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Imprints of latitude, host taxon, and decay stage on fungus-associated arthropod communities

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Abstract

Interactions among fungi and insects involve hundreds of thousands of species. While insect communities on plants have formed some of the classic model systems in ecology, fungus-based communities and the forces structuring them remain poorly studied by comparison. We characterize the arthropod communities associated with fruiting bodies of eight mycorrhizal basidiomycete fungus species from three different orders along a 1200-km latitudinal gradient in northern Europe. We hypothesized that, matching the pattern seen for most insect taxa on plants, we would observe a general decrease in fungal-associated species with latitude. Against this backdrop, we expected local communities to be structured by host identity and phylogeny, with more closely related fungal species sharing more similar communities of associated organisms. As a more unique dimension added by the ephemeral nature of fungal fruiting bodies, we expected further imprints generated by successional change, with younger fruiting bodies harboring communities different from older ones. Using DNA metabarcoding to identify arthropod communities from fungal fruiting bodies, we found that latitude left a clear imprint on fungus-associated arthropod community composition, with host phylogeny and decay stage of fruiting bodies leaving lesser but still-detectable effects. The main latitudinal imprint was on a high arthropod species turnover, with no detectable pattern in overall species richness. Overall, these findings paint a new picture of the drivers of fungus-associated arthropod communities, suggesting that latitude will not affect how many arthropod species inhabit a fruiting body but, rather, what species will occur in it and at what relative abundances (as measured by sequence read counts). These patterns upset simplistic predictions regarding latitudinal gradients in species richness and in the strength of biotic interactions.

KEYWORDS
arthropod, decay, fruiting bodies, fungi, fungivory, fungus–insect interactions, latitudinal gradient, succession

INTRODUCTION

Ecological communities in the natural world are structured through trophic interactions—essentially, who eats whom and where (Gravel et al., 2019; Mougi & Kondoh, 2012; Pimm et al., 1991). Revealing the structure of interaction networks is therefore key to understanding how ecological communities function today. It is also essential for assessing their resilience to future changes in ecosystems (Oliver et al., 2015) and the likely consequences of species loss—such as cascading effects and secondary extinctions (Berg et al., 2015). Mapping out network structure will furthermore inform about the potential effects of climate change, including phenological switches and mismatches across trophic levels (Edwards & Richardson, 2004). From these perspectives, studies of fungus–insect interaction networks are particularly interesting because such food webs are extremely species-rich (Blackwell, 2011), represent a wide spectrum of life histories, and are often abundant and easily accessible to researchers. Yet, where plant-dwelling arthropod communities have formed a cornerstone of community ecology ever since the publication of such works as Ehrlich and Raven (1964) and Strong et al. (1984), fungus-associated communities and the forces structuring them remain poorly studied by comparison.

Three ecological forces in particular can be expected to mold networks of fungi and associated arthropods: (1) large-scale biogeographic forces such as climatic imprints and historical contingencies (Hillebrand, 2004; Peay et al., 2016; Tedersoo et al., 2014); (2) host identity and evolutionary imprints, where more closely related host species can be expected to share more similar communities of associated taxa (Jonsell & Nordlander, 2004; Orledge & Reynolds, 2005; Thorn et al., 2015); and (3) imprints of successional change, reflecting structural and chemical shifts occurring through the growth and decomposition of individual fungal fruiting bodies (Jonsell & Nordlander, 2004; Kadowaki, 2010; Klimaszewski & Peck, 1987; Midtgaard et al., 1998; but see Yamashita & Hijii, 2007). For each of these, our knowledge on fungus–insect interactions lags far behind that on plant–insect interactions (Andrew & Hughes, 2005; Komonen et al., 2003), where latitudinal patterns (Forister et al., 2015; Pennings & Silliman, 2005; Schemske et al., 2009), determinants of host-plant use and the evolution of host-plant associations (Ehrlich & Raven, 1964), and phylogenetic imprints on associations (Nylin et al., 2018; Nyman, 2010) have been studied comprehensively.

In terms of large-scale biogeographic patterns, most plants and plant-associated arthropod groups follow the general latitudinal diversity gradient (Hillebrand, 2004), with regional species richness generally declining with latitude (but see, e.g., Kouki, 1999 and Mateo et al., 2016). While the same pattern generally holds true for the fungi (Lodge et al., 1995; Tedersoo et al., 2014), some notable exceptions have been reported among soil fungi (Shi et al., 2014), as well as in the Agaricomycetes and other ectomycorrhizal taxa (Peay et al., 2016; Varga et al., 2019). Whether these parallel gradients of species diversity translate to change in either the number of interactions or the frequency of types of interaction is a more recent and controversial question (Anstett et al., 2016; Forister et al., 2015; Moles & Ollerton, 2016; Nakadai et al., 2021; Schemske et al., 2009). Comparable continental-scale analyses are still largely lacking for the arthropod component of fungus–arthropod interaction networks (Schigel, 2012), and the few studies done to date have proposed alternative patterns. Komonen et al. (2003) found that insect assemblages on three species of wood-decaying *Fomitopsis* fungi are more diverse and more compartmentalized in the north (Finland) than in the south (China). By contrast, working on the arthropod communities of a specific species of bracket fungus, *Fomes fomentarius*, Friess et al. (2019) found strong turnover in community composition across temperate Europe but little imprint of biogeography, climate, and other systematic factors. Overall, Friess et al. (2019) concluded that fungal fruiting bodies represent similar habitats across large environmental gradients.

In terms of phylogenetic imprints, studies on plant–insect networks have revealed the average herbivore to be fairly specialized in its use of available plant species (Novotny et al., 2002, 2006; Weiblen et al., 2006). Among plants, closely related taxa tend to share a more similar herbivore fauna (Bernays & Graham, 1988; Forister et al., 2015; Mertens et al., 2021; Volf et al., 2017). These patterns are usually attributed to interspecific differences in plant ecological, morphological, phenological, and chemical properties and phylogenetic conservatism in these traits (Futuyma & Agrawal, 2009; Weiblen et al., 2006). Among fungi, one feature that has been shown to affect fungivore community composition is the morphological and structural divide between the hard, perennial fruiting bodies produced by many polypores and the soft and short-lived fruiting bodies produced by many other basidiomycetes such as agarics (e.g., fungi characterized by stipes and caps) (Hanski, 1989; Jakovlev, 2012; Orledge & Reynolds, 2005; Schigel, 2012; Thorn et al., 2015). Within these main types of fruiting bodies, fungivore specialization on single host species appears to be rare (Epps & Arnold, 2018; Ståhls et al., 1989), with some signs of genus-level host specialization (Kobayashi & Sota, 2021; Põldmaa et al., 2016; Tuno et al., 2019).

Both plants and fungi may be characterized by patchy occurrence (e.g., Dixon et al., 1987) and seasonal variation in availability (e.g., Stinson & Brown, 1983). Nonetheless, one important dimension does separate fungi from plant foliage as a resource, that is, quick changes in resource properties. Here, we refer to more dramatic changes than those occurring in the chemistry of maturing plant foliage (e.g., Salminen et al., 2004): in ephemeral mushrooms, an active growth stage is followed by more or less extended, microbially driven decomposition, ultimately converting the originally solid structure into a runny substrate dominated by bacterial cells (Hackman & Meinander, 1979; Krivosheina, 2008). This phase may typically take days or weeks but can be as short as hours in small saprotrophic basidiomycetes. The shifts in the properties and quality of fruiting bodies are akin to those exhibited by dung and carrion, in which gradual decay is reflected as successional change in associated communities of, for example, beetles and dipterans (Gittings & Giller, 1998; Hanski, 1980). As a general rule, younger fruiting bodies tend to host communities of specialized fungivores (Hanski, 1989; Jonsell & Nordlander, 2004; Lipkow & Betz, 2005; Yamashita et al., 2015, but see Jonsell et al., 2016), while fruiting bodies at an advanced stage of decay may be colonized by generalist taxa that are also able to utilize other substrates. Such opportunistic late-stage fungivores include, for example, flies in the family Fanniidae, the ubiquitous house fly *Musca domestica* (Krivosheina, 2008), and even *Nicrophorus* carrion beetles (Nikitsky & Schigel, 2004).

