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RESEARCH ARTICLE

The spatial patterns of community composition, their environmental drivers and their spatial scale dependence vary markedly between fungal ecological guilds

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Abstract

Aim: How community composition varies in space and what governs the variation has been extensively investigated in macroorganisms. However, we have only limited knowledge of microorganisms, especially fungi, despite their ecological and economic significance. Based on previous research, we define and test a series of hypotheses regarding the composition of fungal communities, their most influential drivers and their spatial scale dependence.

Location: Czech Republic.

Time period: Present.

Taxa studied: Fungi.

Methods: We analysed the distance decay relationships, community composition and its drivers (physical distance, litter and soil chemistry, tree composition and climate) in fungi using multivariate analyses. We compared the results across three fungal ecological guilds (ectomycorrhizal fungi, saprotrophs and yeasts), two forest microhabitats (litter and bulk soil) and six spatial scales (from 5 m to 80 km) that comprehensively cover the Czech Republic.

Results: We found that, similar to macroorganisms, the ectomycorrhizal fungi and saprotrophs showed marked distance–decay relationships, and their community composition was driven mainly by vegetation and dispersal at local scales but, at regional scales, by environmental effects. In contrast, the third fungal guild, the unicellular yeasts, showed little distance decay, suggesting extraordinary spatial homogeneity, as often seen in microorganisms, such as bacteria.

Main conclusions: Our results underscore the remarkable variation in the community ecology of fungi, which seems to range well-known patterns both from the macro- and the microworld. Knowledge of these patterns advances our understanding of the ecology of fungi, rather understudied organisms of significant ecological and economic importance, which our findings identify as a potentially suitable model for bridging the gaps between the biogeography of micro- and macroorganisms.

KEYWORDS
dispersal, distance decay, environmental filtering, fungal biogeography, metabarcoding, soil biodiversity, spatial community turnover

1 | INTRODUCTION

Species communities vary in space, and different factors drive community composition at different spatial scales (Leibold & Chase, 2017). While this variation has received significant attention in ecology (Leibold & Chase, 2017; Vellend, 2017), it has been less explored in fungi, due mostly to the relatively recent advent of molecular techniques to adequately capture the composition and diversity of fungal communities (Kauserud, 2023). Knowledge of the drivers of fungal community composition and its spatial variation is important given their pronounced effects on various ecosystem processes (Baldrian, 2017; Crowther et al., 2019; Jacoby et al., 2017). Some studies have shown that fungal communities can vary markedly in space, at least for some taxa and guilds, as a function of dispersal limitation, vegetation, soil chemistry and climate (Odriozola et al., 2021; Peay et al., 2007, 2012; Peguero et al., 2021; Talbot et al., 2014; van der Linde et al., 2018; Větrovský et al., 2019). However, it has yet to be determined whether these effects show spatial scale dependence and what such dependence might look like (e.g., compared to that of macroorganisms and other microorganisms, such as bacteria), especially for fungal groups from different ecological guilds and microhabitats.

The decay in community similarity with spatial distance is a nearly universal biogeographical pattern (Graco-Roza et al., 2021; Green et al., 2004; Nekola & White, 1999; Soininen et al., 2007). The pattern may result from dispersal limitation (i.e., species dispersal tends to decrease as the physical distance from the dispersal point increases) (Condit et al., 2002; Hanson et al., 2012; Nekola & White, 1999; Tuomisto et al., 2003), but it may also arise because physically proximate locations tend to have similar environmental conditions suitable for similar species (Chase & Leibold, 2003; Nekola & White, 1999). Inherently, these effects will depend on the spatial scale of the investigation (Chase et al., 2018; Chase & Leibold, 2003; Nekola & Mcgill, 2014). Even within the same study system, stochastic dispersal effects may be relevant over the shortest spatial distances, where the environment is relatively homogeneous. However, with increasing spatial distance, environmental heterogeneity increases (e.g., vegetation, soil and litter chemistry, climate), and community composition may be associated with that heterogeneity rather than with pure physical distance (Chase, 2014).

Fungal communities are composed of several ecological guilds spanning diverse life forms and ecologies, such as ectomycorrhizal (ECM) fungi, saprotrophic fungi (saprotrophs) and yeasts. ECM fungi and saprotrophs have filamentous growth, can be relatively large and, similar to clonal plants, they are able to translocate resources via their mycelial cords over considerable distances (Cairney, 2005). In contrast, yeasts are unicellular organisms that share several ecological characteristics with bacteria (Mašínová et al., 2017). These physiological differences between guilds presumably lead to differences in their dispersal capacity and their responses to environmental conditions, which, in turn, lead to different spatial patterns and drivers of community composition (Liang et al., 2023; Odriozola et al., 2020, 2021; Peguero et al., 2021; Soininen et al., 2007; Zinger et al., 2019). Several studies have demonstrated that ECM fungi may show biogeographic patterns similar to those of macroorganisms (Bahram et al., 2012; Peay et al., 2007, 2012), and their geographic distributions can be limited by dispersal (Bahram et al., 2013; Talbot et al., 2014). In contrast, yeasts have been shown to resemble bacteria more than filamentous fungi in terms of the drivers of their community composition (Mašínová et al., 2017). Correspondingly, a recent study has shown that the temporal turnover of ECM fungal communities in forest soil is highly stochastic and site-specific, whereas the temporal turnover of yeasts over different sites has more systematic patterns, more similar to those of soil bacteria than of other fungal guilds (Martinović et al., 2021). Last, many studies have shown strong covariation between the spatial distribution of ECM fungi and plant community composition, which has been attributed to their plant-associated lifestyle (Bahram et al., 2013; Liang et al., 2023; Odriozola et al., 2020; Peay et al., 2013; van der Linde et al., 2018). Yet, yeasts and saprotrophs sometimes also show associations with tree identity and plant community composition, even though they are free-living organisms not directly dependent on the association with a host plant (Mašínová et al., 2017; Odriozola et al., 2021; Urbanová et al., 2015).

Community composition might follow different rules across microhabitats such as soil and litter, even when they occur at the same site. Specifically, litter is highly dynamic and undergoes profound seasonal changes, which may act as bottleneck events due to seasonal litter input (Voříšková et al., 2014), and microbial communities in litter are also exposed to larger fluctuations in climate and resources compared with communities in bulk soil. Consequently, litter fungi have been reported to show a high level of spatial variability even at very local scales (<2 m) (Štursová et al., 2016). Similarly, the temporal dynamics of fungal community composition in litter can be highly stochastic, especially when compared with fungal communities in soil (whose community assembly shows more determinism), and too chaotic to capture their rate of temporal community turnover (particularly for ECM fungi) (Martinović et al., 2021).

