Received: 1 November 2021 | Accepted: 20 December 2021

DOI: 10.1111/1365-2745.13839

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Traits and phylogenies modulate the environmental responses of wood-inhabiting fungal communities across spatial scales

Nerea Abrego[1,2] | Claus Bässler[3,4] | Morten Christensen[5] | Jacob Heilmann-Clausen[6]

[1]Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland; [2]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland; [3]Department of Conservation Biology, Institute for Ecology, Evolution and Diversity, Goethe University Frankfurt, Frankfurt, Germany; [4]Bavarian Forest National Park, Grafenau, Germany; [5]Morten Chr. Consult, Sorø, Denmark and [6]Centre for Macroecology, Evolution and Climate, University of Copenhagen, Copenhagen, Denmark

Correspondence
Nerea Abrego
Email: nerea.abrego@helsinki.fi

Funding information
Academy of Finland, Grant/Award Number: 308651; Jacob E. Lange foundation

Handling Editor: Hans Jacquemyn

Abstract

1. Identifying the spatial scales at which community assembly processes operate is fundamental for gaining a mechanistic understanding of the drivers shaping ecological communities. In this study, we examined whether and how traits and phylogenetic relationships structure fungal community assembly across spatial scales.
2. We applied joint species distribution modelling to a European-scale dataset on 215 wood-inhabiting fungal species, which includes data on traits, phylogeny and environmental variables measured at the local (log-level) and regional (site-level) scales.
3. At the local scale, wood-inhabiting fungal communities were mostly structured by deadwood decay stage, and the trait and phylogenetic patterns along this environmental gradient suggested the lack of diversifying selection.
4. At regional scales, fungal communities and their trait distributions were influenced by climatic and connectivity-related variables. The fungal climatic niches were not phylogenetically structured, suggesting that diversifying selection or stabilizing selection for climatic niches has played a strong role in wood-inhabiting communities. In contrast, we found a strong phylogenetic signal in the responses to connectivity-related variables, revealing phylogenetic homogenization in small and isolated forests.
5. *Synthesis*. Altogether, our results show that species-level traits and phylogenies modulate the responses of wood-inhabiting fungi to environmental processes acting at different scales. This result suggests that the evolutionary histories of fungal traits diverge along different environmental axes.

KEYWORDS
biogeography and macroecology, fungal trait, joint species distribution model, phylogenetic signal, phylogeography, trait syndrome, wood decaying fungi

1 | INTRODUCTION

A central goal in community ecology is to elucidate the processes that determine structure and composition of ecological communities. Such processes, can be synthesized as phylogeographic (e.g. speciation and large past migrations) and ecological (e.g. abiotic filtering, biotic filtering and dispersal) assembly processes (Götzenberger et al., 2012; Kraft et al., 2007; Weiher et al., 2011). Compared to analysing community composition in terms of species identities alone, integrating information about the phylogenetic relationships and trait similarity between species provides more explicit insights into the effects of phylogeographic and ecological assembly processes (Cadotte et al., 2011; Cadotte et al., 2015; Mason & de Bello, 2013; McGill et al., 2006; Webb et al., 2002). Functional traits are the characteristics, which impact the fitness differences between species under environmental selection, and thus their detection enables a more mechanistic understanding on how communities are structured over environmental gradients (Violle et al., 2007). The phylogenetic relatedness additionally informs about the shared evolutionary history between species (Mouquet et al., 2012; Webb et al., 2002). Thus, assessing whether closely related species are more similar in their traits and responses to environmental variation (i.e. phylogenetic signal), is a powerful tool to assess the interplay between phylogeographic and ecological assembly processes in structuring ecological communities (Cadotte et al., 2013; Cavender-Bares et al., 2009; Kraft et al., 2007; Webb et al., 2002).

Assembly processes act simultaneously at multiple spatial scales, their relative contributions being scale dependent (Hart et al., 2017; McGill, 2010; Mod et al., 2020; Trisos et al., 2014). While phylogeographic assembly processes act at the broadest scales of community organization (Emerson et al., 2011), ecological assembly processes may act from broadest to finest. For instance, the imprints of filters related to resource availability may be detectable within fine spatial scales ranging from tens to hundreds of kilometres, whereas the imprints of macroclimatic effects may only be detectable within larger spatial scales such as continents (Pearson & Dawson, 2003; Siefert et al., 2012). As the effects of ecological assembly processes are scale dependent, so are the influences of different (response) traits on community assembly (Gianuca et al., 2017; Messier et al., 2010). A less studied but relevant question for understanding evolutionary processes on community assembly is, whether the traits that influence assembly processes at different spatial scales are phylogenetically structured (Cavender-Bares et al., 2006; Silvertown et al., 2006).

Wood-inhabiting fungal communities form species-rich communities organized by environmental factors operating at different scales, and hence represent ideal study system for assessing the scale dependency of ecological assembly processes on community assembly. At the deadwood-unit level, key environmental drivers include the microclimatic conditions related to moisture and temperature (Fukasawa et al., 2009; Pouska et al., 2017), and the physical–chemical properties that change with the diameter, decay stage and tree species of the deadwood (e.g. Abrego & Salcedo, 2013; Heilmann-Clausen & Christensen, 2004; Juutilainen et al., 2017; Krah et al., 2018; Kubartová et al., 2012). At larger scales, anthropogenic pressures reducing the amount, diversity and connectivity of deadwood (e.g. Abrego et al., 2015; Abrego & Salcedo, 2014; Josefsson et al., 2010; Juutilainen et al., 2014; Nordén et al., 2013; Penttilä et al., 2006) and macroclimatic factors related to temperature and precipitation (Abrego, Christensen, et al., 2017; Heilmann-Clausen et al., 2014; Ordynets et al., 2018) have all been found to be important. Ordynets et al. (2018) observed that the contemporary wood-inhabiting fungal community structure was weakly related to the distribution of post-glacial forest refugia in Europe, suggesting that historical dispersal barriers have not been an important determinant of their distributions.

Even if a large body of literature has described how fungal communities respond to environmental variation, it remains poorly understood how these responses are modulated by species traits. Compared to other taxa such as animals or plants, trait-based approaches are only emerging in fungal community ecology (Aguilar-Trigueros et al., 2015; Crowther et al., 2014; Dawson et al., 2019). However, trait-based fungal studies are on the rise, and fungal trait databases are increasingly compiled (e.g. Nguyen et al., 2016; Zanne et al., 2020). At the smallest scale of individual deadwood units, reproductive traits have been found to be linked to deadwood quality, such as size (Bässler et al., 2014), decay stage (Abrego, Norberg, et al., 2017) and tree species (Purhonen et al., 2020). At the larger scale, wood-inhabiting fungi with long-lived reproductive structures have been found to be especially vulnerable to forestry practices, likely due to their affinity of large deadwood units (Abrego, Norberg, et al., 2017; Bässler et al., 2014; Nordén et al., 2013). Dispersal traits characterizing the size and shape of sexual spores have also been linked to deadwood size (Purhonen et al., 2020) as well as to macroclimatic variables of temperature and precipitation (Andrew et al., 2016). Resource use traits such as nutritional mode are linked to deadwood decay stage (Abrego, Norberg, et al., 2017; Mäkipää et al., 2017) as well as to macroclimatic conditions (Andrew et al., 2016). Results from trait-based studies accounting for phylogeny have found a strong phylogenetic signal, suggesting that related species tend to share traits and to respond similarly to the environment (Abrego, Norberg, et al., 2017; Bässler et al., 2014; Thorn et al., 2018).

In this paper, we ask whether the way in which traits and phylogenetic relationships structure community assembly varies across spatial scales. For this, we apply joint species distribution modelling to a large-scale dataset on wood-inhabiting fungi, which includes data on environmental variables measured at different spatial scales, traits and phylogeny. More specifically, we assess (a) how much of the variation in the species responses to the environmental variables measured at different scales can be attributed to variation in reproductive, dispersal and resource use traits, and (b) whether the phylogenetic signal in the species responses to the environmental variables varies across spatial scales. Regarding

the first study question, we hypothesized that (a) dispersal traits would mostly influence the responses of the species to large-scale variables representing forest connectivity, (b) resource use traits would mostly influence the response of the species to small scale variation in deadwood quality and (c) reproductive traits would influence the response of the species both to small-scale variation in deadwood quality and large-scale variation in macroclimate. Regarding the second study question, we followed the framework of Revell et al. (2008) to connect patterns in phylogenetic signal to random drift or selective processes. Namely, trait evolution by random drift is expected to generate a pattern where covariance among species traits equals their phylogenetic relationship (Revell et al., 2008), which we expected for traits modulating the responses to anthropogenic gradients for which the species have had less time to evolve through selective processes. In contrast, selective processes (e.g. diversifying or stabilizing selection) are expected to break the relationship between trait similarity and relatedness, resulting in no or weaker phylogenetic signal, which we expected for traits modulating the responses to natural gradients. Thus, our hypothesis was that phylogenetic signal would be highest in the responses of the species to environmental variables representing anthropogenic gradients (i.e. forest connectivity) rather than those representing natural gradients (i.e. resource quality and climatic conditions).

