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Resource use of wood-inhabiting fungi in different boreal forest types

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Abstract

Generalist species are usually widespread and abundant, and thrive in heterogeneous environments. Specialists, in turn, are generally more restricted in their range, and benefit from more stable conditions. Therefore, increasing human-induced disturbance can have more negative effects on specialist than generalist species. We assessed the specialization of 77 wood-inhabiting fungal species across seven boreal forest types and different substratum qualities. A significantly higher number of specialist species was associated with herb-rich forests and afforested fields than with managed coniferous forests and wood pastures, the number of specialists associated with natural coniferous forests being intermediate. Also, forest type specialists were indicated to be specialists for their substratum tree species as well, but specialization in substratum diameter was not connected with other kinds of specialization. Species with restricted resource or habitat preferences can less readily respond to environmental change, and therefore are more vulnerable to extinction.

Keywords

Introduction

One of the pervasive questions in biology is to understand why certain organisms are present in some places and absent from others. The boundaries of geographic distribution can be assessed on many different scales, which range from global comprehensive approach to local microhabitat level. On the global scale, temperature and moisture are the main limiting factors for the majority of organisms. The gradients of these key physical factors, along with topographic variation, largely define the borderlines of the main climatic and vegetational zones. Other abiotic factors, such as light, pH, bedrock and soil composition operate on a more local scale and generate prerequisites for vegetational types. On the finest scale, suitable environmental conditions, habitat type and available resources combined with interactions among organisms of the same and different species comprise the ecological niche of a species. The realized niche is usually a compromise between the available resources and the biotic interactions limiting the use of them (Vandermeer 1972, Wiens & Graham 2005). Also, behavioral constraints such as preference towards certain resource(s) may confine the species into a subset of potential habitats. Thus, the distribution and the abundance of a species are always affected by a combination of abiotic and biotic factors (Gaston 2003).

It is not known whether the macroclimatic conditions have as important a role in the distribution of wood-inhabiting fungi as they have on vegetation (see, for example Bässler *et al.* (2010)). However, the current distribution patterns of wood-inhabiting fungi seem to be connected to the vegetation zones and largely follow the dominant tree species distribution within the vegetation zones (Hallenberg 1991). At a landscape level, distribution and abundance of wood-inhabiting fungi are heavily dictated by the availability of woody resources (Heilmann-Clausen *et al.* 2014, Abrego *et al.* 2015). Senescence and the exposure of trees to different disturbance factors, such as fire, wind, insect outbreaks, fungal pathogens, periodical drought and flooding, create dead wood in the natural forest landscape. The relative importance of each factor depends on the forest type (Kuuluvainen *et al.* 1998, Gromtsev 2002).

At the forest stand level, dead wood forms a dynamic resource network in both space and time. A continuous supply of variable dead wood units allows the persistence of a diverse species pool. Gaps and fluctuations in the resource availability can lead to local extinctions and recolonizations, if there are healthy source populations within dispersal range (Jonsson *et al.* 2005). At the resource unit level, the quality of dead wood has spatial, temporal and qualitative dimensions: the most studied factors are tree species, size and decay stage, and other factors include decay rate, part of the tree, part of the wood, the cause of mortality of the tree, microenvironment around the wood, and other species' interactions. The number of possible combinations is very high, which creates countless niche specialization opportunities for wood-inhabiting fungi (Boddy *et al.* 2008, Stokland *et al.* 2012).

Human impact on forest ecosystems has been evident for millennia, as exemplified by the historical loss of deciduous forest cover over major parts of central Europe. During recent decades the rate of loss, deterioration and fragmentation of forested landscape has increased and pervaded also boreal and tropical biomes. In the wake of modern forestry practices both the amount and quality of dead wood has been drastically reduced in forest environments. Consequently, especially species associated with large diameter dead wood have suffered from habitat loss (Siitonen 2001). Recently, the growing demand for alternative sources of energy has reached the forests: modern energy-wood harvesting is depleting the forest floor from small diameter dead wood and thus creating a novel threat for associated species (Dahlberg *et al.* 2011, Toivanen *et al.* 2012).

