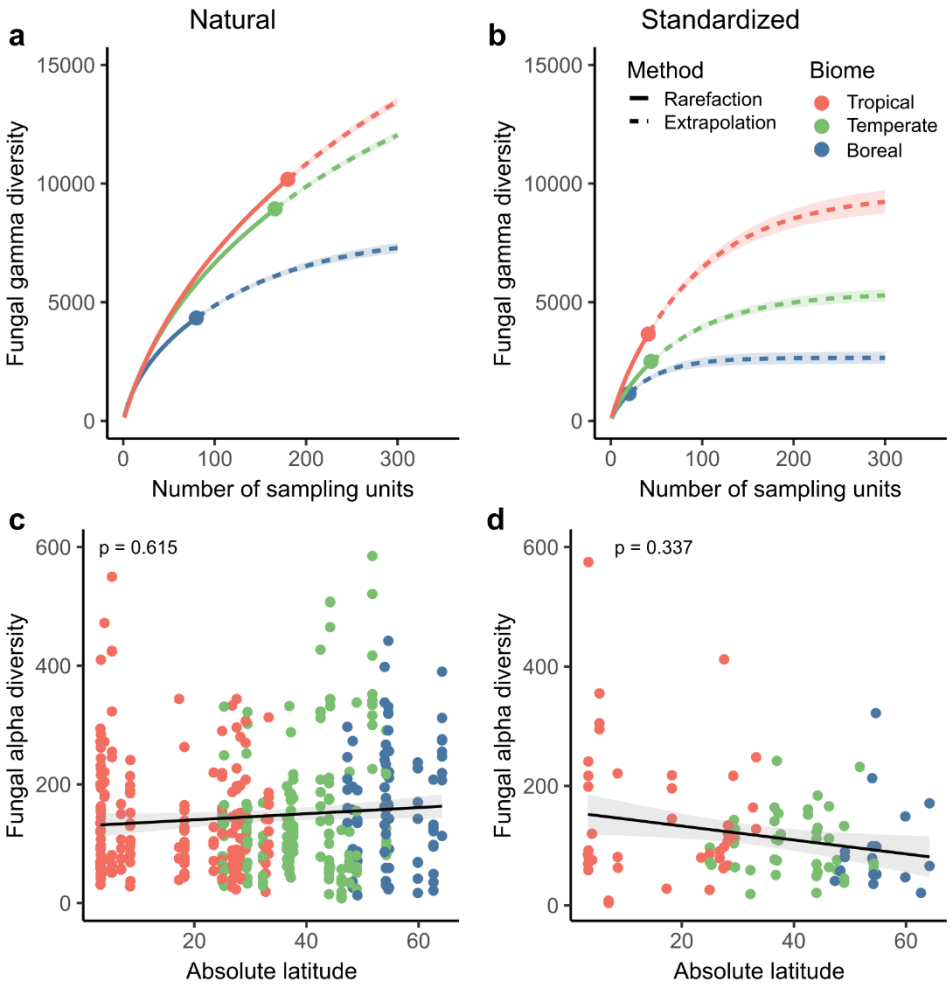

*Figure 6: Main results for the latitudinal diversity gradient in wood-decaying fungal diversity, studied as gamma diversity (**a**, **b**) and alpha diversity (**c**, **d**) along absolute latitude for the natural (left) and the standardised logs (right). Black lines indicate the regression with confidence intervals. Stated p-values correspond to the respective negative binomial generalized linear mixed effect models.*

However, it is important to note that some fungal species were only recorded as fruit bodies, some still miss reference sequences, and both techniques seldom identify the same species simultaneously on the same log. Consequently, relying solely on metabarcoding may lead to the omission of certain threatened fungal species from the overall assessment. For the most comprehensive and accurate assessment, it is therefore recommended utilising both methods in conjunction.

4.2 OBJECTIVE 2: IS THERE A LATITUDINAL DIVERSITY GRADIENT IN GLOBAL SAPROXYLIC FUNGAL DIVERSITY, AND CAN IT EITHER BE EXPLAINED BY INCREASED SPECIALISATION OR TREE SPECIES DIVERSITY?

I analysed metabarcoding fungal data from a global dead-wood experiment to study the global diversity of saproxylic fungi and the mechanisms driving the patterns. In this experiment, 52 plots were installed worldwide, and similar-sized dead-wood of three locally common tree species and three logs of a standardised tree species (*Fagus sylvatica*) were placed. I studied the change of fungal diversity on several scales and specialisation on plot level with latitude and tree species richness to see whether saproxylic fungal diversity follows the patterns of the latitudinal diversity gradient. Further, I examined two hypotheses as the cause of this potential pattern. The ecological specialisation hypothesis expects an increase in ecological specialisation and, thus, higher niche packing in tropical areas (see Chapter 1.2). The tree species diversity hypothesis assumes that the diversity of host tree-dependent species groups increases with tree species diversity (niche space, see Chapter 1.2). I found an increase in gamma diversity against the number of logs per biome from the boreal (7,289 fungal species) to the tropics (13,466 fungal species). Yet, alpha diversity per log did not increase with absolute latitude (Fig. 6a & c). These results were consistent for the standardised logs as well (Fig. 6b & d). The specialisation of fungal networks was generally high (mean H2' 0.79 ± 0.12 (sd)) and increased towards the equator, yet not significantly (Fig. 7a). The resource specialisation on standardised logs was also high (mean d' 0.8 ± 0.17 (sd)) but did not change significantly with latitude (Fig. 7b). Alpha diversity on plot level did increase significantly with increasing tree species diversity (Fig. 7c). To further illuminate the impact of tree species diversity, I examined gamma diversity per biome against the number of sampled tree species (Fig. 7d). Now gamma diversity did not significantly differ between tropical and temperate biomes, but both biomes' gamma diversity significantly differed from the low gamma diversity in the boreal biome.

Latitudinal diversity gradient

I found an overall increasing gamma diversity of saproxylic fungi from the poles towards the equator. Thus, saproxylic fungi follow the latitudinal diversity gradient, like many other species groups (Hillebrand, 2004). This result is especially important for our global understanding of species diversity, as these former studies were mainly conducted on macroorganisms and microbial diversity is largely underrepresented, despite their high diversity and important functional roles (Escalas et al., 2019). Yet, I did not find an increase in diversity on each studied

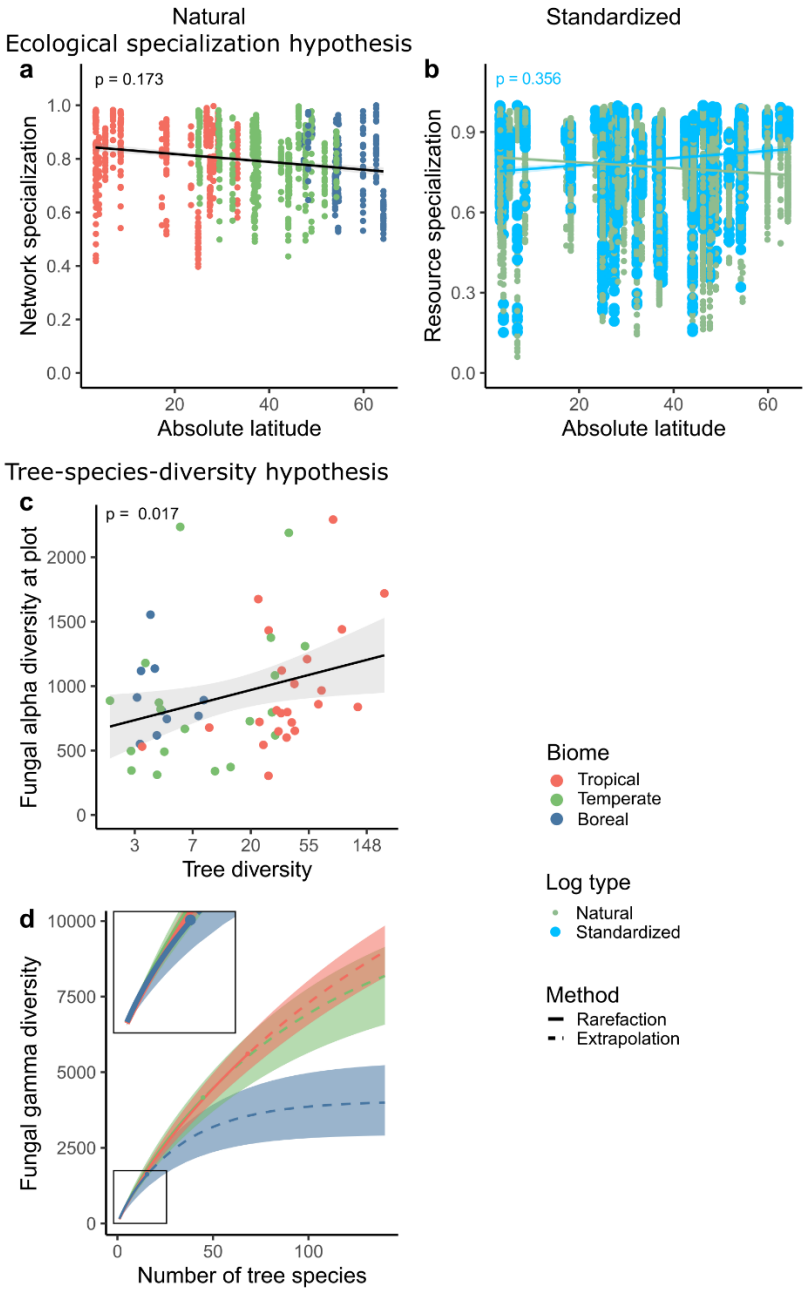

*Figure 7: Main results for the ecological specialisation hypothesis (**a, b**) and the tree-species-diversity hypothesis (**c**) in saproxylic fungal diversity for the natural (left) and the standardised logs (right). **a** displays the network specialisation against absolute latitude. **b** shows the resource specialisation against absolute latitude as the specialisation of fungi on the standardised log (blue)and the mean specialisation on the natural logs (green) on one plot. **c** shows the estimated fungal alpha diversity at plot level on a sample coverage value of 75% against local tree species diversity. **d** displays the fungal gamma diversity against the number of unique tree species per biome. Lines in **a**, **b**, and **c** display the regression with respective confidence intervals. Stated p-values correspond to the respective models.*

scale. Alpha diversity at the log level did not increase towards the equator, which highlights the importance of the studied grain sizes. Only the incorporation of different grain sizes allows for the assessment of all aspects of global diversity patterns within one study. The contrasting results on small grain size, i.e., log level, might be explained by resource availability. Dead-

wood represents a distinct resource with a limited niche space within. Thus, competition among saproxylic species is high, and priority effects by early colonizers (Sakamoto, 2018) and physical barriers, so-called demarcation lines (Boddy, 2000; Boddy and Hiscox, 2016) limit the establishment and spread of fungal species within dead-wood. The niche space within a dead-wood log appears of similar size across the globe, thus not allowing for a higher alpha diversity on similar-sized dead-wood in the tropics. The differences in gamma diversity in the tropics are explained by a higher beta diversity among logs in tropical biomes in contrast to logs in temperate or boreal biomes (Annex A.2).

So far, the only studies focusing on fungi and the latitudinal diversity gradient concerned soil-inhabiting fungi (Tedersoo et al., 2014; Větrovský et al., 2019). However, both studies only examined alpha diversity and found inconsistent results. Tedersoo et al. (2014) confirmed an overall latitudinal diversity gradient. Further, the results differed when studying each functional group separately. Pathogenic and saprotrophic fungal diversity, groups antagonistically linked to their host plants, displayed an increase of alpha diversity towards the equator. Saproxylic fungi can also be seen as plant antagonists since they evolved to bypass the physico-chemical defence of plants in order to access these resources (Floudas et al., 2012). Thus, my results on alpha diversity of saproxylic fungi contradict patterns of plant-antagonistic soil fungi, indicating that generalisations on diversity patterns of different functional guilds are impossible. The observed differences might be due to different assembly processes shaping fungal communities in soil and dead-wood (Bässler et al., 2014; Beck et al., 2015), as the already mentioned competitive interactions might be stronger in dead-wood than in soil. Contrastingly, Větrovský et al. (2019) found a reversed latitudinal diversity pattern in their meta-analysis of common soil fungi, with higher alpha diversity at higher latitudes. This observation might be due to different sensitivity towards environmental factors in species groups of different abundance (see Chapter 4.3). The contradicting results of Tedersoo et al. (2014), Větrovský et al. (2019) and our study further highlight the necessity of considering different spatial and taxonomic grain sizes within one study.

The ecological specialisation hypothesis

As network specialisation did not change significantly with latitude, I have to neglect the ecological specialisation hypothesis and increased specialisation towards the equator as the global mechanism of the observed latitudinal diversity gradient. Thus, my results further strengthen the assumption that the ecological specialisation hypothesis is not generalizable (Moles and Ollerton, 2016). It might have been possible that the evolution and distribution of

host trees could impact the observed specialisation pattern as the share of angiosperm tree species decreases from the boreal to the tropical biome. Former studies found that saproxylic fungi primarily specialize in the deep phylogenetic split between angio- and gymnosperms (Baber et al., 2016; Krah et al., 2018; Purhonen et al., 2017; Yang et al., 2021). I conclude that saproxylic fungi mainly specialize on tree species, and the phylogenetic distribution of host trees does not influence their diversity pattern, as further analyses of mean host phylogenetic distance did not significantly influence the specialisation and a reiteration of the data set using only Angiosperm trees did not change the observed pattern (Annex A.2).

The tree species diversity hypothesis

Alpha diversity on the plot level increased significantly with tree species diversity, thus supporting the tree species diversity hypothesis. Hence the increase of tree species towards the equator (Liang et al., 2022) causes the observed patterns in global saproxylic fungal diversity, as found or suggested in other interaction studies (Novotny et al., 2006; Zanata et al., 2017). This result finds further support in the re-analysation of gamma diversity per biome against the unique number of tree species per biome. The species accumulation curves of the tropical and temperate biome displayed a similar slope and overlap, suggesting equal specialisation. The higher number of tree species thus causes higher gamma diversity in the tropics. In addition, the species accumulation curve of the boreal biome displayed the same slope yet levelled off early, indicating a significant difference from the other two biomes. This discrepancy suggests a decreased ecological specialisation in the boreal areas, negatively impacting saproxylic fungal diversity. Thus, the ecological specialisation hypothesis might not be the primary driver of global saproxylic fungal diversity but partly explains lower diversity in higher latitudes.

4.3 OBJECTIVE 3: AT WHICH SCALE DO CONSERVATION CONCEPTS NEED TO BE IMPLEMENTED TO CONSERVE THE DIVERSITY OF MULTI-TAXONOMIC SAPROXYLIC COMMUNITIES?

In a first step, I analysed the relative importance of beta diversity of multiple saproxylic groups (beetles, fungal fruit bodies, mycelial fungi, bacteria) on several scales for overall gamma diversity using a field experiment (Annex A.3, published as: Rieker et al., 2022). I also compared the differences across scales for rare, common and dominant species. The aim was to assess the diversity of all three species groups on two spatial and host scales and determine whether a unified spatial or host scale conservation concept is sufficient to protect the three

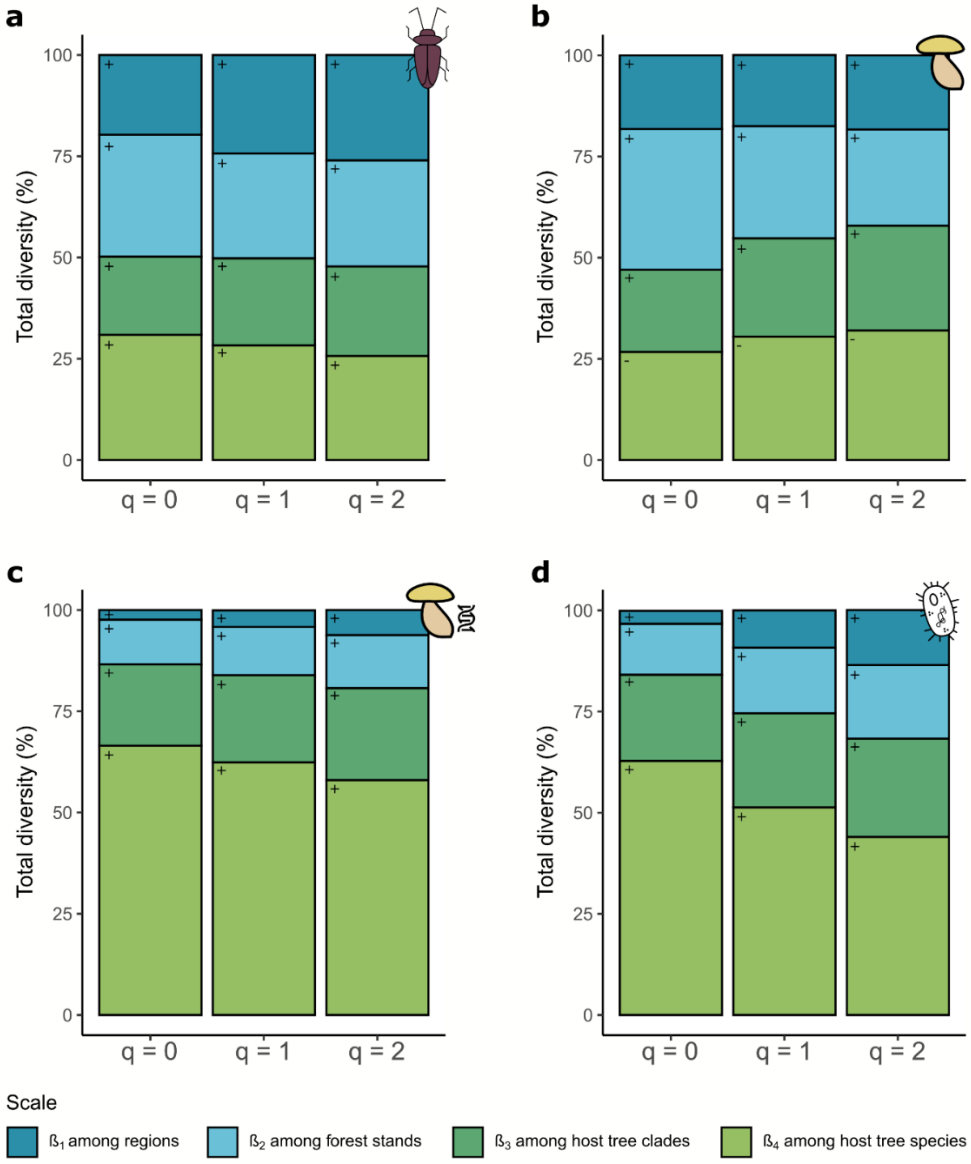

*Figure 8: Stacked bar plots of multiplicative diversity partitioning comparing the relative importance of the beta diversity on different scales for the total diversity of **a** saproxylic beetles, **b** fungal sporocarps, **c** microbial fungi and **d** bacteria. Presented are the number-equivalents of species richness (rare species, q = 0), Shannon entropy (typical species, q = 1), and Simpson diversity (dominant species, q = 2). Note that all observed beta-diversity values are significantly larger (+) or smaller (-) expected based on null modelling. Adapted from Rieker et al. (2022).*

species groups. As spatial scales, I used a regional scale on a macroclimatic gradient among the study regions and a local scale with forests of different management systems standardised across regions. As host scale, I compared the tree lineage scale (angio- vs gymnosperm) and tree species scale. I found that spatial and host scale were almost equally important for the overall gamma diversity of beetles and fungal fruit bodies (Fig. 8 a & b). For mycelial fungi and bacteria, the host scale was way more important than the spatial scale, whereby the results were more pronounced for mycelial fungi than bacteria (Fig. 8 c & d). Within the spatial scale,

the local scale was almost always more important than the regional scale for all species groups. Within the host scale, the species scale was more important than the lineage scale for all species groups. Species scale was most important for mycelial fungi and then bacteria. These results varied among the different diversity indices. Host scale seems more important for rare species than dominant ones, except fungal fruit body diversity, displayed different patterns. These results were not as distinct for beetles and their diversity was approximately equally distributed among all scales.

In a second step, I studied the impact of climate and land use intensity on the diversity and specialisation of mycelial fungi and bacteria using an experimental set up in Bavaria, Germany (Annex A.4, published as shared first author as: Englmeier et al., 2023). Fungal richness at plot level was not determined by climatic variables (Fig. 9a & b) and only slightly higher in near-natural than urban habitats (Fig. 9j), however, the explanatory power of this model was generally low. Bacterial richness at plot level was positively related to MAT but negatively to local temperature (Fig. 9c & d) and higher in grassland and arable than in forest habitats (Fig. 9k). Additionally, it was positively related to MAP. The overall performance of the model was higher than for fungi, but still low. Results for both species groups largely translated to the log level, expect that here fungal richness a was negatively related to MAP. Bacterial richness was higher in grasslands than forests. In addition, large differences in species richness of both species groups were found between dead-wood of different tree species. Community composition of both species groups was under strong influence of the tree species, this effect was larger for fungi (Fig. 10a & b). Climatic and land use variables had no to minor influence. MAP was more important for bacterial than fungal community composition. Specialisation was higher in fungal than in bacterial networks (Fig. 10c). Fungal specialisation was not influenced by climate or land use. Bacterial specialisation was higher in agricultural than near-natural landscapes (Fig. 9p) and positively related to MAP.

Spatial vs host scale

The overall dichotomous results of the first study show that implementing a generally applicable conservation concept on one scale is impossible for the studied saproxylic species groups. Beetles and fungal fruit bodies required both scales equally, while mycelial fungal and bacterial diversity was stronger determined by host scale. This was confirmed by the second study, indicating that environmental variables did not impact mycelial fungal and bacterial communities as much as host related differences. Hence, a combined approach, focusing on spatial- and host scale, seems to be the basis for a comprehensive conservation of saproxylic

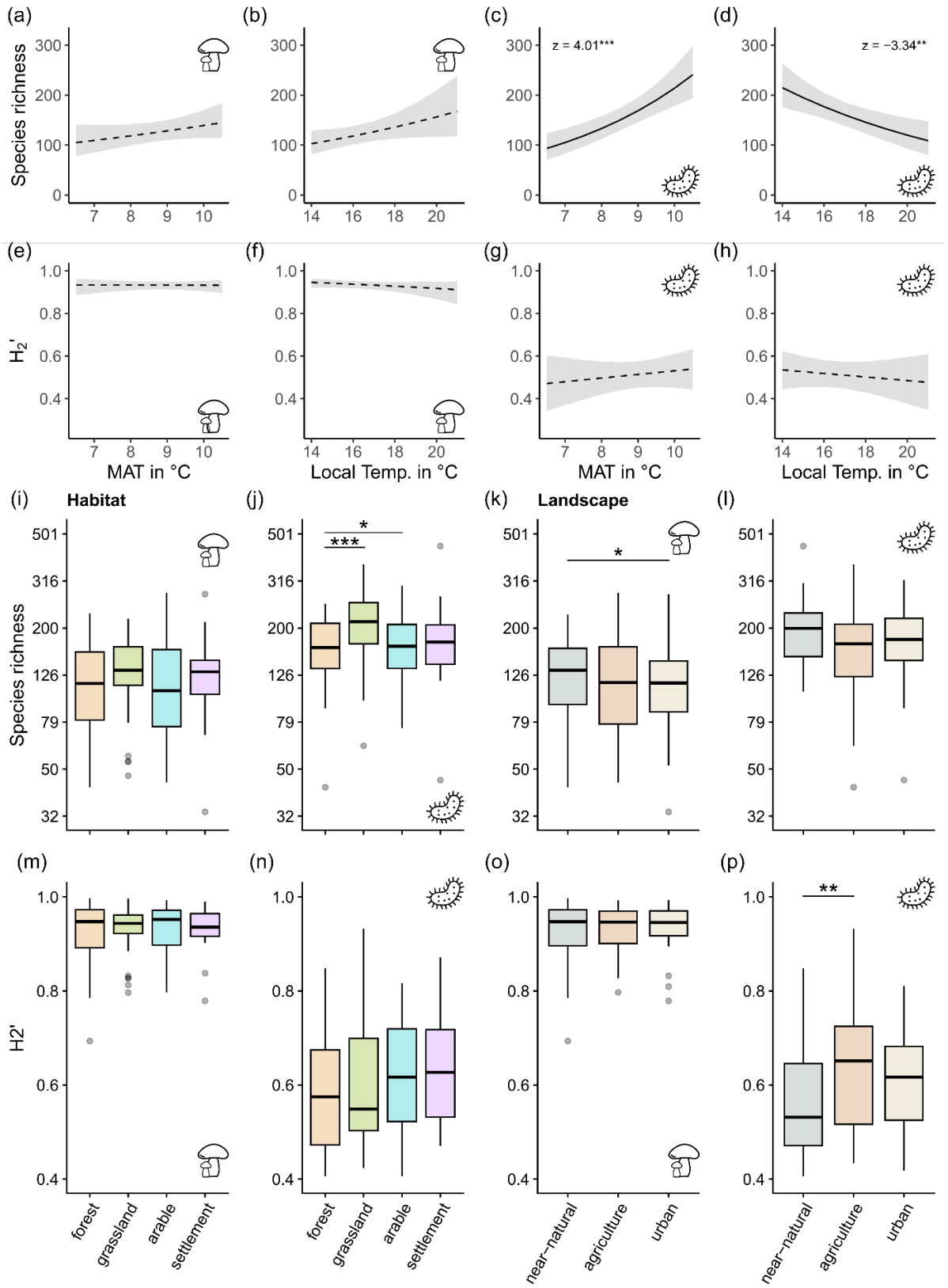

*Figure 9: Regression curves for **a & b** mycelial fungal and **c & d** bacterial species richness and **e & f** fungal and **g & h** bacterial community specialisation at plot-level predicted by the respective models against MAT (**a, c, e & g**) and local temperature (**b, d, f & h**). Dashed lines indicate non-significant changes, reported values are z-values. Boxplots show **i & k** fungal and **j & l** bacterial species richness (log10 transformed) and **m & p** fungal and **n & p** bacterial specialisation among habitat (**i, j, m, n**) and landscape types (**k, l, o, p**) at plot level. Asterisks indicate significant values (* =p <0.05, ** = p <0.01, *** = p <0.001). Adopted from Englmeier et al. (2023).*

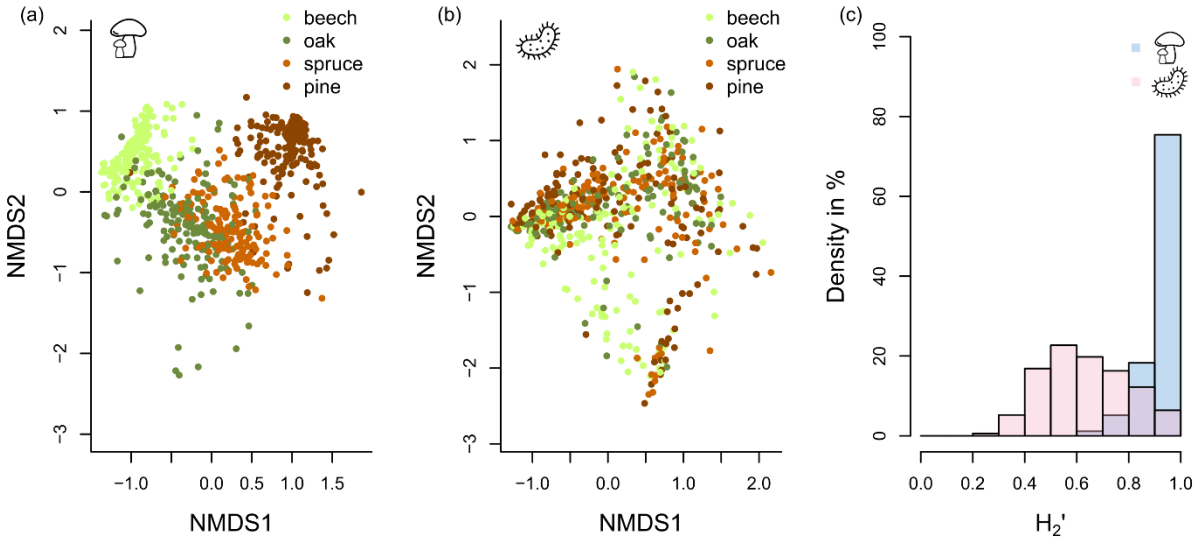

*Figure 10: Ordination plots for **a** fungi (stress = 0.146) and **b** bacteria (stress = 0.150) on log level sorted by tree species. **c** Frequency of observed H_2' values in percent for fungi (blue) and bacteria communities (red). Adopted from Englmeier et al., (2023).*

species. Furthermore, these results show the importance of multi-functional diversity assessments to fully protect all affected species groups and prevent harm to species excluded in such (Gaston and Fuller, 2008).

Regional vs local scale

Within the spatial scale, beta-diversity of all species groups was higher among forest stands than among regions, especially for beetles and fungal fruit bodies. I ruled out dispersal limitation as an important driver of beta diversity, as none of the studied species groups seems to be dispersal limited on the studied scales (Bae et al., 2021; Bovallius et al., 1978; Müller et al., 2020). Rather the differences in forest stand structure and dominant tree species, determined by forest management, can explain the beta diversity on this scale. I studied beech, spruce and pine-dominated forest stands, which result in different forest microclimates through their differing vertical structure and canopy openness (Juchheim et al., 2019). The studied beech forests are darker and thus colder and more humid than the spruce or especially pine forests (Boch et al., 2013). The effect of forest stand microclimate, especially pronounced for beetles, has already been demonstrated by several other studies (e.g., Abrego and Salcedo, 2014; Krah et al., 2018; Hoppe et al., 2015; Müller et al., 2020). The small importance of local scale for mycelial fungi and bacteria finds further support in the second study. Management outside of forests, i.e., land use, had no to little importance on the diversity and community composition of these to study groups. I assumed a decline in diversity caused by a filtering of specialists due

to increased disturbance (van Tienderen, 1991). Specialisation of both species groups was not or only little influenced by land use and hence probably not the driver of potential differences in diversity. An additional influence on the diversity across forest stands might be the dead-wood volume in the surrounding forests, which is higher in the less intensively managed forests (assessed by Schall et al., 2018). Higher dead-wood volumes have a positive influence on the diversity of beetles (Seibold et al., 2017) and fungal fruit bodies (Abrego and Salcedo, 2014; Edman et al., 2004), albeit having no positive effect on the latter in the immediate surrounding (0.1 ha, Krah et al., 2018). For mycelial fungi bacteria, we are still lacking such studies. The higher mycelial fungal richness in near-natural than urban landscapes of the second study could also be explained with limited dead-wood volumes in urban landscapes, which harbour less trees and are cleared from dead-wood more frequently.

On the regional scale, the substantial differences in diversity for beetles, fungal fruit bodies and dominant bacteria are probably caused by (i) the macroclimatic gradient within the study design (6°C to 8.5°C MAT, 500 mm to 1,000 mm MAP). Again, this finds some support in the second study, as bacterial, but not mycelial fungal diversity, community composition and specialisation were under some influence of MAP. A decline of specialisation with MAP could be due to habitat filtering by environmental heterogeneity (higher drought probability), which negatively impacts diversity. Further, MAT had a positive impact on bacterial diversity at log and plot level, indicating that on a stronger gradient, climate becomes more important for bacteria, while mycelial fungi still did not show any response. (ii) A difference in regional tree species composition. Forest management cultivated pine in the northeastern and spruce in the middle and southwestern parts of the study area, which impacts the local species pool and, again, forest microclimates. The low relative importance of regional differences (climate) for overall diversity of fungal mycelia and bacteria is supported by the second study, showing low to no impact of climatic variables on diversity and community composition.

Tree lineage vs tree species scale

On the host scale, the beta diversity among tree species was always higher than among host tree lineages. This indicates a strong specialisation in dead-wood of specific tree species. The second study incorporated in this Chapter also identified the tree species as the main driver of diversity and community composition mycelial fungi and bacteria. The higher specialisation of mycelial fungi over bacteria in both studies is congruent with former research (Lee et al., 2020; Moll et al., 2021), indicating a high dependency of both species groups on tree species.

Beetle and fruit body diversity also differed considerably among host tree lineages. These results support earlier findings of higher host specificity in fungi and bacteria than in beetles (Moll et al., 2021; Müller et al., 2020; Odriozola et al., 2021; Thorn et al., 2018; Wende et al., 2017). This is not surprising, as fungi and bacteria co-evolved as decomposers within their host tree species (Floudas et al., 2012) and adapted to the specific physico-chemical properties of each tree species (Kahl et al., 2017). Beetles only rely partly on dead-wood, as they spend part of their lifecycle outside the wood under stronger environmental influence (Ulyshen, 2018). My results further indicate that the previously assumed host specificity of saproxylic species on the tree lineages is a host specificity on tree species (Hoppe et al., 2015; Kahl et al., 2017; Krah et al., 2018; Moll et al., 2021; Wende et al., 2017).

Further, the lower host specificity of fungal fruit bodies than mycelial fungi is surprising. This could be due to the stronger effect of environmental factors outside dead-wood affecting fruit body formation (Sakamoto, 2018) and detected diversity, like in beetles. Another explanation is the higher number of species in mycelial fungal communities than in fruit body communities, which can result in the detection of a stronger fungi-host relationship. These findings deserve further attention, especially since they contradict former studies detecting similar responses of fungal fruit bodies and mycelial fungi to environmental gradients (Frøslev et al., 2019; Saine et al., 2020).

Rare, common and dominant species

The relative importance of each scale for overall diversity was generally consistent across rare, common and dominant species within each species group. Studying the responses of differently abundant species is important for conservation (Gaston and Fuller, 2008), as rare species are usually targets of nature conservation, but highly abundant species often drive ecosystem processes (Winfree et al., 2015). To ensure their continuous execution, protecting common and dominant species is crucial. In addition, the diversity of rare species seems under a stronger influence of host-related differences than common and dominant ones. This indicates a stronger host specificity within rare species, as already found for fungi (Abrego et al., 2017; Nordén et al., 2013). The diversity of fungal fruit bodies displays a reversed pattern, possibly due to a higher susceptibility towards environmental factors, as discussed above for fungal fruit bodies.

Implications for forest management

In summary, a unified conservation approach for protecting saproxylic diversity in temperate forests, focusing purely on spatial or host scale, is not implementable. This highlights the

importance of evidence-based multi-taxonomic studies to derive conservation methods not to harm non-target species groups. In concrete terms, this means that comprehensive conservation of saproxylic diversity requires supraregional concepts that promote heterogeneous forest structures, i.e., different management systems with heterogeneous tree stands. Within these stands or habitats of other land use, dead-wood of as many native tree species as possible must be accumulated; these tree species should comprise out of angio- and gymnosperms.

5 SYNTHESES AND FUTURE PERSPECTIVES

5.1 FUNGAL DATABASES AND SAMPLING

The advance and advantages of metabarcoding methods for fungal ecology and conservation have become apparent from the various studies published in the last decades and not least the four included in this dissertation. The identification of mycelial fungal diversity shed light on the immense diversity and allowed for the first global assessments of soil fungal diversity (Tedersoo et al., 2014; Větrovský et al., 2019) and now also in dead-wood (Chapter 4.2) and the environmental influences on it. The comparability of both methods in assessing environmental sensitivity and detectability of fungi is not fully resolved, as some studies yielded similar (Frøslev et al., 2019; Saine et al., 2020), and I found differing results (Chapter 4.3) for both methods. The latter results could be attributed to the large differences in sampled species numbers (Annex 3) and partly to the fact that the methods detect different species and individuals (Chapter 4.1). As both methods' ability to detect specific fungi is not yet understood, differences among studies might occur.

Besides the methodological restrictions (Chapter 1.1), one main problem is that large parts of fungal diversity are still unknown (Baldrian et al., 2022). Most of the fungal species we know were described based on a fruit body, but many lack sequences in reference databases (Chapter 4.1, Nilsson et al., 2006). Other species have a deposited sequence, as they were sampled once or several times via metabarcoding, but miss a taxonomic annotation and voucher specimen (Lücking et al., 2020; Abarenkov et al., 2022). This large research gap limits the usefulness of both methods, thus reducing the explanatory power of ecological studies. A pure analysis of the overall fungal community composition and its drivers on the OTU or ASV level might be generally helpful. Nevertheless, within the fungal community, different taxonomic groups or functional guilds display different sensitivity to environmental variables (e.g., Tedersoo et al., 2014). Without a deeper taxonomic resolution, the annotation to functional guilds is not possible, and current studies must involuntarily exclude a large part of fungal communities

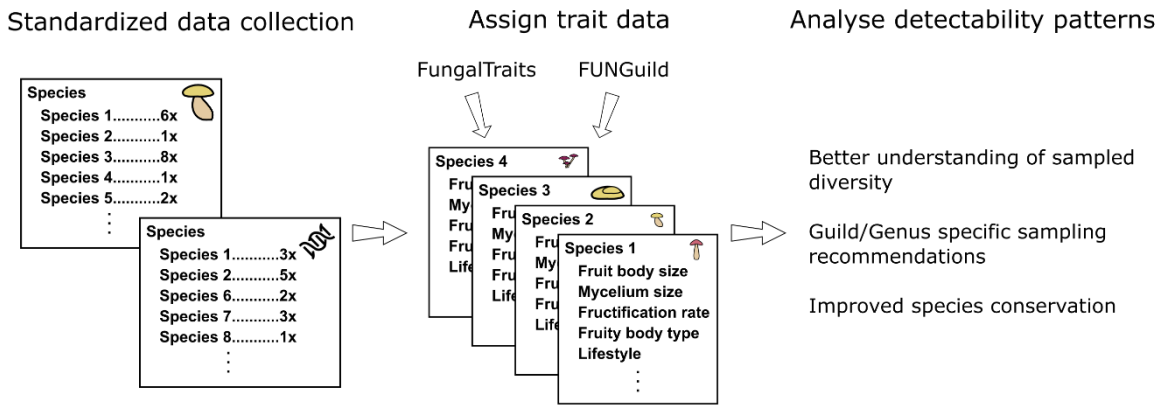

Figure 11: Prospect on further analysis of fruit body and metabarcoding data to further enhance the understanding of both sampling methods and improve species monitoring and conservation.

limiting the generalisation of their results. This research gap is especially pronounced in hyper-diverse areas like the tropics, which are largely understudied regarding saproxylic species (Seibold et al., 2015). These limitations also led to the decision to include all fungal OTUs in Chapter 4.2 (but see Annex A.2) instead of analysing different guilds separately, as large parts of fungal diversity, especially in the tropics, would have been excluded. To improve our taxonomic knowledge and update databases, programs like the "Top 50 most wanted fungi" (Nilsson et al., 2016) try to animate mycologists to help discover the species to very abundant sequences. Other helpful concepts are the demand for a sequence for every new taxon described (Aime et al., 2021) or the somewhat controversial description of uncultured fungi solely by sequencing data (Lücking and Hawksworth, 2018; Nilsson et al., 2023; Thines et al., 2018).

Such advances are necessary to improve the results of mycological studies such as those included in this dissertation. This improvement allows for a better understanding of the results on a taxonomic or functional level, like the different detectability of certain species via fruiting body sampling or metabarcoding. For such analysis, setups used in Chapter 4.1 could be extended to include all sampled fungal species. Assigning traits via trait databases could then help unravel the detection patterns of each method and guilds/species (Fig. 11). At the same time, further studies need to be conducted to illuminate the efficiency of both methods under different environmental conditions and spatial and temporal coverage. That way, we can adapt fungal studies to deepen our understanding of the sensitivity of different fungal groups towards influences like forest management. By increasing our knowledge about both methods and the diversity they sample, we can investigate fungal species, their populations and distribution to assess their threat status and the hazards cause and further improve fungal conservation.

5.2 CHALLENGES UNDER GLOBAL CHANGE

Understanding the increasing impacts of global change on saproxylic species is important to enhance our understanding of its impact on carbon and nutrient cycling is already a common topic (Bradford et al., 2014; Pietsch et al., 2019; Seibold et al., 2021). Biological processes like decomposition tend to increase with increasing temperatures (Seibold et al., 2021). As temperatures are likely to increase with ongoing global change (IPCC, 2022), decomposition processes are likely to accelerate as long as humidity is not limiting (Seibold et al., 2021), resulting in lower carbon sequestration and higher fluxes to the atmosphere, which might have positive feedback on climate change. Further, the impact on long-term nutrient cycling is not well understood. To illuminate the impact of global change on carbon and nutrient cycling, studying its effects on the main decomposers is crucial. Based on the results from Chapter 4.2 and Chapter 4.3, two effects of global change on saproxylic diversity can be derived: i) the direct impact of altered climate on species distribution, ii) the indirect impact of changing host tree species distribution.

Direct effects of increased temperature and drought probability

Species distribution depends on the climatic niche they occupy; changing climate due to global change thus might lead to range shifts of species (Root et al., 2003). The extent and severity of this effect depends on the climatic sensitivity of these species. Chapter 4.3 showed that this sensitivity is highest in beetles and fungal fruit bodies, followed by bacteria and least important for mycelial fungi. The temperature increase is thus more likely to affect the diversity of beetles stronger than fungi and bacteria, increasing local saproxylic beetle diversity as it is positively correlated to temperature (Müller et al., 2015). Nevertheless, since fungi and bacteria are the main agents of decomposition in temperate and boreal areas (Stokland et al., 2012), shifts in community composition due to temperature changes are expected to be small and not affect their share in decomposition. However, in (sub)tropical areas, termites play a major role in dead-wood decomposition; with ongoing climate change, their distribution and decay activity is expected to increase with a strong impact on global carbon cycling (Zanne et al., 2022). Future studies should focus on the climate susceptibility of saproxylic beetles, fungi and bacteria in tropical areas. Due to the benign climate history of the tropics, climatic niches are smaller (“mountain passes are higher in the tropics”, Janzen, 1967). Thus, climate change might impact these species more severely. Such knowledge is crucial to predict future range shifts and impacts on saproxylic communities.

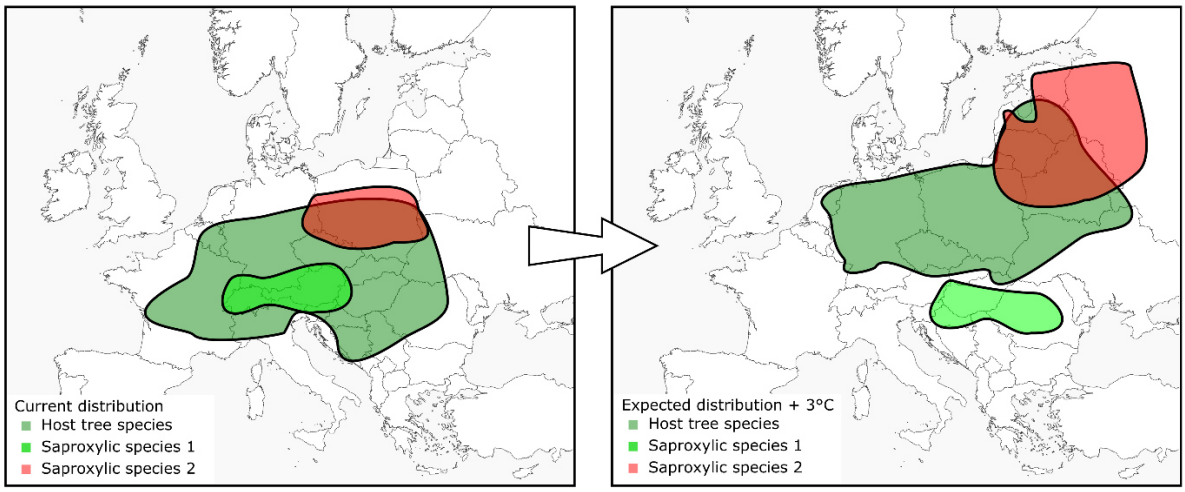

Figure 12: Conceptual analysis of species distribution and hypothetical spatial mismatch under climate change induced temperature increase. Map downloaded from FreeVectorMaps.com (https://freevectormaps.com/world-maps/europe/WRLD-EU-01-0003?ref=atr; 19.06.2023)

Further, it remains unknown how expected changes in drier and wetter periods (Christidis and Stott, 2022) will impact the reproductive success of beetles or the fructification of fungi. The latter is especially critical, as it is not fully resolved how important regular sexual reproduction is for the survival of fungal populations (discussed in Chapter 4.1). As humidity is a limiting factor in decomposition (Seibold et al., 2021), drier periods will negatively impact decomposition (A'Bear et al., 2014; Baldrian et al., 2013). Furthermore, it remains unknown how long and severe dry periods can be without damaging fungal mycelia and, more importantly, bacteria, which are more climate-sensitive than the former (Lennon et al., 2012, Chapter 4.3).

Indirect effects of host range shifts

In Chapter 4.3, I showed a generally strong host specificity of saproxylic species, especially in fungi and bacteria. Further, Chapter 4.2 demonstrated that host specificity is the main driver of fungal diversity on a global scale. Hence these species depend on the occurrence of their host tree species (Yu et al., 2023), for which range shifts are also expected (Root et al., 2003). Host specialists have to track the range shifts of their host, their "habitat". Hence they depend on the abundance of their habitat and its connectivity and thus their dispersal capability, or they go (locally) extinct (Platts et al., 2019). Yet, this will likely play a minor role, as all studied saproxylic species display a high dispersal capability (Bae et al., 2021; Komonen and Müller, 2018). Instead, it is essential to determine whether tree species can disperse fast enough to track changed temperatures or will go (locally) extinct. This would subsequently cause a (local)

extinction of specialized saproxylic species. Due to their high host specificity, this will affect fungi the strongest. Bacteria in temperate areas would be strongly affected by this as well, and, if their host specificity is also globally high, on a global scale. Temperate beetles would only be mildly affected as their specialisation is the lowest. We cannot generalize these patterns to other biomes, as we do not know about the global specialisation patterns of bacteria and beetles. The global drivers of beetle and bacteria diversity, thus, are important research points to better predict the impacts of future host range shifts. Nevertheless, an extinction of host tree species will not impact the decomposition activity of saproxylic species and, thus, unlikely to impact global carbon cycling.

Moreover, migrating tree species will alter forest structures when they establish in new forests. The subsequent impacts of altered microclimate impact the diversity and communities of saproxylic beetles (Gossner and Ammer, 2006). It will also most likely influence the fructification patterns of fungi, while mycelial fungi and bacteria are only slightly impacted by this. Alternated microclimates will also impact the climate-dependent decomposition activity (Gottschall et al., 2019), and migration could thus increase or decrease decomposition rates in forests. The exact impacts on diversity and decomposition will depend on the migrating tree species and tree species composition of the forest being immigrated.

Future research perspectives

The impacts of global change on saproxylic species are as manifold as they are understudied. One main issue will be the assessment of global diversity and its drivers (see Chapter 5.3) to predict the impact of climate change better. Such advances must emphasize currently understudied areas and forest types, as most research on these topics stems from boreal and temperate Europe (Stokland et al., 2012). Increased spatial coverage of studies on saproxylic species is needed to assess the generality of currently known patterns to make the most precise assertions about the influences of global change. For example, the impact of forest management of saproxylic species has not been assessed in tropical and subtropical areas (Chapter 5.3). Further, the impact of increased competition for and lower abundance of dead-wood resources with increased termite activity (Zanne et al., 2022) will be of additional interest in the tropics and subtropics. The fast decomposition by termites could lead to a lower abundance of large dead-wood objects, which probably many saproxylic species depend on as they do in boreal and temperate biomes (e.g., Heilmann-Clausen and Christensen, 2004; Jonsell et al., 2007; Juutilainen et al., 2017; Nordén et al., 2004).