2 | MATERIALS AND METHODS

2.1 | Study area and field data inventories

The data used in the present study were collected from 52 European beech forest reserves (Figure 1a) as used in Abrego, Christensen, et al. (2017); see Figure S1 and Table S1 for the names and locations of the visited sites). The criteria for site (i.e. reserve) selection and survey design were the same as described in Abrego, Christensen, et al. (2017). Briefly, the main criteria were that sites should represent the best reference for natural beech *Fagus sylvatica* forests in each country, and that altogether, the locations of the sites should represent the European beech forest distribution. As the spatial distribution of the visited forest sites was clustered in space, the sites were grouped into eight regions according to their geographical location (see Figure S1).

The fungal fruit-body surveys were carried out between the years 2001 and 2014. Most samplings were carried out visiting each site once during the main fruiting season (from late August to early November, depending on the visited geographical area) except in 2001, when each resource unit was surveyed three times (data used in Ódor et al., 2006). Within each site, individual fallen beech logs of at least 10 cm in diameter, inclusive of their corresponding snag (if it was still present at the time of the survey), were considered individual deadwood units. The selection of the deadwood units was done to

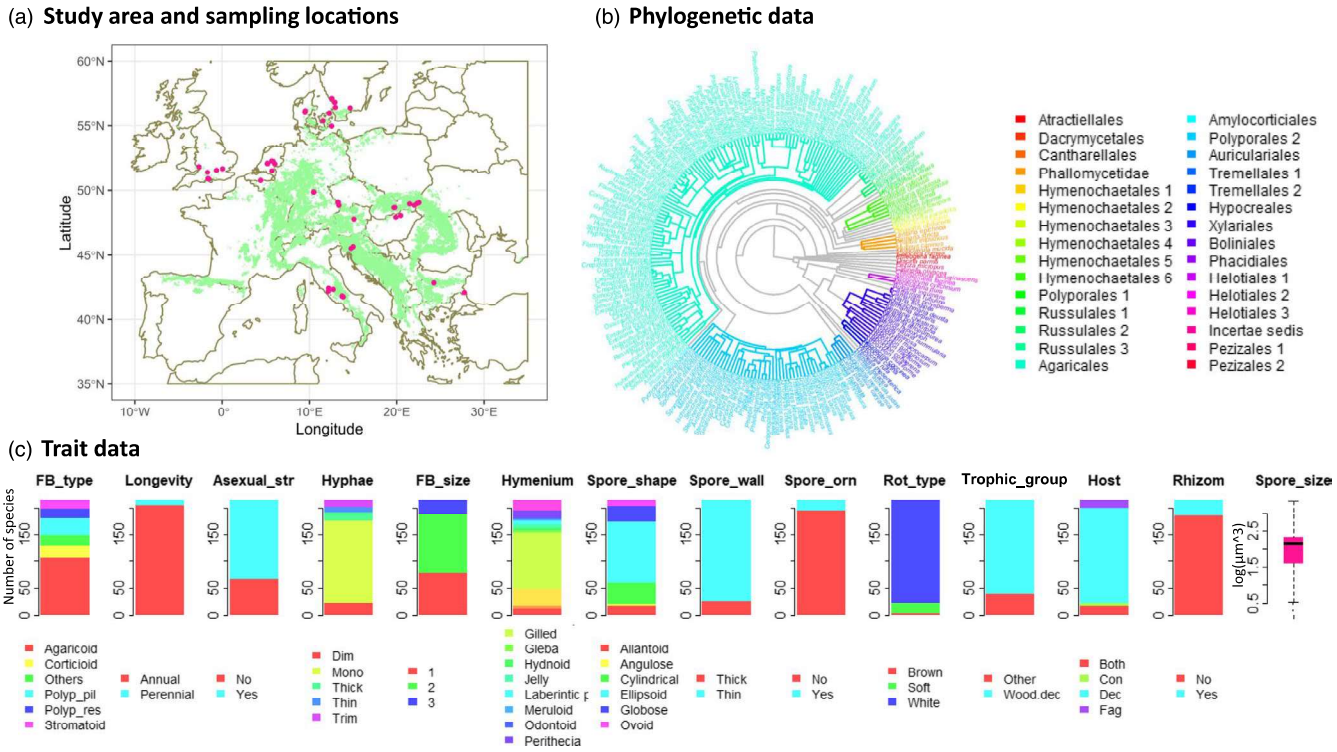

FIGURE 1 Overview of the data used in this study. Panel a shows the visited sampling sites in Europe, panel b illustrates the phylogeny of the fungal dataset and panel c summarizes the fungal trait data. In panel a, the distribution of European beech *Fagus sylvatica* is shown in green and the sampling sites (i.e. beech forest reserves) in pink. In panel b, the phylogenetic tree has been coloured according to 30 clusters of 5% similarity, and the orders to which those clusters belong are given in the legend. In panel c, the *y*-axis shows the number of fungal species in each trait category for categorical traits, and the mean trait value across the species for continuous traits. The list of the species shown in panel B and their colour labels are given in Appendix S3

secure a balanced combination of the main five decay stages within each site (see Christensen et al., 2005 for more details in decay stage classification and log selection procedure). The surveys included all polyporoids and agaricoids, and a subset of corticoids, larger discomycetes and stromatic pyrenomycetes. Most species were identified in the field, but when microscopic identification was necessary, the specimens were collected for further identification in the laboratory.

2.2 | Trait data

We compiled information about all traits that we considered ecologically relevant and for which data were available in the literature (Figure 1c). As described in Table 1, the considered traits were classified into three groups: traits related to the reproductive strategy, traits related to the dispersal capability and traits related to the resource use. The literature sources from which the traits were extracted are given in Appendix S2.

2.3 | Selection of environmental variables

We selected the environmental variables which have been detected to significantly influence fungal species communities, based on results of our previous studies analysing the partially the same data (Abrego et al., 2015; Abrego, Christensen, et al., 2017; Halme et al., 2013; Heilmann-Clausen et al., 2014; Ódor et al., 2006). Thus, in this study we did not perform variable selection, but selected predictors based on the identification of the most influential, representative variables identified in previous studies. Among the local variables describing deadwood quality, we selected deadwood size and decay stage (Abrego, Christensen, et al., 2017). Among the large-scale environmental variables, the size and connectivity of the sites to the surrounding forests have been detected to be the most important drivers, especially for habitat specialist species (Abrego et al., 2015). Finally, among the variables related to climate, the annual temperature range has been detected to have the strongest effect on the composition of wood-inhabiting fungal communities (Abrego et al., 2015; Heilmann-Clausen et al., 2014), followed by precipitation (Abrego, Christensen, et al., 2017; Heilmann-Clausen et al., 2014). Hence, the environmental covariates considered in this study include the diameter at breast height (called henceforth diameter; unit cm) and decay stage of each deadwood unit (scale 1–5), and the 10 km scale connectivity (unitless index), area (ha), annual temperature range (°C) and annual precipitation (mm) of each site. Diameter for trees with a standing snag diameter in breast height was measured at 1.3 m above the forest floor, while for uprooted trees (and broken trees with a low breakpoint) the point was found

TABLE 1 The reproductive, dispersal and resource use trait groups used in the joint species distribution models. In the second column, the categories or units of the traits and the numbers of species within each of the trait categories are given

Traits related to reproduction	**Categories or unit type (number of species)**
Fruit-body type	Agaricoid (106), Corticioid (21), Others (21), Polyporoid pileate (32), Polyporoid resupinate (18), Stromatoid (17)
Fruit-body life span (longevity)	Annual (204), Perennial (11)
The presence of asexual structures in the hymenium	Yes (149), No (66)
Hyphal system type	Monomitic (152), Dimitic (22) and Trimitic (14) in the case of Basidiomycetes, and Thin (10) and Thick (17) in the case of Ascomycetes
Fruit-body size class	One or many small fruit bodies (78), five or less big- or medium-sized fruit bodies (109), Many big fruit bodies (28)
Hymenium shape	Angular pores (11), Branched (5), Circular pores (31), Gilled (107), Gleba/Volva (3), Hydnoid (6), Jelly (6), Labyrinthic pores (6), Meruloid (4), Odontoid (1), Perithecia (15), Reticulate (1), Smooth (19)
Traits related to dispersal	**Categories or unit type (number of species)**
Spore size	Cylinder volume formula: Π x (Spore width/2)^2 x Spore length in μm
Spore shape	Allantoid (16), Angulose (3), Cylindrical (41), Ellipsoid (113), Globose (29), Ovoid (13)
Spore wall	Thin (191), Thick (24)
Ornamented spores	Yes (20), No (195)
Traits related to resource use	**Categories or unit type (number of species)**
Rot type	Brown (4), White (193), Soft (18)
Trophic group	Solely wood decaying (177), nutrients are also taken from other sources than deadwood (38)
Host-tree specialization	Deciduous (177), Beech (16), Conifer (5) or Generalists (17)
The presence of rhizomorphs	Yes (31), No (184)

along the lying log, 1.3 m from the original anchoring of the tree. The connectivity at 10 km spatial scale was based on the beech distribution map in Europe produced by EFI-Alterra (Brus et al., 2012), and we computed it using the Zonation Conservation Planning Software (Lehtomäki & Moilanen, 2013). For characterizing the annual temperature range and the annual precipitation in the reserves, we used the climatic GIS layers BIO7 and BIO12 by Hijmans et al. (2005).

