

RESEARCH ARTICLE

Fungal trait-environment relationships in wood-inhabiting communities of boreal forest patches

Samantha K. Dawson¹  | Håkan Berglund¹ | Otso Ovaskainen^{2,3}  |
Bengt G. Jonsson^{4,5}  | Tord Snäll¹  | Elisabet Ottosson¹  | Mari Jönsson¹ 

¹SLU Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

²Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

³Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

⁴Department of Natural Sciences, Mid Sweden University, Sundsvall, Sweden

⁵Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

Correspondence

Mari Jönsson

Email: mari.jonsson@slu.se

Funding information

Horizon 2020 Framework Programme, Grant/Award Number: 856506; Strategic Research Council, Grant/Award Number: 336212 and 345110; Svenska Forskningsrådet Formas, Grant/Award Number: 2016-00461

Handling Editor: Grace Hoysted

Abstract

1. Fungal traits can provide a mechanistic understanding of how wood-inhabiting fungi interact with their environment and how that influences community assembly in deadwood. However, fungal trait exploration is relatively new and almost no studies measure fungal traits in their environment.
2. In this study we tested species- and trait-environment relationships in reproducing fungal communities inhabiting 571 Norway spruce (*Picea abies*) logs in 55 isolated forest patches (0.1–9.9 ha) of different naturalness types, located in Northern boreal Sweden. The studied patches were (1) semi-natural set-aside patches within highly managed landscapes, or (2) old-growth natural patches located in an unmanaged landscape. We tested species and trait relationships to deadwood substrate and forest patch variables. We measured mean fruit body size and density for each of the 19 species within communities.
3. Traits assembled in relation to log decay stage and forest patch naturalness, illustrating the important role of deterministic environmental filtering in shaping reproducing wood-inhabiting fungal communities. Early decay stage communities had larger, less dense, annual fruiting bodies of half-resupinate type and were more often white-rot fungi. Species rich mid-decay stage communities had mixed trait assemblages with more long lived perennial fruit bodies of intermediate size, and both brown- and white-rot fungi equally represented. Finally, late decay stage communities had smaller, denser and perennial fruit bodies, more often of the brown-rot type.
4. The relationships between the studied traits and decay stages were similar in both set-aside and natural patches. However, set-aside semi-natural patches in highly managed landscapes more frequently supported species with smaller, perennial and resupinate fruit bodies compared to natural patches in an unmanaged landscape.
5. *Synthesis.* We found that log decay stage was the primary driver of fungal community assembly of species and traits in isolated forest patches. Our results suggest that decay stage filters four reproduction traits (fruit body density, size, lifespan

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

and type) and one resource-use trait (white or brown rot). Our results highlights, for the first time, that communities with diverse fungal reproductive traits are maintained foremost across all deadwood decay stages under different forest naturalness conditions.

KEYWORDS

community dynamics, deadwood fungi, decomposition, forest naturalness, fruit-body, functional trait, saprotrophic, spore

1 | INTRODUCTION

Community ecology theory aims to comprehend and predict how both abiotic and biotic species interactions influence the organisation and functioning of communities and functional traits are widely acknowledged as a valuable framework in this undertaking (Violle et al., 2007). An advantage of species traits lies in their direct association of an organism's performance under specific environmental conditions, thereby facilitating a deeper understanding of the mechanisms that govern species distributions and community changes (McGill et al., 2006; Violle et al., 2007). Communities restricted in space and time, such as those living in patchy and ephemeral resources, provide insights to traits' influence in community assembly (Abrego, 2022; Butterworth et al., 2023). Community assembly is often characterised as a 'set of filters', with dispersal serving as the initial filter, allowing species to reach the habitat, and followed by environmental (abiotic) and species interaction (biotic) filters (Leibold et al., 2004; Violle et al., 2012).

Studies of assembly in patchy resources often focus on dispersal filters, assuming that the primary restriction on community assembly is the ability to access resources in space and time (Zambrano et al., 2019). Nevertheless, species growth, size, lifespan, resource use and reproduction, as well as the environmental conditions within the patch, also play crucial roles in structuring patchy communities (Abrego, 2022; Butterworth et al., 2023; Zambrano et al., 2019). For example, the classic trait-based CSR framework proposed by Grime (1977), which categorises species as competitors (C), stress tolerators (S) or ruderals (R), often relies on traits related to competition, size and growth architecture, in addition to dispersal. Although the CSR framework was initially developed for plants, it has also been proposed to be relevant for wood-inhabiting fungi (Boddy & Hiscox, 2017; Lustenhouwer et al., 2020). Communities of wood-inhabiting fungi in patchy and ephemeral resources may be especially influenced by resource-use traits, such as capabilities to degrade wood and adaptability to different wood types, and reproductive traits, like fruit-body size and lifespan influencing spore production. This is particularly true when the colonising fungal species are recognised as effective dispersers (Norros et al., 2014). In such environments, there are more instances where establishment is constrained by conditions upon arrival and niche specialisation, such as the specific deadwood size, decay stage or moisture content, rather than dispersal

ability (Moor et al., 2021). This is in line with deterministic theories in community ecology, which propose that local niche-based processes, such as the ability of wood-inhabiting fungi to exploit specific wood decay stages, are primarily responsible for determining the patterns of species diversity and composition (Leibold, 1995). In contrast, more stochastic theories emphasise the significance of chance colonisation and random extinction (such as neutral theory sensu Hubbell, 2005).

Wood-inhabiting fungi form species-rich communities in deadwood and have small airborne spores that can travel long distances (Norros et al., 2014). Studying fungal trait change in relation to environmental conditions of deadwood substrates, forest patches and landscapes, can help determine environmental filters and scales that have the strongest regulating force on their community assembly (Abrego et al., 2022). A common hypothesis is that environmental filters are more prevalent at coarser scales such as landscapes and forest stands, but have a diminishing relative influence towards the finer substrate scale, dominated by biotic interactions (Abrego et al., 2017; Mod et al., 2020). However, empirical evidence of fungal trait-environment relationships so far is limited and studies rarely include multiple scale dependencies of community assemblages (but see Abrego et al., 2017, 2022).

Finding generalities in processes structuring wood-inhabiting communities is challenging, in part because abiotic conditions and coexistence of fungal species in deadwood is dynamic. From a species-sorting perspective, it has been argued that fungal community assembly should not be looked upon as a simple deterministic pathway but rather a complex dynamic mosaic (Boddy, 2001; Boddy & Hiscox, 2017). Deterministic species-environment interactions have been observed with certain species better adapted to certain environmental conditions (Krah et al., 2018; Nordén et al., 2013) and priority effects from biotic interactions (Lindner et al., 2011; Ottosson et al., 2014). In addition, dispersal limitation and stochastic demographics can influence random neutral processes (Boddy, 2001; Norberg et al., 2019; van der Wal et al., 2016). If assemblages of species and/or traits in communities diverge in response to identical environmental variables, it could indicate that stochastic processes (i.e. unpredictability in species arrival, establishment and death) are more influential drivers of community assembly than deterministic processes. Stochastic processes appear to play a particularly significant role in shaping wood-inhabiting fungal community assembly during early decay stages but diminish over time (Lunde, Jacobsen,

et al., 2022; Norberg et al., 2019; Song et al., 2017; van der Wal et al., 2016). However, accurately quantifying the roles of stochastic processes in community assembly remains challenging, given the high variability of most environments. For example, changes in the net content and concentration of nutrients in deadwood occur with decay stage due to processes such as leaching, fragmentation and export to support the growth of fungal fruit bodies (Fukasawa et al., 2009; Harmon et al., 1994; Krankina et al., 1999). These processes also influence the assembly of microbial communities during the deadwood life cycle (Fukami et al., 2010; Rajala et al., 2012; Rinne et al., 2016). While there is evidence suggesting that both deterministic and stochastic processes contribute to the dynamic and ever-changing nature of fungal communities within deadwood, this observational study primarily focuses on examining deterministic processes.

Managed forests tend to support species with smaller fruit bodies compared to natural forests (Abrego et al., 2017, 2022; Bässler et al., 2014, 2016; Nordén et al., 2013). This is likely because fungal reproduction and fruit-body growth increase with greater deadwood volumes and the higher net content of resources available in natural forests compared to managed forests (Fukasawa, 2021; Nordén et al., 2013). However, one field study indicates that fruit bodies can be larger in semi-natural forests with less deadwood compared to natural old-growth forests with more deadwood, with these differences converging as forests age and deadwood increases (Dawson et al., 2020). Additionally, mean spore size has been shown to both decrease and increase in fungal communities as decay proceeds, leading to contrasting predictions of trait-environment relationships (Abrego et al., 2017, 2022). Given that the study of fungal functional traits is relatively new, it is crucial to test and establish core traits and measurements that provide meaningful insights for developing fungal community ecology theories (Aguilar-Trigueros et al., 2015; Dawson et al., 2019; Zanne et al., 2020).

This study investigates the traits (Table 1) of reproducing fungal communities in 571 Norway spruce logs (downed deadwood substrates) located in 55 isolated boreal forest patches in Northern Sweden. Approximately half of the patches ($n=26$) were semi-natural forest patches, influenced by historical selective logging and set-aside from management in recent decades within highly managed landscapes (hereafter set-aside patches). The other half ($n=29$) were old-growth forest natural patches never influenced by forest management and located in an unmanaged landscape (hereafter natural patches). We examined individual species occurrences, their reproductive and resource-use traits, red-listed status and species richness. We tested their relationships with log decay stage and volume, forest plot-scale (hereafter called patch scale since one plot was centred in each forest patch) summed log volume per hectare, patch area and proportion of clear-cut forest in the surrounding landscape. We tested if community assemblages of fungal species and traits follow the same pathways in relation to log and patch scale environmental variables in natural old-growth forest patches in an unmanaged landscape as in set aside semi-natural forest patches in managed landscapes. We analyse how much variation in the species

responses to environmental variables measured at different scales can be attributed to variation in traits. In Table 1, we present a detailed overview of the examined traits and their hypothesised relationship with fungal function in relation to the environmental variables studied.

