JYX JYVÄSKYLÄN YLIOPISTO UNIVERSITY OF JYVÄSKYLÄ

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

Author(s): Koskinen, Janne; Abrego, Nerea; Vesterinen, Eero; Roslin, Tomas; Nyman, Tommi

Title: Environmental responses of fruiting fungal communities are phylogenetically structured

Year: 2023

Version: Published version

Copyright: © 2023 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of N

Rights: CC BY 4.0

Rights url: https://creativecommons.org/licenses/by/4.0/

Please cite the original version:

Koskinen, J., Abrego, N., Vesterinen, E., Roslin, T., & Nyman, T. (2023). Environmental responses of fruiting fungal communities are phylogenetically structured. Ecography, 2023(10), Article e06333. https://doi.org/10.1111/ecog.06333

ECOGRAPHY

Research article

Environmental responses of fruiting fungal communities are phylogenetically structured

Janne Koskinen[1,2,*], **Nerea Abrego**[2,3,*], **Eero Vesterinen**[4], **Tomas Roslin**[2,5] **and Tommi Nyman**[6]

[1]Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland
[2]Department of Agricultural Sciences, University of Helsinki, Finland
[3]Department of Biological and Environmental Sciences, University of Jyväskylä, Finland
[4]Department of Biology, University of Turku, Finland
[5]Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden
[6]Department of Ecosystems in the Barents Region, Svanhovd Research Station, Norwegian Institute of Bioeconomy Research, Svanvik, Norway

Correspondence: Janne Koskinen (janne.koskinen@helsinki.fi)

Ecography
2023: e06333
doi: 10.1111/ecog.06333

Subject Editor: Vigdis Vandvik
Editor-in-Chief: Miguel Araújo
Accepted 7 June 2023

Through their ephemeral reproductive structures (fruiting bodies), ectomycorrhizal forest soil fungi provide a resource for a plethora of organisms. Thus, resolving what biotic and abiotic factors determine the occurrence and abundance of fruiting bodies is fundamental for understanding the dynamics of forest trophic networks. While the influence of abiotic factors such as moisture and temperature on fungal fruiting are relatively well established, little is known about how these processes interact with the evolutionary history of fungal species to determine when, where, and in which abundance fungal fruiting bodies will emerge. A specific knowledge gap relates to whether species' responses to their environment are phylogenetically structured. Here, we ask whether related fungal taxa respond similarly to climatic factors and forest habitat characteristics, and whether such correlated responses will affect the assembly of fungal fruiting communities. To resolve these questions, we fitted joint species distribution models combining data on the species composition and abundance of fungal fruiting bodies, environmental variation, and phylogenetic relationships among fungal taxa. Our results show that both site-level forest characteristics (dominant tree species and forest age) and climatic factors related to phenology (effective heat sum) greatly influence the occurrence and abundance of fruiting bodies. More importantly, while different fungal species responded unequally to their shared environment, there was a strong phylogenetic signal in their responses, so that related fungal species tended to fruit under similar environmental conditions. Thus, not only are fruiting bodies short-lived and patchily distributed, but the availability of similar resources will be further aggregated in time and space. These strong constraints on resource availability for fungus-associated taxa highlight the potential of fungus-based networks as a model system for studies on the ecology and evolution of resource–consumer relations in ephemeral systems of high spatiotemporal patchiness.

Keywords: forest fungi, fungivory, mycorrhizal fungi, phenology, phylogenetic signal, resource variation, spatial variation, temporal variation

NORDIC SOCIETY OIKOS

www.ecography.org

© 2023 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos
*Shared first authors
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Research into how trophic networks are shaped by ecological and evolutionary forces remains one of the corner stones of modern ecology (Weiblen et al. 2006, Cagnolo et al. 2011, Forister et al. 2015). In this context, phylogenies provide information about evolutionary relationships among species (Baum and Smith 2013, Swenson 2019). Because phylogenetically related species often share similar traits, we expect close relatives to co-occur more often in the same communities, reflecting their shared environmental tolerances. Conversely, if sharing the same traits cause phylogenetically related species to compete strongly, then closely related species may be less likely to co-occur. These and other processes relating functional traits to community composition often result in phylogenetic signatures in how species are distributed among communities (Webb et al. 2002, Davies 2021).

One type of communities on which phylogenetic signatures remain poorly known (Abrego et al. 2022, Bässler et al. 2022) are local assemblages of fungal fruiting bodies. This constitutes an important knowledge gap because fungal fruiting bodies provide a resource for a plethora of organisms (Hanski 1989, Osawa et al. 2011, Kurina et al. 2015, Koskinen et al. 2019, 2022). Fungus-based trophic networks are highly diverse even in the boreal and temperate zones, where thousands of fungal species produce macroscopic fruiting bodies (Salo et al. 2005, Mueller et al. 2007). From the perspective of a fungal consumer, the forces structuring the assembly of communities of fungal fruiting bodies will determine what types of resources occur where, for how long, and at what abundances. Resolving the role of phylogenetic imprints on the assembly of communities of fungal fruiting bodies is then fundamental not only for understanding fungal community dynamics in particular, but the dynamics of trophic networks more generally.

How the local composition and abundance of fungal fruiting bodies affect the associated communities of other taxa is an area of vigorous research (Põldmaa et al. 2016, Koskinen et al. 2019, 2022). Despite their apparent ubiquity, fungal fruiting bodies will namely constitute a spatially and temporally unpredictable resource for fungivorous vertebrates and invertebrates (Butterworth et al. 2023). Theoretically, unpredictable abundance of individual host species favors generalism as a bet-hedging strategy in consumers (Hanski 1989, Poisot et al. 2011). Indeed, many arthropods associated with fruiting bodies of forest fungi show low levels of specialization, or tend to be specialized at the level of host genus rather than species (Ståhls et al. 1989, Thorn et al. 2015, Põldmaa et al. 2016, Koskinen et al. 2019, 2022). In fungivores associated with particular fungal taxa, the specialization tends to target specific features in host ecology or morphology (Orledge and Reynolds 2005, Põldmaa et al. 2015, Lunde et al. 2022). However, the ecology and evolution of fungus-associated arthropod communities remain poorly studied in comparison to, for example, those among plant-feeding insects (Jaenike 1990, Forister et al. 2015).

Local community structures, as well as the overall and species-specific abundance of fungal fruiting bodies available to consumers, are determined by multiple interacting factors. Due to their intricate mutualistic associations with trees, mycorrhiza-forming fungi tend to prefer particular host tree species, forest types, or soil properties (DeBellis et al. 2006, Lang et al. 2011). The availability of fungal fruiting bodies at higher latitudes also shows an annual pattern, with fruiting generally increasing during late summer and decreasing after temperatures drop in the mid- to late autumn (Sato et al. 2012, Büntgen et al. 2013, Boddy et al. 2014). While such phenological changes in fruiting are more or less predictable, they are strongly modulated by interannual and spatial variation in precipitation and temperature (Straatsma and Krisai-Greilhuber 2003, Polevoi et al. 2006, Krebs et al. 2008, Sato et al. 2012, Andrew et al. 2018). Importantly, fungal species and taxa have different phenologies (Pinna et al. 2010, Sato et al. 2012), respond differently to variation in temperature and precipitation (Kauserud et al. 2008, 2012, Büntgen et al. 2012, 2013, Heegaard et al. 2017), and exhibit different preferences with regard to symbiont trees and forest types (Newton and Haigh 1998, Bruns 2002, Lang et al. 2011). These interspecific differences – and the extent to which they are phylogenetically structured – can create highly variable fungal assemblages across space and time.

While a relatively large body of literature has shown how fungal fruiting phenology depends on environmental, seasonal, and climatic variation (Straatsma et al. 2001, Büntgen et al. 2012, Sato et al. 2012, Boddy et al. 2014, Andrew et al. 2018), connections between the determinants of fungal fruiting and the evolutionary history of fungi remain poorly explored. Where sought for, studies of fungal fruiting responses to environmental variation in resource availability, land-use history and macroclimate have generally revealed a strong a strong phylogenetic signal (Bässler et al. 2014, 2022, Abrego et al. 2017, 2022), with related species tending to respond similarly to environmental conditions (Kauserud et al. 2012). While patterns of phylogenetic signal fall short of revealing the exact evolutionary processes underlying the composition of current communities, they do provide useful information to understand and predict community structure (Webb et al. 2002, Cavender-Bares et al. 2009, Cadotte et al. 2013). In the case of forest fungi, any phylogenetic structuring of the spatiotemporal availability of fruiting bodies will come with important consequences for resource availability to forest organisms on higher trophic levels: if related fungal species fruit under similar environmental conditions, then variation in environmental conditions will affect the production of fruiting bodies of entire clades in a non-random manner. Such patterning will directly impact consumers specialized on particular fungal lineages or taxa, as it will increase the spatiotemporal variation and unpredictability of resource availability (Hanski 1989).