2.4 | Phylogenetic data

The fungal phylogeny was constructed as described in detail in Bässler et al. (2014, 2016). Briefly, available nuclear and mitochondrial sequences were mined from the GenBank sequence data repository. For those species that sequences were not available in the database, the species were manually added to the tree, which led to polytomies in some cases (Figure 1b). We used a literature-based guide tree (Hibbett et al., 2007), to successively align the sequences. After removing ambiguously aligned nucleotide position, alignment blocks of all markers were concatenated into a single matrix. Tree topology and branch lengths were modelled in a maximum-likelihood framework using RAxML (Stamatakis, 2014). Sequence evolution was modelled with the GTRCAT approximation for each marker separately on a common topology. The confidence in the tree topology was assessed by 1,000 nonparametric bootstrap replicates.

2.5 | Statistical analyses

The main statistical tool for analysing the data was the Hierarchical Modelling of Species Communities framework (HMSC, Ovaskainen et al., 2017; Ovaskainen & Abrego, 2020). HMSC is a joint species distribution model which includes a hierarchical layer asking how species responses to environmental covariates depend on species traits and phylogenetic relationships (Abrego, Norberg, et al., 2017). Importantly for reaching the aim of this paper, this modelling approach allowed us to simultaneously estimate how the species responded to the environmental covariates measured at different spatial scales, how the traits of the species influenced those responses, and how phylogenetically structured those responses were.

The original fungal data consist of the presence–absence data of 320 wood-inhabiting fungal species surveyed in 1809 logs across 53 European beech forest sites (Figure 1). As high proportions of species with extremely low prevalence result in poor model performance (Norberg et al., 2019), we excluded from the main analyses those 105 species that occurred in four or less logs in the data. While the excluded rare species represented 33% of all species, they represented only 1.1% of all the species occurrences. To assess whether the exclusion of these rare species affected the main trends in the data, we examined whether their environmental responses and trait distributions differed systematically from those species that were included in the main analyses (Appendix S4). The results of these sensitivity analyses showed that the species with four or less occurrences had almost identical environmental responses to the rest of the species (Table S2). Furthermore, they did not systematically differ in terms of their trait distributions (Table S3). Thus, the main analyses are based on the presence–absence data of 215 wood-inhabiting fungal species.

2.5.1 | Model fitting and evaluation

In the HMSC analyses, we considered the individual logs as sampling units. As a response variable, we used the matrix of the presence–absence of all 215 fungal species across the 1,809 logs. To model the presence–absences, we applied probit regression. As fixed effects (i.e. environmental predictors), we included variables measured both at the log and the forest site levels. As log-level variables we included deadwood size (measured as the diameter of the logs at the breast height) and decay stage as continuous covariates. As previous studies using partially the same data have shown that the relationship between deadwood decay stage and wood-inhabiting fungal occurrence is unimodal (Abrego, Christensen, et al., 2017), we also included a second-order term of decay stage as a log-level covariate aimed to capture the non-monotonic responses. At the forest site level, we included the 10 km scale connectivity, reserve area (log-transformed), annual temperature range and annual precipitation, as continuous covariates. To account for the hierarchically spatial nature of the study design, we included the sites (i.e. reserves) and the regions as random effects.

The full trait data matrix consists of 16 traits, out of which six relate to the reproductive strategy, six to the dispersal capability and four to the resource use (henceforth called 'trait groups', Table 1). To avoid over-parameterization due to the large number of traits, we reduced the dimensionality of the trait data matrix following a Principal Component Analysis (PCA) procedure. The PCA analyses were performed using the 'prcomp' function of the R package VEGAN (Oksanen et al., 2020). We constructed three alternative trait data matrices, all including a reduced set of three trait covariates but varying in how the trait information was incorporated. As the trait data included both categorical and continuous traits, the categorical trait variables were converted to binary dummy variables and then all trait variables were scaled to mean zero and unit variance before applying the PCA approach. In the first alternative trait data matrix, we included the first, second and third axes of a PCA applied to the full trait data matrix. These three axes were chosen based on Horn's parallel analysis of principal components (Table S4) using the R package PARAN (Dinno, 2018). In the second trait data matrix, we included the first axes of PCA applied to the reproductive, dispersal and resource use traits respectively. In the third trait data matrix, we included raw trait data, by selecting one trait from each of the three trait groups. This selection was done by assessing the correlations between traits (Table S5) and selecting those that were most correlated with the first axis in the PCA (Figures S2–S4). For categorical traits with more than two levels, the statistical dependencies were

evaluated by Pearson's Chi-square test for cases where the explanatory was also categorical with more than two levels. For categorical traits with two levels, the dependencies were evaluated by logistic regression. For continuous traits, the dependencies were evaluated with linear regression. If the response variable was categorical with more than two levels, and the explanatory variable was either binary or continuous, the roles of the explanatory and response variables were swapped, and then either logistic regression or linear regression was applied respectively. As a result of the dimension reduction procedure, the first alternative trait data matrix includes the most comprehensive information about the traits (in the sense that it includes information about all traits) but does not discriminate among these. In the other extreme, the third trait data matrix includes the most reduced information about the traits (in the sense that it includes information about three traits only) but discriminates both among and within trait groups. The second alternative trait data matrix is an intermediate case, discriminating among trait groups but not within trait groups. We evaluated how phylogenetically correlated the traits were by estimating Pagel's λ parameter with the 'corPagel' function from the APE R package (Paradis et al., 2004; Paradis et al., 2020). For this, we used the first and second alternative trait matrices, as the function required a continuous input variable.

We fitted in total four alternative HMSC models. All four models included the environmental variables, phylogeny and random effects explained above, but differed in whether and how trait data was included. The first three models included the three alternative trait data matrices, while the fourth model did not include trait data. Henceforth we denote the models 'overall PCA model', 'trait group-specific PCA model', 'raw traits model' and 'no traits model'. The fourth model without traits was used as a baseline to which the models including traits were compared.

We fitted the HMSC models with the R-package HMSC (Tikhonov et al., 2020) assuming the default prior distributions (see Chapter 8 of Ovaskainen & Abrego, 2020). We sampled the posterior distribution with four Markov Chain Monte Carlo (MCMC) chains, each of which was run for 375,000 iterations, of which the first 125,000 were removed as burn-in. The chains were thinned by 1,000 to yield 250 posterior samples per chain and so 1,000 posterior samples in total. We examined MCMC convergence by examining the potential scale reduction factors (Gelman & Rubin, 1992) of the model parameters (Table S6).

We evaluated the explanatory and predictive powers of the probit models through species-specific AUC (Pearce & Ferrier, 2000) and Tjur's R^2 (Tjur, 2009) values, which were then averaged across the species to obtain model-specific metrics. To compute explanatory power, we made model predictions based on models fitted to all data. To compute predictive power, we performed fivefold cross-validation, in which the sampling units were assigned randomly to fivefold, and predictions for each fold were based on model fitted to data on the remaining fourfold. The explanatory powers are expected to be higher than the predictive powers because in the case of the explanatory power the model has 'seen' the sampling units for which is predicting. However, if the difference between explanatory power and predictive power is large, it indicates that the model is overparameterized in the sense that it is likely to being capturing not only signal but also noise.

2.5.2 | Assessing the scale dependency in trait responses

We used the fitted joint species distribution models to assess the scale dependency in the trait-level responses of the species to the environment. For this, we first applied a variance partitioning approach to quantify which proportion of the variation on the species' occurrences could be attributed to the variables measured at the deadwood unit and site levels, compared to that explained by the random effects (Ovaskainen et al., 2017). We then computed the amount of variation in the species responses to the environmental variables that was explained by the variation in their traits (Abrego, Norberg, et al., 2017).

We also evaluated how the traits influenced the responses of the species to the environmental covariates measured at different spatial scales (accounting for the phylogenetic structure). In the HMSC modelling framework, the parameters measuring how the traits influence the responses to the environmental covariates are called the γ parameters (Ovaskainen & Abrego, 2020). We evaluated the trait–environment relationship by examining which γ parameters obtained ≥95% posterior probability for being either positive or negative. For those trait–environment relationships showing statistically supported results, we built predictions based on the fitted models. In the predictions, the values of the non-focal variables were set to their expected value conditional on the focal variable.

2.5.3 | Assessing the scale dependency in phylogenetic signal

We first examined the overall phylogenetic signal in each of the fitted joint species distribution models. In the HMSC modelling framework, the phylogenetic signal is measured through the model-specific parameter ρ (Ovaskainen & Abrego, 2020). $\rho = 1$ indicates that after accounting for the effects of the traits, the environmental responses of the species are fully explained by their phylogenetic correlations. Conversely, $\rho = 0$ indicates that the responses of the species to the environment are randomly distributed with respect to the phylogeny. We considered that the phylogenetic signal measured by ρ was statistically supported if the posterior probability of ρ being positive was at least 95%.

We then assessed whether the phylogenetic signal varied across the responses of the species to the environmental variables measured at different spatial scales by fitting phylogenetic regression models with the 'corPagel' function from the APE R package (Paradis et al., 2004; Paradis et al., 2020). The response variable was the posterior estimate measuring how the species respond to each specific environmental variable in the joint species distribution models,

namely the β parameters corresponding to a particular environmental variable (Ovaskainen & Abrego, 2020). From these models, we estimated Pagel's λ parameter to evaluate the strength phylogenetic signal in the community-level responses to each of the covariates. In this case, we assessed the statistical significance of the phylogenetic signal being greater than zero by null hypothesis testing. We note that the Pagel's λ parameter is identical to the ρ parameter of the HMSC package as both determine the weight that is given for the phylogenetic correlation matrix when averaging that with the identity matrix. However, the ρ parameter estimates the average phylogenetic signal across the different β parameters, whereas the above approach enabled us to estimate covariate-specific phylogenetic signals with the λ parameters.