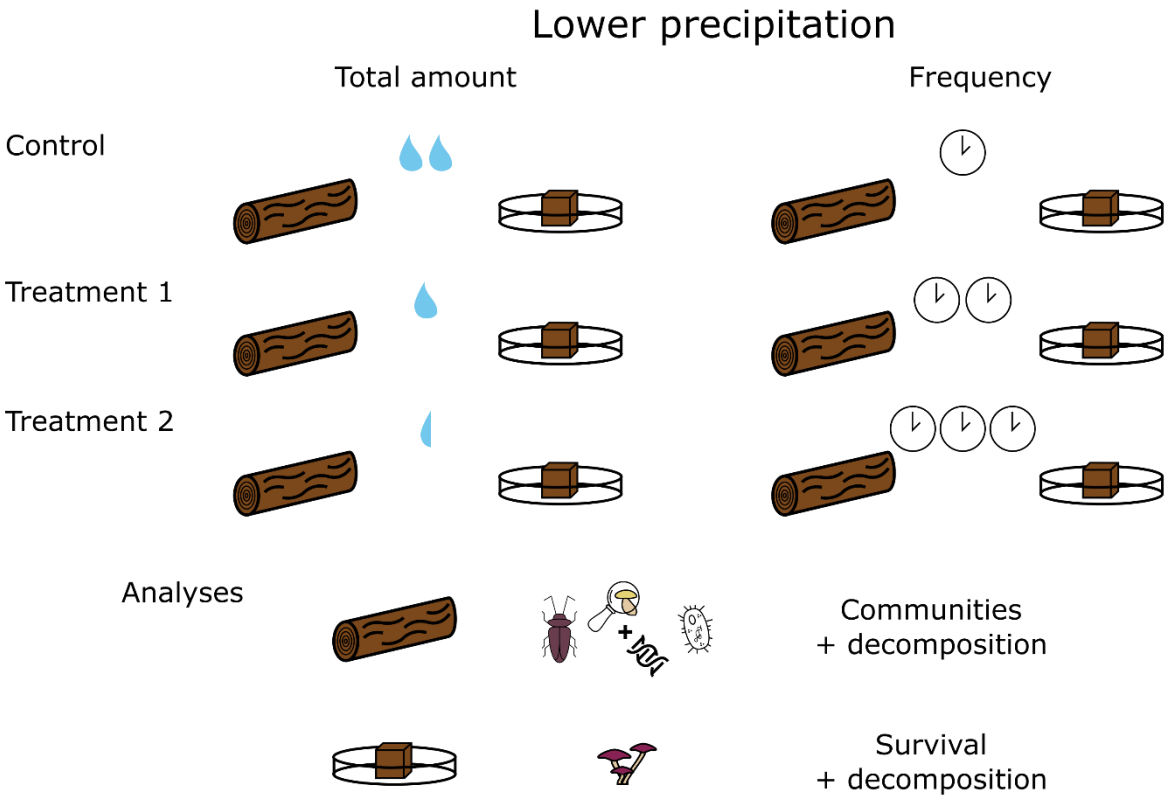

Figure 13: Conceptional study design for studying the effects of lower amounts of precipitation and lower frequency (drought) on saproxylic communities and decomposition in the field and on fungal species and their decomposition in the laboratory.

Estimating the extinction risk of tree species and a subsequent stronger focus on the conservation of critically endangered tree species will most likely also protect the associated saproxylic species. Since the highly diverse tropical areas face great species loss due to deforestation and forest management, stopping deforestation and integrating sustainable forest management will already have a great effect (Barlow et al., 2016; Giam, 2017). Additionally, calculating species distribution models and whether predicted distributions of saproxylic species match the predicted distribution of tree species will show whether distribution mismatches will occur (Fig. 12). Such analysis can further help to estimate the extinction risk of saproxylic species.

Further, the effects of higher climatic variability, especially of droughts, on saproxylic species and the subsequent effects on decompositions processes have to be assessed. Here a combination of laboratory and field experiments controlling for different drought stress intensities can help to identify drought resistance of saproxylic species and the impact on reproduction and fructification of communities and their composition (Fig. 13). Finally, the effects on decomposition can be tracked, which can help to more precisely estimate changes in

global carbon and nutrient cycling. Such knowledge is needed to increase the accuracy of current models estimating alternated decomposition speeds and its impact on global change.

Lastly, other impacts of global change, like increased nitrogen availability or the introduction of non-native tree species, resemble future research topics for saproxylic species. As nitrogen is limited in dead-wood, increased availability might increase decomposition rates. The introduction of tree species for forestry and horticulture can pose threats to native tree species due to gaining dominance or the introduction of new pathogens, and this will also threaten specialized saproxylic species. Additionally, the study on which and how saproxylic species can access the resources (dead-wood) of introduced species will also open a new research field which might reveal more information on the evolution of specialisation.

5.3 GLOBAL PERSPECTIVES ON SAPROXYLIC CONSERVATION

Research on saproxylic diversity and its conservation has increased in recent decades. Conservationists and forest managers recognized the vast importance of dead-wood for the overall forest ecosystem, leading to the implementation of forest management types incorporating dead-wood retention concepts (Bollmann and Braunisch, 2013; Doerfler et al., 2018; Puettmann et al., 2009; Sandström et al., 2019). Most of the generated and applied knowledge comes from temperate and boreal forest areas of Europe and North America, and only little to nothing is known about patterns in tropical areas and the Southern Hemisphere (Seibold et al., 2015). This data lack prevents assessing the general state of the threat of and establishing global conservation concepts for saproxylic species. Two central problems for studying the diversity of saproxylic insects in the tropics have been identified by Grove and Stork (1999): i) forest management is seen as less problematic as ongoing deforestation and hence less studied, and ii) the diversity in tropical areas is immense and hence hard to study – these points also concern overall saproxylic diversity.

Forest management

Studying deforestation and its consequences for biodiversity (Giam, 2017) is important, as saproxylic species depend on tree and forest existence. Albeit this is a severe threat, solely focus neglects the impact of forest management on the remaining forest systems and is not purposeful (Barlow et al., 2016), as saproxylic species seem especially sensitive towards forest management (Stokland et al., 2012). European studies showed the sensitivity of saproxylic species towards forest management-induced changes in forest structure and dead-wood

volume/heterogeneity (Chapter 4.3, Lassauce et al., 2011), which are likely to have similar effects in the tropics. Again, the importance of different influencing factors must be determined to ensure the implementation of efficient conservation concepts in forest management to protect biodiversity while ensuring resource use. Until achieving evidence-based suggestions, conserving more dead-wood is generally advisable to protect the large quantity of saproxylic species via increased resource abundance. Additional enrichment of dead-wood tree species diversity, i.e., increasing niche space by protecting overall tree species diversity, is a key parameter for host-specialized species like fungi and bacteria (Chapter 4.2, Chapter 4.3).

Metabarcoding and remote sensing

The high species diversity in tropical areas (Chapter 4.2, Hillebrand, 2004) and the consequential high workload of sampling and identifying (Lawton et al., 1998) are jointly responsible for their underrepresentation in forest management research. Saproxylic species likely account for a large part of the tropical forest biodiversity (Hammond, 1990; Stokland et al., 2012; Stork, 1987), but their diversity remains unknown (Stokland et al., 2012). Metabarcoding techniques seem promising not only for fungi and bacteria to overcome such problems (Liu et al., 2020). An assessment on OTU or ASV level would help recognize the main drivers of diversity and allow for a derivation of efficient conservation concepts like in Chapter 4.3. Nevertheless, these methods are imperfect (see Chapter 4.1) and still require intensive sampling campaigns and laboratory processing. Due to the elaborate sampling, this might result in low spatial coverage or coarse grain size if it is to be kept feasible (Müller and Brandl, 2009). Here remote sensing methods might provide an additional sampling method for assessing forest structure, which proves to be a good proxy for diversity (Gardner, 2011; Lindenmayer and Franklin, 2002; Storch et al., 2018; Zeller et al., 2022). Remote sensing can be combined with field surveys to estimate species distribution and diversity hotspot evaluation (e.g., Bae et al., 2019; Parisi et al., 2022; Peura et al., 2016). Instead of time-consuming sampling campaigns, areas can thus be specifically assessed, and protective measures can be developed at appropriate scales (Müller and Brandl, 2009).

Until now, these techniques are still underrepresented in saproxylic research in areas of high diversity. It remains to be seen how helpful the inclusion of metabarcoding and remote sensing are in unravelling tropical saproxylic diversity patterns to enhance their conservation.

5.4 KNOWLEDGE GAPS FOR SAPROXYLIC BACTERIA

Research on saproxylic bacteria is sparse, which is surprising, as bacteria are active wood decayers and of high functional importance for the global carbon cycle (Greaves, 1971). The main focus of former bacterial studies was their ability to decompose wood (Eriksson et al., 1990; Johnston et al., 2016; Tláskal and Baldrian, 2021). They strongly interact with fungi by fixating nitrogen and thus impacting their decomposition capability while competing for resources (Tláskal et al., 2017; Tláskal et al., 2021). This basic knowledge about their functional importance should justify further bacterial research, especially regarding environmental factors influencing bacterial diversity and community composition. Surprisingly, we still lack much fundamental knowledge already known for, e.g., beetles and fungi from decades of study. Thus the main influences on diversity and community composition are not assessed, and the conservation of bacteria and connected environmental processes cannot be ensured, which is, in fact, highly needed (Redford, 2023). The mentioned knowledge gaps occur probably because bacteria are a highly diverse group of microbes, with a high proportion being unculturable (Folman et al., 2008). Therefore, it was not until the introduction of DNA techniques such as metabarcoding that bacterial community composition could be sampled in the field, and the species group could be studied in more detail.

Only two studies focus on the assembly processes of bacteria, investigating only one tree species each (Hagge et al., 2019; Kielak et al., 2016). Broader knowledge of bacterial assembly is important to understand habitat requirements, community compositions and, finally, functional roles. As the general decline in forest dead-wood volumes has been identified as the major threat to saproxylic diversity (Lassauce et al., 2011), it is strange to find no study focusing on the effects and importance of dead-wood volumes on and for saproxylic bacterial diversity and community composition. Such studies could be easily conducted, as the experimental setups are already installed (e.g., Krah et al., 2018). In addition, dispersal capabilities are not well known (Johnston et al., 2016); thus, critical dead-wood volume thresholds and the spatial distribution of forest stand and landscape scale to support vital populations are unknown. Also, the impact of dead-wood diameter, i.e. resource amount and dead-wood type (snag, log, stump), on diversity and community composition has not been assessed so far (e.g. Bässler et al., 2010; Uhl et al., 2022).

Last but not least, the impact of forest microclimates and forest management on the diversity of saproxylic bacteria is largely missing from the literature. Chapter 4.3 was among the first studies to assess the environmental influences of saproxylic bacteria in several dead-wood tree species over a broad climatic gradient. Saproxylic bacterial diversity was under a strong

influence of the host tree species (also found by Lee et al., 2020 and Müller et al., 2020), additionally environmental differences, i.e. macroclimate and forest management also played a role in structuring their diversity and community composition (as found by Hoppe et al., 2015). Bacteria seem sensitive to forest management (Hoppe et al., 2015), but as microclimate (open/closed, Müller et al., 2020) is of less importance to bacterial communities, this is most likely an effect of the dominant tree species. The sensitivity of saproxylic bacteria to the surrounding forest structure and management must thus be further investigated. Hoppe et al. (2015) found bacterial richness to be higher in unmanaged forests. Yet, this study was conducted on a subset of the same experimental platform as analysis in Chapter 4.1 and Chapter 4.3. The unmanaged forests in this experimental set-up have been only put out of use for a few decades. Thus, typical natural forest characteristics likely have not established yet (Paillet et al., 2015). Studying saproxylic bacteria in old-growth forests and comparisons with managed forests would further enhance our understanding of the impact of forest management on saproxylic species. All of this knowledge is important to ensure the comprehensive conservation of saproxylic bacteria and ensure the continuity of the ecosystem functions they execute. Recent studies on saproxylic bacteria lack a broad spatial coverage. They are biased towards temperate and boreal forests of Europe, thus requiring a more globally distributed coverage (see Johnston et al. (2016) and references therein).

6 CONCLUSION

The overall decline in saproxylic diversity due to forest management and decreasing dead-wood volumes has received much attention and led to an implication of conservation concepts. However, large knowledge gaps about their diversity and distribution still exist, making comprehensive conservation concepts and actions difficult.

This can be partly explained by their cryptic lifestyle, especially of fungi; their communities could only be genuinely explored with the implementation of metabarcoding. I could now show that metabarcoding detected a high number of threatened fungal species and thus allowed for accurate assessments of fungal species distributions. With further updates of reference databases, the accuracy of this method will increase even more. Implementing metabarcoding in species assessments and subsequently in re-evaluations of fungal Red Lists could thus help to evaluate the more accurate threat statuses, especially as metabarcoding becomes more accurate and readily available due to the fast developments in this field.

Using metabarcoding, I could also prove the latitudinal diversity gradient for the first time in saproxylic fungal diversity. Global patterns of saproxylic fungi were caused by their high level of host specialisation, resulting in high diversity in areas of high tree species diversity. These results highlight the importance of increased forest and tree species conservation, especially in high degradation-endangered tropical areas, to conserve fungal diversity.

However, nature conservation concepts should be based on multi-taxonomic studies, as different saproxylic species groups are differently sensitive to specific environmental factors. While saproxylic beetle diversity is under the similar impact of the host, i.e., tree species and the spatial conditions, i.e., macro-/microclimate, fungal and bacterial diversity is mainly determined by the host tree species. Comprehensive conservation of temperate saproxylic diversity thus requires incorporating host and spatial effects.

Moreover, large research gaps still exist, especially regarding the impacts of global change on saproxylic species and the consequences on decomposition processes. In this regard, it becomes more important to broaden our knowledge about saproxylic bacteria and increase the spatial coverage of studies to currently understudied areas of the tropics. Future research has to focus on these knowledge gaps to ensure comprehensive conservation of saproxylic species and the respective ecosystem functions they execute.

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8 ZUSAMMENFASSUNG

Anthropogene Eingriffe haben Ökosysteme weltweit verändert. Insbesondere Wälder, als Hauptressource für Holz, wurden in ihrer Struktur stark verändert, mit schwerwiegende Auswirkungen auf die Biodiversität im Wald. Insbesondere der Rückgang des Totholzvolumens aufgrund von Holzgewinnung und die Veränderung natürlicher Waldstrukturen hin zu Bestände mit homogenerer Baumartenzusammensetzung bedrohen insbesondere saproxyle (totholzabhängige) Arten, die etwa 20% aller Waldarten ausmachen. Viele dieser Arten, insbesondere die hochdiversen Gruppen Insekten, Pilzen und Bakterien, haben eine hohe funktionale Bedeutung für Zersetzungsprozesse sowie den Kohlenstoff- und Nährstoffkreislauf, was ihren Schutz umso wichtiger macht. Zwar gab es in den letzten Jahren vermehrt Forschung bezüglich besseren Naturschutzes saproxyler Arten, aber diese Studien bezogen sich hauptsächlich auf kleinräumige Gebiete in Europa und meist nur auf eine Artengruppe; globale Studien fehlen komplett. Zudem gibt es noch Unsicherheiten bezüglich der Genauigkeit neuer Pilzerfassungsmethoden, die die Auswertung von Daten erschweren. In dieser Dissertation fokussierte ich mich auf i) einen Methodenvergleich von Fruchtkörperbestimmung und Metabarcoding von gefährdeten saproxylen Pilzen, ii) die globale Diversität von saproxylen Pilzen und die zugrundeliegenden Mechanismen und iii) eine Analyse der Betadiversität auf verschiedenen Skalen für die Gammadiversität von saproxylen Käfern, Pilzen und Bakterien. Die Ergebnisse sollen unser Verständnis über saproxyle Diversität und ihre Treiber auf verschiedenen Skalen stärken. So sollen die Grundlage von evidenzbasiertem Naturschutz saproxyler Arten erweitern, gerade in bisher wenig beachteten Regionen. Dieses Wissen ist nötig, um die Kontinuität der von ihnen ausgeführten Ökosystemprozesse zu gewährleisten.

Im ersten Kapitel konzentrierte ich mich auf die Methoden der Pilzerfassung, nämlich Fruchtkörperbestimmung und Metabarcoding und deren Effizienz bei der Erfassung gefährdeter Pilzarten. Fruchtkörperbestimmung ist die traditionelle Methode Pilzstudien durchzuführen. Die Entwicklung eines Fruchtkörpers ist jedoch stark von der Umwelt beeinflusst, was die Ergebnisse immer stark vom Sammelzeitpunkt abhängig macht. Außerdem gibt es Arten die man leicht übersehen kann, sehr unregelmäßig oder nie Furchtkörper bilden. Metabarcoding detektiert das Pilzmyzel innerhalb einer Bohrprobe des Substrats und ist daher unabhängig von der Fruchtkörperbildung, allerdings werden immer nur sehr kleine Substratproben genommen, was ein Problem bei großen Untersuchungsobjekten darstellt. Bisher wurde noch nicht untersucht, welche der beiden Methoden besser geeignet ist, um bedrohte saproxyle Pilzarten zu erfassen und ob Metabarcoding in der Lage ist Rote Listen zu

informieren. Dazu habe ich die über mehrere Jahre in fünf Gebieten in Zentraleuropa aufgenommen wurden ausgewertet. In drei dieser Gebiete war die Intensität der Metabarcodingprobennahme (Anzahl der Bohrlöcher pro Stamm) gering, in den zwei anderen hoch. In der Auswertung habe ich mich auf Unterschiede und Gemeinsamkeiten in der Gesamtartenzahl, der Artenzahl pro Stamm und die Anzahl von kolonisierten Stämmen konzentriert und untersucht ob die Effizienz einer Methode von substratspezifischen Eigenschaften, wie der Zersetzungsstufe oder ob die Baumart des Stammes zu den Angio- oder Gymnospermen gehört abhängt. Ich fand heraus, dass Metabarcoding beider Intensitäten im Allgemeinen und pro Baumstamm mehr gefährdete Pilzarten detektiert, als mit Fruchtkörperbestimmung. Außerdem hat Metabarcoding mit hoher Probenintensität in allen Zersetzungsstufen, sowie Angio- und Gymnospermenstämmen mehr Arten nachgewiesen. Metabarcoding konnte zudem die gefundenen Arten auf mehr Baumstämmen nachweisen. Die Fruchtkörperbestimmung erfasste jedoch eine einzigartige Gruppe von Arten. Zusätzlich wurden kaum Arten auf demselben Stamm nachgewiesen. Auf Grundlage dieser Ergebnisse lässt sich feststellen, dass Metabarcoding eine sehr effektive Methode ist um gefährdete saproxyle Pilze nachzuweisen und dabei ein breiteres Artenspektrum abdeckt als Fruchtkörperbestimmung. Das ist nicht verwunderlich, da bekannt ist, dass mehr Pilzarten als Myzel vorhanden sind, als gerade Fruchtkörper bilden. Außerdem ist die Wahrscheinlichkeit der Detektion einer gefährdeten Art auf einem Stamm mit Metabarcoding höher, daher ist es bei begrenztem Sammelaufwand (Anzahl zu beprobender Stämme) effizienter. Daher sollte Metabarcoding definitiv als Methode im Pilznaturschutz Anwendung finden. Der hohe Anteil an nur durch Fruchtkörperbestimmung nachgewiesenen Arten entsteht wahrscheinlich aufgrund unvollständiger Referenzdatenbanken für Metabarcoding und artspezifischer Merkmale die die Detektion durch Metabarcoding erschweren. Da die Effektivität von Metabarcoding mit geringer Probenahmeintensität stark von der Zersetzungsstufe des Baumstammes abhängig war empfehle ich für Metabarcoding eine hohe, an die Objektgröße angepasste Probenahmeintensität. Schlussendlich lässt sich sagen, dass Metabarcoding eine geeignete Methode, um gefährdete saproxyle Pilzdiversität zu bewerten und Naturschutzmaßnahmen wie Rote Listen über deren Verbreitung und Häufigkeit zu informieren. Dennoch ist ein ergänzender Ansatz mit Fruchtkörperbestimmung unverzichtbar, um alle gefährdeten Pilzarten zu erfassen.

Im zweiten Teil untersuchte ich, ob die globale Diversität saproxyler Pilze von den Polen zum Äquator hin, zunimmt und somit demselben Muster vieler anderer Artengruppen folgt. Der latitudinale Biodiversitätsgradient ist eines der am meisten untersuchten ökologischen

Phänomene, aber die Ursachen dafür sind noch nicht ausreichend geklärt, und gerade für Mikroorganismen sehr unbekannt. Ich habe mich in meiner Analyse auf den Einfluss biotischer Interaktionen fokussiert und zwei Hypothesen als Ursache für den vermeintlichen Gradienten getestet. i) Die ökologische Spezialisierungshypothese geht davon aus, dass Arten in den Tropen höher spezialisiert sind und weniger Nischenraum beanspruchen, so können mehr Arten nebeneinander existieren. Grundlage für diese Hypothese ist, dass die Tropen klimatisch stabiler und länger eisfrei sind, als gemäßigte oder boreale Biome. Daher sind in den Tropen klimatische Einflüsse weniger selektiv als Interaktionen zwischen Arten, z.B. Konkurrenz und es war mehr Zeit für die Evolution von Spezialisierung vorhanden. ii) Die Baumartendiversitätshypothese geht davon aus, dass die Diversität von hoch spezialisierten wirtsabhängigen Arten, wie es saproxyle Pilze sind, stark von der Diversität der Wirtsbaumarten abhängig sind. Durch die Zunahme der Baumartendiversität zu den Tropen erhöht sich der verfügbare Nischenraum, so können mehr Arten koexistieren. Ich habe ein globales Experiment mit 52 Plots auf denen Totholz von jeweils drei lokal häufigen Baumarten ausgelegt wurde analysiert. Ich habe verschieden Diversitäts- und Spezialiserungsindizes auf unterschiedlichen Skalen analysiert. Die Gammadiversität auf der drei Biome nahm vom borealen über das gemäßigte bis zum tropischen Bereich zu. Alphadiversität auf Stammskala und Spezialisierung auf Plotlevel zeigten keine signifikante Veränderung mit dem Breitengrad. Die Alphadiversität auf Plotlevel nahm mit der lokalen Baumartendiversität zu. Die Zunahme der Gammadiversität vom Boreal zu den Tropen bestätigt den latitudinalen Biodiversitätsgradienten entlang der Breitengrade für sparoxyle Pilze. Allerdings nahm die Alphadiversität pro Stamm nicht signifikant in Richtung Tropen zu, was auf eine Abhängigkeit von der Skalengröße und einen gleichbleibenden Nischenraum innerhalb des Totholzes weltweit hindeutet. Ein Vergleich mit globalen Bodenpilzstudien bestätigte die Wichtigkeit der Inkorporation verschiedener Skalen und zudem funktionellen Gruppen bei Studien solchen Ausmaßes. Da die Spezialisierung der Arten am Plot nicht signifikant mit dem Breitengrad zunahm wurde die Ökologische Spezialisierungshypothese als Treiber des globalen Diversitätsmusters saproxyler Pilze ausgeschlossen. Da die Diversität der saproxylen Pilze signifikant mit der Baumartendiversität zunahm scheint die Baumartenhypothese der Hauptmechanismus für den latitudinalen Biodiversitätsgradienten zu sein. Das wurde durch eine weitere Analyse der Gammadiversität gegen die Anzahl untersuchter Baumarten bestätigt, die jetzt keinen signifikanten Unterschied zwischen den Tropen und dem gemäßigten Biom zeigten. Nur die Diversität im borealen Biom war noch signifikant niedriger, hier scheint die ökologische Spezialisierung also doch eine Erklärung für die Diversitätsunterschiede zu sein.

Die Ergebnisse dieser Studie zeigen insgesamt eine starke Abhängigkeit saproxyler Pilze von ihren Wirtsbaumarten. Daher und dass der weltweite Verlust an Baumarten die saproxyle Pilzdiversität bedroht, mit möglicherweise unberechenbaren Auswirkungen auf den Kohlenstoff- und Nährstoffkreislauf.

Im letzten Kapitel analysierte ich zwei Studien um den Schutz saproxyler Artne zu verbessern. Zunächst untersuche ich die unterschiedliche Betadiversität der drei Hauptzersetzergruppen Käfer, Pilze und Bakterien auf räumlichen und Wirtsskalen. Ziel war es die relative Bedeutung der Betadiversität einzelner Skalen für die Gammadiversität zu berechnen und daraus abzuleiten, welche Faktoren die Diversität am stärksten beeinflussen. Anshcließend sollte evaluiert werden welche Skalen daher für den Schutz saproxler Arten am relevantesten sind und ob ein einheitliches Schutzkonzept eingeführt werden kann, dass alle drei Artengruppen gleichermaßen schützt. Um diese Fragestellung zu beantworten habe ich ein großes Totholzexperiment in drei Regionen Deutschlands verwendet in dem in standardisiert genutzten Wäldern standardisiertes Totholz von 13 Baumarten ausgelegt wurde. Dadurch konnte ich insgesamt vier Skalen auswerten. Auf der räumlichen Skala waren das die regionale Skale, mit starken Unterschieden im Makroklima und der räumlichen Distanz, und die lokale Skala, mit starken Unterschieden im Forstmanagement und daher auch dem Mikroklima. Auf der Wirtsskala untersuchte ich die Baumklassen- und Baumartenskale, hier sind die physisch-chemischen Unterschiede zwischen den Baumarten, die besonders zwischen Bäumen unterschiedlicher Klassen prominent sind ausschlaggebend für Unterschiede in der Diversität. In der zweiten Stude dieses Kapitels untersuche ich die Diversität und Spezialisierung von Pilzen und Bakterien auf Totholz verschiedener Baumarten entlang eines Klima- und Landnutzungsgradienten. Die Frage ist, haben wärmere Temperaturen und geringere Landsnutzung einen positiven Einfluss auf die Diversität. Zeitgliche untersuchte ich den Effekt beider Variablen auf die Spezialisierung. In der Theorie hat stärkere Umweltheterogenität (Klimastrenge, Landnutzungsintensität) einen negativen Einfluss auf die Spezialisierung einer Artgemeinschaft, die Arten nutzen breitere Nischen und weniger Arten können koexistieren. Daher wird Spezialisierung als möglicher Grund für die beobachteten Diversitätsmuster sein. Die Ergebnisse der ersten Studie unterschieden sich stark zwischen den Artengruppen. Während für Käfer und Pilzfruchtkörper die räumliche und die Wirtsskala gleichbedeutend für die Gammadiversität waren, war es bei molekular nachgewiesenen Pilzen und Bakterien hauptsächlich die Wirtsskala. Auf der räumlichen Skala war für alle Artengruppen die lokale Skala wichtiger, auf der Wirtsskala die Baumartenskala. Bei Käfern waren die Ergebnisse nicht so ausgeprägt und jede Skala ungefähr gleich wichtig. Die Ergebnisse dieser Studie erlauben

daher kein einheitliches Schutzkonzept auf einer Skala um die Diversität aller Artengruppen zu schützen. Die Ergebnisse zeigen, dass Artengruppen die außerhalb des Totholzes vorkommen (Käfer, Pilzfruchtkörper) viel stärker von Umweltfaktoren auf den räumlichen Skalen abhängen. In diesem Fall sind es makroklimatische Unterschiede zwischen den Regionen und mikroklimatische Unterschiede zwischen den Beständen unterschiedlichen Forstmanagements. Letzteres beeinflusst die Baumartenzusammensetzung und das Totholzvolumen, was beides wichtige Faktoren für die Diversität von saproxylen Arten sind. Artengruppen innerhalb des Totholzes (molekular nachgewiesene Pilze und Bakterien) sind stärker von den physisch-chemischen Unterschieden zwischen den Bäumen, besonders den Baumarten beeinflusst. Dies zeigen auch die Ergebnisse der zweiten Studie. Die Baumarten hatten den stärksten Einfluss auf die Diversität und Artgemeinschaftszusammensetzung beider Artengruppen. Nur bei Bakterien zeigt der mittlere Gebietsniederschlag einen Einfluss auf die Diversität und Spezialisierung der Gemeinschaften. Solche Studien sind gerade für saproxyle Bakterien noch sehr rar. Eine umfassende Erhaltung der multi-taxonomischen Diversität über Regionen hinweg erfordert daher die Integration mehrerer Skalen. Um die saproxyle Diversität ausreichend zu schützen müssen in verschiedenen makroklimatischen Regionen, Wälder mit unterschiedlichen Mikroklimaten, d.h. Waldmanagement, eingerichtet oder erhalten werden. In diesen Wäldern muss Totholz von verschiedenen Baumklassen, einschließlich Angiospermen und Gymnospermen, und Baumarten bereitgestellt werden.

In meiner Dissertation konnte ich zeigen, dass Metabarcoding eine effiziente Methode zur Erfassung gefährdeter Pilzarten ist und somit im Pilzartenschutz Verwendung finden sollte. Außerdem habe ich den latitudinalen Biodiversitätsgradienten für saproxyle Pilze und die erhöhte Diversität von Baumarten als seinen Hauptmechanismus identifiziert. Außerdem betont meine Arbeit die Bedeutung multi-taxonomischer Studien für einen evidenzbasierten Naturschutz, da verschiedene Artengruppen unterschiedlich sensitiv gegenüber verschiedenen Umweltfaktoren sind und daher unterschiedliche Schutzkonzepte erfordern. Diese Ergebnisse schließen bisherige Wissenslücken und tragen zu einem besseren Verständnis von saproxyler Diversität bei, was hoffentlich in einem besseren Schutz resultiert. Diese Ergebnisse zeigten unter anderem auch, dass eine hohe Wirtsbaumspezialisierung von saproxylen Pilzen kein ausschließlich europäisches Phänomen ist, sondern weltweit auftritt. Daher sind diese Arten besonders vom Verlust von Baumarten unter dem globalen Wandel betroffen. Meine Ergebnisse haben außerdem wichtige Fragen über die Diversität von saproxylen Bakterien beantworten können, allerdings bedarf es hier weiterer Forschung bezüglich des genauen Einflusses von Forstwirtschaft. Allerdings gibt es immer noch große Forschungslücken zu

saproxyler Diversität, besonders in hochdiversen tropischen Gebiete. Ein verstärkter Fokus auf die Treiber der Diversität in diesen Gebieten ist entscheidend, um einen umfassenden saproxylen Naturschutz zu gewährleisten und die verschiedenen von ihnen kontrollierten Ökosystemfunktionen zu erhalten.

10 ANNEX

A.1: RAPID ASSESSMENT OF THREATENED SAPROXYLIC FUNGAL SPECIES – FRUIT BODY SAMPLING VS METABARCODING

Unpublished manuscript

Rapid assessment of threatened saproxylic fungal species – fruit body sampling vs metabarcoding

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Abstract

The ongoing decline of biodiversity challenges politics and conservationists. Effective conservation planning requires rapid assessment of species' presence, distribution and population dynamics, especially threatened species. This can be extremely challenging for species-rich taxa that are difficult to detect and identify, like fungi. In recent years metabarcoding of environmental DNA has proved a promising method for fungal detection. However, its potential advantage against traditional fruit body sampling in monitoring threatened fungal species has rarely been tested. Here, we utilized wood-inhabiting fungi data from 553 dead-wood objects across five sites in Central Europe. We aimed to compare the effectiveness of fruit body sampling and metabarcoding (of low and high sampling intensity) in detecting threatened species. Overall, per site and object, metabarcoding of high and low sampling intensity was more effective in detecting threatened species than fruit body sampling. Approximately 20% of all threatened species at each site could be detected by both methods and ca. 10% exclusively by fruit body inventories. The number of simultaneous species detection by both methods on the same object was very low. Metabarcoding detected threatened species on more objects than fruit body inventories. The comparative effectiveness of either method did not strongly depend on the dead-wood decomposition stage or the host tree identity (angio- or gymnosperm). But metabarcoding of low sampling intensity detected similar numbers of species per object as fruit body sampling in intermediate decay stages. Our findings suggest that metabarcoding, especially of higher sampling intensity is preferred over fruit body inventories when studying the presence or abundance of threatened wood-inhabiting species in a limited number of study objects. Thus, we strongly recommend the increased use of DNA metabarcoding sampling for future wood-inhabiting species conservation assessments. However, fruit body sampling provides further important insights into species numbers and abundances and should be incorporated for an overall species assessment.

Keywords: species conservation, wood-inhabiting fungi, fungal conservation, species detection, red list

Introduction

The increase of human impact on Earth's ecosystems has put biodiversity into a crisis (Nic Lughadha et al., 2020). Despite various conservation efforts, global biodiversity continues to decrease (Cowie et al., 2022). This underpins the need for biodiversity monitoring at relevant spatiotemporal scales to evaluate the presence, distribution and population dynamics of threatened species to inform conservation. However, research commonly addresses only well-known species groups (Lindenmayer & Likens, 2011; Troudet et al., 2017), while taxa that are difficult to detect or identify remain understudied. Hence, for improved biodiversity conservation of such taxa, we need rapid and cost-efficient sampling methods with high spatial and temporal resolution (Hochkirch et al., 2021).

One such taxa is fungi. With 140,000 described species, this group is currently the third-richest eukaryotic kingdom, with predicted species richness of over 6 million (Baldrian et al., 2022). Moreover, fungi are among the most important organisms driving global primary production and the carbon- and nutrient cycle (Boddy & Watkinson, 1995). Still, conservation frameworks largely neglect fungi (Heilmann-Clausen & Vesterholt, 2008; Hochkirch et al., 2021).

Fungal fruit body monitoring is the traditional sampling technique used for years but has shortcomings. Fungal fruit bodies can be highly ephemeral in space and time, as their production depends on intrinsic factors and specific environmental conditions (e.g., weather conditions, Sakamoto, 2018). Therefore, different species can have specific intra-annual (Halme & Kotiaho, 2012; Purhonen et al., 2017) and irregular inter-annual phenologies (Moore et al., 2008; van der Linde et al., 2012). In addition, some species produce small and inconspicuous fruit bodies that are easily overlooked (Lõhmus, 2009), and others need years to collect enough resources for fruit body production (Ovaskainen et al., 2013).

The major advantage of metabarcoding is that it allows the detection of fungal species without visible fruit bodies (A. L. Fischer et al., 2012; Kubartová et al., 2012; Rajala et al., 2011). Further, expert knowledge to identify fungal specimens is not necessary and sampling is easily standardised (Thomsen & Willerslev, 2015). The apparent limitations include the possibility of technical or biological noise, e.g., low-quality or chimeric sequences (Lindahl et al., 2013), remnant DNA from dead organisms (Carini et al., 2016), or randomly present nonviable species (Tuovinen et al., 2015). Moreover, only a minimal amount of substrate is usually sampled, and species not growing in the particular sample (e.g., those with small mycelia) may remain undetected (Kubartová et al., 2012; Ovaskainen et al., 2010). Thus, the effectiveness of metabarcoding might be dependent on the sampling intensity. In addition, species identification via metabarcoding depends on the quality of reference databases (Hibbett et al., 2016).

As a possible solution for improving conservation assessments, a combined use of fruit body sampling and environmental DNA metabarcoding methods (hereafter: metabarcoding) has been discussed for a decade (Runnel et al., 2015). However, empirical evidence is scarce across study systems (e.g., fungal habitats) and spatial scales. One study focusing on soil fungal diversity at country scale (Denmark) found that threatened fungal species can be detected similarly by both methods (Frøslev et al., 2019). However, other equally important fungal habitats are still neglected. One among the most essential terrestrial habitats for fungi is dead-wood. In forest ecosystems, dead-wood can reach 40% of the growing stock (Boddy, 2008). For example, in low range mountain forests in Central Europe, dead-wood can reach more than 250 m^3/ha wood (Müller & Bütler, 2010). However, wood-inhabiting fungi are among the most threatened organisms in forests due to centuries of dead-wood removal and timber extraction (Siitonen, 2001). Dead-wood might be an ideal model system to study the detection efficiency of both methods. First, a dead-wood object is a spatially well-defined and a distinct resource unit for the fungal organisms depending on it. This allows high standardisation and comparability of sampling methods. Second, the diversity of wood-inhabiting fungi continues to decline substantially, and it has only been recently recognized by governments and conservation organisations that fungal diversity is important from a functional and conservational point of view (Mueller et al., 2022). Efficient monitoring concepts might help prevent wood-inhabiting fungal species from further decline via a rapid evaluation and adaption of conservation actions.

Our study aims to compare the efficiency of fungal fruit body sampling and metabarcoding in detecting threatened fungal species on dead-wood. This comparison will improve our understanding of the advantages and limitations of both methods in species assessment to enhance forest nature conservation. We used an extensive dataset comparing species records based on fruit body sampling and metabarcoding of two different sampling intensities from 553 dead-wood objects in five forest sites in central Europe (Fig. 1) sampled over several years. Specifically, we asked: (i) Which method detects threatened species per site/dead-wood object more efficiently? (ii) If both methods detect a threatened species, is it detected on the same object? (iii) Which method better detects threatened species regarding specific resource traits (decay stages, angiosperm/gymnosperm)? (iv) Which method detects threatened species on more objects? Our study defines threatened species as “near threatened” or higher ranks in Central European red lists (Dämmrich et al., 2016; Holec & Antonín, 2006).

Materials and Methods

Study areas and sampling

We used fruit body and metabarcoding data from five sites, from two dead-wood experiments in Germany and a primaeval forest in the Czech Republic (Fig. 1): *1. The study site Alb is located in south Germany, in the* UNESCO Swabian Alb Biosphere Reserve and part of the BELongDead experiment (M. Fischer et al., 2010, www.biodiversity-exploratories.de), at an altitude of 460–860 m a.s.l. Nine plots were established in forests of different management types in each site; three plots in planted conifer stands, even-aged managed beech stands, and unmanaged (for at least 20 years) beech stands each. On each plot, 13 objects (logs of the length 4.0 ± 0.25 m and mean diameter of 31 ± 5.9 cm (SD)) were placed in 2009, resulting in a total of 117 objects. The objects consisted of four conifers (*Larix decidua*, *Picea abies*, *Pinus sylvestris*, and *Pseudotsuga menziesii*) and nine deciduous (*Acer spp.*, *Betula pendula*, *Carpinus betulus, F. sylvatica*, *Fraxinus excelsior*, *Populus spp*., *Prunus avium*, *Quercus spp*., and *Tilia spp*.) tree *species.* 2. The study site Hainich is located in Central Germany, including Hainich National Park. It is also part of the BELongDead experiment at an altitude of 285–550 m a.s.l. Hainich site has nine similar plots to Alb plus three additional plots in forests of selective cutting, resulting in 12 plots. On each plot, objects of the same dimensions and tree species as in the Alb were placed, resulting in 156 objects. 3. The study site Schorfheide is located in north-east Germany in the Schorfheide-Chorin UNESCO Biosphere Reserve and is also part of the BELongDead experiment, on an altitude of 3–140 m a.s.l.. Schorfheide has the exact same plot set up as Alb. *4.* The study site Bavarian Forest is located within the Bavarian Forest National Park in south-eastern Germany, at elevations between 650 and 1450 m a.s.l. In 2011, 67 plots of 0.1 ha were set up in the management zone of the national park (~6,000 ha). Half the plots were cleared of standing trees, and one freshly cut object (logs of the length 5 m and mean diameter of 33 ± 6.5 cm (SD)) of *Fagus sylvatica* and *Abies alba* was placed in each plot. *5.* The study site Zofin is located in the Novohradske Hory mountains, specifically in the 25 ha Zofin ForestGEO® Dynamics Plot (www.forestgeo.si.edu), in the core zone of the Zofínský prales National Nature Reserve in the Czech Republic. The elevation ranges between 735 to 830 m a.s.l. (Anderson-Teixeira et al., 2015). In total, 99 natural logs of different length were sampled (*27 F. sylvatica, 43 Picea abies and 30 Abies alba).* The diameter*: 33 ± 6.5 cm* diameters ranged between 30 - 100 cm and were distributed within each tree species group as evenly as possible. All studied tree species, including non-native *Pseudotsuga menziesii*, are common tree species in Central Europe. For further details on the study sites, see Supplementary Material 1.

Fruit body sampling

The fungal fruit body sampling occurred in the peak fruiting season (September-October) in all study sites. In the Alb, Hainich and Schorfheide sampling took place in 2012, 2015, and 2018,

in the Bavarian Forest in 2012, 2013 and 2015, and in Zofin in September 2013. The threatened fungal species selected for the study were macrofungi, easily visible to the naked eye. Fungi were determined directly in the field or with a microscope in the lab. Fruit body sampling were carried out by the same team of experienced field mycologists (see Acknowledgements).

Metabarcoding

The wood samples for metabarcoding were in most cases collected within the same year as fruit bodies, but in the Alb, Hainich and Schorfheide the last wood samples were collected a year earlier (in 2017). In Alb, Hainich and Schorfheide, one wood sample per object was collected in each sampling campaign. At the sampling location, the bark was removed, minimizing the possibility of including microorganisms occurring on the bark. An auger (20 mm) was driven once from each site with an angle of ~45° vertical middle into the centre of each object. In the Bavarian Forest and Zofin, one vertical sample each was taken at 1/8, 3/8 5/8 and 7/8 of the object length with an auger (8 mm) up to 40 cm deep and pooled. The auger was sterilized between drillings in all sites by rinsing with ethanol and burning. Samples were frozen within a few hours after drilling. Each wood sample was homogenized into fine powder using liquid nitrogen and a swing mill (Retsch, Haan, Germany). Samples of each site were processed following standard laboratory protocols for DNA extraction, PCR amplification and sequencing (see Supplementary Information 1).

Data preparation

Taxonomy assignment for all sequences was performed in PipeCraft 2 bioinformatics platform (Anslan et al., 2017; pipecraft2-manual.readthedocs.io/en/stable/) using blastn algorithm (BLAST v2.11.0+;Camacho et al., 2009) against UNITE v8.3 all eukaryotes database (Abarenkov et al., 2010). Blastn settings were strands=both, e-value=0.001, word size=7, reward=1, penalty=-1, gapopen=1, gapextend=2. For the final analyses, we excluded local singletons from the community matrix(i.e. cells with a value of 1 were set to 0) to reduce possible PCR and sequencing errors (Brown et al., 2015). We aggregated the remaining operational taxonomic units and amplicon sequencing variants assigned to the same species and used the presence-absence of each species on each *object* at each sampling event in further analysis. To compare the sites, we combined the Red Lists of threatened Fungi in Germany (Dämmrich et al., 2016) and the Czech Republic (Holec & Antonín, 2006) to create a regional Red List. We assumed that the spatial proximity of the sites allows this (see Appendix A). In addition, we excluded species listed as “not evaluated”, “least concern”, or “data deficient”. Prior analyses, we excluded twelve species which had no sequence stored in UNITE. We

unified the nomenclatures of each data set and our combined Red List with MycoBank (Crous et al., 2004, accessed: 24.03.2022). Species listed as synonyms in the Red List were also updated and if MycoBank had listed them as an autonomous species, they were included as such in the analyses. A complete species list with abundances (number of objects) is available in Appendix B, Table B1.

Data Analyses

All analyses were conducted using R 4.2.2 (R Core Team, 2022). All Euler plots were created with https://eulerr.co/.

The overall aim of all analyses was to compare the efficiency of the two study methods in detecting threatened species within and across *object*s in each study site. Regarding metabarcoding, we separately tested for low (one drilling hole in three study sites) and high sampling intensity (four drilling holes in two study sites).

To explore the total number of threatened species detected by each method, we counted the number of threatened species sampled by each method within and over all sites and calculated the share. To test whether one method detected more species per *object*, we calculated generalized linear mixed-effects models for negative-binomial distributed count data (function g*lmer.nb,* package *lme4*, Bates et al., 2015). We used the number of threatened species detected per occupied object as a response and sampling method as an explanatory variable; "object ID" was used as a random factor.

To explore if both methods detected threatened species on the same object, we calculated the number of objects a threatened species was sampled on by each method in the same year and set it in relation to the total number of objects occupied by threatened species detected by both methods in the respective sampling year.

To explore if one method performed better in detecting threatened species regarding specific resource traits (decay stages, angiosperm/gymnosperm), we compared the unique number of threatened species sampled by each method and the share across all *object*s from all sites along different decay stages (scale from 1 to 4, Bässler et al., 2010) and whether the host tree was angiosperm or gymnosperm. To test the effectiveness of each method on object-level along decay or between host trees of different host tree lineages, we calculated generalized linear mixed-effects models for negative-binomial count data (*glmer.nb*) for each decay stage and the lineages angiosperm and gymnosperm. Again, we used the number of threatened species detected by each method as a response and the method as an explanatory variable; "object ID" was the random effect.

Finally, to assess if some of the methods can detect threatened species on more objects and to explore the question what is the proportion of objects which inhabit threatened species detected by both methods, we counted the total number of objects occupied by threatened species detected by each method uniquely and the shared. On the object-level, we further calculated generalized linear mixed effects models with the function g*lmer* and a binomial distribution in the package *lme4*. We coded if a method detected an occupied object with 1 (detected) or 0 (not detected) and used this as the response variable. The sampling method was used as the explanatory variable, and "object ID" as a random effect.

Results

We found 2 089 fungal species, of which 137 were considered as threatened.

Which method detects threatened species per site/dead-wood object more efficiently?

Overall, metabarcoding of low and high sampling intensity detected more threatened species (48 species/70.6% and 60 species/63.2%, respectively) than fruit body sampling (7 species/10.3% and 13 species/13.7%, respectively; Fig. 2a &b). Fruit body sampling and metabarcoding of high sampling intensity detected only a slightly higher proportion of shared species (23.2%) than fruit body sampling and metabarcoding of low sampling intensity (19.1%). However, the efficiency of metabarcoding varied strongly among the sites, regardless of sampling intensity from 54.9% up to 87.2% (Fig. 2 b-g). The GLMM showed that metabarcoding detected more threatened species on each dead-wood object than fruit body sampling (Table 1). Additionally, the set of species detected by each method was largely different (Appendix B Fig. B1-B5, Table B2-B6).

If both methods detect a threatened species, is it detected on the same object?

The different sampling methods rarely detected the same species on the same dead-wood object (Table 2). Relative numbers of simultaneously detected species were lower in fruit body sampling paired with metabarcoding of low sampling intensity (5.6-13.5%) than when paired with high sampling intensity (4.9-26.3%). Most high occupancy numbers were driven by a few single species (Appendix B Table B2- B6), but simultaneous detection was only high (15 times) in *Agaricus laevigatus* in Zofin (Appendix B Table B6).

Which method better detects threatened species regarding specific resource traits (decay stages, angiosperm/gymnosperm)?

In each of the four decay stages, both metabarcoding methods always detected higher number of threatened species than fruit body sampling (Fig. 3). The proportion of those species detected uniquely by either method or shared depended on decay stage. Compared to metabarcoding of low sampling intensity, fruit body sampling was most efficient in decay stage two. The highest number of shared species was detected in decay stage one. Fruit body sampling detected no species in decay stage four (Fig. 3g). In turn, compared with high-intensity metabarcoding, fruit body sampling detected most species in decay stages two and three. The number of shared detected species was also highest in these two stages.

Over all sites, metabarcoding detected more threatened species on either lineage than fruit body sampling (Fig. 4). In both comparisons, metabarcoding detected around 60% of all species in angiosperms (sum of all species detected by metabarcoding on angiosperms minus the number of species also detected by fruit body sampling). In gymnosperms, metabarcoding of low sampling intensity detected 38.4% of all species, and metabarcoding of high sampling intensity 65%. Fruit body sampling detected 25.1% of all species in angiosperms when compared with low sampling-intensity metabarcoding and 19.6% when compared with high-intensity metabarcoding. In gymnosperms, fruit body sampling detected 10.4% and 22.8%, respectively.

On the *object*-level, metabarcoding of high sampling intensity detected more threatened species than fruit body sampling independent of decay stage and whether the host tree was angio- or gymnosperm (Table 3). However, metabarcoding of low sampling intensity did not detect significantly more threatened species in decay stages two and three than fruit body sampling.

Which method detects threatened species on more objects?

Overall and per site, metabarcoding detected threatened species on more objects than fruit body sampling (Table 1, Fig. 5, Appendix B Fig. B6). Fruit body sampling detected uniquely more species on objects when compared with low-intensity metabarcoding than when compared with high-intensity metabarcoding. The number of objects both methods detected threatened species on was 32.0% of all occupied objects, when fruit body sampling was paired with metabarcoding of high sampling intensity and 6.7% when compared with low-sampling intensity metabarcoding.

Discussion

To guide efficient future fungal diversity monitoring, we compared fruit body sampling versus metabarcoding in dead-wood, a critical habitat of pivotal conservation concern. We found

overall and at object level that metabarcoding outperforms fruit body sampling. However, ca. 10% of threatened species were detected only via fruit body sampling. More detailed analyses revealed that the number of simultaneous species detection by both methods on the same object was very low. Both methods provide complementary information for a more comprehensive picture of fungal diversity.