In this study, we elucidate the factors that determine the assembly of macrofungal fruiting body communities, and thus resource variability from the perspective fungus-associated consumers. To this aim, we investigated the effects of

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

habitat, space, and time on the occurrence and abundance of the fruiting bodies of forest fungi. Specifically, we tested 1) whether environmental predictors describing climatic and forest habitat characteristics influence the spatiotemporal distribution of fungal fruiting bodies and 2) whether the way in which fruiting fungal communities respond to the focal environmental predictors is phylogenetically structured. For this, we used transect counts of the fruiting bodies of 107 fungal species and operational taxa collected during two consecutive years from 34 forested sites in southeastern Finland. The sites differed with respect to their dominant tree species, soil properties (forest type), and age structure. As the main analytical tool, we fitted joint species distribution models which simultaneously combined the count data on the fungal fruiting bodies, the environmental data, as well as fungal phylogenetic data. Based on previous studies (Büntgen et al. 2013, Boddy et al. 2014, but see Kauserud et al. 2010), we expected the phenology of the fungal fruiting to be driven by the progression of the season, as reflected in accumulating heat sums. We also expected the environmental variables describing forest characteristics to affect the local occurrence and composition of fungal fruiting bodies. Such effects should emerge from the dependency of mycorrhiza-forming fungi on certain host tree species (Newton and Haigh 1998, Bruns 2002), and from environmental variation in microclimate and soil chemistry of relevance to soil fungi (Toljander et al. 2006, Kim et al. 2021). Regarding the phylogenetic patterns, we expected to find a strong phylogenetic signal on where and when fungi fruited, as related taxa should have similar traits and respond similarly to environmental triggers for fruiting (Kauserud et al. 2012, Sato et al. 2012, Diez et al. 2013).

Material and methods

Transect counts, forest characteristics and climatic data

To address the effects of dominant tree species, forest type, forest age, location, and time on the diversity and abundance of ephemeral fungal communities, we conducted fruiting body surveys (transect counts) following a nested sampling scheme. We selected forest sites representing young to old-growth coniferous forests from three main areas in north Karelia, southeastern Finland (Fig. 1). We originally selected 32 study sites, but two of these were logged after the counts in 2016. In 2017, these sites were therefore replaced with nearby sites with similar forest characteristics, resulting in a total of 34 sites being surveyed (7–19 sites per main area). The longest distance between sites was 80.4 km, the mean distance between sites in different areas was 33.6 km, and the mean distance between sites within the same main area was 5.7 km. Among the three areas, Jaamankangas is dominated by young *Pinus sylvestris* forests and Kiihtelysvaara by *Picea abies* forests of various ages, while Patvinsuo has both *Picea*-dominated old-growth forests and *Pinus*-dominated younger forests. Jaamankangas and Kiihtelysvaara are located at the northern margin of the south boreal zone and Patvinsuo at the southern border of the middle boreal zone, and the

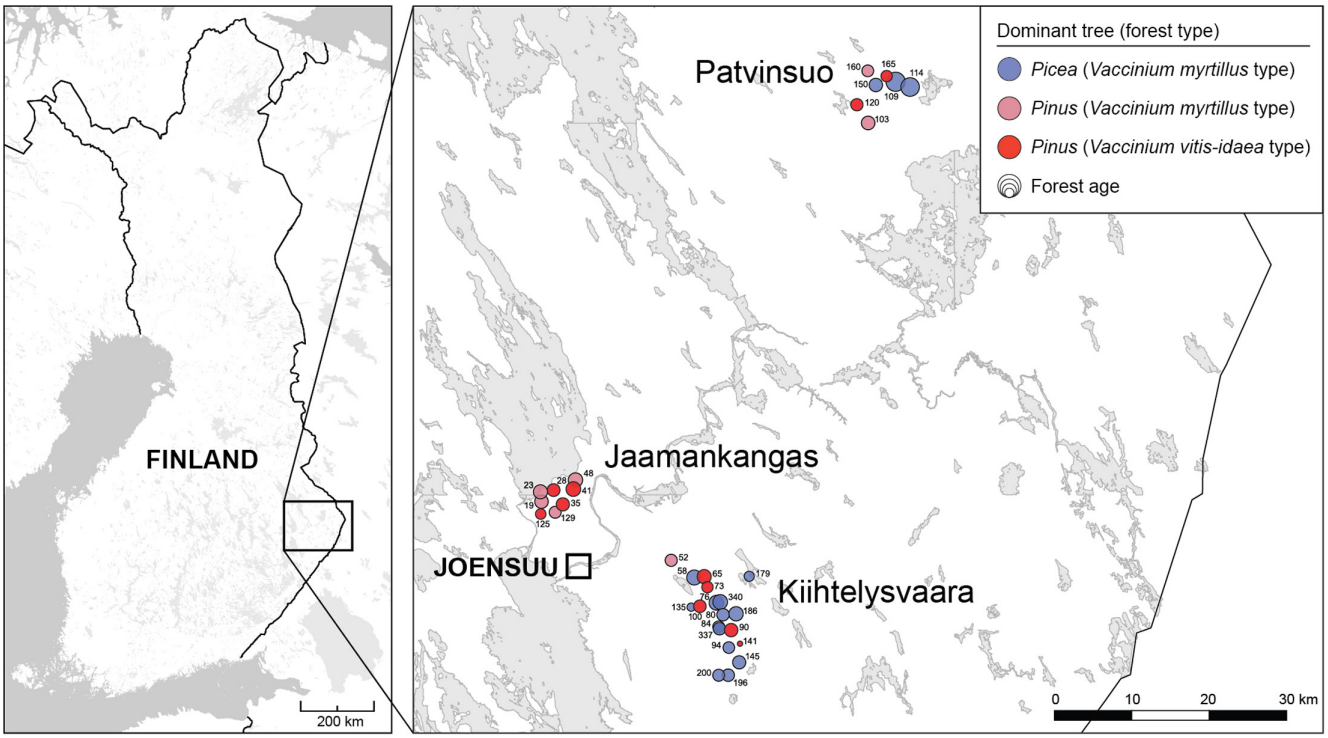

Figure 1. Map showing the locations of the main sampling areas and sites in southeastern Finland. Sampling sites in the main map are shown by circles, circle color denotes dominant tree species and forest type, and circle size is proportional to forest median age (see legend).

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

overall study area is classified as subarctic in the Köppen–Geiger climate classification (Beck et al. 2018).

We conducted three rounds of surveys during two consecutive years: one survey was carried out in July–August 2016, one in September 2016 and one round in August–September 2017 (Supporting information). One to three surveys were conducted per site; in some cases, drought and onset of freezing temperatures, as well as forestry, lowered the number of surveys implementable at a given site. Nonetheless, variation in the number of surveys per site was only slight overall, since out of the targeted 34 × 3 = 102 site-by-date combinations resulting from a fully balanced design, we obtained n = 86 (3 sites were surveyed once, 10 twice, and 21 three times). The analytical methods employed are robust to such variation (Statistical modelling, below).

In each survey, we identified and counted all macrofungal fruiting bodies from a 4 × 200 meters transect running through the site. Fruiting bodies were identified to the taxonomic level achievable in the field. Thus, all fruiting bodies could not be reliably identified to species level (Supporting information). For example, many brown and nondescript *Cortinarius* species were identified to either generic or subgeneric level, and small *Russula* species were identified to generic level only. Furthermore, some small fruiting bodies were lumped into the operational group 'small, white-spored fungi'. We note, however, that taxa attributed to the last group were rare, altogether accounting only for 5.8% of all fruiting bodies encountered (Supporting information), and that all analyses targeting phylogenetic imprints were conducted at the species level.

For each sampling site, we recorded the dominant tree species (*Pinus* or *Picea*) and the forest type according to the vegetation-based Finnish forest classification system (Hotanen et al. 2008). This classification was done during the first survey. The sites (Fig. 1) represented *Vaccinium vitis-idaea* (VT) (n = 11) and *Vaccinium myrtillus* (MT) (n = 23) forest types; the number of MT sites includes a single *Oxalis–Myrtillus* (OMT) type site that was treated as part of the similar MT category. Site-specific median forest age was obtained from remote sensing data of Natural Resources Institute Finland (Mäkisara et al. 2019). For predicting how the advancement of the season influenced the timing of fruiting across fungal species, we adopted the effective heat sum as a widely-used proxy of phenology of seasonal events (Delgado et al. 2020). For each combination of site and sampling date, the date-specific effective heat sum is defined as the sum of the average temperatures of all preceding days within the same year for which the average temperature was over +5°C. In other words, we calculated the heating degree-day sum H of sampling date t at site i as

$$H_{t,i} = \sum_{j=1}^{t} \max\left(T_{j,i} - 5, 0\right)$$

where $T_{j,i}$ is the temperature of day j at site i, and summing over days t starts from 1 January. Daily average temperatures were taken from measurements recorded at the nearest meteorological weather station of the Finnish Meteorological Institute.