In this study, we evaluate how fungal communities vary in space and how the drivers of their community composition change with spatial distance. We make comparisons across two microhabitats (litter and soil) and three fungal guilds (saprotrophs, ECM fungi and yeasts). We build on a newly compiled comprehensive dataset spanning a continuum of spatial scales covering the Czech Republic (Figure 1). For each of the six examined spatial scales (i.e. spatial lags spanning 5 m, 16 m, 62 m, 250 m, 1 km and 80 km), we studied the fungal communities, chemical descriptors of soil and litter and tree composition to address the following questions: i) Do the ecological

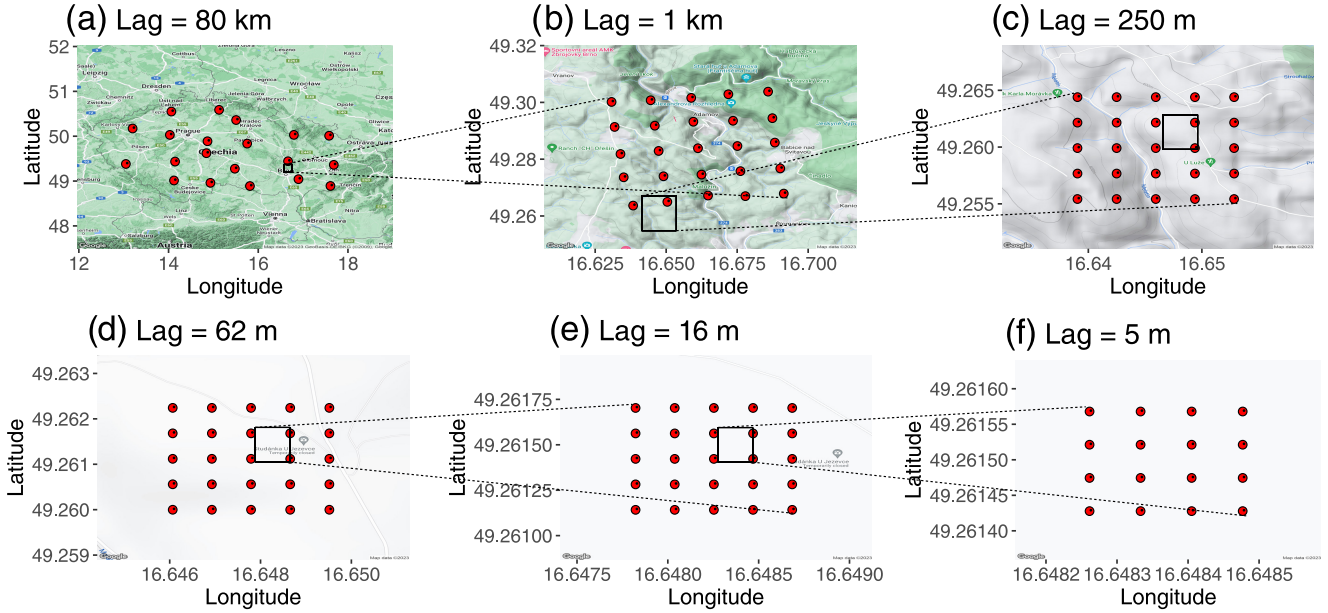

FIGURE 1 A map of the study design showing the sampling areas with six different spatial grains. Each spatial area with a finer-grain scale was embedded within (or located in close proximity to) the area with a coarser-grain spatial scale. Empty squares in the plots indicate the location of the finer grain plot within the area of the coarser grain plot. (a) Sampling area with a spatial lag (i.e., shortest distance that connects all sampling units) of 80 km; (b) sampling area with a spatial lag of 1 km; (c) sampling area with a spatial lag of 250 m; (d) sampling area with a spatial lag of 62 m; (e) sampling area with a spatial lag of 16 m; (f) sampling area with a spatial lag of 5 m.

guilds of fungi differ in their distance decay relationships? ii) Do these relationships vary between microhabitats (i.e. soil and litter)? iii) Are the factors that shape fungal communities spatial scale dependent (physical distance, soil and litter chemistry, vegetation and climate)? iv) Do the factors shaping fungal communities and their spatial dependence differ between the three fungal guilds?

Specifically, we test the following hypotheses: (i) yeasts have weaker distance decay relationships than ECM fungi and saprotrophs, given that yeasts are unicellular and the microenvironments suitable for their establishment tend to be ubiquitous; (ii) litter communities are generally less similar across space than soil communities, given that their community assembly should be more stochastic as a result of rapid litter turnover; (iii) fungal communities are driven by stochastic dispersal effects under relatively homogeneous environmental conditions at local scales, whereas at regional scales, the relative importance of tree composition, soil chemistry and climate increases due to higher environmental variability; (iv) drivers of community composition vary across fungal guilds, and we hypothesize higher covariation of symbiotic ECM fungi with vegetation compared with free-living saprotrophs and yeasts.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

Samples were collected in the territory of the Czech Republic, which encompasses temperate ecoregions, including broadleaf, mixed and montane coniferous forests. Similar ecosystems are found within the same climatic zone throughout much of Europe and North America, but also elsewhere in the world (e.g. parts of Australasia and Southwestern South America), making the results potentially generalizable to temperate ecosystems with comparable climatic vegetation and also soil structures. We sampled the study area at different spatial levels. At the largest spatial scale, 20 sites were sampled, approximately 80 km apart (Figure 1a), each in a stand of the locally dominant tree in fall 2016. The remaining samples at smaller spatial scales were collected within Masaryk Forest Křtiny, the University Forest Enterprise of Mendel University in Brno, a managed temperate mixed forest north of Brno, Czech Republic (49°19′ north latitude, 16°45′ east longitude; Martinović et al., 2021) (Figure 1). Samples were collected in rectangular grids with sample-to-sample distances of 1000 m (25 grid points), 250 m (25 grid points), 62 m (25 grid points), 16 m (25 grid points) and 5 m (16 grid points). In total, this study included 136 plots, and samples were collected in the fall of 2013. Sampling location and metadata are available in Supplementary Table S1.

2.2 | Soil sampling and vegetation survey

To properly represent the spatial variability of fungal communities at each sampling location, five 4-cm-diameter soil cores were collected from each plot: one central core and four additional cores spaced 2 m north, south, east and west of the central core (Martinović et al., 2021). Soil cores were stored at 4°C and processed within 24 h of collection. Litter was collected from the soil

cores, and the top 10 cm of soil was used for further processing. The material from the five cores per site was combined into a composite sample of litter and a composite sample of soil. The litter was cut, and the soil was sieved through a 5-mm sieve. pH was measured in distilled water (1:10). Organic carbon (C) and total nitrogen (N) content measurements were performed in an external laboratory. Total N and organic C contents were determined in a FLASH 2000 Elemental Analyzer (Thermo Scientific). The organic C content was determined after decomposition in HCl (Nelson & Sommers, 2018).

Vegetation variables comprised the composition of the tree layer, represented by species relative abundances. The relative abundance of tree species was estimated as the share of trees with DBH >10 cm growing within 10 m of the centre of sampling. Percent canopy cover derived from a nine-degree Braun–Blanquet scale was assessed in an 8 × 8 m square centred on the sample. The 80 km lag dataset was composed of monodominant stands, 70% of which were dominated by *Picea abies*, 15% by *Fagus sylvatica* and the other 15% by *Quercus* spp. The rest of the datasets were composed of mixed stands. In the 1 km dataset, *Fagus sylvatica* was the most abundant species, with almost 50% relative abundance, followed by *Quercus* spp. and *Picea abies*. *Quercus* spp. was the most abundant species in the 250-m stand, followed by *Carpinus betulus* and *Fagus sylvatica*. The 62-m stand was dominated by *Quercus* spp., followed by *Carpinus betulus*. Lastly, the most abundant species in 16 and 5-m stands was *Quercus* spp., followed by *Carpinus betulus* and *Larix* spp.