3 | RESULTS

3.1 | Overall trait and phylogenetic patterns

The considered fungal traits were generally highly correlated (Table 2). In particular, fruit-body type showed many significant associations with other traits. The PCA applied to the trait data revealed that the traits separated according to fruit-body types, implying that these defined patterns in most of the other traits (Figures S2–S4). The traits were also highly phylogenetically structured. The principal axes of the PCAs applied to all trait data or trait group-specific data were phylogenetically structured in all cases with $p < 0.05$ (Table S7). That is, related species had on average more similar traits than unrelated species.

The four alternative HMSC models yielded basically identical explanatory and predictive powers (Table S8). Measured as AUC, the explanatory and predictive powers of all models were 0.90 and 0.81 respectively. Measured as Tjur's R^2 the explanatory and predictive powers were 0.10 to 0.07 respectively. The small difference between the predictive and explanatory powers indicated a good model fit.

Trait-based variance partitioning revealed that the traits captured the variation in species' responses to the environment more effectively when included in their raw form compared to being included as PCA axes (Table 3; Tables S9 and S10). In the model that included raw trait data, the traits explained 46% of the variation in species occurrences generated by their responses to the environmental variables, whereas in the overall PCA and trait group-specific models, the traits explained 19% and 29.5% respectively.

Overall, the phylogenetic signal parameter ρ which measured whether related wood-inhabiting fungi responded similarly to the environmental conditions (while accounting for the traits included in the models) was high and statistically supported (Figure 3). Thus, closely related species responded more similarly to the considered environmental variables than expected from assuming no phylogenetic signal or from their trait similarities.

3.2 | Scale dependency in trait responses

Most of the explained variation in wood-inhabiting fungal community composition was captured by small-scale variables measured at the deadwood-unit level (Table 3). In all models, most of the community-level explained variation was explained by the deadwood-unit level variable decay stage (28.2%–28.8%, see Table 3 and Tables S9 and S10). The other deadwood-unit level variable, deadwood size, explained only little variation (5.2%–5.3%). Among the larger-scale variables measured at the forest-site level, macroclimatic variables explained slightly more variation than connectivity-related variables. Among macroclimatic variables, precipitation and temperature range explained a similar amount of variation (respectively, 4.4–4.9% and 4.7–4.9%). Among connectivity related variables, forest connectivity explained more variation (4.9%–5.1%) than the area of the reserve (2.4% in all models). The random effects explained a substantial amount of the explained variance in all models, the site-level random effects explaining 32.1%–35.1% and the region-level random effects 14.3%–17.6%.

At the same time, the considered traits explained more variation at the small-scale (deadwood-unit level) responses of fungi than large-scale (forest-site level) responses (Table 3). At the deadwood-unit level, the considered traits explained 19% of variance in the species' responses to decay stage and 4% to deadwood size. At the forest-site level, the traits explained 12% of the variation of species responses to macroclimatic variables (2% to the annual precipitation and 10% to the annual temperature range) and 13% of the variation in species' responses to connectivity-related variables (8% to forest connectivity and 5% to reserve area).

Spore size and fruit-body type were related to deadwood-unit level variation in decay stage, fruit-body type to forest-site level variation in macroclimate, and host-tree specialization to forest-level variation in connectivity (Table 3). Spore size showed a statistically supported negative association to the first-order term of the decay stage but a positive to the second-order term. Thus, spore size was smallest at intermediate values of deadwood decay stage (Figure 2a). Conversely, pileate poroid fruit-body types were negatively associated with the second-order term of decay stage, indicating that the probability of occurrence of pileate poroid species was highest in early-intermediate decay stages (decay stage 2, Figure 2b). Fruit-body type was also associated with macroclimate, in particular the occurrences of resupinate polyporoid species decreased with increasing annual temperature range (Figure 2C). The occurrences of fungi specialized to deciduous trees were positively associated with forest connectivity (Figure 2d). Spore size was negatively associated with connectivity-related variables, species with smaller spores occurring in larger reserves (Figure 2e). The models which compacted the trait information into the main PCA axes captured similar but more masked patterns due to the highly correlated relationships among traits (Tables S9 and S10).

TABLE 2 Trait dependency table showing the *p*-values of the trait associations. The statistical tests to assess the dependency between variables was chosen depending on the nature of the variable that is considered as response (Table S5). *p*-values <0.05 are indicated in bold

	Response													
Explanatory	**Fruit-body type**	**Fruit-body lifespan**	**Asexual structures**	**Hyphal system type**	**Fruit-body size**	**Hymenium shape**	**Spore volume**	**Spore shape**	**Spore wall thickness**	**Ornamented spores**	**Rot type**	**Trophic group**	**Host tree**	**Rhizomorphs**
Fruit-body type		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.24	**0.02**	**0.00**	**0.00**	0.08	**0.00**
Fruit-body life span	**0.00**		**0.01**	**0.00**	**0.00**	**0.00**	0.68	0.59	**0.00**	**0.04**	0.05	0.05	**0.04**	**0.01**
Asexual structures	**0.00**	**0.01**		**0.00**	0.22	**0.00**	**0.00**	**0.00**	0.48	0.83	**0.00**	**0.04**	0.46	**0.03**
Hyphal system type	**0.00**	**0.00**	**0.00**		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.07	**0.00**
Fruit-body size	**0.00**	**0.00**	0.22	**0.00**		**0.00**	0.07	**0.01**	**0.03**	0.14	**0.00**	0.91	**0.03**	0.87
Hymenium shape	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**		**0.00**	**0.00**	**0.05**	**0.03**	**0.00**	**0.00**	0.37	**0.00**
Spore volume	**0.00**	0.69	**0.00**	**0.00**	0.07	**0.00**		**0.00**	**0.00**	0.36	**0.00**	**0.02**	**0.00**	**0.01**
Spore shape	**0.00**	0.59	**0.00**	**0.00**	**0.01**	**0.00**	**0.00**		**0.00**	**0.00**	**0.00**	**0.01**	0.79	0.08
Spore wall thickness	0.24	**0.00**	0.48	0.38	**0.03**	0.05	**0.00**	**0.00**		**0.03**	0.25	**0.04**	0.28	0.68
Ornamented spores	**0.02**	**0.04**	0.83	**0.00**	0.15	**0.03**	0.33	**0.00**	**0.03**		**0.02**	0.81	0.11	0.34
Rot type	**0.00**	0.05	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.25	**0.02**		**0.00**	**0.00**	**0.01**
Trophic group	**0.00**	0.05	**0.04**	**0.00**	0.91	**0.00**	**0.01**	**0.01**	**0.04**	0.81	**0.00**		0.21	0.05
Host tree	0.08	**0.04**	0.46	0.07	**0.03**	0.37	**0.00**	0.79	0.28	0.11	**0.00**	0.21		0.48
Rhizomorphs	**0.00**	**0.01**	**0.03**	**0.00**	0.87	**0.00**	**0.00**	0.08	0.68	0.34	**0.01**	0.05	0.48	

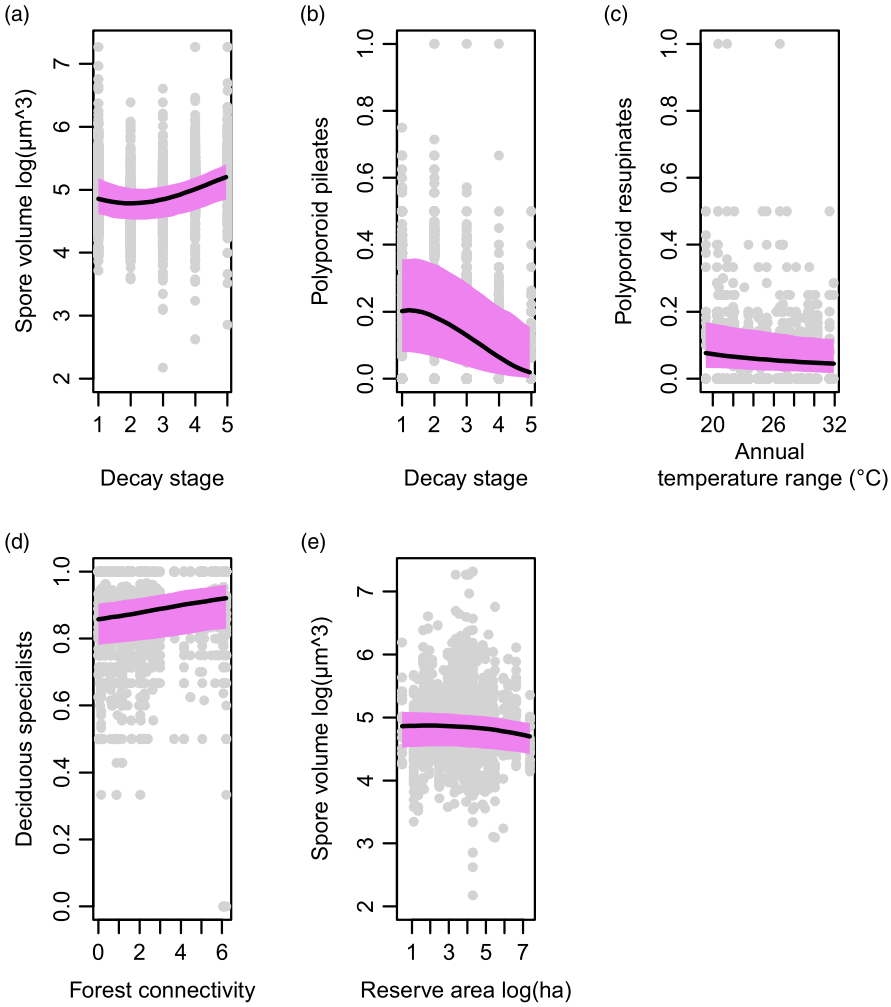

FIGURE 2 Predicted community-weighted mean trait values for different environmental covariates. The panels show the predictions for those trait–environment relationships that were supported by 95% posterior probability (Table 3). The dots show the real values, the lines the mean predicted values and the shaded areas the 95% credible intervals of model prediction