Dataset and phylogeny construction

Based on the transect count data, we created two initial datasets for the analyses. The first dataset contained all 107 operational taxa that were recorded during the surveys. The second dataset – a subset of the first – contained those 81 fungal species for which a phylogenetic tree could be estimated based on the ten 5284-taxon FastDate chronograms provided by Varga et al. (2019) (cf. Koskinen et al. 2022). Varga et al. (2019) reconstructed the phylogeny of the Agaricomycetes based on a backbone-constrained topology inferred from genome-level data (available for 104 species) and on sequence data from up to three nuclear genes (available for 5284 taxa). Because of the comprehensive taxon sampling and robust results of Varga et al. (2019), their phylogenetic trees provide a useful resource for statistical analyses combining information on agaricomycete ecology with estimates of the evolutionary relationships among species. The species included in our second dataset and the corresponding phylogenetic tree were either 1) present in the Varga et al. (2019) trees under the same or a synonym name, or 2) had a close relative that could be presumed to represent the same monophyletic group in the trees (Supporting information). The final phylogenetic tree containing only the focal taxa was constructed by first pruning each tree down to the selected species using the 'ape' ver. 5.2. package (Paradis and Schliep 2019) in R (www.r-project.org), and then calculating a consensus tree with common ancestor node heights using the TreeAnnotator utility of BEAST ver. 2.6.2 (Bouckaert et al. 2019).

Exploratory analyses

Before our main analyses, we characterized overall community similarity, fungal alpha diversity, and taxon-specific and overall abundance across the three main areas and the three combinations of dominant tree and forest type (Supporting information). To evaluate the utility of our continuous explanatory variables for the main modeling analyses, we plotted area- and site-specific distributions of forest age and effective heat sum during each survey, and confirmed the absence of confounding collinearity by constructing pairwise plots of all continuous and categorical explanatory variables (Supporting information).

Statistical modelling

To simultaneously estimate how the fruiting fungal species responded to the environmental covariates and how phylogenetically structured those responses were, we used hierarchical modelling of species communities (HMSC, Ovaskainen et al. 2017, Ovaskainen and Abrego 2020). HMSC is a class of joint species distribution models which allows to account for the dependency structure generated by the sampling scheme,

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and to estimate species-specific responses and their phylogenetic relationships in a multispecies data set.

The original fungal fruiting data consists of the occurrence and counts of fruiting bodies of 107 fungal OTUS surveyed in 34 sites across three areas (Fig. 1). To these data we fitted both multivariate (joint) and univariate species distribution models using the R-package (www.r-project.org) 'Hmsc' ver. 3.0-11 (Tikhonov et al. 2020) (Supporting information). As our response, we considered counts of fruiting bodies per fungal species (in the multivariate models), or the count of fruiting fungal species (in the univariate models). As the sampling units, we considered the 86 individual surveys. Focusing the analyses on the level of individual surveys rather than sites allowed us to utilize within-site data on fruiting phenology, as well as to explicitly account for the slight variation in the number of surveys per site. To account for the zero-inflated nature of the multivariate data, we fitted so called hurdle models. In other words, we first modeled the presence/absence of the species, and then the abundance of the species conditional on its presence. For models of presence–absences, we used a probit-link function, and for models of fruiting body counts conditional on presence, we used a log-normal model. In the univariate model, we modelled the species richness following Poisson regression.

We fitted two versions of the multivariate models, one including the phylogenetic relationships and one excluding them. This is because we could recover the phylogenetic information only for 81 out of the 107 species, but we wanted to test the generality of the results also with respect to the full set of species.

As high proportions of species with extremely low prevalence result in poor model performance (Norberg et al. 2019), we excluded the singleton species (i.e. those occurring in a single sampling unit) from the multivariate joint species distribution models. After the exclusion of singleton species, the multivariate models with and without phylogenetic data comprised 68 and 86 species, respectively. The univariate model on species richness included the data on all the 107 species. By combining models of species occurrence, and of abundance conditional on presence, we were able to answer our study questions both from the single species- and community-level perspective. First, the multivariate models excluding phylogeny allowed us to ask how heat sums and forest habitat characteristics influenced the contribution of individual fungal species to local communities of fungal fruiting bodies. These models reveal which of the environmental covariates increased or decreased the occurrences and counts of each of the fungal species. Second, the multivariate models including phylogenetic data allowed us to assess whether those environmental responses were phylogenetically structured. Finally, the univariate model on species richness allowed us to assess whether the community-level patterns detected by the multivariate models were sensitive to excluding the singleton species – i.e. whether predictions from the multivariate models (from which singleton species had been excluded) matched predictions based on models of species richness as such (which naturally included all species).

The explanatory part of all models was identical. To account for the spatial structure of the study design, we included a spatially structured random effect based on the latitude and longitude of the sites. Since the sites were spatially nested within main areas (Fig. 1), we included the 'main area' as an unstructured random effect. To avoid confounding between the random effect of the area and the spatial random effect of the site, we modified the default prior distribution (Ovaskainen and Abrego 2020) of the spatial scale parameter so that its maximum value did not equal the extent of the study (92 km), but instead a typical distance within areas (10 km). In this way, the random effect of main area models large-scale spatial variation, whereas the random effect of the site captures small-scale spatial variation.

To account for the fact that each site was surveyed in two consecutive years, we further included the year as an unstructured random effect. In the fixed effects part of the models, we included variables describing the forest characteristics and climate. As forest characteristics we included the forest age (continuous), forest type (categorical with MT and VT levels) and dominant tree species (categorical with *Picea* and *Pinus* levels). Since communities of fruiting bodies may show a non-monotonic response to forest age, we included also its second-order term as an explanatory variable. As the most relevant climatic variable affecting fungal fruiting body growth and phenology, we considered the effective heat sum and its second-order term.

We sampled the posterior distribution with four Markov chain Monte Carlo (MCMC) chains, each of which was run for 37 500 iterations, of which the first 12 500 were removed as burn-in. The chains were thinned by 100 to yield 250 posterior samples per chain and so 1000 posterior samples in total. We examined MCMC convergence by examining the potential scale reduction factors (Gelman and Rubin 1992) of the model parameters (Supporting information).

In the multivariate models including phylogeny, we measured the phylogenetic signal through the parameter ρ (Ovaskainen and Abrego 2020). ρ ranges from 0 to 1, so that $\rho = 0$ indicates that the responses of the species to the environment are randomly distributed with respect to the phylogeny, whereas $\rho = 1$ indicates that the environmental responses of the species are fully explained by their phylogenetic correlations. We considered that the existence of a phylogenetic signal was statistically supported if the posterior probability of ρ exceeding zero was at least 95%. We not that with the default prior, the prior probability of ρ exceeding zero is 50% (Ovaskainen and Abrego 2020).

Following Ovaskainen and Abrego (2020), we evaluated the explanatory powers of the probit models through AUC (Pearce and Ferrier 2000) and Tjur's R^2 (Tjur 2009) values. For the log-normal models, we measured explanatory power by the usual R^2 of the linear model, whereas for the Poisson model we used a pseudo-R^2. We then applied a variance-partitioning approach to quantify which proportion of the variation in the fruiting-body occurrences and counts could be attributed to the variables describing forest characteristics and climate. Variation attributed to these factors was compared

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

to that explained by the random effects (Ovaskainen et al. 2017). From the fitted models, we predicted how fruiting fungal abundance and species richness varies with the focal environmental variables, using the *constructGradient* function of the R-package 'Hmsc' (www.r-project.org, Tikhonov et al. 2020). For this purpose, we set all of the non-focal variables to their expected value (for continuous variables) or modes (for categorical variables) conditional on the value of the focal variable.

Results

The variance partitioning results revealed consistent patterns among models (Table 1), indicating that the same environmental factors influence both the occurrences and abundances of fungal species. The fixed effects parts of the models explained ca three times more variance than the random effects parts, suggesting that the predictors included captured most of the variation among areas, sites and years. Among the environmental variables considered, the effective heat sum showed the strongest effects, explaining on average 24.3% of the explained variance in fruiting species occurrence and abundance. The second most influential variable was forest age, explaining on average 19.7% of the explained variance. The dominant tree species explained then on average 14.9% of the explained variance, and forest type 13.0%.

In the variance partitioning applied to the univariate model of species richness, however, most of the variance was explained by the dominant tree species (explaining 22%) and effective heat sum (20%), followed by forest age (10%) and forest type (10%). Among the random effects, most variation was captured at the site level for the presence–absence part of the models (explaining 10.2% of the explained variance), while the variation explained by the area and year was smaller (explaining 7.1 and 6.6%, respectively).

For models of abundance conditional on presence, the amount of variance explained by each of the three random effects was roughly similar (9.8–12.8%). In the species richness model, the random effects explained a larger amount of variance than they did in the hurdle models, with the site, year and area explaining 22, 11 and 6%, respectively, of the explained variance.