2 | MATERIALS AND METHODS

2.1 | Study sites

We studied deadwood fungal communities in boreal forest patches that had been isolated through either natural or anthropogenic processes in Norrbotten County, in Northern Sweden (Berglund & Jonsson, 2003, 2005). Natural patches consisted of old-growth forest patches surrounded by open mire randomly selected within the Granlandet Nature Reserve (ca 27,000ha), a landscape largely unaffected by forest management operations (Lövgren, 1986). Granlandet is primarily protected as a reference landscape for studying Norway spruce old-growth forest dynamics and fragmentation. It has no recreational access roads, but limited hunting is permitted within the reserve. The patches have no signs of forest fires or forest management activities (two cut stumps have been recorded in one of all 29 forest patch plots, likely cut by local hunters for fire wood), and patches have likely been in a natural old-growth state for many centuries with spruces attaining ages up to 300years (Berglund & Jonsson, 2005; Lövgren, 1986). The mean deadwood volume was $30.7 \pm$ standard deviation (SD) $18.5 \text{ m}^3 \text{ ha}^{-1}$ in natural patches. We assume that extinction and colonisation have reached a dynamic equilibrium in these patches (Berglund & Jonsson, 2005). Consequently, the potential long-term impact of forest structure and patch area on species distribution and community assembly should be detectable. Anthropogenic set-aside patches consisted of randomly selected semi-natural forest stand patches located within the managed forest landscape surrounding the natural Granlandet Nature Reserve landscape. The set-aside patches were identified as having high biodiversity and/or conservation value, due to presence of old-growth forest indicator species and/or the forest structure and set-aside from management in the late 1990s (Berglund & Jonsson, 2005). These set-aside patches have been isolated from natural forests at different time points since clear cutting and intensive forest management began in the region in the 1950s and up to the 1990s (Berglund & Jonsson, 2005). The set-aside patches have to different degrees been affected by historical selective logging, but never clear cut (mean $5.6 \pm$ SD 9.1 cut stumps recorded per 0.13 plot). The mean deadwood volume was $19.2 \pm$ SD $17.3 \text{ m}^3 \text{ ha}^{-1}$ in set-aside patches. All patches were dominated by Norway spruce (*Picea abies*), with bilberry dominating the understory layer, and with moist to mesic ground conditions on moraine soils. Surveying permit for Granlandet Nature Reserve (525-8301-17) was issued by the Swedish County Administrative Board of Norrbotten and survey permit for one set-aside patch that was given protected status (Dnr 2018:906) was issued by Jokkmokks Municipality.

TABLE 1 The studied six traits and red-listed status conservation attribute of wood-inhabiting fungi, along with their hypothesised fungal function and corresponding trait-environment relationships at both the log and forest patch scales.

Trait measurement	Hypothesised functions of the traits	Decay stage (†)	Log & summed log volume (†)	Patch area (†)	Clear-cut forest within 1 km (†)	Forest patch naturalness
Spore volume	Dispersal: Smaller spores disperse further but larger spores have greater environmental tolerance and germinability	Contrasting hypothesis of spore volume in relation to decay stage (††)	Spore volume increases with volume (†)	No hypothesis	Contrasting hypothesis of spore volume in relation to increasing proportion of clear-cut forests within 1 km (††)	Contrasting hypothesis of spore volume in relation to patch naturalness (††)
Rot type (brown vs. white)	Resource acquisition: White-rot and brown-rot fungi use different resources and have different physical effects on deadwood, influencing the occurrence of succeeding species	The occurrence of brown-rot fungi decreases (↓) and white-rot fungi increases (↑) with advancing decay stage	No hypothesis	No hypothesis	No hypothesis	No hypothesis
Fruit-body size	Reproduction: Larger fruit bodies survive and sporulate for longer periods than smaller ones, and a larger hymenium result in larger spore production	Fruit-body size decreases with decay stage (↓)	Fruit-body size increases with volume (†)	Fruit-body size increases with patch area (†)	Fruit-body size decreases with increasing proportion clear-cut forests in the surrounding landscape (↓)	Fruit-body size is lower in set-aside patches (↓) compared to natural patches (†)
Dry fruit-body density	Reproduction: A higher density of fruit bodies correlates with a more intricate hyphal structure. This structural complexity serve to maximise the spore-producing surface area and/or provide enhanced protection against a range of abiotic and biotic hazards	Fruit-body density decreases with decay stage (↓)	Fruit-body density increases with volume (†)	Contrasting hypothesis of fruit-body density in relation to patch area (††)	Contrasting hypothesis regarding fruit-body density and an increasing proportion of clear-cut forests in the surrounding landscape (††)	Contrasting hypothesis regarding fruit-body density in relation to patch naturalness (††)
Fruit-body type (pileate, half-resupinate or resupinate)	Reproduction: A pileate (capped) fruit body provide physical protection of the spore-producing surface against abiotic and biotic hazards. A resupinate (uncapped) fruit body maximises the spore-producing surface area, and bait area for vectors of spores. A half-resupinate (small caps but mostly resupinate) fruit body provides both some cap protection and a large spore-producing surface area	Pileate fruit-body types decreases with decay stage (↓). Half-resupinate and resupinate fruit bodies increases with decay stage (†)	Pileate fruit-body types increases with volume (†). Half-resupinate and resupinate fruit bodies are unaffected or decreases with volume (→↓)	Contrasting hypothesis of the occurrence probability of different fruit-body types in relation to increasing proportion of clear-cut forests in the surrounding landscape (††)	Contrasting hypothesis of the occurrence probability of different fruit-body types in relation to increasing proportion of clear-cut forests in the surrounding landscape (††)	Pileate fruit bodies has lower occurrence probability in set-aside patches (↓) compared to natural patches (†). Opposite hypothesis for half-resupinate and resupinate fruit bodies
Fruit-body lifespan (annual vs perennial)	Reproduction: Perennial fruit bodies produce more spores, also by delaying destructive fungivores and desiccation	Perennial species decreases (↓) and annual species increases (†) with decay stage	Perennial species increases (†) and annual species decreases (↓) with volume	Contrasting hypothesis of fruit-body lifespan in relation to patch area (††)	Contrasting hypothesis of fruit-body lifespan in relation to increasing proportion of clear-cut forests in the surrounding landscape (††)	Perennial fruit bodies has lower occurrence probability in set-aside patches (↓) compared to natural patches (†). Opposite hypothesis for annual fruit bodies
Red-listed status	N/A not a functional trait, but often specialist species in relation to log and patch environmental variables	Red-listed species increases with decay stage (†)	Red-listed species increases with volume (†)	Red-listed species increases with patch area (†)	Red-listed species decreases with increasing proportion clear-cut forests in the surrounding (↓)	Red-listed species has lower occurrence probability in set-aside patches (↓) compared to natural patches (†)

Note: The hypothesised relationships for log volume and summed log volume are the same and therefore merged into one column. Scientific support (†9 references) for each hypothesised trait-environment relationship is provided in detail in an extended table (Table S1) in the supporting information. For some trait-environmental relationships, we could not formulate any hypotheses or formulated contrasting or vague hypotheses (†) based on available evidence (Table S1). Arrow ↑ = increasing or higher, → = no trend or difference, and ↓ = decreasing or lower.

2.2 | Fungal survey

In the autumn of 2017 we surveyed wood-inhabiting fungal fruit bodies present on Norway spruce logs originating within circular 0.13 ha plots at the centre of 26 set-aside patches (0.08–6.7 ha) and 29 natural patches (0.17–9.9 ha) (Dawson et al., 2020). All logs with ≥ 10 cm diameter and ≥ 1 m length originating within sample plots were surveyed for fruit bodies. We recorded all polypore species along with six corticoid species considered important indicator and decomposer species in old-growth forest communities (*Asterodon ferruginosus*, *Cystostereum murrayi*, *Laurilia sulcata*, *Phlebia centrifuga*, *Stereum sanguinolentum* and *Veluticeps abietina*). Polypores and corticoids, as pileate and resupinate fruit body types, are especially suitable for studying forest naturalness responses in communities inhabiting Norway spruce (Purhonen et al., 2021) and also provide more reliable results for community composition comparison from single surveys (Abrego et al., 2017). Earlier fruit-body surveys combined with molecular inventories of fungal mycelial abundance in the deadwood show that the most abundant mycelium form fruit bodies (Kubartová et al., 2012; Ovaskainen et al., 2013). It is therefore reasonable that the fruit body size and density of the dominant fruiting species studied here, to some extent also reflect the species mycelial size and resource acquisition in the deadwood. Whilst we acknowledge that the presence of fungal fruit bodies does not give complete information about the fungal species succession, it provides meaningful information from a trait and species association perspective (Saine et al., 2020). The species nomenclature follow the Swedish taxonomic database Dyntaxa (www.artfakta.se).

2.3 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species and traits in communities	Logs in forest patches	571 logs in 55 forest patches

2.4 | Environmental variables

We used six environmental variables in our analysis: log decay stage, log volume, summed log volume per hectare, forest patch area, natural patch versus set-aside patch, and clear cutting in the immediate surrounding 1 km. For individual downed logs sampled within plots, decay stage was categorised into early (deadwood hard and $>50\%$ bark remaining), mid (deadwood hard or starts to soften with smooth texture and $<50\%$ bark remaining) or late (deadwood soft with small crevices, pieces or wood fragments lost and the outline of the log can have started to become deformed), based on McCullough (1948). The individual log volume (m^3) was calculated using the Fraver et al. (2007) conic-paraboloid formula. For individual 0.13-ha plots, the summed log volume per hectare ($m^3 ha^{-1}$)

was calculated. Patch area (ha) and the proportion of surrounding land within 1 km of the patch that experienced clear cutting in the 10 years prior to the survey was calculated using desktop geospatial analyses (Dawson et al., 2020). No environmental variables were strongly correlated ($r \leq 0.6$).

