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# Complex relationship between soil fungi and conservation value assessments in boreal forests

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## Abstract

Large-scale industrial forestry is a threat to biodiversity and imposes long-lasting changes to many forested biomes. Preserving forests as reserves is an important component of the strategy for safeguarding forest biodiversity. Yet, the selection of forests of high biodiversity value is usually based on proxies (i.e., subsets of aboveground habitat characteristics) rather than on direct assessments of species occurrences. This approach is based on the assumption that the diversity and community composition of all organism groups are well represented by the assessed habitat characteristics. We investigated how conservation value, assessed according to common practices based on aboveground habitat heterogeneity, corresponded to the abundance, richness, and community composition of 12 taxonomic and ecological groups of soil fungi across northern and southern Swedish forests. Overall, the assessed conservation value reflected the abundance, diversity, and community composition of deadwood-associated saprotrophs well, likely because they depend directly on the availability of the structures that the assessment is based on. However, the conservation assessment value failed to capture the overall variability for most of the soil-dwelling fungal guilds. Although the assessed value was positively associated with the diversity of ectomycorrhizal fungi, root-associated Ascomycota, and saprotrophic Basidiomycota in the southern region, no such association was evident in the northern region. Soil fertility was the best predictor of the variation in community composition in all fungal guilds. The relative abundance and diversity of most saprotrophic guilds increased as soil fertility increased, whereas root-associated guilds decreased as soil fertility increased. Current methods for assessing conservation value captured only specific subsets of soil fungi, and the predictability of capturing fungal diversity varied depending on the region. To more comprehensively preserve soil fungi, assessment methods should incorporate additional environmental parameters, especially those linked to fungal community composition, such as soil fertility.

**KEYWORDS**
biodiversity, DNA metabarcoding, fungal guilds, PacBio sequencing, woodland key habitats

## INTRODUCTION

In natural forests, disturbances, such as windstorms, wildfires, and pest outbreak, promote multistory and heterogeneous stands, with variable tree species composition and large

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amounts of dead wood (Berglund & Kuuluvainen, 2021; Viljur et al., 2022). In contrast, management for biomass production results in even-aged stands with low habitat diversity, leading to homogenization at the forest stand and landscape scales (Pohjanmies et al., 2021). The simultaneous fragmentation and loss of old-growth forest are additional threats to forest biodiversity (Berglund & Kuuluvainen, 2021; SLU Artdatabanken, 2020). A large part of the boreal biome is managed (Gauthier et al., 2015), and Fennoscandia has a particularly long history of management for wood production (Östlund et al., 1997; Linder & Östlund, 1998), with small remnants of high-conservation-value forests imbedded in an intensively managed forest landscape (Svensson et al., 2019). Multiple small, high-value forests are thought to be of special importance for maintaining a well-connected network of high-biodiversity sites in managed forest landscapes (Hansson, 2001, Laita et al., 2010, Timonen et al., 2010). Reliable methods to identify and map areas of high conservation value is thus key to effective preservation of future biodiversity (Asamoah et al., 2021; Leclère et al., 2020) and an important measure to meet the United Nations post-2020 global biodiversity framework (CBD, 2022).

Because a comprehensive assessment of biodiversity is rarely possible, biodiversity proxies are often used to help identify valuable forests for conservation. Such proxies can be based on habitat characteristics (Bunce et al., 2013; Luque & Vainikainen, 2008); tree microhabitats (Paillet et al., 2018); structural components, such as occurrence of dead wood (Esseen et al., 1997, Hekkala et al., 2023); indicator taxa (Gustafsson, 2000; Pearson, 1994); or measures that combine many variables (Drakenberg & Lindhe, 1999, Hekkala et al., 2023, Larrieu et al., 2021). In a recent study across mature boreal forest stands in Sweden, a score based on a wide range of aboveground habitat heterogeneity characteristics yielded a consistent positive relationship with species richness of defined groups of lichens, bryophytes, macrofungi, and vascular plants (Hekkala et al., 2023). However, it is still largely unknown whether aboveground and belowground biodiversity covaries across habitats and landscapes (Gao et al., 2015; Thakur et al., 2020), and it is uncertain whether current methods used to assess conservation values can further the protection of the functionally important, but yet largely unknown, belowground diversity of fungi.

The fungal kingdom is extremely species rich, with approximately 144,000 species named and classified globally and around 2000 new species described per year (Niskanen et al., 2018). Fungi are also functionally diverse and mediate multiple ecosystem processes. In boreal forest soils, free-living saprotrophic fungi and root-associated mycorrhizal fungi are the dominant fungal guilds (Lindahl et al., 2007). Saprotrophic fungi are the main decomposers of dead organic matter in the form of woody debris and plant litter. Mycorrhizal fungi are symbiotic partners of trees and understory shrubs and form mycelial connections with plant roots, which facilitates plant access to water and nutrients (Smith & Read, 2008). In return, mycorrhizal fungi receive sugars directly from their plant partner, typically 15–30% of net primary production (Smith & Read, 2008), and they play important roles for release and sequestration of organic matter in forest soils (Clemmensen et al., 2013; Frey, 2019).

The inclusion of fungi in forest conservation has lagged behind that of most other organism groups (Heilmann-Clausen & Vesterholt, 2008). Red-listed and rare species are generally surveyed in the field, although the cryptic nature of belowground mycelia and ephemeral production of sporophores challenges the detection and identification of fungal species (Molina et al., 2011; Parker, 2010). Nevertheless, the specific habitat requirements of many fungi make them useful as indicators of conservation values (Heilmann-Clausen et al., 2015). For instance, specialized deadwood-inhabiting fungi can be indicators of forests with high conservation values (Jonsson & Siitonen, 2012). Certain macrofungi, such as *Ramaria* spp., can be useful indicators of old-growth forest ecosystems (Smith et al., 2002). For other ecological groups of soil fungi, such as litter saprotrophs, molds, yeasts, and pathogens, their relation to traditional conservation value is poorly understood.

Progress in DNA technologies has greatly advanced species identification and biodiversity monitoring from environmental samples. The diversity and composition of fungal communities can be assessed directly using DNA-based metabarcoding (Frøslev et al., 2019), and this approach has been used to investigate how fungal communities are related to a variety of biotic and abiotic factors (Kivlin et al., 2014; Kyaschenko, Clemmensen, Karltun, et al., 2017; Sterkenburg et al., 2015; Thomson et al., 2015). Soil fertility (Sterkenburg et al., 2015), host-tree identity (Krah et al., 2018), forestry-related disturbances (Kyaschenko, Clemmensen, Hagenbo, et al., 2017), and past forest fragmentation (Raimbault et al., 2004) have been identified as important determinants of fungal diversity and community composition in forests. The effects of habitat size, amount, and connectivity on large vertebrates and vascular plants in forests and grasslands are rather well studied (Bengtsson et al., 2000; Brudvig et al., 2009; Fahrig, 2003; Kimberley et al., 2021; Lawrence et al., 2018; Ridding et al., 2023), but the relative importance of local habitat quality, forest continuity, and landscape-scale coverage of near-natural forests for soil fungal communities is less well known (Heilmann-Clausen et al., 2017).