TABLE 3 Trait–environmental covariate relationships. The first column shows the proportion of explained variance attributed to each of the environmental variables included in the model, the second column shows the proportion of variance in the species' responses to the environment that is explained by the traits, and the third column indicates which traits showed statistically supported associations to the environmental variables (i.e. which γ parameters obtained ≥95% posterior probability for being either positive or negative). The results shown here correspond to the HMSC model including raw trait data, and the same results but for the models compacting the trait data into PCA axes are given in Tables S9 and S10

Spatial scale	Type of environmental covariate	Environmental covariate	Variance explained by the covariate (%)	Variance explained by traits (%)	Statistically supported trait relationships
Deadwood-unit level	Resource quality	Decay stage	28.2	19	• Spore size negatively associated with the first-order term of the decay stage but positively to the second-order term • Pileate polyporoid fruit-body type negatively associated with the second-order term of decay stage
		Size	5.2	4	None
Forest-site level	Macroclimate	Precipitation	4.9	2	None
		Temperature range	4.9	10	• Resupinate polyporoid fruit-body type negatively associated with temperature range
	Connectivity	10-km connectivity	5	8	• Species specialized to deciduous trees positively associated with forest connectivity
		Reserve area	2.9	5	• Spore volume negatively associated with reserve area

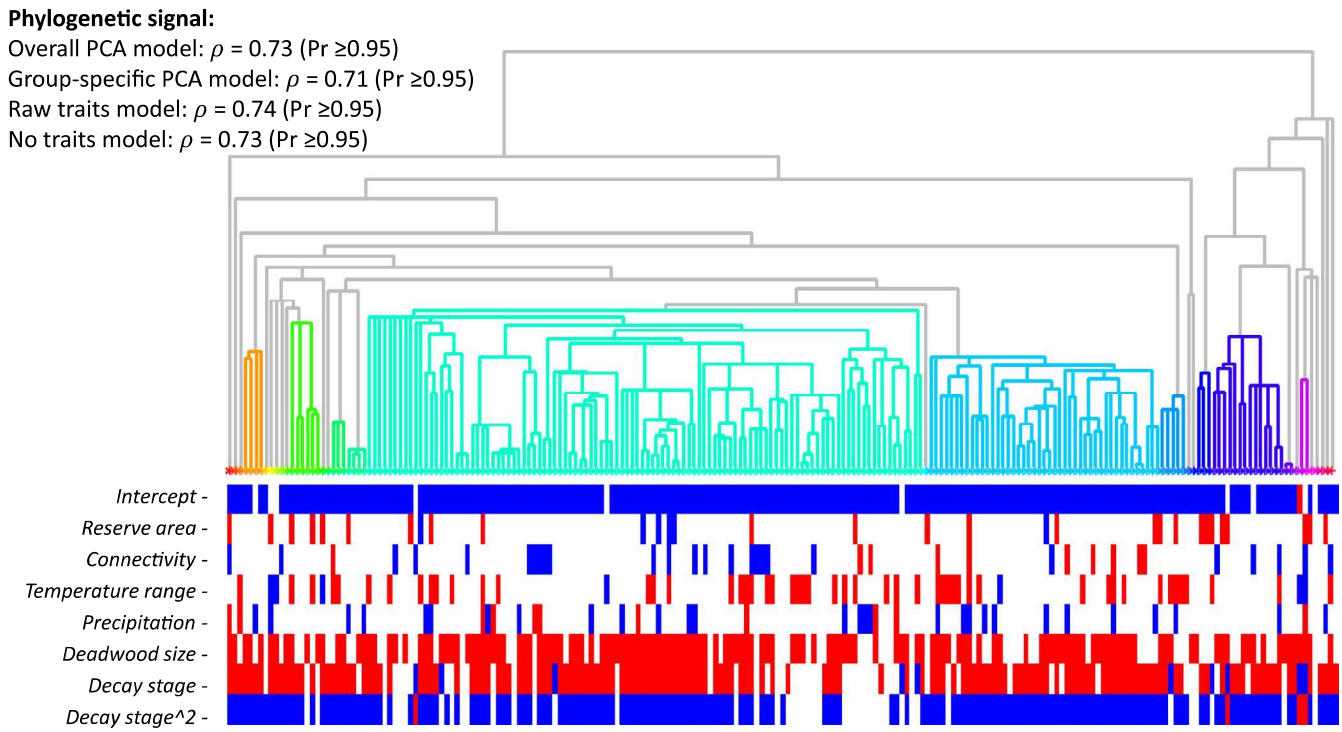

FIGURE 3 Mean posterior regression parameter values measuring the species-specific responses of fungi to each of the environmental covariates included in the HMSC models. Blue colours indicate negative responses and red colours positive responses with ≥0.95 posterior probability. The phylogeny of the species is shown on top of the columns representing the species, and the values of the ρ parameters measuring the overall phylogenetic signal in the four alternative HMSC models are given on top of the tree. The phylogenetic tree has been coloured to reflect phylogenetic similarity as in Figure 1

TABLE 4 Phylogenetic signal in the species' responses to each of the environmental covariates included in the four alternative joint species distribution models. The λ parameter measures the level of phylogenetic signal (from 0 to 1) and the *p*-values indicate whether the level of phylogenetic signal is statistically significant. The significant ($p < 0.05$) values are indicated in bold

Spatial scale	Type of environmental covariate	Environmental variable	Overall PCA model		Group-specific PCA model		Raw traits model		No traits model	
			λ	*p*-value	λ	*p*-value	λ	*p*-value	λ	*p*-value
		Intercept	**0.54**	0.00	**0.52**	0.00	**0.55**	0.00	**0.56**	0.00
Deadwood-unit level	Resource quality	Decay stage	**0.81**	0.00	**0.81**	0.00	**0.81**	0.00	**0.80**	0.00
		Decay stage^2	**0.65**	0.00	**0.64**	0.00	**0.65**	0.00	**0.64**	0.00
		Deadwood size	0.28	0.08	0.27	0.09	0.30	0.05	0.27	0.08
Forest-site level	Macroclimate	Precipitation	0.08	0.71	0.14	0.52	0.38	0.11	0.09	0.67
		Temperature range	0.37	0.16	0.30	0.24	0.11	0.38	0.38	0.20
	Connectivity	Connectivity	0.33	0.06	**0.37**	0.04	0.31	0.07	0.28	0.08
		Reserve area	**0.40**	0.01	**0.37**	0.02	**0.46**	0.00	**0.38**	0.01

3.3 | Scale dependency in phylogenetic signal

The tests examining for phylogenetic signal at the environmental-covariate basis revealed that the overall high phylogenetic signal was determined mostly by the phylogenetically structured responses to the small-scale variables (Figure 3; Table 4). In fact, in all models the λ parameter measuring the phylogenetic signal in the responses of the species to deadwood decay stage (both its first- and second-order terms) was highest and most significant (Table 4). At larger scales, the phylogenetic signal was also significant for the connectivity-related variables, in particular the size of the reserves. The intercept of the models also showed a high and statistically significant phylogenetic signal, revealing that the rarity and commonness of the species were phylogenetically structured.

4 | DISCUSSION

Identifying the critical spatial scales of community organization is fundamental for gaining a mechanistic understanding on how different assembly processes shape ecological communities (Hart et al., 2017; McGill, 2010; Thompson et al., 2020; Trisos et al., 2014). Our study on wood-inhabiting fungal communities demonstrates that environmental and phylogeographic processes act simultaneously at different spatial scales. Environmental constraints structured wood-inhabiting fungal communities both at local (deadwood-unit level) and regional (forest site) scales, and species-level traits and phylogenetic histories influenced the responses of wood-inhabiting fungi at these scales. While several previous studies have highlighted the scale dependency on the environmental factors shaping wood-inhabiting fungal communities (e.g. Abrego et al., 2014; Bässler et al., 2010; Berglund et al., 2011; Heilmann-Clausen et al., 2014; Krah et al., 2018), this is the first large-scale study connecting the scale-dependent responses of wood-inhabiting fungal communities to species-level traits and phylogeny. Furthermore, our results revealed that fungal trait–environment relationships are modulated through response trait syndromes rather than individual response traits (sensu Raffard et al., 2017). Below, we examine each finding in turn.