Efficiency of metabarcoding in detecting threatened species

We found metabarcoding of low and high sampling intensity to detect more threatened fungal species than fruit body sampling. One simple explanation could be that fungi are always present as mycelium but only temporarily as mycelium plus fruit bodies (e.g., Frøslev et al., 2019; Ovaskainen et al., 2013; Saine et al., 2020). A recent study showed that threatened soil fungi could only slightly better detected via both methods (Frøslev et al., 2019). One reason for this discrepancy might be differences in sampling intensity. However, for both studies, the grain size of metabarcoding is very small. Frøslev et al. (2019) sampled 0.01% of the plot surface area representatively and extracted 4 g of soil for eDNA analysis from 5 to 20 kg soil per plot (40 x 40 m). We probably covered less than 0.01% of each dead-wood object's surface in our study. Further, we assume that the intensity of fruit body sampling is comparable. Differences in sampling might, therefore, not explain the observed differences between the studies. Another explanation might be that the relative detection performance between methods depends on the availability of reference sequences in databases. Frøslev et al. noted that many taxa, identified via metabarcoding, missed reference sequences in the UNITE database. As the reference database UNITE is frequently updated (v8.0 in Frøslev et al. and v8.3 in our study), we cannot exclude the possibility that the contrary results are due to the better taxonomic resolution of the recently updated database. Finally, the detection probability of methods might differ between habitats (soil vs. dead-wood). However, we have no convincing explanation for how soil or dead-wood might differ in fructification patterns (e.g., frequency) or mycelia amount and distribution, which would influence the detection probability.

Low share of species and unique set of species

We further found that approximately 20% of the detected species were detected by both methods, and each method detected a unique set of species. Further, both methods rarely detected species simultaneously on the same object. There might be several reasons for this: i) The detection probability might be related to species traits. Some species, especially fungi like the corticioid *Botryobasidium medium* or *Tomentella viridula* are related to the *object*s' surface or bark. Before drilling metabarcoding samples, the bark was removed, to minimize the

detection of nonviable species, and often cleaner parts of the bark are selected for drilling. This should lead to a lower proportion of corticioid species detected by metabarcoding compared to fruit body sampling. However, metabarcoding detected 27 corticoid fungal species (16 uniquely) and fruit body sampling 13 (2 uniquely, FungalTraits, Põlme et al. (2020)), which makes this line of evidence unlikely. Further, detecting species with small mycelia via metabarcoding is less likely due to the small sampling grain size. On the other hand, fruit body sampling might miss species with small or inconspicuous fruit bodies. We have no data on mycelial size and the illumination of the traits which might explain the observed pattern (like Blaschke et al., 2023 did with spore colors) must be left to further studies. ii) Fruit body sampling might have missed a large part of threatened fungal diversity due to unfavourable fruiting conditions, species-specific fruiting phenology outside the main fruiting season, or infrequent fruiting patterns (Halme & Kotiaho, 2012). iii) Soil fungi like ectomycorrhizal species (e.g. *Russula)* can inhabit dead-wood (Mäkipää et al., 2017; Rajala et al., 2015; Tedersoo et al., 2003). Their ability to fructify was assumed to be limited to late decay stages (Holec et al., 2020) and they are thus more likely to be detected via metabarcoding. We also detected more non-saprotrophic fungi with metabarcoding (Appendix B Fig. B7), albeit we could detect fruit bodies of non-saprotrophic fungi in all decay stages (data not shown).

Finally, it is important to note that we detected twelve threatened species without a reference sequence in the utilized databases (8% of all detected threatened species, Appendix B Table B1). The efficiency of metabarcoding in detecting threatened species is thus not at its full potential and will increase with updated databases. Nevertheless, comprehensive conservation requires accurate species detection and identification. As long as not all fungal species occurring in a region of conservation concern do have reference sequences, a combined approach of both methods is necessary for complete species monitoring and threat status evaluation for Red Lists.

The impact of decay and host tree phylogeny

Overall, metabarcoding detected more species than fruit body sampling, independent of the decay stage. However, only for metabarcoding of high sampling intensity, these results also translated to the object-level, while metabarcoding of low sampling intensity performed similarly to fruit body sampling in decay stages two and three. The discrepancies for the latter might be attributed to an increased fructification rate with ongoing decay, as species need time to gather enough resources for fruit body formation (Moore et al., 2008), causing a higher detection probability by fruit body sampling, paired with a simultaneous undersampling of the

increasing (mycelial) diversity (Mäkipää et al., 2017; Rajala et al., 2011) by low-intensity metabarcoding due to the small spatial coverage.

Further, metabarcoding also detected overall more threatened species on dead-wood of angio- and gymnosperms. Metabarcoding of high sampling intensity performed alike in both dead-wood types, while low-intensity metabarcoding detected fewer species in gymnosperms than in angiosperms. On object-level, both metabarcoding methods performed better than fruit body sampling.

We conclude that metabarcoding of high sampling intensity produces more reliable sampling data than metabarcoding of low sampling intensity across decay stages and dead-wood of angio- or gymnosperms. Hence, higher sampling intensity should be the favoured sampling method, as it always detected more species than fruit body sampling.

Detection in relation to the number of objects

Metabarcoding detected threatened species on more objects than fruit body sampling. This indicates that the detection probability of threatened species is higher with metabarcoding, and thus the sampling effort, i.e., the number of studied dead-wood objects, could be lower or deliver better results at equal sampling effort. As resources in conservation are mostly limited and not all dead-wood objects within an area can be sampled for reasons of feasibility, metabarcoding allows a more efficient assessment of threatened dead-wood inhabiting fungal species diversity and abundance. However, results differed among sites, and the share was lower in sites with low-intensity metabarcoding, again implying a higher probability of undersampling and highlighting the importance of a higher sampling effort within dead-wood objects.

Implications for fungal Red Lists

Red Lists are a useful tool to guide conservation priorities. For fungi they are rather new (Mueller et al., 2022), but the current version might already be outdated, as they are purely based on fruit body data. For example, metabarcoding allowed us to detect *Asterostroma cervicolor* and *Athelopsis subinconspicua* in Zofin (the latter also detected once as fruit body). In the Red List of the Czech Republic (Holec & Antonín, 2006), both species are listed as "extinct or lost", which is apparently wrong. Since metabarcoding has proven to be an accurate method to detect fungal species (Blaschke et al., 2023; Frøslev et al., 2019) it might be twofold good for a re-evaluation of fungal Red Lists.

First, metabarcoding allows for the detection of species not producing conspicuous fruit bodies, which should be included for comprehensive fungal conservation. Second, it allows for

more accurate abundance and distribution measures. The current fruit-body based Red Lists are biased, as fruit body development is linked to environmental variables like weather (Sakamoto, 2018), but "only" enables sexual reproduction and long-distance dispersal (Komonen & Müller, 2018). However, the mycelium is the main part of the fungus, spreading through the substrate, acquiring nutrients, competing with others, and thus playing a more pivotal role in the local survival of the fungi (Boddy, 2008). Therefore, it is arguable whether a threat status assessment purely on sexual reproduction events is purposeful. Metabarcoding data on the presence and abundance of fungal species in a region could yield additionally less environmental dependent abundance data. Also it might give more precise information on the ranges and distribution of fungal species (van der Linde et al., 2009). Nevertheless, this does not mean that a pure assessment via metabarcoding is without flaws, as it is unclear how frequently sexual reproduction events need to occur to secure vital fungal meta-populations or whether mycelial endurance and spread through soil is enough for the fungi to endure unfavourable conditions and reach other suitable habitats. An earlier study found a higher environmental susceptibility of fruit body populations than mycelial ones (Rieker et al., 2022). Hence population development estimates (the basis of Red List statuses) based purely on metabarcoding might not detect unfavourable conditions for fructification and necessary dispersal while still detecting species over several years, resulting in an extinction debt (Tilman et al., 1994).

Implications for fungal conservation

We show that metabarcoding is an efficient technique to detect threatened wood-inhabiting fungal species. The accuracy of this technique increases with sampling intensity and with a further completion of reference databases. Moreover, the good performance of metabarcoding in species detection bears potential to gain deeper insights into the real distribution of species. Hence, this technique seems a valuable tool to further developing Red Lists; first to assign novel species so far neglected via fruit body assessments (e.g., those with no or inconspicuous sexual characteristics) and second, to re-evaluate true abundances of species which has been assessed based on fruit bodies. However, as some fungal species were only discovered as fruit bodies, missed reference sequences, and both methods rarely detected the same species on the same object, pure use of metabarcoding will miss parts of the overall threatened fungal diversity. For the most comprehensive picture we, therefore, recommend, using both methods.

Table 1: Results of the GLMMs testing the number of threatened species per dead-wood object and number of dead-wood objects occupied by threatened species using three different sampling methods. Fruit body sampling is the reference group. Asterisks display the significance of each predictor (= p = <0.05, ** = p <0.01, *** = p <0.001).*

	Predictors	z value	R^2m
Number of species ~	Intercept	-10.791***	0.329
	Metabarcoding (high)	19.187***	
	Metabarcoding (low)	5.859***	
Occupied ~	Intercept	-6.041***	0.423
	Metabarcoding (high)	10.099***	
	Metabarcoding (low)	8.702***	

Table 2: Absolute and relative number of objects threatened species were detected on by both methods in the same year.

Fruit body sampling compared with	*No. of simultaneously detected objects*		
	Sampling campaign one	*Sampling campaign two*	*Sampling campaign three*
metabacroding of low sampling intensity	*5.6% (1/18)♦*	*13.5% (5/37)♦*	*NA*
metabacroding of high sampling intensity	*26.3% (41/156)♦*	*17.6% (3/17)♦*	*4.9% (2/41)♦*

♦ *No. of objects threatened species were simultaneously detected/no. of objects occupied by threatened species in the respective year*

Table 3: Results of the linear mixed-effects models on the number of threatened species detected by each method in each decay stage and objects of angio-/gymnosperm trees. Asterisks display the significance of each predictor (= p = <0.05, ** = p <0.01, *** = p <0.001).*

Model group	Number of species ~	z value	R^2m
Decay stage 1	Intercept	-10.494***	0.38
	Metabarcoding (high)	15.154***	
	Metabarcoding (low)	6.648***	
Decay stage 2	Intercept	-1.814	0.287
	Metabarcoding (high)	6.442***	
	Metabarcoding (low)	-0.150	
Decay stage 3	Intercept	-2.134*	0.247
	Metabarcoding (high)	7.509***	
	Metabarcoding (low)	1.285	
Decay stage 4	Intercept	-3.313***	0.384
	Metabarcoding (high)	5.513***	
	Metabarcoding (low)	2.898**	
Angiosperm	Intercept	-7.139***	0.273
	Metabarcoding (high)	12.649***	
	Metabarcoding (low)	2.945**	
Gymnosperm	Intercept	-8.132***	0.363
	Metabarcoding (high)	14.243***	
	Metabarcoding (low)	5.418***	

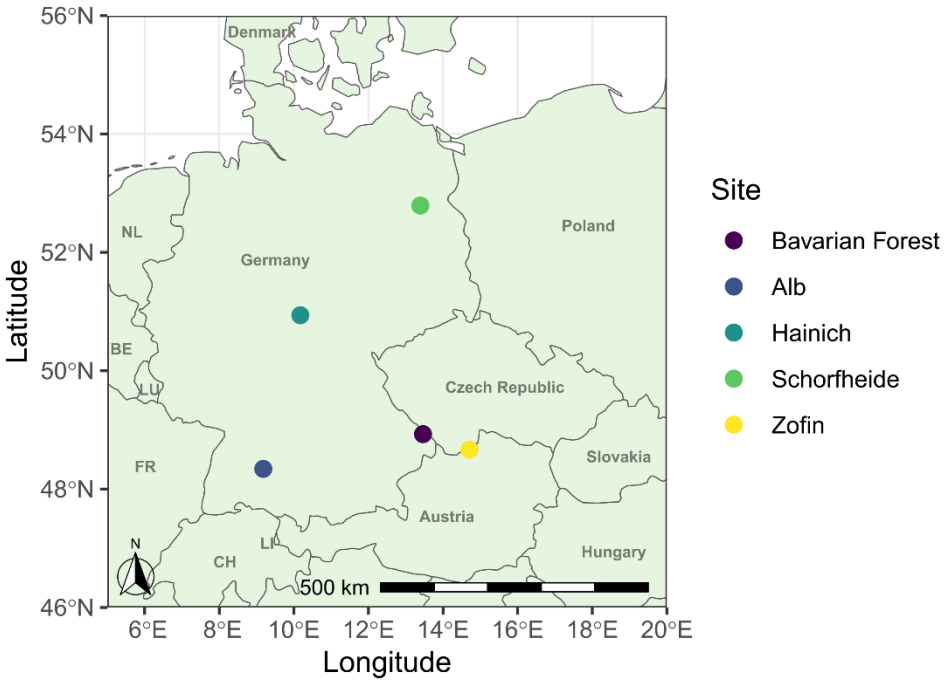

Figure 1: Location of the five sampling sites in Central Europe.

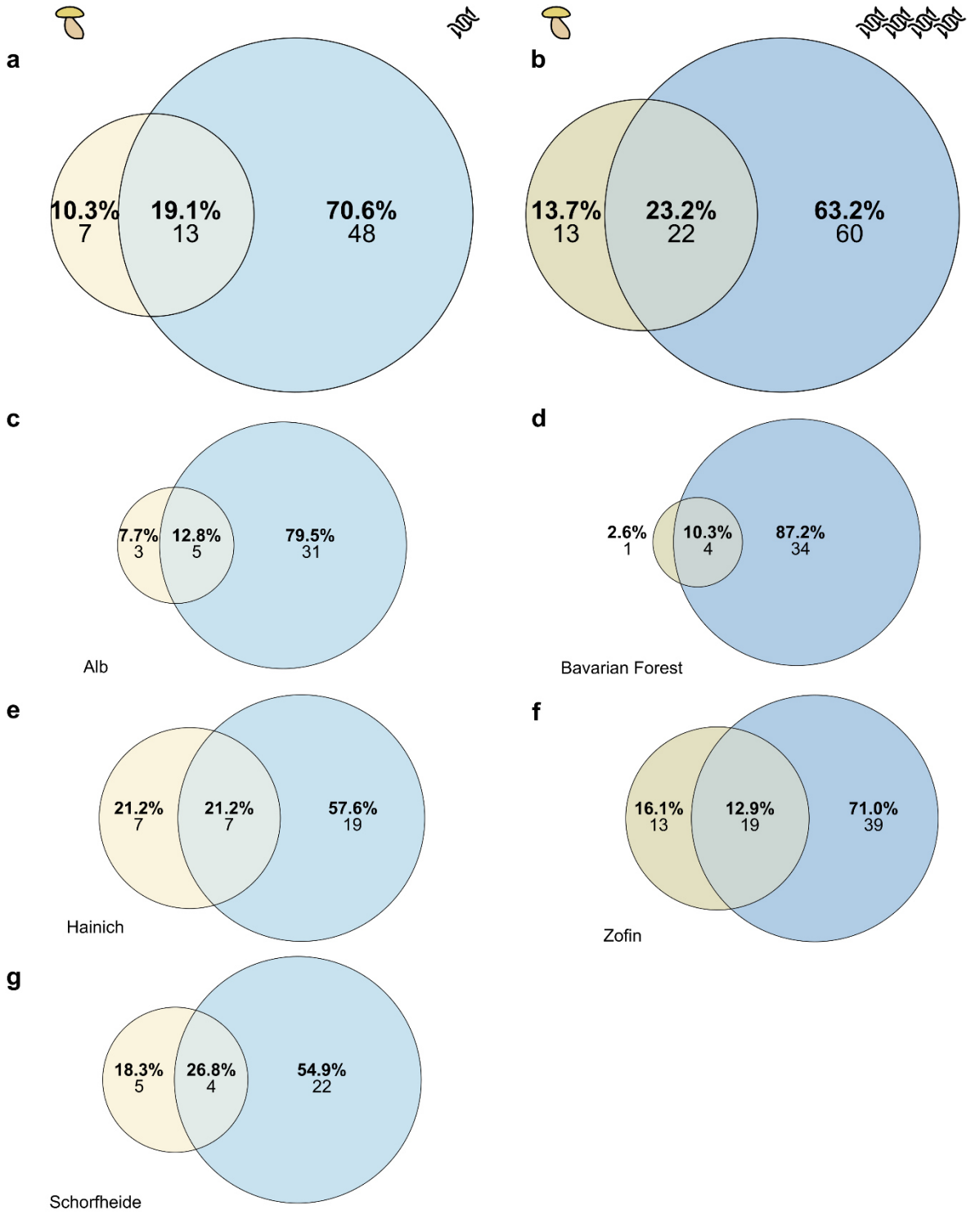

Figure 2: Relative and absolute numbers of threatened species detected by fruit body sampling or metabarcoding with low (a, c, e, g) or high sampling intensity (b, d, f). Figure a and b display the overall comparison of fruit body sampling and metabarcoding of the respective sampling intensity. Figure c – g the site-specific comparisons.

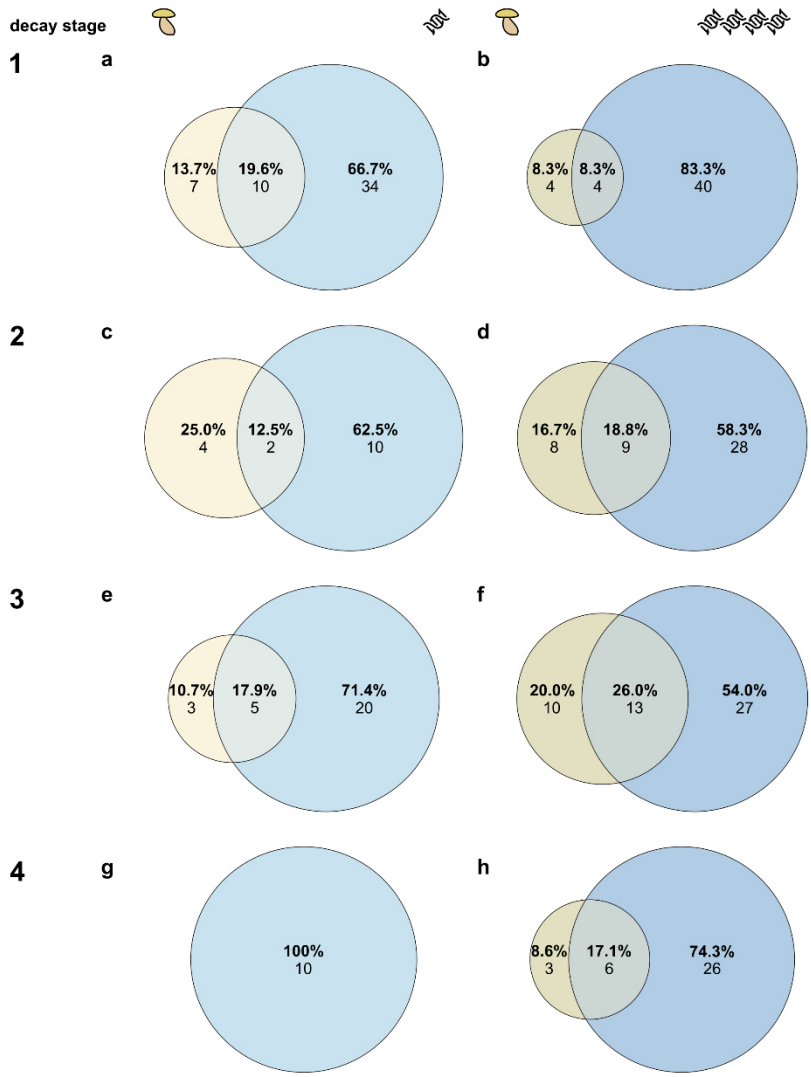

Figure 3: Relative and absolute number of threatened species detected by fruit body or metabarcoding with low (a, c, e, g) or high sampling intensity (b, d, f, h) per decay stage.

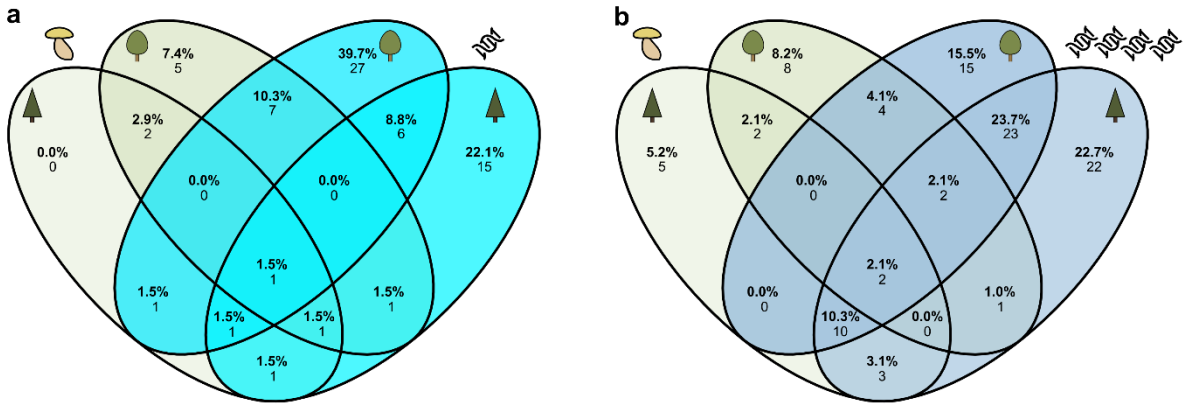

Figure 4: Comparison of the relative and absolute number of threatened species detected on dead-wood objects of angio- and gymnosperm tree species by (a) fruit body sampling and metabarcoding with low sampling intensity, (b) fruit body sampling and metabarcoding with high sampling intensity.

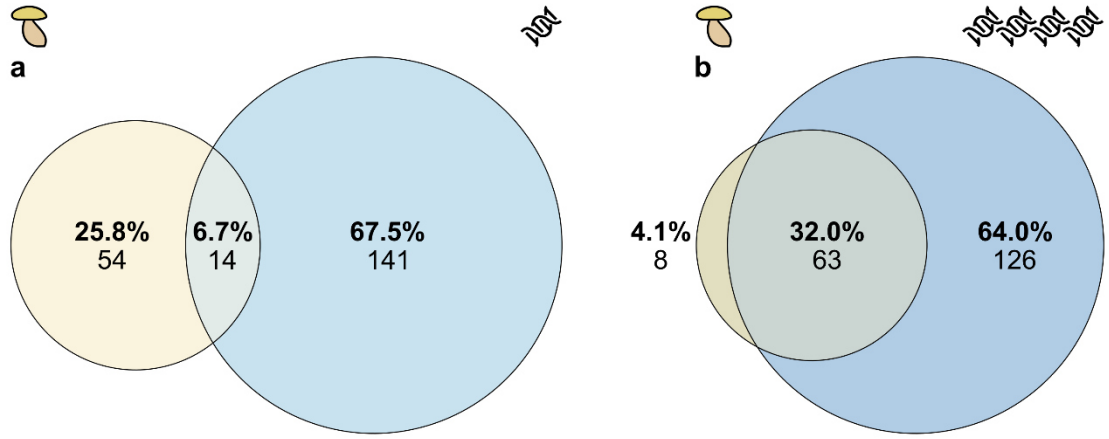

Figure 5: Number of unique and shared dead-wood objects inhabited by threatened fungi species detected by fruit body sampling or metabarcoding.

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Appendix A

Sampling sites

Alb

The study site Alb is, like Hainich and Schorfheide, part of the BELongDead experiment (Fischer et al., 2010). It is located in south-west Germany at the UNESCO Swabian Alb Biosphere Reserve, at an altitude of 460–860 m a.s.l. with 6–7°C (MAT) and 700–1000 mm (MAP), dominated by *F. sylvatica*, *P. abies* makes up to 24% of the forest cover.

Hainich

The Hainich site located in Central Germany, including Hainich National Park, on an altitude of 285–550 m a.s.l. with 6.5–8°C MAT and 500–800 mm MAP, dominated by *F. sylvatica* and a conifer cover of only 12%.

Schorfheide

The Schorfheide study site is located in north-east Germany, in the Schorfheide-Chorin UNESCO Biosphere Reserve, on an altitude of 3–140 m a.s.l. with 8–8.5°C (MAT) and 500–600 mm (MAP), dominated by Scots pine (*Pinus sylvestris*) (39%), and only 12% beech cover.

Bavarian Forest

This experiment was conducted in the mixed montane forests in Bavarian Forest National Park in south-eastern Germany, at elevations between 650 and 1450 m a.s.l. Depending on altitude, the mean annual temperature (MAT, 1972–2001) varies from 3.5 to 7.0°C, and the total annual precipitation varies from 1300 to 1900 mm (MAP, Bässler, 2004). Above about 1100–1200 m a.s.l., the high montane forest is dominated by Norway spruce (*Picea abies*), with a low proportion of European beech (*Fagus sylvatica*) and Mountain ash (*Sorbus aucuparia*); below this altitude, the mixed montane forest is dominated by spruce, beech and Silver fir (*Abies alba*) (Walentowski et al., 2004).

Zofin

The study area was located in the Novohradske Hory mountains, specifically in the 25 ha Zofin ForestGEO® Dynamics Plot (www.forestgeo.si.edu), in the core zone of the Zofínský prales National Nature Reserve in the Czech Republic. The elevation ranges between 735 to 830 m a.s.l. with a slight NW slope. MAP is 866 mm and MAT is 6.2°C (Anderson-Teixeira et al., 2015). At present, the reserve is covered by a mixed forest. *F. sylvatica* predominates (51.5%), followed by *Picea abies* (42.8%) and *Abies alba* (4.8%).

Laboratory protocols for PCR data

BELongDead

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 object (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 ITS2 region of the fungal 16S rRNA gene was amplified in triplicate using the primers fITS7/ITS4, 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. 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. Chimeras were removed using the consensus algorithm. Raw sequences have been deposited to the NCBI short read archive (SRA) and are accessible under BioProject accession number PRJNA756463.

Bavarian forest

Four CWD samples were obtained from each selected *object* in October 2013 using an electric drill with a bit diameter of 8 mm. The length of each CWD unit (or the sum of the lengths of its fragments) was measured, and samples were collected at 1/8, 3/8, 5/8 and 7/8 of the CWD length. Drilling was performed vertically from the middle of the upper surface up to a depth of 40 cm. The drill bit was sterilized between drillings, and sawdust was collected in batches of two adjacent drill holes in sterile plastic bags and frozen within a few hours after drilling.

Zofin

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40 cm. The drill bit was sterilized between drillings, and sawdust was collected in batches of two adjacent drill holes in sterile plastic bags and frozen within a few hours after drilling.

In the laboratory, the sawdust material was freeze-dried and milled using an Ultra Centrifugal Mill ZM 200 (Retsch, Germany), and the resulting fine sawdust was used for subsequent analyses. Total genomic DNA was extracted from 200 mg of material using the NucleoSpin Soil Kit (Macherey-Nagel, Germany) according to the manufacturer's instructions. Briefly, cells were lysed using SL1 lysis buffer. Enhancer SX was added prior to lysis. The samples were homogenized using FastPrep-24 (MP Biomedicals, Santa Anna, USA) at 5 m s^{-1} for 2 × 30 s. In the last step, DNA was eluted from the columns using 50 ml of elution buffer SE (5 mM Tris/HCl, pH 8.5). Two replicate extractions per sample were performed, combining the sawdust obtained from two adjacent drill holes. After extraction, DNA from both extractions was combined to represent the whole CWD. For the microbial community analysis, PCR amplification of the fungal ITS2 region was performed using barcoded gITS7 and ITS4 (Ihrmark et al., 2012) in three PCR reactions per sample as described previously (Žifčáková et al., 2016). Triplicate PCR reactions contained 2.5 ml of 10 × buffer for DyNAzyme DNA Polymerase, 0.75 ml of BSA (20 mg ml^{-1}), 1 µl of each primer (0.01 mM), 0.5 µl of PCR Nucleotide Mix (10 mM each), 0.75 µl polymerase (2 U $µl^{-1}$ DyNAZyme II DNA polymerase 1: 24 Pfu DNA polymerase) and 1 µl of template DNA. Cycling conditions were 94°C for 5 min, 35 cycles of 94°C for 1 min, 62°C for 1 min, and 72°C for 1 min, and a final extension at 72°C for 10 min. Sequencing of amplicons was performed in-house on Illumina MiSeq (2X250 base pair-end run).

The amplicon sequencing data were processed using the pipeline SEED 1.2.1 (Větrovský & Baldrian, 2013). Briefly, pair-end reads were merged using fastq-join (Aronesty, 2013). The ITS2 region was extracted using ITS Extractor 1.0.8 (Nilsson et al., 2010) before processing. Chimeric sequences were detected using Usearch 7.0.1090 (Edgar, 2010) and deleted, and sequences were clustered using UPARSE implemented within Usearch (Edgar, 2013) at a 97% similarity level. Sequence data have been deposited in the MG RAST public database (Meyer et al. (2008), data set number 270336).

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Appendix B

Table B1: Complete species list of threatened species with the number of occupied dead-wood-objects detected with each method (FB = Fruit body; Metab. = Metabarcoding) in each site.

Species	Red List		Alb		Hainich		Schorfheide		Bavarian Forest		Zofin	
	DE†	CZ	FB	Metab.	FB	Metab.	FB	Metab.	FB	Metab.	FB	Metab.
Agaricus devoniensis	G	CR		12								
Agaricus laevigatus		VU		12							19	31
Amaurodon cyaneus	R	CR						1				
Amyloxenasma grisellum	R					3		8		3		
Antrodiella citrinella	R	EN		4								6
Arrhenia epichysium	3	EN									2	
Ascotremella faginea		VU									1	
Asterostroma cervicolor		?EX										1
Athelopsis subinconspicua	D	?EX									1	4
Aurantiporus fissilis	G					1						
Boidinia furfuracea	D	NT			7	6	6	7	1	3		
Bondarzewia mesenterica	V											3
Botryobasidium medium	D	EN							1	5		
Butyrea luteoalba	D	?EX								3		
Calocybe gangraenosa	V	EN		4								
Camarops petersii	R											12
Camarops tubulina	R	NT				2		1		2	3	
Catinella olivacea	3	NT						2		2		2
Clavulicium macounii	R	EN										2
Climacodon septentrionalis	1										1	
Clitocybula lacerata	G	EN		14							1	
Coniophora olivacea	G		1	5							1	10
Conocybe digitalina	D	CR			1						2	
Cortinarius spilomeus	V	DD										1
Crustomyces subabruptus	1	EN				1						3
Cudoniella clavus		NT										3
Cyanosporus subcaesius		EN			2		2		2			
Cystostereum murrayi	2	NT		4								
Dentipellis fragilis	G			2				1			2	2
Desmazierella acicola	D	EN								3		

Ditiola mucida		EN			2		4	2				
Elaphomyces asperulus	3					1						
Entoloma byssisedum	V										1	
Entoloma juncinum		EN							1	1		
Entoloma tjallingiorum	G	EN									2	
Exidia thuretiana		CR				2						
Flammulaster carpophilus	R		1			1						
Flammulaster muricatus		EN							1			
Fomitopsis rosea	G	NT									2	1
Genea hispidula	3											4
Geopora cooperi	R			1								
Gerronema xanthophyllum	R											1
Granulobasidium vellereum		EN				1	1	2				
Gymnopilus bellulus		VU										6
Gymnopilus picreus	V										4	
Gyromitra gigas	3											1
Gyromitra sphaerospora	R	CR										6
Gyrophanopsis polonensis	D	NT				1					1	1
Helvella fastigiata	R	EN				2						
Helvella monachella	V										2	16
Hemipholiota heteroclita	G	VU								1		
Hericium alpestre	2	NT		13							1	6
Hericium cirrhatum	G							1				
Hericium coralloides	G			6				2				4
Hericium erinaceus	2	VU										6
Heyderia abietis	3					1						
Hohenbuehelia auriscalpium	D	EN									2	
Hohenbuehelia fluxilis		EN		1								
Hydnotrya bailii	R			1								
Hydnotrya tulasnei	3									2		3
Hydropus atramentosus	D	EN		3							1	1
Hydropus marginellus	2			2							2	6
Hymenochaete fuliginosa	2	VU										2
Hyphodontia alienata	R											7
Hypholoma ericaeum	G											1
Inocybe corydalina		NT		11								
Inocybe fibrosoides	G			16		1						
Irpex lacteus		EN	2	1			1			1		

Junghuhnia collabens	D	CR						1			2	4
Kneiffiella microspora	R			2						1		
Lachnellula fuscosanguinea	R							3		1		
Lactarius decipiens	V			5								
Lactarius rubrocinctus	G	CR				1						
Lactarius serifluus	V			1								
Lentinellus micheneri	G					1						
Leptosporomyces fuscostratus	R							2				
Lichenomphalia umbellifera	2	CR										2
Lycoperdon lividum	V			2								
Multiclavula mucida		EN										1
Mutinus caninus		NT				1		2		4		
Mycena algeriensis	R											13
Mycena citrinomarginata	G			22								1
Mycena niveipes	G											7
Mycena pearsoniana	G			3								
Mycena pseudocorticola		EN				1						
Mycenella lasiosperma	3			2								
Nemania chestersii	R	EN								3		
Neobulgaria premnophila	R					8						
Neobulgaria pura		NT	1	16	1	1	1	4		1	1	3
Octaviania asterosperma	G					1		1				4
Ophiocordyceps stylophora	R											1
Panellus violaceofulvus		CR	7	31		1						
Peniophora pini	G									2		
Peniophorella echinocystis	R									1		3
Penttilamyces romellii	R								3			
Phaeoclavulina decurrens	R	DD										1
Phaeoclavulina flaccida	G											1
Phellinus igniarius	R			1								
Phellinus nigrolimitatus	2	NT		5							4	6
Phellinus viticola	G										2	
Phlebia centrifuga	1	EN									5	5
Phlebia subserialis	R			1								
Phleogena faginea	3	EN					1			2		
Phloeomana alba	G					1		2				

Pholiota scamba	V										1	2
Pholiota tuberculosa	G				4	1	2	1				
Physisporinus crocatus	1	EN									15	14
Pluteus chrysophaeus	D	NT										1
Pluteus petasatus	V									1		
Pluteus phlebophorus		EN			6	1	1	1	2		9	6
Pluteus podospileus	V	EN						1		1		6
Pluteus thomsonii		EN						1			1	
Pluteus umbrosus	V	VU				1	1				2	3
Polyozellus humicola		CR										1
Porodaedalea pini	V											1
Porotheleum fimbriatum		CR			11	10		1				
Postia balsamea	G						1		1			
Prunulus diosmus		EN								1		
Psathyrella maculata	2	DD				2						
Pseudoplectania nigrella	G	EN		1		1						
Pseudotremella moriformis	R			1								
Pycnoporellus fulgens		NT		5		1	1	1	1	2	1	2
Radulomyces hiemalis	D	CR		5		2				1		
Rhizoctonia ochracea	R					4		3				
Rhodonia placenta	D	EN		2		8		2		3		2
Russula emetica	2										1	
Russula fragrantissima	2					1						
Russula mustelina	V			3								
Russula odorata	3											1
Russula puellula	G	DD		1								
Russula romellii	V					1						
Skeletocutis odora		EN		1								7
Thaxterogaster porphyropus	G	DD										1
Tomentella testaceogilva		EN					1					
Tomentella viridula	R						1					
Tricholoma portentosum	3					1						
Tuber puberulum	G					1		1		1		2
total = 137	97*	69*	5/12♦	38/222♦	8/34♦	36/74♦	14/24♦	26/54♦	9/13♦	26/51♦	32/95♦	58/253♦
Species without reference sequences												
Botryobasidium intertextum	D	NT									3	
Camaropella microspora	3						1					

Chrysomphalina grossula		EN			2						1	
Diplocarpa bloxamii	R										1	
Flammulaster limulatus		EN					1					
Lyomyces juniperi	R				1							
Odonticium septocystidiatum	D	CR							1			
Oxyporus ravidus	R						1					
Phellinus hartigii	V										1	
Phlebia cremeoalutacea	R						1				1	
Pluteus hispidulus	V	VU									6	
Xenasmatella subflavidogrisea	R				1							

† Code: V: near threatened, R: extremely rare, G: threat of unknown extent, 3 threatened, 2: highly threatened, 1: threatened with extinction, 0: extinct or lost

* Only species without data deficiency (“D” in Red List of Germany, “DD” in Red List of Czech Republic) were counted

♦ number of detected species/number of records

Table B2: Absolute number of unique objects threatened species were detected on by each method (FB = Fruit body, Metab. = Metabarcoding) uniquely and by both methods in the Alb.

	2012			2015			2018	2017
Species	FB	Metab.	Shared	FB	Metab.	Shared	FB	Metab.
Amyloxenasma grisellum	0	0	0	0	2	0	0	1
Aurantiporus fissilis	0	0	0	0	1	0	0	0
Boidinia furfuracea	1	0	0	4	2	0	2	4
Camarops tubulina	0	0	0	0	0	0	0	2
Conocybe digitalina	0	0	0	1	0	0	0	0
Crustomyces subabruptus	0	0	0	0	1	0	0	0
Cyanosporus subcaesius	0	0	0	0	0	0	2	0
Ditiola mucida	0	0	0	1	0	0	1	0
Elaphomyces asperulus	0	0	0	0	0	0	0	1
Exidia thuretiana	0	2	0	0	0	0	0	0
Flammulaster carpophilus	0	0	0	0	0	0	0	1
Granulobasidium vellereum	0	1	0	0	0	0	0	0
Gyrophanopsis polonensis	0	0	0	0	1	0	0	0
Helvella fastigiata	0	0	0	0	1	0	0	1
Heyderia abietis	0	0	0	0	1	0	0	0
Inocybe fibrosoides	0	0	0	0	0	0	0	1
Lactarius rubrocinctus	0	0	0	0	1	0	0	0
Lentinellus micheneri	0	1	0	0	0	0	0	0
Mutinus caninus	0	1	0	0	0	0	0	0
Mycena pseudocorticola	0	1	0	0	0	0	0	0
Neobulgaria premnophila	0	4	0	0	2	0	0	2
Neobulgaria pura	1	1	0	0	0	0	0	0
Octaviania asterosperma	0	1	0	0	0	0	0	0
Panellus violaceofulvus	0	1	0	0	0	0	0	0
Phloeomana alba	0	1	0	0	0	0	0	0
Pholiota tuberculosa	0	0	0	3	1	0	1	0
Pluteus phlebophorus	0	0	0	4	0	0	2	1
Pluteus umbrosus	0	0	0	0	0	0	0	1
Porotheleum fimbriatum	4	4	1	4	4	2	3	2
Psathyrella maculata	0	0	0	0	1	0	0	1
Pseudoplectania nigrella	0	0	0	0	0	0	0	1
Pycnoporellus fulgens	0	0	0	0	0	0	0	1
Radulomyces hiemalis	0	2	0	0	0	0	0	0
Rhizoctonia ochracea	0	0	0	0	2	0	0	2
Rhodonia placenta	0	3	0	0	2	0	0	3
Russula fragrantissima	0	0	0	0	0	0	0	1
Russula romellii	0	0	0	0	0	0	0	1
Tricholoma portentosum	0	0	0	0	0	0	0	1
Tuber puberulum	0	1	0	0	0	0	0	0
Sum	6	24	1	17	22	2	11	28
Number of species	3	14	1	6	14	1	6	19

Table B3: Absolute number of unique objects threatened species were detected on by each method (FB = Fruit body, Metab. = Metabarcoding) uniquely and by both methods in Hainich

	2012			2015			2018	2017
Species	FB	Metab.	Shared	FB	Metab.	Shared	FB	Metab.
Amaurodon cyaneus	0	1	0	0	0	0	0	0
Amyloxenasma grisellum	0	2	0	0	5	0	0	1
Boidinia furfuracea	1	0	0	4	2	1	1	5
Camarops tubulina	0	0	0	0	0	0	0	1
Catinella olivacea	0	0	0	0	1	0	0	1
Cyanosporus subcaesius	0	0	0	2	0	0	0	0
Dentipellis fragilis	0	0	0	0	0	0	0	1
Ditiola mucida	1	1	0	3	1	1	0	0
Granulobasidium vellereum	0	1	0	1	0	0	0	1
Hericium cirrhatum	0	0	0	0	1	0	0	0
Hericium coralloides	0	2	0	0	0	0	0	0
Irpex lacteus	0	0	0	1	0	0	0	0
Junghuhnia collabens	0	0	0	0	0	0	0	1

Lachnellula fuscosanguinea	0	0	0	0	2	0	0	1
Leptosporomyces fuscostratus	0	0	0	0	1	0	0	1
Mutinus caninus	0	0	0	0	0	0	0	2
Neobulgaria pura	0	2	0	1	2	0	0	0
Octaviania asterosperma	0	0	0	0	0	0	0	1
Phleogena faginea	0	0	0	1	0	0	0	0
Phloeomana alba	0	1	0	0	1	0	0	0
Pholiota tuberculosa	0	1	0	0	0	0	2	0
Pluteus phlebophorus	0	0	0	1	0	0	0	1
Pluteus podospileus	0	0	0	0	1	0	0	0
Pluteus thomsonii	0	0	0	0	0	0	0	1
Pluteus umbrosus	0	0	0	0	0	0	1	0
Porotheleum fimbriatum	0	0	0	0	1	0	0	0
Postia balsamea	1	0	0	0	0	0	0	0
Pycnoporellus fulgens	0	0	0	0	0	0	1	1
Rhizoctonia ochracea	0	0	0	0	2	0	0	1
Rhodonia placenta	0	0	0	0	1	0	0	1
Tomentella testaceogilva	0	0	0	1	0	0	0	0
Tomentella viridula	0	0	0	1	0	0	0	0
Tuber puberulum	0	0	0	0	1	0	0	0
Sum	3	11	0	16	22	2	5	21
Number of species	4	9	0	11	14	3	5	17

Table B4: Absolute number of unique objects threatened species were detected on by each method (FB = Fruit body, Metab. = Metabarcoding) uniquely and by both methods in Schorfheide

	2012			2015			2018	2017
Species	FB	Metab.	Shared	FB	Metab.	Shared	FB	Metab.
Amyloxenasma grisellum	0	1	0	0	1	0	0	1
Boidinia furfuracea	0	1	0	0	1	0	1	1
Botryobasidium medium	0	0	0	1	2	0	0	3
Butyrea luteoalba	0	0	0	0	1	0	0	2
Camarops tubulina	0	0	0	0	0	0	0	2
Catinella olivacea	0	0	0	0	1	0	0	1
Cyanosporus subcaesius	0	0	0	2	0	0	0	0
Desmazierella acicola	0	1	0	0	0	0	0	2
Entoloma juncinum	0	0	0	0	0	0	1	1
Flammulaster muricatus	0	0	0	1	0	0	0	0
Hemipholiota heteroclita	0	0	0	0	1	0	0	0
Hydnotrya tulasnei	0	1	0	0	1	0	0	0
Irpex lacteus	0	1	0	0	0	0	0	0
Kneiffiella microspora	0	1	0	0	0	0	0	0
Lachnellula fuscosanguinea	0	0	0	0	0	0	0	1
Mutinus caninus	0	0	0	0	0	0	0	4
Nemania chestersii	0	0	0	0	1	0	0	2
Neobulgaria pura	0	1	0	0	0	0	0	0
Peniophora pini	0	0	0	0	1	0	0	1
Peniophorella echinocystis	0	0	0	0	0	0	0	1
Penttilamyces romellii	0	0	0	0	0	0	3	0
Phleogena faginea	0	0	0	0	1	0	0	1
Pluteus petasatus	0	0	0	0	0	0	0	1
Pluteus phlebophorus	0	0	0	0	0	0	2	0
Pluteus podospileus	0	0	0	0	1	0	0	0
Postia balsamea	1	0	0	0	0	0	0	0
Prunulus diosmus	0	0	0	0	0	0	0	1
Pycnoporellus fulgens	0	0	0	1	1	1	0	1
Radulomyces hiemalis	0	0	0	0	0	0	0	1
Rhodonia placenta	0	1	0	0	1	0	0	1
Tuber puberulum	0	0	0	0	1	0	0	0
Sum	1	8	0	5	15	1	7	28
Number of species	1	8	0	4	14	1	4	19

Table B5: Absolute number of unique objects threatened species were detected on by each method (FB = Fruit body, Metab. = Metabarcoding) uniquely and by both methods in the Bavarian Forest.

	2012			2013			2015		
Species	FB	Metab.	Shared	FB	Metab.	Shared	FB	Metab.	Shared
Agaricus devoniensis	0	0	0	0	0	0	0	12	0
Agaricus laevigatus	0	0	0	0	0	0	0	12	0
Antrodiella citrinella	0	0	0	0	0	0	0	4	0
Calocybe gangraenosa	0	0	0	0	0	0	0	4	0
Clitocybula lacerata	0	0	0	0	0	0	0	14	0
Coniophora olivacea	0	0	0	1	0	0	0	5	0
Cystostereum murrayi	0	0	0	0	0	0	0	4	0
Dentipellis fragilis	0	0	0	0	0	0	0	2	0
Flammulaster carpophilus	1	0	0	0	0	0	0	0	0
Geopora cooperi	0	0	0	0	0	0	0	1	0
Hericium alpestre	0	2	0	0	3	0	0	8	0
Hericium coralloides	0	0	0	0	0	0	0	6	0
Hohenbuehelia fluxilis	0	0	0	0	1	0	0	0	0
Hydnotrya bailii	0	1	0	0	0	0	0	0	0
Hydropus atramentosus	0	0	0	0	0	0	0	3	0
Hydropus marginellus	0	0	0	0	0	0	0	2	0
Inocybe corydalina	0	0	0	0	0	0	0	11	0
Inocybe fibrosoides	0	0	0	0	0	0	0	16	0
Irpex lacteus	0	0	0	0	1	0	2	0	0
Kneiffiella microspora	0	0	0	0	0	0	0	2	0
Lactarius decipiens	0	0	0	0	1	0	0	4	0
Lactarius serifluus	0	0	0	0	1	0	0	0	0
Lycoperdon lividum	0	0	0	0	0	0	0	2	0
Mycena citrinomarginata	0	0	0	0	0	0	0	22	0
Mycena pearsoniana	0	0	0	0	0	0	0	3	0
Mycenella lasiosperma	0	0	0	0	0	0	0	2	0
Neobulgaria pura	0	0	0	1	6	1	0	10	0
Panellus violaceofulvus	0	2	0	2	8	2	5	21	2
Phellinus igniarius	0	0	0	0	0	0	0	1	0
Phellinus nigrolimitatus	0	0	0	0	0	0	0	5	0
Phlebia subserialis	0	0	0	0	0	0	0	1	0
Pleurotus cornucopiae	0	0	0	0	0	0	0	0	0
Pseudoplectania nigrella	0	0	0	0	1	0	0	0	0
Pseudotremella moriformis	0	1	0	0	0	0	0	0	0
Pycnoporellus fulgens	0	0	0	0	1	0	0	4	0
Radulomyces hiemalis	0	2	0	0	3	0	0	0	0
Rhodonia placenta	0	0	0	0	0	0	0	2	0
Russula mustelina	0	3	0	0	0	0	0	0	0
Russula puellula	0	0	0	0	0	0	0	1	0
Skeletocutis odora	0	0	0	0	0	0	0	1	0
Sum	1	11	0	4	26	3	7	185	2
Number of species	1	6	0	3	10	2	2	30	1

Table B6: Absolute number of unique objects threatened species were detected on by each method uniquely and by both methods in Zofin.