2.3 | DNA extraction and amplicon-based sequencing

DNA was extracted in triplicate from 250 mg of fresh soil and litter using a modified Miller method (Sagova-Mareckova et al., 2008). Extracted DNA was purified using a GeneClean Turbo Kit (MP Biomedicals). Triplicate extracts were pooled into one sample, which was used as a template for PCR amplification. PCR was also performed in triplicate. The fungal ITS2 region was amplified using barcoded gITS7 and ITS4 primers (Ihrmark et al., 2012) as described previously (Martinović et al., 2021). Each PCR contained 5 μL of 5× buffer for Q5 High-Fidelity DNA polymerase (New England Biolabs, Inc.), 5 μL of 5× Q5 HighGC Enhancer (New England Biolabs, Inc.), 0.5 μL of 10 mM PCR nucleotide mix (Bioline), 1.5 μL of 10 mg ml^{-1} BSA (GeneON), 0.25 μL of Q5 High-Fidelity DNA polymerase (New England Biolabs, Inc.), 1 μL of each 10 μM forward and reverse primer (Sigma–Aldrich), 9.75 μL of H_2O and 1 μL of the template DNA. The PCR conditions were as follows: initial denaturation for 5 min at 94°C; 30 cycles of 30 s at 94°C, 30 s at 56°C and 30 s at 72°C; and an extension at 72°C for 7 min. Amplicons were pooled and purified, and sequencing libraries prepared using the TruSeq DNA PCR-Free Kit (Illumina) were sequenced in house using Illumina MiSeq (2 × 250).

2.4 | Bioinformatics analysis

Amplicon sequencing data were processed using the pipeline Seed 2.0.3 (Větrovský et al., 2018). Briefly, paired-end reads were joined using fastq-join (Aronesty, 2013). The ITS2 region was extracted using ITSx 1.0.8 (Nilsson et al., 2010) before clustering and chimera detection. Chimeric sequences were detected and deleted using USEARCH 8.0.1623 (Edgar, 2010), and sequences were clustered into operational taxonomic units (OTUs) using UPARSE implemented in USEARCH (Edgar, 2013) at a similarity level of 97%. The most abundant sequence of each OTU was selected as a representative. Taxonomic identification was performed using BLASTn against UNITE 9.0 (Nilsson et al., 2019). Sequences identified as nonfungal were discarded. Fungal ecology was determined using FungalTraits (Põlme et al., 2021).

2.5 | Statistical analysis

Since the choice of data type and similarity index (e.g., Sorensen index vs. Bray–Curtis index) may influence distance decay relationships by giving different weights to rare versus abundant or dormant versus active species in the community (Locey et al., 2020), all analyses were performed with relative abundance as well as presence–absence community matrices excluding global singleton occurrences (i.e., OTUs represented by a single sequence in the whole dataset). Although higher average similarities and weaker spatial turnover rates were measured with presence–absence data, very similar overall patterns were obtained with both approaches. Therefore, we only show results based on relative abundances, since relative abundance allows using the well-established Hellinger distance to perform multivariate analyses (Legendre & Gallagher, 2001).

To quantify the rate of community turnover across space, we computed the Bray–Curtis similarity (as 1-dissimilarity) on square root-transformed relative abundance matrices between the samples collected in the same sampling area, and we built distance decay plots (Nekola & White, 1999) between Bray–Curtis similarity and log-transformed spatial distance between samples. The Bray–Curtis index takes values from 0 to 1; thus, it is easily interpreted as the percent difference in community similarity. Then, using linear mixed effect models as implemented in the lme4 package (Bates et al., 2015) in R (R Core Team, 2021), we fitted a model for each studied community using the Bray–Curtis similarity between samples as a response variable and log-transformed spatial distance between samples as a fixed explanatory variable. The estimate of the slope of this relationship represents the overall rate of community turnover across space. We computed 95% bootstrap confidence intervals (with 999 resamplings with replacement) for the regression parameters using the confint.merMod() function of the lme4 package. To model between-sampling area variations in community turnover, we fitted site-level random effects. Using the Akaike information criterion (AIC), we compared models with random slopes and intercepts with

models with only random intercepts. Random intercept-only models were selected in all cases; thus, the sampling area-level random effects accounted for between-area differences in the intercept (i.e., average differences in baseline similarity between samples), but similar rates of turnover were obtained from the datasets encompassing different areas and spatial scales. Analyses were performed for entire fungal communities in soil and litter, as well as independently for saprotrophs, ECM fungi and yeasts.

To identify tentative drivers of soil and litter fungal community composition at different spatial scales, redundancy analysis (RDA) was used (Legendre & Legendre, 2012) through the rda() function of the vegan package in R (Oksanen et al., 2020). A Hellinger-transformed fungal relative abundance table was used as the response community matrix, and each abiotic environmental and vegetation variable (principal components of the Hellinger-transformed tree community composition table) was included as the sole explanatory variable in independent RDAs. Then, to quantify the relative importance of chemistry, climate, tree community composition and spatial autocorrelation, we used RDA-based variation partitioning of fungal community composition (Legendre & Legendre, 2012). The variation partitioning was performed separately for each of the sampling areas (spatial lags of 5 m, 16 m, 62 m, 250 m, 1 km and 80 km). Abiotic environments (including chemistry and climate), vegetation and spatial models were built independently by fitting parsimonious models with a double-stop forward selection procedure (Blanchet et al., 2008). The spatial component was modelled using sets of independent spatial variables constructed using Moran's eigenvector map (MEM) method (Legendre & Legendre, 2012). When constructing the set of spatial descriptors (i.e., MEM variables), the spatial weighting matrix choice was optimized as suggested by Bauman et al. (2018). The partial effect of each group of variables (i.e., the effect of a group once the effects of all other groups had been taken into account) was tested using a permutation test of the partial RDA results (Legendre & Legendre, 2012), and only the significant groups were included in the final variation partitioning. Finally, the total explained variation, adjusted R^2 of the independent effects of each component (i.e., the variation uniquely explained by each group of variables), and the overlap between different components (i.e., the variation jointly explained by different groups of variables) were plotted against the spatial lag of each dataset. Then, trends in the importance of different groups of variables across spatial scales were visually explored. As with distance–decay plots, analyses were performed for entire fungal communities in soil and litter, as well as separately for saprotrophs, ECM fungi and yeasts.

3 | RESULTS

3.1 | Rates of distance decay in community similarity in soil and litter fungi

Distance decay in community similarity of the whole fungal community in litter was slightly stronger than that in soil (Figure 2), but some notable differences emerged across ecological guilds (Figure 3). For saprotrophs and ECM fungi, overall baseline similarity between samples was lower in litter, but the rates of decay were comparable between the two microhabitats (Figure 3a,b,d,e). In contrast, yeasts showed significantly stronger similarity decay across space in litter than in soil (Figure 3f).

When comparing the patterns between fungal ecological guilds, soil saprotrophs and ECM fungi exhibited very similar rates of decay; however, the baseline similarity between samples was markedly lower for ECM fungi than for saprotrophs (Figure 3a,b,d,e),