In this study, we aim to resolve the relative imprint of key structuring forces among arthropods on ephemeral, soft, and short-lived mushrooms. For this purpose, we utilize DNA metabarcoding to resolve the effects of latitude, host identity and phylogeny, and the age (decay stage) of the fruiting body on the diversity and community composition of associated arthropods. We characterize the arthropod communities associated with fruiting bodies of eight mycorrhizal basidiomycete fungus species from three different orders along a 1200-km latitudinal gradient in northern Europe. By applying multivariate statistical methods to these data, we partition the amount of variation into each of these factors, and pose the following questions: (1) How does species richness and community structure vary with latitude? (2) How large is the effect of the identity of the host species and of the phylogenetic relatedness among hosts? (3) How large is the effect of the age (decomposition stage) of individuals within host species? A priori, we hypothesize that (i) overall arthropod species richness decreases with increasing latitude; (ii) the arthropod communities of more closely related host taxa are more similar to each other than to distantly related host taxa; and (iii) the decay stage significantly affects the composition of arthropod communities.

MATERIALS AND METHODS

Sampling design and sample collection

Adopting a factorial design, we sampled mushroom fruiting bodies of a replicate set of fungal species from a total of 11 sites from southern Estonia to northernmost Finland (Figure 1; Appendix S1: Table S1). The sites span a roughly 1200-km climatic and vegetational gradient in the boreal ecotone, from broad-leaved deciduous forests in the south via conifer-dominated taiga forest to low arctic woodlands in the north. From south to north, the sites represent the hemiboreal (three sites), southern boreal (two), middle boreal (three), and northern boreal (two) zones, as well as one northern boreal–arctic site.

Across sites, we targeted eight species of mycorrhizal basidiomycete fungi, which were chosen on the basis of being (i) large and easily identifiable, (ii) representative of different levels of relatedness across the basidiomycete phylogeny, and (iii) widespread and common. These criteria were fulfilled by *Lactarius trivialis* and *Lactarius turpis*, *Russula vinosa* and *Russula decolorans* (Russulales), *Cortinarius caperatus* and *Cortinarius armillatus* (Cortinariales), and *Leccinum scabrum* and *Leccinum versipelle* (Boletales).

Fungal fruiting bodies were collected by local mushroom enthusiasts with known and good identification skills. Collectors were instructed to collect samples from a site where the eight focal species could be found in preferably less than 4–6 h. From each site we aimed at collecting one fruiting body representing each of the five decay stages defined by Hackman and Meinander (1979) for each species. Because of the long north–south gradient involved, the sampling date at each location was adjusted to the site-specific peak harvest from late August to mid-September 2017. Samples were individually placed in labeled sealable bags, frozen, and transported to the University of Helsinki, Finland, for further processing.

DNA extraction, metabarcoding PCR, and high-throughput sequencing

Prior to extraction, samples were thawed and larger fruiting bodies were split into several subsamples. We extracted DNA from the samples following the salt–isopropanol protocol described in Koskinen et al. (2019) but applied dual solid-phase reversible immobilization (SPRI) bead purification (DeAngelis et al., 1995; Vesterinen et al., 2018) on 96-well plates. Thus, a first

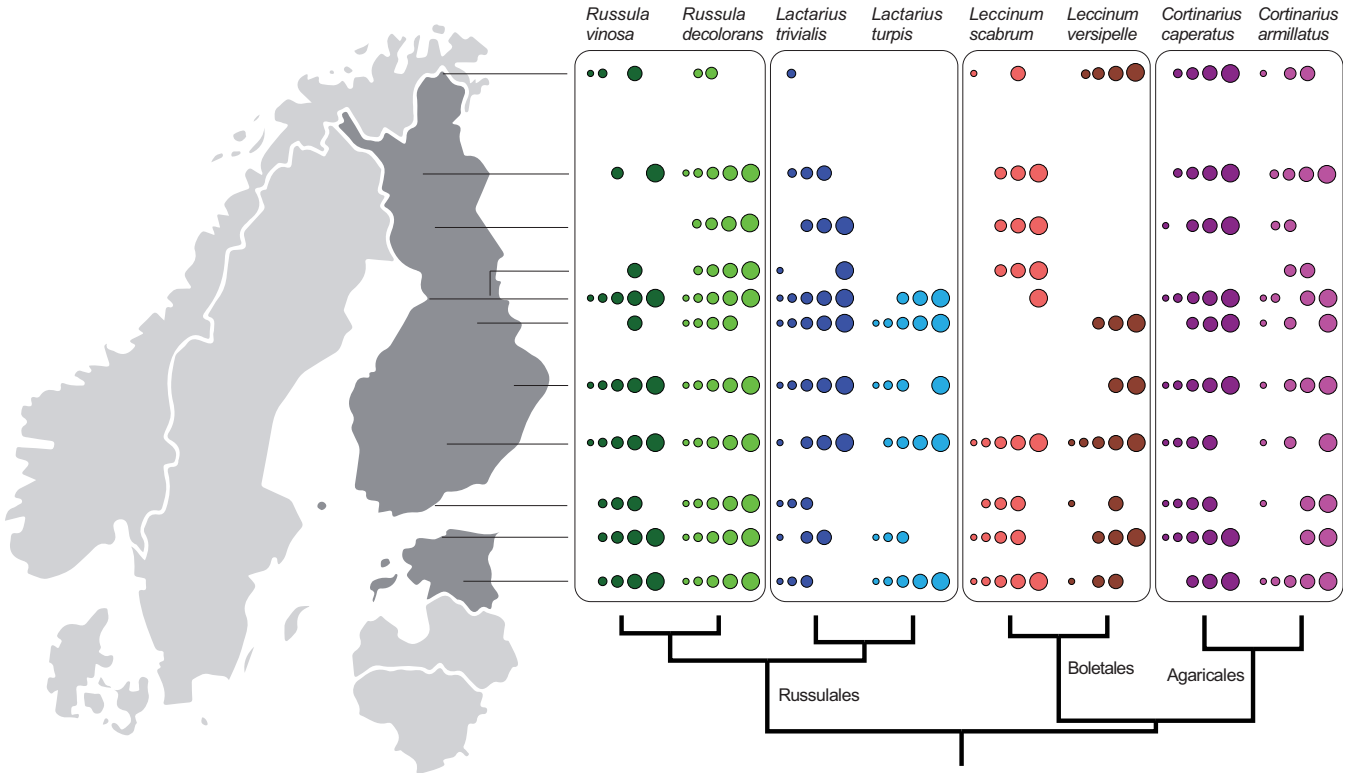

FIGURE 1 Sampling design of our study. Sampling sites along the latitudinal gradient are indicated on the map on the left. Fruiting bodies representing the eight fungal host species are shown as circles, with increasing circle size denoting the five decay stages from least to most decayed. The ultrametric phylogenetic tree of the focal host species is shown under the taxon plot

purification with a 2.0× SPRI bead volume ratio in relation to the sample volume was followed by a second round with a 1.2× ratio. This adjusted protocol enhances DNA purity compared to our earlier approach (Koskinen et al., 2019) with single-step purification. Sterile water samples were included as blank controls in each extraction and purification batch.

To verify the detectability of species present in the samples conditional on the methods employed, as well as to assess polymerase chain reaction (PCR) success and the presence of cross-contamination and tag jumping (also known as sample cross-talk or index leaking), we constructed and purified a mock community consisting of 10 nontarget species representing 9 families in 7 insect orders: *Lasiommata megera* (Lepidoptera, Nymphalidae), *Acheta domesticus* (Orthoptera, Gryllidae), Phasmatidae sp. (Phasmatodea), *Blaptica dubia* (Blattodea, Blaberidae), *Thermobia domestica* (Zygentoma, Lepismatidae), *Parasyrphus tarsatus* (Diptera, Syrphidae), *Drosophila melanogaster* (Diptera, Drosophilidae), *Coelichneumonops occidentalis* (Hymenoptera, Ichneumonidae), and *Euura* sp. (Hymenoptera, Tenthredinidae). DNA extract concentrations were measured with Qubit double-stranded DNA (dsDNA) high-sensitivity (HS) assay (ThermoFisher Scientific), and mock species extracts were combined into an equibalanced 0.45 ng/µl mock pool, of which 48 µl was further purified along with research samples; 2 µl of the purified pool was used as a template for each mock-community PCR.