A species can be considered a specialist if its abundance in a certain habitat or resource type is much higher than elsewhere in its potential range. Inversely, a species distributed evenly among potential resource or habitat types is a generalist. Furthermore, most species tend to have small geographic ranges and only a few are widespread. A positive correlation between regional distribution and local abundance is common among all kinds of organisms: widespread species appear to be more abundant than species with more limited geographical ranges (Gaston *et al.* (1997), but see Komonen *et al.* (2009)). A similar pattern is distinguished for generalist and specialist species, where

the former is usually more widespread and abundant, and the latter more restricted in range. Generalist species are thought to have evolved and thrive in heterogeneous environments, while specialists favor and benefit from more stable conditions (Futuyma & Moreno 1988). Therefore, landscape fragmentation and increasing human-induced disturbance has a more negative effect on specialist than generalist species (Devictor *et al.* 2008b). Environmental degradation can also aggravate biotic homogenization processes in which declining specialist species are increasingly replaced by more mobile and widespread generalists (Olden *et al.* 2004). This has direct consequences for conservation as species with a confined range or specialized habitat requirements tend to have more limited dispersal abilities and are more prone to extinction through changes in their environment or via stochastic events (Henle *et al.* 2004, Berglund & Jonsson 2008). Quantifying species' ecological requirements and measuring their specialization will help identifying which species are more likely than others to prosper in the face of human-induced habitat and climate change, and which species will need our attention and conservation measures.

In this paper, we assess the level of habitat specialization of 77 wood-inhabiting fungal species by assigning them along a generalist-specialist continuum across three habitat and substratum variables: forest type, substratum tree species and substratum diameter. Species ranking from the most generalist to the most specialist species were composed across all possible variable combinations as well as for each variable separately. The connections between the species ranking among different variables was also tested to find out if the specialist species along one gradient are also specialists along other gradients. We also addressed if the level of specialization differed among species associated with alternative habitats or dead wood resource types. Moreover, we studied how specialization is connected to the abundance of the species within the data. Revealing the level of specialization along different environmental gradients and in relation to species' habitat and resource associations will shed light on the ecological requirements of wood-inhabiting fungal species. This can help in understanding and foreseeing the consequences of human-induced habitat

alteration and climate change to fungal species and communities, and, thereby, help in designing appropriate conservation actions.

Materials and methods

Study sites

The study area is located in central Finland and belongs to south and middle boreal zone (Ahti *et al.* 1968). The study sites represent seven different forest types, with four replicates of each type (28 sites in total; Fig. 1). Four of the forest types are conifer dominated and three broadleaved dominated (Table 1). Eight of the 16 coniferous sites belong to mesic *Myrtillus* and *Oxalis-Myrtillus* types (Cajander 1949), dominated by Norway spruce (*Picea abies*), and mixed with variable proportions of Scots pine (*Pinus sylvestris*), birches (*Betula* spp.), European aspen (*Populus tremula*), grey alder (*Alnus incana*), rowan (*Sorbus aucuparia*), and goat willow (*Salix caprea*). The rest of the coniferous sites are drier *Vaccinium* and *Calluna* type forests with Scots pine (*Pinus sylvestris*) as the dominant tree species, mixed occasionally with birches, rowan, alder and spruce. Four of the spruce and four of the pine dominated sites are natural or semi-natural, i.e. no modern logging methods have been applied in these sites. The other half of the coniferous sites have been under intense management regime with regular thinnings. Most of the coniferous study sites are situated in National Parks or other nature reserves, administered by Metsähallitus (Parks and Wildlife Finland), while some of the managed coniferous sites are on privately owned land. See Juutilainen *et al.* (2014) for more detailed description of the coniferous study sites.

The 12 broadleaved study sites belong to natural herb-rich forests, traditional wood pastures and afforested fields. The natural herb-rich forest sites are characterized by diverse mix of various broadleaved tree species including birches, aspen, grey alder, black alder (*A. glutinosa*), rowan, goat willow, bird cherry (*Prunus padus*), Norway maple (*Acer platanoides*), small-leaved lime (*Tilia*

cordata), and wych elm (*Ulmus glabra*), mixed with occasional spruce and pine . The wood pasture

sites are birch dominated, with variable amount of juniper (*Juniperus communis*), grey alder, rowan,

spruce and pine, and are still in use for cattle or sheep grazing. Likewise, the afforested field sites are

birch dominated, with only occasional *Salix spp.* and some spruce saplings, but the trees are of

uniform age and more evenly spaced. See Juutilainen *et al.* (2016) and Oldén *et al.* (2016) for more

details about the broadleaved sites. The natural herb-rich forest sites are located in nature reserves

belonging to the Natura 2000 network. The wood pasture and afforested field study sites are on

privately owned land.