2.5 | Selected functional traits

We assessed species traits that we considered functionally important for dispersal (spore volume; μm^3), resource-use (rot type), and reproduction (fruit body size, density, lifespan and type). Mean fruit body size (mm^3) and dry density (mg/mm^3) per species were measured in the field and laboratory. Measurements and samples were taken from one randomly selected log and up to three random mature fruit bodies of each species growing on each log. A total of 164 fruit bodies were measured, with a mean of nine fruit bodies measured per species. Young undeveloped and overmature decaying fruit bodies were not measured. Data were collected from each species in every set-aside patch and from 11 out of the 29 natural patches (Dawson et al., 2019, 2020). Fruit bodies were randomly selected by numbering the fruit bodies from one end of a log to the other and randomly selecting numbers and corresponding fruit bodies. Mean spore volume (μm^3) and categorical traits such as rot type, fruit body lifespan and type were sourced from the literature (Nordén et al., 2013). No trait or attribute were strongly correlated ($r < 0.5$). A conservation attribute, red-listed status of a species, was also included as it is relevant for management and conservation, and these species are often resource specialists in terms of deadwood amount and quality (SLU Artdatabanken, 2020).

2.6 | Preparation of data and statistical analyses

We included species that occurred in three or more patches (28 of 45 species) for which we had complete trait information (19 of 28 species, see Table S2 for species omitted due to rarity and/or lack of trait measurements). These 19 species contained 93% of all occurrences (i.e. defined as species found fruiting on individual logs), which is above the 80% recommended for trait analyses (Pérez-Harguindeguy et al., 2013). In total, there were 745 fruit-body occurrences across 571 logs in the dataset that was analysed statistically (Table S3).

We analysed the data with hierarchical modelling of species communities (HMSC; Ovaskainen et al., 2017), which is a joint species distribution modelling (JSDM) framework (Warton et al., 2015) that enables the integration of data on species occurrences or abundances, environmental variables, species traits and phylogenetic relationships (Ovaskainen et al., 2017). In the HMSC analyses, the $n_y \times n_s$ response matrix \mathbf{Y} consisted of presence-absences of the $n_s = 19$ species observed in the $n_y = 571$ surveyed logs. We modelled \mathbf{Y} using a probit link function and included a matrix \mathbf{X} of environmental variables at the scale of the log and the patch (i.e. sample

plot), respectively. At the log scale, we included the log transformed log volume and the decay stage classified as early, mid, or late. At the patch scale, we included the log transformed summed deadwood volume per hectare, the log transformed area of the patch, the proportion of land immediately surrounding patches within 1 km that had been clear cut within the 10 years prior to the survey (clear cutting), and patch type classified as natural or set-aside patch. Further, a latent variable approach was used to have a patch-scale random effect to account for the grouping of logs within patches (Ovaskainen et al., 2017). All continuous explanatory environmental variables were scaled (subtracting the mean and dividing by the standard deviation) to improve model performance and facilitate interpretability of model outputs.

Similar to Dawson et al. (2020), species traits and phylogenetic relationships were used for modelling the relationships between X and Y (Abrego et al., 2017; Ovaskainen et al., 2017). Traits used in the T matrix are described above. These included log transformed fruit-body size, fruit-body density, spore volume, decay type (brown or white rot), fruit-body lifespan (annual or perennial), fruit-body type (pileate, resupinate or half-resupinate), and red-listed status (least concern or red-listed following SLU Artdatabanken, 2020). Following Abrego et al. (2017) and Dawson et al. (2020), as no quantitative phylogeny existed, we 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 assuming equal branch length for each level.

We fitted the model using the Hmsc R package (Tikhonov et al., 2020) with default prior distributions. The sampled posterior distribution consisted of 150,000 MCMC iterations, of which 50,000 iterations were discarded as burn-in. We ran two MCMC chains and thinned by 100, giving a posterior distribution sample size of 1000 per chain. We assessed the convergence of the two MCMC chains visually.

We evaluated the explanatory powers of the occurrence probit model through species-specific area under the curve (AUC) values, which were then averaged across the species to obtain the model-specific metric. To compute explanatory power, we made model predictions based on the model fitted to all data. The fitted joint species distribution model was also used to assess the scale dependency in the trait-level responses of the species to the environmental variables (Abrego et al., 2017). We utilised a variance partitioning technique to determine the proportion of variability in the occurrences of species that could be ascribed to the environmental variables at the log- and patch-scales in contrast to that explained by the random effects, following the methodology proposed by Ovaskainen et al. (2017). Next, we calculated the proportion of variation in the species' response to environmental variables that could be accounted for by the variation in their traits (Abrego et al., 2017).

With our analysis, we aimed to answer if traits, as well as species richness and occurrence probabilities of red-listed species, differed with log decay stage and between natural and set-aside patches. To answer these questions, we predicted species

communities on logs within patches based on 2000 draws (1000 draws from each chain) from the joint posterior distribution of the fitted model, with additional non-focal environmental variables held constant at their observed mean values (Dawson et al., 2020). For example, when making the hypothesis for set-aside patches, we set the log volume, summed log volume, patch area, and surrounding clear-cutting to their mean values in this subset of the data. We compared predictions for species richness, red-listed species occurrence probability, as well as trait values (i.e. community weighted mean values of continuous traits and occurrence probabilities of categorical traits). We considered an observed difference to have moderate or strong statistical support if the parameter of interest was greater in one case (i.e. log decay stage or naturalness patch type) than in another with at least 90% or 95% posterior probability, respectively.

3 | RESULTS

There were 800 fruit-body occurrences of 45 species on the 571 logs and 745 occurrences of the 19 species in the dataset modelled. *Trichaptum abietinum* was the most common species, with 145 fruit-body occurrences on 145 logs. The most uncommon species was *Skeletocutis stellae* with only three occurrences. The mean number of occurrences across all logs sampled for a species was 39 and the median was 33 (Tables S2 and S3).

3.1 | Trait-environment relationships

We found a strong influence of fruit-body traits on the occurrence of fungal species across the studied environmental variables. Predictions with the fitted model revealed that across all tested environmental variables, the variation in traits explained a fair amount (34%) of the overall variation in the 19 species' response to all environmental variables. Model predictions showed that traits had a particularly strong influence on the species' response to log decay stage (explaining 54%–73% of the variation in species' response to different decay stages) and patch naturalness (explaining 50% of variation). Compared to later decay stages, early decay stage logs hosted larger (Figure 1a), less dense (Figure 1b), and short-lived annual fruit bodies (Figure 1c), more likely white-rot fungi (Figure 1d) of half-resupinate fruit-body type and the lowest probability of resupinate fungi (Figure 1e). Mid-decay stage logs also hosted less dense fruit bodies than late decay stages, more long lived perennial fruit bodies of intermediate mean size, and with both brown- and white-rot fungi and all fruit-body types represented (Figure 1a–e). Late decay stage logs were associated with smaller, denser and perennial fruit bodies, of all fruit-body types, which were more likely to be of the brown-rot type. Spore volumes were generally small, but we found that spores were larger in late decay stages compared to mid decay stages, although this difference was only supported in set-aside patches (Figure 1f).