In our earlier work (Koskinen et al., 2019), we used a short, 157-bp fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene to identify arthropod communities in fungal samples. In this study, we aimed for increased identification resolution by using a longer fragment with a wider taxonomic coverage, so we applied the more degenerate primers mlCOIIntF (5′-GGWACWGGWTGAACWGTWTAYCCYCC-3′; Leray et al., 2013) and jgHCO2198 (5′-TAIACYTCIGGRTGICCRAARAAYCA-3′; Geller et al., 2013) to amplify a 313-bp region of the COI gene. Our PCR amplification protocols followed those of Vesterinen et al. (2018), with study-specific details as follows. For the first, locus-specific PCR, we used a reaction volume of 10 µl, including 5 µl MyTaq HS Red Mix (BIO-25048, Bioline, UK), 2.6 µl of H_2O, 0.2 µM of each primer, and 2 µl of DNA extract. The PCR cycling conditions were as follows: 1 cycle of 95°C for 5 min; 16 cycles of 95°C for 10 s, 61°C for 30 s with a 1°C step-down per cycle, and 72°C for 1 min; 20 cycles of 95°C for 10 s, 46°C for 30 s, and 72°C for 1 min; 1 cycle of 72°C for 10 min; then hold at 4°C. Sterile water samples were used in each batch as blank PCR controls.

Two replicate metabarcoding plate sets were made of 341 samples from 295 unique fruiting bodies, 4 blank extraction controls, 3 blank PCR controls, 5 blank purification controls, and 4 mock-community extracts. Our barcoding primers were tagged with linkers, so that Illumina-specific adapters and sample-specific indices could be added in a second, library-preparation PCR (Vesterinen et al., 2018). To improve sequencing output by increasing DNA library diversity, we also included different heterogeneity spacers (Fadrosh et al., 2014) in the linker sequences of the first and second plate sets (0 = no spacer and 2 = TC, and 1 = C and 3 = ATC, respectively). Each reaction was dual-indexed with a unique combination of forward and reverse index (Vesterinen et al., 2018). Library preparation followed Vesterinen et al. (2016) with minor modifications: For a reaction volume of 10 μl, we mixed 5 μl MyTaq HS Red Mix, 0.3 μM of each index, and 2.6 μl locus-specific PCR product, filling to 10 μl with H_2O. The PCR cycling conditions were 95°C for 5 min, then 15 cycles of 95°C for 20 s, 60°C for 15 s, and 72°C for 30 s, followed by 72°C for 5 min. After indexing, the 96-well plates were combined into two replicate pools that were purified using SPRI dual library purification (Vesterinen et al., 2018). After measuring DNA concentrations using Qubit dsDNA HS assay, an equal amount of DNA from each pool was combined into a final master library that was sequenced in a MiSeq v3 2×300 run at the Biomedicum Functional Genomics Unit (FuGU) of the University of Helsinki.

Bioinformatics and data processing

The Illumina sequencing yielded 16,280,608 paired-end reads identified to samples with unique dual-index combinations. Trimming and quality control of the sequences were conducted according to Vesterinen et al. (2018). Consequently, paired-end reads were merged and trimmed for quality using USEARCH with the "fastq_maxee_rate" algorithm with threshold 1 (Edgar, 2010). After merging and quality trimming, 15,773,967 reads remained. Primers were removed using the Python program Cutadapt (Martin, 2011), allowing 20% mismatches and with the minimum length set to 100 bp. Primers were found from 99.6% of the reads, of which 14,423,305 were long enough to be retained for the next steps. In the next steps, reads were dereplicated using the USEARCH "fastx_uniques" algorithm with option "minuniquesize 10" (72,633 uniques), and these unique reads were clustered into 3516 zero-radius operational taxonomic units (ZOTUs, Edgar, 2016) (deposited in Dryad: https://doi.org/10.5061/dryad.cjsxksn5d) using the USEARCH "UNOISE3" algorithm. Finally, reads were mapped back to the original trimmed reads to establish the total number of reads in each sample using the USEARCH "usearch_global" algorithm (~93% successfully mapped).

We identified ZOTUs to taxa following the approach of Vesterinen et al. (2016) by applying custom bash scripts utilizing the BOLD systems (Ratnasingham & Hebert, 2007) application programming interface (API) (Vesterinen et al., 2021; Data S1:BOLD_script.txt). To construct the final fruiting body × arthropod species matrix, we first removed nontarget taxa such as fungi and bacteria. We then removed all arthropod taxa with under 97% similarity to any reference database sequence. Next, we kept ZOTUs ≥ 292 bp long with a greater than 98.0% similarity to sequences in the reference database. Finally, we combined into single taxa synonymous barcode index numbers (BINs) as well as ZOTUs with a ≤2% distance to each other.

All mock species were found in the mock-community samples. The *Euura* mock sample was a larva that incidentally was parasitized by *Ichneutes* sp. (Hymenoptera, Ichneumonidae), but this was detected only after sequencing the final library pool. To estimate the proportion of reads that could have been misassigned during index demultiplexing (known as "tag jumping" or "sample cross-talk"), we calculated the proportion of mock reads out of the total number of reads per nonmock sample. This revealed a tag jumping rate of below 0.5%, so we subtracted 0.5% of the total read sum of each ZOTU from each sample-specific read number for that ZOTU, with a minimum of zero. We summed up reads of all taxa across subsamples representing the same fruiting body. To account for potential contamination, we calculated the maximum read number per ZOTU across all negative controls and subtracted that from other read values for that ZOTU (with a minimum of zero). Finally, we removed 24 zero-read fruiting bodies as well as one sample that was judged to be contaminated due to an aberrantly high number of species. The final data matrix consisted of 5,442,060 reads representing 229 arthropod taxa in 270 fruiting bodies (deposited in Dryad: https://doi.org/10.5061/dryad.cjsxksn5d).

Host phylogeny

We constructed a phylogenetic tree for the focal fungal host species based on the ten 5284-taxon FastDate chronograms provided by Varga et al. (2019). We first pruned each tree down to eight species using the ape v.5.2. package (Paradis & Schliep, 2019) in R (R Core Team, 2020), and then calculated a consensus tree with median node heights using the TreeAnnotator utility of BEAST v.2.6.2 (Bouckaert et al., 2019). *R. decolorans*, which was not present in the chronograms, was placed in the location of the related *Russula cessans*.

Statistical analyses

Metrics of arthropod abundance and distribution

In analyzing the communities of fungus-associated arthropods, we are here confined to DNA data. Thus, our focal responses relate to the occurrence and relative abundances of DNA sequences assignable to particular arthropod taxa. Naturally, such metrics will depart from traditional counts of arthropod individuals. Arthropods of different size, integument strength, and mitochondrial densities, for example, as well as taxa with different affinities for exact primers, are likely to produce different read counts per individual and per unit biomass (Elbrecht & Leese, 2015; Marquina et al., 2019; Piñol et al., 2019). However, we see no reason why this fact would compromise ecological analyses across gradients in space or time. As long as biases remain consistent across the gradient, then changes in relative abundances or read counts should be just as reflective of ecological patterns as, say, changes in traditional insect counts (Abrego et al., 2021; Ji et al., 2020). With this reasoning in mind, we will—for simplicity—next refer to data on DNA attributable to a given taxon as data on species occurrence, and data on relative read counts as data on species abundance. We stress that the units are fundamentally different, whereas the ecological inference built on the respective units is not.

Data visualization

We first visualized overall variation in the arthropod communities of individual fruiting bodies using nonmetric multidimensional scaling (NMDS) ordination by applying the "metaMDS" function in the vegan package v. 2.5–6 (Oksanen et al., 2020) in R (Data S2: NMDS_script.R). The ordination was based on Bray–Curtis dissimilarities across a matrix of relative read counts. Samples with zero species-level arthropod ZOTUs ($n = 14$) were excluded from the analysis, and, owing to the high stress values in two dimensions, the analysis was run for 4000 iterations in three dimensions. The results were visualized with R packages ggplot2 (Wickham, 2016) and dichromat (Lumley, 2013).

The relationship between arthropod community structures at the level of host fungal species and the phylogenetic relationships among the hosts was visualized using the Interactive Tree Of Life (iTOL) v.4 online tool (Letunic & Bork, 2019) (Data S3: Heatmap_script.txt). Species-level community structures were calculated by summing up the read numbers of each associate species across conspecific fruiting bodies and then converting the sums to proportions of the total number of reads within the host species (deposited in Dryad: https://doi.org/10.5061/dryad.cjsxksn5d).