Study design and sampling methods

At each study site three 10 X 10 m sampling plots were established according to the methodology

introduced in Juutilainen *et al.* (2011). The afforested field sites were represented with only two

sampling plots due to the limited space in each birch afforestation block and the laborious data

collection in these sites. From the entire sampling plot area all dead wood particles (logs, snags,

stumps, branches) with a minimum diameter of 2 cm were inspected. In addition, a 2 X 2 m subplot

was set at each corner of every sampling plot. More comprehensive sampling was conducted in the

subplots, including the smallest twigs and cones. The investigated dead wood material was divided

into six diameter categories: <0.5 cm, 0.5-<1 cm, 1-<2 cm, 2-<5 cm, 5-<10 cm and ≥10 cm. In

addition, cones were separated as the seventh substrate "diameter" category. Dead wood units

were identified to species level whenever possible. Sometimes, especially with more decayed units,

identification was impossible. Therefore, some dead wood units were labelled as "Unidentified

deciduous/conifer/ tree species".

Every dead wood unit was carefully inspected for the presence of fungal fruit bodies or mycelial

cords. In this study corticioid and polyporoid fungi including resupinate Heterobasidiomycetes

("Corticiaceae" *s.l.*) were collected. The majority of the species are true wood decayers, but some

are mostly associated with forest floor litter, and a few species are ectomycorrhizal with trees. What

all these species have in common is that they form fruit bodies on dead wood, regardless of their primary nutritional strategy. The measure of species' abundance used in this study was the total number of dead wood units from which the species was recorded. The observed fungi were identified to species level *in situ*, or collected and dried as specimens for later microscopic identification, using compound microscope with magnification of 40-1600X. The nomenclature follows mostly Kotiranta *et al.* (2009), with some exceptions from Bernicchia & Gorjón (2010) and Ryvarden & Melo (2014). Voucher specimens are preserved in the herbaria of National History Museum of University of Jyväskylä (JYV) and personal collections of the authors K.J and H.K. Unfortunately, we did not separate the observations based on fungal cords, and therefore the number of *Piloderma fallax* in the material is inflated. Moreover, *Piloderma* taxonomy has proven to be more varied than previously thought. Currently it seems that the cord material we have named *P. fallax* can potentially include some observations from *P. byssinum* or extremely rare *P. olivaceum.*

Data selection

The abundance data used in this paper combines the datasets of two earlier studies (Juutilainen *et al.* 2014, Juutilainen *et al.* 2016). The complete data comprises over 10 000 observations of wood-inhabiting fungi, including species and genus level observations as well as unidentified specimens belonging to higher level taxa (Supplementary Appendix B). For this study only species with minimum number of 10 observations were included. The filtered dataset includes 4331 fungal observations of 77 species (see Supplementary Appendix C for the number of fungal species on different substrate categories/forest types).

Data analyses

We calculated species' abundances (occurrences per dead wood unit) across seven forest types (SN, PN, SM, PM, HR, WP, AF; Table 1.), seven dead wood substratum diameter categories (<0.5 cm, 0.5-<1 cm, 1-<2 cm, 2-<5 cm, 5-<10 cm, 10≤ cm; cones as the seventh "diameter" category), and four

substratum tree species (*Betula*, other deciduous wood combined, *Picea* and *Pinus*). Other coniferous substrata as well as unidentified substrata were omitted from the analyses.

To quantify each species' specialization we calculated Species Specialization Index (SSI, *sensu* (Julliard *et al.* 2006)), which is simply the ratio of standard deviation to mean of the species relative abundance, across all resource classes, as well as for forest types, substratum diameter categories and substratum tree species separately.

Standard deviation of abundances can be expected to be biased by low sample size. Hence, we used the formula $\sqrt{K/n}$ (where K is the number of resource classes and n is the total number of observations of a species) to estimate bias for each species (see Devictor *et al.* (2008a) for detailed explanation). In the final analyses we used the bias-corrected values (SSIc). In general, the small values of SSIc refer to a generalist species, and the level of specialization for certain resource type(s) increases with increasing SSIc value. There is, however, no specific borderline value which could divide strictly the generalists and the specialists. Rather, the SSIc values form a continuum from the most generalist to the most specialist species.