The absolute amount of explained variance was on average 17.0% for the presence–absence part of the models and 57.5% for the abundance (conditional on presence) part of the hurdle models (Table 1). This nominal difference in the degree of determination does not, however, indicate that explaining whether a given fungal species will occur as fruiting bodies would per necessity be any more challenging than explaining the abundance of such fruiting bodies once we know that the species is present. The discrepancy in numbers can equally well be attributed to the fact that the former is measured in terms of Tjur's R^2 and the latter by R^2, and that the two currencies are not directly comparable. The absolute amount of explained variance for species richness was high, i.e. 69%.

In line with the variance partitioning results, the regression parameters measuring how the species responded to the environmental variables revealed statistically supported responses to the effective heat sum for most species (Fig. 2). This result was consistent for both the presence–absence and abundance conditional on presence models. For the effective heat sum, the responses to the first order term were positive, while to the second order term were negative. This result indicates that the phenology of fungi (when and in which abundance a given species fruits) peaks after a particular effective heat sum has been exceeded (Fig. 3a–b). At the level of individual species, this is seen in that the occurrence probability of most species increases until the end of the season, with only a minority of the species reaching their peak earlier (Fig. 3c). For the presence–absence part of the models, most species also showed statistically supported responses to forest age (Fig. 2a), with

Table 1. Variance partitioning of the HMSC models. The numbers show the proportion (unit %) of explained variance captured by each of the variables included in the models. The last column shows the total amount of variance explained by the models (unit %).

		Fixed effects				Random effects			
Response variable	Model characteristics	Forest age	Forest type	Dominant tree	Effective heat sum	Site	Area	Year	Explanatory power
Presence–absence	No singleton species, no phylogeny	20	14.3	14.9	25.8	10.7	7.5	6.8	16.8 Tjur R^2 and 87 AUC
Abundance conditional on presence	No singleton species, no phylogeny	19.8	11.8	12.8	26.7	9	9.7	10.2	50 R^2
Presence–absence	No singleton species, phylogeny included	21.6	12.8	18.4	24.5	9.7	6.7	6.3	17.2 Tjur R^2 and 87 AUC
Abundance conditional on presence	No singleton species, phylogeny included	17.2	13.1	13.3	20	16.6	9.9	10	65 R^2
Species richness	All species included	10	10	22	20	22	6	11	69 pseudo R^2

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

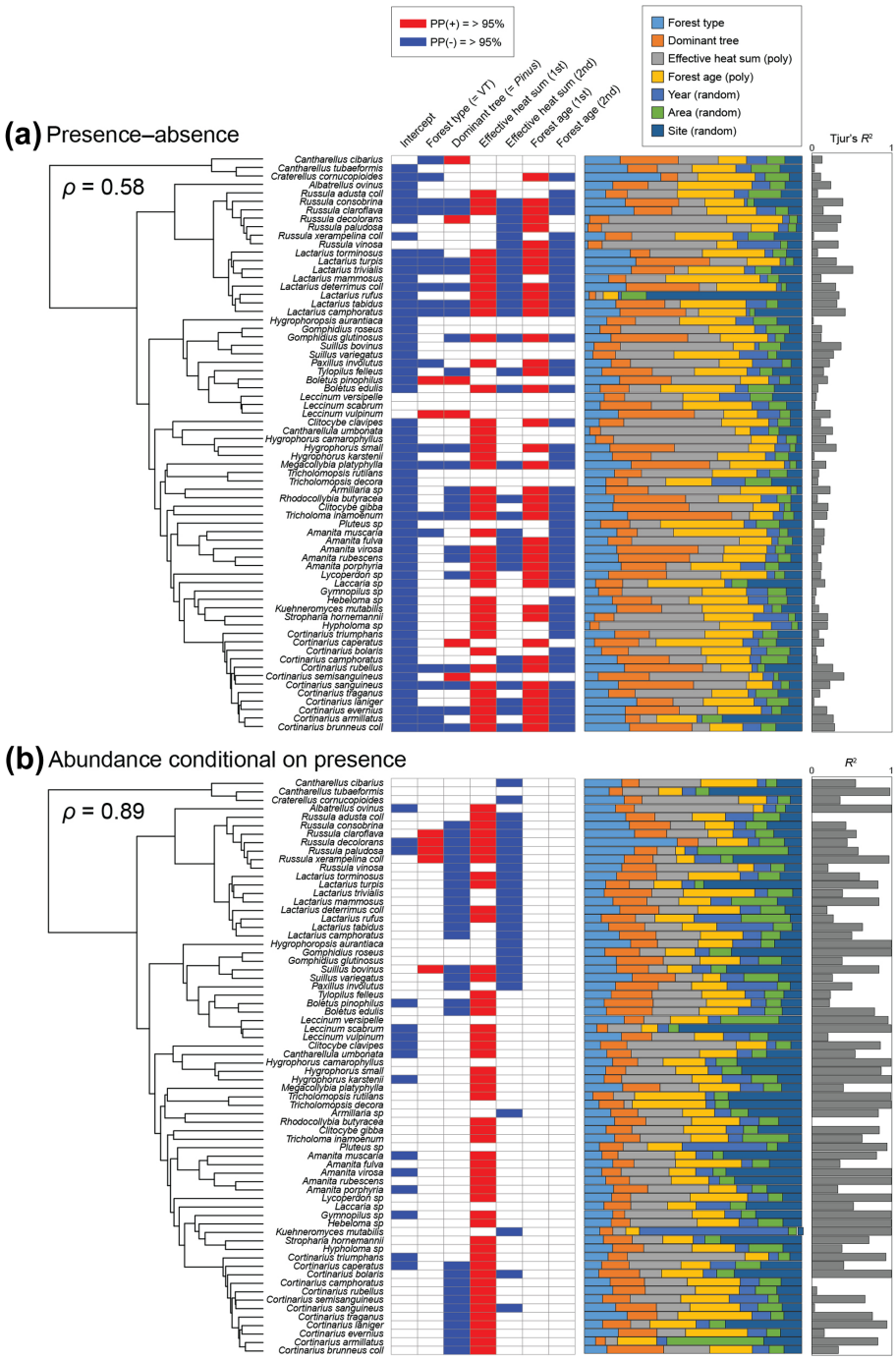

Figure 2. Mean posterior regression parameters measuring the species-specific responses of fungi to each of the environmental covariates included in the presence–absence (a) and abundance conditional on presence (b) models. The phylogeny of the species is shown on the left-hand side, with the tips representing the fungal species and the estimated phylogenetic signal parameter ρ shown inside each tree. In the first (response) matrix, blue colors indicate negative responses and red colors positive responses with ≥ 0.95 posterior probability. The variance-partitioning plots show the variance explained by each focal variable (see legend) in relation to the explained variance. Bar plots on the right-hand side show proportions of variance explained by the models (Tjur's R^2 for the presence–absence and R^2 for abundance conditional on presence model).

many species preferring the oldest forests and roughly equally many species preferring forests of intermediate age (Fig. 3d, f). The occurrence of nearly half of the species showed statistically supported responses to forest type and dominant tree species (Fig. 2a), with most of these species preferring *Picea*-dominated MT forests (Fig. 3g, i, Supporting information). For the abundance models, fewer statistically supported responses were detected (Fig. 2b). Nonetheless, the results