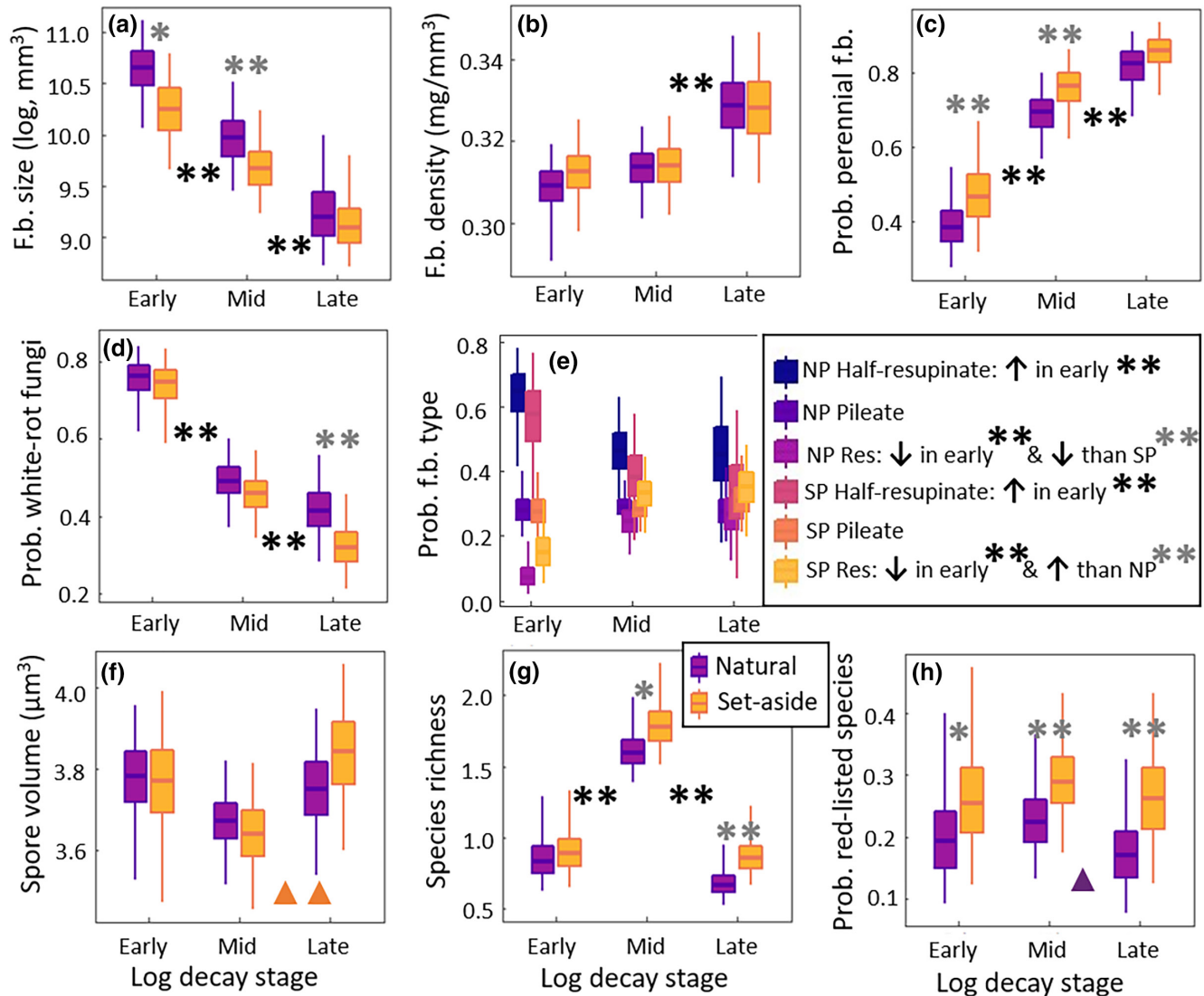


FIGURE 1 Predicted values from the fitted HMSC model for log-scale community-weighted mean trait values of (a) fruit-body size and (b) fruit-body density, in relation to log decay stage and forest patch naturalness type. The model also predicts the occurrence probability of (c) perennial fungi, (d) white-rot fungi, (e) different fruit-body types (with supported differences indicated in text next to the graph), (f) community-weighted mean spore volume, (g) species richness and (h) the occurrence probability of a red-listed species. Box and whisker plots show the distribution (0.025, 0.25, 0.5, 0.75 and 0.975 quantiles) of the predicted species communities based on draws from the joint posterior distributions. Differences between decay stages are denoted by symbols: ** indicates a strongly supported difference and * indicates a supported difference. A black asterisk represents differences between decay stages for both patch types, while a grey asterisk represents differences between patch types within decay stages. A purple triangle signifies a supported higher occurrence probability of red-listed species in mid decay stages compared to late decay stages in natural patches. Two orange triangles indicate a strongly supported larger spore volume in communities of late decay stages in set-aside patches. F.b. = fruit body, NP=natural patch and SP=set-aside patch, and Res=resupinate.

Mid and late decay stage logs in set-aside patches had slightly higher species richness and occurrence probabilities of red-listed species compared to natural patches (Figure 1g,h). Early and mid-decay stage logs in set-aside patches generally hosted species with smaller fruit-bodies (Figure 1a) and fruit-bodies were more often of the perennial type (Figure 1c), compared to natural patches where species with annual fruit-bodies were more likely to occur. White-rot fungi were more likely to occur on late decay stage logs in natural patches, compared to set-aside patches where brown-rot fungi were more likely to occur (Figure 1d). The occurrence

probability of resupinate (uncapped) fungi was lowest in the early decay stage in both set-aside and natural patches, but was overall higher in set-aside forest patches compared to natural patches (Figure 1e).

Decay stage had the highest number of statistically supported hypotheses concerning relationships with fungal traits (Table 2). Except for log decay stage and patch naturalness, no other trait- or attribute-environment relationship that we tested was statistically supported. As such, traits explained a relatively small part of the variation among species niches in terms of their occurrence

TABLE 2 Results for the hypothesised trait and conservation attribute relationships of wood-inhabiting fungi with the studied environmental variables, as presented in Table 1 and Table S1.

Trait	Log decay stage (†)	Log volume & summed log volume (†)	Patch area (†)	Clear-cut forest within 1 km (†)	Forest patch naturalness
Spore volume	H ↓↑: SP ↑ mid to late decay & NP →	H ↑ NO SUPPORT	NO HYPOTHESIS	H ↓↑ NO SUPPORT	H ↓↑ NO SUPPORT
Rot type	H1 Brown rot ↓ FALSE: ↓ H2 White rot ↑ FALSE: ↑	NO HYPOTHESIS	NO HYPOTHESIS	NO HYPOTHESIS	NO HYPOTHESIS. White rot ↑ mid to late decay in NP
Fruit-body size	H ↓ TRUE: ↓	H ↑ NO SUPPORT	H ↑ NO SUPPORT	H ↓ NO SUPPORT	H SP ↓ & NP ↑ TRUE: SP ↓ & NP ↑
Fruit-body density	H ↓ FALSE: ↑	H ↑ NO SUPPORT	H ↓↑ NO SUPPORT	H ↓↑ NO SUPPORT	H ↓↑ NO SUPPORT
Fruit-body type	H1 Pileate ↓ FALSE: → H2 Half-res. ↑ FALSE: ↓ H3 Resup. ↑ TRUE: ↑	H1 Pileate ↑ NO SUPPORT H2 Half-res. →↓ NO SUPPORT H3 Resup. →↓ NO SUPPORT	H ↓↑ NO SUPPORT	H ↓↑ NO SUPPORT	H1 Pileate SP ↓ & NP ↑ FALSE: SP & NP → H2 Half-res. SP ↑ & NP ↓ FALSE: SP & NP → H3 Resup. SP ↑ & NP ↓ TRUE: SP ↑ & NP ↓
Fruit-body lifespan	H1 Perennial ↓ FALSE: ↑ H2 Annual ↑ FALSE: ↓	H1 Perennial ↑ NO SUPPORT H2 Annual ↓ NO SUPPORT	H ↓↑ NO SUPPORT	H ↓↑ NO SUPPORT	H1 Perennial SP ↓ & NP ↑ FALSE: SP ↑ & NP ↓ H2 Annual SP ↑ & NP ↓ FALSE: SP ↓ & NP ↑
Red-list status	H1 Red-listed ↑ FALSE: SP → & NP ↓	H ↑ NO SUPPORT	H ↑ NO SUPPORT	H ↓ NO SUPPORT	H1 Red-listed SP ↓ & NP ↑ FALSE: SP ↑ NP ↓

Note: Green boxes = supported relationships, yellow boxes = partly supported relationships and orange boxes = opposite relationships to the hypothesis. White boxes denote the many unsupported relationships or no hypothesised relationship. Arrow ↑ = increasing or higher, → = no trend or difference and ↓ = decreasing or lower. H = hypothesis, SP = set-aside patch, NP = natural patch, Half-res. = half-resupinate and Res = resupinate.

probability in relation to individual downed log's volume (15%), summed log volume per hectare (19%), forest patch area (21%) and clear cutting in the surrounding area (35%). With limited statistical support for any of these relationships, we only include them in Figure S1.

There was no evidence for a phylogenetic (taxonomic) signal on the species' occurrence responses to the environmental conditions, beyond that explained by the included traits. The results suggest that the 19 species analysed primarily respond individually to environmental variation through the studied traits, rather than exhibiting dependencies based on taxonomic relatedness among the species. Given the small size of the dataset consisting of only 19 species, this outcome was expected. Measured as averaged species specific AUC values, the explanatory power of the models was sufficient at 0.81 for making inferences (Figure S2).

3.2 | Species-environment relationships

The majority of strongly supported relationships were between species occurrence and decay stage, with most species occurring in mid or late decay stages (Figure 2). There were a few exceptions to this, with *Amylocystis lapponica*, *Leptoporus mollis*, *Phellinus*

chrysoloma, *Stereum sanguinolentum*, *Trichaptum abietinum* and *Trichaptum fuscoiolaceum* fruiting more likely in the early decay stages. The occurrence probability of several species increased with log volume, including *Fomitopsis* and *Trichaptum* species. The occurrence probability of red-listed *F. rosea* and *Phellinus ferrugineofuscus* increased with forest patch area and was higher in set-asides than in natural patches. A few species, including *Butyrea luteoalba*, *F. rosea* and *Veluticeps abietina*, exhibited lower occurrence probability with increasing proportion of clear-cut forest in the surrounding landscape.

3.3 | Partitioning variance in species occurrence into environmental variables

Log decay stage explained most of the variance (mean 44.8%) in species occupancy (Figure 3). The second most important variable was the proportion of surrounding clear-cut forest area within 1 km (mean 12.3%), followed by the random variation among patches (11.7%) and then patch area (9.7%). The set-aside patch versus natural patch variable explained a low part of the variance (mean 8.0%). The deadwood volume of the individual log and summed log volume per hectare explained the least variance with mean values of 7.3% and 6.1%, respectively.

