



Morphological traits predict host-tree specialization in wood-inhabiting fungal communities

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ARTICLE INFO

Article history:

Received 10 December 2018

Received in revised form

8 August 2019

Accepted 13 August 2019

Available online 15 October 2019

Corresponding Editor: Thomas W. Crowther

Index descriptors:

Broadleaved

Coniferous

Dead wood

Functional trait

Fruit body

Morphology

Specialization

Spore

Tree species

ABSTRACT

Tree species is one of the most important determinants of wood-inhabiting fungal community composition, yet its relationship with fungal reproductive and dispersal traits remains poorly understood. We studied fungal communities (total of 657 species) inhabiting broadleaved and coniferous dead wood (total of 192 logs) in 12 semi-natural boreal forests. We utilized a trait-based hierarchical joint species distribution model to examine how the relationship between dead wood quality and species occurrence correlates with reproductive and dispersal morphological traits. Broadleaved trees had higher species richness than conifers, due to discomycetoids and pyrenomycetoids specializing in them. Resupinate and pileate species were generally specialized in coniferous dead wood. Fungi inhabiting broadleaved trees had larger and more elongated spores than fungi in conifers. Spore size was larger and spore shape more spherical in species occupying large dead wood units. These results indicate the selective effect of dead wood quality, visible not only in species diversity, but also in reproductive and dispersal traits.

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1. Introduction

Functional traits in fungi can be defined as any morphological, physiological or phenological feature affecting the fitness of an individual fungus (Dawson et al., 2018). Knowledge of the relationship between species traits and species responses to environmental conditions provides understanding of the mechanisms influencing community assembly in different environments (McGill et al., 2006; Weiher et al., 2011). Although trait-based assessments of community-level responses in the fungal kingdom have lagged

behind that of animal and plant communities, currently fungal ecological research is undergoing a proliferation of empirical and conceptual studies addressing this issue (Peay et al., 2008; Crowther et al., 2014; Aguilar-Trigueros et al., 2015; Dawson et al., 2018).

Wood-inhabiting fungi constitute a highly species-rich and functionally important group regulating nutrient cycling in forest ecosystems (Dowding, 1981; Boddy et al., 2008; Stokland et al., 2012; Kahl et al., 2017). Wood-inhabiting fungal communities strongly respond to changes in environmental variables such as climatic conditions (Lindblad, 2001; Heilmann-Clausen and Christensen, 2005; Boddy and Heilmann-Clausen, 2008; Bässler et al., 2010; Heilmann-Clausen et al., 2014; Pouska et al., 2017), resource quality (Renvall, 1995; Küffer et al., 2008; Abrego and

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Salcedo, 2013; Juutilainen et al., 2017) and habitat naturalness (Bader et al., 1995; Sippola and Renvall, 1999; Sippola et al., 2001; Lõhmus, 2011; Abrego and Salcedo, 2014). Given the strong responses of wood-inhabiting fungal communities to the environment and their high taxonomical and morphological diversity, many recent studies have focused on understanding how fungal functional diversity is influenced by environmental conditions (e.g. Kauserud et al., 2011; Nordén et al., 2013; Bässler et al., 2014; Norros et al., 2015; Abrego et al., 2017; Caiafa et al., 2017; Calhim et al., 2018).

Traits related to spore and fruit body morphology are among the very few traits that are comprehensively available for wood-inhabiting fungi (Dawson et al., 2018). In previous studies, these traits have been found to be important in determining the occurrences of fungal species on dead wood of different sizes and decay stages (Nordén et al., 2013; Abrego et al., 2017). In terms of fruit body morphology, wood-inhabiting fungal species with robust pileate and resupinate fruit bodies require large dead wood (Bässler et al., 2016; Abrego et al., 2017), while fungi with ramarioid fruit bodies and resupinate polypores are correlated with strongly decayed wood (Abrego et al., 2017). In terms of spore morphology, dead wood in advanced decay stages harbours more wood-inhabiting fungal species with thick-walled and ornamented spores (Abrego et al., 2017). The links between spore size and dead wood characteristics, however, remain unresolved. Nordén et al. (2013) found that spore size slightly decreased as log size increased, while Abrego et al. (2017) discovered that larger logs hold species with somewhat larger spores. The discrepancy in the results between the cited studies most likely arises from the differences in the taxonomical coverage and host-tree species.