	2017		
species	Fruit body	Metabarcoding	Shared
Agaricus laevigatus	19	31	15
Antrodiella citrinella	0	6	0
Arrhenia epichysium	2	0	0
Ascotremella faginea	1	0	0
Asterostroma cervicolor	0	1	0
Athelopsis subinconspicua	1	4	0
Bondarzewia mesenterica	0	3	0
Camarops petersii	0	12	0
Camarops tubulina	3	0	0
Catinella olivacea	0	2	0
Clavulicium macounii	0	2	0
Climacodon septentrionalis	1	0	0

Clitocybula lacerata	1	0	0
Coniophora olivacea	1	10	1
Conocybe digitalina	2	0	0
Cortinarius spilomeus	0	1	0
Crustomyces subabruptus	0	3	0
Cudoniella clavus	0	3	0
Dentipellis fragilis	2	2	1
Entoloma byssisedum	1	0	0
Entoloma tjallingiorum	2	0	0
Fomitopsis rosea	2	1	1
Genea hispidula	0	4	0
Gerronema xanthophyllum	0	1	0
Gymnopilus bellulus	0	6	0
Gymnopilus picreus	4	0	0
Gyromitra gigas	0	1	0
Gyromitra sphaerospora	0	6	0
Gyrophanopsis polonensis	1	1	0
Helvella monachella	2	16	1
Hericium alpestre	1	6	1
Hericium coralloides	0	4	0
Hericium erinaceus	0	6	0
Hohenbuehelia auriscalpium	2	0	0
Hydnotrya tulasnei	0	3	0
Hydropus atramentosus	1	1	1
Hydropus marginellus	2	6	0
Hymenochaete fuliginosa	0	2	0
Hyphodontia alienata	0	7	0
Hypholoma ericaeum	0	1	0
Junghuhnia collabens	2	4	2
Lichenomphalia umbellifera	0	2	0
Multiclavula mucida	0	1	0
Mycena algeriensis	0	13	0
Mycena citrinomarginata	0	1	0
Mycena niveipes	0	7	0
Neobulgaria pura	1	3	1
Octaviania asterosperma	0	4	0
Ophiocordyceps stylophora	0	1	0
Peniophorella echinocystis	0	3	0
Phaeoclavulina decurrens	0	1	0
Phaeoclavulina flaccida	0	1	0
Phellinus nigrolimitatus	4	6	3
Phellinus viticola	2	0	0
Phlebia centrifuga	5	5	3
Pholiota scamba	1	2	0
Physisporinus crocatus	15	14	5
Pluteus chrysophaeus	0	1	0
Pluteus phlebophorus	9	6	4
Pluteus podospileus	0	6	0
Pluteus thomsonii	1	0	0
Pluteus umbrosus	2	3	1
Polyozellus humicola	0	1	0
Porodaedalea pini	0	1	0
Pycnoporellus fulgens	1	2	1
Rhodonia placenta	0	2	0
Russula emetica	1	0	0
Russula odorata	0	1	0
Skeletocutis odora	0	7	0
Thaxterogaster porphyropus	0	1	0
Tuber puberulum	0	2	0
Sum	95	253	41
Number of species	32	58	15

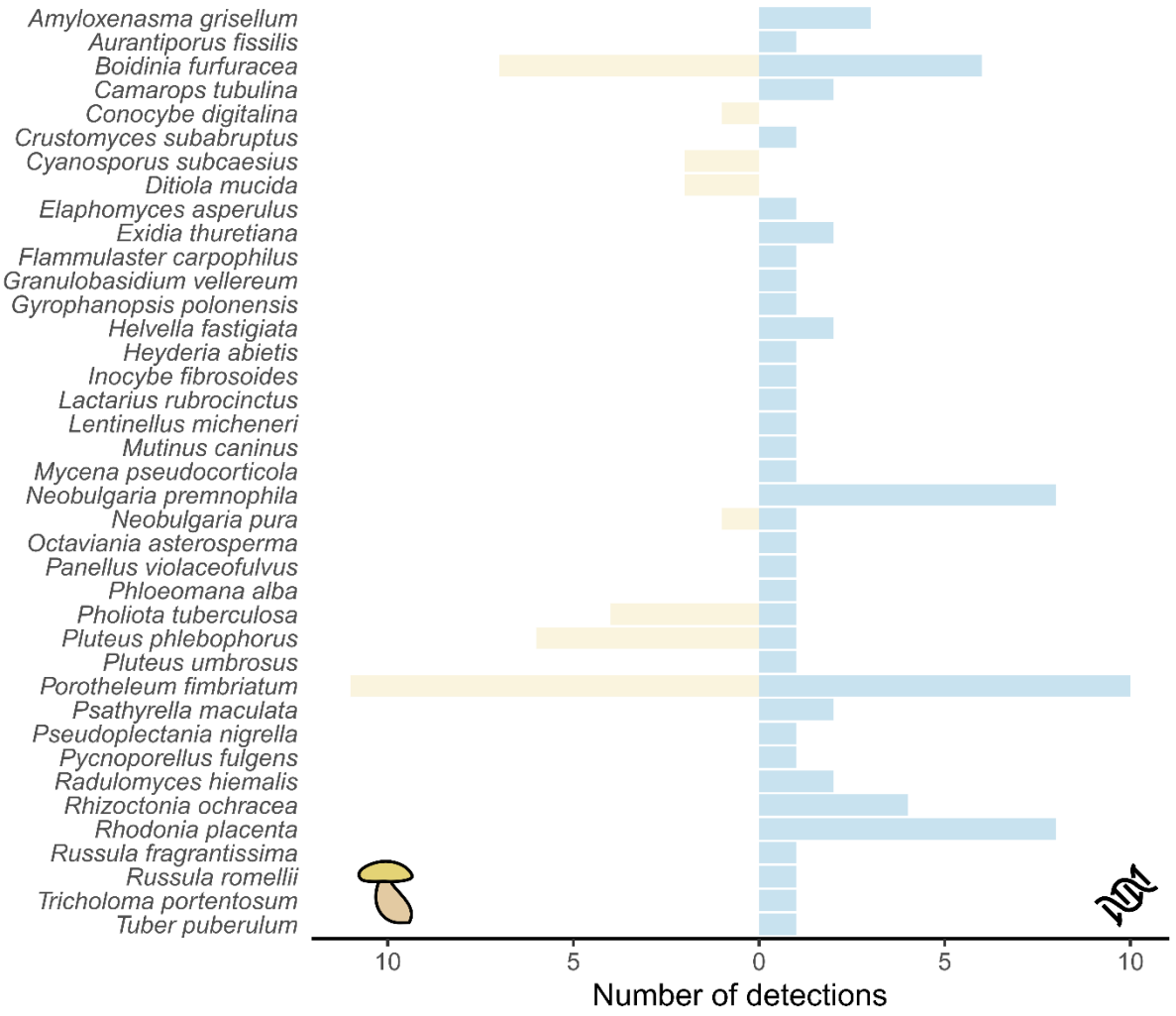

Figure B1: All threatened fungal species detected in the Alb with the number of times they have been detected by fruit body sampling or metabarcoding.

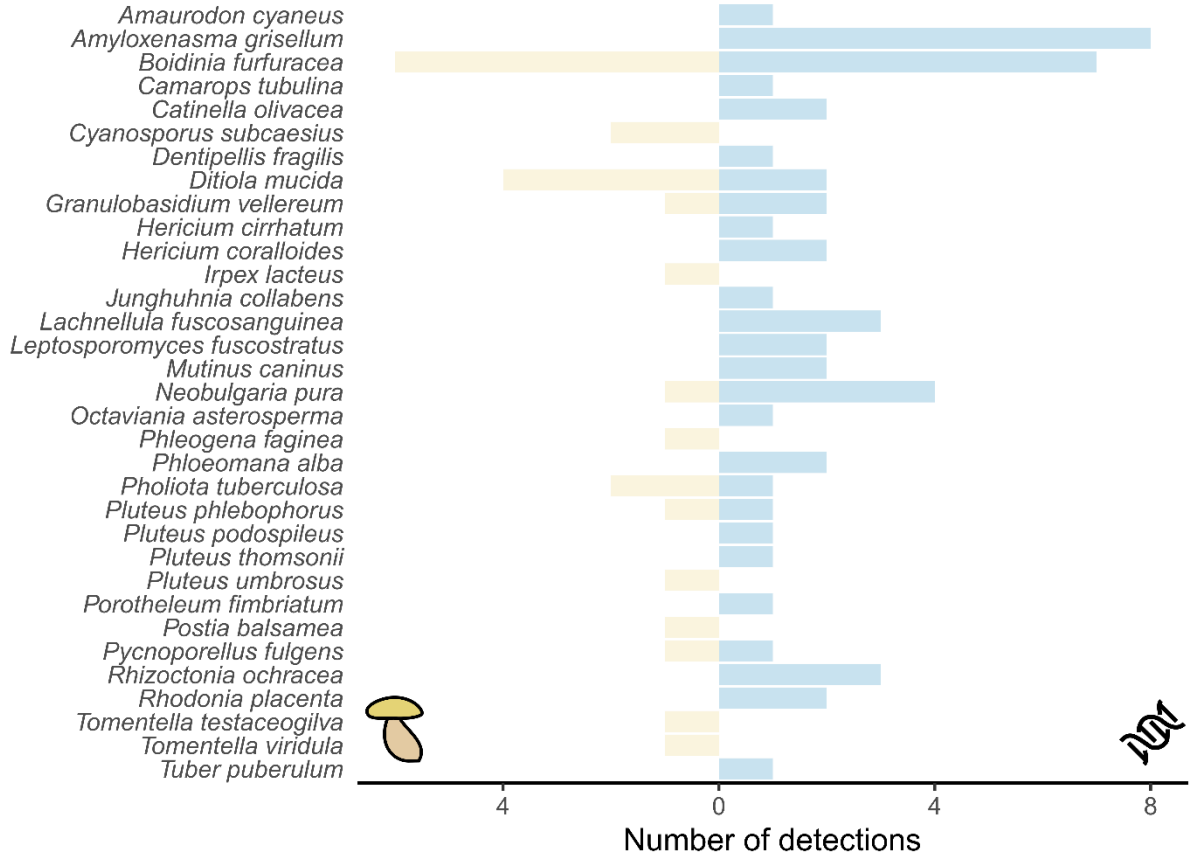

Figure B2: All threatened fungal species detected in Hainich with the number of times they have been detected by fruit body sampling or metabarcoding.

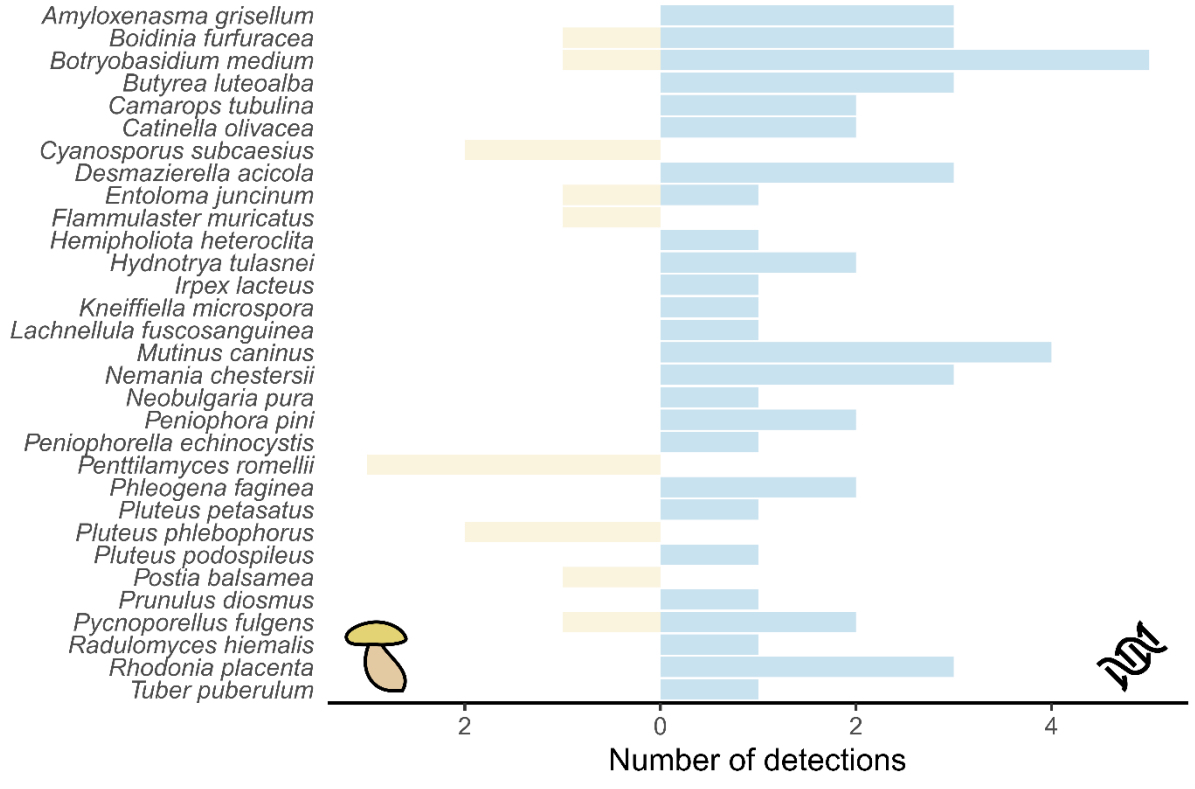

Figure B3: All threatened fungal species detected in the Schorfheide with the number of times they have been detected by fruit body sampling or metabarcoding.

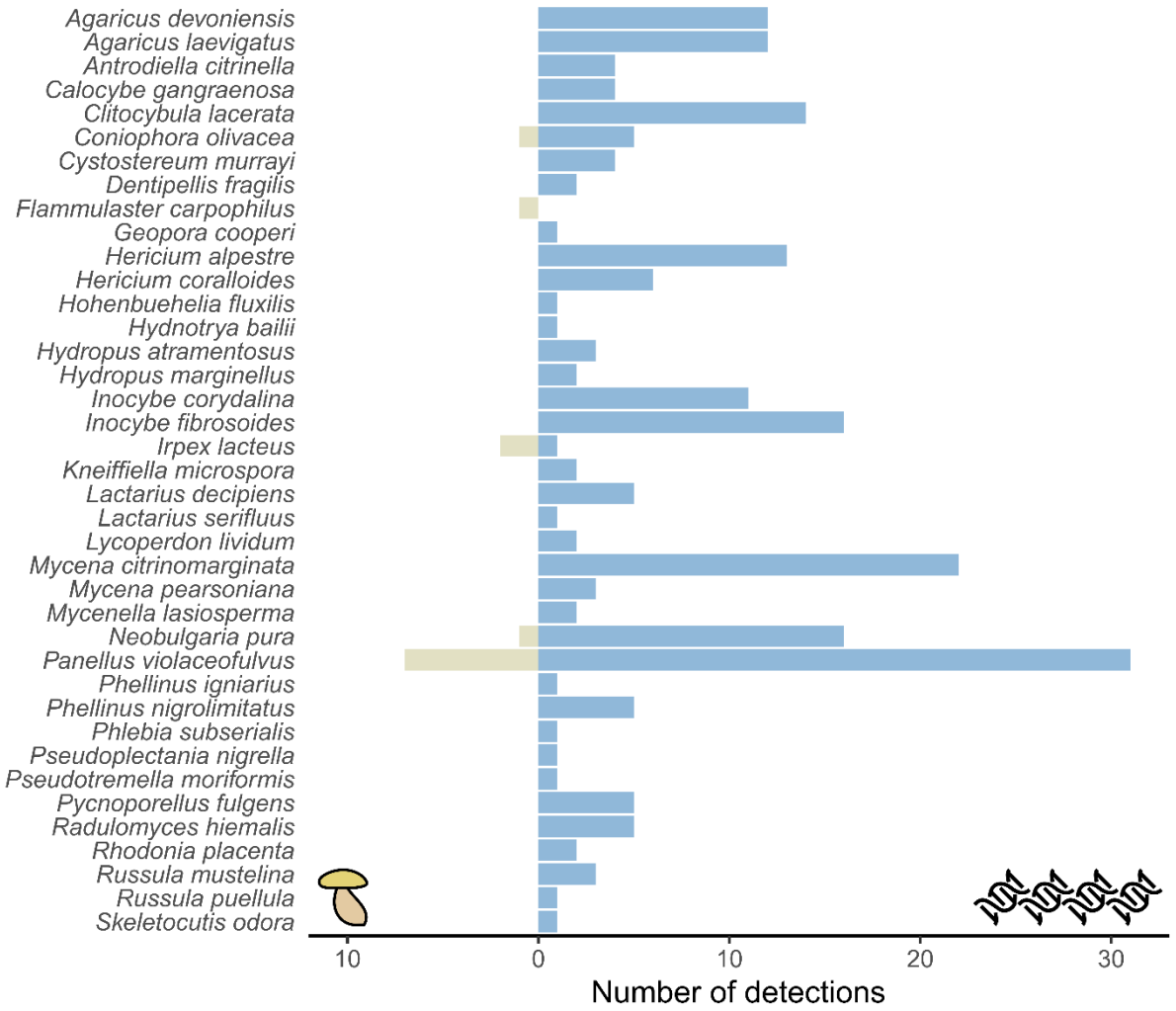

Figure B4: All threatened fungal species detected in the Bavarian Forest with the number of times they have been detected by fruit body sampling or metabarcoding.

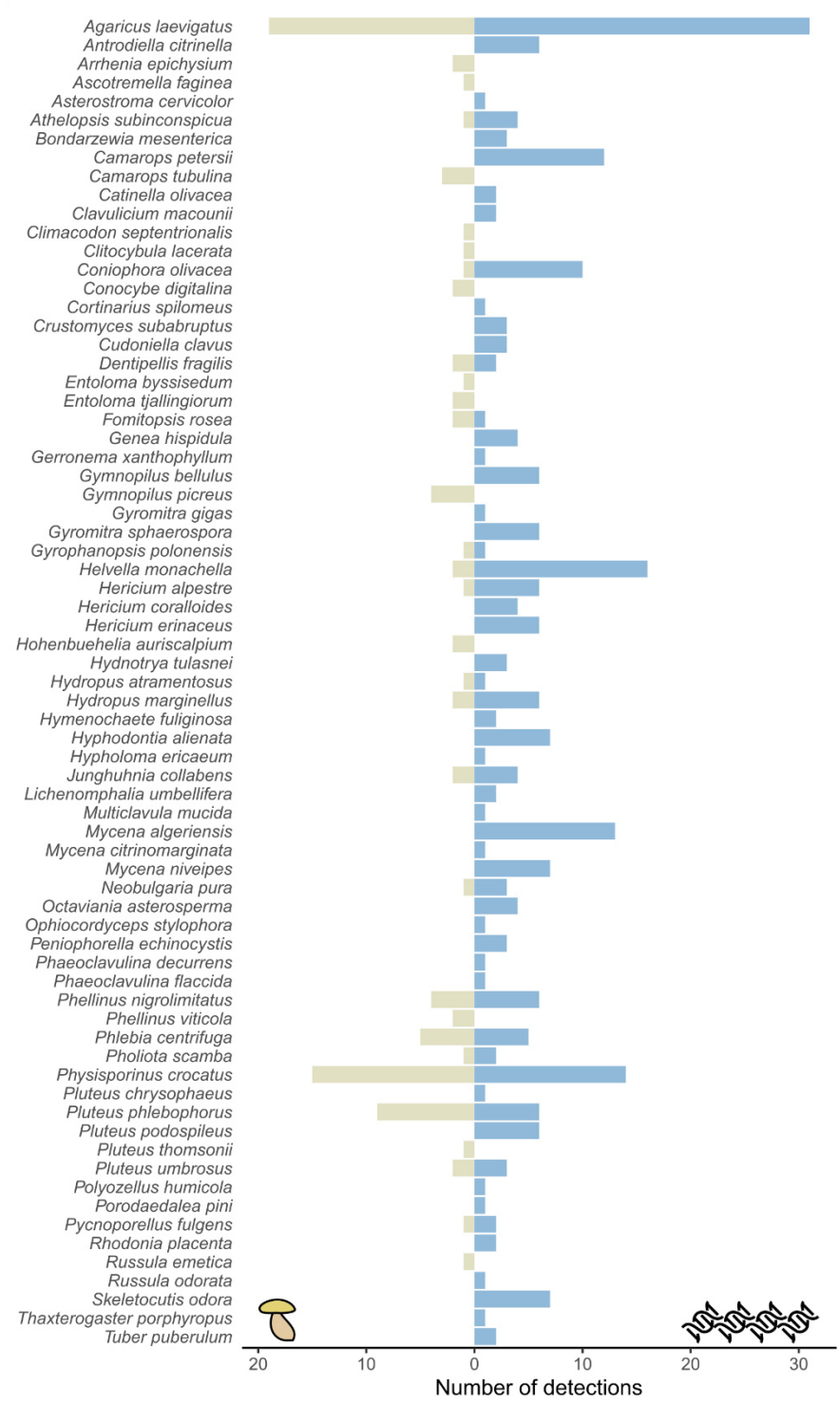

Figure B5: All threatened fungal species detected in Zofin with the number of times they have been detected by fruit body sampling or metabarcoding.

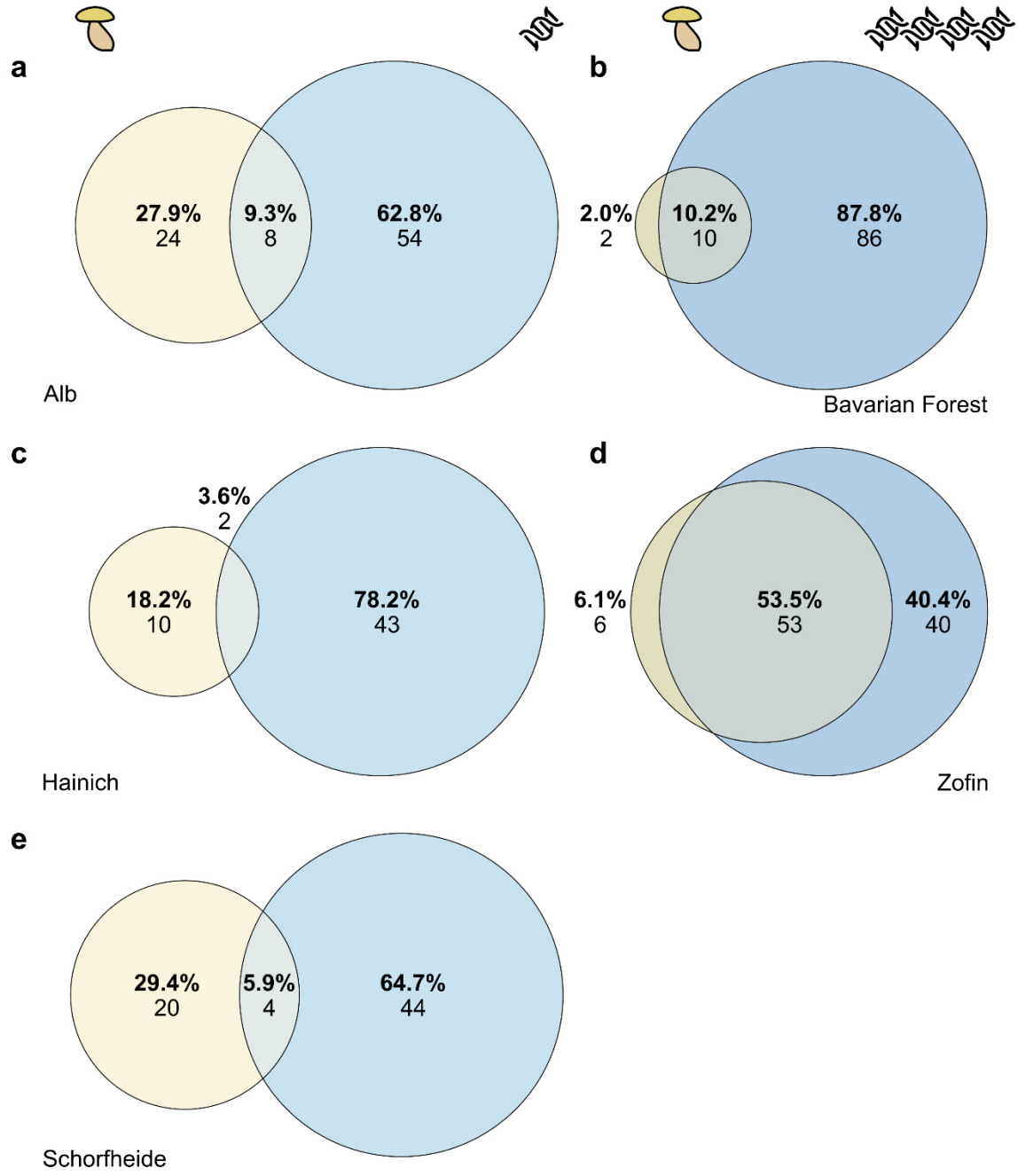

Figure B6: Relative and absolute numbers of dead-wood objects occupied by threatened species, detected by fruit body sampling and metabarcoding of low (a, c, e) and high sampling intensity (b, d) within each site.

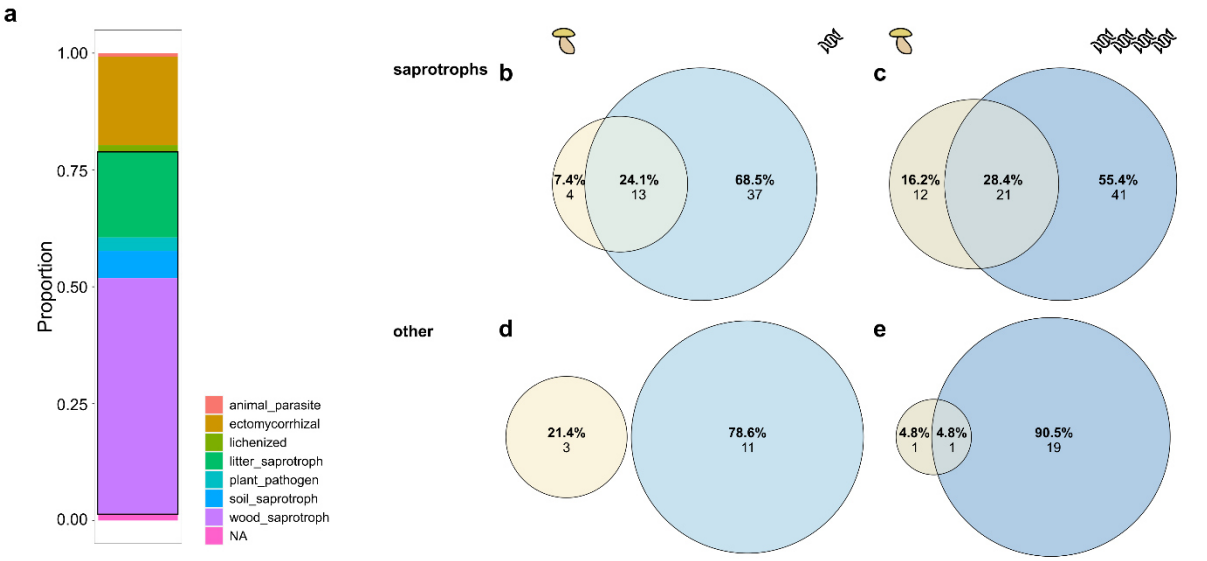

Figure B7: Classification of sampled fungi into functional groups based on Põlme et al. (2020). a) displays the proportion of species found in each functional group, to overall number of species. The black outline includes all guilds we count as saprotrophs in plots b) and c). Plots b) and d) show the number of species detected by fruit body and metabarcoding of low sampling intensity, plots c) and e) the number of species detected by fruit body sampling and high-intensity metabarcoding, both categorized either as saprotrophs (b-c) or other (d-e).

A.2: TREE DIVERSITY, NOT HOST SPECIFICITY, DRIVES GLOBAL WOOD-DECAYING FUNGAL DIVERSITY

Unpublished manuscript

Tree diversity, not host specificity, drives global wood-decaying fungal diversity

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Summary

Understanding the mechanisms that shape global biodiversity patterns can provide an important baseline for predictions about how biodiversity will respond to global change. Greater ecological specialisation has been suggested to be one fundamental mechanism explaining the higher biodiversity in the tropics compared to temperate and boreal biomes [1]. However, for diverse wood-decaying fungi, key agents of global carbon cycling [2] with a high host-tree specificity [3,4], we have a poor understanding of the mechanisms that drive global diversity patterns.

Here we show that wood-decaying fungal species richness increased from the poles towards the tropics, supporting the generality of the latitudinal diversity gradient. We did not find support for increasing specialisation, thus rejecting host specificity as a major mechanism driving global diversity patterns of wood-decaying fungi. Instead, the latitudinal diversity gradient in wood-decaying fungi is most likely caused by higher species richness of woody plants at lower latitudes. These results suggest that global wood-decaying fungal diversity is threatened particularly by the ongoing loss of tropical forests and their tree diversity in the Anthropocene with unknown consequences on decomposition processes and carbon cycles.

Keywords: global diversity, latitudinal diversity gradient, fungal diversity, niche packing

Main text

Tropical ecosystems are characterized by an enormous diversity of species across kingdoms, while ecosystems in temperate and boreal regions are typified by smaller numbers of species [5]. Exploring the generality of the latitudinal diversity gradient for different taxa and identifying the ecological mechanisms that underlie this pattern has been the subject of many studies over the past few decades [6]. Yet, the mechanisms of this pattern are complex and rather poorly understood [7]. However, a better mechanistic understanding of global diversity is crucial as this would allow more accurate predictions about biodiversity decline and resulting changes in ecosystem processes caused by global change.

Biotic interactions have been suggested to play a key role in the origin and maintenance of species diversity, causing the latitudinal diversity gradient [1]. One heavily debated mechanism is whether ecological specialisation increases towards the tropics, often referred to as the ecological-specialisation hypothesis [8–11]. Ecological specialisation and species richness are linked[12], as specialisation should facilitate species coexistence by partitioning niche space and thus reducing interspecific competition [13]. Therefore, when fitness equalizing mechanisms are not predominant (e.g. Janzen-Connell effects [14,15]), species richness and specialisation can increase simultaneously (niche packing) [16,17] based on the character divergence of species in response to competition [18].

Equatorial biomes are geologically older, have been climatically more stable and less impacted by drastic environmental changes than poleward biomes. Stable environmental conditions over long periods could foster speciation through niche divergence and increasing resource specialisation resulting in higher total species number per biome (gamma diversity) and higher niche packing in the tropics [8,19–21]. An increase in ecological specialisation towards the tropics has been tested several times with idiosyncratic results [22–26], which seems to disprove the generality of the ecological-specialisation hypothesis across systems and taxa [9,11]. Alternatively, higher species numbers of heterotrophic taxa, such as herbivores or decomposers in the tropics, could also be explained by higher plant diversity and a thus larger niche space without higher levels of specialisation [25–27]. We call this the tree-species-diversity hypothesis.

Here, we tested the latitudinal diversity gradient and the ecological-specialisation hypothesis versus the tree-species-diversity hypothesis as underlying mechanisms for the strong co-evolutionary interaction system of wood-decaying fungi and their host trees, using a global experiment covering all major biomes. Even though strongly host-dependent and ubiquitous across forested biomes, wood-decaying fungi have been entirely ignored in studies addressing the ecological-specialisation or tree-species-diversity hypotheses. Wood-decaying fungi are among the most specialised organisms on Earth and share a long history of coevolution with

their host plants [28]. They adapted to bypass plants' secondary metabolite defence mechanisms and evolved a complex portfolio of extracellular enzymes to break down lignin and cellulose from their hosts [29]. The ability to degrade lignin was a game changer in recycling plant necromass with profound consequences for global carbon dynamics [30,31], making wood-decaying fungi one of the most important groups driving decay processes [2]. Wood-decaying fungi are thus an ideal study system for comparing the ecological-specialisation and tree-species-diversity hypothesis.

We set up experiments in 52 locations covering the climate envelope of global forests from the tropics to the boreal zone (Fig. 1a). We sampled wood-decaying fungi via high-throughput sequencing from experimental consistently sized small-diameter logs of three locally common tree species (133 tree species in total) and standardised logs in all sites (industrial dried, debarked and sized wooden log of European beech, *Fagus sylvatica*). We first explored the latitudinal diversity gradient based on rarefaction-extrapolation curves of gamma diversity as the number of species across dead-wood objects for the three biomes (i.e., tropical including subtropical, temperate, and boreal including hemi-boreal). Second, we tested patterns of species richness within wooden logs (alpha diversity on log) versus latitude. We hypothesized that wood-decaying fungal alpha and gamma diversity decreases with increasing latitude (Fig. 1). Third, we tested whether the latitudinal diversity gradient can be explained by ecological specialisation using species-host interaction networks (H_2' and d', Blüthgen et al., 2006) as specialisation measures. Consistent with the ecological-specialisation hypothesis, we expect a negative linear relationship between specialisation and latitude. In addition, we expect differences in the slope of fungal species richness – tree species accumulation curves among biomes, which should be indicative of the ecological-specialisation hypothesis (Fig. 1). In contrast, a positive linear relationship between fungal alpha diversity on a plot and the number of tree species in a region [32], as well as similar slopes of the fungal species richness – tree species accumulation curves among biomes (similar specialisation rates) would indicate that simply the differences in tree species diversity among biomes cause the latitudinal diversity gradient (Fig. 1, tree-species-diversity hypothesis).

Latitudinal diversity gradient

We found a total of 20,685 fungal OTUs (referred to as "species" here on). Considering a common sampling effort (gamma diversity extrapolated to a sample size of 300 logs per biome), a decrease in species number from the tropics (13,466 species) towards the poles (12,039 and 7,289 species in the temperate and boreal biome, respectively, Fig. 2a-b) is evident which is

consistent with the latitudinal diversity gradient. Alpha diversity, i.e., species richness per log, did not change significantly with latitude (Fig. 2c-d, Extended Data Table 1).

There is broad evidence for a latitudinal diversity gradient across taxa [6]. However, most of our knowledge is based on eukaryotic macroorganism clades from the plant and animal kingdoms. Despite recent advances in molecular methods, global diversity patterns of microbes are still underexplored, particularly those dependent on host species [32]. Our results indicate that global patterns of gamma diversity of wood-decaying fungi follow the latitudinal diversity gradient. However, there was no latitudinal pattern for alpha diversity. This underpins an important factor that has been part of the debate about inconsistencies in research on the latitudinal diversity gradient, namely, the grain size of the study. The non-significant relationship between species richness per log and latitude might be caused by colonization and establishing (assembly) constraints (priority effects). When fungi colonize a dead-wood object, individuals within and across species rapidly and strongly compete for resources and fix claims via so-called demarcation lines inhibiting further colonization by other species [33–35]. This assembly process characterized by high competition might limit the total number of species per log, causing similar alpha diversity levels across biomes, indicating that local communities are saturated [36]. Higher gamma diversity despite similar alpha diversity in the tropics was associated with higher beta diversity among logs (Extended Data Fig. 1a-b), supporting this view. This highlights the importance of grain size and the related scaling of assembly processes and hence the need to consider multiple grain sizes in latitudinal diversity gradient studies.

The first studies exploring global diversity patterns of fungi focused solely on alpha diversity of soil fungi and found inconsistent results. While Tedersoo et al. [37] found support for the latitudinal diversity gradient, the meta-analyses by Větrovský et al. [38] found high numbers of species at high latitudes. However, the response of species diversity to latitude seems dependent on the ecology and life-history strategy of the examined fungi. Tedersoo et al. [37] showed that fungi antagonistically linked to plant resources (saprotrophic and pathogenic) followed the latitudinal diversity gradient. Wood-decaying fungi can be seen as plant antagonists and therefore, our findings on alpha diversity level are in contrast to soil-saprotrophic fungi. One reason for this inconsistency could be that assembly processes in soil differ from those observed in dead-wood. The strength of biotic interactions within dead wood (competitive interactions) might be more pronounced than in soil [39,40]. However, we need more studies that explore the latitudinal diversity gradient and related assembly processes in fungi across lifestyles and habitats in a unified framework with standardised spatial grain size and extend at alpha and gamma levels.

Specialisation as a potential driver of the latitudinal diversity gradient

Network specialisation among natural logs of different tree species and resource specialisation on standardised logs did not change significantly with latitude (Fig. 3a-b, Extended Data Table 1). Therefore, ecological specialisation of wood-decaying fungal communities appears consistent across latitudes and biomes, and thus we suggest that the ecological-specialisation hypothesis is not a robust mechanism explaining the observed latitudinal diversity gradient. One explanation for why we found no significant relationship between specialisation and latitude might be related to the evolution and distribution of host tree species across the globe. It is important to note that angiosperm trees predominantly characterize the tropics, while angiosperm and gymnosperm trees coexist in temperate and boreal biomes. A high degree of host specialisation of fungi has been attributed to this deep phylogenetic split in many local studies in the northern hemisphere [41–44]. To address this potential explanation, we first regressed network specialisation versus mean phylogenetic distance between tree species for each plot but found no significant relationship (Extended Data Table 1, Extended Data Fig. 1c). Therefore, specialisation seems unrelated to the deep phylogenetic host tree distances (e.g., plant classes). Second, we repeated our analyses using only angiosperm wood and found similar patterns when considering all host tree species (Extended Data Table 1, Extended Data Fig. 2). This indicates that the deep phylogenetic split among host species is not an important driver for fungi specialisation. Finally, to explore at which taxonomic level specialisation of fungi matters, we correlated the community composition with different taxonomic levels (genus, family, order, class). These analyses revealed strong effect sizes with the level host tree genera and weaker effect sizes with family, order or class (Extended Data Table 2). Consistent with findings from a temperate forest [45], our results suggest that globally, specialisation at genus level is more important than at higher taxonomic levels.

Tree species diversity as a potential driver of the latitudinal diversity gradient

We observed a significant positive relationship between wood-decaying fungal diversity and tree species diversity at the regional level (Fig. 3c, Extended Data Table 1). Moreover, the species accumulation curves versus the number of tree species considerably overlap among the tropical and temperate biome (Fig. 3d). The accumulation curve of the boreal biome overlapped only at a low number of tree species which is the apparent outcome of the very low number of tree species in this biome. However, the large overall overlap and similar slopes for the tropical and temperate biomes suggest a similar rate of specialisation. Therefore, higher tree species diversity at low latitudes is likely to be the main driver of the high fungal gamma diversity observed in our study. However, in all models, specialisation on natural logs showed a negative,

even though non-significant relationship, with latitude. We, therefore, cannot entirely rule out that ecological specialisation might play a marginal role in explaining the observed diversity pattern. Nevertheless, the tree species diversity effect is predominantly important; hence, our study supports the view that the generality of the ecological-specialisation hypothesis has to be rejected.

Global change implications

Our results show that host specialisation of wood-decaying fungi is high across biomes suggesting that tree species diversity is the primary driver of wood-decaying fungal diversity in the tropics. Therefore, the loss of tropical forests due to land use [46] and climate change [47] threatens fungal diversity and may already cause unobserved losses of fungal species. Furthermore, the declining diversity of wood-decaying fungi may alter decomposition processes and carbon cycles since wood-decaying fungi are among the most important organisms driving the global carbon- and nutrient cycle [2].

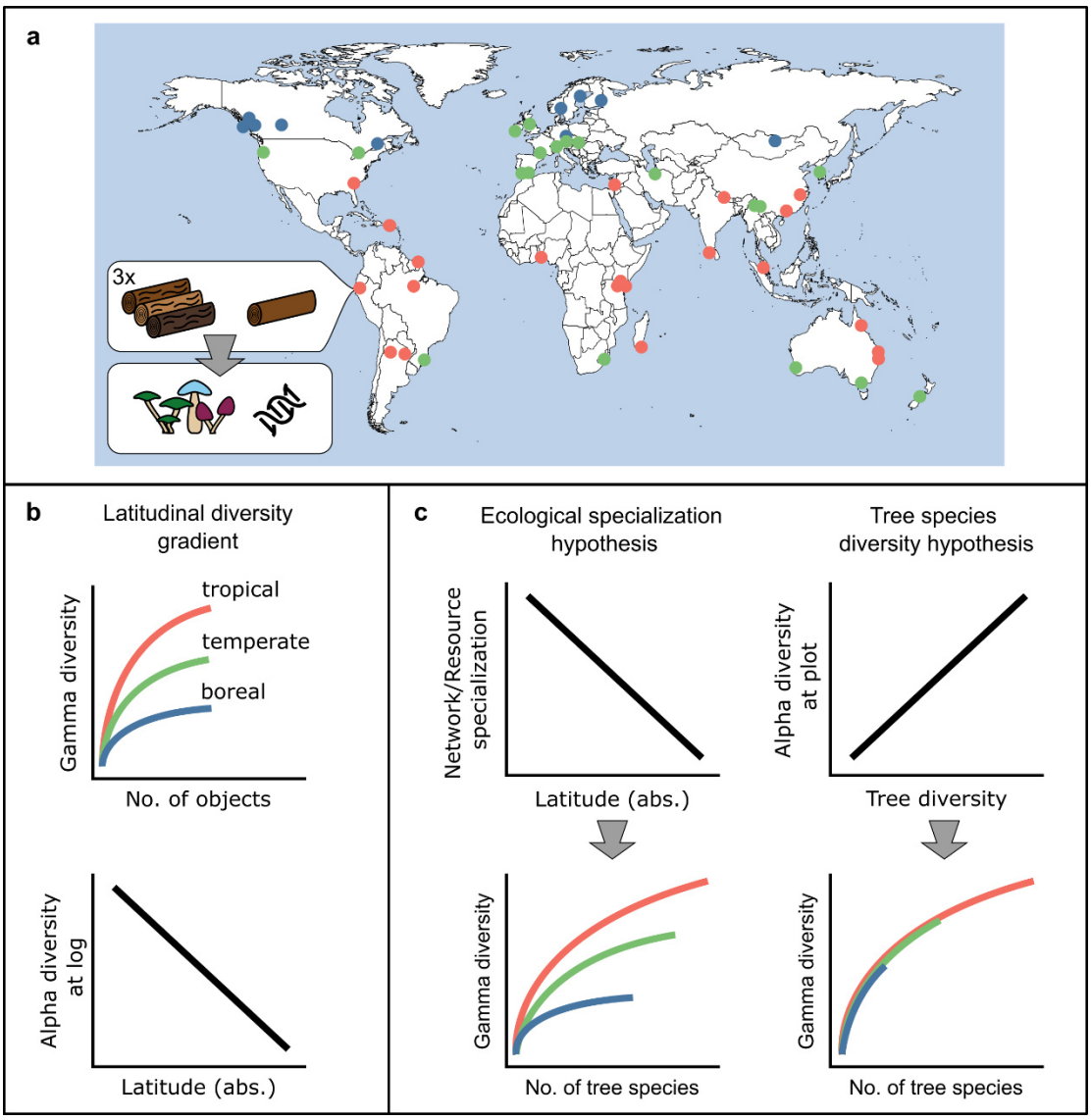

Figure 6: Conceptional figure of how the latitudinal diversity gradient of wood-decaying fungi caused either by ecological specialisation or tree species diversity. ***a*** *Global map showing the sampling sites assigned to three different biomes, boreal (blue), temperate (green), and tropical (red) with experimental set-up and sampling method.* ***b*** *Expected gamma and alpha diversity patterns at log of all sampled objects under the assumption of the latitudinal diversity gradient.* ***c*** *Expected patterns of specialisation indices and gamma diversity against the number of sampled tree species if the ecological specialisation hypothesis (left column), or alpha diversity at plot level and gamma diversity against the number of sampled tree species if tree species diversity hypothesis (right column) is assumed as the cause of the latitudinal diversity gradient.*

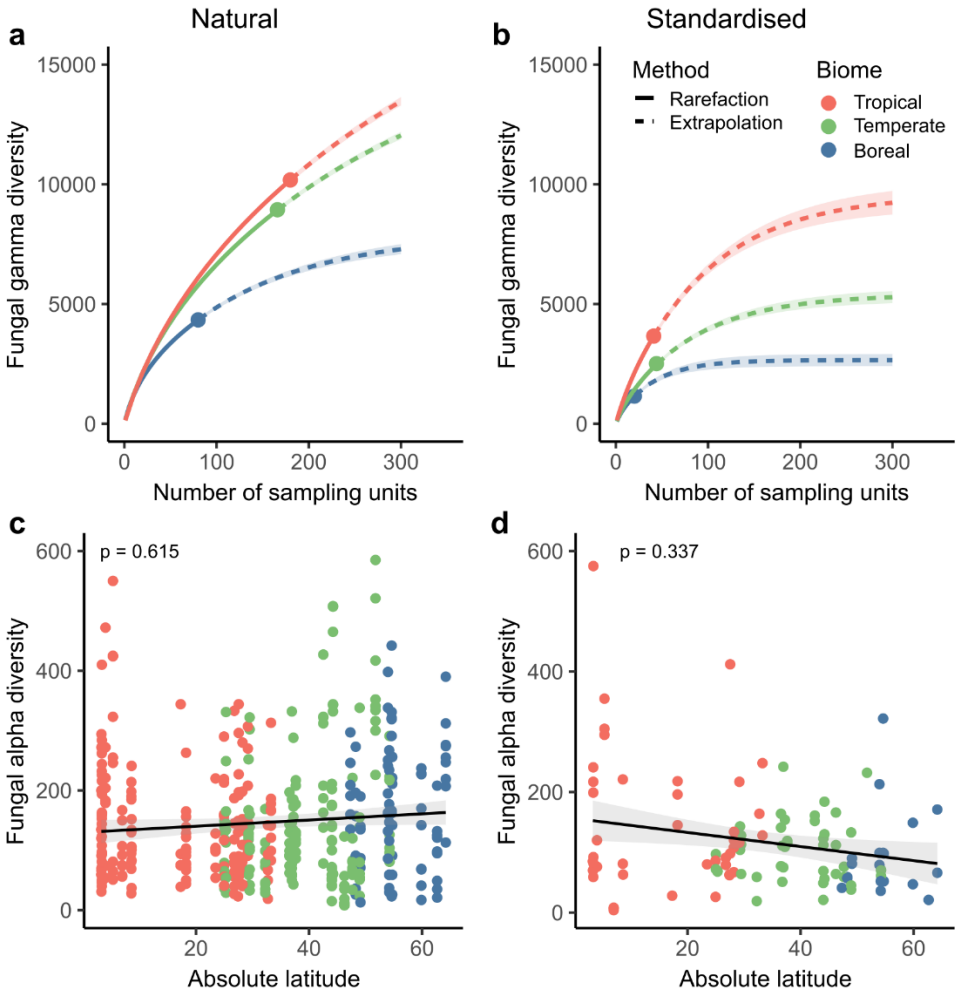

*Figure 7: Main results for the latitudinal diversity gradient in wood-decaying fungal diversity, studied as gamma diversity (**a**, **b**) and alpha diversity (**c**, **d**) along absolute latitude for the natural (left) and the standardised logs (right). Stated p-values correspond to the respective negative binomial generalized linear mixed effect models.*

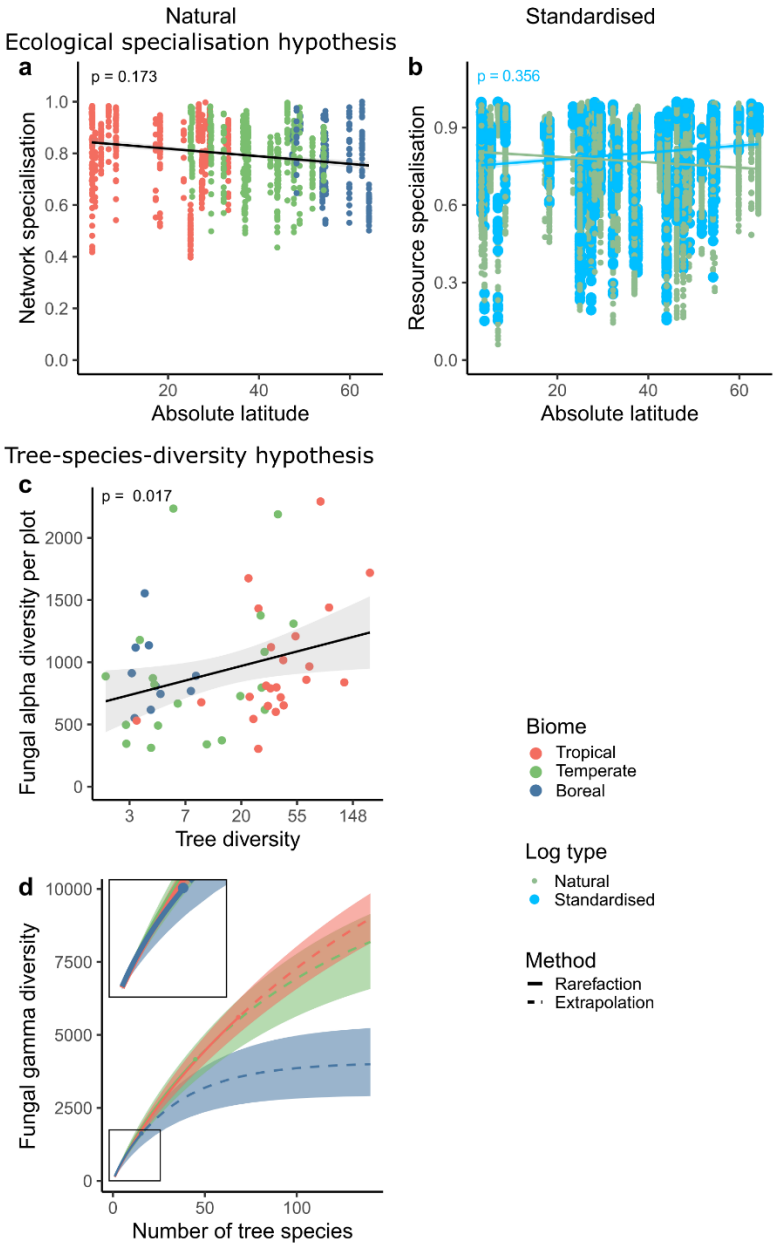

*Figure 3: Main results for the ecological specialisation hypothesis (**a, b**) and the tree-species-diversity hypothesis (**c**) in wood-saprotrophic fungal diversity for the natural (left) and the standardised logs (right). **a** displays the network specialisation against absolute latitude. **b** shows the resource specialisation against absolute latitude as the specialisation of fungi on the standardised log (blue)and the mean specialisation on the natural logs (green) on one plot. **c** shows the estimated fungal alpha diversity at plot level on a sample coverage value of 75% against local tree species diversity [48]. Alpha diversity at plot was calculated as the extra- or interpolated species richness of 75% sampling coverage at each plot (function* iNEXT*, package* iNEXT *[49]). **d** displays the fungal gamma diversity against the number of unique tree species per biome. Stated p-values correspond to the respective models.*

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Methods

Field experiment

We established a global network of 52 experimental forest sites across boreal, temperate and tropical biomes, with sites covering a wide range in temperature and precipitation across and within biomes (Fig. 1, see Seibold et al. [1] for more details). Site installation took place between March 2015 and July 2016, depending on seasonality (see Seibold et al. [1]). At each site, either branches or stems of young trees (~3 cm in diameter, 50 cm in length) from three of the most common tree species were freshly cut from trees without signs of insect or fungal damage

(termed natural logs in the following). Three natural logs per tree species (9 objects altogether) were placed next to each other on the forest floor after removing the topmost layer of leaf litter to ensure all logs had complete soil contact. Alongside the natural logs, we exposed three dried and barkless dowels of *Fagus sylvatica* of the same origin (termed standardised logs in the following). This standardised resource accounts for alternations in specialisation along latitude caused by changes in host phylogeny. Altogether we exposed 468 natural logs representing 131 different tree species and 156 standardised logs. However, we lost samples due to disturbance of the logs or laboratory problems. Therefore, our final data set consisted of 426 natural and 105 standardised logs.