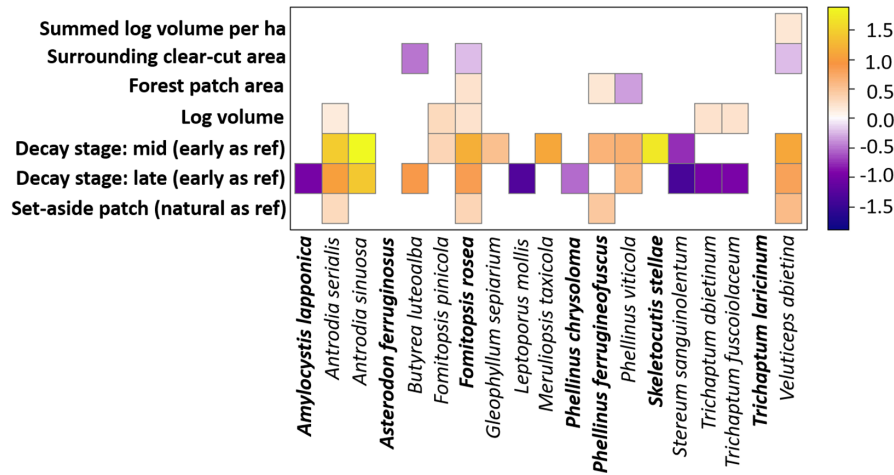


FIGURE 2 Estimated species-specific mean posterior regression parameter values (beta values) for which the 95% posterior strongly support a relationship between the species' occurrence and each of the environmental variables included in the HMSC model. Environmental variables at log scale were mid and late decay stage (early as reference) and log volume and patch-scale variables were the summed log volume per hectare, proportion of clear-cut area in the surrounding 1 km, forest patch area and set-aside patches (natural patches as reference). Purple colours indicate negative responses and yellow colours positive responses with ≥ 0.95 posterior probability. The intensity of the colour represents the posterior mean estimate of the parameter (variables were scaled for comparison). Species with recent name changes are *A. serialis* (new name *Neoantrodia serialis*), Ant. sin. = *A. sinuosa* (*Amyloporia sinuosa*), *F. rosea* (*Rhodofomes roseus*), *P. chrysoloma* (*Porodaedalea chrysoloma*), *P. ferrugineofuscus* (*Phellinidium ferrugineofuscum*) and *P. viticola* (*Fuscoporia viticola*). Red-listed species are marked in bold.

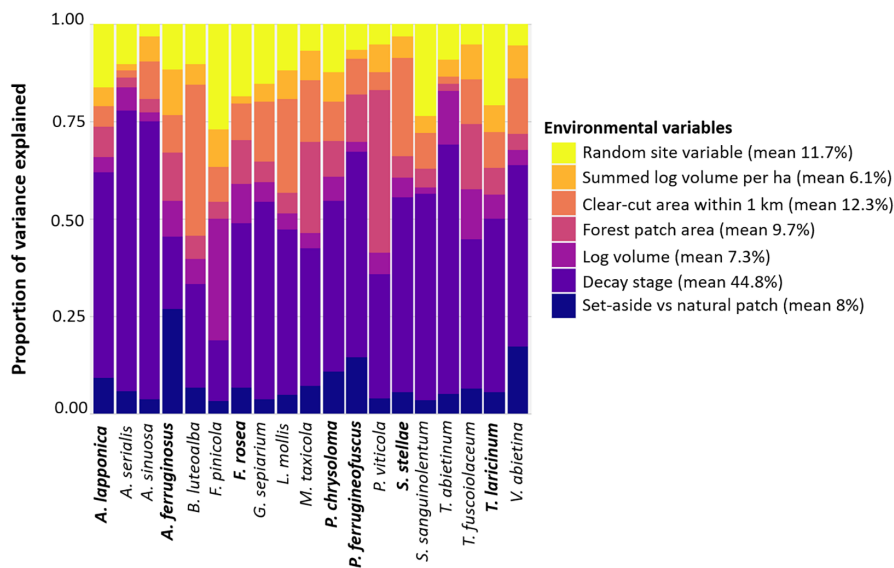


FIGURE 3 Proportion of variance explained by each environmental variable for each species' occupancy in the communities studied (for full species names and recent name changes, see [Figure 2](#)). The mean explained variance (in %) across species is shown in the legend. Red-listed species are marked in bold.

4 | DISCUSSION

4.1 | Assembly of fungal species and traits with decay stage and patch naturalness

We found that log decay stage was the primary driver of community assembly of species and traits of wood-inhabiting fungi in isolated forest patches, adhering to theories of deterministic niche-based assembly processes. The decay stage was strongly associated with four reproduction traits (fruit-body density, size, lifespan and type) and one resource-use trait (rot type), although

these traits were also filtered by patch naturalness. Communities of natural patches in an unmanaged landscape hosted larger mean fruit-body sizes and higher occurrence probabilities of annually fruiting fungi, compared with communities of set-aside patches in managed landscapes. While patch naturalness often influenced traits ([Figure 1](#)), it generally did not relate as strongly to individual species' occurrences ([Figures 2 and 3](#)). This is likely because traits are more directly linked to how well organisms perform or function in relation to patch naturalness and their conditions. Our theory that fungal traits could potentially explain community assembly beyond species identity was only partially supported, that is in the

case of patch naturalness, but not decay stage which was strongly related to both species and traits. We discuss the specific trait- and species-environment relationships in greater detail in the subsequent sections.

4.2 | Trait-decay stage relationships

Traits were more effective in explaining differences in how fungal species responded to log decay stage (54%–73%) compared to their responses to summed log volume per hectare (19%), patch area (21%), and proportion of surrounding clear cutting (35%) at the patch scale. However, patch naturalness was an exception, where fungal traits explained a significant portion of the variation (50%). This is in agreement with Abrego et al. (2022), who found that complexes of correlated traits, such as fruit-body type correlated to multiple other fruit body morphological traits, explained more of the variation in the substrate-scale responses (decay stage) of wood-inhabiting fungi than the forest-site responses (forest area, macroclimate and connectivity). However, fungal trait studies in temperate European beech (*Fagus sylvatica*) forests (Abrego et al., 2017, 2022) and boreal forests (Purhonen et al., 2020) have established relatively few statistically supported individual trait-environment relationships. In our study, decay stage had the highest number of statistically supported hypotheses concerning relationships with fungal traits (Table 2). In agreement with our hypothesis, mean fruit-body size decreased with increasing decay stage. This may result from reduced or more unreliable deadwood resources with increasing decay stage (e.g. Bässler et al., 2014, 2016; Halbwachs et al., 2016; Nordén et al., 2013). Wood-inhabiting fungal communities are well known to follow successional dynamics during decay related to both changes in deadwood resources, microclimate, and biotic interactions (Abrego et al., 2017; Ottosson et al., 2014; Rajala et al., 2015).

As deadwood decays, density decreases and moisture content increases, making the substrate more physically heterogeneous with greater niche availability in a spatially non-uniform way, at least during mid-decay stages before resources are depleted (Boddy, 2001; Hart et al., 2023). This, in turn, allow for higher diversity, competition and filtering of species and traits (Boddy, 2001). Opposite to our original hypotheses, fruit-body density and perennial species increased in communities of late decay stages. This could potentially result from multiple factors, including evidence suggesting that late decay stages often exhibit high moisture levels and concentrations of nitrogen. This may alleviate nitrogen limitation in deadwood, a factor known to influence microbial composition at the end of the deadwood life cycle (Rajala et al., 2012; Rinne et al., 2016). While we did not directly assess the nutrient content of deadwood or fungal fruit bodies in this study, future investigations into fungal community traits would benefit from including measurements of nutrient-acquisition traits. Additionally, there may be competitive advantages associated with durability and longevity, allowing species to exploit resources over extended periods and reproduce primarily in late decay stages when resources become more limited. This has been

demonstrated in studies such as that of *Phellopilus nigrolimitatus* (Kubartová et al., 2012; Ovaskainen et al., 2013). Furthermore, an investment in fruit-body structure and toughness may enhance protective functions (Halbwachs et al., 2016; Krah et al., 2022). However, the potential advantages in terms of competition with other fungi, protection against fungivores and survival in late decay deadwood warrant further research.

As hypothesised, fruit-body traits can potentially have multiple functions (e.g. reproduction, dispersal and protection) and there may be trade-offs between functional traits that explain the decay-dependent assembly of these organisms (Boddy & Hiscox, 2017; Dawson et al., 2019). According to Grime (1977), potential trade-offs could exist between highly competitive, short lived, fast-growing and fast-decaying R-selected species and stress-tolerant, long lived, slow-growing and poor-decaying C- and/or S-selected species (Lustenhouwer et al., 2020). Reproductive traits characterising wood-inhabiting fungi of early decay stage (larger, less dense, and more often short-lived annual species), agrees strongly with ecological theories of R-selected species (Grime, 1977). These include rapid spore germination, growth, high investment in reproduction, and low investment in persistence traits within the resource (Boddy & Hiscox, 2017). Large fruit-body size has been proposed as a C-selected and/or S-selected life strategy, with higher competitiveness, stress tolerance (e.g. to desiccation and predation pressure) and chance of survival for longer periods (Bässler et al., 2014; Halbwachs et al., 2016; Krah et al., 2022). Early decay stage deadwood may represent microclimatically and chemically stressful habitats, but the large fruit-body sizes measured in our study more likely reflect reproductive advantages where larger spore-producing surface areas (hymenium) leads to higher reproduction and dispersal capacity. The lower density and higher probability of annual fruit-bodies in early decay stages also support an alignment with the life strategies of R-selected species. In comparison to fruit-body size, the dry fruit-body density likely correspond more closely to resource investment in reinforcing hyphal structure with protective (e.g. structural support and protection against rain, desiccation, heat, insolation and predators) and provisioning (water and nutrients to hymenium, bait for vectors, spore production) functions (Halbwachs et al., 2016). We found a tendency for smaller spore size in mid decay stages compared to late decay stages, although only strongly supported in set-aside patches. This could be indicative of an r-selected strategy. Smaller spores are often produced in greater numbers, which aligns with the strategy of maximising reproductive output to exploit temporary or less stable environments. Norros et al. (2023) summarised that smaller spore size may be correlated to several other traits (e.g. more spores, low spore viability, low deposition rate, larger fruit bodies, higher sensitivity to fragmentation) that are typical for sensitive saprotrophs tracking rare colonisation opportunities. We could detect similar patterns for larger fruit-body size and greater species richness, although not for the occurrence of red-listed rare species, in mid decay stage compared to late decay stage.