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

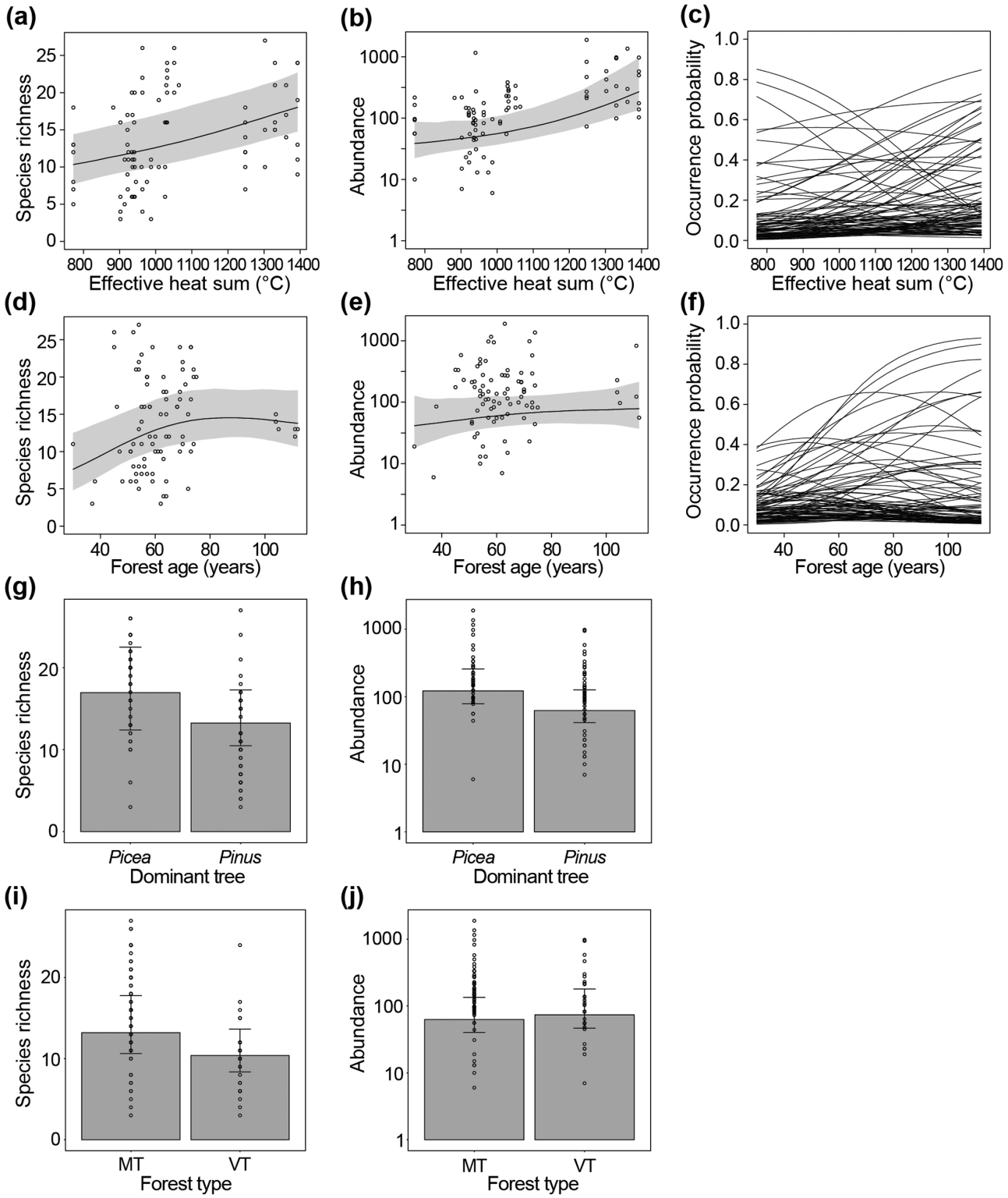

Figure 3. Predicted species richness and abundance of fungal fruiting bodies per survey and site combination in relation to effective heat sum (a, b), forest age (d, e), dominant tree species (g, h), and forest type (i, j), based on the fitted joint species distribution models. In (c, f), the lines show the predicted species-specific responses to effective heat sum and forest age, respectively. In (a, b, d, e), the lines show the predicted relationship, the shaded areas the 95% credible intervals of the predicted relationship, and the dots the raw data. In (g–j), the boxes show the predicted relationship, the bars the 95% credible intervals of the predicted relationship, and the dots the raw data. All predictions were generated by setting all of the non-focal variables to their expected value (for the continuous variables) or modes (for the categorical variables) conditional on the value of the focal variable.

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

were generally consistent with those of the presence–absence parts of the models (Fig. 3h). The main difference between the two model types (occurrence *vs* abundance conditional on presence) was that abundances of most species were either independent of forest type or higher in VT forests (Fig. 3j), and that the abundances of fruiting bodies did not depend on forest age (Fig. 3e).

The phylogenetic signal parameter ρ, which measures whether related fungal species responded similarly to the environmental conditions, was high and statistically supported (with posterior probability for positive value ≥ 0.95). For the models of presence–absence, the posterior mean of ρ was 0.58, and for models of abundance conditional on presence, the posterior mean of ρ was 0.89. Thus, closely related species responded more similarly to the environmental variables considered than one would expect in the absence of a phylogenetic signal (Fig. 2).

Discussion

If phylogenetically related species respond similarly to their environment, then more similar species are more likely to co-occur more often in the same communities (Davies 2021). Conversely, if sharing the same traits causes related species to interact more negatively, then similar species are less likely to co-occur (Liu et al. 2012, Treseder et al. 2014). The consequences of these general assembly processes will be particularly accentuated for any organism associated with the fruiting bodies of particular fungi. For such species, resource availability will per necessity be patchy and ephemeral in space and time (Hanski 1989, O'Connell and Bolger 1997, Epps and Arnold 2019, Butterworth et al. 2023) – with phylogenetic imprints potentially adding to the challenges. While many fungivores may have adopted taxon-level generalism as a bet-hedging strategy to safeguard against local unavailability of the fruiting bodies of particular fungal species (Põldmaa et al. 2016, Koskinen et al. 2022), the efficacy of such genus- or family-level host specialization will vary with the strength of phylogenetic imprints on the environmental responses of fungal fruiting – on whether related fungal species resemble each other in their responses to environmental properties and phenological cues that facilitate or suppress fruiting. In this study, we assessed whether the production of fruiting bodies by ectomycorrhizal forest fungi shows phylogenetic conservatism in relation to seasonality and local forest characteristics. Drawing on a set of more than a hundred macrofungal species, we modelled the distribution and abundance of fruiting bodies in space and time. We found strong patterns of seasonal change, signaled by an imprint of effective heat sum. Of site-level features, the dominant tree species emerged as the most important environmental factor influencing community structure, along with forest age. Importantly, while different fungal species responded unequally to their shared environment, a strong phylogenetic signal was evident across the species-level responses (Fig. 2). All of these patterns come with strong implications for fungus-associated taxa. Below, we will discuss each one in turn, starting from the environmental responses before turning to patterns of response-sharing among related taxa (i.e. phylogenetic imprints).

Factors shaping the communities of fungal fruiting bodies

Phenological differences among fungal taxa – within and between seasons and years – are known to structure the assemblages of fruiting bodies (Pinna et al. 2010, Sato et al. 2012). Our analyses, however, revealed a strong effect of the effective heat sum but a relatively weak effect of the year (Table 1, Supporting information). Effective heat sum had a clear effect on predicted species richness and on the predicted abundance of fruiting bodies, with the diversity and number of fruiting bodies generally increasing during the late summer and early autumn (Fig. 3a–c). However, the fruiting of many species peaked before the end of the sampling period. The lack of strong interannual variation in fruiting fungal communities (cf. Straatsma et al. 2001, Straatsma and Krisai-Greilhuber 2003) may perhaps be attributed to the fact that our study only included data from two consecutive years. As for other organismal groups, longer time series data may be needed to robustly capture interannual differences in fruiting fungal communities (Heegaard et al. 2017, White 2019).

Against the backdrop of seasonal change, we found pronounced impacts of site-level forest characteristics, whereas location as such (as captured by main area and site) appeared less important for fungal alpha diversity and abundance (Supporting information): Site explained more out of the explained variation in the presence–absence and abundance models than did the main area (Table 1, Fig. 2), and variation among the main areas appeared predominantly attributable to differences in the availability of different forests (Fig. 1).

Among site-level characteristics, the dominant tree species emerged as a factor highly influential in structuring the presence and abundance of fungal fruiting bodies (Table 1, Supporting information). The strong influence of the dominant tree species is likely reflective of mycorrhizal fungus–tree associations (Newton and Haigh 1998, Bruns 2002, Tedersoo et al. 2008). However, reflecting the fact that the preferred symbiont plant species and the level of specialization varies across fungal species (Newton and Haigh 1998, Bruns 2002, DeBellis et al. 2006, Ishida et al. 2007, Tedersoo et al. 2009), we found great variation in how the species responded to the dominant tree species (Fig. 2). Nonetheless, we note that from our data it is not possible to separate the indirect effect of factors with an impact on tree species composition from direct effects of tree species composition as such. Despite wide transect- and taxon-level variation, *Picea*-dominated sites generally harbored higher fruiting body diversity than did *Pinus*-dominated forests (Fig. 3g, Supporting information). In this context, the effect of dominant tree species may reflect a higher diversity of other forest tree species in *Picea*-dominated forests. In our focal area, even managed *Picea*-dominated forests often contain a mixture of, for example, *Betula* and *Populus* species, each of which partner

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

with their own mycorrhizal symbionts (Salo et al. 2005). The higher abundance of fruiting bodies in *Picea*-dominated forests (Fig. 3h), in turn, is apparently indicative of a general diversity–productivity relationship (Mittelbach et al. 2001, Straatsma et al. 2001), since spruce is competitively strongest on comparatively nutrient-rich soils (Lahti and Väisänen 1987, Tonteri et al. 1990, Levula et al. 2003). Furthermore, spruce forests will often come with a substantial element of deciduous trees. Since such trees facilitate nutrient cycling (Melvin et al. 2015), they may perhaps affect fungal fruiting. However, higher abundances of fruiting bodies in *Picea*-dominated forests may also be due to higher soil moisture, as also shown to stimulate fruiting in forest fungi (Boddy et al. 2014, Bose et al. 2022).