Host-tree identity is an important determinant of the species composition of wood-inhabiting fungal communities (Lumley et al., 2001; Rajala et al., 2010; Krah et al., 2018b; Ordynets et al., 2018). In some cases, host-tree identity can determine wood-inhabiting fungal diversity more than microclimatic conditions and local dead wood amount or heterogeneity (Krah et al., 2018b). In general, broadleaved and coniferous dead trees hold quite distinct fungal communities, broadleaved trees being more species rich (Rajala et al., 2010; Stokland, 2012a; Abrego et al., 2016). According to Rajala et al. (2010), the higher species richness in broadleaved trees results from a higher diversity of Ascomycota. Despite the clear influence of host-tree species on wood-inhabiting fungal community composition, to our knowledge, the effect of host-tree identity on the functional composition of wood-inhabiting fungal communities has not been thoroughly investigated (but see Kauserud et al., 2008 for polypores).

Fennoscandian boreal forests represent a suitable ecosystem for studying the effect of host-tree identity on wood-inhabiting fungal communities. These forests are composed of a relatively small set of broadleaved and coniferous tree species, which all produce high amounts of dead wood (Esseen et al., 1997; Siitonen, 2001). In the southern boreal zone in Finland, (Ahti et al., 1968), the dominant tree species are Norway spruce (*Picea abies*, hereafter called spruce), Scots pine (*Pinus sylvestris*, pine), birches (*Betula* spp.) and European aspen (*Populus tremula*, aspen). While the fungal communities inhabiting dead spruce wood have been extensively studied (Kruys et al., 1999; Edman et al., 2004; Kubartová et al., 2012; Ottosson et al., 2015), the fungal communities inhabiting the other dominant tree species, especially birch and aspen, have been less studied (but see Lumley et al., 2001; Rajala et al., 2010; Ruokolainen et al., 2018).

The main aim of the present study is to evaluate how host-tree characteristics relate to the morphological composition of fruiting wood-inhabiting fungi. For this, we used an extensive dataset consisting of 657 species of non-lichenized fungi producing sexual

fruit bodies. We surveyed large logs (base diameter > 15 cm) belonging to the four dominant tree species in Fennoscandian boreal forests (spruce, pine, birch and aspen) in 12 semi-natural forest sites. More specifically, we determined how much of the variation in species occurrences is explained by the host-tree species and volume, and how much of the variation in community composition is explained by the morphological characteristics of the fruit bodies and spores.

We expected differences in trait composition to arise from the differences in the wood composition and distributional patterns of coniferous versus broadleaved trees. Coniferous and broadleaved wood differ in their chemical and physical characteristics, coniferous wood having generally higher amounts of toxic compounds for saproxylic organisms (Stokland, 2012a). In terms of distributional patterns, in Finnish boreal forests broadleaved trees are less abundant and show more clumped distributions than coniferous trees. Thus, the fungal species growing on each of the wood types should be well adapted to colonize and exploit the wood resources accordingly.

We hypothesized that the manner by which species exploit the wood resources is reflected in the morphological traits, as these may be linked to resource-use and dispersal strategies. Our main working hypotheses related to fruit body morphology are: (1) species producing small-sized fruit bodies, such as some Ascomycota, are most prevalent on broadleaved wood because unlike other fungi, they are able to decompose bark through soft rot, and bark is more abundant in decomposing broadleaved logs than in coniferous logs; (2) Agaricoids are most prevalent on broadleaved wood, because they have lignin-decomposing enzymes (causing white rot) which are especially efficient in exploiting wood of broadleaved trees (Krah et al., 2018a); (3) Species with pileate and resupinate fruit bodies are expected to be equally prevalent in broadleaved and coniferous logs, because these include lineages which equally well decompose cellulose and mostly occur on coniferous logs (i.e. brown-rot fungi), or mainly decompose lignin and mostly occur on broadleaved logs (i.e. white-rot fungi) (Krah et al., 2018a). Our working hypothesis about how spore morphology is linked to host-tree is that (4) coniferous trees host species with smaller spores because their wood is easier to penetrate, compared to wood of broadleaved trees (Kauserud et al., 2008); and (5) broadleaved trees with clumped distributions in the forest landscape (e.g. aspen) also have species with small-sized spores, because they should be able to disperse longer distances (Norros et al., 2014).