Several studies have found that species with pileate fruit bodies occur mostly in early mid-decay stages (Abrego et al., 2017,

2022; Bässler et al., 2014; Nordén et al., 2013). Our results differed from these findings, probably because we divided this group further into pileate (capped) and half-resupinate (a resupinate with a pileate part) fruit-body types. In doing so, we found strong support for half-resupinate fruit-body types in early decay stages possibly indicating a trade-off for efficient capture of resources in the outer sapwood (e.g. white-rot *Trichaptum* species), where the cap protect the spore-bearing structures and the resupinate part maximises the size of the spore-bearing tissue. However, further comparative studies on the functional performance of different fruit-body types are needed to better understand their functional biomechanics (Lapichino et al., 2021), relation to abiotic and biotic filtering (Dawson et al., 2019; Halbwegs et al., 2018). For example, the arthropod diversity is higher in fruit bodies with a larger surface area-to-volume ratio (resupinates), suggesting that colonisation via a large surface area is crucial to maintain arthropod populations and potential spore vectors (Lunde, Birkemoe, et al., 2022).

Contrary to our hypothesis, the proportion of reproducing white-rot fungi decreased with decay stage, while brown-rot fungi increased. Our original hypothesis was partly based on Rajala et al. (2015), who found a succession from brown-rot to white-rot communities using DNA sequencing data of fungal mycelia in Norway spruce wood (Table S1). Our focus on the dominant reproducing species likely accounts for the difference in results. To gain deeper insights, it would be beneficial to refine and relate various resource-use traits to species' metacommunity dynamics (Moor et al., 2021), such as the prevailing rot types or nutrient acquisition of colonising and extinct species in communities, with increasing decay stage. Nonetheless, our results provide valuable insights, because the dominant wood rot types alter the physicochemical properties of deadwood, which affects carbon sequestration in forests (Lustenhower et al., 2020) and can have indirect long-lasting cascading impacts on forest biodiversity (Fukasawa, 2021).

4.3 | Patch naturalness relationships

Set-aside patches more often filtered for species with smaller, perennial and resupinate fruit-bodies compared to natural patches. Hence, fruit-body size, type and lifespan were linked to the responses of wood-inhabiting fungi to relatively small variation in naturalness from semi-natural forests in managed landscapes to natural forests in an unmanaged landscape. Our results partially agree with earlier studies that found forest management filters out species with large and long-lived fruit-bodies (Abrego et al., 2017, 2022; Bässler et al., 2014, 2016; Nordén et al., 2013). More generally, the role of increasing forest naturalness (e.g. long structural continuity, high connectivity, and less intensive land use) has been illustrated as an important driver of the occurrence (Nordén et al., 2013) and dynamics (Moor et al., 2021) of specialised wood fungi, and the occurrence of pileate and resupinate morpho-groups inhabiting spruce (Purhonen et al., 2021). Further research is needed to establish conclusive evidence for the performance of the traits presented in this

study, as well as for other functional traits, over a broader range of boreal forest environments (including managed forests). Moreover, relatively few species (*Antrrodia serialis*, *Fomitopsis rosea*, *P. ferrugineofuscus* and *Veluticeps abietina*) were more likely to be found on logs in set-aside patches than natural patches (Figure 2), and these four species may have been particularly influential on trait-patch naturalness results. The forest history of set-aside patches, originally part of a much larger intact forest area, suggests that community members and traits may still be transitioning towards a new equilibrium. Encouragingly, logs within set-aside patches exhibited a higher species richness and likelihood of hosting red-listed species compared to natural patches in the unmanaged reference landscape. Consistent with earlier research (Timonen et al., 2011), these results indicate that the deadwood in set-aside patches effectively supports species-rich fungal communities, including red-listed species. The increased likelihood of red-listed species in set-aside patches can be partially attributed to the presence of red-listed species such as *F. rosea* and *P. ferrugineofuscus* within set-asides. Notably, these were the only species positively associated with increasing patch area, suggesting that their presence in set-aside patches may reflect these patches' historically larger intact forest areas. The two species are also among the most abundant and least specialised red-listed species in our study (SLU Artdatabanken, 2020). Hence, it is important to note that the rarest and most specialised species were not included in this study (Table S2), which may also influence these findings. Even though species richness was higher on logs in set-aside patches, the mean species richness of all red-listed species per plot was 4.0 in set-aside patches and 7.2 in natural patches (see Table S2). This difference is likely due to the lower average amount of deadwood in set-aside patches (19 m³/ha) compared to natural patches (31 m³/ha) in our study. We did not test if variables other than decay stage and patch naturalness were associated with log-level fungal species richness. However, earlier research has shown that both the local amount of deadwood within patches and the potential source habitat in the surrounding landscape are important drivers of wood fungal richness in boreal forest patches (Junninen & Komonen, 2011; Kärvelo et al., 2021).

4.4 | Unsupported environmental relationships

The large number of unsupported hypotheses (Table 2) for patch-scale summed log volume, patch area, and clear-cutting in the surrounding 1 km do not agree with the standard hypothesis of environmental filters being more prevalent at coarser scales (e.g. Mod et al., 2020). These results may stem from various factors and many of our trait hypotheses were exploratory in nature, reflecting the limited studies and knowledge regarding trait performance in the field. Similar to Abrego et al. (2022), these coarser scale variables may indeed not be very influential on fungal trait assemblages. Alternatively, we may need larger sample sizes and/or a greater environmental gradients to observe some of the trait differences. These relationships are also expected to be heavily reliant on different fungal groups,

particularly relating to dispersal capacities and habitat specialisation (Moor et al., 2021; Nordén et al., 2013; Purhonen et al., 2021), and need to be tested for a broader range of fungi. Moreover, in order to disentangle the influence of stochastic processes to these results, experimental approaches are needed. Intraspecific variation of traits within fungal species may also account for the lack of supported hypotheses, especially since intraspecific variation of fungal traits is very large compared to other organisms (Dawson & Jönsson, 2020). At last, we were unable to address the time between colonisation and fruiting in our study, raising questions about whether late decay stage fruiterers were present in the deadwood since early decay stages or if they colonise later. This area requires further exploration (see Kubartová et al., 2012; Ovaskainen et al., 2013).

Both the volume of individual downed logs and the summed volume of logs per hectare are considered strong determinants of occurrence (Nordén et al., 2013) and colonisation (Moor et al., 2021) of fungal old-growth indicator species and fruit-body morphological traits (Abrego et al., 2017; Bässler et al., 2014). Yet, they both had a relatively small impact in our study system, similar to Abrego et al. (2022). This is likely because our forest patches had relatively high summed log volumes per hectare, above or close to the $20\text{m}^3\text{ha}^{-1}$ threshold suggested important for maintaining polypore diversity (Junninen & Komonen, 2011). Furthermore, as shown by Dawson et al. (2020) the patch-scale trait composition of semi-natural set-aside forests in this study area have converged with natural patches over time. The lack of strong effects could also be because we focused on coarse logs ($>10\text{cm}$ diameter) which hold more uniform communities compared to smaller substrates (Juutilainen et al., 2011).

5 | CONCLUSIONS

In this study, we show that fungal reproductive traits and environmental filters, particularly log decay stage and forest patch naturalness, influence the assembly of wood-inhabiting fungal communities. We found relationships between four fungal reproductive traits and one resource-use trait with log decay stage. These results indicate that deterministic niche-based processes play an important role in the assembly of species and traits, although we could not disentangle the stochastic components in community assembly. Fungal fruit-body traits can have multiple functions in terms of reproduction, dispersal, and protection, and our results indicate there may be trade-offs between functional traits that explain the observed decay-dependent assembly of communities. The observed trait-decay stage relationships followed the same trajectories in forest patches of different naturalness type, illustrating that fungal reproduction traits can capture assembly processes related to deadwood decomposition in different forest environments. Patch naturalness did nonetheless modulate this response within decay stages, where semi-natural set-aside patches in managed landscapes more often filtered for species with smaller, perennial and resupinate fruit-bodies compared to natural patches in an unmanaged landscape. Taken collectively, these insights not only deepen our understanding of fungal ecology and function but also

emphasise the utility of trait-based approaches for comprehending community assembly dynamics across a spectrum of ecological contexts. Future studies should explore, preferably by field studies as well as experimental approaches, these and other fungal traits to better understand their functional performance and relation to abiotic and biotic filtering in community assembly (Fukami et al., 2010). Future studies should strive to measure fungal traits across a broad environmental spectrum, taking into account intraspecific trait variation. Additionally, exploring the role of fungal traits in metacommunity dynamics—such as the colonisation, persistence, and extinction of species—will enhance our current understanding of wood-inhabiting community assembly processes and theories. Investigations into the role of biotic interactions in deadwood ecosystems will also contribute significantly to advancing our knowledge in this field.

AUTHOR CONTRIBUTIONS

SKD, HB, BGJ, TS, EO and MJ conceived the ideas and designed methodology; SKD, HB, EO and MJ collected the data; SKD and OO analysed the data; SKD and MJ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank the field assistants Torbjörn Josefsson and Sofia Nygård. The study was funded by the Swedish University of Agricultural Sciences to SKD and FORMAS (grant 2016-00461) to SKD, HB, BGJ, TS, EO and MJ. OO was funded by Academy of Finland (grant no. 336212 and 345110), and the European Union: the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 856506; ERC-synergy project LIFEPLAN). We thank two anonymous reviewers for valuable comments that greatly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data upon which this study is based are available through the Dryad Digital Repository <https://doi.org/10.5061/dryad.pg4f4qrzc> (Dawson et al., 2024).