We analyzed the correlation between the species' specialization level (SSIc) and mean abundance (observations/dead wood particle) across all resource classes. The correlation is expected to be negative, if the generalist species are more abundant than the specialists.

Differences in species' SSIc-values were tested among species associated with different forest types, substratum tree species and substratum diameter categories. We classified species being associated with the forest types, substratum tree species and diameter category, based on their highest abundance among the categories. For example, a species was classified being associated with natural spruce forests if its abundance was highest in that forest type. To avoid too small sample sizes, some classes were pooled together to create ecologically sound combinations: Among forest types SN and PN were combined as "coniferous forests with low human influence"; SM, PM and WP

were combined as "forests with high human influence"; HR was left separate as "deciduous forest with low human influence" and AF as "novel ecosystem with high human influence". Among substratum diameter categories the three smallest fractions (<2 cm) were combined to represent very fine woody debris, and the cones were omitted because of low number of occurrences. The other diameter fractions were left separate. Regarding substratum tree species, dead wood from spruce, pine and birch were analyzed separately. Dead wood from all other deciduous tree species, as well as from unidentified deciduous (other than birch) trees were combined as a fourth substratum tree "species". The differences were tested with one-way analysis of variance (1-way ANOVA). For significant results also pairwise *post hoc* –comparisons were performed using least significant distance (LSD) measure.

To compare the generalist-specialist continuum among forest types, substratum tree species and substratum diameter categories, we ran rank correlations of the species' SSIc values for all possible combinations (forest type vs. substratum tree species, substratum diameter category vs. substratum tree species, and substratum diameter category vs. forest type). All analyses were conducted with IBM SPSS Statistics 22.0 software for Windows.

Results

Among the 77 species analyzed across all habitat and substratum type combinations, the SSIc values ranged from 1.81 for the most generalist species (*Botryobasidium subcoronatum*) to 11.10 for the most specialist species (*Trechispora byssinella*) (Table 2). There was only a slight negative correlation between SSIc and the mean abundance across all combinations (r=-0.179, df=75, p=0.119; Fig.2). However, when the less abundant species (<20 observations) were omitted, the negative correlation strengthened (r=-0.299, df=39, p=0.057). The bias/SSI ratio was at least 50% for nine species out of

77, and thus interpreting the SSIc values for these species should be done cautiously (Supplementary Table A1).

When analyzed separately, SSIc values across forest types ranged from 0 for the most generalist species (*Ceratobasidium cornigerum*) to 2.22 for the most specialist species (*Phlebiella* aff. *insperata*) (Table 2 and Supplementary Table A2). Species' SSIc values differed significantly among the species associated with different forest types (F=2.994, p=0.036). The pairwise comparisons revealed a significantly higher mean level of specialization among species associated with herb-rich forests (HR) and afforested fields (AF) than among species associated with forests with high human influence (SM+PM+WP combined). Also, AF tended to have a higher mean level of species' specialization than natural forests (SN+PN), but the difference was not significant (Fig.3).

Across substratum tree species classes the SSIc values ranged from 0 for the most generalist species (*Botryobasidium subcoronatum*) to 1.52 for the most specialist species (*Phlebiella* aff. *insperata*) (Table 2 and Supplementary Table A3). As the assumption of the homogeneity of variance was not met for substratum tree species, the original SSIc values were replaced by rank numbering to provide a non-parametric equivalent for the analysis of variance. The mean level of species' specialization did not differ significantly among species associated with different substratum tree species (F=0.526, p=0.666).

The SSIc values across substratum diameter categories ranged from 0.35 for the most generalist species (*Scopuloides rimosa*) to 1.61 for the most specialist species (*Sistotrema cf. oblongisporum*) (Tables 2 and A4). Also for substratum diameter categories the variances were unequal; hence the SSIc values were replaced by ranks. There were no significant differences in the mean level of specialization among species associated with different substratum diameter categories (F=0.956, p=0.418).

Species' rank of their SSIc values showed strong positive correlation between forest types and substratum tree species (r=0.663, p<0.01, Fig. 4A) indicating that the forest type specialists tend to be specialists also in terms of their substratum tree species. Species' forest type specialization rank did not correlate with the rank based on specialization with respect to substratum diameter categories (r=0.055, p=0.636, Fig. 4B). There was a weak negative correlation between species' rank based on specialization with respect to different substratum diameter categories and the rank based on specialization with respect to substratum tree species (r=-0.106, p=0.360, Fig. 4C).