We investigated whether boreal forest conservation value, as assessed based on aboveground forest structures (Hekkala et al., 2023), correlates with abundance, richness, and community composition of the major fungal guilds in the topsoil as assessed by DNA-based methods. We also examined whether soil fertility, tree species composition, and stand- and landscape-level tree continuity correlate with these fungal variables or modify their relationships with conservation value. Integrated evaluation of relationships with assessed conservation value and environment can inform improvement of conservation assessment methods. Our study is based on 74 mature coniferous forests across northern and southern boreal regions. These forests represented a wide range of assessment scores or conservation values. The northern region is less affected by forestry because it has a shorter history of industrial forestry and a larger portion of old-growth forest compared with the southern region.

We expected that the abundance, species richness, and composition of fungal guilds in the topsoil would be reflected in our assessed conservation values. Given that conservation value mainly reflects aboveground characteristics, we expected

strong (positive, for richness) relationships for fungal guilds that depend directly on assessed aboveground structures, such as deadwood-dependent saprotrophs and root-associated (including mycorrhizal) fungi, and weak relationships for soil- and litter-saprotrophic fungi that depend less directly on aboveground structures. We also expected that relationships between assessed conservation value and the abundance, species richness, and community composition of assessed taxonomic and ecological fungal groups would be stronger in the southern than in the northern boreal forest, as previously found for aboveground species diversity (Hekkala et al., 2023).

# METHODS

## Study sites and assessment of conservation value

A total of 74 coniferous-dominated (more than 65 % basal area of Scots pine [*Pinus sylvestris*] and Norway spruce [*Picea abies*]), mature (>65 years old in the southern region, $n = 36$, and >75 years old in the northern region, $n = 38$), 2-ha forest stands were selected to represent a wide range of conservation values across the Swedish forest landscape (Figure 1). These ranged from uniform forests with presumed low conservation values to heterogeneous forests with presumed high conservation values (Appendix S1). The sampling covered southern and northern regions of boreal forest to capture areas that vary greatly in climate (Ahti et al., 1968), silvicultural histories (Josefsson & Östlund, 2011; Linder & Östlund, 1998), and the extent of reserves and remnants of natural forest in the surrounding landscape (Svensson et al., 2019). To ensure we considered a broad range of conservation values, half the stands included were woodland key habitats, presumably representing medium to high conservation values, and the other half were production forests, presumably representing low to medium conservation values. We ensured even distribution of woodland key habitats and production forests across both regions based on information from the forest company Sveaskog AB and from the publicly available database on woodland key habitats in Sweden, curated by the Swedish Forest Agency (https://kartor.skogsstyrelsen.se/kartor/). In addition to tree species composition (coniferous dominated), we used information on soil type, slope, field vegetation type, and occurrences of boulders to further select sites in accordance with the following predefined criteria. To avoid extreme soil characteristics that might not represent the typical soils of the region, we deliberately omitted stands in steep terrain, wet sites on peaty soils (peat layer >30 cm), dry sites (indicated by lichen-rich vegetation types), and boulder-rich sites. The sites included for study were thus all on well-drained to mesic soils, with understory vegetation spanning from *Vaccinium–Empetrum* to *Vaccinium–Myrtillus* types.

We assessed conservation value based on the habitat heterogeneity score (Hekkala et al., 2023), developed by a consultant company AB Skogsbiologerna (Drakenberg & Lindhe, 1999), which is the most commonly used method for assessing forest conservation value in Sweden. The method is based on a systematic search for structural components and stand characteristics important for biodiversity according to a score sheet with 50 features per forest type (Appendix S1). The presence of each feature, such as amounts and types of dead wood, understory vegetation, and indications of natural disturbance dynamics (e.g., signs of past wild fires, such as fire scars), was recorded on the score sheet. The scores can theoretically sum to 50, but the sum rarely exceeds 30 (Drakenberg & Lindhe, 1999). The mean conservation values in the northern and southern regions were 17 (SE 1.15) (range 4–34) and 14 (0.97) (range 3–27), respectively. Further details on the conservation value assessment are in Hekkala et al. (2023).

## Stand- and landscape-level forest continuity

In each stand, we sampled tree ring increment cores (at 1.3 m height) from the 2 oldest pines and the 2 oldest spruce trees (visually judged). We used the maximum tree age estimated from tree ring counts as a proxy for stand-level tree continuity (i.e., this was the proxy for minimum duration of tree cover at the site, rather than forest age, which cannot be assessed in near-natural forests). We used the total area of old-growth forest (>120 years old), estimated in 2018 from national satellite images, forest monitoring, and logging data, within a 2-km radius around each 2-ha study site as a proxy for landscape-level forest continuity. These data were obtained from Kärvemo et al. (2021).

## Tree species composition

We placed multiple belt transects (4-m wide and 20-m long) systematically throughout the 2-ha study site to survey a total area of 0.2 ha (Hekkala et al., 2023). We measured diameter at breast height (dbh) for all living trees with dbh >4.5 cm in each transect and used the measurements to calculate the basal area of Scots pine, Norway spruce, and 2 birch species (*Betula pendula* and *Betula pubescens*) for each site. Because all the sites were conifer dominated and the basal area of the Norway spruce and Scots pine was strongly negatively correlated ($R^2 = -0.63$, $p < 0.001$), the basal area of Norway spruce (square meters per hectare) was used as a proxy for tree species composition to avoid multicollinearity among predictors.

## Soil sampling

We collected soil samples in September 2019. In each of the 74 forest sites, 60 soil cores with a diameter of 3 cm were systematically sampled along transects. Sampling points were separated by 10 m throughout the 2-ha plot. We sampled to a maximum depth of 30 cm (corresponding to the deepest organic soils) and included the complete sample volume for organic soils. For soils with an organic layer of <30 cm, we included the entire organic horizon and the uppermost 5 cm of mineral soil. For sampling points on rocks, we sampled any material present on top,