Sampling fungal communities

Natural and standardised logs were collected after two years and in a few cases, after one year due to high decomposition rates or three years if another sample was lost. Note that a sensitivity analysis using only logs of year two did not yield different results (Extended Data Table 1, Extended Data Fig. 3). Logs were dried at 40°C until mass remained constant. One 5 cm long sample was cut from each log and placed in a sealed plastic bag with silica gel until transferred to a freezer (-20°C). Each wood sample was drilled, driving an augur lengthwise horizontally through the wood sample, hollowing it out. The resulting material was then freeze-dried, milled and homogenized using a ball mill (Retsch, Germany). Total fungal genomic DNA was extracted from each milled wood sample using the Quick-DNA Fecal/Soil Microbe Mini Prep Kit (Zymo Research, Freiburg, Germany) following the protocol of [2]. PCR amplification of the fungal ITS2 region was performed using barcoded gITS7 and ITS4 [3]. PCR follows the protocol of [4]. Sequencing of amplicons was performed on Illumina MiSeq. The amplicon sequencing data were processed using the pipeline SEED 2 [5], and sequences were clustered using UPARSE implemented within Usearch [6] at a 97% similarity level or using DADA2 [7]. Consensus sequences were constructed for each cluster, and the closest hits at the species level were identified using BLASTn against UNITE [8] version 9 and GenBank. Finally, we assigned each putative species a lifestyle (e.g., wood saprotroph) via matching with the FungalTraits database [9].

Data analysis

Data preparation and analyses were performed in R 4.2.2 [10].

Data preparation

We used raw read data tables for the final analyses and excluded local singleton reads from the species-by-site community matrix (i.e., setting matrix cells with the value of 1 to 0). Singletons are likely PCR and sequencing errors and would lead to an overestimation of rare species, inflating diversity estimates [11,12]. Nevertheless, since transformations and rarefaction are widely used for data normalization, we checked the robustness of our results against the model outcome based on rarefied data (thresholds 5000; Extended Data Table 1, Extended Data Fig. 4; function *rrarefy*, R package *vegan*, [13]). For network and resource specialisation analyses, we used only logs with a minimum of five OTUs, which excluded only one standardised log. We are aware that the OTUs in our data set consist of different guilds. Even though not all OTUs detected in a log might have decay capabilities, they are all related to the log as environment. Further, our knowledge to assign the OTUs detected to a specific lifestyle is still limited and probably biased towards species related to better-studied areas (Europe, North Amerika). For simplicity, we used all OTUs in our analyses and termed it wood-decaying fungi. Nevertheless, as sensitivity analysis, we calculated a subset filtering only to those OTUs with the assigned primary and secondary lifestyle "wood saprotroph" according to the data set provided by Polme et al [9](Extended Data Table 1, Extended Data Fig. 5). Although we are aware that OTUs are only putative species, to enhance readability, we use the term "species" for fungal OTUs.

Statistical analysis

To address our first hypothesis that wood-decaying fungi display the latitudinal diversity gradient, we calculated sample-based rarefaction/interpolation curves via the R package *iNEXT* [14] for natural and standardised logs. Further, we calculated alpha diversity as species richness per log. For rarefied data, alpha diversity was species richness based on the function *rarefy* on thresholds of 5000 (package vegan [13]). We calculated a negative binomial linear mixed effect model for alpha diversity using the *glmer.nb* function from the *lme4* package [15]. We considered the site as a random effect to account for repeated measurements.

To address our second hypothesis that the observed latitudinal diversity gradient in wood-decaying fungi can be explained by specialisation (ecological-specialisation hypothesis), we calculated the specialisation within networks of fungi and natural logs on each plot. Wood-decaying fungi were chosen as a suitable study system to test for ecological specialisation as their host-relation is spatially distinct, with clear boundaries, making controlling for resource availability experimentally feasible. Finally, the use of standardised organic materials can control for cofounding effects of the resource type across latitude helping to overcome some constraints of previous studies [16]. Per plot, we created a matrix for each possible combination

of natural logs of different tree species. For each of these matrices, we calculated the standardised two-dimensional Shannon entropy index H_2' [17] with the function *H2fun* in the *bipartite* package [18]. H_2' is defined as complementary specialisation of a given network (referred to as network specialisation) and ranges from 0 (complete generalism = all species use all resources) to 1 (complete specialisation = each species uses only one resource) [19]. It is independent of network size and sampling effort [17]. All observed H_2' values were checked for significant difference from random against 1,000 null models (*r2d*, keeps row and column sums constant, package *vegan* [13]). All observed H_2' values were significantly different from random and we, therefore, used all samples in our analyses.

For the standardised logs, we calculated the standardised Kullback-Leibler distance d' [17] with the function *specieslevel* in the *bipartite* package [18]. d' is a measure of specialisation on species level, thus allowing specialisation assessments in relation to the standardised log. More specifically, like H_2', the index d' is defined as complementary specialisation but of a given species, accounting for specialisation on a specific partner, i.e., the standardised log (from now on, resource specialisation). It ranges from 0 (generalist interaction = all species use this resource) to 1 (specialist interaction = only one species uses this resource) [19]. It also is independent of network size and sampling effort [17]. We calculated d' for each standardised log in each matrix of natural logs created for H_2'. All observed d' values were checked for significant differences from random against 1,000 null models (*r2d*, keeps row and column sums constant, package *vegan* [13]), yet none had to be excluded as all were significantly different from random.

If the ecological-specialisation hypothesis applies, we expect network and resource specialisation to show a negative relationship with latitude. We calculated a model for each specialisation measure. Each model included the measure as a dependent variable and absolute latitude as an independent variable. We calculated beta regression models with the *gam* function from the *mgcv* package[20]. In each model, we considered the site as a random effect to account for repeated measurement. In the d' model, we put the log ID as an additional random effect to account for the repeated sampling of each standardised log per plot.

To address our alternative hypothesis that the latitudinal diversity gradient in wood-decaying fungi is caused by tree species diversity, we calculated the expected species richness per plot on a sample coverage value of 75% with the package *iNEXT* [14] over all logs on a plot. Note that exploring sample coverage across our setting showed that all sites were sampled in a saturating way (data not shown). Based on this procedure, we considered both sampling effort and sampling coverage in our analyses. We used local tree diversity values from Liang et al. [21]. If no data was available for the coordinates of a plot, we used the nearest neighbor approach, with the *extract* function from the package *raster* [22]. For the nearest neighbour approach, we used

the smallest buffer (fun = "max") to extract a value for each plot. We calculated a negative binomial generalized linear model for expected species richness with tree diversity as explanatory variable using the *glm.nb* function from the *MASS* package [23].

To illuminate the effect of specialisation and tree species diversity on gamma diversity, we calculated gamma diversity against the number of unique tree species. We randomly selected a natural log of each unique tree species per biome, starting in the boreal and ending in the tropical biome and calculated the sample-based rarefaction/interpolation as described above. We repeated this a hundred times and used the mean as the final curve and the range between min and max as the confidence interval.

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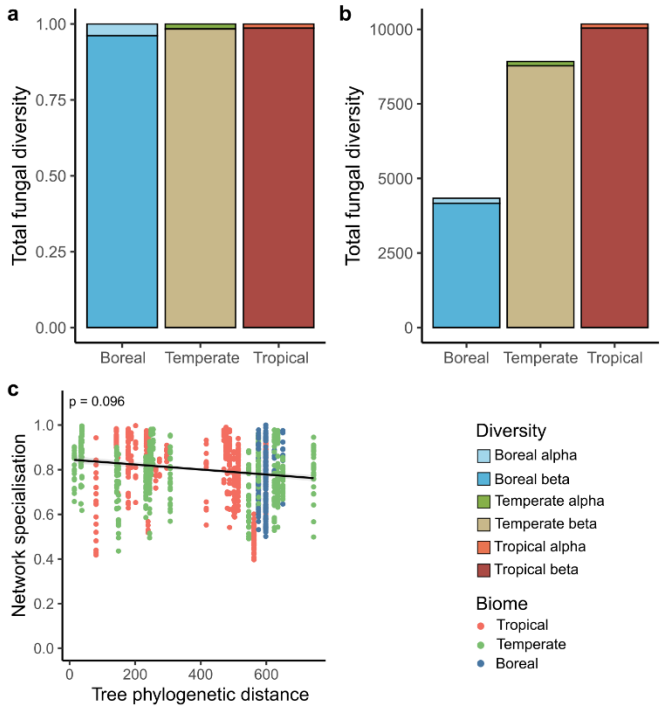
Extended data

Extended Data Table 1: Results for all models used in testing the latitudinal diversity gradient (LDG), ecological specialisation hypothesis (ESH) and the tree species diversity hypothesis (TSDH) for different subsets of the data of wood-decaying fungi.

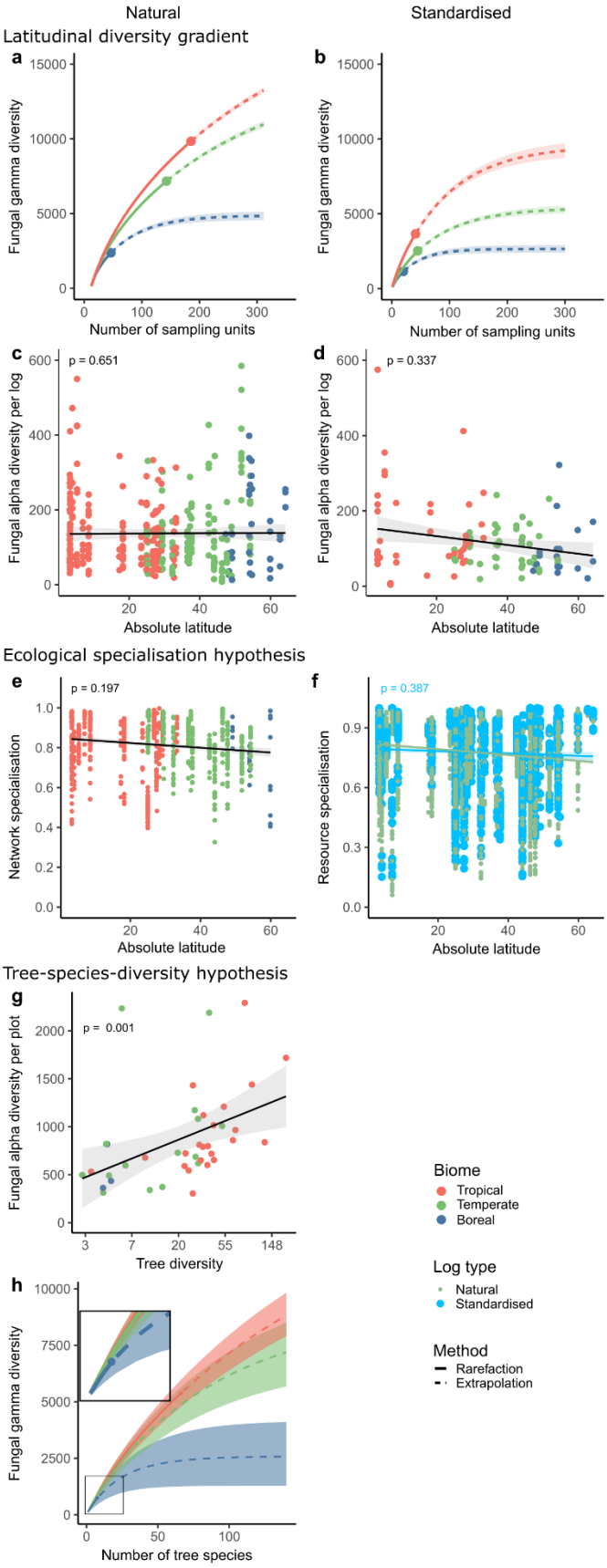
Data subset	Log type	Hypothesis	Response	Explanatory	Type	Df	z-value	p-value
all fungal OTUs	natural	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	0.502	0.615
		ESH	Network specialisation	Absolute latitude	betareg	1	-1.364	0.173
		TSDH	Alpha diversity per plot	Tree species diversity	glm.nb	1	2.294	**0.017**
	standardised	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	-0.959	0.337
		ESH	Resource specialisation	Absolute latitude	betareg	1	0.923	0.356
only sampling year two	natural	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	0.308	0.758
		ESH	Network specialisation	Absolute latitude	betareg	1	-1.343	0.179
		TSDH	Alpha diversity per plot	Tree species diversity	glm.nb	1	2.207	**0.022**
	standardised	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	-0.986	0.324
		ESH	Resource specialisation	Absolute latitude	betareg	1	0.846	0.398
rrarefy (5000)	natural	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	0.723	0.469
		ESH	Network specialisation	Absolute latitude	betareg	1	-1.891	0.059
		TSDH	Alpha diversity per plot	Tree species diversity	glm.nb	1	1.805	0.077
	standardised	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	-0.62	0.535
		ESH	Resource specialisation	Absolute latitude	betareg	1	0.849	0.396
wood saprotrophs	natural	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	0.499	0.618
		ESH	Network specialisation	Absolute latitude	betareg	1	-0.773	0.439
		TSDH	Alpha diversity per plot	Tree species diversity	glm.nb	1	2.423	**0.013**
	standardised	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	-1.096	0.273
		ESH	Resource specialisation	Absolute latitude	betareg	1	0.679	0.497
only angiosperms	natural	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	-0.453	0.651
		ESH	Network specialisation	Absolute latitude	betareg	1	-1.291	0.197
		TSDH	Alpha diversity per plot	Tree species diversity	glm.nb	1	3.361	**0.001**
	standardised	LDG	Alpha diversity per log	Absolute latitude	glmer.nb	1	-0.959	0.337
		ESH	Resource specialisation	Absolute latitude	betareg	1	0.865	0.387

Extended Data Table 2: Permanova on the communities of wood-decaying fungi on natural logs and explanatory power of different host taxonomical resolutions.

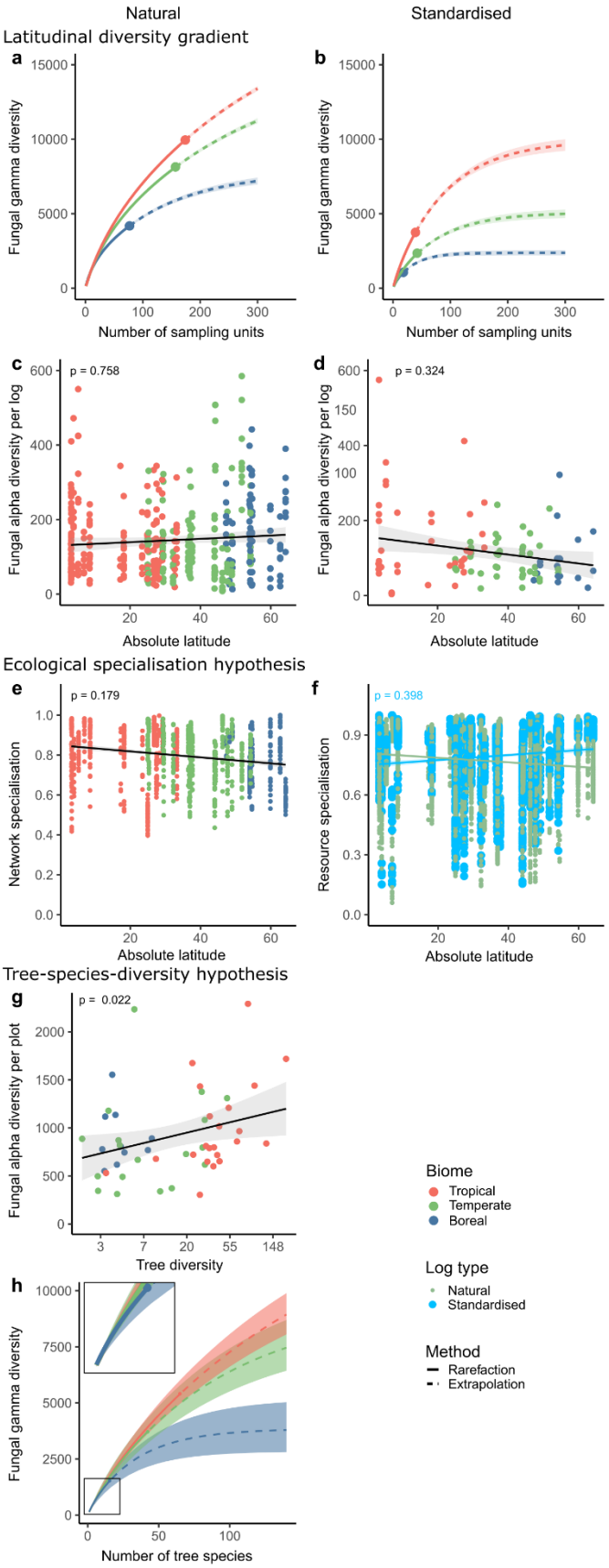
	Df	SumOfSqs	R2	F	p
Class	1	2.2	0.011	5.954	<0.001
Order	22	17	0.081	2.076	<0.001
Family	23	16.8	0.08	1.959	<0.001
Genus	46	33.6	0.161	1.961	<0.001
Species	38	29.3	0.141	2.074	<0.001
Residual	295	109.8	0.526		
Total	425	208.7	1		



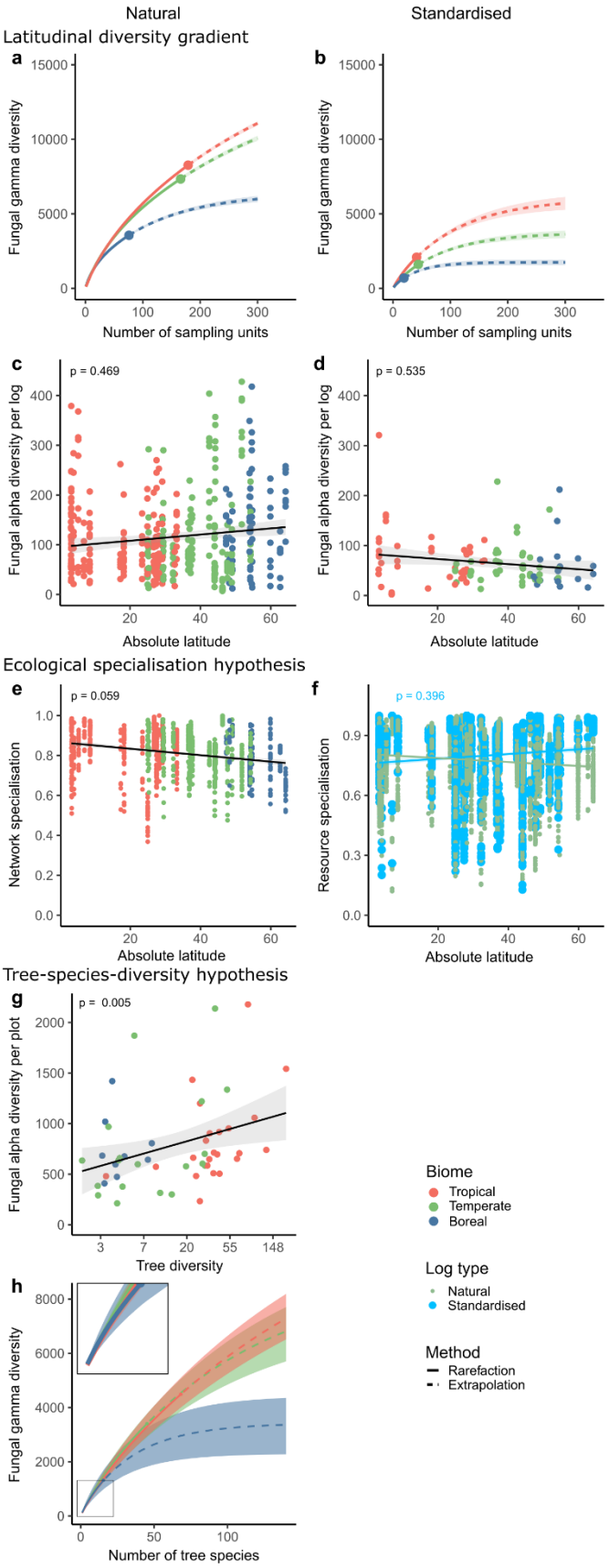
*Extended Data Figure 1: Additional diversity and specialisation analysis for wood-decaying fungi on natural logs. Figure **a** and **b** display additive diversity partitioning (*adipart, vegan [1]*) among all logs within each biome into the **a** relative and **b** total share of alpha and beta diversity in total diversity. Figure **c** displays the network specialisation against tree phylogenetic distance of the natural logs on the respective plot.*



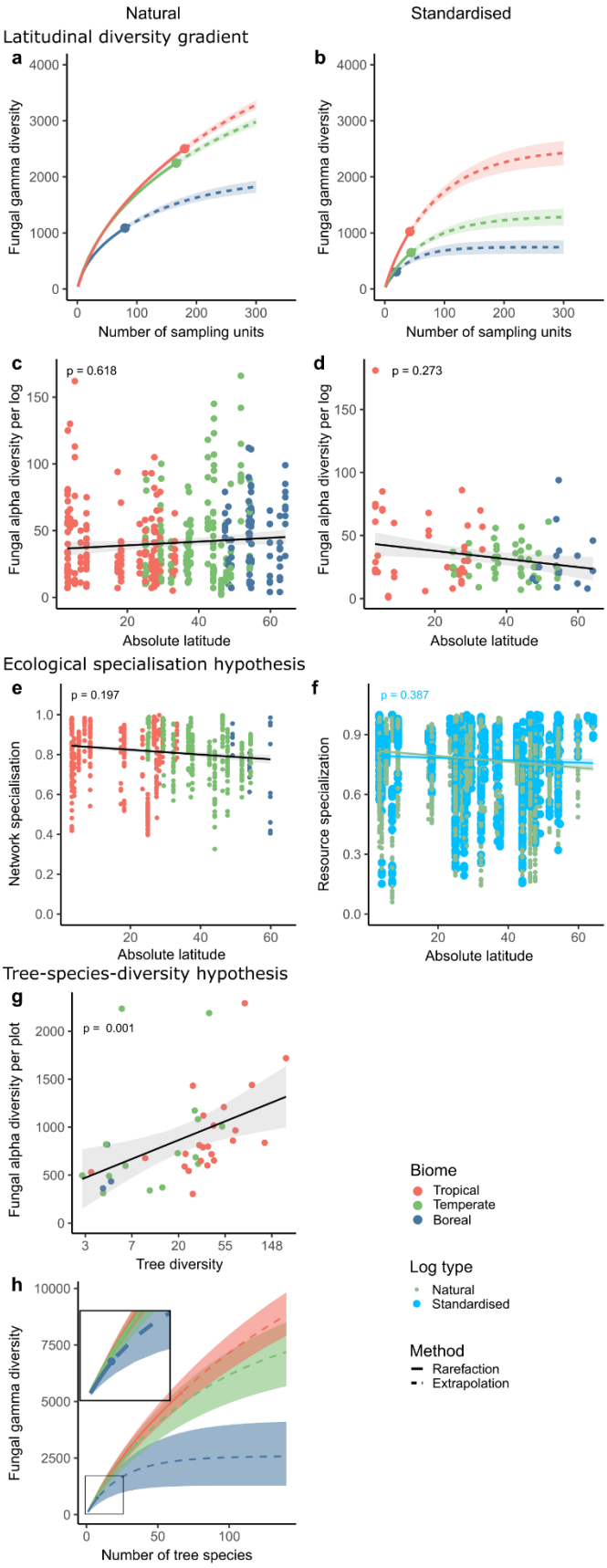
*Extended Data Figure 2: Main results for the latitudinal diversity gradient **a-d**, ecological specialisation hypothesis **e, f** and the tree-species-diversity hypothesis **g, h** in wood-decaying fungal diversity on logs of angiosperm trees for the natural (left) and the standardised logs (right). **a** and **b** display the fungal gamma diversity against the number of sampled objects per biome. **c** and **d** display the fungal alpha diversity on log level against absolute latitude. **e** displays the network specialisation against absolute latitude. **f** shows the resource specialisation against absolute latitude as the specialisation of fungi on the standardised log (blue)and the mean specialisation on the natural logs (green) on one plot. **g** shows the estimated fungal alpha diversity at plot level on a sample coverage value of 75% against local tree species diversity [2]. Alpha diversity at plot was calculated as the extra- or interpolated species richness of 75% sampling coverage at each plot (function* iNEXT*, package* iNEXT *[3]). **h** displays the fungal gamma diversity against the number of unique tree species per biome. Stated p-values correspond to the respective models*



*Extended Data Figure 3: Main results for the latitudinal diversity gradient **a-d**, ecological specialisation hypothesis **e, f** and the tree-species-diversity hypothesis **g, h** in wood-decaying fungal diversity, standardised on logs of the second sampling campaign, for the natural (left) and the standardised logs (right). **a** and **b** display the fungal gamma diversity against the number of sampled objects per biome. **c** and **d** display the fungal alpha diversity on log level against absolute latitude. **e** displays the network specialisation against absolute latitude. **f** shows the resource specialisation against absolute latitude as the specialisation of fungi on the standardised log (blue)and the mean specialisation on the natural logs (green) on one plot. **g** shows the estimated fungal alpha diversity at plot level on a sample coverage value of 75% against local tree species diversity [2]. Alpha diversity at plot was calculated as the extra- or interpolated species richness of 75% sampling coverage at each plot (function* iNEXT, *package* iNEXT *[3]). **h** displays the fungal gamma diversity against the number of unique tree species per biome. Stated p-values correspond to the respective models*



*Extended Data Figure 4: Main results for the latitudinal diversity gradient **a-d**, ecological specialisation hypothesis **e, f** and the tree-species-diversity hypothesis **g, h** in wood-decaying fungal diversity, rarefied to a threshold of 5,000, for the natural (left) and the standardised logs (right). **a** and **b** display the fungal gamma diversity against the number of sampled objects per biome. **c** and **d** display the fungal alpha diversity on log level against absolute latitude. **e** displays the network specialisation against absolute latitude. **f** shows the resource specialisation against absolute latitude as the specialisation of fungi on the standardised log (blue)and the mean specialisation on the natural logs (green) on one plot. **g** shows the estimated fungal alpha diversity at plot level on a sample coverage value of 75% against local tree species diversity [2]. Alpha diversity at plot was calculated as the extra- or interpolated species richness of 75% sampling coverage at each plot (function* iNEXT*, package* iNEXT *[3]). **h** displays the fungal gamma diversity against the number of unique tree species per biome. Stated p-values correspond to the respective models*



*Extended Data Figure 5: Main results for the latitudinal diversity gradient **a-d**, ecological specialisation hypothesis **e, f** and the tree-species-diversity hypothesis **g, h** in wood-saprotrophic fungal diversity for the natural (left) and the standardised logs (right). **a** and **b** display the fungal gamma diversity against the number of sampled objects per biome. **c** and **d** display the fungal alpha diversity on log level against absolute latitude. **e** displays the network specialisation against absolute latitude. **f** shows the resource specialisation against absolute latitude as the specialisation of fungi on the standardised log (blue)and the mean specialisation on the natural logs (green) on one plot. **g** shows the estimated fungal alpha diversity at plot level on a sample coverage value of 75% against local tree species diversity [2]. Alpha diversity at plot was calculated as the extra- or interpolated species richness of 75% sampling coverage at each plot (function* iNEXT, *package* iNEXT [3]*). **h** displays the fungal gamma diversity against the number of unique tree species per biome. Stated p-values correspond to the respective models.*

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A.3: DISENTANGLING THE IMPORTANCE OF SPACE AND HOST TREE FOR THE BETA-DIVERSITY OF BEETLES, FUNGI, AND BACTERIA: LESSONS FROM A LARGE DEAD-WOOD EXPERIMENT

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Policy analysis

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

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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.

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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

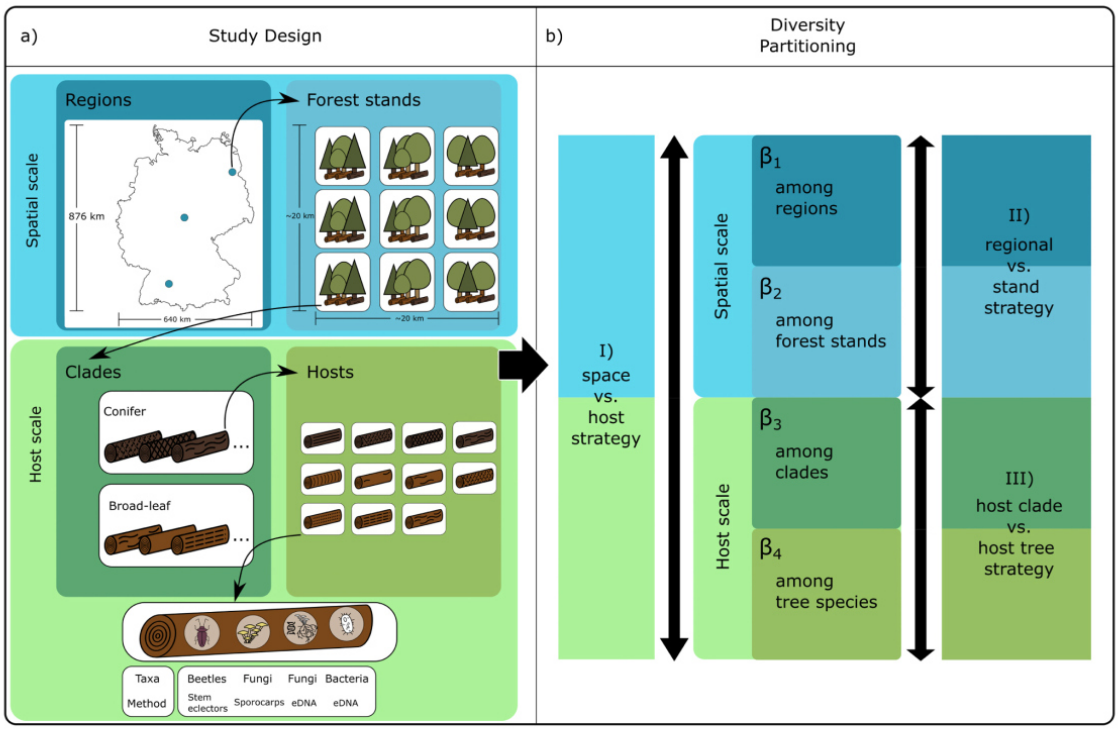

Fig. 1. Sampling design, methods, and conservation strategies. a) Sampling design: Over 7 years, the diversity of saproxylic beetles, fungal sporocarps, microbial fungi, and bacteria was studied at different scales: in three regions of Germany (regional scale) and in 27 forest stands, with 11 logs of 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.

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 km^2 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 700–1000 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, ~1560 km^2), 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, ~1300 km^2), 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, 1672 of the 1782 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 Section 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 6926 sequence reads per sample for fungal ITS and 1879 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 and Fuller, 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 species"), Shannon entropy ($q = 1$) reflects the species' sampled abundance, without favoring rare or dominant species (hereafter "typical species", after Gotelli and Chao (2013)), while Simpson diversity ($q = 2$) assigns most weight to dominant species (hereafter "dominant species") (Jost, 2007). Each observed beta-diversity value calculated was compared to a null model with 1000 randomizations, based on complete randomizations at all levels but keeping species frequencies and species richness constant (function *r2dtable*). Null modeling indicated whether the observed beta-diversity at a given scale was larger or smaller than expected or not different from random.

The overall gamma-diversity of each species group was partitioned simultaneously into spatial and host scales, resulting in four levels (Fig. 1): spatial scale was partitioned into β_1, representing the beta-diversity among regions, and β_2, the beta-diversity among forests stands; host scale was partitioned into β_3, among host tree clades and β_4, among host tree species. This output addresses the first study question (space vs. host), with β_1 and β_2 summed into the overall space component and β_3 and β_4 into the overall host component, scaled to 100%.

The imbalance resulting from the inclusion of seven broad-leaved vs. four conifer host tree species was taken into account by analyzing subsets of the data containing only four broad-leaved species each time together with all four conifer host trees. Accordingly, 35 matrices covering all possible combinations of four broad-leaved and the four conifer tree species were created. For each matrix, the beta-diversity and respective null models were calculated for each group and diversity index as described above. Mean beta-diversity and variance for each beta-diversity scale were then calculated and the results of each of the 35 null models recorded. This was followed by a calculation for each beta-diversity scale of the percentage of observed values larger or smaller than or not different from random (Appendix B Table B.1). It should be noted that: (i) we are aware that reads do not necessarily represent the actual abundance of ASVs (Lamb et al., 2019). However, using sample-based relative abundance in our analysis did not change the inferences (data not shown). Furthermore, incidence data were accounted for in the analysis of species richness ($q = 0$, see Section 2.3.2). Possible sequence errors (Modin et al., 2020) were accounted for by excluding singletons, through the rarefaction of the data, and by comparison with null models. (ii) Separate analyses of the data for 2012 (2011 for beetles), 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 Sections 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, 5690 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 Section 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

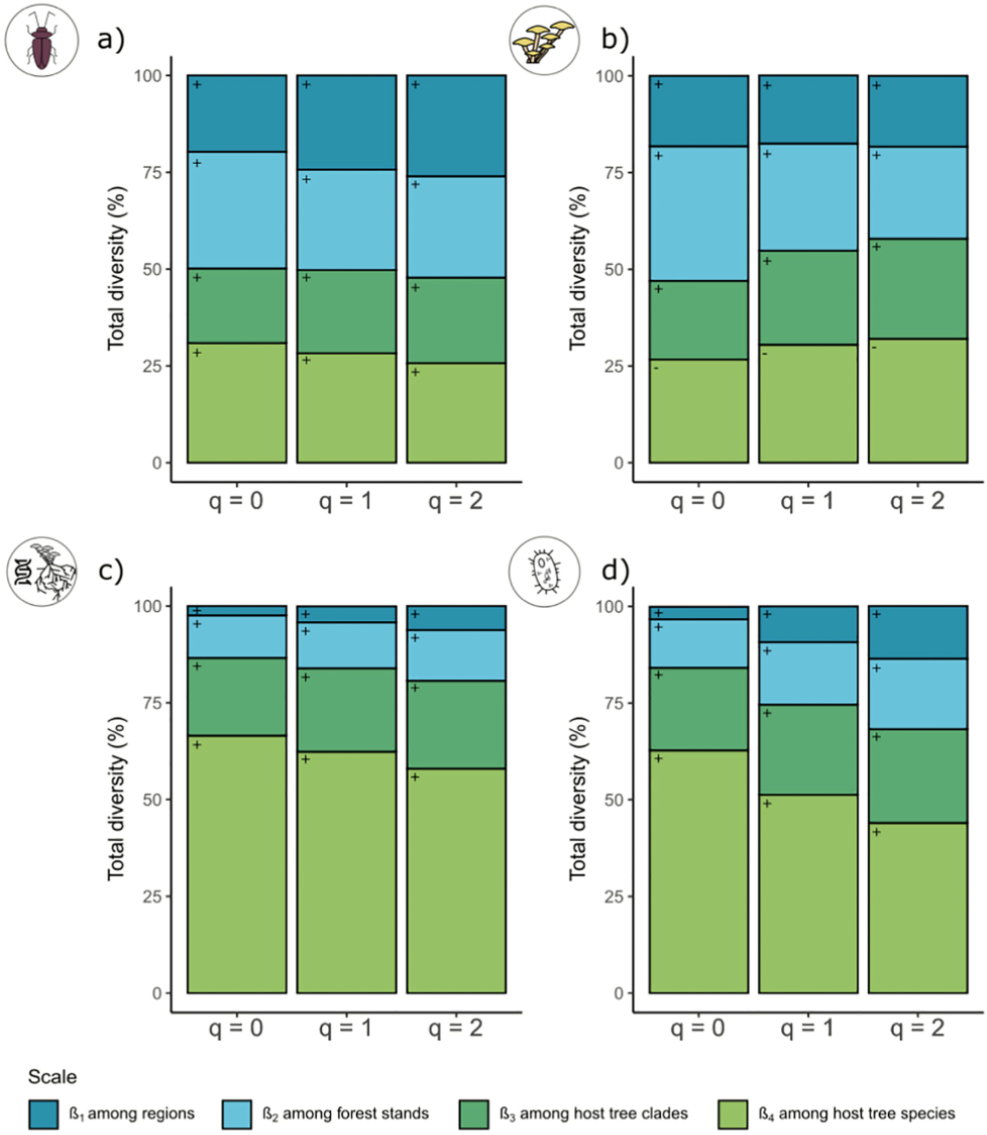

Fig. 2. Stacked bar plots of multiplicative diversity partitioning comparing the relative importance of the beta diversity on different scales for the total diversity of saproxylic beetles (a), fungal sporocarps (b), microbial fungi (c), and bacteria (d). Presented are the number-equivalents of species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

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-wood amount in the 9000 m^2 plot was higher. This was also supported by Abrego and Salcedo (2014), who studied the influence of forest management on fungal sporocarp diversity at the plot scale of 100 m^2. For saproxylic beetles, an increased dead-wood amount in a 40 m radius around the plot had a positive effect on the species richness (Seibold et al., 2017). Although further studies are needed, our results clearly underline the importance of among-stand environmental variability for saproxylic diversity.

While the among forest stand scale seems to be more important than the among regions scale across taxa, the variability of environmental conditions among regions explained a considerable amount of the beta-diversity of beetles and fungal sporocarps. Additional evidence is needed, but dispersal limitation is unlikely to be the reason for this finding. In fact, in a previous study, the beta-diversity of beetles at a scale similar to that used in our study was better explained by environmental conditions than by spatial structure, with the latter serving as a surrogate for dispersal limitation (Bae et al., 2021). Müller and Gossner (2010) also concluded that dispersal limitation is not the primary reason for beetle diversity at scales around 240 km. In their analysis, the scale between forest sites, likewise separated by non-forest land, was of minor importance. These arguments for beetles should also apply to fungi since, at the regional scale, they are less dispersal-limited than beetles (Komonen and Müller, 2018; Bae et al., 2021).

The spatial pattern determined for bacterial beta-diversity was between that of fungal sporocarps and that of molecular fungi. To the best of our knowledge, bacterial beta-diversity across these spatial scales has not been analyzed previously in this context. Our study demonstrated that the beta-diversity caused by spatial variation contributed more to the gamma-diversity of bacteria than to that of molecular fungi (Fig. 2c). If bacteria are also assumed to have no dispersal limitation at the examined spatial scale, spatial environmental variability would also be the most plausible explanation of their high beta-diversity (Van der Gucht et al., 2007; Barberán et al., 2014). This would also point to bacterial communities' stronger sensitivity than fungal molecular communities to environmental variability across space.

The importance of the among regions scale for beetles, fungal sporocarp, and bacteria (dominant 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 700–1000 mm and 6–7 °C, to the north where the MAP and MAT are 500–600 mm and 8–8.5 °C; see Section 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 Section 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, Tables 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 and Fuller, 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 is 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

This work is based on data elaborated by the BELongDead Experiment of the Biodiversity Exploratories program (DFG Priority Program 1374). Data for beetles (ID: 31124) and fungal sporocarps (ID: 31058) can be downloaded at: https://www.bexis.uni-jena.de/ddm/publicsearch/index. However, to give data owners and collectors time to perform their analysis the Biodiversity Exploratories' data and publication policy includes by default an embargo period of three years from the end of data collection/data assembly. These datasets will be made publicly available via the same data repository. Molecular data is available at: https://dataview.ncbi.nlm.nih.gov/object/PRJNA756463?reviewer=csfdp5h8htnmrqq37qs5l7qj88.

CRediT authorship contribution statement

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Declaration of competing interest

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

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Appendix A. Supplementary data

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Appendix A – Species lists with abundances, red-list and old-growth indicator categories

Table A.1: Species list of saproxylic beetles with abundances on logs and samples, as well as assigned red list status in Germany (Schmidl and Büche, 2017) and primeval forest relict beetles (Eckelt et al., 2018).