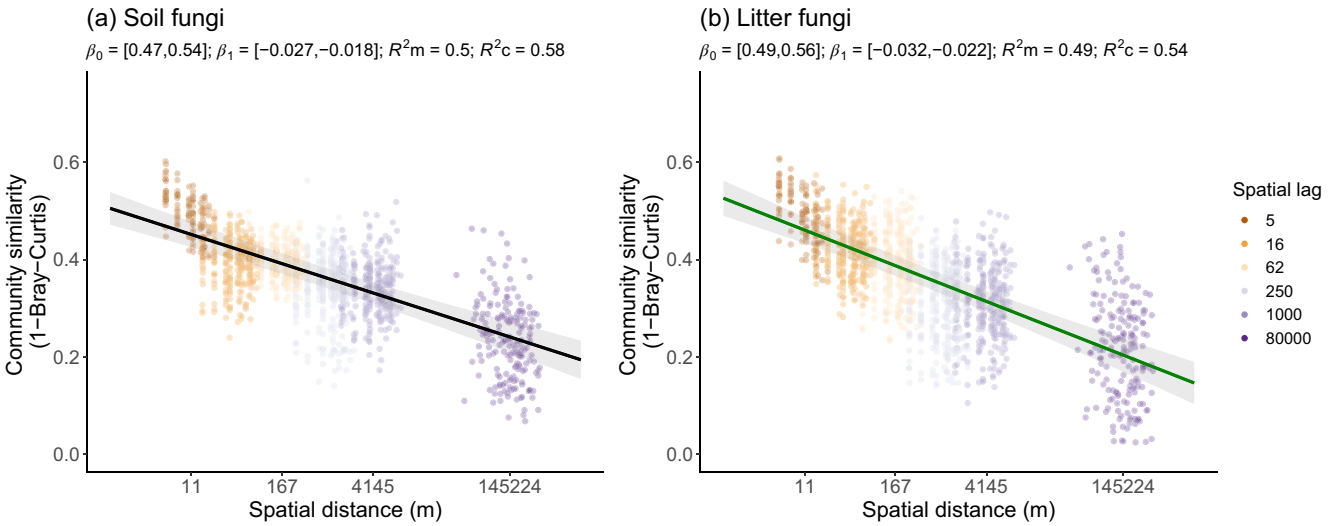

FIGURE 2 Spatial distance decay of fungal community similarity. (a) Soil fungal communities and (b) litter fungal communities. β_0 is the model intercept; β_1 is the slope; square brackets contain the 95% bootstrap confidence intervals; R^2m is the marginal coefficient of determination or the variance explained by the fixed effect spatial distance; R^2c is the conditional coefficient of determination or the variance explained by fixed and random effects together; the difference between R^2c and R^2m is the variance explained by random effects, i.e., between-sampling area variations in the model intercept.

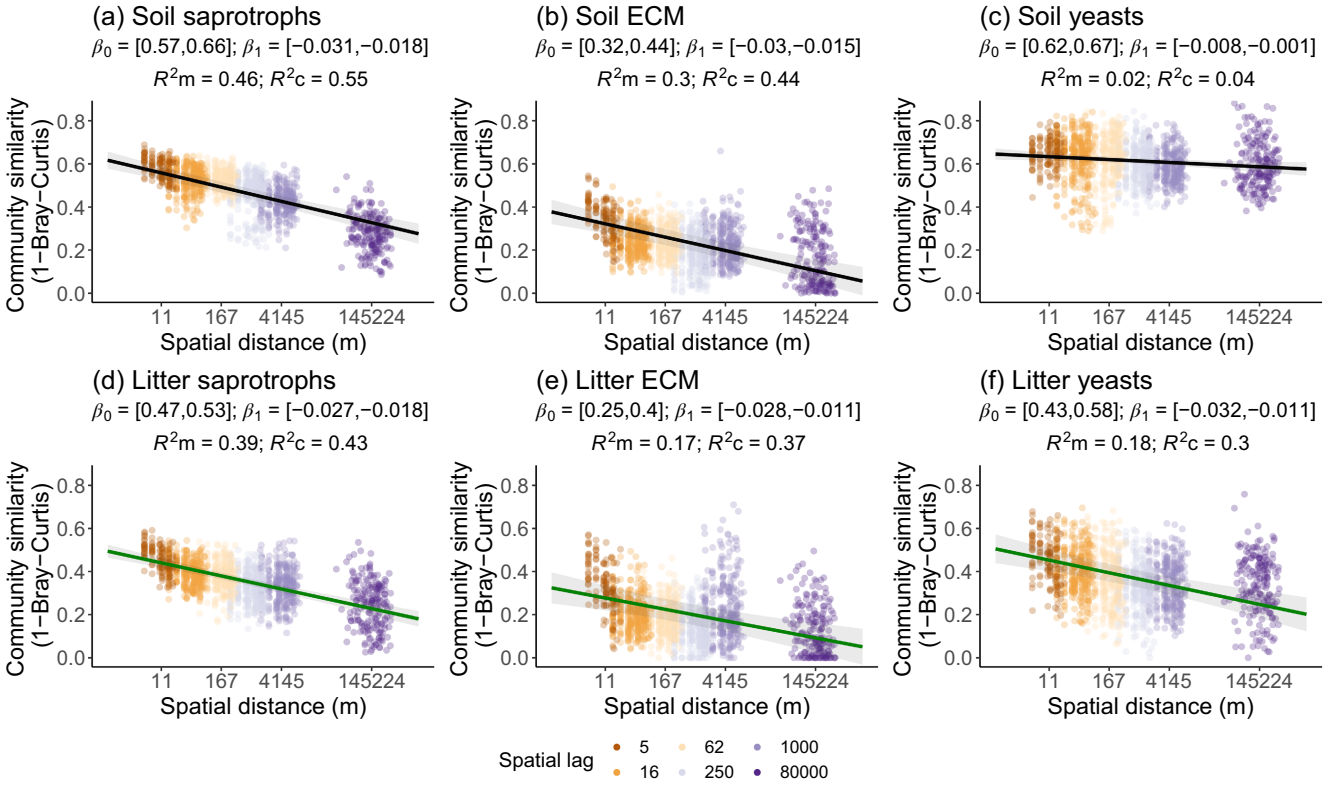

FIGURE 3 Spatial distance decay of community similarity of soil fungal ecological guilds. (a) Soil saprotrophs, (b) soil ECM fungi, (c) soil yeasts, (d) litter saprotrophs, (e) litter ECM fungi and (f) litter yeasts. β_0 is the model intercept; β_1 is the slope; square brackets contain the 95% bootstrap confidence intervals; R^2m is the marginal coefficient of determination or the variance explained by the fixed effect spatial distance; R^2c is the conditional coefficient of determination or the variance explained by fixed and random effects together; the difference between R^2c and R^2m is the variance explained by random effects, i.e., between-sampling area variations in the model intercept.

regardless of the microhabitat. On the other hand, yeasts had significantly weaker decay as well as high baseline similarity as compared to the other guilds in soil (Figure 3c), whereas the rate of decay was comparable to saprotrophs in litter (Figure 3e).

Looking at species' prevalence (i.e., the number of samples in which a species occurs) across spatial scales, there were no ubiquitous soil ECM species in sampling areas above a 62 m spatial lag, whereas there were ubiquitous saprotrophs and yeasts (Figure 4). Those few yeast species that were present in all samples were extremely dominant (i.e., they reached very high relative abundances across samples) (Figure 5). Similarly, the most widespread soil saprotroph species also tended to be the most dominant, whereas there was no clear relationship between ECM species prevalence and relative abundance across samples (Figure 5). In the litter microhabitat, again, there were no ubiquitous ECM fungal species at the broadest scales, but there were ubiquitous saprotrophs and yeasts (Supplementary Figure S1). As in soil, the most prevalent litter saprotrophs and yeasts tended to be the most locally abundant, but this relationship was not as clear as in soil, particularly for yeasts (Supplementary Figure S2). There was no relationship between the prevalence and relative abundance of litter ECM fungi (Supplementary Figure S2).