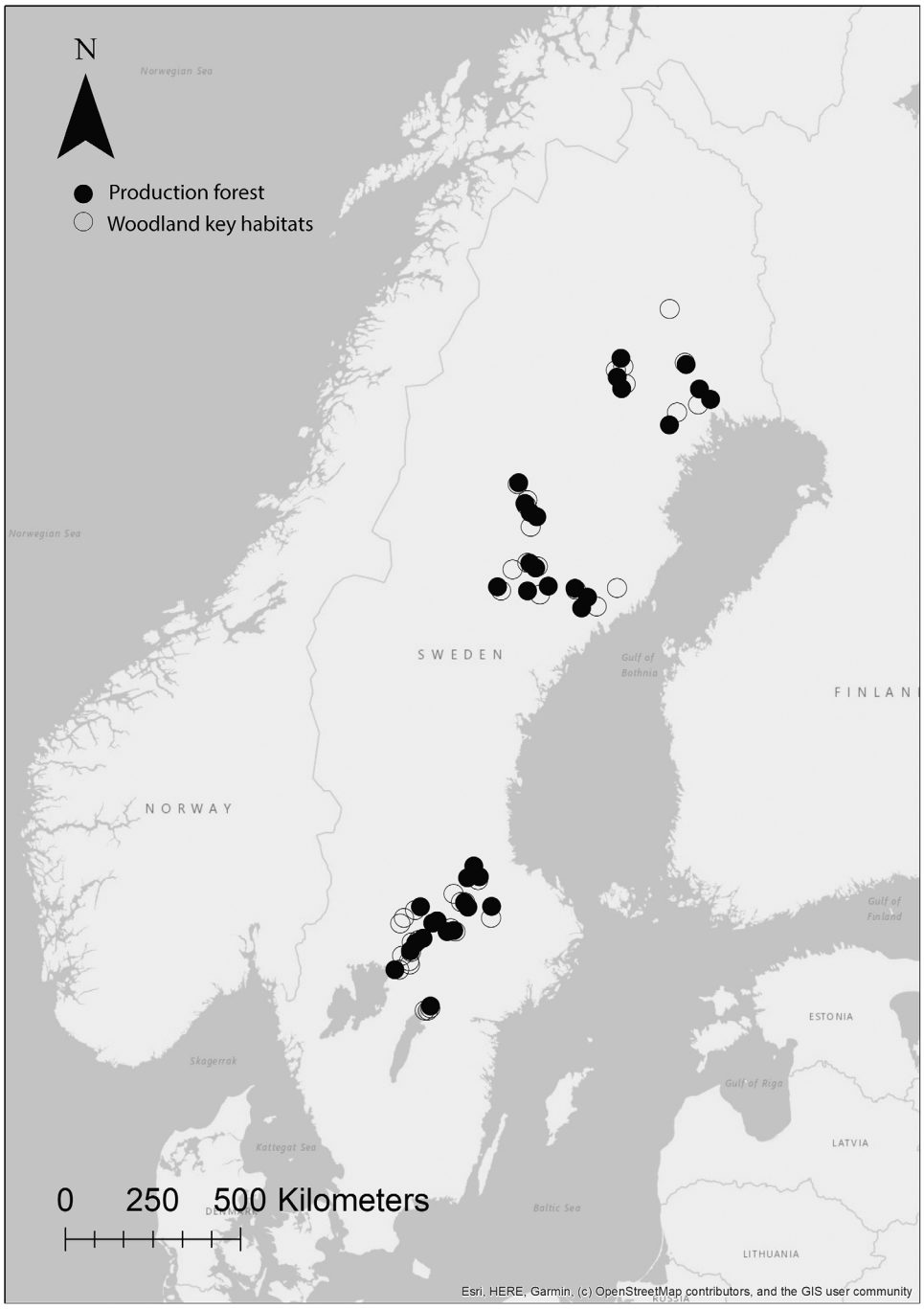


**FIGURE 1** Study sites in northern (38 sites) and southern (36 sites) Swedish boreal forest.

adhering strictly to the same area sampled in all stands. Large, green plant parts were removed, but the litter layer and any dead wood pieces were kept in the sample. The 60 cores from each site were pooled to a composite sample and frozen at −20°C within 4–8 h. The composite sample was weighed and homogenized in frozen condition in a custom-made mill, and a 100-g subsample was used to determine pH in 1:3 soil:water volume slurry with a 744 pH meter (Metrohm). A 100-g subsample was freeze-dried and homogenized in a ball mill to a fine powder. Subsamples of the freeze-dried and milled samples were used to extract DNA (see below) and determine organic matter content from mass loss on ignition (6 h at 550°C) and carbon and nitrogen concentration with an elemental analyzer (Flash EA 2000; Thermo Fisher Scientific).

## DNA extraction and amplification

Depending on the soil organic matter content, we extracted DNA from 50–450 mg of dried and milled soil aliquots with

the NucleoSpin Soil kit (Macherey-Nagel) and checked the quality of the extracted DNA with Nanodrop. Library preparation by polymerase chain reaction (PCR) amplification, purification, and pooling of samples for sequencing of the fungal ITS2 region was performed as described by Clemmensen et al. (2023) and Castaño et al. (2020). Adaptor ligation and Pacific Biosciences sequencing on 4 Sequel I SMRT cells were performed by Uppsala Genome Center (SciLifeLab). We archived sequence data at NCBI-SRA (PRJNA1103361).

## Sequence analyses

Sequences were quality filtered and clustered using the SCATA pipeline (https://scata.mykopat.slu.se/). Sequences of <150 bases were removed, after which the remaining sequences were screened for primers (requiring 90% match) and sample tags (requiring 100% match). Sequences with an average amplicon quality score of <20 or with a score of <3 at any position were removed. Sequences were compared pairwise with USEARCH (Edgar et al., 2011) and clustered into species-level clusters with single-linkage clustering with a minimum similarity of 99% to the closest neighbor required to enter a cluster.

After we identified and removed nonfungal sequences with the support of a neighbor-joining tree (7% of the total reads), we manually assigned all clusters that accounted for more than 0.25% of the sequences in any sample to species hypotheses in the UNITE database at 99% similarity (Kõljalg et al., 2013; Nilsson et al., 2019). Using this cutoff, we assigned the most abundant 767 fungal clusters (hereafter referred to as species), together representing 86.7% of the sequences, to taxonomic or ecological groups (Appendix S1). We included a large data set from Swedish National Soil Inventory (Lindahl et al., 2021) directly in the clustering process in SCATA to facilitate taxonomic identification and assignment of fungal species to ecological groups. Although clusters may sometimes map to more than one species, we used them as a proxy of species because the 99% threshold is a rather conservative approach that minimizes the lumping of species, and variation in the threshold usually has a negligible effect on the outcomes of analyses (Botnen et al., 2018).

All identified fungal species were first categorized into the 2 major taxonomic groups Ascomycota (group 1) and Basidiomycota (group 2) (Appendix S2). We further assigned fungal species to the following 4 ecological groups: root Ascomycota (associated with living roots, e.g., ericoid mycorrhizal fungi and root endophytes, including species in Archaeorhizomycetes) (group 3) and ectomycorrhizal fungi (mostly Basidiomycota, some Ascomycota) (group 4). The sum of groups 3 and 4 resulted in group 5: root-associated fungi (associated with living roots). Free-living fungi were classified as saprotrophic Ascomycota (associated with plant litter) (group 6), saprotrophic Basidiomycota (associated with plant litter) (group 7), and wood saprotrophs (dead-wood dependent) (group 8). Groups 6–8 were summed to create group 9, saprotrophs (fungi associated with plant litter). Other groups (group 10) were yeasts (species in Microbotryomycetes and Tremellomycetes, Basidiomycota, and Saccharomycetales, Ascomycota), molds (species in Mortierellales, Mortierellomycota, and Mucorales, Mucoromycota, and some species in Eurotiales, Hypocreales, and Capnodiales, Ascomycota) (group 11), and pathogens (some species in Sordariomycetes and Leotiomycetes, Ascomycota, and one species in the genus *Athelia*, Basidiomycota) (group 12). Relative abundances of fungal species were calculated for each sample by division of reads assigned to a specific fungal species by the total fungal reads in the sample (Appendix S3).

## Statistical analyses

To avoid losing valid data, we did not rarefy the data based on minimum read counts per sample. Instead, we included total fungal reads as an explanatory variable in all analyses to account for variation in sequencing depth per sample, but this had very little effect on the results. Both the association of the conservation value with relative abundance (out of total fungal amplicons [transformed to the square root]) and species richness were tested using linear models implemented with the lm function from the base R package for the 12 taxonomic and ecological groups (hereafter referred to as fungal groups). The association with conservation value was tested first with region as an additional predictor and then with and without the region as an interaction term with conservation value. The best fitting model was selected based on the Akaike information criterion (AIC) in the AICcmodavg package (Mazerolle, 2023). In the same way, we tested the associations between each fungal group (relative abundance and richness) and the following environmental variables: spruce basal area, stand- and landscape-level forest continuity, and soil fertility (expressed as the first axis ordination scores of a principal component analysis [PCA] of soil pH and C:N ratio [Appendix S4]). We tested these associations again with and without region and the interaction with region. Thus, we used PCA to handle collinearity of soil pH and C:N ratio ($p < 0.001$, $r = -0.61$), both related to soil fertility.