Species	Red List status *	Primeval forest relict **	Occurence on No. of logs	Occurence in No. of samples
Total	76	8	297	1 672
Abdera flexuosa	U		1	1
Abraeus granulum	U		24	25
Abraeus perpusillus	U		44	76
Acalles camelus	U		37	41
Acalles echinatus	U		11	12
Acritus minutus	3		12	15
Acrulia inflata	U		5	6
Aderus populneus	U		4	4
Aeletes atomarius	3		8	8
Aesalus scarabaeoides	1	2	1	1
Agaricochara latissima	U		11	11
Agathidium nigripenne	U		37	37
Agrilus laticornis	U		1	1
Alosterna tabacicolor	U		5	5
Ampedus balteatus	U		27	41
Ampedus cinnabarinus	2		12	14
Ampedus elongatulus	U		4	5
Ampedus nigerrimus	3		1	1
Ampedus nigrinus	U		2	3
Ampedus pomorum	U		123	271
Ampedus rufipennis	2		11	12
Ampedus sanguineus	U		35	55
Amphotis marginata	U		3	3
Anaglyptus mysticus	U		1	1
Anaspis flava	U		28	31
Anaspis frontalis	U		27	32
Anaspis humeralis	U		2	2
Anaspis maculata	U		8	9
Anaspis marginicollis	D		14	16
Anaspis ruficollis	U		43	63
Anaspis rufilabris	U		46	50
Anaspis thoracica	U		61	71
Anidorus nigrinus	U		4	5
Anisotoma castanea	U		9	9
Anisotoma glabra	U		1	1
Anisotoma humeralis	U		159	281
Anisotoma orbicularis	U		83	124
Anobium costatum	U		7	7
Anobium nitidum	U		1	1
Anobium pertinax	U		19	24
Anomognathus cuspidatus	U		80	90
Anostirus castaneus	U		1	1
Anthribus albinus	U		44	69
Aplocnemus nigricornis	U		1	2
Arhopalus rusticus	U		9	14
Arpidiphorus orbiculatus	U		51	64
Arthrolips obscurus	D		1	1
Atheta oblita	U		1	1
Atheta picipes	U		80	86
Atheta pilicornis	U		2	2
Atomaria atrata	D		2	2
Atomaria bella	D		20	20

Atomaria diluta	U		7	8
Atomaria elongatula	D		8	10
Atomaria lohsei	U		4	5
Atomaria ornata	U		7	7
Atomaria procerula	U		2	2
Atomaria pulchra	D		23	28
Atomaria turgida	U		38	42
Atomaria umbrina	U		15	17
Atrecus affinis	U		78	97
Batrisodes venustus	U		10	16
Bibloporus bicolor	U		222	431
Bibloporus mayeti	U		3	3
Bibloporus minutus	U		80	119
Bitoma crenata	U		14	30
Bolitochara lucida	U	2	4	4
Bolitochara mulsanti	U		4	4
Bolitochara obliqua	U		100	131
Bolitophagus reticulatus	3		6	6
Caenoscelis ferruginea	U		9	9
Calyptomerus alpestris			3	3
Cerylon fagi	U		166	253
Cerylon ferrugineum	U		246	560
Cerylon histeroides	U		231	500
Choragus sheppardi	U		15	16
Cis bidentatus	U		17	17
Cis boleti	U		76	118
Cis castaneus	U		20	21
Cis dentatus	U		18	21
Cis fagi	D		3	3
Cis glabratus	U		29	35
Cis hispidus	U		18	22
Cis jacquemartii	D		9	9
Cis lineatocribratus	U		11	11
Cis micans	U		36	44
Cis nitidus	U		71	97
Cis punctulatus	U		4	4
Cis rugulosus	U		9	10
Cis setiger	U		1	1
Corticaria abietorum	U		82	142
Corticaria alleni	D		1	1
Corticaria linearis	D		7	8
Corticaria longicollis	U		39	57
Corticaria pineti	D		1	1
Corticarina lambiana	U		52	58
Corticarina obfuscata	D		32	34
Corticeus unicolor	U		41	63
Corymbia rubra	U		74	161
Corymbia scutellata	3		10	14
Coryphium angusticolle	U		28	31
Cossonus linearis	U		4	4
Cryphalus abietis	U		10	11
Cryptolestes corticinus	U		7	8
Cryptolestes duplicatus	U		7	7
Cryptophagus cylindrus	U		1	1
Cryptophagus dorsalis	U		59	84
Cryptophagus labilis	V		5	5
Cryptophagus micaceus	U		3	3
Cryptophagus subdepressus	U		2	2
Crypturgus cinereus	U		25	26
Crypturgus hispidulus	U		54	83
Crypturgus pusillus	U		21	23
Crypturgus subcribrosus			17	17
Cychramus luteus	U		5	6

Cychramus variegatus	U	18	23
Cypha pulicaria	U	1	1
Dacne bipustulata	U	9	9
Dadobia immersa	U	65	73
Dasytes aeratus	U	2	3
Dasytes caeruleus	U	31	34
Dasytes plumbeus	U	15	15
Dasytes virens	U	1	1
Denticollis linearis	U	102	130
Denticollis rubens	3	22	25
Dexiogya corticina	U	28	32
Diaperis boleti	U	8	13
Dinaraea aequata	U	33	35
Dinaraea linearis	U	22	23
Diplocoelus fagi	U	23	29
Dirhagus lepidus	U	13	13
Dissoleucas niveirostris	U	3	3
Dorcatoma dresdensis	U	1	1
Dorcus parallelipipedus	U	15	20
Dryocoetes autographus	U	56	76
Dryocoetes villosus	U	8	8
Dryophilus pusillus	U	8	8
Eblisia minor	U	1	1
Endomychus coccineus	U	20	20
Enicmus atriceps	U	10	10
Enicmus brevicornis	U	4	4
Enicmus fungicola	U	4	4
Enicmus planipennis	D	4	4
Enicmus testaceus	U	20	28
Ennearthron cornutum	U	40	50
Epuraea biguttata	D	1	1
Epuraea limbata	U	2	2
Epuraea longula	U	1	1
Epuraea marseuli	U	11	12
Epuraea neglecta	U	4	4
Epuraea pallescens	U	5	5
Epuraea pygmaea	U	49	51
Epuraea terminalis	U	23	24
Epuraea variegata	U	77	93
Ernobius abietinus	U	12	13
Ernobius abietis	U	13	14
Ernobius mollis	U	2	2
Ernobius nigrinus	U	1	1
Ernoporicus fagi	U	22	22
Euconnus pragensis	G	1	1
Euglenes oculatus	3	21	26
Euglenes pygmaeus	3	10	14
Euplectus bescidicus	D	3	3
Euplectus bonvouloiri	R	2	2
Euplectus brunneus	U	23	28
Euplectus decipiens	R	27	37
Euplectus fauveli	U	22	24
Euplectus infirmus	D	15	18
Euplectus karsteni	U	64	66
Euplectus kirbyi	U	80	176
Euplectus nanus	U	119	224
Euplectus piceus	U	51	66
Euplectus punctatus	U	62	86
Euplectus tholini	U	2	2
Euryusa castanoptera	U	11	11
Euthiconus conicicollis	2	7	7
Gabrius splendidulus	U	205	297
Glischrochilus quadriguttatus	U	2	2

Glischrochilus quadripunctatus	U	3	3
Grammoptera ruficornis	U	1	1
Gyrophaena angustata	U	3	3
Gyrophaena boleti	U	33	35
Gyrophaena minima	U	6	6
Gyrophaena polita	U	1	1
Hallomenus axillaris	3	2	2
Hallomenus binotatus	U	12	13
Hapalaraea pygmaea	U	1	1
Hedobia imperialis	U	4	4
Holobus apicatus	U	10	10
Hololepta plana	U	1	1
Homalota plana	U	5	5
Hylastes attenuatus	U	2	2
Hylastes cunicularius	U	15	17
Hylastes opacus	U	1	1
Hylecoetus dermestoides	U	54	75
Hylesinus crenatus	U	3	3
Hylis cariniceps	3	13	14
Hylis foveicollis	V	15	15
Hylis olexai	V	30	38
Hylobius abietis	U	9	9
Hylurgops palliatus	U	45	56
Hypnogyra glabra	U	5	5
Hypoganus inunctus	V	1	1
Hypopycna rufula	U	5	5
Ips typographus	U	2	2
Ischnoglossa obscura	U	2	2
Ischnoglossa prolixa	U	2	2
Ischnomera sanguinicollis	3	1	1
Isorhipis melasoides	3	1	1
Kyklioacalles navieresi	U	1	1
Kyklioacalles roboris		6	6
Laemophloeus monilis	V	1	1
Latridius consimilis	D	39	47
Latridius hirtus	U	30	34
Leiopus linnei		2	2
Leiopus nebulosus	U	1	1
Leperisinus fraxini	U	9	14
Leptophloeus alternans	U	4	4
Leptoplectus spinolae	U	48	70
Leptura quadrifasciata	U	10	11
Leptusa fumida	U	46	52
Leptusa pulchella	U	105	125
Liodopria serricornis	U	7	7
Lissodema denticolle	U	8	10
Litargus connexus	U	12	12
Magdalis rufa	U	1	1
Malachius bipustulatus	U	3	3
Malthinus facialis	V	3	3
Malthinus punctatus	U	7	7
Malthinus seriepunctatus	U	3	3
Malthodes crassicornis	3	20	24
Malthodes flavoguttatus	V	1	1
Malthodes guttifer	U	4	4
Malthodes hexacanthus	U	4	5
Malthodes holdhausi	U	5	5
Malthodes lobatus	D	8	8
Malthodes marginatus	U	4	4
Malthodes mysticus	U	8	8
Malthodes pumilus	U	52	58
Malthodes spathifer	U	14	14
Megatoma undata	U	8	8

Melandrya barbata	2		3	4
Melandrya caraboides	V		6	8
Melanotus castanipes	U		162	266
Melanotus rufipes	U		29	29
Melasis buprestoides	U		15	23
Micrambe abietis	U		59	96
Micridium halidaii	G		23	29
Microscydmus minimus	U		95	124
Mordellistena neuwaldeggiana	U		5	5
Mordellistena variegata	U		2	2
Mordellochroa abdominalis	U		58	93
Mycetina cruciata	U		32	45
Mycetophagus atomarius	U		6	8
Mycetophagus fulvicollis	2		2	2
Mycetophagus multipunctatus	U		2	2
Mycetophagus quadripustulatus	U		11	12
Nemadus colonoides	U		1	1
Nemosoma elongatum	U		3	4
Neuraphes carinatus	U		86	118
Neuraphes plicicollis	U		1	1
Neuraphes ruthenus	U		15	15
Nosodendron fasciculare	3		1	1
Nudobius lentus	U		16	17
Octotemnus glabriculus	U		98	165
Oligota granaria	U		5	5
Opilo mollis	U		6	6
Oplosia fennica	3		1	1
Orchesia minor	U		3	3
Orchesia undulata	U		25	40
Orthocis alni	U		12	14
Orthocis festivus	U		18	19
Orthoperus atomus	U		106	136
Orthoperus mundus	U		85	110
Orthoperus nigrescens	D		4	4
Orthoperus punctulatus	D		1	1
Orthotomicus laricis	U		1	1
Osphya bipunctata	3		2	2
Oxymirus cursor	U		3	3
Oxypoda recondita	U		21	27
Pachytodes cerambyciformis	U		1	1
Paromalus flavicornis	U		25	28
Paromalus parallelepipedus	U		16	16
Pediacus depressus	U		16	17
Philothermus evanescens	R	2	37	54
Phloeocharis subtilissima	U		171	327
Phloeonomus punctipennis	U		131	154
Phloeonomus pusillus	U		7	7
Phloeophagus lignarius	V		4	4
Phloeopora corticalis	U		26	26
Phloeopora teres	U		1	1
Phloeopora testacea	U		6	6
Phloeostiba lapponicus	U		4	4
Phloeostiba planus	U		10	11
Phloiotrya rufipes	V		3	3
Phthorophloeus spinulosus	U		1	1
Phyllodrepa ioptera	U		13	13
Phyllodrepa linearis	D		18	20
Phyllodrepa melanocephala	U		1	1
Phyllodrepa nigra	U		8	8
Phyllodrepoidea crenata	U		1	1
Pissodes pini	U		1	1
Pityogenes bidentatus	U		2	2
Pityogenes chalcographus	U		5	5

Pityophagus ferrugineus	U		12	12
Pityophthorus pityographus	U		3	3
Pityophthorus pubescens	U		2	2
Placonotus testaceus	U		7	7
Placusa atrata	U		4	4
Placusa depressa	U		2	2
Placusa incompleta	D		2	2
Placusa pumilio	U		11	11
Placusa tachyporoides	U		45	45
Platycerus caraboides	U		6	6
Platycis cosnardi	3		10	14
Platycis minutus	U		5	5
Platydema violaceum	U		1	1
Platyrhinus resinosus	U		15	16
Platysoma compressum	U		4	5
Plectophloeus fischeri	U		71	101
Plectophloeus nitidus	U		40	55
Plectophloeus nubigena	U		143	227
Plegaderus caesus	U		14	16
Plegaderus dissectus	U		114	234
Plegaderus vulneratus	U		1	1
Pogonocherus fasciculatus	U		3	3
Pogonocherus hispidus	U		2	2
Prionocyphon serricornis	G		5	5
Prionychus ater	V		3	3
Prionychus melanarius	2	2	2	2
Pseudocistela ceramboides	3		1	1
Ptenidium gressneri	3		2	2
Ptenidium turgidum	G		104	149
Pteryngium crenatum	U		42	69
Pteryx suturalis	U		212	439
Ptilinus pectinicornis	U		76	121
Ptinella aptera	U		135	185
Ptinella denticollis	G		2	2
Ptinella limbata	U		98	148
Ptinella microscopica	G		1	1
Ptinella tenella	G		64	85
Ptinus sexpunctatus	U		2	2
Pycnomerus terebrans	3	2	2	2
Pyrochroa coccinea	U		66	88
Pyropterus nigroruber	U		2	2
Pytho depressus	U		2	2
Quedius maurus	U		11	11
Quedius scitus	U		36	57
Quedius xanthopus	U		65	75
Rabocerus foveolatus	U		3	3
Rhagium bifasciatum	U		6	7
Rhagium inquisitor	U		23	24
Rhagium mordax	U		54	70
Rhizophagus bipustulatus	U		231	443
Rhizophagus cribratus	U		8	9
Rhizophagus depressus	U		27	27
Rhizophagus dispar	U		192	279
Rhizophagus ferrugineus	U		3	3
Rhizophagus nitidulus	U		18	20
Rhizophagus parvulus	U		17	17
Rhizophagus perforatus	U		2	3
Rhizophagus picipes	U		1	1
Rhyncolus ater	U		13	16
Rhyncolus elongatus	3		7	8
Rhyncolus sculpturatus	2		3	4
Ropalodontus perforatus	U		3	3
Ruteria hypocrita			47	76

Rutpela maculata			5	6
Sacium pusillum	U		1	1
Salpingus planirostris	U		9	9
Salpingus ruficollis	U		14	14
Saperda scalaris	U		1	1
Saulcyella schmidtii	R		7	8
Scaphidium quadrimaculatum	U		33	46
Scaphisoma agaricinum	U		100	217
Scaphisoma balcanicum	D		8	8
Scaphisoma boreale	R		1	1
Schizotus pectinicornis	U		36	42
Scolytus intricatus	U		1	1
Scydmaenus perrisii	G		1	1
Scydmoraphes minutus	G		2	2
Sepedophilus testaceus	U		42	53
Serropalpus barbatus	U		2	2
Siagonium quadricorne	U		1	1
Silvanoprus fagi			9	9
Silvanus bidentatus			30	30
Silvanus unidentatus			50	54
Sinodendron cylindricum	V		48	90
Sphaeriestes castaneus	U		1	1
Sphaerites glabratus	U		6	6
Sphindus dubius	U		9	10
Stenagostus rhombeus	U		8	8
Stenichnus bicolor	U		115	150
Stenichnus godarti	U		87	166
Stephostethus alternans	U		46	67
Stephostethus rugicollis	U		3	3
Stereocorynes truncorum	U		3	3
Sulcacis affinis	U		21	30
Sulcacis bicornis	U		6	6
Sulcacis fronticornis	U		15	16
Synchita humeralis	U		9	10
Tachyta nana	U		7	9
Tachyusida gracilis	2	1	4	4
Taphrorychus bicolor	U		25	27
Tetratoma fungorum	U		10	10
Thamiaraea cinnamomea	U		2	2
Thanasimus femoralis	U		1	1
Thanasimus formicarius	U		11	13
Thanasimus pectoralis			1	1
Tillus elongatus	U		4	5
Tomicus piniperda	U		2	2
Tomoxia bucephala	U		7	9
Trachodes hispidus	U		43	55
Triphyllus bicolor	3		10	10
Triplax aenea	3		3	3
Triplax russica	U		2	2
Tritoma bipustulata	U		13	13
Tropideres albirostris	U		1	1
Trypodendron lineatum			7	7
Tyrus mucronatus	U		39	55
Uleiota planata			47	56
Uloma culinaris	3		10	10
Vincenzellus ruficollis	U		41	47
Xyleborus dispar	U		48	56
Xyleborus germanus	U		156	250
Xyleborus monographus	U		12	14
Xyleborus saxeseni	U		70	90
Xylechinus pilosus	U		1	1
Xylita laevigata	3		1	1
Xylita livida	2		2	2

Xylostiba bosnicus	U	2	2
Xylostiba monilicornis	U	8	8
Xyloterus domesticus	U	102	110
Xyloterus signatus	U	26	26

* Categories: 0: Extinct or Lost, 1: Threatened with Extinction, 2: Highly Threatened, 3: Threatened, G: Threat of Unknown Extent, R: Extremely Rare, V: Near Threatened, U: Not Threatened, D: Data Deficient, Empty space: No Information

** Categories: 1: *sensu stricto*, restricted to primeval forests; 2: *sensu lato* might appear in production forests

Table A.2: Species list of saproxylic fungal sporocarps with abundances on logs and samples, as well as assigned red list status in Germany (Bundesamt für Naturschutz, 2017) and indication for old growth forests (Blaschke et al., 2009).

species	red list status *	old-growth indicator **	Occurence on No. of logs	Occurence in No. of samples
total	8	5	297	866
Achroomyces effusus			1	1
Albonectria spec.			1	1
Alutaceodontia alutacea			2	2
Amphinema byssoides			5	5
Amylostereum areolatum			3	3
Amylostereum chailletii			1	2
Annulohypoxylon multiforme			62	107
Antrodia serialis			43	61
Antrodia sinuosa			1	1
Antrodia xantha	D		1	1
Antrodiella onychoides			1	1
Antrodiella romellii	D		1	1
Antrodiella semisupina			2	2
Armillaria borealis	D		2	2
Armillaria lutea			160	263
Ascocoryne cylichnium			38	44
Ascocoryne sarcoides			29	32
Athelia			1	1
Athelia bombacina	D		4	4
Athelia decipiens	D		2	2
Athelia epiphylla			9	9
Athelia epiphylla agg.			16	16
Athelia neuhoffii	D		1	1
Auricularia auricula			2	2
Basidiodendron caesiocinereum	D		3	3
Basidiodendron eyrei	D		2	2
Bertia moriformis			10	10
Bispora antennata			3	4
Bisporella citrina			19	24
Bisporella pallescens	D		1	1
Bisporella subpallida	D		1	1
Bjerkandera adusta			68	77
Boidinia furfuracea	D		11	13
Bombardia fasciculata			1	1
Botryobasidium			1	1
Botryobasidium aureum			10	11
Botryobasidium botryosum			7	7
Botryobasidium conspersum			3	3
Botryobasidium laeve			4	4
Botryobasidium medium	D		1	1
Botryobasidium pruinatum	D		22	26
Botryobasidium subcoronatum			39	49
Botryohypochnus isabellinus			43	65
Brevicellicium olivascens			3	3
Byssocorticium atrovirens			1	1
Calocera cornea			35	39
Calocera furcata			21	23
Calocera viscosa			3	3
Calycina spec.			1	1
Calycina trabinella			1	1
Camarophyllus grossulus			2	2
Camarops microspora	3		1	1
Ceriporia			1	1

Ceriporia excelsa			10	10
Ceriporia viridans			4	4
Cerrena unicolor			1	1
Chaetosphaeria cupulifera			1	1
Chaetosphaeria innumera			4	4
Chaetosphaeria myriocarpa			1	1
Chaetosphaeria preussii			1	1
Chaetosphaeria pulviscula			1	1
Cinereomyces lindbladii			3	3
Clavulina coralloides			1	1
Clitopilus hobsonii			6	6
Collybia cookei			2	2
Coniochaeta ligniaria			1	1
Coniophora arida			7	7
Coniophora fusispora	D		2	2
Coniophora puteana			1	1
Conocybe subpubescens	D		1	1
Coprinellus disseminatus			1	1
Coprinellus domesticus s.l.			14	17
Coprinellus micaceus			17	19
Crepidotus applanatus			8	8
Crepidotus mollis			20	21
Cristinia helvetica			2	2
Cyathus striatus			1	1
Cyphellopsis anomala			7	7
Dacrymyces capitatus			1	1
Dacrymyces stillatus			8	8
Dacrymyces stillatus agg.			95	108
Dacryobolus karstenii			3	3
Daedalea quercina			3	3
Dasyscyphella nivea			1	1
Datronia mollis			45	59
Dialonectria episphaeria			3	3
Diaporthe eres			1	1
Diatrype stigma			1	1
Eleutheromycella mycophila			1	1
Entoloma juncinum			1	1
Entoloma spec.			1	1
Eriopezia caesia			11	15
Eutypa flavovirens			1	1
Eutypa lata	D		32	35
Eutypa maura			1	1
Eutypa spinosa			13	21
Eutypa velutina			1	1
Exidia glandulosa			1	1
Exidia nigricans			7	7
Exidiopsis effusa			3	3
Fibulomyces mutabilis			2	2
Flammulaster muricatus		x	1	1
Flammulina velutipes			1	1
Fomes fomentarius			32	54
Fomitopsis pinicola			47	109
Galerina marginata			8	8
Ganoderma applanatum			38	74
Gloeocystidiellum porosum			2	2
Gloeophyllum odoratum			4	7
Gloeophyllum sepiarium			3	4
Glonium lineare			2	2
Glonium nitidum			1	1
Grandinia barba jovis			2	3
Grandinia barba jovis jovis			1	1
Granulobasidium vellereum			1	1
Gymnopilus penetrans			4	4

Gymnopilus sapineus			2	2
Helicogloea lagerheimii	D		1	1
Helvella lacunosa			1	1
Hemipholiota populnea			9	9
Henningsomyces fasciculatus			1	1
Heterobasidion annosum			1	1
Heterobasidion annosum agg.			19	27
Holwaya mucida			4	5
Hyalorbilia inflatula			12	12
Hyaloscypha albohyalina var. spiralis			2	2
Hyaloscypha aureliella			23	23
Hydnomerulius pinastri			4	4
Hygrophoropsis aurantiaca			1	2
Hymenochaete rubiginosa			1	1
Hymenoscyphus serotinus			1	1
Hyphoderma argillaceum			7	7
Hyphoderma guttuliferum		x	1	1
Hyphoderma mutatum			3	3
Hyphoderma occidentale	D		1	1
Hyphoderma pallidum			2	2
Hyphoderma roseocremeum			1	1
Hyphoderma setigerum			15	16
Hyphodiscus hemiamyloideus			2	2
Hyphodontia alutaria			7	9
Hyphodontia arguta			4	4
Hyphodontia pallidula			13	14
Hyphodontia sambuci			2	2
Hypholoma capnoides			34	40
Hypholoma fasciculare			48	62
Hypholoma sublateritium			8	8
Hypochniciellum ovoideum	D		1	1
Hypochnicium erikssonii	D		1	1
Hypochnicium geogenium			1	1
Hypochnicium punctulatum			3	3
Hypochnus fusisporus			2	2
Hypomyces aurantius			2	2
Hypoxylon fragiforme	D		32	34
Hypoxylon fuscum			14	14
Hypoxylon macrocarpum	D		8	8
Hypoxylon perforatum			5	5
Hypoxylon rubiginosum			24	24
Hypoxylon rubiginosum agg.			112	149
Hysterium angustatum			3	4
Hysterium pulicare			2	3
Ischnoderma resinosum		x	9	17
Jackrogersella cohaerens			26	42
Junghuhnia nitida			2	2
Kretzschmaria deusta			10	10
Kuehneromyces mutabilis			15	16
Laccaria laccata			1	1
Lachnum brevipilosum			2	2
Lachnum impudicum			13	13
Lactarius subdulcis			7	8
Lasiosphaeria ovina			35	37
Lasiosphaeria strigosa			4	4
Lasiosphaeris hirsuta			14	14
Laxitextum bicolor			3	3
Lenzites betulina			3	3
Leptosporomyces mutabilis	D		3	3
Leptosporomyces roseus	D		4	4
Leucogyrophana mollusca			11	16
Leucogyrophana romellii	R		3	3
Leucogyrophana spec.			1	1

Lycoperdon foetidum			1	1
Lycoperdon perlatum			3	3
Lycoperdon pyriforme			7	7
Lyomyces sambuci			8	9
Marasmius androsaceus			5	5
Marasmius rotula			1	1
Melanomma juniperinum			1	1
Melanomma pulvis pyrius			83	88
Melanomma pulvis pyriuspyrius			6	6
Mollisia fusca			22	22
Mollisia olivaceocinerea			67	69
Mucronella calva			10	11
Mycena bulbosa			1	1
Mycena crocata			2	2
Mycena galericulata			4	4
Mycena galopus			5	5
Mycena haematopus			31	35
Mycena inclinata			1	1
Mycena leptocephala			3	3
Mycena meliigena			8	8
Mycena purpureofusca			7	8
Mycena renati			2	2
Mycena rubromarginata			1	1
Mycena sanguinolenta			4	4
Mycena silvae nigrae			1	1
Mycena stipata			7	7
Mycena tintinnabulum			1	1
Mycetinis alliaceus			2	2
Mycoacia aurea			2	2
Mycoacia nothofagi		x	7	7
Mycoacia uda			2	2
Mytilinidion gemmigenum			1	1
Nectria cinnabarina			7	7
Nectria coccinea			8	8
Nectria peziza			6	6
Nemania diffusa	D		1	1
Nemania serpens agg.			19	19
Neodasyscypha cerina			9	9
Ombrophila pura			2	2
Ombrophila spp.			1	1
Ombrophila violacea	D		1	1
Orbilia sarraziniana			2	2
Orbilia xanthostigma agg.			83	91
Oxyporus obducens			3	4
Panellus serotinus			10	11
Panellus stipticus			27	32
Panellus stypticus			3	3
Parasola leiocephala			1	1
Peniophora cinerea			3	3
Peniophora incarnata			1	1
Peniophora limitata			3	3
Peniophorella pubera			47	51
Peziza micropus			3	3
Phanerochaete laevis			3	3
Phanerochaete sanguinea			1	1
Phanerochaete septocystidia	D		1	1
Phanerochaete sordida agg.			1	1
Phanerochaete tuberculata			3	3
Phanerochaete velutina			2	2
Phlebia cremeoalutacea	R		1	1
Phlebia livida			5	5
Phlebia radiata			14	16
Phlebia rufa			1	1

Phlebia tremellosa			5	7
Phlebiella vaga			17	21
Phlebiopsis gigantea			8	8
Phleogena faginea	3		1	1
Phloeomana hiemalis			1	1
Phloeomana speirea			14	15
Pholiota flammans			1	1
Pholiota lucifera			1	1
Pholiota populnea			5	6
Pholiota tuberculosa	G		3	3
Pholiotina brunnea			1	1
Physisporinus vitreus			4	4
Pleonectria coryli			1	1
Pleurotus dryinus			2	2
Pleurotus ostreatus			2	2
Plicaturopsis crispa			1	1
Pluteus cervinus			31	31
Pluteus phlebophorus			7	7
Pluteus plautus			1	1
Pluteus pouzarianus			3	3
Pluteus romellii			1	1
Pluteus salicinus			1	1
Pluteus semibulbosus			1	1
Pluteus umbrosus	V	x	1	1
Polydesmia pruinosa			20	20
Polyporus badius			1	1
Polyporus varius			4	5
Porotheleum fimbriatum			7	9
Postia balsamea	G		2	2
Postia caesia			12	12
Postia stiptica			10	12
Postia subcaesia			6	6
Postia tephroleuca			7	8
Proliferodiscus pulveraceus			1	1
Protocrea farinosa			1	1
Protodontia subgelatinosa	D		1	1
Psathyrella piluliformis	D		1	1
Pseudoclitocybe cyathiformis			1	1
Pseudotomentella spec			1	1
Pycnoporellus fulgens			2	2
Pycnoporus cinnabarinus			1	1
Radulomyces confluens			2	2
Ramaria stricta			7	7
Resinicium bicolor			35	48
Rhizochaete radicata			2	3
Rickenella fibula			3	3
Rigidoporus sanguinolentus			12	12
Rosellinia aquila			1	1
Ruzenia spermoides			61	82
Saccoblastia farinacea			1	1
Schizophyllum commune			4	4
Schizopora flavipora			11	11
Schizopora paradoxa			11	11
Schizopora radula			3	3
Scopuloides rimosa			11	11
Scutellinia cejpii	D		2	2
Scutellinia scutellata			9	9
Scutellinia subhirtella	D		1	1
Sebacina dimitica	D		1	1
Sebacina epigaea			6	6
Sebacina incrustans			11	11
Serpula himantioides			19	30
Serpula lacrimans			1	1

Simocybe centunculus		6	6
Simocybe rubi		1	1
Simocybe sumptosa		2	2
Simocybe sumptuosa		1	1
Sistotrema brinkmannii		15	16
Sistotrema coroniferum	D	1	1
Skeletocutis amorpha		26	32
Skeletocutis carneogrisea		1	1
Skeletocutis nivea		19	21
Sphaerobolus stellatus		4	5
Steccherinum ochraceum		2	2
Steccherinum ochraceum s.l.		1	1
Stereum gausapatum		8	8
Stereum hirsutum		78	121
Stereum ochraceoflavum		1	1
Stereum rugosum		45	64
Stereum sanguinolentum		91	109
Stereum subtomentosum		7	7
Stylonectria purtonii		1	1
Subulicystidium longisporum		4	4
Thelephora terrestris		2	2
Thelephora terrestris agg.		1	1
Tomentella atroarenicolor	D	1	1
Tomentella bryophila		1	1
Tomentella lateritia	D	1	1
Tomentella punicea		1	1
Tomentella stuposa		1	1
Tomentella sublilacina		3	3
Trametes gibbosa		10	15
Trametes hirsuta		13	13
Trametes ochracea		3	3
Trametes versicolor		83	141
Trechispora cohaerens		1	1
Trechispora confinis		1	1
Trechispora farinacea		5	5
Trechispora hymenocystis		2	2
Trechispora microspora	D	1	1
Trechispora minima	D	1	1
Trechispora mollusca agg.		1	1
Trechispora stevensonii	D	1	1
Trichaptum abietinum		16	19
Trichoderma citrinum		1	1
Trichoderma gelatinosum agg. agg.		3	3
Trichoderma pulvinata		1	1
Trichoderma pulvinatum		1	1
Trichoderma viride agg.		39	44
Tubaria furfuracea agg.		1	1
Tulasnella eichleriana		6	6
Tulasnella tomaculum	D	1	1
Tulasnella violea		2	2
Vesiculomyces citrinus		1	1
Xenasmatella subflavidogrisea	R	1	1
Xylaria hypoxylon		67	104
Xylaria longipes		1	1
Xylaria polymorpha		3	3
Xylodon asperus		13	13
Xylodon brevisetus		4	4
Xylodon raduloides		5	5
Xylodon spathulatus	D	6	6

* Categories: 0: Extinct or Lost, 1: Threatened with Extinction, 2:Highly Threatened, 3: Threatened, G: Threat of Unknown Extent, R: Extremely Rare, V: Near Threatened, D: Data Deficient, Empty space: Not Threatened

Table A.3: Species list of saproxylic molecular fungi taxonomical assigned using the UNITE database (version 8.0; UNITE Community, 2019) with abundances on logs and samples, as well as assigned red list status in Germany (Bundesamt für Naturschutz, 2017) and indication for old growth forests (Blaschke et al. 2009).

species	red list status*	old-growth indicator	Occurence on No. of logs	Occurences in No. of samples
total	26	5	297	889
undefined ASVs = 5150	-	-	-	-
Abortiporus biennis			1	1
Acephala applanata			1	1
Acidomelania panicicola			1	1
Acremonium cavaraeanum			36	57
Acremonium furcatum			3	3
Acremonium spinosum			14	16
Acrodontium virellum			1	1
Acrostalagmus luteoalbus			2	2
Aequabiliella effusa			2	2
Agaricus comtulus	D		1	1
Agaricus matrum			1	1
Agonimia allobata			1	1
Agrocybe praecox			1	1
Alatospora acuminata			2	2
Albertiniella polyporicola			1	1
Alternaria eichhorniae			13	15
Alternaria hordeicola			3	3
Alutaceodontia alutacea			4	4
Amanita fulva			1	1
Amphinema byssoides			1	1
Amphiporthe hranicensis			1	1
Ampulloclitocybe clavipes			3	3
Amyloporia sinuosa			2	3
Amylostereum areolatum			5	5
Amylostereum chailletii			5	6
Amyloxenasma allantosporum	D		2	3
Angustimassarina acerina			32	35
Anhellia nectandrae			1	1
Annulohypoxylon cohaerens			27	39
Annulohypoxylon multiforme			54	95
Antennariella placitae			2	2
Antrodia serialis			48	101
Antrodia xantha	D		1	3
Antrodiella serpula			1	1
Aphanobasidium pseudotsugae			13	15
Apiognomonia errabunda			9	9
Apiotrichum dulcitum			6	6
Apiotrichum laibachii			1	1
Apiotrichum xylopini			47	55
Apodus deciduus			16	17
Arachnopeziza aurata			8	8
Arachnopeziza aurelia			10	11
Arbusculina fragmentans			1	1
Arthopyrenia salicis			4	4
Arthrocatena tenebrio			1	1
Articulospora proliferata			1	1
Ascocoryne cylichnium			297	646
Athelia decipiens	D		2	2
Athelia epiphylla			33	47
Athelopsis lembospora	D		2	2
Atractium stilbaster			4	5

Atractospora reticulata			1	1
Aurantiporus fissilis		x	1	1
Aureobasidium pullulans			50	53
Auxarthron umbrinum			3	3
Bacidina sulphurella			4	4
Barbatosphaeria arboricola			2	2
Barbatosphaeria barbirostris			70	94
Barbatosphaeria hippocrepida			9	9
Barbatosphaeria varioseptata			2	2
Basidiobolus ranarum			1	1
Basidiodendron caesiocinereum	D		15	21
Basidiodendron eyrei	D		8	8
Beauveria caledonica			48	53
Beauveria pseudobassiana			4	4
Biatriospora mackinnonii			6	6
Bisporella citrina			3	3
Bjerkandera adusta			96	135
Blastobotrys nivea			3	3
Blastobotrys parvus			1	1
Bolbitius reticulatus			4	4
Botryobasidium conspersum			6	6
Botryobasidium laeve			17	19
Botryobasidium subcoronatum			41	56
Botryodiplodia fraxini			22	28
Botrytis porri			1	1
Brevicellicium olivascens			2	2
Buckleyzyma aurantiaca			4	4
Bulgaria inquinans			7	8
Bullera alba			1	1
Bullera crocea			2	2
Burgoa verzuoliana			10	12
Byssochlamys spectabilis			1	1
Byssocorticium atrovirens			1	1
Byssomerulius corium			3	3
Cadophora luteo olivacea			1	1
Cadophora melinii			117	190
Calcarisporium arbuscula			2	2
Calycina ellisii			7	7
Camptophora hylomeconis			2	2
Candida chilensis			8	9
Candida ponderosae			2	2
Candida santamariae			2	2
Candida sophiae reginae			1	1
Candida sphagnicola			1	1
Candida viswanathii			2	2
Candida zeylanoides			1	1
Capronia epimyces			1	1
Capronia pilosella			58	82
Capronia pulcherrima			81	124
Capronia semi immersa			1	1
Catinella olivacea	3		2	3
Celerioriella prunicola			12	12
Cenangium acuum			1	1
Cenococcum geophilum			1	1
Cephalotrichum asperulum			1	1
Cephalotrichum stemonitis			1	1
Ceraceomyces serpens			1	2
Ceratocystiopsis minuta			1	1
Ceratocystiopsis rollhanseniana			1	1
Ceriporia aurantiocarnescens	D		6	6
Ceriporia excelsa			3	3
Ceriporia reticulata			3	3
Ceriporia viridans			14	15

Ceriporiopsis gilvescens		2	2
Chaetomium angustispirale		1	1
Chaetosphaeria vermicularioides		3	4
Chalara holubovae		7	7
Chalara hyalocuspica		24	26
Chalara longipes		1	1
Chalara piceae abietis		4	4
Chlorociboria halonata		1	1
Cinereomyces lindbladii		2	3
Circinotrichum maculiforme		1	1
Cladobotryum mycophilum		1	1
Cladonia fimbriata		2	2
Cladophialophora chaetospira		100	117
Cladophialophora humicola		79	97
Cladophialophora sylvestris		28	30
Cladorrhinum foecundissimum		1	1
Cladosporium flabelliforme		53	59
Cladosporium halotolerans		1	1
Claussenomyces olivaceus		1	1
Clavulina coralloides		1	1
Clitocybe gibba		2	2
Clitocybe nebularis		5	5
Clitopilus hobsonii		7	7
Coccinonectria rusci		1	1
Colacogloea eucalyptica		8	8
Colacogloea peniophorae		2	2
Colacogloea philyla		33	35
Coniochaeta fodinicola		23	26
Coniochaeta ligniaria		3	3
Coniophora arida		7	8
Coniophora puteana		10	12
Coniothyrium carteri		2	2
Conocybe macrospora	R	2	2
Coprinellus disseminatus		1	3
Coprinellus micaceus		58	85
Coprinellus radians		5	6
Cordana ellipsoidea		15	16
Cordana inaequalis		5	6
Cordana terrestris		1	1
Cordyceps bassiana		1	1
Corticium confine		7	7
Cortinarius diasemospermus	D	1	1
Cosmospora arxii		21	25
Cotylidia undulata	2	1	1
Crepidotus cesatii		1	2
Crepidotus mollis		8	17
Crocicreas epicalamia		4	4
Cryptocoryneum condensatum		27	27
Cryptodiscus pallidus		1	2
Cryptosphaeria eunomia		4	4
Cryptosphaeria subcutanea		16	20
Cuniculitrema polymorpha		76	93
Curvibasidium cygneicollum		5	5
Cutaneotrichosporon curvatus		1	1
Cyathus striatus		1	1
Cylindrobasidium evolvens		5	5
Cylindrocarpon faginatum		21	23
Cylindrocarpostylus gregarius		8	10
Cyphellophora europaea		2	2
Cyphellophora pauciseptata		2	2
Cyphellophora sessilis		13	13
Cyphellopsis anomala		40	61
Cystobasidium pinicola		6	6

Cystobasidium psychroaquaticum		1	1
Cystofilobasidium capitatum		1	1
Cytospora ribis		4	4
Dacrymyces novae zelandiae		22	25
Dactylellina cionopaga		3	3
Daedalea quercina		1	2
Daedaleopsis confragosa		1	1
Darkera picea		1	1
Dasyscyphella nivea		3	3
Datronia mollis		23	31
Debaryomyces hansenii		2	2
Deconica phyllogena		1	1
Dendryphion europaeum		1	1
Desmazierella acicola	D	2	2
Devriesia pseudoamericana		5	6
Devriesia strelitziicola		29	33
Dictyochaeta simplex		1	1
Dictyosporium digitatum		3	4
Dinemasporium morbidum		1	1
Durella macrospora		2	2
Elaphomyces asperulus	3	1	1
Elaphomyces muricatus		2	2
Eleutheromyces pseudosubulatus		2	2
Endoconidioma populi		9	9
Endosporium aviarium		3	3
Entoloma juncinum		1	1
Erythrobasidium hasegawianum		1	1
Eucasphaeria capensis		12	12
Eutypa lata	D	58	71
Eutypa spinosa		22	40
Exidia glandulosa		9	9
Exidia pithya		1	1
Exidia saccharina		9	16
Exobasidium arescens	D	3	3
Exobasidium kishianum		1	1
Exobasidium maculosum		1	1
Exobasidium yoshinagae		1	1
Exophiala bergeri		10	13
Exophiala castellanii		8	8
Exophiala equina		4	4
Exophiala moniliae		120	163
Exophiala psychrophila		51	70
Exophiala salmonis		2	2
Exophiala sideris		8	8
Exophiala xenobiotica		5	5
Exserohilum rostratum		1	1
Extremus antarcticus		1	1
Fellomyces horovitziae		1	1
Fellozyma inositophila		3	3
Fibroporia norrlandica		1	1
Fibulobasidium inconspicuum		3	4
Filobasidium stepposum		2	2
Filobasidium wieringae		13	13
Flabellascus tenuirostris		18	20
Flagelloscypha minutissima		3	3
Flammulaster carpophilus		3	3
Flammulina velutipes		6	6
Fomes fomentarius		24	29
Fomitopsis pinicola		68	122
Fulgidea sierrae		3	3
Fusarium fujikuroi		2	2
Fusicolla aquaeductuum		10	11
Fusicolla violacea		1	1

Galerina cephalotricha	D		1	1
Galerina hygrophila			4	4
Galerina sideroides			2	2
Genolevuria amylolytica			9	9
Geomyces auratus			9	10
Geosmithia langdonii			1	1
Gibberella pulicaris			1	1
Gibberella tricincta			2	2
Gibberella zeae			1	1
Gloeocystidiellum kenyense			1	1
Gloeophyllum odoratum			6	9
Goffeauzyma gastrica			1	1
Gorgomyces hungaricus			1	1
Graphium fabiforme			5	5
Grosmannia cucullata			6	6
Grosmannia francke grosmanniae			4	5
Grosmannia laricis			5	5
Guehomyces pullulans			12	14
Gymnopilus penetrans			5	7
Gymnopus androsaceus			2	2
Gymnopus confluens			1	1
Gymnopus perforans			1	1
Gymnopus peronatus			1	2
Gyoerffyella entomobryoides			1	1
Gyoerffyella tricapillata			1	1
Gyromitra slonevskii			1	2
Gyrophanopsis polonensis			1	1
Hamamotoa lignophila			71	92
Helicodendron luteoalbum			2	2
Helicogloea farinacea			2	2
Helicoma fumosum			6	6
Helicoma isiola			3	3
Helicoma morganii			14	17
Hemipholiota heteroclita	G		1	1
Hericium coralloides	G	x	1	1
Hericium erinaceus	2	x	1	1
Herpotrichia juniperi			4	4
Heterobasidion australe			53	76
Hirsutella rhossiliensis			1	1
Hirsutella subulata			1	1
Holtermanniella takashimae			2	2
Hormonema macrosporum			27	28
Humaria hemisphaerica			2	2
Humicola grisea			5	5
Hyaloscypha aureliella			64	96
Hyaloscypha leuconica var bulbopilosa			12	13
Hydnotrya tulasnei	3		1	1
Hydnum ellipsosporum	D		1	1
Hydropisphaera fungicola			1	1
Hygrophorus eburneus			1	1
Hymenochaete rubiginosa			3	3
Hymenogaster griseus	G		1	1
Hymenoscyphus caudatus	D		1	1
Hyphoderma definitum	D		5	5
Hyphoderma mutatum			2	2
Hyphoderma setigerum			37	44
Hyphodermella corrugata			1	1
Hyphodiscus brachyconius			26	32
Hyphodiscus hymeniophilus			22	26
Hyphodiscus luxurians			3	4
Hyphodontia abieticola			1	1
Hyphodontia alutaria			10	18
Hyphodontia aspera			7	15

Hyphodontia pallidula			27	39
Hyphodontia radula			13	14
Hyphodontia subalutacea			1	2
Hypholoma capnoides			75	115
Hypholoma dispersum			2	3
Hypholoma fasciculare			51	76
Hypholoma lateritium			8	12
Hypholoma radicosum			2	2
Hypochnicium geogenium			18	27
Hypochnicium punctulatum			10	10
Hypochnicium subrigescens	D		2	3
Hypogymnia physodes			1	1
Hypomyces aurantius			2	2
Hypoxylon carneum			1	1
Hypoxylon cercidicola			2	2
Hypoxylon fragiforme	D		19	21
Hypoxylon howeanum			19	25
Hypoxylon macrocarpum	D		7	10
Hypoxylon petriniae	D		2	2
Hypoxylon rubiginosum			75	126
Ilyonectria macrodidyma			1	1
Ilyonectria mors panacis			1	1
Ilyonectria robusta			1	1
Imleria badia			1	1
Infundichalara minuta			10	11
Inocybe cookei			2	2
Inocybe fibrosoides	G		1	1
Inocybe maculata			1	1
Inocybe rhodiola			1	1
Inocybe sindonia			1	1
Irpex hacksungii			1	1
Ischnoderma resinosum		x	30	46
Itersonilia pannonica			1	1
Jattaea aphanospora			10	14
Jattaea discreta			1	1
Jattaea prunicola			2	2
Jattaea ribicola			1	1
Junghuhnia luteoalba	D		3	3
Kockovaella machilophila			1	1
Kondoa yuccicola			1	1
Krasilnikovozyma huempii			2	2
Kretzschmaria deusta			10	18
Kuehneromyces mutabilis			27	38
Kuraishia capsulata			9	10
Kurtzmaniella cleridarum			1	1
Kurtzmanomyces nectairei			1	1
Kurtzmanomyces tardus			1	1
Lachnella villosa			2	2
Lachnellula calyciformis	D		2	2
Lachnum fuscescens			1	1
Lachnum pygmaeum			6	6
Lachnum soppittii			1	1
Lactarius blennius			1	1
Lactarius camphoratus			2	2
Lactarius rubrocinctus	G		1	1
Lactarius subdulcis			10	12
Lanzia echinophila			1	1
Lapidomyces hispanicus			8	8
Lasiosphaeria glabrata			4	5
Lasiosphaeria ovina			29	37
Lasiosphaeris hispida			55	72
Laxitextum incrustatum			4	4
Lecania cyrtella			1	1

Lecanicillium fungicola		1	1
Lecanicillium fusisporum		2	2
Lecanicillium muscarium		1	1
Lecanora hagenii		1	1
Lentinus crinitus		1	1
Lenzites betulina		2	2
Leptodontidium boreale		2	2
Leptodontidium trabinellum		280	605
Leptographium lundbergii		17	18
Leptospora rubella		1	1
Leptosporomyces galzinii		1	1
Leucosporidium creatinivorum		2	2
Leucosporidium drummii		5	5
Limacella delicata	D	1	1
Lirula macrospora		1	1
Lophiostoma cynaroidis		7	7
Lophiotrema eburnoides		2	2
Lophiotrema rubi		66	95
Lophodermium piceae		19	21
Lophodermium pinastri		4	4
Luellia recondita	D	16	17
Lycoperdon echinatum		3	3
Lycoperdon pratense		1	1
Lycoperdon pyriforme		4	6
Lycoperdon subumbrinum		1	1
Malassezia restricta		5	5
Mariannaea samuelsii		32	43
Massarina eburnea		1	1
Megacollybia platyphylla		42	55
Melanconiella spodiaea		1	1
Melanogaster ambiguus		2	2
Melanogaster broomeanus		8	9
Melanogaster variegatus	D	1	1
Meliniomyces bicolor		18	18
Meliniomyces variabilis		6	8
Menispora ciliata		5	5
Menispora manitobaensis		41	44
Merismodes fasciculata		23	37
Metacordyceps chlamydosporia		1	1
Metarhizium carneum		2	2
Metarhizium robertsii		5	5
Meyerozyma caribbica		1	1
Micarea hedlundii		3	3
Microascus longirostris		1	1
Microcera larvarum		3	3
Microcera rubra		1	1
Microdochium phragmitis		2	2
Microsporomyces pini		3	3
Minimelanolocus asiaticus		2	2
Mollisia cinerea		19	23
Monochaetia monochaeta		1	1
Moristroma quercinum		20	27
Mortierella alliacea		2	2
Mortierella alpina		1	1
Mortierella amoeboidea		9	9
Mortierella angusta		1	1
Mortierella cystojenkinii		1	1
Mortierella exigua		6	6
Mortierella gamsii		25	26
Mortierella gemmifera		13	13
Mortierella humilis		6	6
Mortierella hyalina		28	31
Mortierella jenkinii		7	7

Mortierella lignicola			3	3
Mortierella macrocystis			5	5
Mortierella macrocystopsis			23	24
Mortierella minutissima			3	3
Mortierella parvispora			33	38
Mortierella pseudozygospora			1	1
Mortierella pulchella			29	33
Mortierella sclerotiella			1	1
Mortierella turficola			5	5
Mortierella zychae			1	1
Mrakia frigida			32	33
Mrakiella aquatica			4	4
Mucor abundans			2	2
Mucor hiemalis			1	1
Mutinus caninus			5	5
Mycena abramsii			20	25
Mycena alba			6	6
Mycena amicta			10	12
Mycena crocata			4	4
Mycena cyanorhiza	D		3	3
Mycena diosma			2	2
Mycena floridula			1	1
Mycena galericulata			11	11
Mycena haematopus			28	33
Mycena laevigata			3	3
Mycena meliigena			1	1
Mycena metata			7	8
Mycena pelianthina			3	3
Mycena plumipes			1	1
Mycena pura			3	3
Mycena rebaudengoi			4	4
Mycena renati			9	9
Mycena rosea			1	1
Mycena sanguinolenta			16	16
Mycena septentrionalis	D		1	1
Mycena silvae nigrae			1	1
Mycena speirea			6	8
Mycena zephirus			20	21
Mycetinis alliaceus			7	8
Mycoacia aurea			6	7
Mycoacia fuscoatra			1	1
Mycoacia nothofagi		x	2	2
Mycoacia uda			5	7
Mycosphaerella punctiformis			3	3
Myxocephala albida			1	1
Naganishia liquefaciens			1	1
Nakazawaea holstii			5	5
Natantiella ligneola			25	29
Nectria cinnabarina			1	1
Nectria ramulariae			12	12
Nectria zangii			1	1
Nectriopsis rexiana			3	3
Nectriopsis tremellicola			1	1
Nemania chestersii	R		2	3
Nemania diffusa	D		3	3
Nemania serpens			13	14
Neoascochyta exitialis			2	2
Neobulgaria pura			6	6
Neocatenulostroma microsporum			3	3
Neofabraea malicorticis			23	25
Neolentinus kauffmanii			1	1
Neonectria fuckeliana			1	1
Nidulariopsis iowensis			3	3

none		329	980
Oberwinklerozyma yarrowii		4	4
Octaviania asterosperma	G	5	5
Odontia ferruginea		1	1
Ogataea pilisensis		1	1
Oidiodendron echinulatum		1	1
Oidiodendron griseum		25	31
Oidiodendron maius		2	2
Oidiodendron periconioides		12	13
Oidiodendron rhodogenum		18	18
Operculomyces laminatus		1	1
Ophiostoma angusticollis		1	1
Ophiostoma aurorae		1	1
Ophiostoma denticiliatum		1	1
Ophiostoma tsotsi		4	4
Oxyporus populinus		9	14
Panellus serotinus		23	32
Panellus stipticus		7	12
Panus conchatus		1	1
Papiliotrema flavescens		2	2
Papiliotrema laurentii		1	1
Papiliotrema terrestris		1	1
Paraphoma chrysanthemicola		1	1
Parathyridaria percutanea		1	1
Peltaster fructicola		1	1
Penicillium carneum		3	3
Penicillium lignorum		1	1
Penicillium paczoskii		1	1
Peniophora lycii		7	7
Peniophora piceae	2	2	2
Peniophorella guttulifera	D	4	6
Peniophorella pallida		3	4
Peniophorella praetermissa		74	87
Peniophorella pubera		60	84
Perusta inaequalis		12	12
Pesotum piceae		41	56
Peterozyma toletana		35	36
Pezicula neosporulosa		10	11
Pezicula sporulosa		3	5
Peziza arvernensis		1	1
Peziza michelii		1	1
Phacidium lacerum		7	8
Phaeoacremonium angustius		39	68
Phaeoacremonium croatiense		52	69
Phaeoacremonium inflatipes		3	9
Phaeococcomyces catenatus		3	3
Phaeomollisia piceae		48	64
Phaeosclera dematioides		4	4
Phaeosphaeria caricicola		1	1
Phaeosphaeria podocarpi		1	1
Phaeotheca fissurella		2	2
Phaeotremella skinneri		1	1
Phallus impudicus		75	102
Phanerochaete laevis		2	3
Phanerochaete sordida		7	9
Phanerochaete velutina		4	5
Phialemoniopsis cornearis		1	1
Phialemoniopsis ocularis		7	7
Phialocephala compacta		16	17
Phialocephala glacialis		1	1
Phialocephala humicola		2	2
Phialocephala repens		28	37
Phialocephala scopiformis		19	21