3.2 | Predictors of fungal community composition in litter and soil across spatial scales

Different factors explained fungal community composition at different spatial scales in soil (Table 1) and litter (Table 2). Soil fungal community composition was largely explained by tree composition across all spatial scales (Table 1). However, the effects of soil chemical variables were significant beyond 16 m and with bioclimatic variables beyond 62 m (Table 1). Litter fungal community composition was also explained by tree composition across all scales, but by litter chemistry beyond 62 m, and it was independent of the bioclimatic variables, regardless of the scale analyzed (Table 2). How much the different variables explained at each scale might be, at least to some extent, associated with the spatial variation that we found within these variables (Supplementary Figure S3). Namely, the areas that spanned over 62 m encompassed sizable variation in soil chemistry (as measured by the average between-sample similarities in soil chemical variables) (Supplementary Figure S3a), but variation in litter chemistry showed limited spatial dependence (Supplementary Figure S3b). Bioclimatic variables from the CHELSA database do not capture variability at spatial distances smaller than 250 m (Supplementary Figure S3c), so it is not surprising that

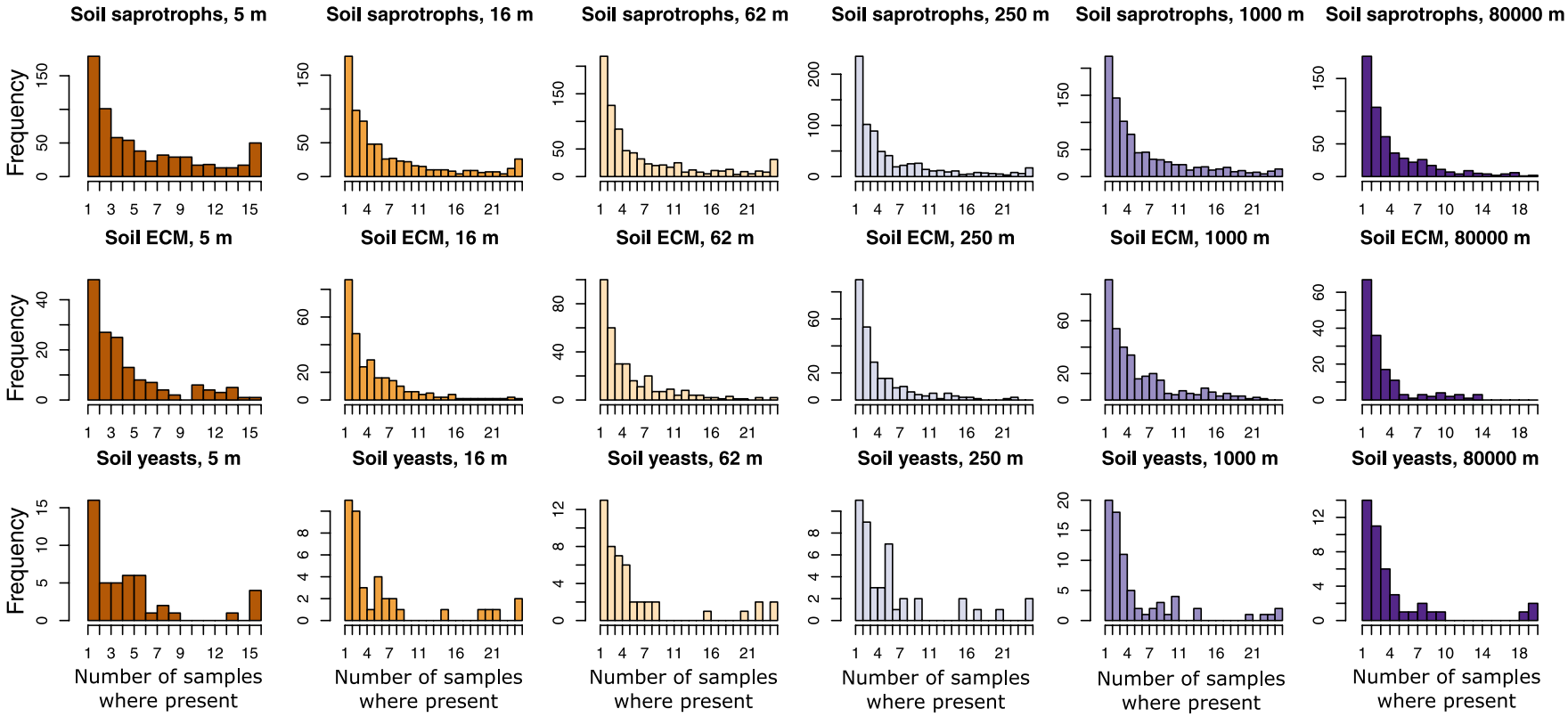

FIGURE 4 Frequencies of soil fungal taxa with different numbers of samples where they occur across fungal guilds and spatial scales. Panels are organized from finer-grained to coarser-grained spatial scales from left to right. Top panels are for soil saprotrophs, middle panels are for soil ECM fungi and bottom panels are for soil yeasts.

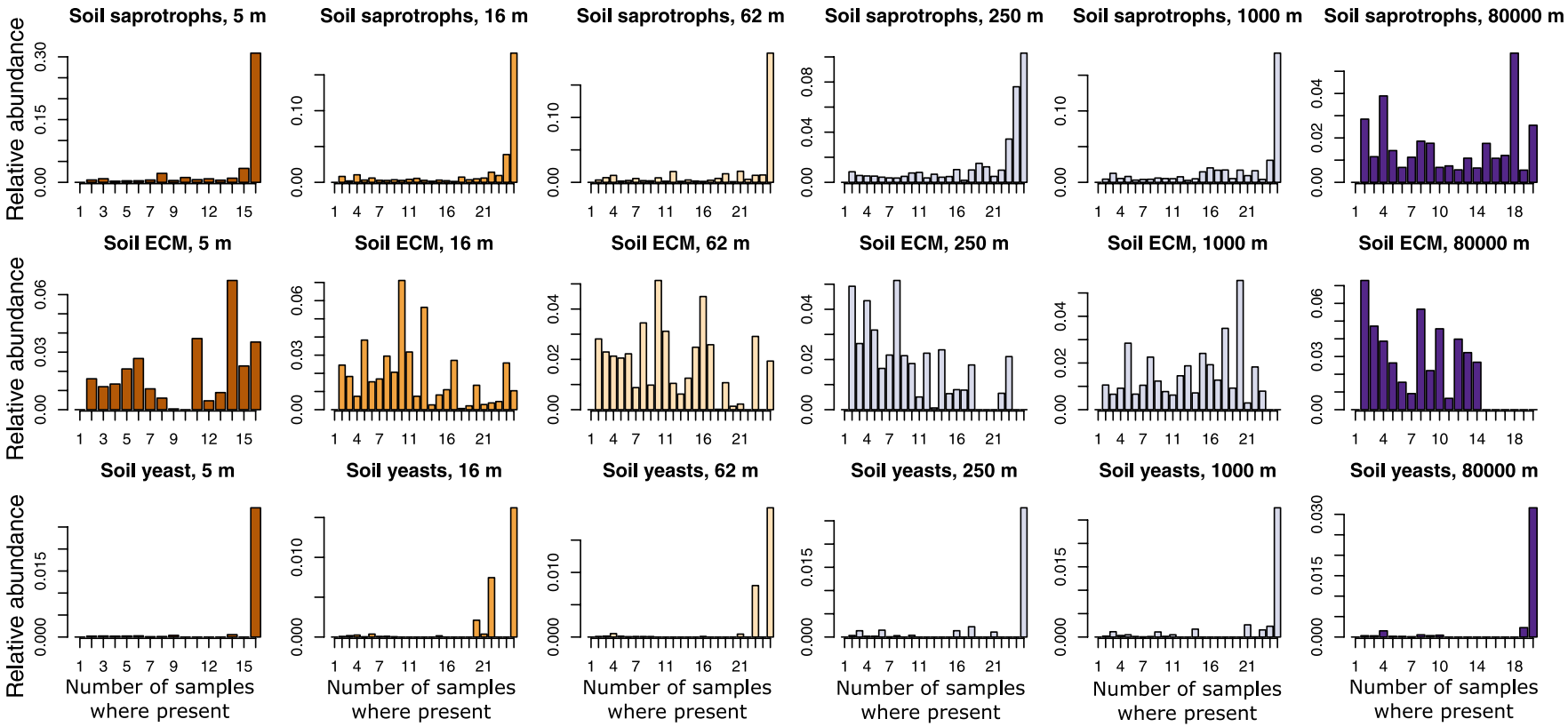

FIGURE 5 Relative abundances of soil fungal taxa with different numbers of samples where they occur across fungal guilds and spatial scales. Panels are organized from finer-grained to coarser-grained spatial scales from left to right. Top panels are for soil saprotrophs, middle panels are for soil ECM fungi and bottom panels are for soil yeasts.