Due to clear effects of region, we built separate linear models for the 2 regions, testing all relations between each fungal group (relative abundance and richness) and conservation value and environmental variables (fertility, spruce basal area, stand- and landscape-level continuity). All 2-way interactions between conservation value and the environmental variables were included to test context dependencies of relationships with conservation value in each region.

In all cases, the best fitting models (per fungal group) were selected based on lowest AIC in the AICcmodavg package (Mazerolle, 2023). Correlation matrices of the 5 explanatory variables were inspected across all 74 sites and for the 2 regions separately (Appendix S5). Collinearity between explanatory variables was checked with variance inflation factor (VIF) analysis; a threshold of 2 was applied to identify potential multicollinearity (vif function in the car package) (Fox & Weisberg, 2019). Model fit was evaluated by examining the residuals for normality and homoscedasticity. The effect sizes and confidence intervals

for the best fitting models were illustrated using the dotwhisker package (Solt & Hu, 2021). All analyses were performed in R 4.1.2 (R Core Team, 2022).

We used detrended correspondence analysis (DCA) to visualize fungal community composition within and across both regions. We used canonical correspondence analysis (CCA) to test whether fungal community composition differed between regions. We further investigated relationships between conservation value and total and group-wise fungal community composition in each region. The best predictors of community composition in each region (soil fertility and spruce basal area) were identified using CCAs with forward selection of environmental variables. Similarly, we used CCAs with forward selection procedure to test the potential effect of the interaction between the conservation value and selected environmental variables on community composition. Correlations between community composition and stand- and landscape-level continuity were tested on the total data set, but because they were not significant, these explanatory variables were excluded from further analyses. To reduce the influence of the most frequent species, relative abundances were transformed to the square root (i.e., Hellinger transformed) for ordination analyses, and $p$ values were adjusted by Holm correction for multiple comparisons. All ordination analyses were performed in CANOCO 5 (Microcomputer Power).

# RESULTS

## Fungal communities

Sequence clustering resulted in 4548 fungal species (283,722 reads) with an average of 3822 (ranging between 1279 and 9889) high-quality reads per sample. Most of the fungal reads belonged to Ascomycota (65% on average), followed by Basidiomycota (15%), Mucoromycota (4.3%), Mortierellomycota (1.6%), and fungal species with another phylum-level classification (0.4%) (Appendix S3). Among Ascomycota, the most common classes were Leotiomycetes (35% on average), Archaeorhizomycetes (9%), Dothideomycetes (9%), Eurotiomycetes (8%), and Sordariomycetes (3%). Among Basidiomycota, the most common classes were Agaricomycetes (12% on average), Tremellomycetes (2%), and Microbotryomycetes (1%) (Appendix S3).

## Regional differences in fungal communities

The relative abundance of most soil fungal guilds differed between the 2 regions (Figure 2a; Appendix S3). The relative abundances of ectomycorrhizal fungi, molds, and yeasts were higher in the southern region, and the relative abundances of all other saprotrophic fungal guilds were higher in the northern region ($p < 0.005$ for all) (Appendix S6). Root-associated Ascomycota made up the largest community fraction (45%) in both regions (Figure 2a; Appendix S6). Species richness differed in corresponding ways between the 2 regions, except that richness of saprotrophic Basidiomycota and wood saprotrophs (as well as total Basidiomycota) was highest in the southern region (i.e., opposite to their relative abundance), and molds and yeast had similar richness in the 2 regions (Appendix S6). Fungal community composition at species level also differed between the regions for both the total community and individual taxonomic and ecological groups (Figure 2; Appendix S7).

## Associations of fungal communities with conservation value

Conservation value was generally not related to the relative abundance and richness of taxonomic and ecological groups of soil fungi (Figure 3a; Appendix S6). Wood-saprotrophic fungi increased in relative abundance and richness with increasing conservation value, whereas the relative abundance of molds and yeasts, and richness of yeasts, decreased with conservation value. Contrary to expectations, the root-associated groups did not uniformly relate to conservation value across all sites. The richness of root-associated Ascomycota overall declined with increasing conservation value (Figure 3a; Appendix S6). However, there were clear regional dependencies, as indicated by interactions between conservation value and region, particularly regarding the richness of ectomycorrhizal fungi and saprotrophic Basidiomycota. These dependencies observed at finer fungal groups extended consistently to broader groupings, encompassing total Basidiomycota and total root-associated fungi (Figure 3a; Appendix S6).

Accordingly, in the northern region, richness of ectomycorrhizal Basidiomycota (and total root-associated fungi) declined with increasing conservation value (Table 1). The relative abundance of ectomycorrhizal fungi was not directly associated with the conservation value in any region, but in the northern region, the relationship with the conservation value became stronger with increasing spruce basal area and decreasing soil fertility (Table 1).

When regions were analyzed separately, the richness of saprotrophic Basidiomycota was positively associated with the conservation value in the north. Further, in the northern region, the relationship between richness and the conservation value became stronger at higher soil fertility. Similarly, in the southern region, the relationship between the relative abundance of saprotrophic Basidiomycota and the conservation value was more pronounced in forests with higher soil fertility (Table 1).

The richness and relative abundance of wood saprotrophs and saprotrophic Ascomycota were also unrelated to conservation values when regions were analyzed separately. The relationship between the relative abundance of wood saprotrophs and conservation value weakened with increasing landscape continuity in the southern region (Table 1).

The relative abundance of yeasts and molds was negatively associated with the conservation value across both regions (Appendix S6), but this relationship was mainly due to a negative relationship in the northern region (Table 1), although molds also depended on soil fertility and landscape continuity