2. Materials and methods

2.1. Study sites and design

We carried out the study in central Finland, which belongs to the southern boreal vegetation zone (Ahti et al., 1968). All of the 12 study sites were spruce dominated forests characterized by *Myrtillus* or *Oxalis-Myrtillus* forest types (Cajander, 1949). All study sites were semi-natural, and varied relatively little in their age and management history. To control for the quality variation among the study sites in the analyses, we used a forest naturalness index described in Supplementary Material 1. From each forest, we chose four large (base diameter ≥ 15 cm), fallen logs of birch, spruce, pine and aspen (these species produce the majority of the coarse dead wood (diameter at breast height > 10 cm) in the area), that had died naturally, in total 16 logs at each site and 192 logs in the whole study. To minimize the variation in log quality, only logs that had decay stage between 2 and 4 (Renvall, 1995), and moss cover < 50% were selected. For each log, we measured the base and top diameter and the length of the logs, and calculated the volume by using the

formula of a truncated cone.

2.2. Fungal data collection and identification

We thoroughly surveyed the fungal sexual fruit bodies on each study log. All fruit bodies from the same taxon within a study log were considered as one occurrence of the taxon. To better account for the species-specific variation in the timing and duration of fruit body production (see Purhonen et al., 2017), two subsequent inspections were conducted for each log. The first inspection was performed between 21st of May and 6th of June, and the second between 20th of August and 26th of September. To enable multiple surveys of the same logs, moss and bark cover were left intact and the logs were not turned over. The fruit bodies were identified to species in the field or collected for microscopic identification (about 7500 specimens collected). When species-level identification was not possible, we identified the specimens to the highest possible taxonomical level and named them with unique labels according to their morphology (e.g. pyrenomycete sp1, sp2 etc.). Some of the classified taxa include multiple species (i.e. species complexes), as their taxonomy is still unresolved. The nomenclature follows Index Fungorum (Royal Botanic Gardens Kew et al., 2015).

2.3. Fungal trait data collection

The identified species were classified into seven groups according to their fruit body morphology; agaricoids were species having a soft pileus and stipe (also pleurotoid fungi were grouped here). We classified species with disc-to cup-shaped fruit bodies as discomycetoids. Pileates were species that grow as crusts over the log surface when young but the majority of the fruit body is a pileus or erected on the edges when adults. As pyrenomycetoids, we classified those fungi whose fruit bodies were individual round or flask shaped bags (i.e. perithecia). Ramarioids had fruit bodies with a branched structure. As resupinates, we classified those species that mostly grow as a crust over the log surface, but some may be slightly pileate as well. Stromatoids were fungi whose fruit bodies were round or flask shaped bags embedded in a mass-like structure.

For the spore morphology, we gathered information about spore length, width and presence of ornamentation (meaning that the surface of the spore is not smooth but has some texture) from the literature. For those specimens that we could only identify to the genus level, but still recognize as unique taxa, we measured the spore size and noted the shape during the identification procedure (see detailed trait variable data and literature used for the spore morphology in Supplementary Material 2).

To account for phylogenetic relationships between species, the phylogenetic relationships were estimated based on the taxonomic levels. As the data include a large number of poorly known species and species that are not yet described, it was not possible to use a quantitative phylogenetic tree. For each species, we included the taxonomic levels of the genus, family, order and class, using the Index Fungorum and Mycobank online databases (International Mycological Association, 2017; Royal Botanic Gardens Kew et al., 2017).

2.4. Statistical analyses

We analyzed the data with Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017). HMSC is a joint species distribution modelling framework (Warton et al., 2015) that enables the integration of data on species occurrences or abundances, environmental covariates, species traits and phylogenetic relationships, as well as the spatio-temporal nature of the study

design (Ovaskainen et al., 2017).