TABLE 1 Hypothesis testing and explanatory power of abiotic environment and plant variables (principal components of tree community composition) for soil fungi are included in the RDA variation partitioning shown in Figure 6a and Supplementary Figure S4a–c.

	df_{Model}	$df_{Residual}$	Adjusted R^2	*F* value	*p* value
5 m					
pH	1	14	0	1.02	0.388
Total N	1	14	0.02	1.26	0.133
C/N ratio	1	14	0.02	1.24	0.108
Plant PC1	1	14	0.05	1.73	0.008
Plant PC2	1	14	0.01	1.21	0.139
Plant PC3	1	14	0.04	1.55	0.018
16 m					
pH	1	23	0	1.11	0.36
Total N	1	23	0	1.15	0.183
C/N ratio	1	23	0	0.82	0.833
Plant PC1	1	23	0.04	2	0.001
Plant PC2	1	23	0	0.98	0.51
Plant PC3	1	23	0	0.86	0.747
62 m					
pH	1	23	0	0.9	0.701
Total N	1	23	0.01	1.13	0.195
C/N ratio	1	23	0.01	1.31	0.037
Plant PC1	1	23	0.02	1.58	0.004
Plant PC2	1	23	0	0.9	0.737
Plant PC3	1	23	0.01	1.2	0.059
250 m					
MAT	1	23	0.01	1.16	0.128
MAP	1	23	0.02	1.49	0.008
pH	1	23	0.01	1.14	0.168
Total N	1	23	0.03	1.8	0.001
C/N ratio	1	23	0.02	1.51	0.004
Plant PC1	1	23	0	1.11	0.216
Plant PC2	1	23	0.02	1.41	0.014
Plant PC3	1	23	0.02	1.45	0.017
1000 m					
MAT	1	23	0	1.09	0.289
MAP	1	23	0	1.08	0.318
pH	1	23	0.02	1.49	0.005
Total N	1	23	0.01	1.26	0.06
C/N ratio	1	23	0.04	2	0.001
Plant PC1	1	23	0.02	1.41	0.014
Plant PC2	1	23	0.02	1.52	0.002
Plant PC3	1	23	0	0.95	0.557
80,000 m					
MAT	1	18	0.01	1.15	0.182
MAP	1	18	0.01	1.1	0.26
pH	1	18	0.07	2.35	0.001
Total N	1	18	0	0.95	0.549
C/N ratio	1	18	0.08	2.68	0.001
Plant PC1	1	18	0.09	2.93	0.001
Plant PC2	1	18	0.02	1.4	0.04

Note: Explanatory power is measured by including the variables in the models as single explanatory variables. The tests are based on a permutation procedure with 999 permutations.

TABLE 2 Hypothesis testing and explanatory power of abiotic environment and plant variables (principal components of tree community composition) for litter fungi, included in the RDA variation partitioning shown in Figure 6b and Supplementary Figure S4d–f.

	df_{Model}	$df_{Residual}$	Adjusted R^2	*F* value	*p* value
5 m					
pH	1	14	0	1.06	0.308
Total N	1	14	0.02	1.34	0.083
C/N ratio	1	14	0.02	1.27	0.104
Plant PC1	1	14	0.04	1.63	0.021
Plant PC2	1	14	0	0.86	0.726
Plant PC3	1	14	0.02	1.33	0.089
16 m					
pH	1	23	0	0.81	0.89
Total N	1	23	0	0.94	0.62
C/N ratio	1	23	0	0.77	0.904
Plant PC1	1	23	0.05	2.34	0.001
Plant PC2	1	23	0.02	1.37	0.034
Plant PC3	1	23	0.01	1.18	0.158
62 m					
pH	1	23	0.01	1.26	0.112
Total N	1	23	0	0.61	0.994
C/N ratio	1	23	0	1.04	0.367
Plant PC1	1	23	0.04	1.92	0.004
Plant PC2	1	23	0.04	2.1	0.003
Plant PC3	1	23	0.01	1.14	0.219
250 m					
MAT	1	23	0.01	1.18	0.136
MAP	1	23	0.01	1.25	0.081
pH	1	23	0.01	1.25	0.083
Total N	1	23	0.02	1.43	0.02
C/N ratio	1	23	0.01	1.19	0.14
Plant PC1	1	23	0.02	1.48	0.009
Plant PC2	1	23	0.02	1.38	0.034
Plant PC3	1	23	0.04	2.1	0.001
1000 m					
MAT	1	23	0.01	1.15	0.2
MAP	1	23	0.01	1.15	0.22
pH	1	23	0	0.99	0.476
Total N	1	23	0	1.09	0.305
C/N ratio	1	23	0.02	1.5	0.01
Plant PC1	1	23	0.01	1.27	0.083
Plant PC2	1	23	0.03	1.8	0.001
Plant PC3	1	23	0.03	1.65	0.003
80,000 m					
MAT	1	18	0.01	1.26	0.102
MAP	1	18	0.02	1.33	0.067
pH	1	18	0.06	2.26	0.001
Total N	1	18	0	0.85	0.761
C/N ratio	1	18	0	0.98	0.465
Plant PC1	1	18	0.09	2.81	0.001
Plant PC2	1	18	0.04	1.71	0.007

Note: Explanatory power is measured by including the variables in the models as single explanatory variables. The tests are based on a permutation procedure with 999 permutations.