Discussion

Comparison of SSIc values across all habitat and substratum type combinations revealed great variability among the species' resource preferences. The species in the generalist end of the continuum were present in varying combinations across all variables. The species in the specialist end of the list were more restricted with their preferences for either forest type, substratum tree species, substratum diameter category, or for some combination of these. We did not find strong negative correlation between species specialization index and mean abundance across all habitat and substratum type combinations, which would have been expected if locally more abundant species were habitat and substratum type generalists. In our data, specialist species were always rare but generalists included both locally abundant and rare species. The species that were opposite to expectation (locally rare generalists) included several species loosely associated with deciduous and small diameter dead wood, but we could not identify any single common characteristic for them. This is an intriguing pattern and deserves more study.

One should also note that as the number of different habitat-resource combinations is large (152 combinations in total), the abundances of species in each class are inevitably small. This decreases the power of the analysis and reduces the interpretability of the SSIc values. When the SSIc values

were examined separately for the three classifying variables, interpreting species' preferences was more reasonable. Concerning the forest type, all species at the generalist end of the list were present in four to six out of seven types of forests whereas the most specialized ones were found only in one, two or three forest types. It is notable that the majority of the most specialized species are growing almost exclusively in (some of the) deciduous forest types, or at least they are completely absent from the managed coniferous forests. There did not appear to be any species specialized to managed coniferous forest types. Furthermore, specialization in natural coniferous forests seems to be relatively rare among wood-inhabiting fungi occupying fine woody debris, which is in contrast with earlier results on species occupying coarse woody debris (Nordén *et al.* 2013). This is logical since the number of small dead wood units per hectare is very similar in spruce and pine dominated natural and managed forests (Table 3.) (Juutilainen *et al.* 2014). It suggests equal availability of resources in natural and managed coniferous forests for species associated with fine woody debris. An interesting question is whether the physiochemical conditions of fine woody debris are also similar in managed and natural coniferous forests. Our data do not provide any hard evidence for this, but suggests that there are no major differences; otherwise there would, probably, be more specialized species.

Most likely the specialization in some particular forest type is, in fact, specialization in a certain combination of substratum tree species, stand age structure, and most importantly, the amount and quality of decaying wood. Most wood-inhabiting fungi acquire necessary energy and nutrients from the woody substratum they are living in. Therefore, the question whether a fungal species is present in a certain forest type or not, is largely determined by the available resources. A well-known example is the comparison of fungal species richness and community composition in natural and managed forests. The differences in fungal assemblages are mostly explained by the differences in the dead wood profile of the forests (Penttilä *et al.* 2004, Hottola *et al.* 2009, Abrego & Salcedo 2013). However, the dead wood profile does not seem to be the only determining factor explaining the differences in fungal communities among different forest types. For example, previously

(Juutilainen *et al.* 2016) we found that the dead wood profile did not explain why the fungal species richness and the number of rare species was relatively high in afforested fields compared to other habitats, even though the amount and diversity of dead wood in the afforested fields is very limited.

The generalists for substratum tree species were able to utilize both coniferous and deciduous wood whereas the specialists had clear preferences for either one tree species or for deciduous vs. coniferous wood. Species that were present only on one substratum tree species were very rare, and were mainly associated with birch. Some of them (*Phlebiella* aff.*insperata*, *Sistotrema oblongisporum*, *Tomentella galzinii*) represent species associated with small diameter dead wood, whose ecology and substratum preferences are poorly known. *Phlebiella* aff.*insperata* is a mystery species to us; it was found solely on birch twigs from afforested field sites. We have no hypotheses to explain this pattern, as birch twigs were present in all studied forest types. *Sistotrema oblongisporum* is usually common on several kinds of fine deciduous woody material. In our data it was tightly associated with birch, but this can be partly explained by the fact that it was encountered mostly in afforested field and wood pasture sites where birch trees are dominant and other deciduous material is very scarce. *S. oblongisporum* fruit bodies emerge usually shortly after rain and disappear rather quickly. The detectability of the fruit bodies is, therefore, strongly affected by local conditions and sampling time, which, in turn, can be reflected in the data. This might partly explain why we found so few *S. oblongisporum* occurrences in natural herb-rich sites. *Tomentella galzinii* is one of the few ectomycorrhizal corticioids in our data. As it is largely associated with birch trees, it probably grows fruit bodies on the most readily available substrata, which tend to be the fallen branches of the companion tree.