In comparison with the effect of the dominant tree species, the impact of local forest type on the composition and abundance of fungal fruiting bodies was less obvious (Table 1, Fig. 3i, j). The Finnish forest type classification is based on the composition of the understory vegetation, and forest type is thus reflective of a full syndrome of local productivity and soil properties, such as average pH and nutrient status (Lahti and Väisänen 1987). Hence, the generally *Pinus*-dominated VT type represents xeric habitats with often acidic, poor sandy soils, while MT-type *Pinus* or *Picea*-dominated forests are more mesic and productive. It is well known that soil chemistry will directly affect soil-fungal communities (Saarsalmi and Mälkönen 2001, Toljander et al. 2006, Tedersoo et al. 2009, 2014, Erlandson et al. 2016). In our study, the understory vegetation had a relatively small effect on the fruiting fungal communities compared to the dominant tree species. This apparently contradictory result might be due to the fact that our study is based on fruit-body surveys, which compared to DNA-based surveys (Tedersoo et al. 2008, 2014, Kim et al. 2021) are more biased toward ectomycorrhizal taxa with stronger symbiotic links with tree species.

As expected, forest age had a strong effect on the fruiting fungal communities. For the presence–absence part of the models, most species showed positive responses to the first term and negative responses to the second term of forest age (Fig. 2a), indicating that the occurrence of fruiting bodies peaks at particular forest ages (Fig. 3d, f). While this result may at first glance seem surprising, it matches other studies showing highest fungal species richness in forests of a given age (Twieg et al. 2007, Tomao et al. 2020). Modern intensive forestry practices reduce landscape-level average forest age (Kuuluvainen 2009, Kuuluvainen et al. 2012), which in turn reduces the diversity of forest-dwelling fungi. The impact of intensive forestry was also reflected in our study, as forests between 80 and 100 years of age were largely absent from our study areas. It is noteworthy, however, that forest age had no discernible effect on the overall abundance of fruiting bodies (Fig. 3e). This result may be attributable to the lack of very young forests from our study design. Including recently clear-cut forests in our study design most likely would have added variation in fruiting body diversity and abundance, because most forest-dwelling ectomycorrhizal fungi are killed after clear-cutting (Sterkenburg et al. 2019, Tomao et al. 2020, Kim et al. 2021).

Phylogenetic signal in the assembly of fungal fruiting body communities: consequences for fungivores and ecosystems

We found that species-level responses to forest characteristics, space, and time are strongly structured with respect to the phylogenetic relationships among fungal taxa – a pattern suggestive of phylogenetic niche conservatism (Losos 2008, Wiens et al. 2010). Likewise, previous studies have suggested that related groups of soil-inhabiting mycorrhizal fungi may respond similarly to environmental conditions: Chen et al. (2017) demonstrated that arbuscular endomycorrhizal taxa show low specialization but clear phylogenetic signal with respect to associations with woody hosts, while Hibbett et al. (2000) showed that fungus–host associations are more labile across ectomycorrhizal groups. However, only few studies have so far probed for a phylogenetic signal in how fungal communities respond to environmental constraints (Abrego et al. 2022, Bässler et al. 2022). Here, our study offers a seminal contribution by building on a quantitative phylogeny, rather than on using taxonomy as a proxy for relationships among taxa (cf. Kauserud et al. 2012).

From the perspective of consumers associated with fungal fruiting bodies, a phylogenetic signal in the fruiting of fungi will further amplify variation in resource availability: if several species of fruiting bodies occur together under similar (favorable) conditions, then it also means that they will also each be absent under other (unfavorable) conditions. While arthropods feeding on fungal fruiting bodies are rarely specialized on particular host species, many fungivores feed on sets of related fungal hosts (Orledge and Reynolds 2005, Põldmaa et al. 2016, Koskinen et al. 2019). Such clade-level specificity was also revealed by Koskinen et al. (2022), who found the overall similarity of arthropod communities to decrease with an increasing phylogenetic distance among fungal hosts. For consumers specializing on particular fungal taxa or clades, non-random responses of entire fungal clades to spatiotemporal variation in environmental conditions will therefore introduce further unpredictability in resource availability: not only are fruiting bodies as such short-lived and patchily distributed, but the occurrence and abundance of entire host groups is further clumped in time and space.

However, phylogenetic niche conservatism in ectomycorrhizal fungi also has wider implications for forest ecosystems. At the species level, the production of visible fruiting bodies above ground is a short-term phenomenon that is reflective of earlier, long-term processes below ground (Kauserud et al. 2010, Kim et al. 2021). While these processes are invisible to a human observer, understanding how species-level responses are constrained by the phylogenetic relationships among forest fungi is central for predicting how decomposition, nutrient cycling, and symbioses with forest trees will change as a result of anthropogenic environmental changes (Abrego et al. 2022, Bässler et al. 2022). Clearly, the nature of our current data prevents us from providing

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

in-depth inference of such effects: what we explored were patterns in the occurrence of fruiting bodies, as providing evidence only for the presence but not the absence of fungal mycelia. Here, the ever-increasing availability of molecularly-based assessment of fungal occurrence (Pauvert et al. 2019, Tedersoo et al. 2022), as combined with comprehensive phylogenetic trees (Varga et al. 2019, Li et al. 2021, Kim et al. 2023) will greatly facilitate studies incorporating phylogenetic data into analyses of fungal community ecology. Overall, our findings show how evolutionary history and ecological context are weaved together in shaping modern communities, highlighting the need for ecophylogenetic approaches (Davies 2021) in research on plant–fungus–fungivore networks.

Acknowledgements – We would like to thank Eija Takala and Marjo Kilpinen for their invaluable support. We thank Jari Kouki for valuable insights regarding potential data collection sites. Kari Ratilainen provided excellent feedback and technical support, and Tiina Kolari, Ville Puttonen and Pirita Latja assisted in data collection. We also thank Hanna Tuovila, Outi Laakso and Seppo Huhtinen for providing background knowledge for fungal field identification.
Funding – JK was funded by Bätty Väänäsen rahasto, Emil Aaltosen säätiö, Olvi-säätiö and Oskar Öflunds stiftelse. JK was funded with junior researcher position by University of Eastern Finland. JK was provided with facilities and support from University of Helsinki. NA and TN received funding from Academy of Finland (grant no. 342374 and 294466, respectively).

Author contributions

Janne Koskinen and **Nerea Abregi** share first authorship. **Janne Koskinen**: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (supporting). **Nerea Abrego**: Conceptualization (equal); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Eero Vesterinen**: Project administration (equal). **Tomas Roslin**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Supervision (lead); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Tommi Nyman**: Conceptualization (equal); Methodology (equal); Project administration (lead); Supervision (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.06333.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8sf7m0cqh (Koskinen et al. 2023). Scripts used in the analyses are available in Zenodo (https://doi.org/10.5281/zenodo.6308171).

Supporting information

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

References

Abrego, N., Norberg, A. and Ovaskainen, O. 2017. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. – J. Ecol. 105: 1070–1081.
Abrego, N., Bässler, C., Christensen, M. and Heilmann-Clausen, J. 2022. Traits and phylogenies modulate the environmental responses of wood-inhabiting fungal communities across spatial scales. – J. Ecol. 110: 784–798.
Andrew, C., Heegaard, E., Høiland, K., Senn-Irlet, B., Kuyper, T. W., Krisai-Greilhuber, I., Kirk, P. M., Heilmann-Clausen, J., Gange, A. C., Egli, S., Bässler, C., Büntgen, U., Boddy, L. and Kauserud, H. 2018. Explaining European fungal fruiting phenology with climate variability. – Ecology 99: 1306–1315.
Bässler, C., Ernst, R., Cadotte, M., Heibl, C. and Müller, J. 2014. Near-to-nature logging influences fungal community assembly processes in a temperate forest. – J. Appl. Ecol. 51: 939–948.
Bässler, C., Heilmann-Clausen, J., Andrew, C., Boddy, L., Büntgen, U., Diez, J., Heegaard, E., Egli, S., Gange, A. C., Halvorsen, R., Kauserud, H., Kirk, P. M., Krisai-Greilhuber, I., Kuyper, T. W., Nordén, J., Senn-Irlet, B. and Krah, F. 2022. European mushroom assemblages are phylogenetically structured by temperature. – Ecography 2022: e06206.
Baum, D. A. and Smith, S. D. 2013. Tree thinking: an introduction to phylogenetic biology. – Roberts and Company Publishers.
Beck, H. E., Zimmermann, N. E., McVicar, T. R., Vergopolan, N., Berg, A. and Wood, E. F. 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. – Sci. Data 5: e180214.
Boddy, L., Büntgen, U., Egli, S., Gange, A. C., Heegaard, E., Kirk, P. M., Mohammad, A. and Kauserud, H. 2014. Climate variation effects on fungal fruiting. – Fung. Ecol. 10: 20–33.
Bose, A. K. et al. 2022. Lessons learned from a long-term irrigation experiment in a dry Scots pine forest: impacts on traits and functioning. – Ecol. Monogr. 92: e1507.
Bouckaert, R. et al. 2019. BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. – PLoS Comput. Biol. 15: e1006650.
Bruns, T. D. 2002. Host specificity in ectomycorrhizal communities: what do the exceptions tell us? – Integr. Compar. Biol. 42: 352–359.
Büntgen, U., Kauserud, H. and Egli, S. 2012. Linking climate variability to mushroom productivity and phenology. – Front. Ecol. Environ. 10: 14–19.
Büntgen, U., Peter, M., Kauserud, H. and Egli, S. 2013. Unraveling environmental drivers of a recent increase in Swiss fungi fruiting. – Global Change Biol. 19: 2785–2794.
Butterworth, N. J., Benbow, M. E. and Barton, P. S. 2023. The ephemeral resource patch concept. – Biol. Rev. 98: 697–726.
Cadotte, M., Albert, C. H. and Walker, S. C. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. – Ecol. Lett. 16: 1234–1244.