When connecting fungal traits to the species-specific responses to the environment, we observed that fungal traits formed complexes of correlated traits that simultaneously influenced species' responses to the environment. In evolutionary biology, such groups of correlated traits that together affect species' responses are termed 'response trait syndromes' (Raffard et al., 2017). In particular, fruit-body type summarized a complex set of correlated traits that influenced simultaneously the species' response to many aspects of environmental variation at different spatial scales. Some local studies have also found fruit-body type to be the most general trait to understand how fungal species responded to local environmental variation (Abrego, Norberg, et al., 2017; Heilmann-Clausen, 2001; Purhonen et al., 2020). Interestingly, fruit-body morphology has recently been identified as the major driver of diversification in macrofungi (Sánchez-García et al., 2020). Our results bring strong evidence for fruit-body type being ecologically meaningful as well as a good proxy of many other traits, and hence support the recent proposal of Dawson et al. (2019) to consider fruit-body type as one of the standard traits in macrofungal trait studies.

The considered fungal traits explained more variation for the local-scale responses of fungi than the regional-scale responses. In particular, traits explained a substantial part of the variation in how wood-inhabiting fungi occurred along the deadwood decay process measured at the deadwood-unit level. Wood-inhabiting fungal communities are well known to follow successional dynamics during decay (Ottosson et al., 2014; Rajala et al., 2015), but to our knowledge this process has not previously been assessed in a trait syndrome perspective. The strongest result was that species with pileate polyporoid fruit bodies occurred mostly in early-intermediate decay stage (as it has also been found in earlier studies, Nordén et al., 2013; Abrego, Norberg, et al., 2017; Bässler et al., 2014), and that spore size was smallest at this decay stage. In fact, pileate polyporoid species had the smallest spores, and hence these two signals are inter-dependent. How the traits considered in this study functionally relate to the decay process remains, however, largely unsolved from our study. Unmeasured traits that relate to species' colonization (Moor et al., 2021) and competitive capabilities (Hiscox et al., 2015; Holmer & Stenlid, 1997) as well as more refined resource-use traits (Lustenhouwer et al., 2020) than those used in our study would most likely bring deeper insights into this issue. We note that while previous studies have found a strong relationship between fruit-body morphological traits and deadwood size (Bässler et al., 2014; Abrego, Norberg, et al., 2017), in our study we did not find a strong trait relationship for deadwood size. The explanation for this apparent contradiction most likely lies on the fact that our study involves coarse deadwood (>10 cm DBH) only, which is known to hold rather uniform communities compared to deadwood of smaller sizes (Abrego & Salcedo, 2013; Juutilainen et al., 2011; Küffer et al., 2008; Nordén et al., 2004).

At regional scales, the considered traits also explained variation in the responses of fungal communities to the annual temperature range and forest connectivity. Species with resupinate polyporoid fruit bodies occurred mostly in forest sites located in areas with narrow temperature ranges, suggesting that annual, soft and thin fruit bodies are an adaptation to Atlantic climates. Some previous studies have suggested that fruit-body morphology of wood-inhabiting fungi is related to their tolerance to climate (Bässler et al., 2010; Lindblad, 2001). Likewise, in a local-scale study, Abrego, Norberg, et al. (2017) found that species with resupinate polyporoid fruit bodies preferred forest interiors where climatic fluctuations are smaller than in forest edges. Our study confirms that fruit-body type is related to species' responses to climate. Even if temperature range was the strongest climatic predictor, we suggest that the effect is rather related to fluctuations in air humidity, which are tightly related to temperature, and likely to exhibit a more direct selective pressure on fungal communities than temperature *per se*.

The responses of fungi to the regional-scale variable of forest connectivity were mostly explained by host-tree specialization. Deciduous specialist fungal species were the most sensitive to lack of forest connectivity. This is in agreement with several previous studies, that have shown specialists wood-inhabiting fungal to be more impacted by forest fragmentation than generalists (Abrego et al., 2015; Nordén et al., 2013; Ruete et al., 2017). Given the drastic forest cover reduction that European deciduous forests have suffered due to human land use (Roberts et al., 2018), this result highlights the threat that many wood-inhabiting fungi are exposed to in the European continent (Abrego et al., 2015). A more surprising result was that spore volume increased with decreasing reserve area. An experimental study found that smaller spores can disperse larger distances within forests (2014). Thus, many studies have hypothesized that isolated and small forest remnants should select for fungal species with smaller spores (e.g. Abrego, Norberg, et al., 2017;

Bässler et al., 2014; Nordén et al., 2013). However, Abrego, Norberg, et al. (2017) found that managed forests selected for species with larger spores compared to natural forests with higher deadwood connectivity, and Halbwachs et al. (2017) found that spore size increases with decreasing resource availability. Our continental-scale study is in line with these two studies by showing that spore size is larger in small and more isolated forest sites. The explanation for this most likely lies on the trait-syndrome issue discussed above: Rather than spore size alone, the complex of traits associated with small spore volume and their trade-offs in how they influence species' fitness might be behind the occurrence patterns of wood-inhabiting fungi. In fact, species with pileate fruit bodies had smaller spores, and these are at the same time the species that are most resource specialized and require well-connected forests (Abrego, Norberg, et al., 2017; Nordén et al., 2013).

Fungal responses were phylogenetically structured especially for the local-scale variable of deadwood decay stage. Namely, not only species similar in their traits but also in their phylogenetic position responded similarly to decay stage. Because deadwood decay stage is a natural environmental gradient, we expected fungal communities to be shaped by selective processes along this gradient. It is well known that during the decay process fungal communities show strong turnover, and as conceptualized by Heilmann-Clausen (2001), this turnover is related to substantial changes in substrate quality, as well as competition and stress responses. Thus, a priori, we expected no phylogenetic signal along the decay gradient. This assumption followed from the suggestion that diversifying selection consistently leads to lack of phylogenetic signal (Revell et al., 2008). Contrary to this expectation, we found a strong phylogenetic signal in the community responses to decay stage. High phylogenetic signal might be caused by multiple evolutionary and ecological mechanisms such as genetic drift (i.e. the lack of strong diversifying or stabilizing selection), fluctuating selection, limited genetic variation, gene flow or competition (Crisp & Cook, 2012; Losos, 2008; Revell et al., 2008; Wiens et al., 2010).

The only regional-scale variables for which we found a strong phylogenetic signal in the responses of wood-inhabiting fungal communities were related to forest connectivity. This could support the hypothesis that fungi have had too little time to evolve for anthropogenic gradients, but also alternative explanations remain, as mentioned above (genetic drift, fluctuating selection, limited genetic variation, gene flow or competition; Crisp & Cook, 2012; Losos, 2008; Revell et al., 2008; Wiens et al., 2010). From a conservation perspective, the fact that related fungal species respond similarly to forest fragmentation reveals that as forests become more fragmented, entire clades may be lost and consequently communities become phylogenetically and functionally more homogeneous (McKinney, 1997). This might be because some fungal clades are adapted to environmental conditions that are degraded by anthropogenic disturbances (e.g. very large fallen logs, old veteran trees). As expected, we did not find fungal climatic niches to be phylogenetically structured. This result is in contrast with patterns known for animals and plants (Liu et al., 2020). This suggest that compared to animals and plants, diversifying selection or strong stabilizing selection for climatic niches has played a stronger role in the case of fungi, at least within the groups and geographical scales considered in our study.

5 | CONCLUSIONS

Our study demonstrates that disentangling among spatial scales is essential for understanding how assembly processes structure ecological communities. In fact, our results show that species-level traits and phylogenies influence the responses of wood-inhabiting fungi to environmental processes acting at different scales, suggesting that fungal traits have followed diverging evolutionary histories of along different environmental axes. Furthermore, our results show that rather than individual traits, trait syndromes influence the responses of the species to environmental variation. How these trait syndromes have evolved and their functional relationship with the environment remains, however, unresolved from our study, providing an exciting avenue of future research.

ACKNOWLEDGEMENTS

We are grateful to the original NatMan myco-team, Andrej Piltaver, Mirjam Veerkamp, Ruben Walleyn† and Irén Siller for collecting part of the dataset. Slavomír Adamčík, Stanislav Glejdura, Ján Holec, Soňa Jančovičová, Vladimír Kunca, Alfedo Di Filippo, Gianluca Piovesan, Alan Lucas, Rosemary Davies, Helen Read, Jeremy Dagley and George Peterken are thanked for their great help and a great time in the field, and for arranging field work during data collection in Slovakia, Italy and the United Kingdom. We are also grateful to all land owners/managers who kindly granted us access to the sampling sites. Reinhard Pekny is thanked for guiding and helping us to access Rothwald. The other members of the Beech Boys, Erik Aude, Rasmus Fuglsang Frederiksen, Örjan Fritz, Péter Òdor and Klaas van Dort are thanked for their great company on the numerous field trips behind this study. We acknowledge the Danish Mycological Society and the Jacob E. Lange foundation for supporting part of the field work and the Academy of Finland for supporting the first author during the preparation of this manuscript (grant no. 308651).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.C. and J.H.-C. designed and coordinated the sampling strategy, and all authors took part in the data collection; N.A., C.B. and J.H.-C. conceived the idea of the study; N.A. carried out the statistical analyses and N.A. and J.H.-C. wrote the first draft of the manuscript. All authors contributed to the revisions.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13838.

DATA AVAILABILITY STATEMENT

The data and R-scripts for reproducing the results are available in Dryad Digital Repository https://doi.org/10.5061/dryad.t76hdr82r (Abrego et al., 2022).