Phialocephala trigonospora		24	28
Phialocephala urceolata		1	2
Phialophora chinensis		4	4
Phialophora livistonae		1	1
Phialophora phaeophora		3	3
Phlebia livida		3	4
Phlebia radiata		19	26
Phlebia rufa		2	2
Phlebia tremellosa		3	4
Phlebia tuberculata		5	5
Phlebiopsis gigantea		15	18
Pholiota adiposa		6	8
Pholiota lenta		1	1
Pholiota tuberculosa	G	2	2
Phomatospora dinemasporium		1	1
Phomatospora striatigera		1	1
Phyllactinia fraxini		2	2
Phyllozyma coprosmicola		1	1
Physcia adscendens		4	4
Piloderma lanatum	D	2	2
Piloderma olivaceum		1	1
Piskurozyma cylindrica		8	9
Placynthiella dasaea		13	14
Plectosphaerella alismatis		1	1
Plectosphaerella cucumerina		2	2
Plectosphaerella oratosquillae		1	1
Plectosphaerella populi		1	1
Plenodomus biglobosus		33	37
Pleurophoma ossicola		1	1
Pleurotopsis longinqua		1	1
Pleurotus dryinus		1	1
Pleurotus ostreatus		4	4
Pleurotus pulmonarius		3	3
Plicaturopsis crispa		2	2
Pluteus atromarginatus		4	5
Pluteus brunneidiscus		7	8
Pluteus cervinus		6	6
Pluteus eludens		2	2
Pluteus exiguus	V	1	1
Pluteus hongoi		16	18
Pluteus leoninus		2	2
Pluteus longistriatus		2	2
Pluteus phlebophorus		2	2
Pluteus plautus		6	6
Pluteus podospileus	V	2	2
Pluteus romellii		2	2
Pluteus salicinus		1	2
Pluteus satur		1	2
Pluteus semibulbosus		1	1
Pluteus shikae		1	1
Pluteus thomsonii		8	9
Pochonia bulbillosa		15	15
Pochonia cordycepisociata		1	1
Polydesmia pruinosa		4	4
Polyporus varius		5	7
Porotheleum fimbriatum		8	11
Postia caesia		8	9
Postia fragilis		1	1
Postia guttulata		2	3
Postia rennyi		2	2
Postia sericeomollis		1	1
Postia tephroleuca		4	4
Preussia flanaganii		7	7

Priceomyces haplophilus		1	1
Protocrea pallida	D	1	1
Psathyrella candolleana	D	3	3
Psathyrella fagetophila	D	2	2
Psathyrella fennoscandica		1	1
Psathyrella maculata	2	2	2
Psathyrella obtusata	D	5	7
Pseudaegerita corticalis		3	4
Pseudogymnoascus appendiculatus		3	3
Pseudomicrostroma phylloplanum		1	1
Pseudoplectania nigrella	G	1	1
Pseudovalsaria ferruginea		2	2
Pucciniastrum areolatum		1	1
Pycnoporellus fulgens		3	4
Pycnopulvinus aurantiacus		4	4
Pyrenochaetopsis leptospora		3	3
Pyrenopeziza revincta		2	2
Pyrigemmula aurantiaca		4	4
Ramaria stricta		3	4
Ramichloridium anceps		3	5
Ramichloridium cucurbitae		1	1
Ramichloridium pini		1	1
Ramimonilia apicalis		1	1
Ramophialophora humicola		6	6
Resinicium bicolor		78	129
Resinicium furfuraceum	D	1	2
Resupinatus poriaeformis	D	1	1
Reticulascus clavatus		1	1
Reticulascus tulasneorum		3	3
Rhinocladiella fasciculata		52	69
Rhizoctonia fusispora		5	6
Rhizodermea veluwensis		2	2
Rhizophlyctis rosea		1	1
Rhizopogon rudus		2	2
Rhizosphaera kalkhoffii		4	4
Rhodocollybia butyracea f asema		2	2
Rhodonia placenta	D	6	13
Rhodosporidiobolus colostri		5	5
Rhodotorula cycloclastica		3	3
Rhodotorula toruloides		1	1
Rhodoveronaea varioseptata		54	62
Rickenella fibula		6	7
Rickenella swartzii		1	1
Rigidoporus sanguinolentus		38	50
Rosasphaeria moravica		15	16
Rosellinia abscondita		1	1
Russula fellea		2	2
Russula ionochlora		4	6
Russula nobilis		5	5
Russula ochroleuca		3	3
Russula puellaris		1	1
Russula rosea		1	2
Saitozyma podzolica		7	7
Sakaguchia lamellibrachiae		10	10
Sarcoleotia globosa	R	1	1
Sarocladium kiliense		1	1
Sarocladium strictum		2	2
Sawadaea bicornis		3	3
Saxophila tyrrhenica		4	4
Scheffersomyces ergatensis		41	59
Scheffersomyces parashehatae		72	91
Scheffersomyces stipitis		4	5
Schizopora flavipora		10	10

Schizopora paradoxa		3	3
Schizothecium miniglutinans		1	1
Schwanniomyces polymorphus		1	1
Sclerostagonospora cycadis		1	1
Sclerostagonospora opuntiae		1	1
Scopuloides hydnoides		35	43
Scopuloides rimosa		1	1
Scutellinia crinita	D	9	9
Scutellinia olivascens		4	5
Scytalidium album		69	96
Scytalidium lignicola		27	30
Sebacina epigaea		4	4
Sebacina flagelliformis		4	4
Sebacina incrustans		1	1
Septoriella hirta		1	1
Serendipita herbamans		2	2
Serendipita indica		1	1
Serpula himantioides		15	28
Simocybe sumptuosa		8	8
Simplicillium lamellicola		2	2
Simplicillium minatense		2	2
Sistotrema brinkmannii		218	333
Sistotrema raduloides	R	1	1
Skeletocutis amorpha		12	15
Skeletocutis kuehneri	D	4	5
Slooffia pilatii		19	20
Slooffia tsugae		1	1
Solicoccozyma aeria		3	3
Solicoccozyma terricola		19	19
Sphaerobolus stellatus		1	1
Sporobolomyces roseus		2	2
Sporobolomyces symmetricus		1	1
Sporoschisma hemipsilum		13	19
Sporothrix fumea		4	4
Sporothrix rossii		3	3
Steccherinum ochraceum		1	1
Stereum gausapatum		21	36
Stereum hirsutum		48	68
Stereum ostrea		3	3
Stereum rugosum		36	50
Stereum sanguinolentum		72	92
Subulicystidium longisporum		42	52
Sugitazyma miyagiana		2	2
Sugiyamaella japonica		3	5
Sugiyamaella paludigena		49	63
Sydowia polyspora		2	2
Symbiotaphrina buchneri		3	3
Sympodiella acicola		2	2
Sympoventuria capensis		1	1
Talaromyces acaricola		3	3
Talaromyces diversus		6	9
Talaromyces rademirici		27	36
Talaromyces ruber		1	1
Talaromyces rugulosus		4	4
Teichospora rubriostiolata		4	4
Tetracladium marchalianum		6	7
Thekopsora rubiae		1	1
Thelonectria mammoidea		4	4
Thelonectria pinea		1	1
Tolypocladium album		3	3
Tolypocladium pustulatum		1	1
Tomentella badia	D	1	1
Tomentella coerulea		1	1

Tomentella lapida	D	1	1
Tomentella pilosa	D	1	1
Tomentella punicea		4	4
Tomentella stuposa		1	1
Tomentella subclavigera	R	1	1
Tomentella sublilacina		4	4
Tomentella terrestris	D	1	1
Torula hollandica		1	1
Tothia fuscella		10	10
Trametes gibbosa		9	11
Trametes versicolor		86	135
Trapeliopsis flexuosa		4	4
Trechispora farinacea		5	6
Trechispora hymenocystis		6	6
Trechispora invisitata	R	3	3
Trechispora stevensonii	D	13	14
Trematosphaeria pertusa		2	2
Tremella aurantia	D	8	8
Tremella encephala		2	2
Tremella fuciformis	D	2	3
Tremella indecorata	D	6	6
Tremella roseotincta		1	1
Trichaptum abietinum		9	10
Trichoderma aerugineum		3	3
Trichoderma asperellum		1	1
Trichoderma atroviride		23	36
Trichoderma deliquescens		20	26
Trichoderma harzianum		24	26
Trichoderma luteocrystallinum		1	1
Trichoderma minutisporum		81	108
Trichoderma oblongisporum		2	2
Trichoderma parapiluliferum		24	31
Trichoderma pulvinatum		1	1
Trichoderma rhododendri		1	1
Trichoderma sinuosum		1	1
Trichoderma spirale		3	3
Trichoderma stellatum		45	55
Trichoderma stilbohypoxyli		10	11
Trichoderma trixiae		59	75
Tricholoma portentosum	3	1	1
Tricholomopsis rutilans		1	1
Trichomerium dioscoreae		8	8
Trichomonascus petasosporus		5	5
Trichothecium crotocinigenum		1	1
Trichothecium roseum		1	1
Tricladium splendens		2	2
Truncatella spadicea		3	3
Tubaria furfuracea		1	1
Tubaria praestans	D	1	1
Tuber anniae		2	2
Tuber borchii	3	1	1
Tuber puberulum	G	2	2
Udeniozyma ferulica		2	2
Umbelopsis angularis		13	13
Umbelopsis changbaiensis		3	3
Umbelopsis dimorpha		1	1
Umbelopsis isabellina		25	26
Umbelopsis ramanniana		17	20
Unilacryma unispora		1	1
Urocystis eranthidis		1	1
Ustilago nunavutica		1	1
Veronaea compacta		34	37
Veronaea japonica		2	2

Verticillium leptobactrum	1	1
Vishniacozyma dimennae	1	1
Vishniacozyma victoriae	25	26
Wallemia mellicola	1	1
Wardomyces inflatus	1	1
Wickerhamomyces bisporus	6	6
Xanthoporia radiata	2	2
Xenasma tulasnelloideum	5	5
Xenasmatella borealis	1	1
Xenasmatella vaga	11	12
Xenoacremonium recifei	12	12
Xenopolyscytalum pinea	78	107
Xerocomellus porosporus	1	1
Xerocomellus pruinatus	2	2
Xylaria cubensis	3	3
Xylaria hypoxylon	13	17
Xylaria polymorpha	8	10
Xylodon detriticus	2	2
Xylodon nespori	1	1
Xylodon sambuci	17	17
Yurkovia mendeliana	11	11
Zalerion arboricola	25	27
Zopfiella marina	2	2

* Categories: 0: Extinct or Lost, 1: Threatened with Extinction, 2: Highly Threatened, 3: Threatened, G: Threat of Unknown Extent, R: Extremely Rare, V: Near Threatened, D: Data Deficient, Empty space: Not Threatened

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Appendix B - Supplementary figures and tables

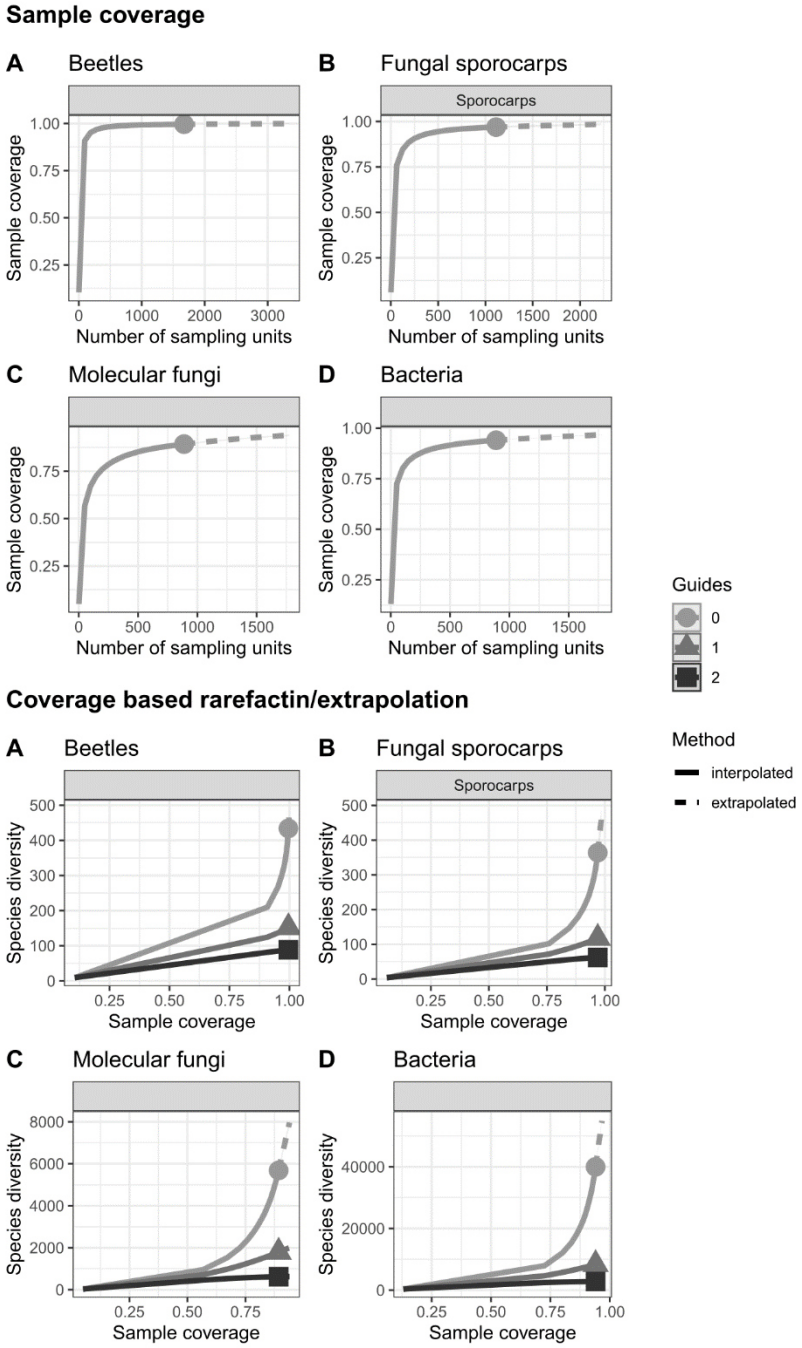

Figure B.1: Incidence-based observed and extrapolated sample coverage for beetles (a), fungal sporocarps (b), microbial fungi (c), and bacteria (c). Coverage-based rarefaction and extrapolation of the incidence data of beetles (e), fungal sporocarps (f), fungal mycelium (g), and bacterial (h) ASVs, computed for the Hill number-equivalents q = 0,1,2. All computations were carried out using the package *iNEXT* in R.

Table B.1: Results of the multiplicative diversity partitioning of space for saproxylic beetles, fungal sporocarps, microbial fungi, and bacteria in Germany among three regions (β_1) with a total of 27 forest stands (β_2) where logs of 2 tree clades (β_3) and 11 tree species (β_4) where placed. .

Species group diversity index	β-level	Mean percentage of total diversity (± variance)*	Percentage of observed values greater/smaller than or equal to the null-model computation
Beetles			
Species richness	β_1	19.7 ± 0.04	100/0/0
	β_2	30.1 ± 0.05	100/0/0
	β_3	19.3 ± 0.02	100/0/0
	β_4	30.9 ± 0.06	71.4/2.9/25.7
Shannon entropy	β_1	24.3 ± 0.04	100/0/0
	β_2	25.9 ± 0.1	100/0/0
	β_3	21.5 ± 0.02	100/0/0
	β_4	28.3 ± 0.14	91.4/0/8.6
Simpson diversity	β_1	26.0 ± 0.67	100/0/0
	β_2	26.2 ± 0.57	100/0/0
	β_3	22.1 ± 0.29	100/0/0
	β_4	25.7 ± 0.81	100/0/0
Fungal sporocarps			
Species richness	β_1	18.2 ± 0.19	100/0/0
	β_2	34.8 ± 1.92	100/0/0
	β_3	20.3 ± 1.29	100/0/0
	β_4	26.7 ± 6.51	0/100/0
Shannon entropy	β_1	17.6 ± 0.32	100/0/0
	β_2	27.7 ± 1.53	100/0/0
	β_3	24.3 ± 1.35	100/0/0
	β_4	30.5 ± 6.41	0/100/0
Simpson diversity	β_1	18.3 ± 0.28	100/0/0
	β_2	23.8 ± 0.65	100/0/0
	β_3	25.9 ± 1.49	100/0/0
	β_4	32.0 ± 4.53	0/82.9/17.1
Molecular fungi			
Species richness	β_1	2.4 ± 0	100/0/0
	β_2	11.0 ± 0	100/0/0
	β_3	20.1 ± 0.01	100/0/0
	β_4	66.5 ± 0.03	100/0/0
Shannon entropy	β_1	4.1 ± 0.02	100/0/0
	β_2	11.9 ± 0.01	100/0/0
	β_3	21.5 ± 0.03	100/0/0
	β_4	62.4 ± 0.14	100/0/0
Simpson diversity	β_1	6.2 ± 0.04	100/0/0
	β_2	13.1 ± 0.01	100/0/0
	β_3	22.7 ± 0.11	100/0/0
	β_4	58.0 ± 0.23	100/0/0
Bacteria			
Species richness	β_1	3.2 ± 0	100/0/0
	β_2	12.6 ± 0.02	100/0/0
	β_3	21.3 ± 0.01	100/0/0
	β_4	62.8 ± 0.04	100/0/0
Shannon entropy	β_1	9.2 ± 0.08	100/0/0
	β_2	16.2 ± 0.13	100/0/0
	β_3	23.3 ± 0.02	100/0/0
	β_4	51.3 ± 0.39	100/0/0
Simpson diversity	β_1	13.6 ± 0.45	100/0/0
	β_2	18.2 ± 0.24	100/0/0
	β_3	24.3 ± 0.13	100/0/0
	β_4	44.0 ± 0.82	100/0/0

* Mean beta diversity values of 35 sub-computations, each comparing logs of the four conifer tree species with one of the possible four combinations of the seven deciduous tree species, were calculated.

Table B.2: Comparison of the annual percentage beta diversity of all studied species groups in comparison to the aggregated observed values.

Species group diversity index	*β-level*	*Year 1*	*Year 2*	*Year 3*	*3 year mean*	*Observed*
Beetles						
Species richness	β_1	21.1	17.7	18.7	19.2	19.7
	β_2	29.3	32.8	33.6	31.9	30.1
	β_3	17.6	18.3	17.5	17.8	19.3
	β_4	32.1	31.2	30.2	31.2	30.9
Shannon entropy	β_1	22.2	18.3	23.3	21.3	24.3
	β_2	22.2	28.6	26.3	25.7	25.9
	β_3	22.8	20.7	19.4	21.0	21.5
	β_4	32.8	32.4	31.0	32.1	28.3
Simpson diversity	β_1	25.2	19.5	26.5	23.7	26.0
	β_2	19.7	25.9	22.5	22.7	26.2
	β_3	25.1	22.4	20.6	22.7	22.1
	β_4	30.0	32.2	30.4	30.9	25.7
Fungal sporocarps						
Species richness	β_1	17.6	16.2	16.1	16.7	18.2
	β_2	31.0	32.7	35.7	33.2	34.8
	β_3	20.7	19.2	19.1	19.7	20.3
	β_4	30.7	31.9	29.1	30.5	26.7
Shannon entropy	β_1	16.7	15.7	15.2	15.9	17.6
	β_2	23.3	26.6	30.8	26.9	27.7
	β_3	26.0	22.4	21.5	23.3	24.3
	β_4	34.0	35.3	32.5	34.0	30.5
Simpson diversity	β_1	17.1	16.3	15.1	16.2	18.3
	β_2	20.0	22.9	28.1	23.7	23.8
	β_3	28.4	24.0	22.5	25.0	25.9
	β_4	34.5	36.9	34.3	35.2	32.0
Mircobial fungi						
Species richness	β_1	2.0	2.0	2.0	2.0	2.4
	β_2	10.3	10.4	10.4	10.4	11.0
	β_3	19.4	19.5	19.6	19.5	20.1
	β_4	68.3	68.1	68.0	68.1	66.5
Shannon entropy	β_1	3.4	3.2	3.1	3.2	4.1
	β_2	11.3	11.6	11.6	11.5	11.9
	β_3	21.1	21.3	21.3	21.2	21.5
	β_4	64.2	63.9	64.1	64.1	62.4
Simpson diversity	β_1	4.5	4.7	4.5	4.6	6.2
	β_2	12.3	12.6	12.9	12.6	13.1
	β_3	22.4	22.5	22.5	22.5	22.7
	β_4	60.8	60.2	60.2	60.4	58.0
Bacteria						
Species richness	β_1	2.6	2.7	2.6	2.7	3.2
	β_2	11.6	11.7	11.7	11.7	12.6
	β_3	20.4	20.6	20.5	20.5	21.3
	β_4	65.4	65.0	65.2	65.2	62.8
Shannon entropy	β_1	6.6	6.7	6.9	6.7	9.2
	β_2	14.7	14.6	14.9	14.7	16.2
	β_3	22.6	22.8	22.7	22.7	23.3
	β_4	56.1	55.9	55.5	55.8	51.4
Simpson diversity	β_1	11.1	10.7	10.9	10.9	13.6
	β_2	17.9	17.8	17.5	17.7	18.1
	β_3	25.1	25.4	24.4	25.0	24.3
	β_4	46.0	46.1	47.2	46.4	44.0

Table B.3: Number of sampled species and ASVs, bold are the highest numbers of species/ASVs respective to the two host tree clades.

Tree clade and species	Beetle species	individuals	Sporocarp species	total cover in %*	mircobial fungi** ASVs	bacteria** ASVs
broad-leaved	399	32014	333	4254.7	3808	32384
Betula pendula	229	4179	103	670.3	694	7932
Carpinus betulus	**270**	7781	131	843.8	851	10232
Fagus sylvatica	255	5739	**149**	814.8	889	10150
Fraxinus exzelsior	217	2612	92	408.8	834	8832
Populus sp.	222	3072	102	460	1121	9117
Quercus sp.	220	5315	105	471.5	**1349**	**11122**
Tilia sp.	255	3316	129	585.3	849	10873
coniferous	338	12996	164	1662.2	3041	18991
Larix decidua	205	2156	**89**	391.5	1177	8543
Picea abies	**248**	5995	82	446.8	1214	**8600**
Pinus sylvestris	223	2621	82	455.8	1089	7806
Pseudotsuga menziesii	226	2224	71	368	**1263**	8581

* summed up from all logs over all years

** because reads were rarefyed number of reads was the same for each host tree species/clade and is not printed here

Table B.4: Results of the multiplicative diversity partitioning of space and host for saproxylic beetles, fungal sporocarps, microbial fungi, and bacteria among 297 logs of 11 tree species of two clades (added up to host scale) placed in 27 forest stands in three regions (added up to spatial scale) in Germany.

Species group diversity index	*Scale*	*Mean percentage of total diversity*
Beetles		
Species richness	Host	50.2
	Spatial	49.8
Shannon entropy	Host	49.8
	Spatial	50.2
Simpson diversity	Host	47.8
	Spatial	52.2
Fungal sporocarps		
Species richness	Host	47.0
	Spatial	53.0
Shannon entropy	Host	54.8
	Spatial	45.2
Simpson diversity	Host	57.8
	Spatial	42.2
Microbial fungi		
Species richness	Host	86.7
	Spatial	13.3
Shannon entropy	Host	84.0
	Spatial	16.0
Simpson diversity	Host	80.7
	Spatial	19.3
Bacteria		
Species richness	Host	84.2
	Spatial	15.8
Shannon entropy	Host	74.6
	Spatial	25.4
Simpson diversity	Host	68.3
	Spatial	31.7

Appendix C – Community matrices

This appendix was excluded due to layout restrictions and can be accessed at: https://doi.org/10.1016/j.biocon.2022.109521.

A.4 DIVERSITY AND SPECIALISATION RESPONSES TO CLIMATE AND LAND USE DIFFER BETWEEN DEADWOOD FUNGI AND BACTERIA

ECOGRAPHY

Research article

Diversity and specialization responses to climate and land use differ between deadwood fungi and bacteria

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Climate and land use are major determinants of biodiversity, and declines in species richness in cold and human exploited landscapes can be caused by lower rates of biotic interactions. Deadwood fungi and bacteria interact strongly with their hosts due to long-lasting evolutionary trajectories. However, how rates of biotic interactions (specialization) change with temperature and land-use intensity are unknown for both microbial groups. We hypothesize a decrease in species richness and specialization of communities with decreasing temperature and increasing land use intensity while controlling for precipitation. We used a full-factorial nested design to disentangle land use at habitat and landscape scale and temperature spanning an area of 300 × 300 km in Germany. We exposed four deadwood objects representing the main tree species in Central Europe (beech, oak, spruce, pine) in 175 study plots. Overall, we found that fungal and bacterial richness, community composition and specialization were weakly related to temperature and land use. Fungal richness was slightly higher in near-natural than in urban landscapes. Bacterial richness was positively associated with mean annual temperature, negatively associated with local temperature and highest in

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grassland habitats. Bacterial richness was positively related to the covariate mean annual precipitation. We found strong effects of host-tree identity on species richness and community composition. A generally high level of fungal host-tree specialization might explain the weak response to temperature and land use. Effects of host-tree identity and specialization were more pronounced in fungi. We suggest that host tree changes caused by land use and climate change will be more important for fungal communities, while changes in climate will affect bacterial communities more directly. Contrasting responses of the two taxonomic groups suggest a reorganization of deadwood microbial communities, which might have further consequences on diversity and decomposition in the Anthropocene.

Keywords: climate change, land-use intensification, microbes, network analysis, saproxylic, urbanization

Introduction

Climate and land use are major drivers of species diversity at various spatial scales (Storch et al. 2007). In many taxonomic groups, species richness decreases with decreasing temperature (Lomolino 2001) and increasing land-use intensity (Murphy and Romanuk 2014, Newbold et al. 2015). However, the mechanisms are often poorly understood but are key to improving predictions about how climate change and land-use intensification will affect species richness (Urban et al. 2016). Along with climate and land-use gradients, a decline in the richness of species which strongly interact with a host (ecological specialization) can be mechanistically linked to lower levels of biotic specialization (Pellissier et al. 2018).

Fungi and bacteria are tremendously speciose and are the main decomposers of deadwood (Boddy and Watkinson 1995, Johnston et al. 2016). They are thus particularly important for the global carbon and nutrient cycle (Bani et al. 2018), considering that the amount of carbon stored in deadwood is equivalent to about 8% of the global forest carbon stocks (Pan et al. 2011). Strong co-evolution of deadwood-dependent fungal and bacterial species with their hosts has caused a high level of specialization (Floudas et al. 2012, Moll et al. 2021). However, fungi show a slightly stronger specialization than bacteria (Moll et al. 2021). Still, our knowledge of how temperature and land use affect fungal and bacterial species richness and how this is linked to changes in biotic interactions (specialization) is limited.

In this study, we used a full-factorial design to disentangle temperature and land-use effects on fungal and bacterial richness, community composition and host tree specialization along climate and land-use gradients in southern Germany. We expect that the level of specialization within fungal and bacterial communities decreases with decreasing temperature and increasing land-use intensity caused by increasing environmental variability for the following reasons. First, theory predicts an increase of generalist species, thereby reducing community specialization with decreasing mean temperature at different spatial scales (latitudinal and altitudinal niche breadth hypothesis, MacArthur 1972), caused by a higher temperature variability in cold environments (Rasmann et al. 2014). Second, land-use intensification causes environmental variability via disturbance and perturbation of habitats (Polasky et al. 2011, Tittensor et al. 2014, Dudley and Alexander 2017, Curtis et al. 2018) and hence, anthropogenic habitats should support generalist species, thereby decreasing specialization within communities. This assumption is supported by an empirical study suggesting that the observed decline in specialist species can be attributed to habitat destruction and degradation (Clavel et al. 2011). Variability of environmental conditions, e.g. in terms of temperature and land-use intensity, is crucial for niche evolution; the evolution of specialization has been attributed to stable environmental conditions, while generalist species are thought to have evolved under variable heterogeneous environmental conditions (van Tienderen 1991). Environmental unpredictability causes variability in species population sizes and hence supports the evolution of generalists (Whittaker 1975). This evolutionary mechanism should translate into the structuring of communities observed today (ecological mechanism) and can be tested via specialization measures of communities in a given environment.

To test these expectations, we experimentally exposed four deadwood objects representing the main tree species in central Europe (beech, oak, spruce, pine) in 175 study plots across a large climate and land-use gradient. We characterized fungal and bacterial communities via high-throughput sequencing and determined species richness and specialization (H_2' index). We tested the following hypotheses: Species richness and specialization 1) decrease with decreasing temperature, and 2) decrease with increasing land-use intensity.

Material and methods

Study design

In April 2019, we placed deadwood objects along a climate and land-use gradient in Bavaria, Germany. To establish these gradients, five climate zones based on mean annual temperature (< 7.5°C, 7.5–8°C, 8–8.5°C, 8.5–9°C, > 9°C) from 1981 to 2010 (Deutscher Wetterdienst 2020) and three land-use categories (near-natural: > 85% natural vegetation including a minimum of 50% forest, n = 58; agricultural: > 40% arable land and managed grassland, n = 58; urban: > 14% housing, industry and traffic structure, n = 59) were defined and assigned to a matrix of grid cells (5.8 × 5.8 km) across Bavaria. Grid cells were selected to represent all 15 possible combinations of climate and land-use categories with four replicates, resulting in 60 grid cells (following: 'study region').

Within each of the 60 study regions, three study plots (3 × 30 m) were embedded, representing the most dominant habitat types (out of forest, grassland, arable fields, and settlements), resulting in 175 study plots in total (one study region contained only two study plots, Supporting information). The number of study plots was distributed as follows: forest: 53, grassland: 45, arable: 43, settlement: 34 (Supporting information for distribution across habitat types). For reasons of standardization, study plots were established on an open area with herbaceous vegetation, such as forest clearings, meadows, crop field margins, and green spaces within settlements or cities. The study area covers an area of 300 × 300 km and 1000 m in elevation. More details about the study design can be found in Redlich et al. (2021).

As deadwood, the four dominant tree genera in German forests were chosen, i.e. beech *Fagus sylvatica*, oak *Quercus* sp., spruce *Picea abies*, and pine *Pinus sylvestris*. All deadwood branches originated from the Steigerwald Forest, northern Bavaria, to ensure equal starting conditions in microbial communities. On each study plot, one branch (10 cm in diameter, 50 cm length) of each of the four tree genera was vertically positioned on a pole, with direct soil contact, for one growing season (April–September 2019).

Environmental parameters

The information on mean annual temperature (MAT) for each study plot was extracted from gridded monthly datasets with a horizontal resolution of 1 km using the nearest source to destination approach. Subsequently, long-term averages were calculated for the period 1991 to 2020. The raw input datasets were provided free of charge by the German Meteorological Service (DWD) and are described in Kaspar et al. (2013). To characterize small-scale habitat-related temperature, we used iButton thermologgers (type DS1923, Hygrochron iButton, Whitewater, WI, USA) on each study plot (average day and night temperature from April to September 2019). Each datalogger was mounted on a wooden pole at 1.10 m height, facing north and with a roof panel to protect against direct sun exposure. These measurements are hereafter referred to as 'local temperature'. Furthermore, we used the covariate mean annual sum of precipitation (MAP) to account for offset effects. MAP was assessed analogously to MAT, using data from the German Meteorological Service (DWD), described in Kaspar et al. (2013). We also considered the four habitat types (forest, grassland, arable field, settlements) embedded within near-natural, agricultural, or urban landscapes.

Microbial sample processing

To assess the microbiome in the deadwood, we removed the bark from each branch with a sterilized knife before drilling three holes (diameter ca 0.5 cm) horizontally into the middle of the branch. The knife and drill were sterilized after each sample using a Bunsen burner and 99% ethanol. Five grams of the extracted powdery debris were pulverized using liquid nitrogen in a swing mill (MM400, Retsch, Haan, Germany). Total environmental (i.e. bacterial and fungal) DNA was isolated from 0.25 g of each homogenized, powdery wood sample using the Quick-DNA Fecal/Soil Microbe Miniprep kit (D6010) (Zymoresearch, Irvine, CA, USA) following the manufacturer's instructions. PCR amplification, sequencing and bioinformatics were performed externally by LGC Genomics, Berlin (Germany). Briefly, the fungal ITS (internal transcribed spacer) region was amplified using the region-specific primers fITS7 (*forward*) [GTGARTCATCGAATCTTTG] and ITS4 (*reverse*) [TCCTCCGCTTATTGATATGC] and corresponding amplification protocols described by Ihrmark et al. (2012), including no template control samples. Likewise, bacterial 16S gene (V4 region) was amplified using the region-specific primers 515F (*forward*) [GTGYCAGCMGCCGCGGTAA] and 806R (*reverse*) [GGACTACNVGGGTWTCTAAT] modified by Caporaso et al. (2011, 2012). Subsequently, dual barcoded amplicons were sequenced on an Illumina MiSeq system. For data analysis, read libraries were demultiplexed allowing one or two mismatches or Ns in the barcode and sorted by amplicon inline barcodes (allowing for one mismatch per barcode) with Illumina bcl2fastq ver. 2.20 software. Amplicon barcodes and adapter remnants were clipped from the sequences and reads consisting of < 100 bases were discarded. Primer sequences were used for identification (three mismatches allowed) and separation of fungal and bacterial reads before being removed. Forward and reverse reads were combined using BBMerge ver. 34.48 (Bushnell et al. 2017). All reads with a similarity > 97% were clustered to an OTU (operational taxonomic unit) using Mothur software, which also implemented the removal of chimeric sequences (Schloss et al. 2009). Each bacterial OTU (with at least two observed sequences) was queried against the ribosomal database project (RDP) release 11.4 (Cole et al. 2014) using a blastn search (NCBI BLAST+ ver. 2.10.0, E ≤ 0.1, percent identity ≥ 90%). Fungal OTUs were queried against the curated database UNITE ver. 6 (Nilsson et al. 2019). All bacterial and fungal hits were counted per sample and integrated in a count table, filtering and removing for example amplified and sequenced mitochondrial 16S, plant ITS or other non-target sequences. Further, all singletons were removed (i.e. setting community matrix cells with the value of 1 to 0) from the dataset prior to statistical analysis (potential sequence errors, Brown et al. 2015).

Response variables

To determine fungal and bacterial species richness and community composition, we first rarefied each community matrix (function *rrarefy*, package 'vegan' by Oksanen et al. 2020). We then calculated species richness for each object and plot. To determine a suitable rarefaction depth, we first calculated the read sums for each sample. We visualized all read sums based on sorted histograms. This allows identifying samples with relatively low read sums, which might indicate low sequence quality. Removal of samples with relatively low read sums increases data quality for further

analysis (Tedersoo et al. 2022). Further, with this procedure, we maintain as many samples as possible while keeping the rarefaction depth sufficiently high for a representative sampling effort. Minimum read sum per sample considered as the threshold for rarefaction was 1345 for fungi and 373 for bacteria. Based on this procedure, we retained 92% of all objects for the fungal analysis and 86% for the bacterial analysis. Note that results based on rarefaction to the lowest sum of reads and therefore maintaining all objects and plots for the analysis showed largely consistent results (data not shown). However, it is recommended to remove samples with rather low read sums and further avoid a too-low threshold of the minimum read sums because it can substantially reduce the explained variance (Tedersoo et al. 2022). We therefore present the results based on the above-mentioned rarefaction procedure. Finally, we are aware that OTUs are not equivalent to species, but we chose the term 'species' throughout the manuscript for readability.

Based on the rarefied community matrix, community specialization was calculated by a network analysis using the package 'bipartite' (Dormann et al. 2009). Here, the standardized two-dimensional Shannon entropy (H_2', Blüthgen et al. 2006) serves as a measure of fungal and bacterial community specialization on host trees and ranges between 0 (no host-tree preference) and 1 (total specialization). H_2' calculates the interaction frequencies of two groups of different trophic levels (number of species per host tree) in relation to all possible interactions, hence being network-size independent. This allows comparisons across networks and along ecological gradients, i.e. whether community specialization shifts to a more specialized or generalistic resource use with a shift in MAT, local temperature, or land use. After calculating H_2', we compared the observed H_2' values with a null model with full randomization that kept frequencies and richness constant (function *r2dtable*, 1000 simulations). Specialization differed from random ($p < 0.05$) in all plots and were hence considered in further analyses. Since branches with insufficient reads were excluded from further analysis due to rarefaction (above), not all plots contained all four tree species anymore. Hence, we standardized the data set to plots characterized by the full set of branches for the analyses on plot level (species richness per plot, community specialization). Therefore, we kept 81% of all plots for fungi and 67% for bacteria. The remaining plots were still equally distributed across the environmental gradients with sufficient replications (Supporting information).

Statistics

All statistical analyses were performed using R ver. 4.3.2 (www.r-project.org).

To test the relationship between fungal and bacterial richness vs MAT, local temperature and land use at habitat and landscape scale, we used four separate negative-binomial generalized linear mixed effect models, one for each microbial group and each resolution level (plot level and object level) using the function *glmer.nb* from the 'lme4' package (Bates et al. 2015). As main predictors, we used MAT, local temperature, habitat type and landscape type. Since MAT and local temperature were only moderately correlated (spearman's rho = 0.50 and $p < 0.05$), both variables were included in the models. Elevation was highly correlated with MAT (spearman's rho = −0.83 and $p < 0.001$) and thus excluded from the models. As outlined above, we used MAP ($\log_{10}$-transformed for normality) as a covariate in our models. Further, we included 'study region' at plot level and 'study plot' nested within 'study region' as random effect to account for the nested design and repeated measures (four objects on each plot). We compared the effects between fungi and bacteria based on the models' effect sizes (z-values). Conditional and marginal R^2 were calculated with the function *r.squaredGLMM* in the package 'MuMIn' (Bartoń 2023). Note that R^2 outside of the range between 0 and 1 are possible, indicating rather poor fits. We interpret these models with care. Finally, we applied post-hoc tests to assess effects among host tree identity, habitat type landscape type respectively, using function *glht* in the package 'multcomp' (Hothorn et al. 2008).

Effects of host tree identity, MAT, local temperature and land use at habitat and landscape scale on fungal and bacterial species composition were analyzed using Bray-Curtis dissimilarity matrices (function *vegdist*, package 'vegan', Oksanen et al. 2020). Based on these matrices (fungi and bacteria separately), non-metric multidimensional scaling ordination plots (function *metaMDS*, package 'vegan') were created. We applied a permutational multivariate analysis of variance (permanova, function *adonis2*, package 'vegan') with 999 permutations to test the relative importance of our set of predictors on the composition of fungal and bacterial communities. We compared the effects between fungi and bacteria based on the models' partial R^2-values.

To test the relationship between fungal and bacterial specialization vs MAT, local temperature and land use at habitat and landscape scale, we built a generalized linear mixed model (function *glmmTMB*, package 'glmmTMB', Brooks et al. 2017) for both fungi and bacteria using H_2' as response variable. Models were specified as described above for the richness models at plot level.

To analyze species richness and specialization at plot level and the community composition at object level, we also explored interaction effects between temperature (MAT, local temperature) and land use (landscape-, habitat scale). At plot level, we specified two-way interactions (temperature variable and land use variable). At object level, we specified three-way interactions (between host, temperature variable, and land use variable). We did not include interaction terms in the original models, as the main effects of interaction models would generally be conditional, while our hypotheses rely on marginal effects. Complex interaction models with numbers of predictors, as in our study, can be flawed and prone to inferential errors (Brambor et al. 2006, Kuhn and Johnson 2013). As a conservative approach, we therefore considered only those interaction terms in which one of the interaction variables was significant in our main models

based on marginal (independent) effects. We also refrained from presenting p-values for the interaction approach to avoid violation of statistical principles, i.e. testing identical response and predictor variables in the second model. We point towards hypothesis generating, but not traditionally confirmatory interpretation of the additional model. Other predictors not involved in interaction terms were added as covariates to be consistent with the main models, including also precipitation as a covariate. Thus, all predictors were represented as main effects. For example, if only landscape was significant in the main marginal model (above), we specified the following model: landscape × MAT + landscape × local temperature + Habitat + MAP.

Results

Across all study plots, we observed 4136 fungal and 6999 bacterial putative species (OTUs). Most fungal species belonged to the phyla Ascomycota and Basidiomycota (Supporting information). The most dominant bacteria phyla were Proteobacteria, Actinobacteria and Bacteroidetes (Supporting information). The appearance and distribution of the main fungal and bacterial taxa across our environmental gradients were largely consistent (Supporting information).

Microbial richness at study-plot level

Fungal species richness was unrelated to MAT or local temperature (Table 1, Fig. 1a–b). In contrast, bacteria species richness was positively related to MAT but negatively to local temperature (Table 1, Fig. 1c–d). Fungal species richness was higher in near-natural landscapes compared to urban landscapes (Table 1, Fig. 1k). Bacteria richness was higher in grassland and arable than in forest habitats but unaffected by landscape (Table 1, Fig. 1j, l). Bacterial richness was significantly positively related to the covariate MAP (Table 1, Supporting information). R^2 values of the overall models were generally low; model performance was better for bacteria (marginal R^2: 27.8%) than fungi (marginal R^2: 14.3%). Post-hoc test results for all pairwise comparisons among habitats and landscapes can be found in the Supporting information. Our models suggest no interactions among temperature and land use predictors based on the effect sizes (z-values), about 1.55 at maximum (Supporting information).

Microbial richness at object level

The results gained from the model at object level showed strong significant differences in richness between tree genera for both fungi and bacteria (Supporting information). The post-hoc test revealed significant differences in fungal richness between each tree genera. Fungal richness was lowest in beech branches, followed by pine, oak and was highest in spruce (Supporting information). Bacterial richness was also lowest in beech branches and lower in pine than oak and spruce branches (Supporting information). Effects of climate and land use variables on fungal and bacterial species richness at object level were largely consistent with plot-level models (Table 1, Supporting information). We found no relationship between fungal richness and MAT and local temperature. Bacterial richness was positively related to MAT but negatively to local temperature. Fungal richness was lower in urban compared to near-natural landscapes. Bacterial richness was significantly higher in grasslands compared to forest habitats. Fungal richness at object level was negatively related to the covariate MAP, whereas bacterial richness showed a positive relationship to MAP (Supporting information). The marginal R^2 value for the fungal model was 58.9% (conditional R^2 62.9%), while the marginal R^2 value for the bacterial model was 14.6% (conditional R^2: 18.8%).

Table 1. Effects of the main predictors mean annual temperature (MAT), local temperature and land use at habitat and landscape scale) and the covariate mean annual sum of precipitation (MAP, log_{10}-transformed) on the richness and degree of community specialization on host tree (H_2') of fungi and bacteria estimated by generalized linear mixed effects models (negative binomial) and beta-regression models, respectively. Results are described by z-values. Significant values are indicated in bold and by asterisks (*=p < 0.05, **=p < 0.01, ***=p < 0.001). Note that R^2s out of the range from 0 to 1 indicate low model performance and poor fits.

		Fungi		Bacteria	
		Richness	H_2'	Richness	H_2'
Predictors		z-value	z-value	z-value	z-value
	(Intercept)	3.08**	1.83	−0.08	−2.80**
Main predictors					
Temperature	MAT in °C	1.18	−0.06	**4.01****	0.69
	Local temp. in °C	1.83	−1.14	**−3.34****	−0.62
Habitat type	Grassland vs forest	1.30	−0.13	**3.70*****	1.17
	Arable vs forest	−0.61	−0.09	**1.97***	1.92
	Settlement vs forest	−0.17	−0.22	1.65	0.95
Landscape type	Agric. vs near-natural	−1.31	−0.42	−0.59	**3.26****
	Urban vs near-natural	**−1.97***	0.36	−0.45	1.26
Covariate					
Precipitation	MAP in mm (log10)	−1.51	−0.50	**4.10*****	**3.39****
Observations		146	146	120	120
Marginal R^2/Conditional R^2		0.143/0.262	−0.506/−0.907	0.278/0.467	0.572/1.156

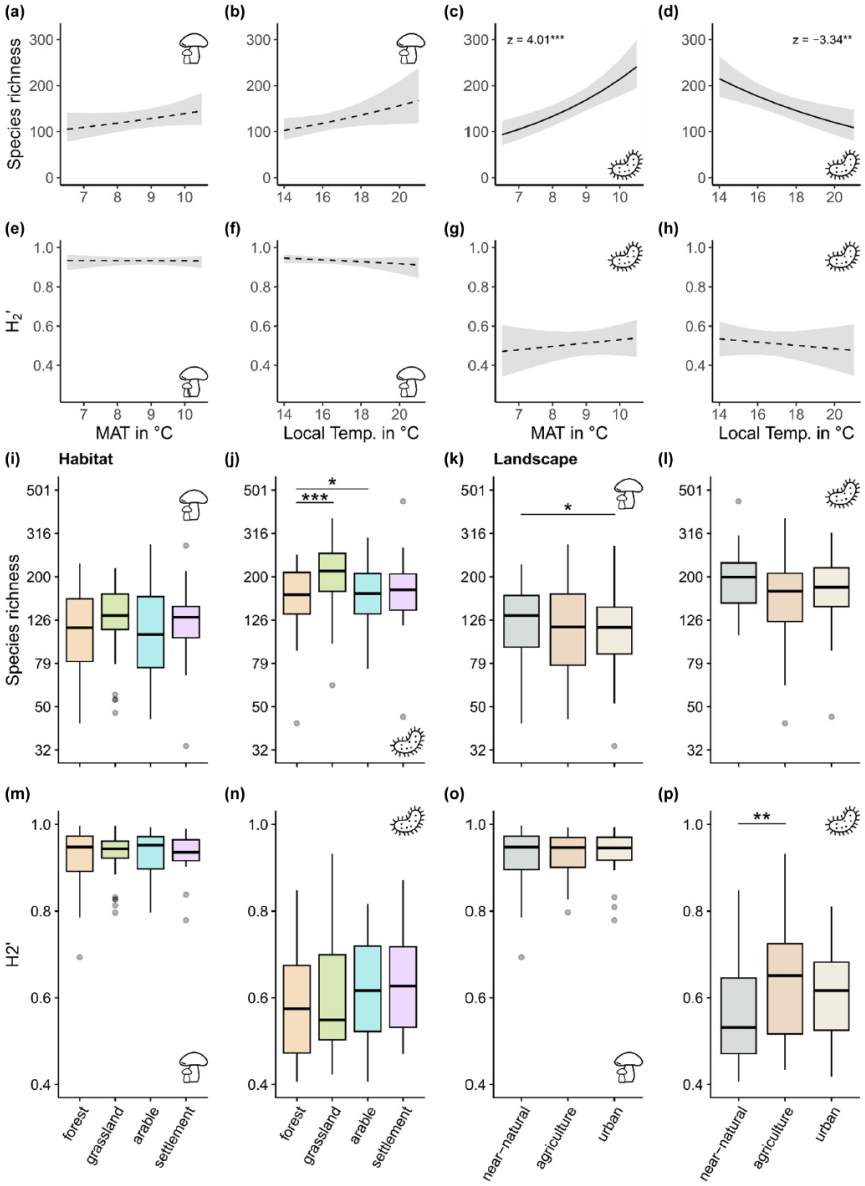

Figure 1. Regression curves showing fungal (a, b) and bacterial (c, d) species richness and community specialization (fungi: e, f; bacteria: g, h) at study-plot level predicted by the generalized linear mixed model (glmer.nb: richness; glmmTMB: specialization) and mean annual temperature (MAT; a, c, e, g) and local temperature (b, d, f, h). Non-significant changes are indicated by dashed lines. Boxplots show fungal (i, k) and bacterial (j, l) species richness (log10 transformed) and specialization (fungi: m, o; bacteria: n, p) among habitat (i, j, m, n) and landscape types (k, l, o, p) at plot level. Significant values are indicated by z-values and asterisks (* = p < 0.05, ** = p < 0.01, *** = p < 0.001). Detailed results can be found in Table 1.

Community composition

Permanova at object level revealed the host-tree identity as the most important factor determining fungal community composition (Table 2, Fig. 2a, Supporting information). Bacterial community composition was also strongly related to host tree identity, but the partial R^2 value was lower compared to fungi (33.7% for fungi, 8.1% for bacteria, Table 2, Fig. 2b). All other predictors showed a low partial R^2 value. MAT explained only 0.2% of fungal and 0.5% of bacterial community composition. Effects of land-use variables on bacterial communities were slightly higher (Habitat type: 0.9%, Landscape type: 0.5%) compared to the fungal community (Habitat type: 0.4%, Landscape type: 0.2%). The effect of the covariate MAP on the community composition was more pronounced for bacteria than fungi (7% for bacteria, 0.3% for fungi, Table 2). Based on effect sizes, the additional interaction model did not suggest strong three-way interaction (between host, temperature, and land use) effects for fungal and bacterial community compositions (Supporting information).