In the HMSC analyses, the $n_y \times n_s$ response matrix **Y** consisted of presence-absences of the $n_s = 657$ species observed in the $n_y = 192$ logs, called henceforth sampling units. We modelled **Y** with probit-regression, including in the predictor matrix **X** the environmental covariates of the tree species (categorical variable with four levels: aspen, birch, spruce and pine), the size of the dead wood unit (log-transformed volume), decay class (categorical variable with two levels: decay class 2; and decay classes 3 and 4 combined, as only four logs had decay class four), and the forest naturalness index. We modelled the mapping from **X** to **Y** as a function of species traits and phylogenetic relationships following Abrego et al. (2017) and Ovaskainen et al. (2017). We included in the matrix of species traits **T** the fruit body morphology (categorical variable with seven levels: agaricoid, discomycetoid, pileate, pyrenomycetoid, ramarioid, resupinate, stromatoid), the presence of ornamentation on the spores (categorical variable with two levels: yes or no), spore shape (log-transformed ratio of length to width), and spore size (log-transformed volume). In the absence of a quantitative phylogeny, we followed Abrego et al. (2017) and used as a proxy for the phylogenetic correlation matrix **C** a taxonomical correlation matrix, constructed from the five levels of class, order, family, genus and species, and assumed equal branch length for each level. As a community-level random effect, implemented through a latent variable approach (Ovaskainen et al., 2016, 2017), we included the study site, with 12 levels.

We fitted the model to the data using the HMSC-R package (Tikhonov et al., 2019). We assumed the default prior distributions, and sampled the posterior distribution for 150*thinning iterations, out of which the first 50*thinning iterations were discarded as burn-in. We used thinning = 100 and thus run the MCMC chain for a total of 15,000 iterations. We assessed the convergence of the MCMC chain visually, and examining the convergence of the results between thinning = 1, thinning = 10, and thinning = 100.

To examine host-tree specialization at the levels of species and functional groups, we used the fitted model to predict species occurrences to new sampling units that were standardized to be of average size and decay stage and consisted of each of the four host-tree species. To examine host-tree specialization at the species level, we used these predictions to classify the host-tree use of each fungal species to one of the following seven classes: generalist, coniferous generalist, spruce specialist, pine specialist, broadleaved generalist, birch specialist, and aspen specialist. We first classified the species as generalists, broadleaved species or coniferous species by asking whether the predicted mean occurrence probability over broadleaved trees (birch and aspen) was smaller or greater than that for coniferous trees (pine and spruce) with at least 95% posterior probability. We further classified the broadleaved species as aspen specialists, birch specialists or broadleaved generalists by examining if the occurrence probability on aspen was smaller or greater than that for birch with at least 95% posterior probability. Similarly, we classified the coniferous species as spruce specialists, pine specialists and coniferous generalists.

To examine host-use specialization at the functional group level, we counted for each seven host-tree use classes the numbers of species belonging to each of the seven fruit body types. We then asked if a particular fruit body type was over- or under-represented in a given host-tree type by conducting a randomization test, in which we randomly permuted the fruit body types among the species, and examined if the observed value was greater or smaller than the 95% quantile in 1000 randomizations. To examine the association among host-tree use and spore-related traits (presence of ornamentation and the shape and size of spores), we computed the posterior distributions of community-weighted mean traits for species predicted to occur on each of the four tree species.

3. Results

3.1. Morphological traits and species richness

In total, we recorded 657 species, which occurred 5714 times (Supplementary Material 2). A large proportion of the species was resupinates (288 species, 44%), followed by discomycetes (148, 22.5%), agaricoids (73, 11%), pyrenomycetoids (71, 11%), pileates (49, 7%), stromatoids (18, 3%), and ramarioids (10, 1.5%).

Aspen dead wood had the highest fungal species richness (239 spp.), followed by birch (221), spruce (209) and pine (186). All tree species shared 68 species, on top of which the two broadleaved species shared 107 species, the two conifers shared 70, whereas all other combinations of coniferous and broadleaved tree species shared less than 20 fungal species. Discomycetoids, pyrenomycetoids, ramarioids and stromatoids had significantly higher species richness on broadleaved host-trees than on conifers (Supplementary Material 3).

Spore size (volume) and shape (length/width) showed a weak but statistically significant negative association (in linear regression, $p = 0.02$, $R^2 = 0.008$). While pyrenomycetoids had the largest and most elongated spores, agaricoids had large and spherical spores, whereas pileates and resupinates had the smallest spores (Fig. 1).