ORCID

Nerea Abrego https://orcid.org/0000-0001-6347-6127
Jacob Heilmann-Clausen https://orcid.org/0000-0003-4713-6004

REFERENCES

Abrego, N., Bässler, C., Christensen, M., & Heilmann-Clausen, J. (2015). Implications of reserve size and forest connectivity for the conservation of wood-inhabiting fungi in Europe. *Biological Conservation*, *191*, 469–477.

Abrego, N., Bässler, C., Christensen, M., Heilmann-Clausen, J.. (2022). Data from: Traits and phylogenies modulate the environmental responses of wood-inhabiting fungal communities across spatial scales. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.t76hdr82r

Abrego, N., Christensen, M., Bässler, C., Ainsworth, A. M., & Heilmann-Clausen, J. (2017). Understanding the distribution of wood-inhabiting fungi in European beech reserves from species-specific habitat models. *Fungal Ecology*, *27*, 168–174.

Abrego, N., García-Baquero, G., Halme, P., Ovaskainen, O., & Salcedo, I. (2014). Community turnover of wood-inhabiting fungi across hierarchical spatial scales. *PLoS One*, *9*, e103416.

Abrego, N., Norberg, A., & Ovaskainen, O. (2017). Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. *Journal of Ecology*, *105*, 1070–1081.

Abrego, N., & Salcedo, I. (2013). Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality? *Forest Ecology and Management*, *291*, 377–385.

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

Aguilar-Trigueros, C. A., Hempel, S., Powell, J. R., Anderson, I. C., Antonovics, J., Bergmann, J., Cavagnaro, T. R., Chen, B., Hart, M. M., Klironomos, J., Petermann, J. S., Verbruggen, E., Veresoglou, S. D., & Rillig, M. C. (2015). Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biology Reviews*, *29*, 34–41.

Andrew, C., Heegaard, E., Halvorsen, R., Martinez-Peña, F., Egli, S., Kirk, P. M., Bässler, C., Büntgen, U., Aldea, J., Høiland, K., Boddy, L., & Kauserud, H. (2016). Climate impacts on fungal community and trait dynamics. *Fungal Ecology*, *22*, 17–25.

Bässler, C., Ernst, R., Cadotte, M., Heibl, C., & Müller, J. (2014). Near-to-nature logging influences fungal community assembly processes in a temperate forest. *Journal of Applied Ecology*, *51*, 939–948.

Bässler, C., Müller, J., Cadotte, M. W., Heibl, C., Bradtka, J. H., Thorn, S., & Halbwachs, H. (2016). Functional response of lignicolous fungal guilds to bark beetle deforestation. *Ecological Indicators*, *65*, 149–160.

Bässler, C., Müller, J., Dziock, F., & Brandl, R. (2010). Effects of resource availability and climate on the diversity of wood-decaying fungi. *Journal of Ecology*, *98*, 822–832.

Berglund, H., Hottola, J., Penttilä, R., & Siitonen, J. (2011). Linking substrate and habitat requirements of wood-inhabiting fungi to their regional extinction vulnerability. *Ecography*, *34*, 864–875.

Brus, D. J., Hengeveld, G. M., Walvoort, D. J. J., Goedhart, P. W., Heidema, A. H., Nabuurs, G. J., & Gunia, K. (2012). Statistical mapping of tree species over Europe. *European Journal of Forest Research*, *131*, 145–157.

Cadotte, M., Albert, C. H., & Walker, S. C. (2013). The ecology of differences: Assessing community assembly with trait and evolutionary distances. *Ecology Letters*, *16*, 1234–1244.

Cadotte, M. W., Arnillas, C. A., Livingstone, S. W., & Yasui, S. E. (2015). Predicting communities from functional traits. *Trends in Ecology & Evolution*, *30*, 510–511.

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*, 1079–1087.

Cavender-Bares, J., Keen, A., & Miles, B. (2006). Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology*, *87*, S109–S122.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*, 693–715.

Christensen, M., Hahn, K., Mountford, E. P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S., & Vrska, T. (2005). Dead wood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecology and Management*, *210*, 267–282.

Crisp, M. D., & Cook, L. G. (2012). Phylogenetic niche conservatism: What are the underlying evolutionary and ecological causes? *New Phytologist*, *196*, 681–694.

Crowther, T. W., Maynard, D. S., Crowther, T. R., Peccia, J., Smith, J. R., & Bradford, M. A. (2014). Untangling the fungal niche: The trait-based approach. *Frontiers in Microbiology*, *5*, 579.

Dawson, S. K., Boddy, L., Halbwachs, H., Bässler, C., Andrew, C., Crowther, T. W., Heilmann-Clausen, J., Nordén, J., Ovaskainen, O., & Jönsson, M. (2019). Handbook for the measurement of macrofungal functional traits: A start with basidiomycete wood fungi. *Functional Ecology*, *33*, 372–387.

Dinno, A. (2018). *Paran: Horn's test of principal components/factors*. R package version 1.5.2.

Emerson, B. C., Cicconardi, F., Fanciulli, P. P., & Shaw, P. J. A. (2011). Phylogeny, phylogeography, phylobetadiversity and the molecular analysis of biological communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2391–2402.

Fukasawa, Y., Osono, T., & Takeda, H. (2009). Dynamics of physicochemical properties and occurrence of fungal fruit bodies during decomposition of coarse woody debris of *Fagus crenata*. *Journal of Forest Research*, *14*, 20–29.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*, 457–472.

Gianuca, A. T., Declerck, S. A. J., Cadotte, M. W., Souffreau, C., De Bie, T., & De Meester, L. (2017). Integrating trait and phylogenetic distances to assess scale-dependent community assembly processes. *Ecography*, *40*, 742–752.

Götzenberger, L., de Bello, F., Bråthen, K. A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., & Zobel, M. (2012). Ecological assembly rules in plant communities-approaches, patterns and prospects. *Biological Reviews*, *87*, 111–127.

Halbwachs, H., Heilmann-Clausen, J., & Bässler, C. (2017). Mean spore size and shape in ectomycorrhizal and saprotrophic assemblages show strong responses under resource constraints. *Fungal Ecology*, *26*, 59–64.

Halme, P., Ódor, P., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I., & Heilmann-Clausen, J. (2013). The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. *Biological Conservation*, *168*, 24–30.

Hart, S. P., Usinowicz, J., & Levine, J. M. (2017). The spatial scales of species coexistence. *Nature Ecology & Evolution*, *1*, 1066–1073.

Heilmann-Clausen, J. (2001). A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. *Mycological Research*, *105*, 575–596.

Heilmann-Clausen, J., Aude, E., van Dort, K., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I., Standovár, T., & Òdor, P. (2014). Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe – Reflecting substrate quality or shaped by climate and forest conditions? *Journal of Biogeography*, *41*, 2269–2282.

Heilmann-Clausen, J., & Christensen, M. (2004). Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. *Forest Ecology and Management*, *201*, 105–117.

Hibbett, D. S., Binder, M., Bischoff, J. F., Blackwell, M., Cannon, P. F., Eriksson, O. E., Huhndorf, S., James, T., Kirk, P. M., Lücking, R., Thorsten Lumbsch, H., Lutzoni, F., Matheny, P. B., McLaughlin, D. J., Powell, M. J., Redhead, S., Schoch, C. L., Spatafora, J. W., Stalpers, J. A., … Zhang, N. (2007). A higher-level phylogenetic classification of the fungi. *Mycological Research*, *111*, 509–547.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978.

Hiscox, J., Savoury, M., Muller, C. T., Lindahl, B. D., Rogers, H. J., & Boddy, L. (2015). Priority effects during fungal community establishment in beech wood. *The ISME Journal*, *9*, 2246–2260.

Holmer, L., & Stenlid, J. (1997). Competitive hierarchies of wood decomposing basidiomycetes in artificial systems based on variable inoculum sizes. *Oikos*, *79*, 77–84.

Josefsson, T., Olsson, J., & Östlund, L. (2010). Linking forest history and conservation efforts: Long-term impact of low-intensity timber harvest on forest structure and wood-inhabiting fungi in northern Sweden. *Biological Conservation*, *143*, 1803–1811.

Juutilainen, K., Halme, P., Kotiranta, H., & Mönkkönen, M. (2011). Size matters in studies of dead wood and wood-inhabiting fungi. *Fungal Ecology*, *4*, 342–349.

Juutilainen, K., Mönkkönen, M., Kotiranta, H., & Halme, P. (2014). The effects of forest management on wood-inhabiting fungi occupying dead wood of different diameter fractions. *Forest Ecology and Management*, *313*, 283–291.

Juutilainen, K., Mönkkönen, M., Kotiranta, H., & Halme, P. (2017). Resource use of wood-inhabiting fungi in different boreal forest types. *Fungal Ecology*, *27*, 96–106.

Kraft, N. J. B., Cornwell, W. K., Webb, C. O., & Ackerly, D. D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist*, *170*, 271–283.

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

Kubartová, A., Ottosson, E., Dahlberg, A., & Stenlid, J. (2012). Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Molecular Ecology*, *21*, 4514–4532.

Küffer, N., Gillet, F., Senn-Irlet, B., Aragno, M., & Job, D. (2008). Ecological determinants of fungal diversity on deadwood in European forests. *Fungal Diversity*, *30*, 83–95.