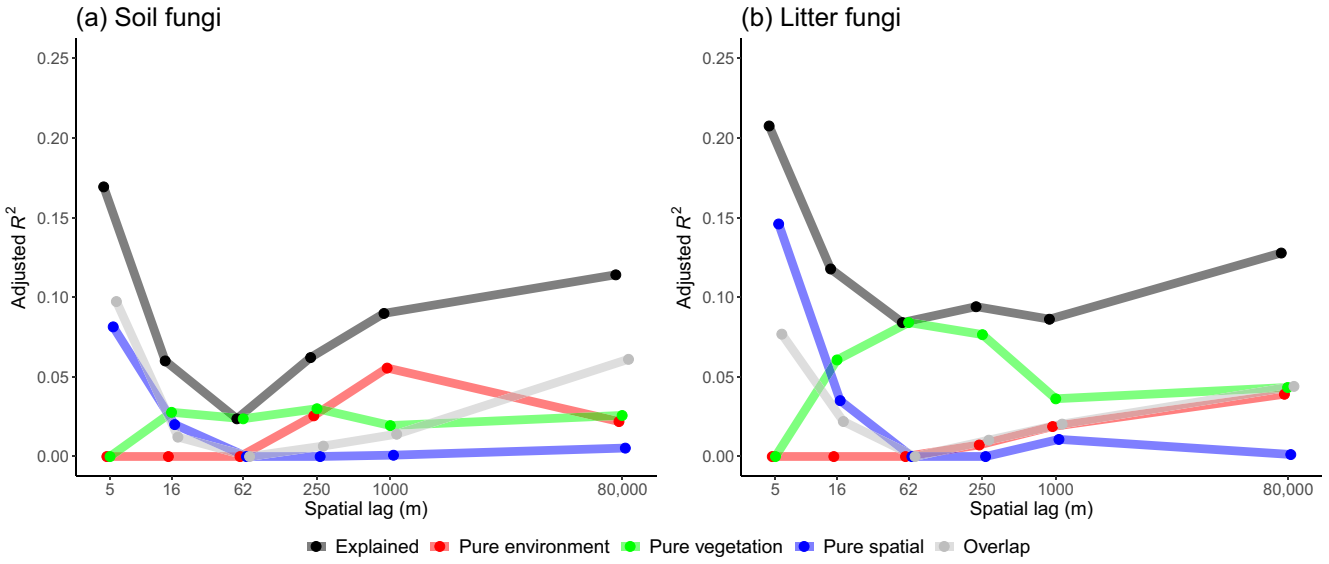

FIGURE 6 Explanatory power of abiotic environmental variables, tree composition, spatial variables and overlapping effects for (a) soil and (b) litter fungal communities. Explanatory power is based on RDA variation partitioning conducted independently in sampling areas of different spatial scales. Pure effects represent the effect of a group of variables once the effect of the other groups has been taken into account. Overlap represents the variation jointly explained by several groups of variables. Explained represents the total explained variance.

significant statistical associations occurred only above this threshold. Nevertheless, microclimatic variability below these spatial scales is not expected in our study system. Areas beyond the 250 m spatial lag tended to encompass higher variability in vegetation (as measured by the average between-sample similarities in tree community composition) than areas corresponding to shorter spatial lags (Supplementary Figure S3d).

We found pronounced spatial scale dependence in the total amount of variance explained in the fungal community composition (in both soil and litter) and also in the relative importance of the different groups of explanatory variables. The total explanatory power of the model for soil fungal community composition was highest at the finest grain scale of 5 m, then, it dropped between 16 and 250 m and increased again beyond that scale (Figure 6a). A similar but much weaker drop in explanatory power was also observed for litter fungi at intermediate spatial scales (Figure 6b). Fungal community composition in soil and litter was strongly spatially structured (i.e. spatial variables were the main predictors of community composition) at the shortest spatial distances of 5 and 16 m; none of the other variables were significantly associated with fungal composition at the 5 m distance after accounting for spatial autocorrelation (Figure 6). The pure effect of vegetation peaked at intermediate distances from 16 to 250 m, where none of the other variables were associated with fungal composition (Figure 6). The effect of abiotic environmental variables (chemistry and climate) on fungal composition increased beyond distances of 62 m in both soil and litter. A drop in the independent effect of the abiotic environment was observed for soil fungi at 80-km distance; however, the drop was associated with a strong increase in the overlapping effects (Figure 6a). Similarly, a drop in the pure vegetation effect was observed above 250 m in litter fungi, but this drop was again associated with an increase in overlapping effects (Figure 6b). This indicates that abiotic environment, vegetation and space became more strongly intercorrelated at the largest distances, rather than a decreased association between fungal composition and abiotic environment and vegetation.

The spatial scale dependence was sizable also when analysing the fungal guilds separately. Patterns of explanatory power across space observed for the entire soil fungal community were observed in soil saprotrophs and, to some degree, in soil ECM (Supplementary Figure S4a,b). In contrast, soil yeasts showed completely different trends: the strong spatial structure observed at the shortest distances in soil saprotrophs and ECM was absent in yeasts (Supplementary Figure S4c). Nevertheless, a stronger association with abiotic environmental variables at the longest distances was also observed in soil yeasts (Supplementary Figure S4c). The patterns observed for entire litter fungal communities were only visible in litter saprotrophs (Supplementary Figure S4d). Litter ECM were spatially structured at the shortest distance and associated with vegetation and abiotic factors at the longest distances (Supplementary Figure S4e). Last, litter yeasts were spatially structured at the shortest distances and associated with vegetation across spatial scales but, particularly, at the longest distances (Supplementary Figure S4f).

4 | DISCUSSION

This study provides a multiscale assessment of community composition and its drivers in fungi. While microorganisms differ dramatically in their biology from macroorganisms, we find that the changes in their community composition are spatial scale dependent and, more interestingly, the scale dependence follows well-known

rules in biogeography. Namely, dispersal limitation and vegetation (i.e., biotic effects) seem to shape community composition at small scales, while soil chemistry and climate (i.e., abiotic environmental effects) are important at large scales (>250 m). We found that the scale dependence is largely similar between saprotrophic and ECM fungi but differs markedly from the guild of yeasts, which showed comparatively spatially homogeneous communities. These results are based on a comprehensive dataset that spans a continuum of spatial scales, from 5 m to 80 km between the sampled fungal communities, encompassing the entire Czech Republic. Altogether, these findings advance our knowledge of the community composition of fungi, its scale dependence and biogeography. Interestingly, while some fungi show patterns well known from macroorganisms, others show microorganism-like patterns.

Patterns of spatial distance–decay differed strongly between the studied fungal ecological guilds. Soil yeasts showed the most distinct pattern, with very high baseline community similarity between samples and a very weak distance–decay relationship, a pattern typically observed in bacteria (Luan et al., 2020; Peguero et al., 2021; Zinger et al., 2019). The comparative homogeneity of yeast communities across scales was driven by a few ubiquitous taxa that strongly dominated all samples (i.e. *Cryptococcus terricola and Cryptococcus podzolicus*). Previous studies have shown that yeasts resemble bacteria more than filamentous fungi in terms of the drivers of their community composition (Mašínová et al., 2017) and their temporal dynamics (Martinović et al., 2021), and our study reports similar results also for the geographic space. The homogeneity of communities in unicellular organisms at regional scales is usually attributed to their higher dispersal ability due to their small propagules, large populations and short generation times (Hanson et al., 2012; Martiny et al., 2006; Peguero et al., 2021). However, we argue that the ability to exploit microniches and establish viable populations may play a larger role in this case since many filamentous fungi also produce spores that are capable of long-distance dispersal. Soil ECM fungi showed the lowest baseline similarity and a strong distance–decay relationship. Our results agree with those of many other studies on ECM fungal biogeography showing that these communities are strongly spatially structured (i.e. they show strong spatial autocorrelation that is not induced by environmental variation), with distance–decay relationships comparable to those in animals and plants, due presumably to similar limitations to dispersal and the establishment of stable populations (Bahram et al., 2013; Peay et al., 2007, 2012; Talbot et al., 2014).

Our study also revealed a low baseline similarity across samples for ECM fungi, with no ubiquitous taxa above 0.625 km^2 and no positive association between species' range sizes and their local dominance. This indicates a high level of stochasticity in the ECM community assembly. These observations correspond with those recently reported by Martinović et al. (2021), in which the temporal dynamics of soil ECM fungi were also highly unpredictable, likely due to the stochasticity of the process of recolonization of fine tree roots that emerge newly every year (Dumbrell et al., 2011) and the priority effects subsequently exerted by the successful colonizers (Kennedy et al., 2009). Similar processes might also explain the low baseline similarity observed for ECM fungi. Namely, stochasticity in fine root colonization coupled with priority effects might have resulted in different ECM fugal taxa dominating in different locations. This, in turn, would have dropped the overall similarity in ECM fungal composition across locations. Alternative explanations might include colonization tradeoffs or limited room for coexistence due to high biomass (compared to other microbes). Soil saprotrophs showed patterns intermediate to those observed in yeasts and ECM fungi, with a rate of spatial community turnover comparable to that of ECM fungi but a baseline similarity more similar to that in yeasts. Widespread species tended to be locally dominant, but the trend was not as clear as for yeasts. These results were not surprising since saprotrophs resemble ECM fungi in their life form but are similar to yeasts in their free-living saprotrophic lifestyle. The results from litter were comparable to those from soil, with the exception that yeasts had stronger distance decay in litter than soil, with overall patterns similar to those of litter saprotrophs.