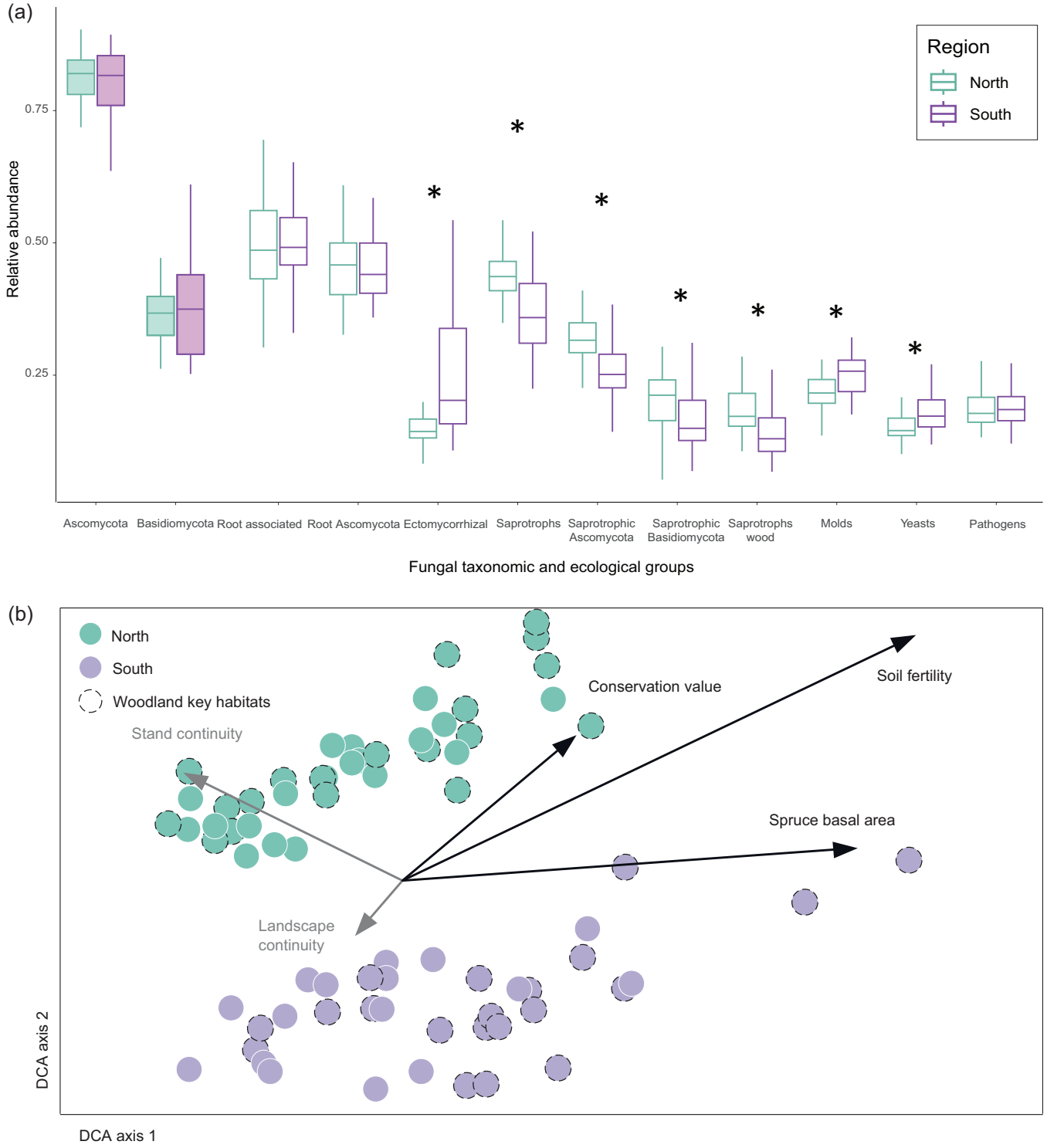


**FIGURE 2** Regional differences in (a) relative abundance of major fungal taxonomic (shaded boxes) and ecological groups (unshaded boxes) and (b) species-level fungal community composition (DCA, detrended correspondence analysis) in soil in northern (green; $n = 38$) and southern (purple; $n = 36$) Swedish boreal forests as determined by DNA sequencing of ITS2 markers (*, significant differences between regions in relative abundance of taxonomical and ecological groups; boxes, the interquartile range [IQR]; horizontal lines inside boxes, median value; whiskers, the smallest and the largest value within 1.5 times the IQR; circles with dashed borders, woodland key habitats; other circles, production forests; black arrows, variables significantly correlated with fungal community composition across all forests; gray arrows, variables that did not correlate with fungal community composition). Relative abundances were transformed to the square root prior to analyses.

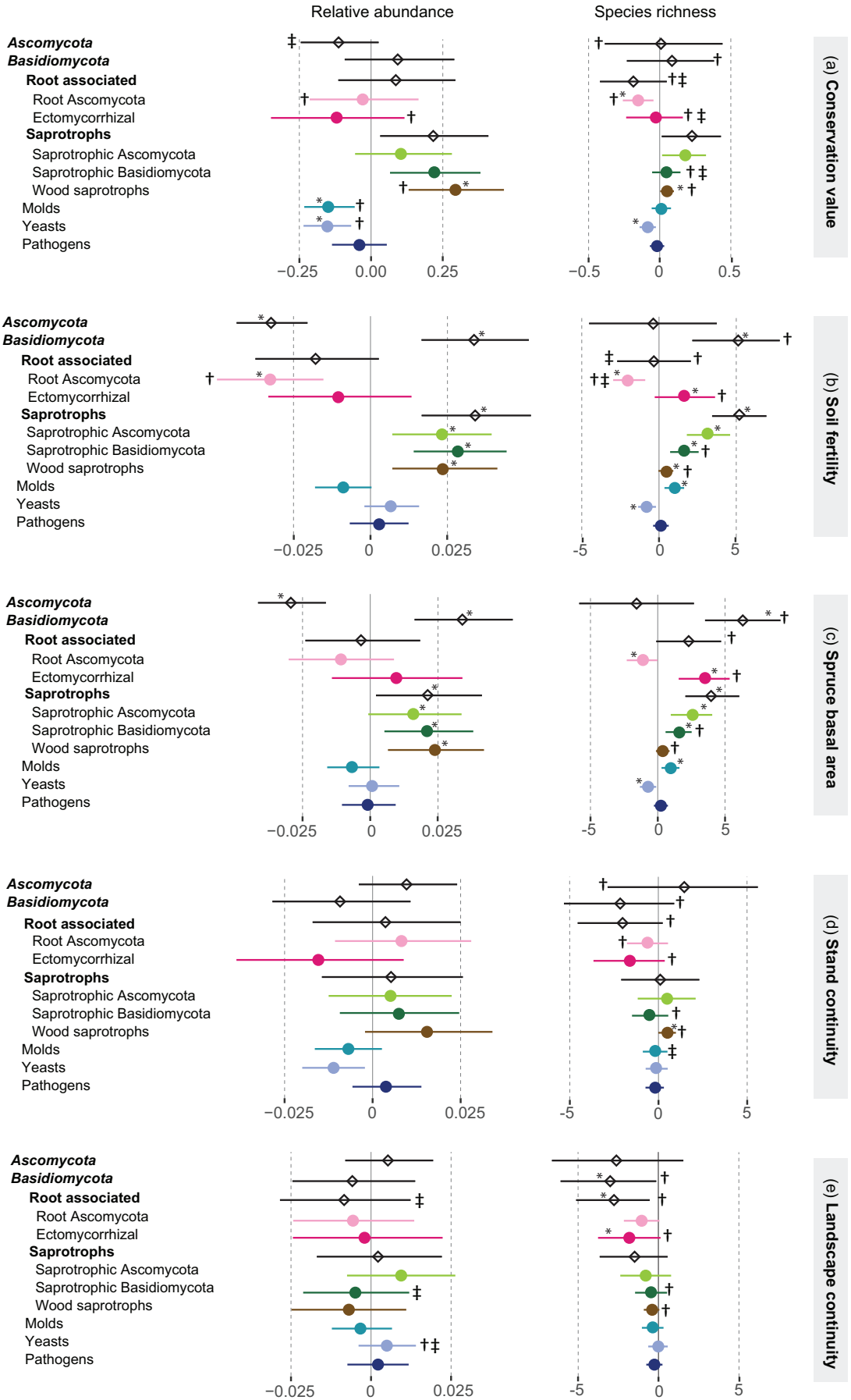

**FIGURE 3** Linear model coefficients of soil fungi in relation to (a) conservation value, (b) soil fertility, (c) spruce basal area, (d) stand continuity, and (e) landscape continuity across 74 Swedish boreal forests (filled circles, ecological groups; open diamonds, taxonomic groups; *, significant main effects of explanatory variables; †, significant main effects of region; ‡, interaction with region [north = 0, south = 1]; ‡ on the right of each fungal group, positive effects; ‡ on left side of each fungal group, negative effects; whiskers, 95% confidence intervals). Correlations between conservation value and fungal guild relative abundance and species richness visualized in (a) corresponds to the statistical results reported in Appendix S6.

(Table 1). In the southern region, the relationships of yeasts and molds with the conservation value depended on spruce basal area and stand- and landscape-level continuity (Table 1).