Species accumulation rates

With more fruiting bodies inspected, we will detect increasing numbers of associated taxa. We first estimated sampling effects for arthropod species richness within each fungal species by fruiting-body rarefaction within the vegan R package. However, the overall accumulation of new arthropod species with increasing numbers of fruiting bodies examined can be split into components reflecting the contribution of including new locations, host species, and decay stages. To reveal their respective effects, we performed explicit sequential resampling of fruiting bodies from our data matrix. Starting from a random fruiting body, we added fruiting bodies from the same or different reference groups, resampling each chain 1000 times or until all potential combinations had been sampled. These analyses were performed using custom R scripts (Data S4: Resampling_script.Rmd), and results were visualized using the ggplot2 R package.

First, to measure host species effects, we resampled fruiting bodies within a site, adding further fruiting bodies from (i) the same host species, (ii) a different species from the same host genus, and (iii) across all host species, adding new species not already present in the particular sampling chain. Second, to examine the effect of including further sites, we resampled within the same host species, starting from a randomly selected fruiting body and adding fruiting bodies from (i) the same site and (ii) from all sites, adding sites not already present in the sampling chain. Third, to examine differences between decay stages, we resampled within species by adding further fruiting bodies from (i) among decay stages within sites, (ii) among sites and decay stages, and (iii) among sampling sites within decay stages.

Variance partitioning and predicting latitudinal and decay-stage trends

To more formally quantify the contributions of latitude, host phylogeny, and host decomposition stage on fungus-associated arthropod communities, we used joint species distribution modeling (Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017) with the Hmsc R package (Tikhonov et al., 2020). For computational reasons, we included only those arthropods that occurred in at least 5 fruiting bodies in the data (134 out of 229 species). Because the data were dominated by zeros and there was

little variation in abundance, we applied the following hurdle-type models: we modeled the presence–absence data with probit regression and the abundances (i.e., sequence counts) conditional on presence using a log-normal model. As fixed explanatory variables, we included the latitude where the fruiting bodies were collected from and their decay stage as continuous variables. We also added second-order terms of these variables to allow for unimodal responses (i.e., to allow for nonlinear responses). As a measure of observation effect, we included the total number of ZOTU reads per sample as a log-transformed continuous explanatory variable. This term adjusts for the fact that the number of reads may vary not only with the abundance of a species but also with, for example, the total biomass of a particular fruiting body. Thus, it makes it possible to separate the effect of focal variables from that of sequencing depth as such. As random effects, we included the localities where the fruiting bodies were collected from and the phylogenetic relationships among the host fungi, assuming a nested structure with the levels of species, genus, and order.

In the analyses (Data S5: HMSC_script.R), we assumed the default prior distributions and applied the Markov chain Monte Carlo (MCMC) scheme of the R package Hmsc (Tikhonov et al., 2020). We sampled the posterior distributions with four chains. We run each chain for 375 × thin iterations, of which we discarded 125 × thin as burn-in and thinned the remaining ones by the thinning factor thin to result in 250 samples per chain and, thus, 1000 samples in total. We increased the thinning factor as thin = 1, 10, 100, ..., until we reached satisfactory MCMC convergence, which we considered as having taken place when the potential scale reduction factor was smaller than 1.05 for all of the beta parameters that measure the responses of the species to the environmental covariates (Tikhonov et al., 2020). This was reached with thin = 1000 for the presence–absence model and thin = 100 for the abundance model.

We calculated the explanatory power of the presence–absence and abundance models by calculating Tjur's (2009) coefficient of discrimination and the R^2 coefficient of determination, respectively, and applied a variance-partitioning approach to evaluate the proportion of variance attributable to each of the explanatory variables. In interpreting the results, we point to two caveats. First, the explanatory power of the presence–absence versus abundance models are quantified by different metrics and are thus not directly comparable since traditional R^2 values are invalid for presence–absence data (Tjur, 2009). Second, the variance explained by a given explanatory variable can be characterized in two different ways: as the proportion of all variation or as the proportion of all variation explained. Since variance explained will always be a subset of total variance, a proportion out of variance explained will always be higher than a proportion out of all variance. From the fitted models, we predicted how arthropod species richness and abundances varied along with latitude and decay stage of the fruiting body using the constructGradient function of the Hmsc package by setting all of the nonfocal variables to their means over the data.

Beta-diversity partitioning

Finally, to test the significance of community change across latitudinal, phylogenetic, and decay-stage gradients, we constructed distance–decay plots in which pairwise differences in species composition among fruiting bodies were plotted against their distance in terms of the three focal factors. We followed the beta-diversity partitioning framework of Baselga (2010) to separate the overall beta diversity (variation in arthropod species composition across fruiting bodies) into its turnover (species replacement) and nestedness (species loss or gain) components (Data S6: Beta_diversity_script.R).

Overall beta diversity was measured by calculating the Sørensen dissimilarity between fruiting-body pairs, the turnover component was measured by calculating the Simpson dissimilarity between samples, and the nestedness component was the difference between the former two (Baselga, 2010). Distances in latitude, phylogeny, and decay stage were all characterized by continuous metrics—latitudinal distance among fruiting bodies was measured as the Euclidean distance between the latitudes from where the samples had been collected. Phylogenetic distance was calculated by converting the aforementioned ultrametric phylogenetic tree of the fungal host species into a phylogenetic correlation assuming a Brownian model with the phytools (Revell, 2012) R package. Differences in fruiting-body decay stages were measured by calculating the Euclidean dissimilarity among samples. We then constructed linear models for quantitatively assessing how the overall beta diversity and its turnover and nestedness components varied across the different measures of distance.

Note that in these linear models, each data point consists of a pair of samples, so the data points are not independent of each other, rendering the standard test of statistical significance invalid. For this reason, we tested for the significance of the linear models by applying a permutation test where we compared the observed *t*-values to the null expectation based on 1000 permutations among the sampling units. Since the observed value was compared to the distribution generated by explicit permutations, it was independent of assumptions regarding the theoretical distributions of the test statistic or its degrees of freedom.

Importantly, the beta-diversity partitioning provides an analysis complementary to the Hmsc analyses outlined earlier, since in partitioning the beta diversity we focused on the total rather than marginal effect of each variable. For example, when analyzing how the Sørensen similarity depends on spatial distance, the marginal effect would describe how Sørensen similarity changes if only spatial distance changes, whereas other factors remain unchanged. In contrast, the total effect described here shows how Sørensen similarity changes when spatial distance changes along with a change in other factors. Thus, where the Hmsc analyses specifically examine marginal effects through a model that simultaneously controls for all the environmental and spatial variables, the approach of Baselga (2010) describes the effect of concerted change.

RESULTS

Diversity and overall similarity

The final species-level data matrix across the 270 fruiting bodies of the 8 focal basidiomycete species consisted of 229 arthropod taxa (deposited in Dryad: https://doi.org/10.5061/dryad.cjsxksn5d). The associates represented 90 dipteran, 40 coleopteran, 16 hymenopteran, 4 hemipteran, 3 psocopteran, and 2 mecopteran insect species, in addition to 35 collembolan, 34 acarid, 1 arachnid, 1 opilionid, 2 diplopod, and 1 symphylan species (Appendix S1: Figure S1). The 155 insect species observed represent 41 families, of which the Staphylinidae (Coleoptera), Mycetophilidae (Diptera), and Ichneumonidae (Hymenoptera) were the most diverse. In terms of number of reads, the most common families were the dipteran families Mycetophilidae, Anthomyiidae, Limoniidae, and Phoridae and the coleopteran family Staphylinidae. On average, 10.68 arthropod species (standard error of the mean [SEM] = 0.47; range 0–41) were found per fruiting body, while the total number of taxa observed per mushroom species ranged from 60 in *C. armillatus* to 162 in *R. decolorans* (mean total arthropod species per host species = 111.50, SEM = 12.61) (Appendix S1: Figure S2).

Arthropod communities showed substantial overlap across fungal host species (Figure 2, Appendix S1: Figure S1). However, the overlap in NMDS ordination space (Figure 2) is largely caused by wide dispersion of *Cortinarius*-associated community samples, while the associated communities of *Leccinum*, *Russula*, and *Lactarius* species were clearly grouped according to genus. By contrast, no clustering was evident in terms of latitude or decay stage (Appendix S1: Figure S3).

Sequential resampling of conspecific fruiting bodies within sites showed no discernible difference in terms of accumulation of arthropod species richness as compared to resampling across all host taxa within sites, and the same held true also for sampling pairs of congeneric hosts (Appendix S1: Figure S4a). Likewise, adding conspecific fruiting bodies from one and the same site provided results very similar to those obtained by adding conspecific fruiting bodies across all sites (Appendix S1: Figure S4b). Turning to the potential imprint of decay stage, the effect of adding fruiting bodies among decay stages within host species and sites was very similar to that of adding fruiting bodies from the same host but among sites and decay stages—a pattern repeated when adding fruiting bodies within decay stages and host species, but among sites (Appendix S1: Figure S4c).