Previous studies showed that litter fungal communities are highly heterogeneous even at very short spatial distances (Štursová et al., 2016) and that they undergo profound seasonal and annual changes (Martinović et al., 2021; Voříšková et al., 2014). Therefore, we hypothesized to observe lower overall similarities between samples in litter compared to soil. Contrary to this hypothesis, we observed very similar distance–decay relationships in both microhabitats; however, there were differences when the ecological guilds were examined separately: the baseline similarities were lower in litter for the three guilds, and yeasts had stronger distance–decay relationship in litter than in soil. Moreover, Štursová et al. (2016) focused on a small area of a few m^2, and therefore compared samples were represented by individual soil cores, while our results are based on a mixed sample of five cores that better represent each location. This could explain why we found comparable sample-to-sample similarities in soil and litter.

The drivers of fungal community composition changed with the spatial scale. As hypothesized, spatial distance was the best predictor of community composition at the smallest, local scales (5 m). Vegetation effects peaked at intermediate scales (16–62 m), and the covariation between tree composition and abiotic environmental variables explained most of the variance in fungal composition at the largest scales (>250 m). These results support the idea that the processes through which fungal communities are assembled are spatial scale dependent (Chase, 2014). Together, they also motivate a careful consideration of spatial scale when designing a study, analysing and interpreting the resultant patterns pertaining to the community ecology and biogeography of fungi (Chase et al., 2018; Leibold & Chase, 2017; Nekola & Mcgill, 2014).

Importantly, the spatial scale dependence of the drivers of community composition differed across the three fungal guilds. Namely, strong spatial structure captured at the shortest spatial distances was present in ECM fungi and saprotrophs but not in yeasts; therefore, it likely captured the mycelial growth of the large, filamentous fungal species, which have been demonstrated to grow up to several metres long (Cairney, 2005). The vegetation effect observed

at intermediate scales in our study corresponds with the results of other studies conducted at similar scales, where vegetation has been shown to affect fungal communities (Bahram et al., 2013; Liang et al., 2023; Odriozola et al., 2020, 2021; Peay et al., 2013; Tedersoo et al., 2020; Urbanová et al., 2015). In contrast to our hypothesis, the distribution of ECM fungi did not show stronger coupling with vegetation than the distribution of saprotrophs and yeasts. We believe that similar processes that explained the low baseline similarity across locations exhibited by ECM fungal communities might explain the lower than expected coupling with vegetation, too. Even if ECM fungal species show some level of host-specificity, the same ECM tree species may establish symbioses with different ECM fungal taxa (Brundrett & Tedersoo, 2018). Given the above-mentioned stochasticity in the seasonal colonization of fine roots by ECM fungi, the same tree species may establish a symbiosis with different ECM fungal taxa in different locations, thus reducing the coupling between ECM fungi and tree community composition. For instance, Liang et al. (2023) reported strong vegetation effects on ECM fungal composition when analysing samples dominated by host trees with mixed mycorrhizal types, but soil variables were the main predictors when analysing only the samples dominated by ECM-associated trees. All samples in our study were dominated by ECM-associated trees, which might have contributed to the weaker vegetation effects on ECM fungi. Yet, we did find some indication of stronger direct effects of vegetation in ECM fungi than in yeasts and saprotrophs. The association between vegetation and ECM fungal composition was stronger in soil than in litter (where ECM fungi were highly unpredictable), whereas, for saprotrophs and yeasts, the association was stronger in litter than in soil. This indicates that the influence of vegetation on ECM fungi was likely direct, while the influence on free-living guilds was likely mediated by the effects on litter characteristics (not included in litter chemical variables). Lastly, climatic variables were associated with fungal composition at all spatial scales and across all three fungal guilds, which agrees with the recent reports that climate governs large-scale fungal distributions (Tedersoo et al., 2014; van der Linde et al., 2018; Větrovský et al., 2019).

Our findings encompass multiple scales, covering the Czech Republic. However, it seems plausible that the main conclusions, namely the spatial scale dependence of the drivers of community composition and the cross-guild differences (ECM fungi, saprotrophs and yeast), might hold in other systems, too, especially in those with similar spatial, climatic, vegetation and soil structures (e.g. temperate ecoregions of Europe and North America). We can speculate that ecoregions with higher heterogeneity (e.g. zonal montane or tropical ecoregions) show similar qualitative patterns (e.g. yeast communities tend to be more homogeneous than saprotroph and ECM fungal communities), but the patterns emerge over quantitatively different scales, reflecting the spatial granularity of the particular ecoregion. Still, some interesting differences emerge when comparing our results to similar studies conducted in other parts of the world. For example, Eagar et al. (2023) studied temperate forests in the Adirondack Mountains (New York, USA) and showed that the statistical association between fungal community composition and dominant tree mycorrhizal types was stronger in the warmer, dryer sites and weaker in the cooler, wetter sites. Glassman et al. (2017), studying isolated single pine tree islands at high temperate altitudes of the Yosemite Park (California, USA), found relatively strong effects of soil chemistry at fine spatial scales and only weak effects of host plants when compared with our results. Altogether, these findings underscore the utility of further research, covering an extended range of spatial scales and ecoregions. Our findings might motivate more work in this direction and offer potentially useful insights into workable methodology and the formulation of testable hypotheses for future studies.

5 | CONCLUSION

We report that community composition in fungi is driven by multiple factors whose relative importance depends on the ecological guild (saprotrophs, ECM fungi and yeasts) and the spatial scale of the study (5 m to 80 km distance between sampling units). Similar to macroorganisms, ECM fungi and saprotrophs showed marked distance–decay relationships, and their community composition was driven by dispersal and vegetation at local scales but by abiotic environmental effects at regional scales. In yeasts, we found contrasting results, namely, a high degree of community homogeneity across samples and spatial scales, similar to what has been previously reported in bacteria. These results reveal remarkable variation in the community ecology of fungi. While some guilds show little to no detectable spatial scale dependence (at least at the country-wide scale of the Czech Republic), others require spatial scale to be explicitly considered when studying their community composition and its drivers (such as dispersal limitation, soil and litter chemistry, vegetation and climate). To efficiently safeguard and understand biodiversity across different domains of life, we might need to continue to search for parallels between macro- and microbiology, and also develop an appreciation for the rich diversity within the community ecology of fungi, which seems to span both worlds, including geographic patterns well known from macro- and microorganisms.

AUTHOR CONTRIBUTIONS

Petr Baldrian and Barbara Doreen Bahnmann designed the study. Michal Tomšovský and Petr Sedlák selected the study sites. Barbara Doreen Bahnmann, Tereza Mašínová, Michal Tomšovský, Petr Sedlák and Petr Baldrian performed the sampling and sample processing. Tereza Mašínová and Tijana Martinović performed the laboratory work. Tereza Mašínová and Barbara Doreen Bahnmann performed the vegetation survey. Iñaki Odriozola and Petr Baldrian analysed the data. Iñaki Odriozola drafted the manuscript with contribution from all coauthors.

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CONFLICT OF INTEREST STATEMENT

All authors declare that there are no competing interests.

DATA AVAILABILITY STATEMENT

Sequencing data have been deposited in MG-RAST under accession code 4696490.3 and the Sequence Read Archive under accession code PRJNA873923. The R script and datasets necessary to run the analysis are publicly available in the Zenodo and Dryad (https://doi.org/10.5061/dryad.zpc866tcv) repositories, respectively.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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