The relative abundance and richness of root-associated Ascomycota were not directly related to conservation values across regions. However, in the southern region, the relationships between conservation value and the relative abundance of root-associated Ascomycota (and total root-associated fungi) were negatively related to stands with higher soil fertility and longer tree continuity (Table 1). Pathogens were not directly related to the conservation value in any of the regions, but the interactions with the environmental parameters suggest that some relationships depended on soil fertility, as well as stand- and landscape-level continuity.

Conservation value was associated with total fungal community composition at species-level across all 74 stands (Figure 4). However, in the northern region (when analyzed alone), the conservation value appeared unrelated to community composition, both across the entire fungal community and for all individual fungal groups (Figure 4a,b; Appendix S8). When conservation value was tested in CCAs, alongside other potential predictors (soil fertility, spruce basal area, and their interactions with conservation value), the conservation value explained part of the community variation in several fungal groups. However, this was mainly contingent on soil fertility level (for total root-associated fungi, ectomycorrhizal fungi, wood saprotrophs, and pathogens) or spruce basal area (for all fungi, total root-associated fungi, and yeasts) (Appendix S9). Conversely, in the southern region, the conservation value explained a significant proportion of community composition of the entire community and of all fungal groups individually (Figure 4c,d; Appendix S8). When analyzed together with fertility and spruce basal area as potential explanatory variables in the southern region, conservation value still explained a significant proportion of community composition of total Ascomycota, yeasts and pathogens, without interactive dependencies on the other factors. However, for most fungal groups, relationships with the conservation value depended on soil fertility (for all fungi, Basidiomycota, all root-associated fungi, ectomycorrhizal fungi, all saprotrophs, saprotrophic Basidiomycota, and molds) and spruce basal area (for ectomycorrhizal fungi) (Figure 4; Appendix S9).

### Associations between fungal communities and forest characteristics

Across all 74 stands, the associations among the relative abundances and richness of fungal groups and soil fertility and spruce basal area paralleled their associations with conservation value but with more and much stronger significant effects (Figure 3a–c). Basidiomycota (both saprotrophic and ectomycorrhizal) were positively associated with soil fertility and spruce basal area, whereas root-associated Ascomycota and yeasts were negatively associated with soil fertility and spruce basal area (Figure 3b,c). Only the richness of wood-dependent saprotrophs was positively associated with stand-level tree continuity (Figure 3d). In contrast, the richness of root-associated fungi (Basidiomycota) was negatively associated with landscape continuity (Figure 3e).

When tested across all forests (Figure 3b,c), and separately in each region (Table 1), the relative abundance of Basidiomycota was positively and that of Ascomycota negatively associated with soil fertility (northern region) or spruce basal area (southern region) because these groups made up the majority of the reads and thus had complementary responses. In the southern region, all saprotrophic groups, molds, and pathogens were positively associated with soil fertility, whereas the relative abundance of root-associated Ascomycota was associated negatively with fertility (Table 1; Figure 3b,c). Root-associated fungi were negatively associated with stand continuity in the northern region (Table 1; Figure 3e).

In the separate analyses of the 2 regions, forward selection of explanatory variables also demonstrated that soil fertility explained the largest share of variation in community composition in all fungal groups (Appendix S9). Spruce basal area was the second most important predictor of fungal community composition across all sites (Figure 4) and for the regions separately (Appendix S9). Overall, stand and landscape continuity were the least important explanatory variables of fungal abundance, richness, and community composition (Figure 4; Table 1).

The 2 variables, soil fertility and spruce basal area, were positively correlated across all plots ($p = 0.007$, $r = 0.59$) and within regions ($p < 0.001$, $r = 0.77$ in the northern region; $p = 0.002$, $r = 0.49$ in the southern region) (Appendix S5).

## DISCUSSION

### Forest conservation value as a predictor of belowground fungi

We found that the assessed conservation value overall did not reflect the variation in most of the studied fungal guilds. Across all investigated forests, only the abundance and richness of wood-dependent saprotrophs were positively associated with the conservation value, whereas the abundance of molds and yeasts and the richness of yeasts and root-associated Ascomycota were negatively associated with conservation values. Other groups, such as ectomycorrhizal fungi, saprotrophic fungi, and pathogens, did not relate significantly to assessed

**TABLE 1** Results from linear models testing the effect of conservation value, soil fertility, spruce basal area, stand continuity, and landscape continuity and all 2-way interactions with conservation value on relative abundance (upper lines) and richness (lower lines) of fungal groups across 38 northern and 36 southern boreal forests.

| | | Main effect[a] | | | | | Context dependency[a] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Region | Fungal group | Conservation value (CV) | Soil fertility (F) | Spruce basal area (SBA) | Stand continuity (SC) | Landscape continuity (LC) | CV × F | CV × SBA | CV × SC | CV × LC |
| North | Ascomycota | 0.431(+) | 5.123***(−) | | | 0.69(+) | 1.499(−) | | | 1.734(+) |
| | | | | 1.400(−) | | | | | | |
| | Basidiomycota | 0.179(+) | 4.215***(+) | | | 0.396(−) | | | | 2.221*(−) |
| | | 0.260(+) | 0.005(+) | 1.744(+) | | | 1.354(+) | | | |
| | Root associated | | | | | | | | | |
| | | 2.380*(−) | 1.357(+) | | 1.334(−) | 2.137*(−) | | | | 1.376(+) |
| | Root associated (Ascomycota) | | | 1.461(−) | | | | | | |
| | | | | 1.586(−) | 2.396*(−) | 1.850(−) | | | | |
| | Ectomycorrhizal (Basidiomycota) | 1.039(−) | 0.687(+) | 0.552(+) | 0.849(−) | 1.212(−) | 2.422*(−) | 2.113*(+) | 1.454(−) | 1.608(+) |
| | | 2.683**(−) | 1.672(+) | 2.070(+) | | 2.322(−) | | | | |
| | Saprotrophs | | | 2.041*(+) | | | | | | |
| | | 0.082(−) | 3.370**(+) | | | | 1.582(+) | | | |
| | Saprotrophs (Ascomycota) | | | 1.737(+) | | 1.578(+) | | | | |
| | | | 3.430*(+) | | | | | | | |
| | Saprotrophs (Basidiomycota) | 1.090(+) | | | | 0.761(−) | | | | 1.789(−) |
| | | 0.350(−) | 0.717(+) | | 1.945(−) | | 2.038*(+) | | | |
| | Wood saprotrophs | 1.619(+) | | 1.602(+) | | | | | | |
| | | | | 1.716(+) | | | | | | |
| | Molds | 2.720**(−) | 0.705(−) | 1.249(+) | | 2.148(−) | 2.004*(+) | 1.659(+) | | 1.595*(+) |
| | | 0.037(−) | 1.129(+) | 0.725(+) | | 2.002*(−) | 1.846(+) | 1.913(−) | | |
| | Yeasts | 2.538*(−) | 3.293**(+) | | | 1.423(−) | | | | |
| | | 2.536*(−) | 3.160**(+) | | | | | | | |
| | Pathogens | | | | 1.42(+) | | | | | |

(Continues)