3.2. Effects of environmental variables on community composition

The fitted joint species distribution model explained 6% of the variation in the fungal community composition, as measured by the average Tjur (2009) R^2 value over the species. Of the variables included in the model, host-tree species was by far the most important one, as 71% of the explained variation in species occurrence was attributed to it. The percentages of explained variation attributed to other variables were 15% for log-characteristics (size and decay class), 5% for forest naturalness, and 9% for the random effect of the site. Considering only associations that had at least 95% posterior support, the occurrence probability of 86 species increased and of 0 species decreased with the size of the log, 16 species were most prevalent in decay class 3 and 11 species in decay class 2, and the occurrence probability of 10 species increased and of 1 species decreased with the increasing value of the naturalness index.

Among the 293 species that occurred at least four times in the

data, 66 were generalists, 95 broadleaved generalists, 30 birch specialists, 14 aspen specialists, 41 coniferous specialists, 27 spruce specialists and 20 pine specialists (Fig. 2).

3.3. Effects of morphological traits on the responses to the environment

The traits explained 7% of the variation in the species responses to the environmental variables. The posterior mean of the phylogenetic signal parameter ρ was 0.20 and its 95% credibility interval was [0.11, 0.35]. As the prior for ρ has probability mass of 0.5 at $\rho = 0$ (no phylogenetic signal) and the remaining probability is distributed evenly in [0, 1], the model revealed a moderate but

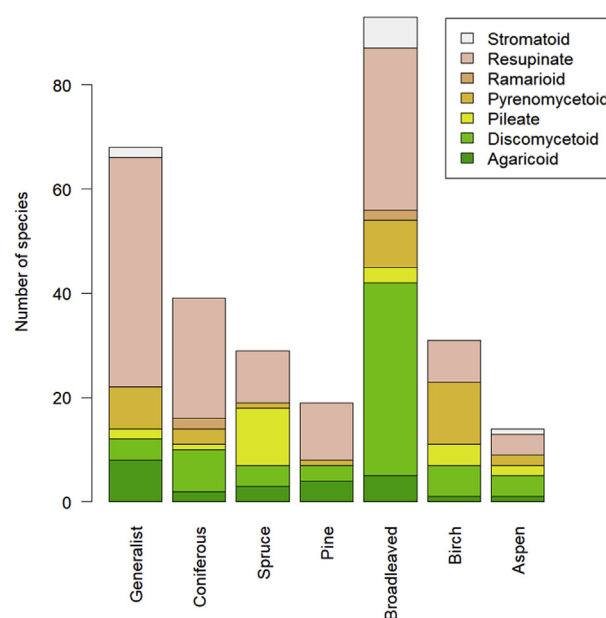


Fig. 2. Numbers of host-tree generalist and specialist fungal species. The bars show the numbers of fungal species classified to the seven host-tree specialization classes, with colours representing different fruit body types. Note that the figure includes only those species that occur at least four times in the data, as reliable classification for host-tree specialization is not possible for rare species.

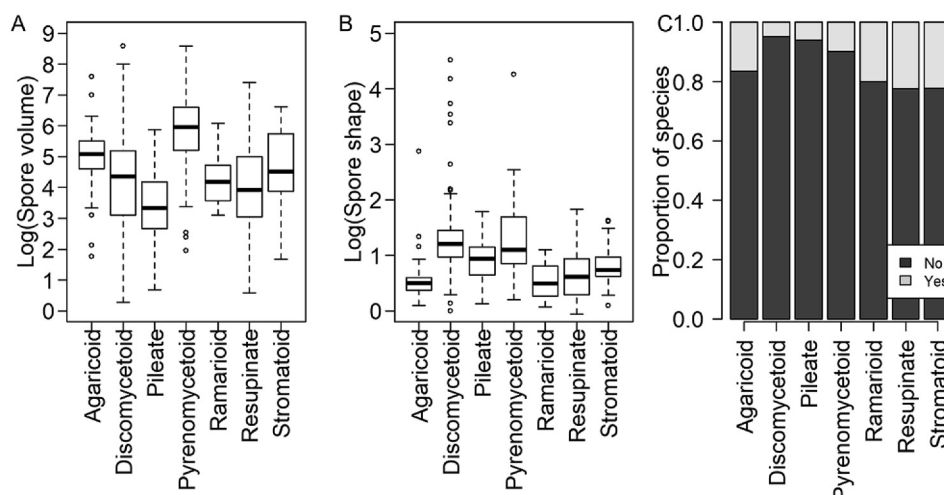


Fig. 1. Relationship between spore morphological traits and fruit body types. The relationship between (A) the fruit body type and spore volume, (B) spore shape, (C) and spore ornamentation.