In general, the preference for substratum tree species is commonly observed among wood-inhabiting fungi (Gange *et al.* 2011, Heilmann-Clausen & Læssøe 2012). Many wood-inhabiting fungal species seem to have a preference for a certain tree species, tree genus or for a few similar tree species as a resource (Boddy *et al.* 2008). The proportion of specialist species tends to be higher

among the species that interact with living host trees, such as latent decay and heart rot fungi (Boddy *et al.* 2008). Perhaps the lack of latent decayers and heart rot agents among the community occupying fine woody debris explains the scarcity of facultative specialists in our data.

True substratum generalist species, with the ability to utilize a very wide variety of tree species (both deciduous and coniferous wood) were relatively common in our data. There were 24 species (31% of the studied species) with at least one occurrence on all studied tree species (when other deciduous trees than birch were pooled together). Among the species associated with very fine woody debris, the substratum tree species generalists include several fungi from the genera *Athelia*, *Piloderma*, *Sistotrema* and *Trechispora*. Interestingly, many of these species are often found in well-decayed wood or even litter, which suggests preference for advanced decay stages over other attributes of the substratum. Also, it is possible that the defence chemicals, which are largely specific to each tree species, have smaller effect on fungi during the late decay stages (Boddy *et al.* 2008).

In our study the proportion of substratum generalist species was higher than in earlier studies of fungi associated with coarse woody debris. For example, Nordén *et al.* (2013) found that only 26 (22%; mainly polypore) species out of 119 were generalists for substratum tree species, and the majority of fungi showed clear preference for either coniferous or deciduous wood. Kueffer *et al.* (2008) found that only 20 species out of 230 were tightly associated with one host tree species, whereas the main factor dividing fungal species was coniferous vs. deciduous hosts. Stokland & Larsson (2011), however, found that 69 (33 %) species out of 208 occurring on pine logs and 90 (38 %) species out of 232 occurring on spruce logs were generalists, while the rest showed preference for either pine, spruce or coniferous substrata. The varying proportion of generalists among the abovementioned studies might stem from the methods used for measuring substratum specialization, which differed among studies. In general it is difficult to compare the results of specialization analyses conducted in different systems because the detected specialization is always

dependent on the methodology, and the analyses always catch only a subset of the local species pool.

The division of species into generalists and specialists according to substratum diameter was also evident. The generalist species for substratum diameter category were present in both small and large diameter dead wood and many species also in cones. The specialist species were more restricted to either fine or coarse woody debris. However, we did not find any species strictly specialized on one particular diameter class. The size of dead wood unit affects the variation of physical conditions, for example temperature (Halme *et al.* 2013) within the wood. Moreover, it is likely that the chemical conditions also vary depending on dead wood size, and those conditions have an effect on how different species are able to utilize the wood (Venugopal *et al.* 2016).

Fine woody debris is a very abundant resource in most forest types (Juutilainen *et al.* 2011, Juutilainen *et al.* 2014, Juutilainen *et al.* 2016) and its supply is continuous in most forests. Thus, specialization in finest woody debris could rationally be a winning evolutionary strategy. Interestingly, Kueffer *et al.* (2008) also found that only nine fungal species out of 230 showed strong preference for substratum diameter (in this case for small twigs, intermediate and larger branches). The main diameter thresholds, 0.72 cm and 1.35 cm, discovered in their study were surprisingly small, and effectively categorize all dead wood from intermediate branches to large trunks into the same category of coarse woody debris. However, our results support earlier studies in that many species of wood-inhabiting fungi show some preference for either large or small sized dead wood substrata. Especially, the connection of several polypore species with large diameter dead wood is widely acknowledged (Junninen & Komonen 2011). Indeed, in natural forests coarse woody debris is a very abundant resource (Siitonen 2001) and it is logical to expect specialization in it, too. To summarize, it seems that clear preferences for different dead wood dimensions exist among wood-inhabiting fungi but most often these preferences do not manifest as strict specialization in a certain substratum diameter or narrow diameter range.