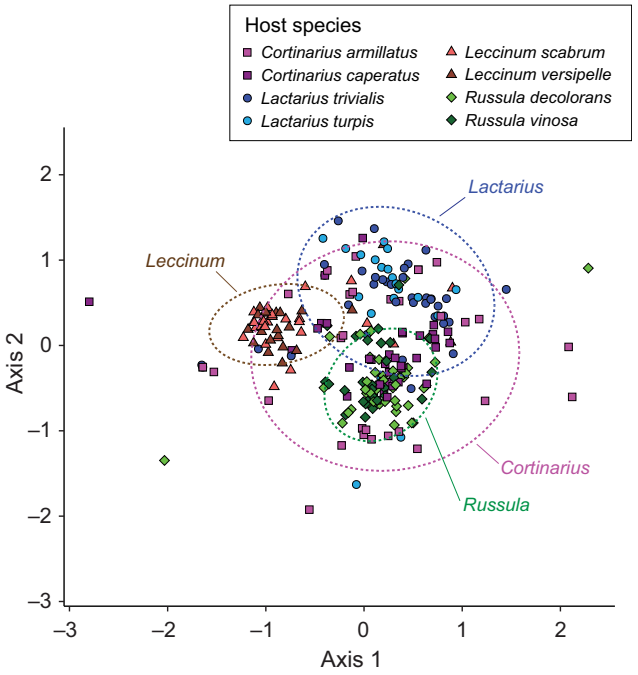

FIGURE 2 Nonmetric multidimensional scaling ordination of individual fungal fruiting bodies based on Bray–Curtis dissimilarities among their arthropod communities. Symbols denote fungal genera and are colored by host species. Circles in the plot represent 95% confidence intervals at the level of host genera. Final stress = 0.22

Variance partitioning and predicting latitudinal and decay-stage trends

Overall, the joint species distribution models of presence–absence (Figure 3a) and abundance conditional on presence (Figure 3b) explained 12.4% and 61.1%, respectively, of all variation in the response. Latitude explained 2.1% and 5.4% of all variation in the presence–absence and abundance models, respectively (with the

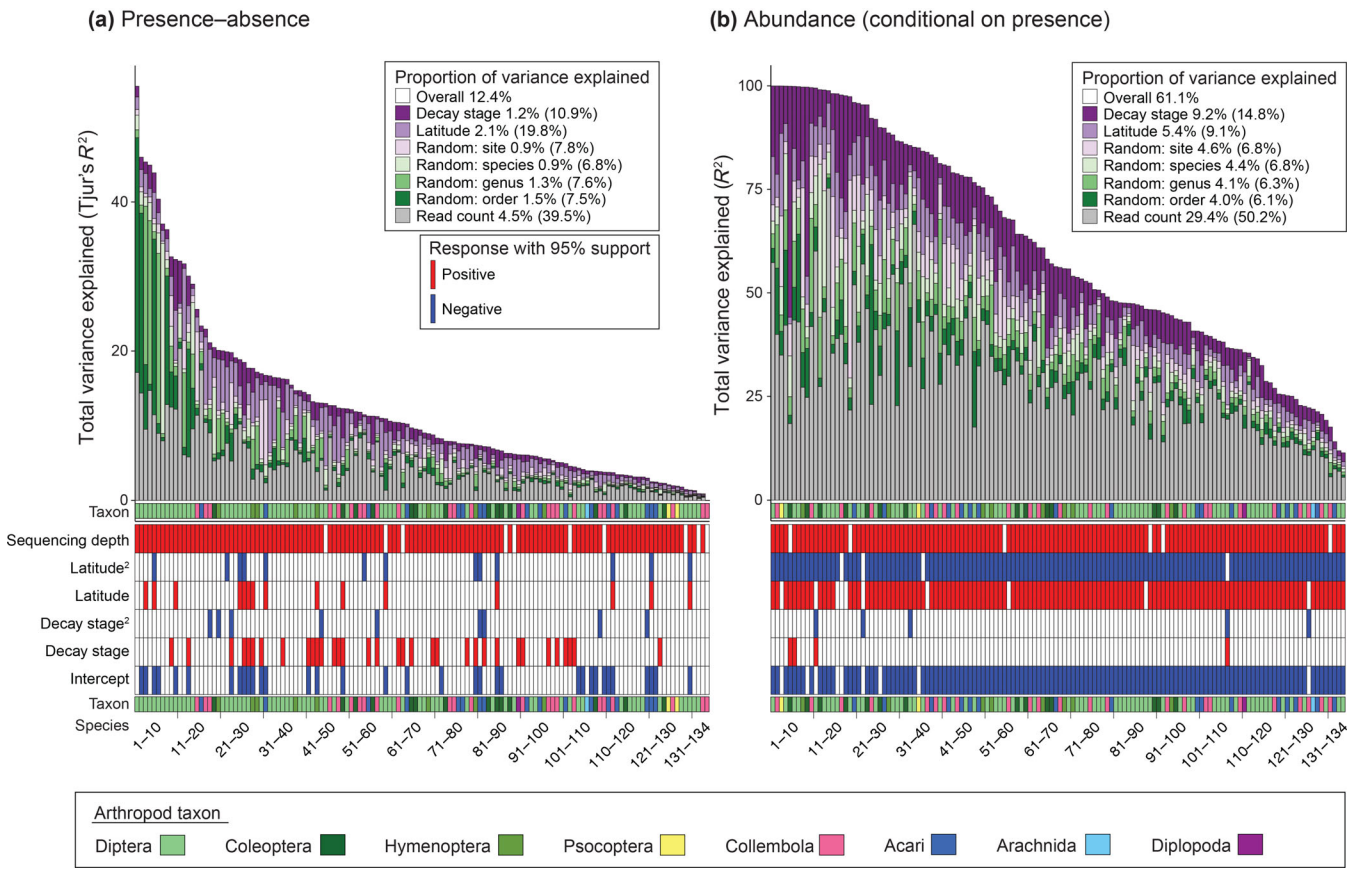

FIGURE 3 Variance-partitioning and parameter-estimate plots for (a) presence–absence and (b) abundance conditional on presence joint species distribution models. In the upper variance-partitioning parts, each bar represents an arthropod species, ordered in descending order according to the absolute variance explained by the models. Heights of subsections within bars indicate the proportion of variance explained by different explanatory variables, and the arthropod taxa are indicated below the bars (see legend). The relative amount of variance (averaged over the species) explained by each of the variables included in the models is shown in the figure legends (numbers in parentheses show the corresponding proportions of the total variance explained by the model). The lower parameter-estimate plots indicate the sign of regression parameters measuring species-specific responses to sequencing depth and the environmental covariates included the two models. Bars representing species are in the same order as in the variance-partitioning plots, and the red and blue colors indicate positive and negative responses with at least 95% posterior support, respectively. Species numbers under the lower taxon indicator stripes correspond to the numbers used in Appendix S1: Figure S5a,b, which show the names of the associate taxa

corresponding proportions out of the explained variation being 19.8% and 9.1%). Sequencing depth accounted for 4.5% and 29.4% of the total variation in the presence–absence and abundance models, and for 39.5% and 50.2% of the variation explained by the two models, respectively. Host species and taxonomy (genus and order) collectively explained 3.7% of the variation in the presence–absence model and 12.5% in the abundance model, with the proportions of explained variation being 21.9% and 19.2%, respectively. In the presence–absence model, order and genus were the most important taxonomic levels, while species explained the highest amount of variance in the abundance model. Noticeably, in the presence–absence analysis, the associated species with the highest overall R^2 values had high proportions of host taxonomy components and represented mainly dipteran fungivore groups (Figure 3a). Decay stage explained more variation in species abundances than in presence–absences (9.2% vs. 1.2% for total variation; 14.8% vs. 10.9% for explained variation). Finally, site-level random effects explained 0.9% and 4.6% of the total, and 7.8% versus 6.8% of explained, variation in the presence–absence and abundance models, respectively.