statistically well supported phylogenetic signal in species responses to environmental covariates. In other words, phylogenetically (taxonomically) related species showed more similar responses to the environmental covariates than could be predicted solely based on their traits. We recorded a large number of non-random associations between host-tree use and fruit body type (Fig. 3). In particular, species with resupinate fruit bodies were typically conifer generalists, while species with pileate fruit bodies were often specific to spruce. Species with discomycetoid fruit bodies were typically broadleaved generalists, whereas species with pyrenomycetoid fruit bodies were often birch specialists.

The fungal species occurring on broadleaved dead wood had on average larger spores than those occurring on coniferous dead wood (Fig. 4A). The fungal species occurring on aspen had the most elongated spores, whereas those occurring on spruce had the most spherical spores (Fig. 4B). The proportion of species with ornamented spores varied between 12% and 16% on all host-trees, with birch having the largest and spruce the smallest proportion of species with ornamented spores (Fig. 4C). Larger logs had larger and more spherical spores, whereas smaller logs had smaller and more elongated spores (Fig. 4D and E). Spore ornamentation did not vary with log size (Fig. 4F).

4. Discussion

Our study shows that the occurrence of fungal species in dead wood with different characteristics relates to the morphological traits of the fungal fruit bodies and sexual spores. While it is well known that many wood-inhabiting fungal species are specific to certain host-tree species (Stokland et al., 2004; Küffer et al., 2008; Berglund et al., 2011; Stokland, 2012a), to our knowledge, this is the first time that the importance of the fruit body and spore morphology in determining host-tree specialization is revealed. We next discuss in turn, how and why fruit body and spore morphology are linked to host-tree identity.

Specialization to host-tree species was related to fruit body morphology. In line with our hypothesis that species developing small-sized fruit bodies from the Ascomycota lineages are more prevalent on broadleaved wood, we found discomycetes to be specialized to broadleaved trees in general, and pyrenomycetes to birch in particular. This association may relate to the fact that broadleaved dead wood generally has a higher proportion of bark, which is decomposed most efficiently through the so called soft-rot

carried out by some Ascomycota species (Stokland, 2012b). While we expected species with pileate and resupinate fruit bodies to be equally prevalent in broadleaved and coniferous wood, we found resupinate species to be specific to conifer tree species in general and pileates to spruce in particular. Because of the small-scale of our study (forests from central Finland), it remains to be tested by larger scale studies whether this is a general pattern in wood-inhabiting fungal communities.

Our results also revealed an association between host-tree species and spore size. Fungal species on broadleaved trees had on average larger spores than those inhabiting conifers. This result is in line with Kauserud et al. (2008) who found that polypore species inhabiting broadleaved dead wood had significantly larger spores than species inhabiting coniferous dead wood. They speculated that because coniferous trees are evolutionary older, their wood is easier to penetrate and thus colonizing spores do not need as much energy and inoculum potential as spores colonizing broadleaved trees. Our results show that this may also relate to the relationship between fruit body morphology and spore size, as pyrenomycetoids had on average the largest and most elongated spores, and they were also as a group specialized on broadleaved trees (birch in particular).

We expected aspen dead trees to have species with smaller spores, because these trees show clustered and isolated distributional patterns in the boreal forest landscape, and smaller spores are able to disperse larger distances (Norros et al., 2014). Yet, our results showed the opposite, the fungal species occurring on broadleaved dead wood having on average larger, and more specifically more elongated, spores. Some studies have suggested that spore elongation increases attachment to substrates (Ingold, 1965; Calhim et al., 2018). It remains to be tested what is the primary reason for larger spore size on species inhabiting broadleaved trees.