**TABLE 1** (Continued)

| Region | Fungal group | Main effect[a] | | | | | Context dependency[a] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Conservation value (CV) | Soil fertility (F) | Spruce basal area (SBA) | Stand continuity (SC) | Landscape continuity (LC) | CV × F | CV × SBA | CV × SC | CV × LC |
| South | Ascomycota | 0.585(−) | 0.697(−) | 2.135*(−) | | | 2.445*(−) | | | |
| | | 0.032(−) | 1.246(+) | 0.879(+) | 0.068(−) | | 2.646**(−) | 1.256(+) | 1.738(+) | |
| | Basidiomycota | 0.198(−) | 0.053(+) | 2.042*(+) | | | 1.549(+) | | | |
| | | 2.052*(−) | 3.652**(+) | | | 2.758**(−) | 1.633(+) | | | |
| | Root associated | 0.139(+) | 1.372(−) | | 0.611(−) | 1.538(−) | 2.020*(−) | | 2.056*(−) | |
| | | 1.552(+) | 0.523(−) | | | | 1.679(−) | | | |
| | Root associated (Ascomycota) | 1.350(+) | 4.006**(−) | 1.461(−) | 3.120**(−) | | 3.120**(−) | | 2.009*(−) | |
| | | 1.033(−) | 1.637(−) | | | 1.792(−) | 1.934(−) | | | |
| | Ectomycorrhizal (Basidiomycota) | 1.829(+) | | | | | | | | |
| | Saprotrophs | 0.247(+) | 3.575**(+) | 1.459(+) | 0.202(+) | 0.474(−) | | | 1.543(+) | 1.329(−) |
| | | 0.555(−) | 3.220**(+) | 3.679**(+) | | | | | 0.713(+) | 1.800(+) |
| | Saprotrophs (Ascomycota) | | 2.390*(+) | 2.267*(+) | | 2.191*(+) | | | | |
| | | 0.387(−) | 2.646**(+) | 3.043**(+) | 0.941(−) | 0.811(+) | 1.511(−) | | 1.859(+) | 1.859(+) |
| | Saprotrophs (Basidiomycota) | 0.127(+) | 2.234*(+) | 1.731(+) | 1.939(+) | | 2.329*(+) | | | |
| | | 3.004**(+) | 1.398(+) | | | | | | | |
| | Wood saprotrophs | 0.975(+) | 3.637**(+) | | | 0.845(−) | | | | 2.467*(−) |
| | | 0.409(+) | 2.574*(+) | 1.647(+) | 1.545(+) | 0.329(−) | | 1.470(+) | | 1.594(−) |
| | Molds | | | 1.850(−) | 3.265**(−) | | 1.436(−) | | | |
| | | 1.824(−) | 2.758**(+) | 2.270*(+) | 3.294**(+) | 0.633(+) | | | 2.925**(+) | 2.548*(−) |
| | Yeasts | | | | | | | 3.129 **(−) | 1.445(+) | |
| | | 0.434(−) | | 2.232*(−) | 0.376(−) | 1.183(−) | | 1.625(−) | 1.243(+) | 2.383*(−) |
| | Pathogens | 1.092(−) | 3.574**(+) | 0.787(−) | | | 3.886**(−) | | | 3.886*(−) |
| | | 0.144(−) | 2.24*(+) | | 0.66(−) | | 2.98**(−) | | 2.17*(+) | |

*Note*: For each fungal group and response metric, only the best fitting model is presented (according to AIC-based selection). Signs: +, main or context-dependent effects of explanatory variables is positive; −, main or context-dependent effects of explanatory variables is negative. Relative abundances of fungal groups were square root-transformed prior to the analyses.

[a]Statistical significance of *T* values: ***$p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$.

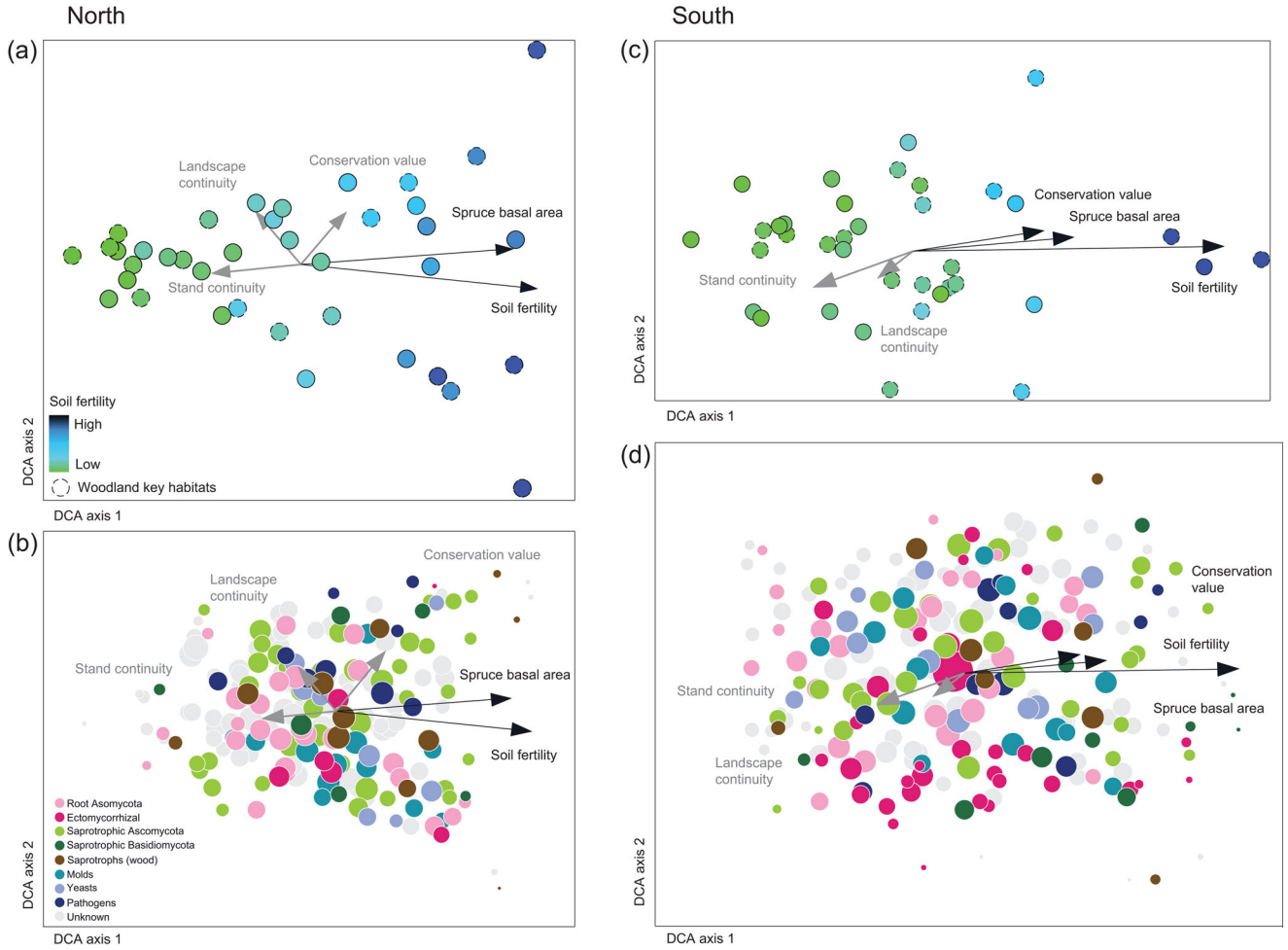


**FIGURE 4** Example plot of detrended correspondence analysis (DCA) of (a, c) fungal communities and the (b, d) most abundant 190 fungal species in soil in northern (a, b) ($n = 38$) and southern (c, d) ($n = 36$) Swedish boreal forests (dots, samples; soil fertility, an index based on ordination scores on the first axis of a principal component analysis of pH and soil C:N ratio; circles with dashed borders, woodland key habitats; circles with solid borders, production forests; circle size, proportional to average relative abundance of the species across all sites; arrows, correlation between the environmental variables and the ordination axes; arrow length, relative magnitude of correlations; position of arrow in the ordination space, direction of the correlations; black arrows, variables that correlate significantly with fungal community composition; gray arrows, variables do not correlate significantly with fungal community composition, as reported in Appendices S8 & S9).