Our rank correlation results showed that the generalist species for different forest types are generalists considering their substratum tree species as well. This connection is tangible: if a fungal species can utilize many different tree species as a substratum, it can potentially survive in many kinds of habitats where suitable substrata are present, as long as dead wood input is constant. Consequently, the generalist species are able to thrive in different forest environments due to their ability to utilize the variety of tree species available in each forest type. On the other hand, some species highly specialized for the substratum tree species and forest type were present only in one forest type and abundant only within a certain substratum type. These species were rare or completely absent from other forest types even if the apparently preferred substratum was plentiful in other habitats as well. An extreme example is, again, *Phlebiella* aff*. insperata*, which was one of the most abundant species in afforested fields, but absent from every other forest type. This species was practically always found on small diameter birch wood (only one additional observation from unidentified deciduous wood), a substratum very common in all the deciduous forest types (Juutilainen *et al.* 2016) and also present in all coniferous forests (Juutilainen *et al.* 2014). It seems that some unknown factors play an additional role in the habitat selection of this and of other similar species. For example, it is possible that the quality of dead wood differs among forest types due to differences in the age, growth rate or competitive environment of the trees. Growth rate of the tree has certainly been shown to affect wood-inhabiting fungi (Edman *et al.* 2006). The high level of specialization of species in afforested fields is a surprising result, as one may expect that only opportunistic species with wide niche are able to inhabit novel habitats. It may be that some specialists that we found in afforested fields are actually species associated with habitats our sampling did not include such as peatland forests, riverine/shore forests or shrub lands (see also discussion in Juutilainen *et al.* (2016)). Therefore, to resolve the habitat requirements of the specialist species found in afforested fields requires that future studies should also encompass non-forest habitats in addition to the main forest types we studied.

Species ranking in relation to specialization for forest types was not correlated with ranking in relation to specialization for substratum diameter categories. Thus, there appears to be no ecological connection between fungal species' specialization for forest type and substratum diameter. Accordingly, a forest type specialist could be either a generalist or a specialist for substratum diameter, and *vice versa*. It is also possible that this result derives from different dead wood profiles of the forest types. In natural spruce and pine dominated and herb-rich forests all dead wood diameter fractions are present, whereas in managed spruce and pine dominated forests, wood pastures and afforested fields the available dead wood diameter range is limited from small to medium.

The weak negative correlation in species specialization ranking between substratum tree species and substratum diameter categories suggests some trade-off between the ability to use a wide variety of substratum tree species and a large range in substrate diameter simultaneously. The true existence of the correlation remains to be tested with a larger data set, because in our data the correlation was weak and not significant. Such trade-off sounds plausible, because narrow niches along several niche dimensions simultaneously render a species vulnerable to extinction in highly variable and disturbance prone boreal forests. Narrow niche with respect to tree species and along diameter gradient may only be possible if the host tree species is common enough.

The width of species' ecological niche is rarely controlled by only one variable. For most species the niche comprises the variation of several parameters, which form a multi-dimensional niche space (Hutchinson 1957, Vandermeer 1972). In our study, the most important feature in the multidimensional niche space separating generalist from specialists was forest type. However, one must remember that we did not record all the possible niche dimensions. Most importantly, we did not record decay stage for the smallest dead wood units due to the difficulty of estimating it reliably (but see Lõhmus & Kraut (2010)). Decay stage is definitely an important additional dimension to the niche space and its interaction with other variables weakens the interpretability of our results

(Junninen & Komonen 2011, Abrego & Salcedo 2013, Nordén *et al.* 2013). Moreover, we could not study interspecific interactions and their role in the specialization. We know that some species have tight interactions with other species, both positive and negative (Abrego *et al.* 2016), and, consequently, some species are most likely associated with a combination of some dead wood attributes and presence-absence patterns of some other species.

Conclusions

Species associated with small diameter dead wood have widely been neglected in the past research of wood-inhabiting fungi. Recently, the existence of these inconspicuous species has gained more attention and their ecology is slowly being revealed (Kueffer *et al.* 2008, Abrego & Salcedo 2015). Increased research effort has yielded better knowledge of their substratum requirements. Many species that were formerly considered rare appear to be common in the forested landscape, and seem to have rather wide substratum preferences. However, although the awareness of these species increases and surveying methods become more accurate, concurrently more previously unknown or rarely collected species are revealed. Accumulation of comprehensive knowledge about these species' ecology, distribution and abundance is important in order to make reliable conservation assessments. To sort out which species are actually rare and endangered is an extensive task, as is to unveil the underlying reasons behind their current status. We can only conserve species if we protect their resources and habitats as well.

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