Considering the relationship between log characteristics and spore morphology, previous studies have reported weak and/or contrasting results (e. g. Nordén et al., 2013; Abrego et al. 2017). Interestingly, we found a clear relationship between spore size and shape and the log size. Species with spherical and large spores were more common on large logs, whereas species with elongated and small spores were more common on smaller logs. Bässler et al. (2014) hypothesized that wood-inhabiting fungal species with smaller and more elongated spores, follow the *r* reproductive strategy (sensu Grime, 1988), and thus cope better in managed environments where dead wood items are typically smaller. We cannot conclude how spore morphology relates to the *K/r* reproductive strategy since we did not collect data about spore production. Yet, our results are in line with Bässler et al. (2014) hypothesis that species with smaller and more elongated spores occur more often in smaller dead trees; thus, their proportion can be expected to be higher in forests where most dead wood is small due to management actions (Eräjää et al., 2010; Abrego and Salcedo, 2013).

We did not find clear differences in spore ornamentation frequency between the tree species. This might be because the spore ornamentation is not likely to influence airborne dispersal substantially (Hussein et al., 2013). Instead, ornamentation may be important for attaching to animal vectors for dispersal. Especially mycorrhizal species are characterized by ornamented spore walls (Halbwachs et al., 2015), which are suggested to aid in transportation to deeper soil layers via arthropod vectors (Calhim et al., 2018). However, in our study the proportion of species with ornamented spores was equal in totally saprotrophic groups (ramarioids and stromatoids) and a group encompassing many mycorrhizal fungi (resupinates) (Kotiranta et al., 2009). We note that we treated spore ornamentation as a categorical variable (classified as yes/no), and thus ignored the great variation of ornamentation types and

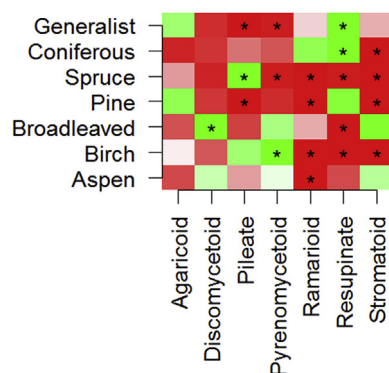


Fig. 3. Host-tree specialization-level of fungi with different fruit body types. Green colours (respectively, red colours) indicate that the fungal species groups have a given host-tree classification more often (respectively, less often) than expected by chance, the asterisks indicating those results that are supported by at least 95% posterior probability. Note that this analysis is restricted to those species that occur at least 4 times in the data.