ORCID

Samantha K. Dawson  <https://orcid.org/0000-0001-5165-9591>

Otso Ovaskainen  <https://orcid.org/0000-0001-9750-4421>

Bengt G. Jonsson  <https://orcid.org/0000-0001-7307-1940>

Tord Snäll  <https://orcid.org/0000-0001-5856-5539>

Elisabet Ottosson  <https://orcid.org/0000-0003-4678-4210>

Mari Jönsson  <https://orcid.org/0000-0002-5465-7820>

REFERENCES

Abrego, N. (2022). Wood-inhabiting fungal communities: Opportunities for integration of empirical and theoretical community ecology. *Fungal Ecology*, 59, 101112. <https://doi.org/10.1016/j.funeco.2021.101112>

- Abrego, N., Bässler, C., Christensen, M., & Heilmann-Clausen, J. (2022). Traits and phylogenies modulate the environmental responses of wood-inhabiting fungal communities across spatial scales. *Journal of Ecology*, 110, 784–798. <https://doi.org/10.1111/1365-2745.13839>
- Abrego, N., Norberg, A., & Ovaskainen, O. (2017). Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. *Journal of Ecology*, 105, 1070–1081. <https://doi.org/10.1111/1365-2745.12722>
- Aguilar-Trigueros, C. A., Hempel, S., Powell, J. R., Anderson, I. C., Antonovics, J., Bergmann, J., Cavignaro, T. R., Chen, B., Hart, M. M., Klironomos, J., Petermann, J. S., Verbruggen, E., Veresoglou, S. D., & Rillig, M. C. (2015). Branching out: Towards a trait-based understanding of fungal ecology. *Fungal Biology Reviews*, 29, 34–41. <https://doi.org/10.1016/j.fbr.2015.03.001>
- Bässler, C., Ernst, R., Cadotte, M., Heibl, C., & Müller, J. (2014). Near-to-nature logging influences fungal community assembly processes in a temperate forest. *Journal of Applied Ecology*, 51, 939–948. <https://doi.org/10.1111/1365-2664.12267>
- Bässler, C., Halbwegs, H., Karasch, P., Holzer, H., Gminder, A., Kriegelsteiner, L., Gonzalez, R. S., Müller, J., & Brandl, R. (2016). Mean reproductive traits of fungal assemblages are correlated with resource availability. *Ecology and Evolution*, 6, 582–592. <https://doi.org/10.1002/ece3.1911>
- Berglund, H., & Jonsson, B. G. (2003). Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. *Biological Conservation*, 112, 319–328. [https://doi.org/10.1016/S0006-3207\(02\)00329-4](https://doi.org/10.1016/S0006-3207(02)00329-4)
- Berglund, H., & Jonsson, B. G. (2005). Verifying an extinction debt among lichens and fungi in northern Swedish boreal forests. *Conservation Biology*, 19, 338–348. <https://doi.org/10.1111/j.1523-1739.2005.00550.x>
- Boddy, L. (2001). Fungal community ecology and wood decomposition processes in angiosperms: From standing tree to complete decay of coarse woody debris. *Ecological Bulletins*, 49, 43–56.
- Boddy, L., & Hiscox, J. (2017). Fungal ecology: Principles and mechanisms of colonization and competition by saprotrophic fungi. In J. Heitman, B. J. Howlett, P. W. Crous, E. H. Stukenbrock, T. Y. James, & N. A. R. Gow (Eds.), *The fungal kingdom*. American Society of Microbiology. <https://doi.org/10.1128/9781555819583.ch13>
- Butterworth, N. J., Benbow, M. E., & Barton, P. S. (2023). The ephemeral resource patch concept. *Biological Reviews*, 98, 697–726. <https://doi.org/10.1111/ecog.06333>
- Dawson, S. K., Berglund, H., Ovaskainen, O., Jonsson, B. G., Snäll, T., Ottosson, E., & Jönsson, M. (2024). Data from: Fungal trait-environment relationships in wood-inhabiting communities of boreal forest patches. Dryad Digital Repository, <https://doi.org/10.5061/dryad.pg4f4qzrc>
- Dawson, S. K., Berglund, H., Ovaskainen, O., Snäll, T., Jonsson, B. G., & Jönsson, M. (2020). Convergence of fungal traits over time in natural and forestry-fragmented patches. *Biological Conservation*, 251, 108789. <https://doi.org/10.1016/j.biocon.2020.108789>
- Dawson, S. K., Boddy, L., Halbwegs, H., Bässler, C., Andrew, C., Crowther, T. W., Heilmann-Clausen, J., Nordén, J., Ovaskainen, O., & Jönsson, M. (2019). Handbook for the measurement of macro-fungal functional traits; a start with basidiomycete wood fungi. *Functional Ecology*, 33, 1365–1387. <https://doi.org/10.1111/1365-2435.13239>
- Dawson, S. K., & Jönsson, M. (2020). Just how big is intraspecific trait variation in basidiomycete wood fungal fruit bodies? *Fungal Ecology*, 46, 100865. <https://doi.org/10.1016/j.funeco.2019.100865>
- Fraver, S., Ringvall, A., & Jonsson, B. G. (2007). Refining volume estimates of down woody debris. *Canadian Journal of Forest Research*, 37, 627–633. <https://doi.org/10.1139/X06-269>
- Fukami, T., Dickie, I. A., Wilkie, J. P., Paulus, B. C., Park, D., Roberts, A., Buchanan, P. K., & Allen, R. B. (2010). Assembly history dictates ecosystem functioning: Evidence from wood decomposer communities. *Ecology Letters*, 13, 675–684. <https://doi.org/10.1111/j.1461-0248.2010.01465.x>
- Fukasawa, Y. (2021). Ecological impacts of fungal wood decay types: A review of current knowledge and future research directions. *Ecological Research*, 36, 910–931. <https://doi.org/10.1111/1440-1703.12260>
- Fukasawa, Y., Osono, T., & Takeda, H. (2009). Dynamics of physicochemical properties and occurrence of fungal fruit bodies during decomposition of coarse woody debris of *Fagus crenata*. *Journal of Forest Research*, 14, 20–29. <https://doi.org/10.1007/s10310-008-0098-0>
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111, 1169–1194. <https://doi.org/10.1086/283244>
- Halbwachs, H., Karasch, P., & Simmel, J. (2018). Small can be beautiful: Ecological trade-offs related to basidiospore size. *Asian Journal of Mycology*, 1, 15–21. https://asianjournalofmycology.org/pdf/AJOM_1_1_3.pdf
- Halbwachs, H., Simmel, J., & Bässler, C. (2016). Tales and mysteries of fungal fruiting: How morphological and physiological traits affect a pileate lifestyle. *Fungal Biology Reviews*, 30, 36–61. <https://doi.org/10.1016/j.fbr.2016.04.002>
- Harmon, M. E., Sexton, J., Caldwell, B. A., & Carpenter, S. E. (1994). Fungal sporocarp mediated losses of Ca, Fe, K, Mg, Mn, N, P, and Zn from conifer logs in the early stages of decomposition. *Canadian Journal of Forest Research*, 24, 1883–1893. <https://doi.org/10.1139/x94-243>
- Hart, S. C., Porter, T. M., Basiliko, N., Venier, L., Hajibabaei, M., & Morris, D. (2023). Fungal community dynamics in coarse woody debris across decay stage, tree species, and stand development stage in northern boreal forests. *Canadian Journal of Forest Research*, 54, 12–30. <https://doi.org/10.1139/cjfr-2023-0061>
- Hubbell, S. P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, 19, 166–172. <https://doi.org/10.1111/j.0269-8463.2005.00965.x>
- Junninen, K., & Komonen, A. (2011). Conservation ecology of boreal polypores: A review. *Biological Conservation*, 144, 11–20. <https://doi.org/10.1016/j.biocon.2010.07.010>
- Juutilainen, K., Halme, P., Kotiranta, H., & Mönkkönen, M. (2011). Size matters in studies of dead wood and wood-inhabiting fungi. *Fungal Ecology*, 4, 342–349. <https://doi.org/10.1016/j.funeco.2011.05.004>
- Kärvelö, S., Jönsson, M., Hekkala, A.-M., Sjögren, J., & Strengbom, J. (2021). Multitaxon conservation in northern forest hot-spots: The role of forest characteristics and spatial scales. *Landscape Ecology*, 36, 989–1002. <https://doi.org/10.1007/s10980-021-01205-x>
- Krah, F. S., Hagge, J., Schreiber, J., Brandl, R., Müller, J., & Bässler, C. (2022). Fungal fruit body assemblages are tougher in harsh microclimates. *Scientific Reports*, 12, 1633. <https://doi.org/10.1038/s41598-022-05715-9>
- Krah, F. S., Seibold, S., Brandl, R., Baldrian, P., Müller, J., & Bässler, C. (2018). Independent effects of host and environment on the diversity of wood-inhabiting fungi. *Journal of Ecology*, 106, 1428–1442. <https://doi.org/10.1111/1365-2745.12939>
- Krankina, O. N., Harmon, M. E., & Griazkin, A. V. (1999). Nutrient stores and dynamics of woody detritus in a boreal forest: Modeling potential implications at the stand level. *Canadian Journal of Forest Research*, 29, 20–32. <https://doi.org/10.1139/x98-162>
- Kubartová, A., Ottosson, E., Dahlberg, A., & Stenlid, J. (2012). Patterns of fungal communities among and within decaying logs, revealed by 454 sequencing. *Molecular Ecology*, 21, 4514–4532. <https://doi.org/10.1111/j.1365-294X.2012.05723.x>
- Lapichino, M., Wang, Y. W., Gentry, S., Pringle, A., & Seminara, A. (2021). A precise relationship among Buller's drop, ballistospore, and gill