The effect of different imprints can be gleaned from the regression parameters of the fitted Hierarchical Modeling of Species Communities (HMSC) models. As expected, sequencing depth had a positive effect on nearly all species in both the presence–absence (Figure 3a) and abundance (Figure 3b) models. By contrast, the two models revealed differing responses to the environmental covariates: The occurrences of nearly half of the focal arthropod species increased with decay stage

(regression parameters for the first-order term were positive with 95% posterior support), while latitude influenced only some species (Figure 3a). By contrast, decay stage did not have a general effect on abundance conditional on presence, while abundances commonly peaked at intermediate latitudes (regression parameters for the first- and second-order terms were positive and negative, respectively, with 95% posterior support) (Figure 3b).

Community-level predictions based on the parameterized joint species distribution models showed that arthropod species richness per fruiting body did not vary across latitudes (Figure 4a) but increased along with the decay stage of the fruiting body (Figure 4b). In addition, abundance showed a slight peak at intermediate latitudes and decay stages (Figure 4c,d).

Beta-diversity partitioning

Partitioning the variation in arthropod community composition among individual fruiting bodies across latitudinal, phylogenetic, and decay-stage gradients showed that overall beta diversity was generally high and mainly reflected turnover rather than loss or gain of species: The mean overall beta diversity was 0.88, out of which on average 0.8 was attributed to species turnover and only 0.08 to nestedness (Figure 5). The dissimilarity of arthropod communities among fruiting bodies increased along with geographic distance; the pattern mostly reflected species turnover, while differences in nested species richness were weakly but statistically significantly negatively correlated with distance (Figure 5a). Community dissimilarity was also associated with the phylogenetic distance among fruiting-body pairs (Figure 5b), again due to slightly increasing differences in species composition. Finally, overall beta diversity among fruiting bodies increased along with dissimilarity in decay stage, but in this case the effects of the turnover and nestedness components were statistically nonsignificant when analyzed separately (Figure 5c).

DISCUSSION

In this paper, we investigated the arthropod communities inhabiting the ephemeral fruiting bodies of eight species of basidiomycete fungi across a 1200-km north–south gradient. Using metabarcoding, we identified 229 arthropod taxa

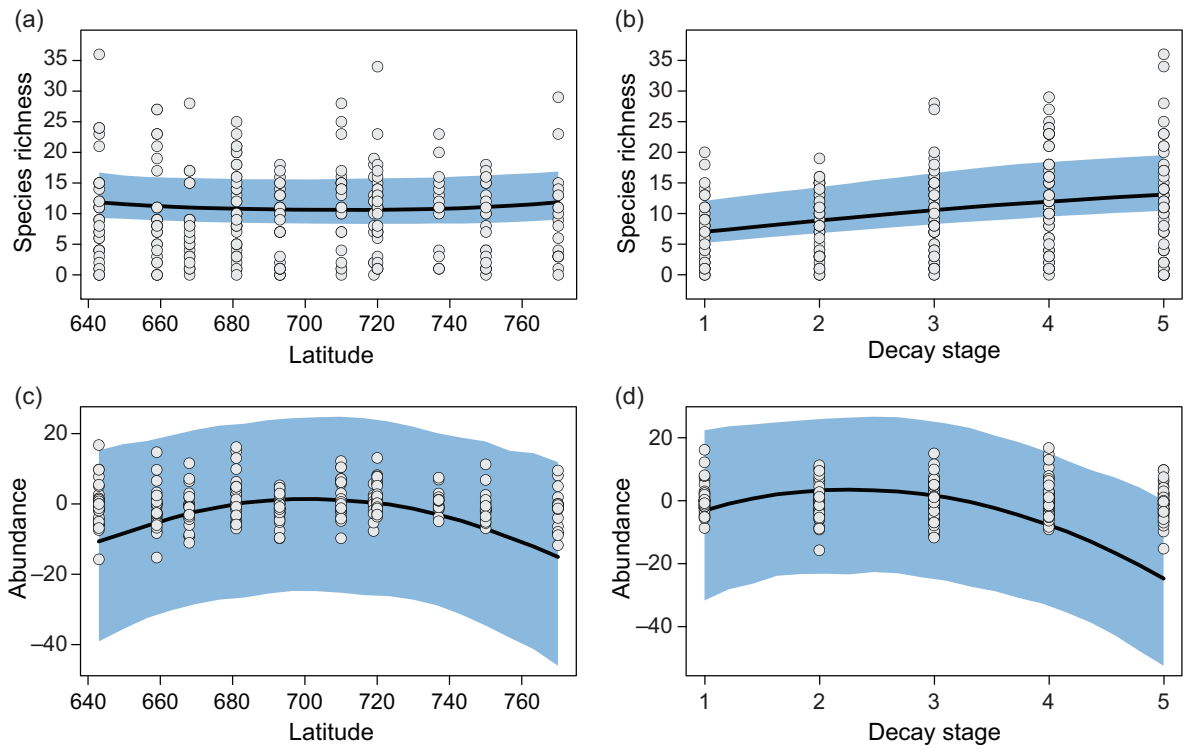

FIGURE 4 (a, b) Predicted arthropod-associated species richness and (c, d) summed abundance conditional on presence per fruiting body in relation to latitude and decay stage based on fitted joint species distribution models. The lines show the predicted relationship, the shaded areas the 95% credible intervals of the predicted relationship, and the dots the raw data. The predictions were generated with the constructGradient function of the Hmsc R package by setting nonfocal variables to their means over the data. The posterior probability by which the response variable (i.e., the variable on the *y*-axis) is higher for the highest value of the predictor variable (i.e., the variable on the *x*-axis) than for the lowest value of the predictor variable is (a) 0.46, (b) 1.00, (c) 0.61, and (d) 0.03