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Cagnolo, L., Salvo, A. and Valladares, G. 2011. Network topology: patterns and mechanisms in plant–herbivore and host–parasitoid food webs. – J. Anim. Ecol. 80: 342–351.
Cavender-Bares, J., Kozak, K. H., Fine, P. V. A. and Kembel, S. W. 2009. The merging of community ecology and phylogenetic biology. – Ecol. Lett. 12: 693–715.
Chen, L., Zheng, Y., Gao, C., Mi, X.-C., Ma, K.-P., Wubet, T. and Guo, L.-D. 2017. Phylogenetic relatedness explains highly interconnected and nested symbiotic networks of woody plants and arbuscular mycorrhizal fungi in a Chinese subtropical forest. – Mol. Ecol. 26: 2563–2575.
Davies, T. J. 2021. Ecophylogenetics redux. – Ecol. Lett. 24: 1073–1088.
DeBellis, T., Kernaghan, G., Bradley, R. and Widden, P. 2006. Relationships between stand composition and ectomycorrhizal community structure in boreal mixed-wood forests. – Microbial Ecol. 52: 114–126.
Delgado, M. D. M. et al. 2020. Differences in spatial versus temporal reaction norms for spring and autumn phenological events. – Proc. Natl Acad. Sci. USA 117: 31249–31258.
Diez, J. M., James, T. Y., McMunn, M. and Ibáñez, I. 2013. Predicting species-specific responses of fungi to climatic variation using historical records. – Global Change Biol. 19: 3145–3154.
Epps, M. J. and Arnold, A. E. 2019. Interaction networks of macrofungi and mycophagous beetles reflect diurnal variation and the size and spatial arrangement of resources. – Fung. Ecol. 37: 48–56.
Erlandson, S. R., Savage, J. A., Cavender-Bares, J. M. and Peay, K. G. 2016. Soil moisture and chemistry influence diversity of ectomycorrhizal fungal communities associating with willow along an hydrologic gradient. – FEMS Microbiol. Ecol. 92: fiv148.
Forister, M. L. et al. 2015. The global distribution of diet breadth in insect herbivores. – Proc. Natl Acad. Sci. USA 112: 442–447.
Gelman, A. and Rubin, D. B. 1992. Inference from iterative simulation using multiple sequences. – Stat. Sci. 7: 15–51.
Hanski, I. 1989. Fungivory: fungi, insects and ecology. – In: Wilding, N., Collins, N. M., Hammon, P. M. and Webber, J. F., (eds), Insect–fungus interactions. Academic Press., pp. 25–68.
Heegaard, E., Boddy, L., Diez, J. M., Halvorsen, R., Kauserud, H., Kuyper, T. W., Bässler, C., Büntgen, U., Gange, A. C., Krisai-Greilhuber, I., Andrew, C. J., Ayer, F., Høiland, K., Kirk, P. M. and Egli, S. 2017. Fine-scale spatiotemporal dynamics of fungal fruiting: prevalence, amplitude, range and continuity. – Ecography 40: 947–959.
Hibbett, D. S., Gilbert, L. and Donoghue, M. J. 2000. Evolutionary instability of ectomycorrhizal symbioses in basidiomycetes. – Nature 407: 506–508.
Hotanen, J.-P., Nousiainen, H., Mäkipää, R., Reinikainen, A. and Tonteri, T. 2008. Metsätyypit - Opas kasvupaikkojen luokitteluun. – Metsäkustannus oy, Hämeenlinna.
Ishida, T. A., Nara, K. and Hogetsu, T. 2007. Host effects on ectomycorrhizal fungal communities: insight from eight host species in mixed conifer–broadleaf forests. – New Phytol. 174:430–440.
Jaenike, J. 1990. Host specialization in phytophagous insects. – Annu. Rev. Ecol. Syst. 21: 243–273.
Kauserud, H., Stige, L. C., Vik, J. O., Okland, R. H., Hoiland, K. and Stenseth, N. C. 2008. Mushroom fruiting and climate change. – Proc. Natl Acad. Sci. USA 105: 3811–3814.
Kauserud, H., Heegaard, E., Semenov, M. A., Boddy, L., Halvorsen, R., Tige, L. C. S., Sparks, T. H., Gange, A. C. and Stenseth, N. C. 2010. Climate change and spring-fruiting fungi. – Proc. R. Soc. B 277: 1169–1177.
Kauserud, H., Heegaard, E., Büntgen, U., Halvorsen, R., Egli, S., Senn-Irlet, B., Krisai-Greilhuber, I., Dämon, W., Sparks, T., Nordén, J., Høiland, K., Kirk, P., Semenov, M., Boddy, L. and Stenseth, N. C. 2012. Warming-induced shift in European mushroom fruiting phenology. – Proc. Natl Acad. Sci. USA 109: 14488–14493.
Kim, S., Axelsson, E. P., Girona, M. M. and Senior, J. K. 2021. Continuous-cover forestry maintains soil fungal communities in Norway spruce dominated boreal forests. – For. Ecol. Manage. 480: e118659.
Kim, D., Gilchrist, C. L. M., Chun, J. and Steinegger, M. 2023. UFCG: database of universal fungal core genes and pipeline for genome-wide phylogenetic analysis of fungi. – Nucl. Acids Res. 51:D777–D784.
Koskinen, J., Roslin, T., Nyman, T., Abrego, N., Michell, C. and Vesterinen, E. J. 2019. Finding flies in the mushroom soup: host specificity of fungus-associated communities revisited with a novel molecular method. – Mol. Ecol. 28: 190–202.
Koskinen, J. S., Abrego, N., Vesterinen, E. J., Schulz, T., Roslin, T. and Nyman, T. 2022. Imprints of latitude, host taxon, and decay stage on fungus-associated arthropod communities. – Ecol. Monogr. 92: e1516.
Koskinen, J., Abrego, N., Vesterinen, E., Roslin, T. and Nyman, T. 2023. Data from: Environmental responses of fruiting fungal communities are phylogenetically structured. – Dryad Digital Repository, https://doi.org/10.5061/dryad.8sf7m0cqh.
Krebs, C. J., Carrier, P., Boutin, S., Boonstra, R. and Hofer, E. 2008. Mushroom crops in relation to weather in the southwestern Yukon. – Botany 86: 1497–1502.
Kurina, O., Unap, E. and Põldmaa, K. 2015. Two new Neuratelia Rondani (Diptera, Mycetophilidae) species from western palaearctic: a case of limited congruence between morphology and DNA sequence data. – ZooKeys 129: 105–129.
Kuuluvainen, T. 2009. Forest Management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. – Ambio 38: 309–315.
Kuuluvainen, T., Tahvonen, O. and Aakala, T. 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. – Ambio 41: 720–737.
Lahti, T. and Väisänen, R. A. 1987. Ecological gradients of boreal forests in south Finland: an ordination test of Cajander's forest site type theory. – Vegetatio 68: 145–156.
Lang, C., Seven, J. and Polle, A. 2011. Host preferences and differential contributions of deciduous tree species shape mycorrhizal species richness in a mixed central European forest. – Mycorrhiza 21: 297–308.
Levula, J., Ilvesniemi, H. and Westman, C. 2003. Relation between soil properties and tree species composition in a Scots pine–Norway spruce stand in southern Finland. – Silva Fenn. 37: 205–218.
Li, Y., Steenwyk, J. L., Chang, Y., Wang, Y., James, T. Y., Stajich, J. E., Spatafora, J. W., Groenewald, M., Dunn, C. W., Hittinger, C. T., Shen, X.-X. and Rokas, A. 2021. A genome-scale phylogeny of the kingdom Fungi. – Curr. Biol. 31: 1653–1665.
Liu, X., Liang, M., Etienne, R. S., Wang, Y., Staehelin, C. and Yu, S. 2012. Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. – Ecol. Lett. 15: 111–118.
Losos, J. B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. – Ecol. Lett. 11: 995–1003.
Lunde, L. F., Birkemoe, T., Kauserud, H., Boddy, L., Jacobsen, R. M., Morgado, L., Sverdrup-Thygeson, A. and Maurice, S. 2022. DNA metabarcoding reveals host-specific communities of arthropods residing in fungal fruit bodies. – Proc. R. Soc. B 289: e20212622.
Mäkisara, K., Katila, M. and Peräsaari, J. 2019. The multi-source national forest intentory of Finland – Methods and results