Community specialization

Fungal specialization showed no significant relationship with climate and land-use variables (Table 1, Fig. 1e, f, m, o). Bacterial specialization was significantly higher in agricultural than in near-natural landscapes (Table 1, Fig. 1p, Supporting information) and showed a positive relationship with the covariate MAP (Table 1, Supporting information). The overall performance of the models was weak (Table 1). The specialization index of fungi was close to 1.0 (H_2' mean value of 0.93 (± 0.05 SD), Fig. 2c). The specialization index of bacteria peaked at ca 0.5 (mean $H_2' = 0.58 \pm 0.14$ SD, Fig. 2c). For fungi, we did not explore interactions (no significant variable in the overall model). The interaction terms in bacteria indicated only small effects (Supporting information).

Discussion

We hypothesized that species richness and specialization decrease with decreasing temperature and increasing land-use intensity. However, this could only be partially confirmed for bacterial species richness, which was positively related to MAT, and for fungal richness, which was slightly higher in near-natural than urban landscapes. Further, we found no support for the hypothesis that specialization decreases with increasing land-use intensity. Fungal and bacterial richness and community composition were more strongly related to host-tree identity than temperature and land use.

Species richness and temperature

We found no significant relationship between fungal species richness and temperature. This is in contrast to studies showing a positive relationship between fungal species richness and temperature within and across landscapes. For example, Bässler et al. (2010) found an increase in fungal species richness on fine woody debris (similar to branches used in our study) with temperature at landscape scale. In another study, Thorn et al. (2018) found a decrease in fungal species richness on coarse and fine woody debris with increasing elevation, i.e. decreasing temperature across landscapes. However, both studies used species richness based on fruit

Table 2. Permanova results for the effects of host tree identity, mean annual temperature (MAT), local temperature, habitat and landscape type on community composition of deadwood-inhabiting fungi and bacteria. We used mean annual sum of precipitation as a covariate. Significant values are indicated in bold and by asterisks (*=p < 0.05, **=p < 0.01, ***=p < 0.001).

Fungi	Df	SumOfSqs	partial R^2	F	Pr(> F)
Main predictors					
Host tree	3	94.118	0.337	111.355	**0.001*****
MAT in °C	1	0.525	0.002	1.864	**0.046***
Local temp. in °C	1	0.408	0.001	1.447	0.136
Habitat type	3	1.221	0.004	1.445	0.051
Landscape type	2	0.645	0.002	1.144	0.267
Covariate					
MAP (log10) in mm	1	0.938	0.003	3.33	**0.002****
Residual	644	181.438	0.65		
Total	655	279.293	1		
Bacteria					
Main predictors					
Host tree	3	15.848	0.081	19.458	**0.001*****
MAT in °C	1	0.51	0.003	1.877	**0.043***
Local temp. in °C	1	0.354	0.002	1.305	0.196
Habitat type	3	1.76	0.009	2.16	**0.001*****
Landscape type	2	1.07	0.005	1.97	**0.016****
Covariate					
MAP (log10) in mm	1	13.758	0.07	50.674	**0.001*****
Residual	601	163.169	0.831		
Total	612	196.469	1		

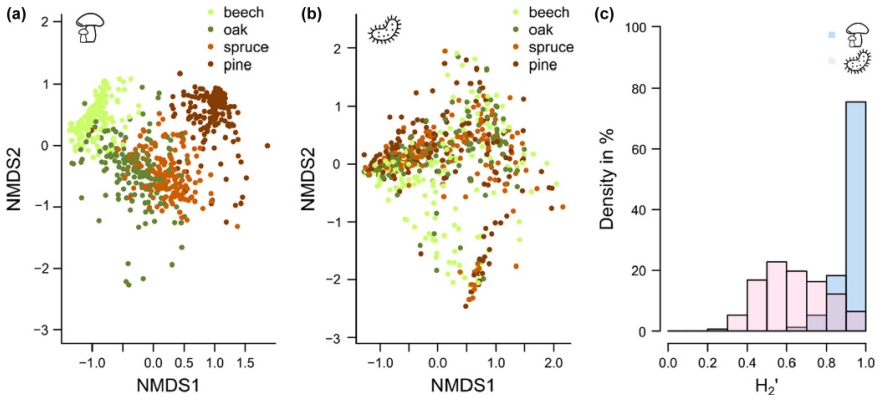

Figure 2. (a) and (b) Ordinations based on non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices (a: fungi: k = 3, stress = 0.146; b: bacteria: k = 3, stress = 0.150). Dots indicate communities in individual deadwood objects (beech: light green, oak: dark green, spruce: light brown, pine: dark brown). The closer the dots, the higher the proportion of species shared. (c) Frequency of observed H_2' values (community specialization) in percent for fungi (blue) and bacteria communities (red).

body inventories. We instead used species richness based on metabarcoding from within the woody substrate. Rieker et al. (2022) suggested that the fruiting communities are more sensitive to environmental gradients than the within-substrate (mycelial) communities due to the stronger exposure of fruit bodies to environmental constraints. This might explain the discrepancy between these studies and our findings. Another explanation might be that the studies mentioned are based on an observational survey at plot level (deadwood originating from forest stands). In contrast, our study is based on an experiment (all deadwood types standardized exposed across landscapes). Hence, confounding effects cannot be excluded in observational studies, which might explain the discrepancy (e.g. temperature changes confounded with changes in host species).

In contrast to fungal communities, bacterial species richness showed a significant positive relationship with MAT. Studies of deadwood-inhabiting bacterial diversity at larger scale are scarce. However, those studies that do exist found environmental conditions (e.g. macroclimate) as weak explanations for deadwood-inhabiting bacterial community composition (Lee et al. 2020) and beta-diversity at a larger scale (Rieker et al. 2022). A low beta-diversity and low differences in community composition might indicate that differences among study plots are not very pronounced, which disagrees with our findings. However, our study used a considerably stronger macroclimate gradient (Material and methods). The large extension of the climate gradient might explain this discrepancy and why we found lower species richness in cold environments. Moreover, we found a decrease in bacterial richness with increasing local temperature. Open habitats, as in our study, coincide with higher variability in temperature and probably with the prevalence of temperature extremes (De Frenne et al. 2019). Extreme microclimatic conditions causing stress might restrain some bacteria species from colonizing and hence decrease the species richness of communities. A loss of species across taxa under extreme environmental conditions was also described by Lomolino (2001). However, our models' effects and overall performance are weak; hence, our results must be interpreted with care. This is furthermore reflected by the interaction models where no strong effects were observed. We cannot exclude that other, yet unmeasured more local factors, like deadwood- or soil properties, would be important to explain the observed patterns better. We used standardized wood material from the same origin across our spatial setting and therefore assume similar wood chemistry throughout the design. Nevertheless, our deadwood objects had minor soil contact and soil chemical properties may vary across our design. Therefore, we cannot exclude deadwood colonization by fungal and bacterial species from the soil (below). This, however, is unlikely to be important for the fungal communities assessed in this study since community composition within one study plot would be more similar than among host trees. Analyzing the branches' chemical- and physical characteristics in future might shed more light on the assembly processes.

Species richness and land use

We showed that fungal richness was only influenced by land-use intensity at landscape scales, although the effect was not pronounced, being lower in urban than in near-natural landscapes.

The availability of deadwood as a resource is a key determinant of fungal diversity (Bässler et al. 2010, Thorn et al. 2018). The amount and diversity of deadwood in urban landscapes might be reduced by anthropogenic interventions, e.g. due to deforestation in anthropogenic areas (Dudley and Alexander 2017, Curtis et al. 2018). Therefore, in urban areas, the availability of deadwood might be reduced and

depends mainly on the type of green space. Moreover, deadwood in urban areas is often removed for safety or aesthetics (Fröhlich and Ciach 2020). Taken together, the availability of diverse deadwood that fuels species richness on an object is expected to be significantly lower in urban than in near-natural dominated landscapes, which might explain the observed pattern (i.e. island biogeography, MacArthur and Wilson 1967). This furthermore indicates that fungal species might be dispersal limited to some extent at the scale of our study. Komonen and Müller (2018) suggested that fungi are not dispersal limited at landscape scales. Across landscapes, Abrego et al. (2017) found that airborne fungal communities differed if distances exceeded 100 km, supporting our finding. However, even though significant, the effects are not very pronounced (Fig. 1k). Our results also suggest only a weak role of dispersal limitation through similar relationships of fungal communities with their hosts (specialization) irrespective of environmental and geographic variability.

Another explanation for lower fungal richness in urban landscapes, although unlikely, is that fungi are constrained by environmental conditions preventing species from successful colonization and establishment on the exposed deadwood objects in urban plots. One important factor in this respect might be microclimatic extremes. As outlined above, forests buffer microclimate extremes even if there are small clearings (Thorn et al. 2020) in contrast to rather wide open habitats in urban areas. However, we suggest this mechanism is less plausible for the following reasons. We considered a measure of local microclimate within our models (local temperature), and the habitat categories might serve as proxies for environmental conditions not directly measured in our project. As all these covariates are not significantly related to fungal species richness, we do not expect this mechanism to explain the observed pattern.

In contrast to fungi, bacterial species richness showed no relationship with land use at landscape scale but was significantly higher in grasslands than in forests. Even though speculative, the latter finding might be explained by higher colonization of deadwood by soil-inhabiting bacteria in grassland. A study from Germany showed that soil inhabiting bacterial diversity is also higher in grassland than in forests, mainly due to differences in soil pH (Kaiser et al. 2016). Further, genes related to lignin degradation seem more abundant in bacterial communities occurring in grassland (Kaiser et al. 2016), which could thus allow a larger number of taxa of grassland soil bacteria to utilize deadwood than forest soil inhabiting bacteria. However, further studies are needed on how deadwood will be colonized in different environmental conditions. Moreover, the contrasting effects between the microbial taxa observed in our study suggest differences in assembly processes between bacteria and fungi depending on the land-use type. Finally, it is important to note that many more studies exist for deadwood fungi than deadwood bacteria. More comparative studies are therefore needed to better understand assembly mechanisms at different spatial scales among deadwood microbial taxa.

Specialization of communities along temperature and land-use gradients

Fungal specialization showed no significant relationship with temperature and land use. Previous studies showed that deadwood-inhabiting fungi are highly specialized with their hosts (Lee et al. 2020, Moll et al. 2021). However, no study focused on how specialization might change along pronounced environmental gradients. Our results support a high specialization level in fungi that remains unchanged across large environmental gradients. Our community composition analysis at object level supports the results based on the specialization index (H_2'). Here we show highly distinct communities depending on host tree identity. These findings suggest that, despite their strong relationship to certain host tree species, fungal species are characterized by broad environmental niches (e.g. thermal niches). This additionally suggests a strong co-evolution of fungi with their hosts under various environmental conditions (Floudas et al. 2012).

Similar to fungi, bacterial specialization did not show significant effects with temperature, even though bacteria seem less specialized than fungi. The latter finding supports an earlier study, demonstrating that fungi are more specialized to their host than bacteria when averaging across different tree species, local environmental conditions and regions (Moll et al. 2021). We cannot explain why bacteria specialization is higher in agricultural than in near-natural landscapes. Therefore, further studies are needed to focus on how strongly bacteria species are related to certain substrates (e.g. soil vs wood) and how selection and preferences for specific substrates change with environmental factors.

Importance of precipitation for bacterial richness and specialization

We found that bacteria richness and specialization were significantly positively correlated with MAP. Further, the bacteria community composition was significantly driven by MAP. Effect sizes of MAP were larger than for MAT. Even though moisture has been shown to affect bacterial communities at log scale (Hoppe et al. 2014, Moll et al. 2018), our study is the first, to our knowledge, to consider a large MAP gradient with a focus on deadwood bacteria. One explanation for species richness and specialization associated positively with MAP might be that moisture can be temporarily limited in areas with a low precipitation level. Drier and more variable moisture conditions might act as a habitat filter, thereby reducing the number of species and favoring generalists as we expected for MAT (Introduction). However, further studies are needed on how climate variability and constraints affect the assembly of generalist and specialist species. However, for microbial species, our ecological knowledge that would allow assigning a species to a generalist or specialist is still limited.

Conclusions

Fungal and bacterial communities are more strongly driven by host-tree identity than temperature and land use due

to a high level of specialization. However, specialization is more pronounced for fungi than bacteria. Fungi, therefore, sustain their high host specificity even in extreme climates and anthropogenically modified landscapes. Bacterial richness, community composition and specialization responded more strongly to climate and land use than fungi. These findings suggest different responses of both microbial communities in times of global change. However, it is suggested that both microbial groups interact strongly within deadwood (Odriozola et al. 2021). Consequently, disruption of microbial communities caused by global change could have severe consequences on deadwood diversity and subsequent decomposition processes. Hence more studies are needed to illuminate the role of bacteria communities and their interaction with fungi on decomposition processes under global change.

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Author contributions

Jana Englmeier: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Daniel Rieker**: Formal analysis (equal); Visualization (equal); Writing – review and editing (lead). **Oliver Mitesser**: Formal analysis (equal). **Caryl Benjamin**: Investigation (equal); Writing – review and editing (equal). **Ute Fricke**: Investigation (equal); Writing – review and editing (equal). **Cristina Ganuza**: Investigation (equal); Writing – review and editing (equal). **Maria Haensel**: Investigation (equal); Writing – review and editing (equal). **Harald Kellner**: Writing – review and editing (equal). **Janina Lorz**: Investigation (equal). **Sarah Redlich**: Project administration (equal); Writing – review and editing (equal). **Rebekka Riebl**: Investigation (equal); Writing – review and editing (equal). **Sandra Rojas**: Botero Investigation (equal); Writing – review and editing (equal). **Thomas Rummler**: Data curation (equal); Resources (equal). **Ingolf Steffan-Dewenter**: Project administration (equal); Writing – review and editing (equal). **Elisa Stengel**: Investigation (equal). **Cynthia Tobisch**: Investigation (equal); Writing – review and editing (equal). **Johannes Uhler**: Investigation (equal); Writing – review and editing (equal). **Lars Uphus**: Investigation (equal); Writing – review and editing (equal). **Jie Zhang**: Data curation (equal); Resources (equal). **Jorg Muller**: Conceptualization (equal); Project administration (equal); Supervision (equal). **Claus Bässler**: Conceptualization (lead); Formal analysis (equal); Supervision (equal); Writing – review and editing (lead).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.06807.

Data availability statement

All raw sequence data were submitted to the short read archive (SRA, www.ncbi.nlm.nih.gov/sra/) and are accessible under SUB13062688.

Data are available from the Dryad Digital Repository: https://doi.org/doi:10.5061/dryad.ttdz08m2p (Englmeier et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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Diversity and specialisation responses to climate and land use differ between deadwood fungi and bacteria

Names of all Authors as they appear on the manuscript

The data that support the findings of this study are available in datadryad at https://datadryad.org/stash/share/e1va3HUw9mPZyV1GiE5XwwX1boAmAckQq0CIIOAPueA (double-blinded version for peer-review)

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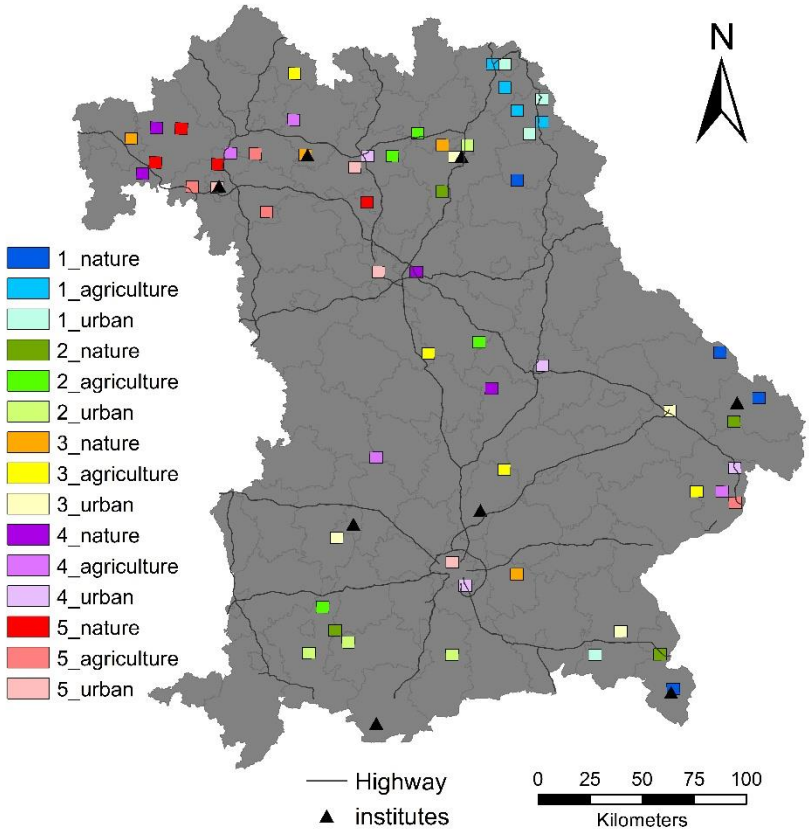

Figure S1: Location of study plots across Bavaria. Numbers (1-5; 1: cold, 5: warm) indicate climate zones; landscapes are defined as nature (near-natural), agriculture, and urban.

Table S2: Overview about the distribution of the plots in the four habitat types across the three land-use categories. The first value in each cell refers to the overall number of plots used for analyses on log level. The second and third value refer to the number of plots considered in the plot level analyses of fungi and bacteria, respectively, in which we standardised to plots containing four deadwood objects after rarefication. See Redlich et al (2021) for more details on the conceptual design.

Land-use category	**Habitat type**				
	Forest	*Grassland*	*Arable*	*Settlement*	*sum*
Near-natural	21/18/13	17/15/12	13/12/10	7/7/7	58/52/42
Agriculture	17/14/10	15/15/13	19/17/16	7/7/7	58/53/46
Urban	15/11/7	13/7/7	11/10/9	20/16/11	59/44/34
sum	53/43/30	45/37/32	43/39/35	34/30/25	175/149/122

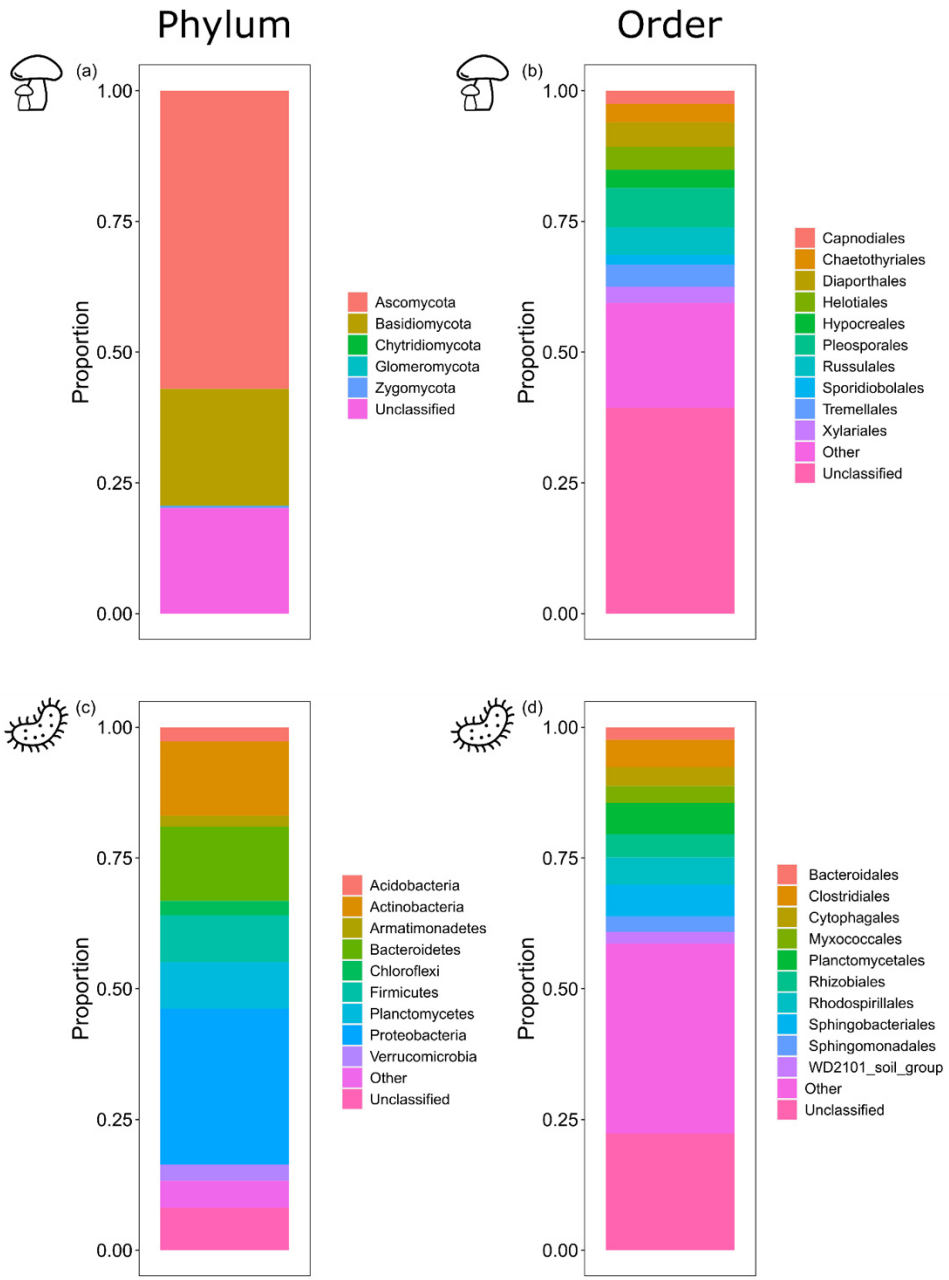

Figure S3: Overall taxonomic distribution of bacteria and fungi across all samples at phyla and order level. Note that many putative fungal and bacterial species are still unclassified due to methodological constraints or knowledge gaps. The "WD2101_soil_group" is the official name of an uncultured strain of *Planctomycetes* bacteria of the class *Phycisphaerae* (Dedysh et al., 2020).

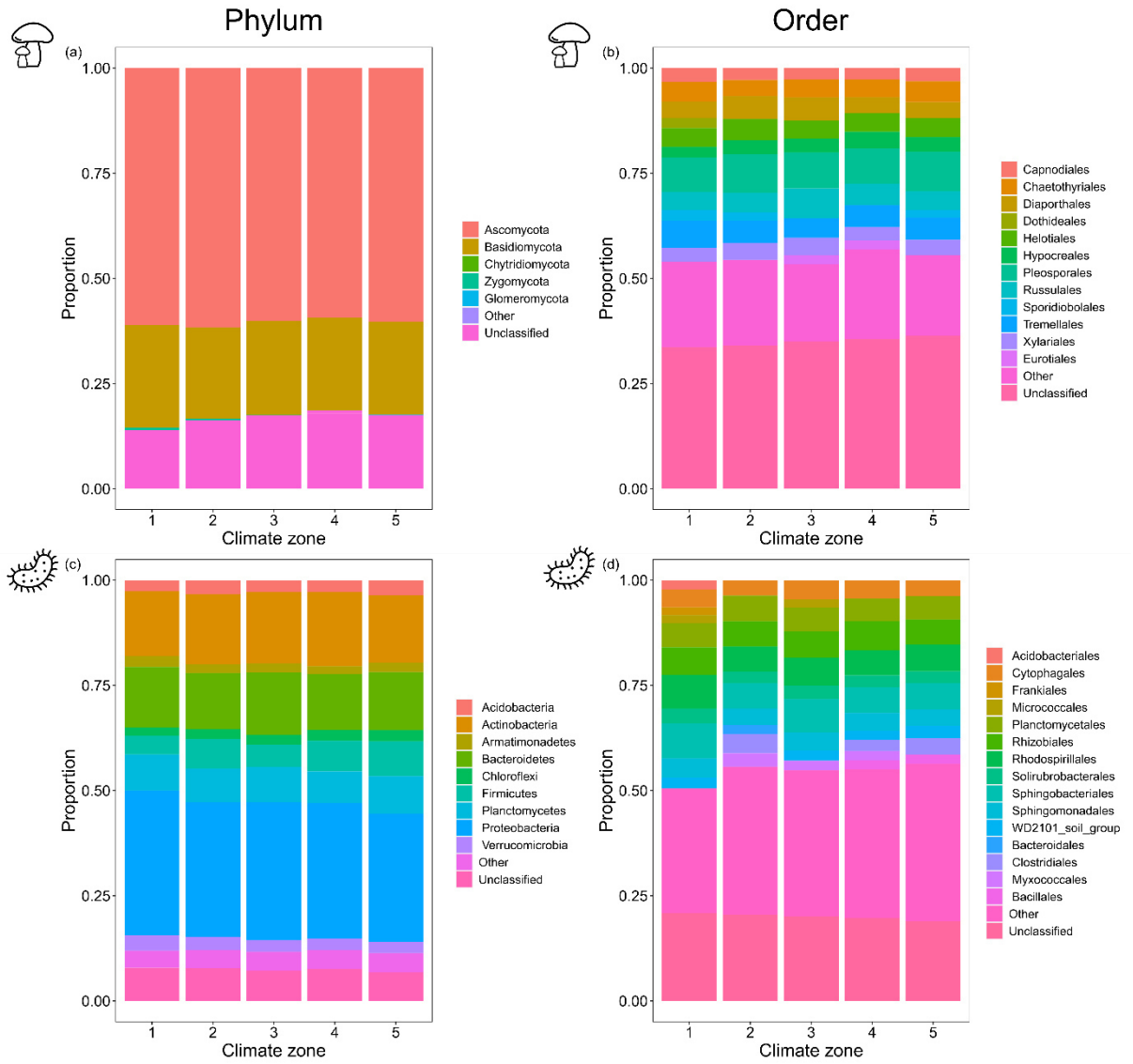

Figure S4: Taxonomic distribution of bacteria and fungi across all samples at phyla and order level categorized by climate zone (1: cold – 5: warm). Note that many putative fungal and bacterial species are still unclassified due to methodological constraints or knowledge gaps. The "WD2101_soil_group" is the official name of an uncultured strain of *Planctomycetes* bacteria of the class *Phycisphaerae* (Dedysh et al., 2020).

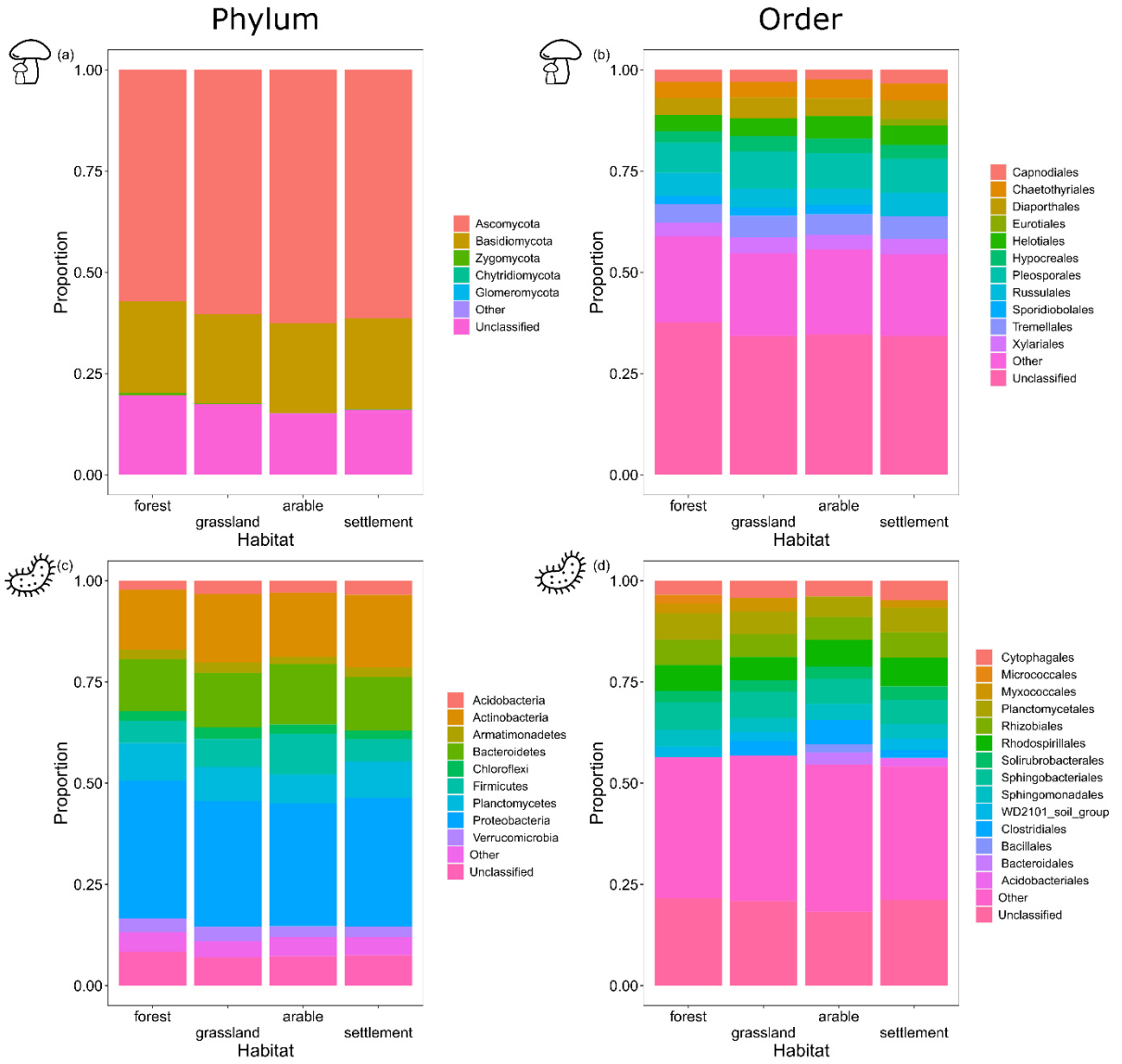

Figure S5: Taxonomic distribution of bacteria and fungi across all samples at phyla and order level categorized by habitat type. Note that many putative fungal and bacterial species are still unclassified due to methodological constraints or knowledge gaps. The "WD2101_soil_group" is the official name of an uncultured strain of *Planctomycetes* bacteria of the class *Phycisphaerae* (Dedysh et al., 2020).

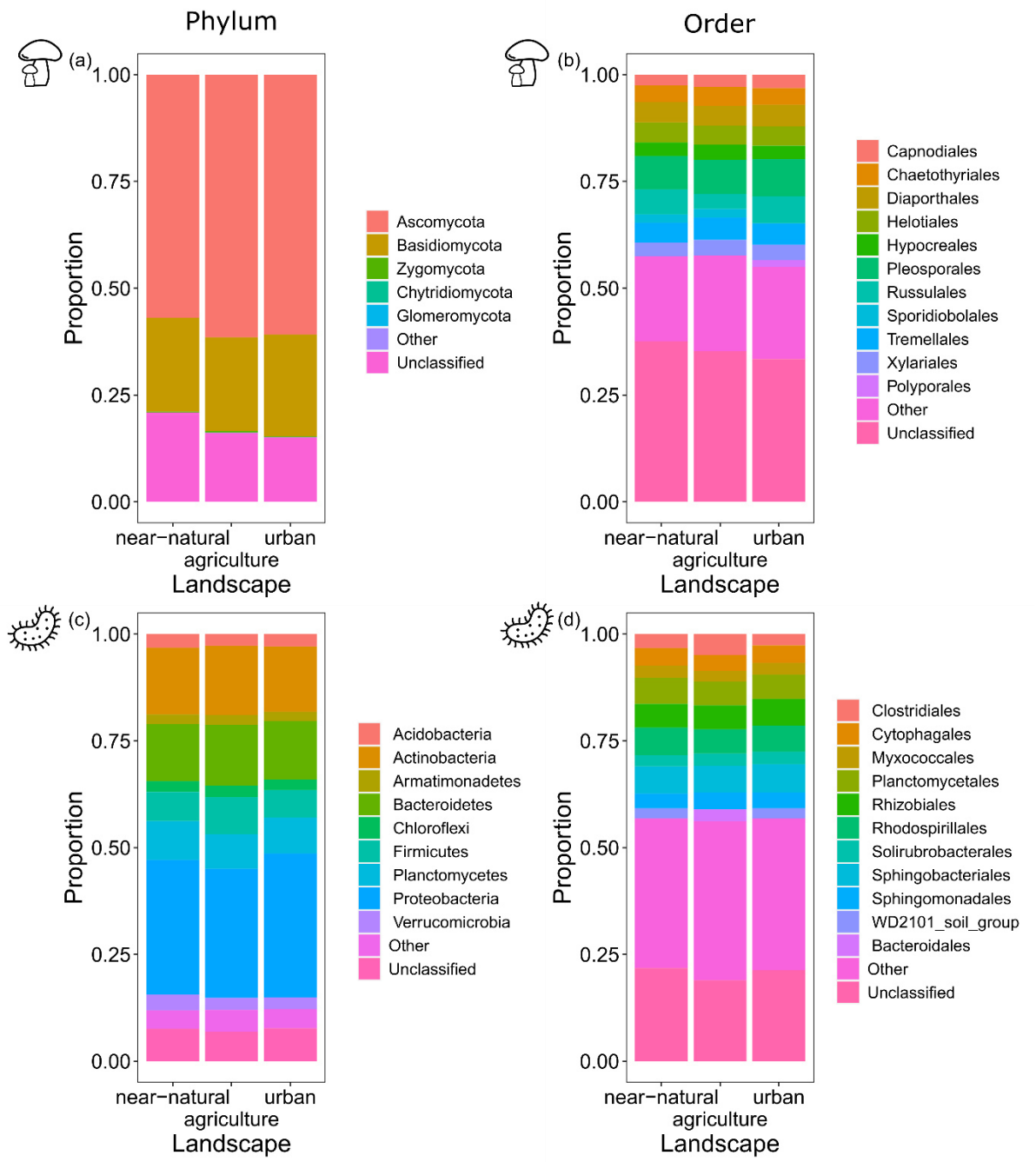

Figure S6: Taxonomic distribution of bacteria and fungi across all samples at phyla and order level categorized by landscape type. Note that many putative fungal and bacterial species are still unclassified due to methodological constraints or knowledge gaps. The "WD2101_soil_group" is the official name of an uncultured strain of *Planctomycetes* bacteria of the class *Phycisphaerae* (Dedysh et al., 2020).

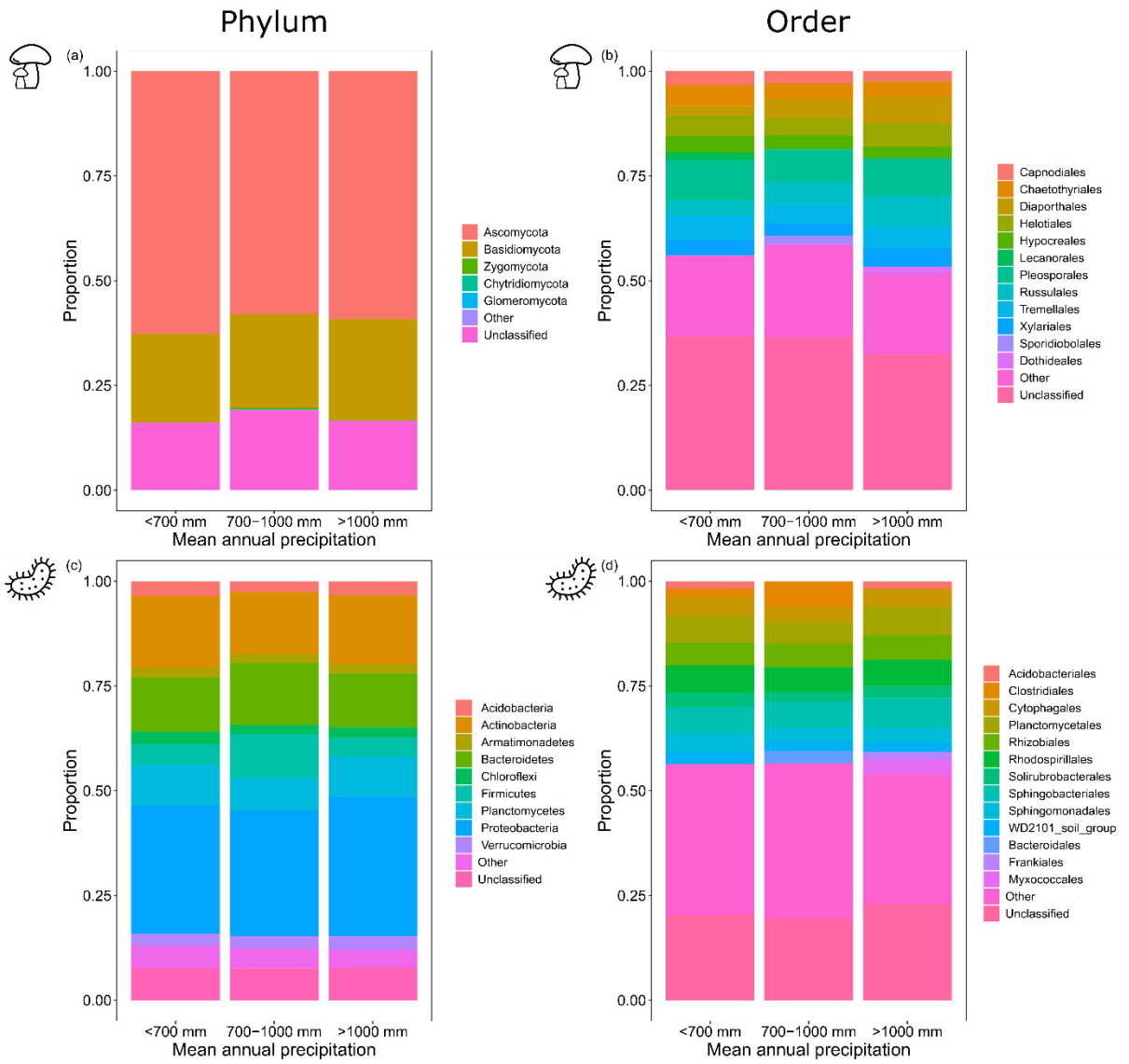

Figure S7: Taxonomic distribution of bacteria and fungi across all samples at phyla and order level categorized by low (<700 mm), medium (700-1000 mm), and high (>1000 mm) mean annual precipitation amounts. Note that many putative fungal and bacterial species are still unclassified due to methodological constraints or knowledge gaps. The "WD2101_soil_group" is the official name of an uncultured strain of *Planctomycetes* bacteria of the class *Phycisphaerae* (Dedysh et al., 2020).

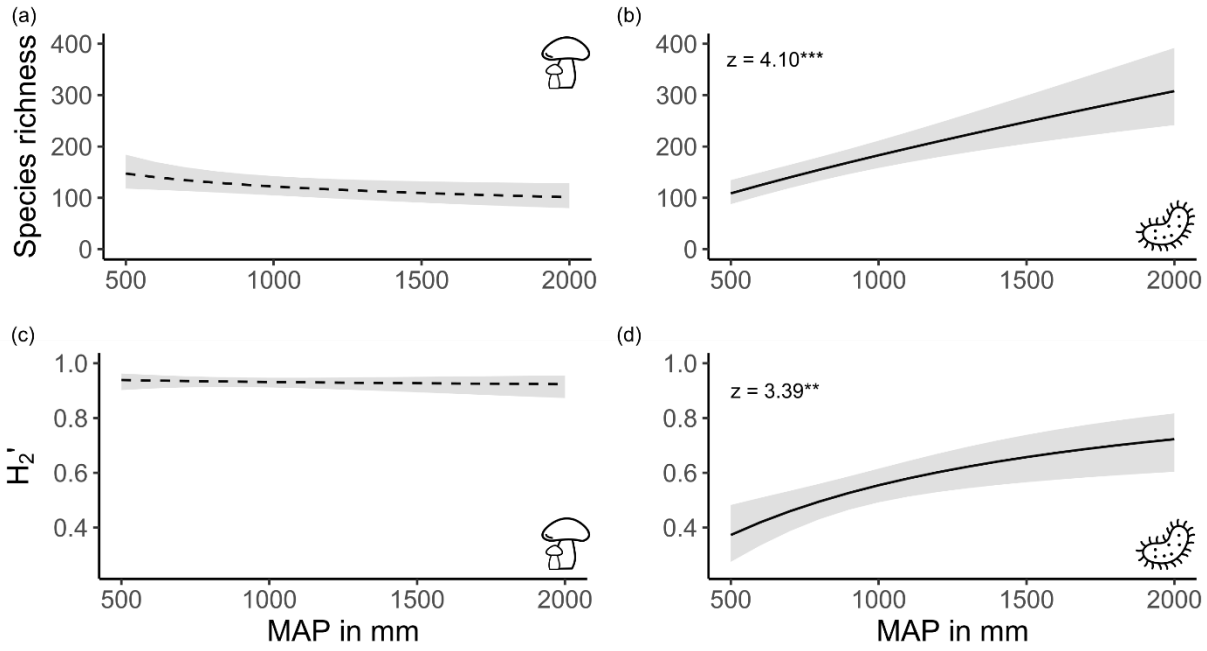

Figure S8: Regression curves showing microbial richness (a, b) and community specialisation H_2' (c, d) at study-plot level predicted by the glmer.nb (richness) and glmmTMB (specialisation) (a, c: fungi; b, d: bacteria) and mean annual precipitation (MAP). H_2' is the two-dimensional Shannon entropy (Blüthgen et al. 2006) and measures community specialisation (0 = only generalist interactions, 1 = total specialisation). Significant changes in richness and specialisation are indicated by z-values and asterisks (*: p = <0.05, **: p = <0.01, ***: p = <0.001). Non-significant changes are indicated by a dashed line.

Table S9: Post-hoc comparison of fungal and bacterial OTU richness among habitat types and landscape types. Significant values are indicated by asterisks (* =p <0.05, ** = p <0.01, *** = p <0.001).

	Fungi		**Bacteria**	
	Richness	**H_2'**	**Richness**	**H_2'**
	z-value	*z-value*	*z-value*	*z-value*
Habitat				
grassland – forest	1.300	-0.132	**3.696****	1.174
arable – forest	-0.611	-0.088	1.972	1.916
settlement – forest	-0.170	-0.216	1.654	0.954
arable – grassland	-1.796	0.036	-1.703	0.776
settlement – grassland	-1.265	-0.107	-1.655	-0.091
settlement – arable	0.387	-0.146	-0.155	-0.831
Landscape				
Agric. – near-natural	-1.311	-0.421	-0.588	**3.262****
urban – near-natural	-1.966	0.362	-0.446	1.264
urban – agric.	-0.612	0.737	0.146	-1.977

Table S10: Results of the interaction models estimating the interaction effects of mean annual temperature (MAT), and local temperature with local and regional land use, and the covariate mean annual precipitation (MAP) on the richness of bacteria on host-tree level and community specialisation (H_2') of bacteria on plot level. Only interaction terms with at least one significant effect of temperature and land use variables based on the main model (Table 1 main body) were considered. We provide no p-values to avoid violation of statistical assumption as the predictors were tested already in the marginal models (Table 1 main body, for more details see Method section main body). Note that R^2s out of the range from to 1 indicate low model performance and poor fits.

	Fungi	**Bacteria**	
	Richness	**Richness**	**H_2'**
Predictors	*z-value*	*z-value*	*z-value*
Intercept	63.98	64.48	0.12
MAT in °C	1.56	2.24	-0.27
Local temp. in °C	1.29	-1.44	0.02
Landscape agriculture	-1.27	-0.69	3.18
Landscape urban	-2.17	-0.42	1.30
Habitat grassland	1.28	3.44	1.19
Habitat arable	-0.44	1.81	1.81
Habitat settlement	-0.18	1.43	0.98
MAP in mm (log10)	-1.19	4.18	3.24
MAT in °C * Landscape agriculture	-1.41	1.59	0.83
MAT in °C * Landscape urban	-0.03	-0.35	0.68
MAT in °C * Habitat grassland		0.48	
MAT in °C * Habitat arable		-1.55	
MAT in °C * Habitat settlement		0.56	
Habitat grassland * Local temp. in °C		-1.32	
Habitat arable * Local temp. in °C		1.50	
Habitat settlement * Local temp. in °C		-0.97	
Landscape agriculture * Local temp. in °C	0.00	-0.75	-0.32
Landscape urban * Local temp. in °C	-0.05	1.07	-0.60
Observations	146	120	120
Marginal R^2 / Conditional R^2	0.167/0.246	0.349/0.963	0.568/1.148

Table S11: Results of the negative-binomial generalized linear mixed effect model estimating the effects of host-tree genera, local and regional land use, mean annual temperature (MAT), mean annual precipitation (MAP), and local temperature on the richness of fungi and bacteria on host-tree level. Significant values are indicated by asterisks (* =p <0.05, ** = p <0.01, *** = p <0.001).

	Fungal richness	**Bacterial richness**
Predictors	*z-value*	*z-value*
(Intercept)	**3.61*** **	-0.21
oak vs. beech	**18.23*** **	**6.28*** **
spruce vs. beech	**28.07*** **	**7.76*** **
pine vs. beech	**7.70*** **	**3.41** **
MAT in °C	-1.49	**2.69** **
Local temp in °C	1.95	**-2.75** **
Habitat grassland vs. forest	0.87	**2.88** **
Habitat arable vs. forest	-1.16	1.77
Habitat settlement vs. forest	0.14	1.82
Landscp. agric. vs. near-nature	-1.38	-1.17
Landscp. urban vs. near-nature	**-2.00***	-0.84
MAP (log10) in mm	**-2.88** **	**3.41*** **
Observations	656	614
Marginal R^2 / Conditional R^2	0.589/0.629	0.146/0.188

Table S12: Post-hoc comparison of fungal and bacterial richness among different tree genera. Significant values are indicated by asterisks (*: p = <0.05, **: p = <0.01, ***: p = <0.001).

	Fungi		**Bacteria**	
	z-value	*p-value*	*z-value*	*p-value*
oak – beech	18.234	**<0.001*****	6.277	**<0.001*****
spruce – beech	28.072	**<0.001*****	7.756	**<0.001*****
pine – beech	7.697	**<0.001*****	3.409	**0.004****
spruce – oak	10.070	**<0.001*****	1.266	0.584
pine – oak	-10.940	**<0.001*****	-3.019	**0.013***
pine – spruce	-20.983	**<0.001*****	-4.426	**<0.001*****

Table S13: Permanova results for the interaction effects of host tree identity, mean annual temperature (MAT), local temperature, habitat and landscape type on community composition of deadwood-inhabiting fungi and bacteria. We used mean annual sum of precipitation as a co-variate. Only interaction terms with at least one significant effect of temperature and land use variables based on the main model (Table 1 main body) were considered. We provide no p-values to avoid violation of statistical assumption as the predictors were tested already in the marginal models (Table 1 main body, for more details see Method section main body).

Fungi	partial R^2	***Bacteria***	partial R^2
Main predictors		**Main predictors**	
Host tree	0.337	Host tree	0.081
MAT in °C	0.002	MAT in °C	0.002
Local temp. in °C	0.002	Local temp. in °C	0.002
Landscape	0.002	Landscape	0.005
Habitat	0.004	Habitat	0.009
MAP in mm	0.003	MAP in mm (log10)	0.07
Host tree * Habitat	0.011	Host tree * Habitat	0.011
Host tree * MAT in °C	0.004	Host tree * MAT in °C	0.005
Habitat * MAT in °C	0.003	Habitat * MAT in °C	0.004
Host tree * Landscape	0.006	Host tree * Landscape	0.007
MAT in °C * Landscape	0.002	MAT in °C * Landscape	0.007
Host tree * Local temp. in °C	0.005	Host tree * Local temp. in °C	0.004
Habitat * Local temp. in °C	0.003	Habitat * Local temp. in °C	0.004
Landscape * Local temp. in °C	0.002	Landscape * Local temp. in °C	0.004
Host tree * Habitat * MAT in °C	0.008	Host tree * Habitat * MAT in °C	0.01
Host tree * MAT in °C * Landscape	0.005	Host tree * MAT in °C * Landscape	0.008
Host tree * Habitat * Local temp. in °C	0.009	Host tree * Habitat * Local temp. in °C	0.011
Host tree * Landscape * Local temp. in °C	0.006	Host tree * Landscape * Local temp. in °C	0.006

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