- morphologies enables maximum packing of spores within gilled mushrooms. *Mycologia*, 113, 300–311. <https://doi.org/10.1080/00275514.2020.1823175>
- Leibold, M. A. (1995). The niche concept revisited—Mechanistic models and community context. *Ecology*, 76, 1371–1382. <https://doi.org/10.2307/1938141>
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- Lindner, D. L., Vasaitis, R., Kubartová, A., Allmér, J., Johansson, H., Banik, M. T., & Stenlid, J. (2011). Initial fungal colonizer affects mass loss and fungal community development in *Picea abies* logs 6 yr after inoculation. *Fungal Ecology*, 4, 359–460. <https://doi.org/10.1016/j.funeco.2011.07.001>
- Lövgren, R. (1986). *Urskogar. Inventering av urskogsartade områden i Sverige. Del 3 - Norra Sverige*. Report 1509. Swedish Environmental Protection Agency.
- Lunde, L. F., Birkemoe, T., Kauserud, H., Boddy, L., Jacobsen, R. M., Morgado, L., Sverdrup-Thygeson, A., & Maurice, S. (2022). DNA metabarcoding reveals host-specific communities of arthropods residing in fungal fruit bodies. *Proceedings of the Royal Society B*, 289, 20212622. <https://doi.org/10.1098/rspb.2021.2622>
- Lunde, L. F., Jacobsen, R., Kauserud, H., Boddy, L., Nybakken, L., Sverdrup-Thygeson, A., & Birkemoe, T. (2022). Legacies of invertebrate exclusion and tree secondary metabolites control fungal communities in dead wood. *Molecular Ecology*, 31, 3241–3253. <https://doi.org/10.1111/mec.16448>
- Lustenhauer, N., Maynard, D. S., Bradford, M. A., Lindner, D. L., Oberle, B., Zanne, A. E., & Crowther, T. W. (2020). A trait-based understanding of wood decomposition by fungi. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 11551–11558. <https://doi.org/10.1073/pnas.1909166117>
- McCullough, H. A. (1948). Plant succession on fallen logs in a virgin spruce-fir Forest. *Ecology*, 29, 508–513. <https://doi.org/10.2307/1932645>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Mod, H. K., Chevalier, M., Luoto, M., & Guisan, A. (2020). Scale dependence of ecological assembly rules: Insights from empirical datasets and joint species distribution modelling. *Journal of Ecology*, 108, 1967–1977. <https://doi.org/10.1111/1365-2745.13434>
- Moor, H., Nordén, J., Penttilä, R., Siitonen, J., & Snäll, T. (2021). Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. *Journal of Ecology*, 109, 491–503. <https://doi.org/10.1111/1365-2745.13526>
- Norberg, A., Halme, P., Kotiaho, J. S., Toivanen, T., & Ovaskainen, O. (2019). Experimentally induced community assembly of polypores reveals the importance of both environmental filtering and assembly history. *Fungal Ecology*, 41, 137–146. <https://doi.org/10.1016/j.funeco.2019.05.003>
- Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., & Ovaskainen, O. (2013). Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *Journal of Ecology*, 101, 701–712. <https://doi.org/10.1111/1365-2745.12085>
- Norros, V., Halme, P., Norberg, A., & Ovaskainen, O. (2023). Spore production monitoring reveals contrasting seasonal strategies and a trade-off between spore size and number in wood-inhabiting fungi. *Functional Ecology*, 37, 551–563. <https://doi.org/10.1111/1365-2435.14254>
- Norros, V., Rannik, Ü., Hussein, T., Petäjä, T., Vesala, T., & Ovaskainen, O. (2014). Do small spores disperse further than large spores? *Ecology*, 95, 1612–1621. <https://doi.org/10.1890/13-0877.1>
- Ottosson, E., Nordén, J., Dahlberg, A., Edman, M., Jönsson, M., Larsson, K., Olsson, J., Penttilä, R., Stenlid, J., & Ovaskainen, O. (2014). Species associations during the succession of wood-inhabiting fungal communities. *Fungal Ecology*, 11, 17–28. <https://doi.org/10.1016/j.funeco.2014.03.003>
- Ovaskainen, O., Schigel, D., Ali-Kovero, H., Auvinen, P., Paulin, L., Nordén, B., & Nordén, J. (2013). Data from combining high-throughput sequencing with fruitbody surveys reveals contrasting life-history strategies in fungi. *The ISME Journal*, 7, 1696–1709. <https://doi.org/10.1038/ismej.2013.61>
- Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, G. F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20, 561–576. <https://doi.org/10.1111/ele.12757>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–213. <https://doi.org/10.1071/BT12225>
- Purhonen, J., Abrego, N., Komonen, A., Huhtinen, S., Kotiranta, H., Læssøe, T., & Halme, P. (2021). Wood-inhabiting fungal responses to forest naturalness vary among morpho-groups. *Scientific Reports*, 11, 14585. <https://doi.org/10.1038/s41598-021-93900-7>
- Purhonen, J., Ovaskainen, O., Halme, P., Komonen, A., Huhtinen, S., Kotiranta, H., Læssøe, T., & Abrego, N. (2020). Morphological traits predict host-tree specialization in wood-inhabiting fungal communities. *Fungal Ecology*, 46, 100863. <https://doi.org/10.1016/j.funeco.2019.08.007>
- Rajala, T., Peltoniemi, M., Pennanen, T., & Makipää, R. (2012). Fungal community dynamics in relation to substrate quality of decaying Norway spruce (*Picea abies* [L.] Karst.) logs in boreal forests. *FEMS Microbiology Ecology*, 81, 494–505. <https://doi.org/10.1111/j.1574-6941.2012.01376.x>
- Rajala, T., Tuomivirta, T., Pennanen, T., & Mäkipää, R. (2015). Habitat models of wood-inhabiting fungi along a decay gradient of Norway spruce logs. *Fungal Ecology*, 18, 48–55. <https://doi.org/10.1016/j.funeco.2015.08.007>
- Rinne, K. T., Rajala, T., Peltoniemi, K., Chen, J., Smolander, A., & Mäkipää, R. (2016). Accumulation rates and sources of external nitrogen in decaying wood in a Norway spruce dominated forest. *Functional Ecology*, 31, 530–541. <https://doi.org/10.1111/1365-2435.12734>
- Saine, S., Ovaskainen, O., Somervuo, P., & Abrego, N. (2020). Data collected by fruit body- and DNA-based survey methods yield consistent species-to-species association networks in wood-inhabiting fungal communities. *Oikos*, 129, 1833–1843. <https://doi.org/10.1111/oik.07502>
- SLU Artdatabanken. (2020). *Red-listed species in Sweden 2020*. SLU.
- Song, Z., Kennedy, P. G., Liew, F. J., & Schilling, J. S. (2017). Fungal endophytes as priority colonizers initiating wood decomposition. *Functional Ecology*, 31, 407–418. <https://doi.org/10.1111/1365-2435.12735>
- Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehtikoinen, A., Jonge, M. M. J., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the r-package Hmsc. *Methods in Ecology and Evolution*, 11, 442–447. <https://doi.org/10.1111/2041-210X.13345>
- Timonen, J., Gustafsson, L., Kotiaho, J. S., & Mönkkönen, M. (2011). Hotspots in cold climate: Conservation value of woodland key habitats in boreal forests. *Biological Conservation*, 144, 2061–2067. <https://doi.org/10.1016/j.biocon.2011.02.016>
- van der Wal, A., Klein Gunnewiek, P. J. A., Cornelissen, J. H. C., Crowther, T. W., & de Boer, W. (2016). Patterns of natural fungal community assembly during initial decay of coniferous and broadleaf tree logs. *Ecosphere*, 7, e01393. <https://doi.org/10.1002/ecs2.1393>

- Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27, 244–252. <https://doi.org/10.1016/j.tree.2011.11.014>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology & Evolution*, 30, 766–779. <https://doi.org/10.1016/j.tree.2015.09.007>
- Zambrano, J., Garzon-Lopez, C. X., Yeager, L., Fortunel, C., Cordeiro, N. J., & Beckman, N. G. (2019). The effects of habitat loss and fragmentation on plant functional traits and functional diversity: What do we know so far? *Oecologia*, 191, 505–518. <https://doi.org/10.1007/s00442-019-04505-x>
- Zanne, A. E., Abarenkov, K., Afkhami, M. E., Aguilar-Trigueros, C. A., Bates, S., Bhatnagar, J. M., Busby, P. E., Christian, N., Cornwell, W., Crowther, T. W., & Moreno, H. F. (2020). Fungal functional ecology: Bringing a trait-based approach to plant-associated fungi. *Biological Review*, 95, 409–433. <https://doi.org/10.1111/brv.12570>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: The studied six traits and red-list conservation attribute of wood-inhabiting fungi, along with their hypothesized relationships

with fungal function and corresponding trait-environment relationships at both the log and forest patch scales.

Table S2: Table of species occurrences (once per log) in natural and set-aside forest patches and sub-setting of species data to account for low species occurrence and lack of trait information.

Table S3: Summary table of the final model data set of species occurrences (once per log) and their traits values and red-list category.

Figure S1: Unsupported relationships of fungal traits and the red-listed status conservation attribute with the quantitative environmental variables in the model.

Figure S2: Species-specific area under the curve (AUC) values for each species in the model obtained from model predictions fitted to all data.

How to cite this article: Dawson, S. K., Berglund, H., Ovaskainen, O., Jonsson, B. G., Snäll, T., Ottosson, E., & Jönsson, M. (2024). Fungal trait-environment relationships in wood-inhabiting communities of boreal forest patches. *Functional Ecology*, 38, 1944–1958. <https://doi.org/10.1111/1365-2435.14627>