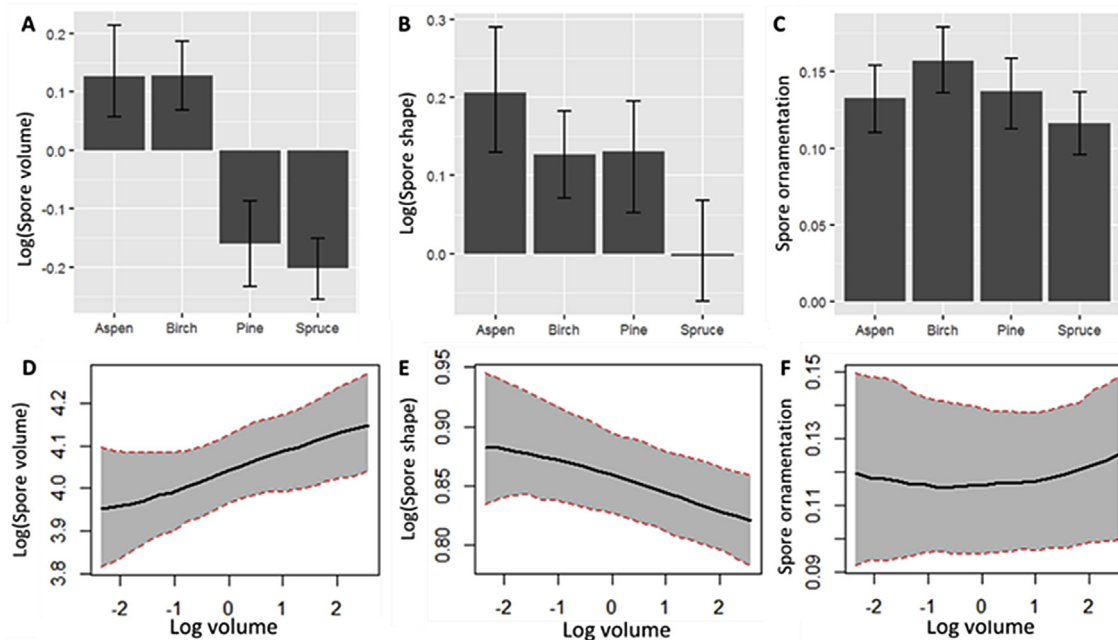


Fig. 4. Community-weighted mean spore trait values for (A–C) different host-tree species and for (D–F) logs of different sizes. The first column shows the mean spore volume, the second column shows the mean spore shape, and the third column shows the mean proportions of species with ornamented spores. The error bars (A–C) and shaded areas (D–F) show the 95% credibility interval.

their possible functional roles.

The vast majority of the variation in species occurrences at the level of logs was not explained by the fitted model. This result is in accordance with previous studies from temperate Europe (Bässler et al., 2012; Abrego et al., 2014, 2017), which concluded that random processes dominate in shaping wood-inhabiting fungal communities at small spatial scales. Most fungal species were rare (55% occurring three or fewer times), which is a common feature of ecological communities in which random processes dominate (White et al., 2006; Vellend, 2016). However, there might be many other variables we did not include, but which could have improved the models predictive power, such as microclimatic factors or direct measurements of wood composition such as C/N ratio. This result was also partially influenced by the fact that we conducted only two surveys, one in each of the peak fruiting seasons in boreal forests (Halme and Kotiaho, 2012; Abrego et al., 2016; Purhonen et al., 2017). Since many wood-inhabiting fungi have ephemeral fruit bodies, repeating surveys over several years in the peak fruiting seasons would have decreased the proportion of rare species and thus increased the predictive power of our model. Also molecular surveys of mycelia might have decreased the proportion of rare species and increased predictability of their occurrence (e.g. Kubartová et al., 2012; Mäkipää et al., 2017). However, in comparison to molecular surveys, fruit body based surveys provide direct information about the “breeding” populations of fungi. As a large portion of the species groups in the present study is taxonomically poorly known, some of the results should be considered with caution. For example *Mollisia* sp., which shared several host-tree species, might indeed be specialized in different host-trees (see also Runnel et al., 2014).

We found that broadleaved dead trees have higher species richness than coniferous dead trees. In particular, aspen hosted the highest and pine the lowest species richness. Higher species richness in broadleaved trees may result from the lack of defensive chemicals that conifer tree species have, making them easier to colonize and decay (Stokland, 2012a; Hoppe et al., 2016). However,

fungal fruiting patterns may differ between tree species, and thus to observe the true differences in species richness between tree species, fruit body surveys should be accompanied by molecular data of mycelia within wood. Furthermore, different tree species have different residence times, and thus the total species richness may be higher for tree species with longer life-span as a log.

5. Conclusions

Our study showed that the occurrence of fungal species in dead wood with different characteristics is related to the morphological traits of fungi. Our results also revealed that specialization to host-tree species occurs at the level of fruit body morphological groups, and that the size and shape of the fungal spores relate to the preference for logs of different sizes.

Acknowledgements

We are grateful to Katja Juutilainen for contributing to the fungal surveys, Titta Kauppinen for help with dead wood and trait data collection and Leena Nikolajev-Wikström for trait data collection. Anni Rintoo, Jorma Pennanen, Matti Kulju, Unto Söderholm, Timo Kosonen and Tea von Bonsdorff helped with identification of difficult fungal specimens. We want to thank also Panu Kuokkanen from Metsähallitus for providing the forest age information of the study sites. We also thank the two anonymous reviewers for their constructive comments on an earlier version of the manuscript. This study was funded by the Ministry of the Environment of Finland (PUTTE grant to Halme), the Finnish Foundation of Nature Conservation and the Finnish Cultural Foundation (grants to Purhonen), Academy of Finland (grants 309581 and 284601 to Ovaskainen and grant 308651 to Nerea Abrego), Jane and Aatos Erkko Foundation (grant to Ovaskainen), and Research Council of Norway through its Centres of Excellence Funding Scheme (223257) to Ovaskainen via Centre for Biodiversity Dynamics.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.funeco.2019.08.007>.

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