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

2015. – In: Natural resources and bioeconomy studies 8/2019. Natural Resources Institute Finland, Helsinki. 57 p. https://jukuri.luke.fi/handle/10024/543826.
Melvin, A. M., Mack, M. C., Johnstone, J. F., David McGuire, A., Genet, H. and Schuur, E. A. G. 2015. Differences in ecosystem carbon distribution and nutrient cycling linked to forest tree species composition in a mid-successional boreal forest. – Ecosystems 18: 1472–1488.
Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L, Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I., Gough, L. and Kellogg, W. K. 2001. What is the observed relationship between species richness and productivity? – Ecology 82: 2381–2396.
Mueller, G. M., Schmit, J. P., Leacock, P. R., Buyck, B., Cifuentes, J., Desjardin, D. E., Halling, R. E., Hjortstam, K., Iturriaga, T., Larsson, K.-H., Lodge, D. J., May, T. W., Minter, D., Rajchenberg, M., Redhead, S. A., Ryvarden, L., Trappe, J. M., Watling, R. and Wu, Q. 2007. Global diversity and distribution of macrofungi. – Biodivers. Conserv. 16: 37–48.
Newton, A. C. and Haigh, J. M. 1998. Diversity of ectomycorrhizal fungi in Britain: a test of the species–area relationship, and the role of host specificity. – New Phytol. 138: 619–627.
Norberg, A. et al. 2019. A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. – Ecol. Monogr. 89: e01370.
O'Connell, T. and Bolger, T. 1997. Stability, ephemerality and dispersal ability: microarthropod assemblages on fungal sporophores. – Biol. J. Linn. Soc. 62: 111–131.
Orledge, G. M. and Reynolds, S. E. 2005. Fungivore host-use groups from cluster analysis: patterns of utilisation of fungal fruiting bodies by ciid beetles. – Ecol. Entomol. 30: 620–641.
Osawa, N., Toft, R., Tuno, N., Kadowaki, K., Fukiharu, T., Buchanan, P. K. and Tanaka, C. 2011. The community structures of fungivorous insects on *Amanita muscaria* in New Zealand. – N. Z. Entomol. 34: 40–44.
Ovaskainen, O. and Abrego, N. 2020. Joint species distribution modelling: with applications in R. – Cambridge Univ. Press.
Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T. and Abrego, N. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. – Ecol. Lett. 20: 561–576.
Paradis, E. and Schliep, K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. – Bioinformatics 35: 526–528.
Pauvert, C., Buée, M., Laval, V., Edel-Hermann, V., Fauchery, L., Gautier, A., Lesur, I., Vallance, J. and Vacher, C. 2019. Bioinformatics matters: the accuracy of plant and soil fungal community data is highly dependent on the metabarcoding pipeline. – Fung. Ecol. 41: 23–33.
Pearce, J. and Ferrier, S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. – Ecol. Model. 133: 225–245.
Pinna, S., Gévry, M.-F., Côté, M. and Sirois, L. 2010. Factors influencing fructification phenology of edible mushrooms in a boreal mixed forest of eastern Canada. – For. Ecol. Manage. 260: 294–301.
Poisot, T., Bever, J. D., Nemri, A., Thrall, P. H. and Hochberg, M. E. 2011. A conceptual framework for the evolution of ecological specialisation. – Ecol. Lett. 14: 841–851.
Põldmaa, K., Jürgenstein, S., Bahram, M., Teder, T. and Kurina, O. 2015. Host diversity and trophic status as determinants of species richness and community composition of fungus gnats. – Basic Appl. Ecol. 16: 46–53.
Põldmaa, K., Kaasik, A., Tammaru, T., Kurina, O., Jürgenstein, S. and Teder, T. 2016. Polyphagy on unpredictable resources does not exclude host specialization: insects feeding on mushrooms. – Ecology 97: 2824–2833.
Polevoi, A., Jakovlev, J. and Zaitzev, A. 2006. Fungus gnats (Diptera Bolitophilidae, Diadocidiidae, Keroplatidae and Mycetophilidae) new to Finland. – Entomol. Fenn. 17: 161–169.
Saarsalmi, A. and Mälkönen, E. 2001. Forest fertilization research in Finland: a literature review. – Scand. J. For. Res. 16: 514–535.
Salo, P., Niemelä, T., Nummela-Salo, U. and Ohenoja, E. 2005. Suomen helttasienten ja tattien ekologia, levinneisyys ja uhanalaisuus. – In: Ohenoja, E. (ed.), Suomen ympäristökeskus.
Sato, H., Morimoto, S. and Hattori, T. 2012. A thirty-year survey reveals that ecosystem function of fungi predicts phenology of mushroom fruiting. – PLoS One 7: e49777.
Ståhls, G., Ribeiro, E. and Hanski, I. 1989. Fungivorous *Pegomya* flies: spatial and temporal variation in a guild of competitors. – Ann. Zool. Fenn. 26: 103–112.
Sterkenburg, E., Clemmensen, K. E., Lindahl, B. D. and Dahlberg, A. 2019. The significance of retention trees for survival of ectomycorrhizal fungi in clear-cut Scots pine forests. – J. Appl. Ecol. 56: 1367–1378.
Straatsma, G. and Krisai-Greilhuber, I. 2003. Assemblage structure, species richness, abundance, and distribution of fungal fruit bodies in a seven year plot-based survey near Vienna. – Mycol. Res. 107: 632–640.
Straatsma, G., Ayer, F. and Egli, S. 2001. Species richness, abundance, and phenology of fungal fruit bodies over 21 years in a Swiss forest plot. – Mycol. Res. 105: 515–523.
Swenson, N. G. 2019. Phylogenetic ecology: a history, critique and remodeling. – Univ. of Chicago Press.
Tedersoo, L., Jairus, T., Horton, B. M., Abarenkov, K., Suvi, T., Saar, I. and Kõljalg, U. 2008. Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. – New Phytol. 180: 479–490.
Tedersoo, L., Suvi, T., Jairus, T., Ostonen, I. and Põlme, S. 2009. Revisiting ectomycorrhizal fungi of the genus Alnus: differential host specificity, diversity and determinants of the fungal community. – New Phytol. 182: 727–735.
Tedersoo, L. et al. 2014. Global diversity and geography of soil fungi. – Science 346: e1256688.
Tedersoo, L., Bahram, M., Zinger, L., Nilsson, R. H., Kennedy, P. G., Yang, T., Anslan, S. and Mikryukov, V. 2022. Best practices in metabarcoding of fungi: from experimental design to results. – Mol. Ecol. 31: 2769–2795.
Thorn, S., Müller, J., Bässler, C., Gminder, A., Brandl, R. and Heibl, C. 2015. Host abundance, durability, basidiome form and phylogenetic isolation determine fungivore species richness. – Biol. J. Linn. Soc. 114: 699–708.
Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., Jonge, M. M. J., Oksanen, J. and Ovaskainen, O. 2020. Joint species distribution modelling with the R-package Hmsc. – Methods Ecol. Evol. 11: 442–447.
Tjur, T. 2009. Coefficients of determination in logistic regression models – a new proposal: the coefficient of discrimination. – Am. Stat. 63: 366–372.
Toljander, J. F., Eberhardt, U., Toljander, Y. K., Paul, L. R. and Taylor, A. F. S. 2006. Species composition of an ectomycorrhizal fungal community along a local nutrient gradient in a boreal forest. – New Phytol. 170: 873–884.

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Tomao, A., Antonio Bonet, J., Castaño, C. and De-Miguel, S. 2020. How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. – For. Ecol. Manage. 457:117678.

Tonteri, T., Hotanen, J. P. and Kuusipalo, J. 1990. The Finnish forest site type approach: ordination and classification studies of mesic forest sites in southern Finland. – Vegetatio 87: 85–98.

Treseder, K. K., Bent, E., Borneman, J. and McGuire, K. L. 2014. Shifts in fungal communities during decomposition of boreal forest litter. – Fung. Ecol. 10: 58–69.

Twieg, B. D., Durall, D. M. and Simard, S. W. 2007. Ectomycorrhizal fungal succession in mixed temperate forests. – New Phytol. 176: 437–447.

Varga, T. et al. 2019. Megaphylogeny resolves global patterns of mushroom evolution. – Nat. Ecol. Evol. 3: 668–678.

Webb, C. O., Ackerly, D. D., McPeek, M. A. and Donoghue, M. J. 2002. Phylogenies and community ecology. – Annu. Rev. Ecol. Syst. 33: 475–505.

Weiblen, G. D., Webb, C. O., Novotny, V., Basset, Y. and Miller, S. E. 2006. Phylogenetic dispersion of host use in a tropical insect herbivore community. – Ecology 87: 62–75.

White, E. R. 2019. Minimum time required to detect population trends: the need for long-term monitoring programs. – BioScience 69: 40–46.

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

16000587, 0, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/ecog.06333 by University Of Jyväskylä Library, Wiley Online Library on [16/08/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License