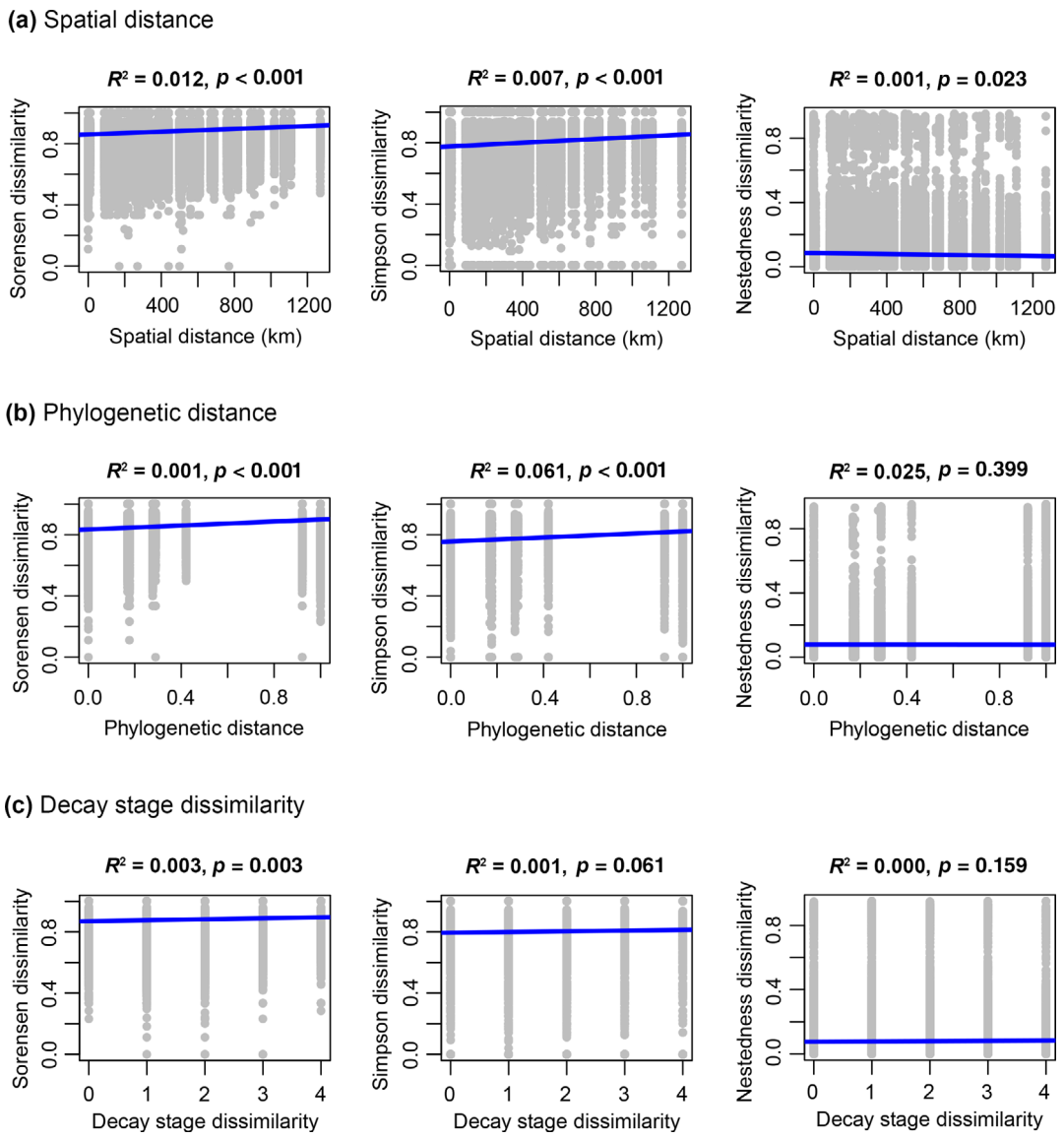

FIGURE 5 Distance–decay plots for arthropod community similarity among fungal fruiting bodies along gradients of (a) spatial distance, (b) phylogenetic distance, and (c) decay-stage dissimilarity. The first column shows overall beta diversity (measured as Sørensen dissimilarity), the second its turnover component (Simpson dissimilarity), and the third its nestedness component (difference between Sørensen and Simpson dissimilarities). Gray dots are community dissimilarity values of individual fruiting-body pairs; the blue lines show the linear regression between community dissimilarity and the focal gradient. The coefficient of determination and statistical significance of each regression analysis is shown above the corresponding panel

from 270 fruiting bodies and then examined and partitioned the variation observed into components related to latitude, host identity and phylogeny, and the decay stage of the fruiting body. We found a clear effect of latitude and host phylogeny on arthropod species turnover, whereas overall species richness remained remarkably stable over the latitudinal gradient. Decay stage had a detectable impact on overall dissimilarity in community structures, but this effect was weak and hard to partition among its nestedness and species turnover components. The abundance of arthropods peaked at intermediate latitudes. Overall, we conclude that latitude contributes to structuring the arthropod communities inhabiting fruiting bodies and that this effect is seen as species turnover among sites along the gradient rather than as changes in overall species richness. In what follows, we examine each finding in turn.

A latitudinal gradient in species richness?

Species diversity generally decreases toward higher latitudes (Hillebrand, 2004; Willig et al., 2003). By extension, it has been proposed that the number of species present in local communities should be reflected in the network

structures and ecological processes within them, so that biotic interactions are more complex and prevalent at lower latitudes (Schemske et al., 2009). Many studies have found evidence in support of this hypothesis, in the form of, for example, intensified herbivory (Salazar & Marquis, 2012; Zvereva et al., 2020) and arthropod predation (Jeanne, 1979; Roslin et al., 2017; Zvereva et al., 2019), as well as increased herbivore specialization (Forister et al., 2015), toward the tropics.

In our study, we found no evidence of a latitudinal gradient in overall species richness (Figure 4a) but clear latitudinal imprints on the abundance and distribution of species (Figures 3 and 4c). Since our analyses explicitly concerned the number of species per fruiting body of a given fungal species, they also directly reflected the complexity of biotic interactions. Where ordination (Appendix S1: Figure S3) and resampling analyses (Appendix S1: Figure S4) indicated little geographic structuring of community composition, latitude had a relatively high explanatory power in HMSC models of species-level presence and abundance. While the absolute proportion of variance explained may seem low by traditional standards (2.1% for variation in presence–absence, 5.4% of variation in read numbers conditional on presence), we reiterate that these numbers should be evaluated against their relevant background. First of all, the explanatory power of a factor will vary with the scale at which the response is measured. In the current case, we measured species occurrence and abundance at the level of individual fungal fruiting bodies—for which it is naturally challenging to achieve high explanatory powers. Clearly, it is more challenging to predict whether a given species will occur in a specific fruiting body than at a site for which many fruiting bodies are inspected. In the current case, our interest is explicitly at the level of individual mushrooms, so explanatory power should be calculated at this smallest scale.

Second, the low previously cited figures concerned the absolute proportion of variance explained by the variables—not relative proportions out of all variation explained. For clarity, we note that all variables together explained 12.4% out of all variation in presence–absence (a typical figure, given that the responses consist of zeros and ones) and 61.1% of variation in abundance (conditional on presence). In relative terms (i.e., expressed as proportions out of the overall 12.4% versus 61.1% of variance explained), these values were naturally much higher (Figure 3). What is more, their relative magnitudes were even reversed between the two models, being 19.8% for presence–absence and 9.1% for abundance, respectively. Given the overall lack of latitudinal imprints on species richness, we infer that latitude will not affect how many arthropod species inhabit a fruiting body, but it will indeed affect what species occur in it and at what abundances. These results are consistent with the pattern of increasing differences among communities with an increasing distance in space: Partitioning of the beta diversity resulting from species-level responses revealed a slight but statistically significant increase in turnover along with geographical distance among fruiting bodies (Figure 5a).

In terms of the strength of the patterns detected, it is evident that much variation remains unaccounted for (cf. Figures 3 and 5). This variation seems a key characteristic of fungus-associated arthropod communities. When communities form in ephemeral resource patches such as fungal fruiting bodies, dung, or carrion (Gittings & Giller, 1998; Hanski, 1980), there is always a major element of chance in terms of what species reach a specific resource patch. For this reason, the pattern would likely remain the same no matter how many descriptors of the fruiting bodies and their environment we were to measure; no systematic factor accounts for more than a fraction of all variation. This observation is fully consistent with current theory on community assembly in ephemeral habitats (O'Neill, 2016; Orrock & Watling, 2010; Reigada et al., 2015).

Our finding of a lack of detectable richness gradient runs contrary to assumptions regarding the ubiquity of trends in diversity with latitude (Hillebrand, 2004; Willig et al., 2003). In contrast, they resonate with studies reporting a lack of (or even reversed) latitudinal gradients in the species richness of, for example, wetland birds (Järvinen et al., 1987), sawflies (Kouki, 1999), and aphids (Dixon et al., 1987). Among fungi, many groups—including the ectomycorrhizal fungi studied here—exhibit a reversed latitudinal gradient in species diversity (Peay et al., 2016; Tedersoo et al., 2014) as well as diversification rates (Looney et al., 2016; Varga et al., 2019). High community-level diversity of fungal hosts even in the northernmost parts of Europe could therefore support roughly equal levels of arthropod-associated diversity across our focal gradient. Furthermore, Hebert et al. (2016) recently demonstrated, based on barcode-based screening of Canadian insect communities, that the diversity of several dipteran groups, including the largely fungus-associated Sciariidae, may be substantially higher in the north than previously thought. Our observation that change across latitudes is reflected as change in species composition rather than diversity runs contrary to the findings of Komonen et al. (2003), who compared communities on *Fomitopsis* bracket fungi in Finland and China. By contrast, our results are consistent with patterns found by Friess et al. (2019) for arthropods associated with the polypore *F. fomentarius* across Central Europe. In their study, the diversity of specialist associates decreased toward the

north, but the relationship was weak and the effect of latitude disappeared when the community was considered as a whole rather than filtering out the presumptively specialized species.

Our second finding of hump-shaped patterns of species' site-specific abundances (where present, Figures 3 and 4) is only logical given the general shape of species' niches. Because species are generally confined to specific envelopes of climatic conditions, abundances are likely to peak under optimal conditions (Renwick et al., 2012; Russell et al., 2015). With different species peaking at different latitudes, the net effect on overall abundance is still a slight peak halfway along the latitudinal gradient. The average fruiting body will then be attacked by a slightly higher abundance of consumers halfway along the latitudinal gradient observed by us. Overall, our results attest to a general consistency in the diversity of interaction partners per fungal fruiting body, rather than to any pronounced latitudinal cline in such associations. In terms of abundance, they attest to a general latitudinal pattern, but with a particular twist to previous suggestions of monotonic trends (Anstett et al., 2016; Moles et al., 2011; Moles & Ollerton, 2016; Roslin et al., 2017)—since here, the number of individual interaction partners actually peaked midrange. Whether such hump-shaped distributions may also occur in other biotic interactions is currently an open question (Schemske et al., 2009).

An imprint of host identity and phylogeny?