Lehtomäki, J., & Moilanen, A. (2013). Methods and workflow for spatial conservation prioritization using zonation. *Environmental Modelling and Software*, *47*, 128–137.

Lindblad, I. (2001). Diversity of poroid and some corticoid wood-inhabiting fungi along the rainfall gradient in tropical forests, Costa Rica. *Journal of Tropical Ecology*, *17*, 353–369.

Liu, H., Ye, Q., & Wiens, J. J. (2020). Climatic-niche evolution follows similar rules in plants and animals. *Nature Ecology & Evolution*, *4*, 753–763.

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, *11*, 995–1003.

Lustenhouwer, N., Maynard, D. S., Bradford, M. A., Lindner, D. L., Oberle, B., Zanne, A. E., & Crowther, T. W. (2020). A trait-based understanding of wood decomposition by fungi. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 11551–11558.

Mäkipää, R., Rajala, T., Schigel, D., Rinne, K. T., Pennanen, T., Abrego, N., & Ovaskainen, O. (2017). Interactions between soil- and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. *The ISME Journal*, *11*, 1964–1974.

Mason, N. W. H., & de Bello, F. (2013). Functional diversity: A tool for answering challenging ecological questions. *Journal of Vegetation Science*, *24*, 777–780.

McGill, B. J. (2010). Matters of scale. *Science*, *328*, 575–576.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 178–185.

McKinney, M. L. (1997). Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, *28*, 495–516.

Messier, J., McGill, B. J., & Lechowicz, M. J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, *13*, 838–848.

Mod, H. K., Chevalier, M., Luoto, M., & Guisan, A. (2020). Scale dependence of ecological assembly rules: Insights from empirical datasets and joint species distribution modelling. *Journal of Ecology*, *108*, 1967–1977.

Moor, H., Nordén, J., Penttilä, R., Siitonen, J., & Snäll, T. (2021). Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. *Journal of Ecology*, *109*, 491–503.

Mouquet, N., Devictor, V., Meynard, C. N., Munoz, F., Bersier, L.-F., Chave, J., Couteron, P., Dalecky, A., Fontaine, C., Gravel, D., Hardy, O. J., Jabot, F., Lavergne, S., Leibold, M., Mouillot, D., Münkemüller, T., Pavoine, S., Prinzing, A., Rodrigues, A. S., … Thuiller, W. (2012). Ecophylogenetics: Advances and perspectives. *Biological Reviews*, *87*, 769–785.

Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, J. S., & Kennedy, P. G. (2016). FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology*, *20*, 241–248.

Norberg, A., Abrego, N., Blanchet, F. G., Adler, F. R., Anderson, B. J., Anttila, J., Araújo, M. B., Dallas, T., Dunson, D., Elith, J., Foster, S. D., Fox, R., Franklin, J., Godsoe, W., Guisan, A., O'Hara, B., Hill, N. A., Holt, R. D., Hui, F. K. C., … Ovaskainen, O. (2019). A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. *Ecological Monographs*, *89*(3), e01370.

Nordén, B., Ryberg, M., Götmark, F., & Olausson, B. (2004). Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. *Biological Conservation*, *117*, 1–10.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., & Ovaskainen, O. (2013). Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology*, *101*, 701–712.

Ódor, P., Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K. W., Piltaver, A., Siller, I., Veerkamp, M. T., Walleyn, R., Standovár, T., van Hees, A. F. M., Kosec, J., Matočec, N., Kraigher, H., & Grebenc, T. (2006). Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forest in Europe. *Biological Conservation*, *131*, 58–71.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., & Wagner, H. (2020). *Vegan: Community ecology package*. R package version 2.5-7.

Ordynets, A., Heilmann-Clausen, J., Savchenko, A., Bässler, C., Volobuev, S., Akulov, O., Karadelev, M., Kotiranta, H., Saitta, A., Langer, E., & Abrego, N. (2018). Do plant-based biogeographical regions shape aphyllophoroid fungal communities in Europe? *Journal of Biogeography*, *45*, 1182–1195.

Ottosson, E., Nordén, J., Dahlberg, A., Edman, M., Jönsson, M., Larsson, K., Olsson, J., Penttilä, R., Stenlid, J., & Ovaskainen, O. (2014). Species associations during the succession of wood-inhabiting fungal communities. *Fungal Ecology*, *11*, 17–28.

Ovaskainen, O., & Abrego, N. (2020). *Joint species distribution modelling: With applications in R*. Cambridge University Press.

Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*, 561–576.

Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claramunt, S., Claude, J., Cuong, H. S., Desper, R., Didier, G., Durand, B., Dutheil, J., Ewing, R. J., Gascuel, O., Guillerme, T., Heibl, C., Ives, A., Jones, B., Krah, F., Lawson, D., … de Vienne, D. (2020). *Ape: Analysis of phylogenetics and evolution*. R package version 5.4-1.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290.

Pearce, J., & Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, *133*(3), 225–245.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, *12*, 361–371.

Penttilä, R., Lindgren, M., Miettinen, O., Rita, H., & Hanski, I. (2006). Consequences of forest fragmentation for polyporous fungi at two spatial scales. *Oikos*, *114*, 225–240.

Pouska, V., Macek, P., Zíbarová, L., & Ostrow, H. (2017). How does the richness of wood-decaying fungi relate to wood microclimate? *Fungal Ecology*, *27*, 178–181.

Purhonen, J., Ovaskainen, O., Halme, P., Komonen, A., Huhtinen, S., Kotiranta, H., Læssøe, T., & Abrego, N. (2020). Morphological traits predict host-tree specialization in wood-inhabiting fungal communities. *Fungal Ecology*, *46*, 100863.

Raffard, A., Lecerf, A., Cote, J., Buoro, M., Lassus, R., & Cucherousset, J. (2017). The functional syndrome: Linking individual trait variability to ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171893.

Rajala, T., Tuomivirta, T., Pennanen, T., & Mäkipää, R. (2015). Habitat models of wood-inhabiting fungi along a decay gradient of Norway spruce logs. *Fungal Ecology*, *18*, 48–55.

Revell, L. J., Harmon, L. J., & Collar, D. C. (2008). Phylogenetic signal, evolutionary process, and rate. *Systematic Biology*, *57*, 591–601.

Roberts, N., Fyfe, R. M., Woodbridge, J., Gaillard, M.-. J., Davis, B. A. S., Kaplan, J. O., Marquer, L., Mazier, F., Nielsen, A. B., Sugita, S., Trondman, A.-K., & Leydet, M. (2018). Europe's lost forests: A pollen-based synthesis for the last 11,000 years. *Scientific Reports*, *8*, 716.

Ruete, A., Snäll, T., Jonsson, B. G., & Jönsson, M. (2017). Contrasting long-term effects of transient anthropogenic edges and forest fragment size on generalist and specialist deadwood-dwelling fungi. *Journal of Applied Ecology*, *54*, 1142–1151.

Sánchez-García, M., Ryberg, M., Khan, F. K., Varga, T., Nagy, L. G., & Hibbett, D. S. (2020). Fruiting body form, not nutritional mode, is the major driver of diversification in mushroom-forming fungi. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 32528–32534.

Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yépiz, J. C., Carter, B. E., Glennon, K. L., Heberling, J. M., Jo, I. S., Pontes, A., Sauer, A., Willis, A., & Fridley, J. D. (2012). Scale dependence of vegetation–environment relationships: A meta-analysis of multivariate data. *Journal of Vegetation Science*, *23*, 942–951.

Silvertown, J., Dodd, M., Gowing, D., Lawson, C., & McConway, K. (2006). Phylogeny and the hierarchical organization of plant diversity. *Ecology*, *87*, S39–S49.

Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*, 1312–1313.

Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., Viana, D. S., & Chase, J. M. (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecology Letters*, *23*, 1314–1329.

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

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., de Jonge Melinda, M. J., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the R-package Hmsc. *Methods in Ecology and Evolution*, *11*, 442–447.

Tjur, T. (2009). Coefficients of determination in logistic regression models – A new proposal: The coefficient of discrimination. *The American Statistician*, *63*, 366–372.

Trisos, C. H., Petchey, O. L., & Tobias, J. A. (2014). Unraveling the interplay of community assembly processes acting on multiple niche axes across spatial scales. *The American Naturalist*, *184*, 593–608.

Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892.

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*, 475–505.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., & Bentivenga, S. (2011). Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*, 2403–2413.

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Damschen, E. I., Jonathan Davies, T., Grytnes, J. A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., & Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*, 1310–1324.

Zanne, A. E., Abarenkov, K., Afkhami, M. E., Aguilar-Trigueros, C., Bates, S., Bhatnagar, J. M., Busby, P. E., Christian, N., Cornwell, W. K., Crowther, T. W., Flores-Moreno, H., Floudas, D., Gazis, R., Hibbett, D., Kennedy, P., Lindner, D. L., Maynard, D. S., Milo, A. M., Nilsson, R. H., … Treseder, K. K. (2020). Fungal functional ecology: Bringing a trait-based approach to plant-associated fungi. *Biological Reviews*, *95*, 409–433.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Abrego, N., Bässler, C., Christensen, M., & Heilmann-Clausen, J. (2022). Traits and phylogenies modulate the environmental responses of wood-inhabiting fungal communities across spatial scales. *Journal of Ecology*, 110, 784–798. https://doi.org/10.1111/1365-2745.13839