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Research article

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

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

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

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

Introduction

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

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

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

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

Material and methods

Study design

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

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

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

Environmental parameters

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

Microbial sample processing

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

Response variables

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

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

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

Statistics

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

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

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

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

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

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

Results

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

Microbial richness at study-plot level

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

Microbial richness at object level

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

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

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

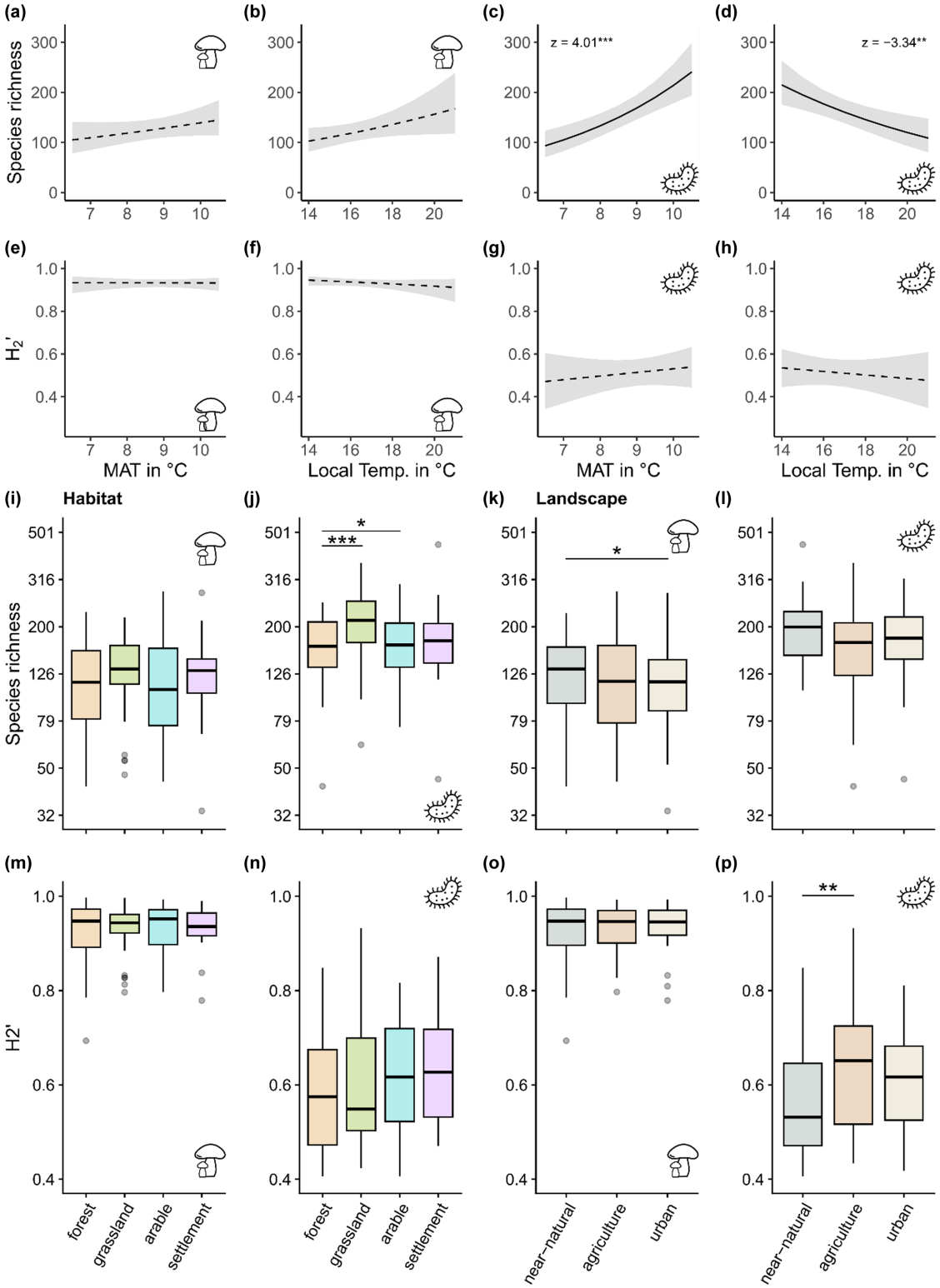

Figure 1. Regression curves showing fungal (a, b) and bacterial (c, d) species richness and community specialization (fungi: e, f; bacteria: g, h) at study-plot level predicted by the generalized linear mixed model (glmer.nb: richness; glmmTMB: specialization) and mean annual temperature (MAT; a, c,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

Community composition

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

Community specialization

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

Discussion

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

Species richness and temperature

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

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

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

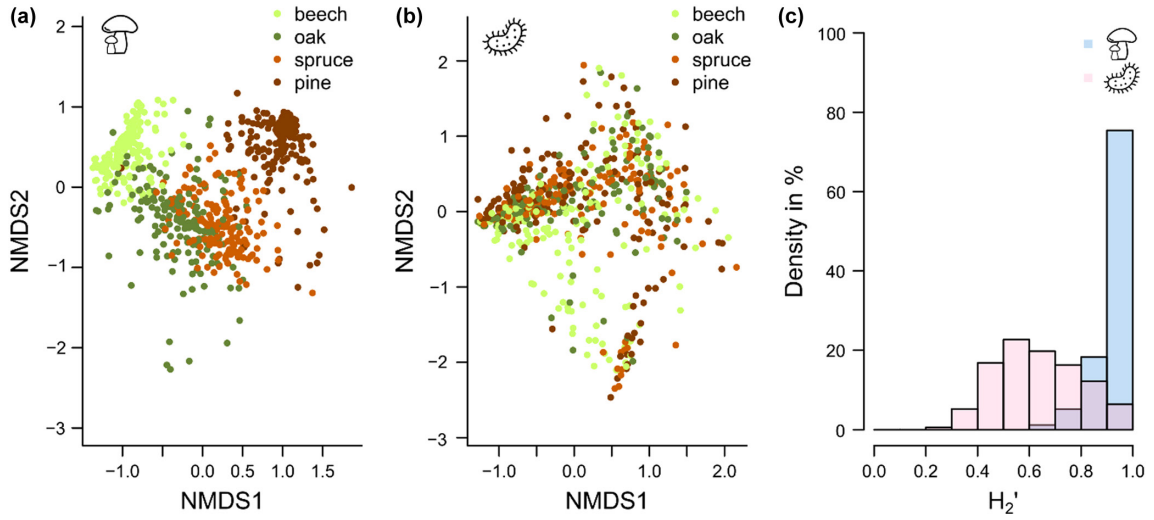

Figure 2. (a) and (b) Ordinations based on non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices (a: fungi: k = 3, stress = 0.146; b: bacteria: k = 3, stress = 0.150). Dots indicate communities in individual deadwood objects (beech: light green, oak: dark green, spruce: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

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

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

Species richness and land use

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

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

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

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

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

Specialization of communities along temperature and land-use gradients

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

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

Importance of precipitation for bacterial richness and specialization

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

Conclusions

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

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

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Author contributions

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

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Data availability statement

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

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

Supporting information

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

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