Fungal fruiting bodies support a diverse community of arthropods whose members either feed directly on the fungal tissue or consume the other inhabitants. Of the taxa feeding on fungal tissues, some can be considered typical "parasites" of fungi (e.g., dipteran larvae restricted to a single fruiting body) or "micropredators" (e.g., adult beetles, which can move among multiple fruiting bodies) (cf. Lafferty et al., 2015). In general, a parasitic lifestyle—with each consumer feeding on a single host individual—promotes specialization with respect to available hosts (Nylin et al., 2018). In such systems, pronounced host specificity and marked phylogenetic imprints on host-use evolution have often been observed as likely adaptations to interspecific differences and phylogenetic conservatism in host morphology and defenses (Futuyma & Agrawal, 2009; Weiblen et al., 2006). However, as pointed out by Kobayashi and Sota (2021), phylogeny-based approaches have thus far been rarely applied in studies on long-term associations between insects and fungi. Given that forest fungi exhibit marked interspecific variation in ecological traits, fruiting-body morphology, and chemical defenses and that these traits are phylogenetically conserved (Varga et al., 2019; Yin et al., 2019), insects living in fruiting bodies would be expected to specialize in using particular host species and taxa.

In our study, host taxonomy emerged as a secondary, yet clear structuring force with regard to the overall arthropod communities of individual fruiting bodies (Figures 3 and 5b). Many arthropod associates proved broad generalists (Appendix S1: Figure S1), as reflected in widely overlapping clusters in the NMDS ordination (Figure 2) and in similar rates of species accumulation within versus across host taxa (Appendix S1: Figure S4). On the other hand, sample-based rarefaction showed interspecific differences among the hosts in associated diversity (Appendix S1: Figure S2); within several host genera, the associated communities of individual fruiting bodies clustered together in the ordination results (Figure 2), the turnover component of community beta diversity among fruiting bodies was correlated with phylogenetic distance (Figure 5b), and HMSC variance partitioning revealed a clear taxonomic impact on the occurrence and abundance of many associated taxa (Figure 3a). Notably, the species for which we found the highest effect of host identity and taxonomy on occurrence patterns were all dipteran species in families Anthomyiidae and Mycetophilidae, which, with regard to lifestyle, are typical parasites of fungi. When examining the imprints of host identity and phylogeny on the patterns found, it is important to understand the effects of study design. The strength of phylogenetic signal in resource–consumer networks is generally dependent on the scale at which it is analyzed (Cagnolo et al., 2011; Desneux et al., 2012; Leppänen et al., 2013). Therefore, had we compared fundamentally different fruiting bodies (like hard polypores vs. soft agarics), then fungal species and phylogeny undoubtedly would have explained even more of the variation. However, such a result might be seen as trivial, since it was already known that hard polypores sustain arthropod communities different from those of soft agarics (Hanski, 1989; Jakovlev, 2012; Orledge & Reynolds, 2005; Schigel, 2012; Thorn et al., 2015). What we were primarily interested in was rather whether, among agarics, there was a phylogenetic signal in the patterning by fungal species. For this reason, we explicitly included a set of soft, ephemeral species varying internally in relatedness and compared differences in community similarity with differences in relatedness within a comparatively a restricted range of fungal phylogeny.

Our metabarcoding-based inferences are in broad agreement with previous molecular (Koskinen et al., 2019) and rearing-based (Jakovlev, 2011; Põldmaa et al., 2016; Ståhls et al., 1989; Tuno et al., 2019) analyses of fungus-associated insect communities, each of which has indicated frequent generalism in the use of available hosts.

That fungus-associated arthropods have wider host ranges than plant-feeding insects was previously attributed to the temporally and spatially unpredictable occurrence of fungal fruiting bodies. Such unpredictability in the resource distribution may enforce generalism as a bet-hedging strategy, despite potential differences in quality among hosts (Põldmaa et al., 2016). Nevertheless, several studies have revealed that even fungus feeders can exhibit clear preferences for particular fungal families or genera (Jakovlev, 2012; Põldmaa et al., 2016; Ståhls et al., 1989). All in all, our study provides added support for a modest, yet demonstrable, level of host specialization among fungus-associated arthropods, detectable as imprints on both the presence–absence and abundance of individual associated taxa.

A signature of decay stage?

Individual fungal fruiting bodies constitute an ephemeral, ever-changing resource for consumers and, therefore, also for the diverse parasites, parasitoids, and scavengers relying on the consumers. As fruiting bodies grow and decay, their structural and biochemical composition changes (Barros et al., 2007), partly as a result of shifts in the microbial fauna within them (Gohar et al., 2020; Ye et al., 2018). The rapid and pronounced temporal changes in resource properties are akin to those observed in decaying dung and carrion, in which arthropod communities exhibit predictable successional sequences across time (Anderson, 2000; Gittings & Giller, 1998). In the case of fungal fruiting bodies, Jonsell and Nordlander (2004) suggested that progressing decay should in particular lead to an increasing proportion of generalists in the associated communities.

We found the overall imprint of decay stage on associated communities to be detectable but slight (Figure 3). This conclusion is supported by the NMDS analyses (showing no clear clustering by decay stage, Figure 2) and the resampling procedures (with little separate increment in species through complementary sampling of decay stages) (Appendix S1: Figure S4). Nevertheless, a temporal effect is observable in the variance-partitioning results, where decay stage affects the occurrence of many species (Figure 3); in the beta-diversity partitioning results, where overall community dissimilarity among fruiting bodies increases with an increase in the pairwise differences in decay stage (Figure 5c); and in that the predicted number of arthropods per fruiting body increased from young to old fruiting bodies (Figure 4b).

An effect of fruiting-body age or decay stage was previously observed among fungus-feeding beetles (Epps & Arnold, 2018) and in insects associated with polypores (Jonsell & Nordlander, 2004; Kadowaki, 2010; but see Yamashita & Hijii, 2007). A general increase in species richness with decay stage can be explained in several ways. First, further-decayed fruiting bodies are generally older and have therefore been available for colonization for a longer time, resulting in more taxa co-occurring in older fruiting bodies. But second, and potentially adding to the preceding point, is the ecology of DNA itself (Bálint et al., 2018): Metabarcoding may produce a summation of taxa that are and have been present in a fruiting body since DNA may remain in, for example, fungivore feces, shed skins, pupae, and even predator guts. Hence, to achieve maximal resolution, the elucidation of temporal variation in community structure may require a combination of rearing and molecular methods or repeated sampling of the same fruiting bodies through time.

CONCLUSIONS

While arthropod communities on plants have provided some of the classic model systems in ecology, fungus-based communities and the forces structuring them remain poorly studied. In this paper, we paint a new picture of fungus–arthropod interactions, pointing to key differences in the forces governing the assembly of fungus-associated arthropod communities as compared to plant-associated communities. We show that latitude leaves a clear imprint on the composition of fungus-associated arthropod communities, affecting what species occur where and at what abundances, without corresponding effects on net species richness. Thus, the structuring impact of latitude is mediated by high species turnover. Phylogeny and decay stage play lesser but still detectable roles. The lack of patterns in species richness indicate high spatial turnover, with low nestedness across latitudes, decay stages, and host phylogeny. Overall, our findings suggest that from an arthropod community perspective, large-scale variation in environmental conditions (affecting local species pools) and local stochastic elements (affecting what species out of that pool colonize individual fruiting bodies) predominate over finer differences in the physicochemical properties of fruiting bodies. Since metabarcoding provides an efficient tool for screening of arthropod communities in individual fungal fruiting bodies, we propose that future research should embark on a sweeping survey of host specificity across arthropods of widely different host taxa, traits, and ecologies. A true quest for generalities in host use is now finally within reach.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Tommi Nyman, Tomas Roslin, and Janne S. Koskinen planned the study, and Janne S. Koskinen, Tomas Roslin, and Tommi Nyman wrote the manuscript with input from Nerea Abrego, Eero J. Vesterinen, and Torsti Schulz. Eero J. Vesterinen designed the molecular approach and performed the bioinformatics processing, and Janne S. Koskinen fine-tuned the taxonomic assignments. Nerea Abrego performed and wrote the joint species distribution modeling and beta-diversity analyses, and Torsti Schulz wrote analytical scripts for resampling scenarios. All authors read and accepted the final manuscript.

DATA AVAILABILITY STATEMENT

Data (Koskinen et al., 2022a) are available in Dryad at https://doi.org/10.5061/dryad.cjsxksn5d. Novel scripts (Koskinen et al., 2022b) used in the analyses are available on Zenodo at https://doi.org/10.5281/zenodo.6103067 and are also available in the Supporting Information in Data S1–S6.

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