conservation values across all our studied forests. The positive association of wood saprotrophs with the assessed conservation value was most likely related to the positive effect of the substrate heterogeneity and amount of dead wood on the diversity of wood-decaying fungi (Hoppe et al., 2016; Stenlid et al., 2008; Tomao et al., 2020). Similarly, forest naturalness (a combined measure of dead wood volume, number of cut stumps, and canopy tree age) has been found to correlate positively with the overall diversity of wood-inhabiting fungi (Purhonen et al., 2021). Consistent with our expectations, the composite nature of the assessed conservation value, encompassing multiple aboveground structures, likely accounts for the contrasting associations observed for different fungal groups. These findings suggest that the most commonly used conservation assessment methods may be insufficient for selecting forests that protect highly diverse soil microbiomes, particularly in boreal forests.

## Context dependencies of fungal relations with conservation value

We found a clear regional difference in relationships between assessed conservation value and richness, abundance, and community composition for most fungal groups. In particular, species richness of major fungal groups (Basidiomycota, ectomycorrhizal and saprotrophic fungi) was positively associated with the assessed conservation value, but only in the southern region. Community composition of all fungal guilds also correlated with the assessed conservation value in the southern region, but not in the northern region. Southern forests have higher overall tree species diversity and productivity, which allows them to support a higher fungal diversity. This is mainly due to large variation in soil conditions and nutrient availability, which may strengthen the relationship between assessed conservation value and fungal diversity relative to more uniform

northern forests that contain higher proportions of coniferous trees. Further, the observed regional differences could be related to differences in management history because the southern region is characterized by a longer history of intensive forest management and the northern region has a relatively shorter history of intensive management and a greater share of remaining seminatural forests (Östlund et al, 1997; Linder & Östlund, 1998; Josefsson & Östlund, 2011; Svensson et al., 2019). Our results suggest that belowground fungi are more heavily affected by forest management practices in the south. In the north, where fewer forests have been clearcut, belowground fungi remain less affected, which may explain weaker associations with aboveground structures.

We also found that the correlation between assessed conservation value and species richness and relative abundance of many of the fungal groups was contingent on environmental parameters. Richness of saprotrophic Basidiomycota (in both regions) and abundance of molds (in the northern region) correlated positively with conservation value, particularly in more fertile sites (Table 1), because increasing soil fertility creates extra resources and potentially greater niche heterogeneity. Greater natural soil fertility has been associated with more complex fungal community assemblages and increased diversity among fungal guilds (Guo et al., 2020; Nguyen et al., 2016). This relationship may be particularly significant in generally nutrient-poor boreal forest landscapes, potentially explaining the positive associations with fertility observed in our study.

Soil fertility explained more of the overall variation in relative abundance, species richness, and community composition than the assessed conservation value for all fungal guilds. The relative abundance and species richness of almost all fungal guilds were associated with soil fertility, but the direction of associations varied among fungal groups and regions. In particular, the relative abundance of Ascomycota (driven by root-associated species) decreased as soil fertility increased, whereas the relative abundance of Basidiomycota (particularly saprotrophic species), yeasts, and pathogens increased as soil fertility increased (Table 1). Soil fertility is one of the most important edaphic variables that relates to fungal community composition, even within fungal guilds (e.g., Sterkenburg et al., 2015). In the boreal forest, Ascomycota are usually more abundant in nutrient-poor and more acidic forest soils, whereas both saprotrophic and ectomycorrhizal Basidiomycota tend to dominate in forest soils with larger pools of available nitrogen and less acidic soils, likely driven by the higher tree productivity there (Clemmensen et al., 2015; Grau et al., 2017; Siciliano et al., 2014; Sterkenburg et al., 2015; Tedersoo et al., 2014). Our results are consistent with this pattern; Ascomycota and Basidiomycota responded in opposite directions to soil fertility (in the northern region) and (the tightly correlated) spruce basal area (in the southern region). Further, abundance and richness of saprotrophic fungi were positively associated with soil fertility, although mainly in the southern region. This may be related to reduced belowground carbon allocation by trees under higher soil fertility, resulting in decreased dominance of ectomycorrhizal fungi relative to saprotrophic fungi in the soil fungal community (Högberg et al., 2003; Kyaschenko, Clemmensen, Karltun, et al., 2017; Sterkenburg et al., 2015).

Soil fertility is a well-known mediator of fungal community composition (Guo et al., 2020; Sterkenburg et al., 2015), fungal decomposition, and nutrient cycling activities in soils (Brabcová et al., 2018; Hagenbo et al., 2022; Mayer et al., 2023). Our results confirm the crucial role of soil fertility for fungal community composition and diversity across boreal landscapes. Understanding fertility–fungal relationships can help predict the impact of forest management practices and conservation efforts on ecosystem function and conservation value. Our observations suggest that conservation value primarily relates to fungal community composition under higher soil fertility levels. Moreover, soil fertility overall predicted more of the variation in fungal richness and community composition than conservation value across the boreal forest landscape, despite the study being specifically designed to assess forests with a diverse range of conservation values rather than representing the boreal forest in general.

## Weak associations between fungal variables and stand- and landscape-level continuity

Surprisingly, we found no correlation between stand- and landscape-level continuity and fungal community composition for any fungal groups, although we used a rather simple proxy for stand continuity. Ecological continuity is used to describe attributes that persist in a stand over a prolonged period, such as understory vegetation, old trees, and dead wood of certain quality, which takes decades or centuries to develop. In Fennoscandia, such attributes are considered to be one of the key criteria for selecting sites to be set aside to protect biodiversity (Nilsson et al., 1995). Studies of effects of local forest continuity on fungi have mainly investigated the diversity and community composition of wood-inhabiting fungi, and stand-level continuity is of limited significance for this fungal guild (Nordén et al., 2014; Saine et al., 2018). However, the need for further landscape-scale studies investigating the effects of ecological continuity on fungi has also been emphasized (Sverdrup-Thygeson & Lindenmayer, 2003), as supported by our results. Ectomycorrhizal fungal species are often considered more sensitive to changes in continuity in tree cover compared with other fungal groups (Peay & Bruns, 2014), and a meta-analysis (Spake et al., 2015) suggests that it may take, on average, 90 years for disturbed forests to regain old-growth levels of ectomycorrhizal fungi richness. However, studies of continuity effects vary with regard to the type of disturbance or management action, which complicates comparisons with our tree age continuity value. At the same time, the concept of ecological continuity has been criticized because it may underestimate the complexity of the history of forests (Bradshaw et al., 2015). In particular, the diversity of insects, fungi, lichens, and bryophytes has been associated with the frequency of natural forest disturbances, amounts of dead wood, or the number of

deciduous trees in coniferous forests, rather than stand continuity (Bradshaw et al., 2015: Hekkala et al, 2023; Ohlson et al., 1997; Rudolphi & Gustafsson, 2011). This supports the view that forest continuity per se may be less important for high biodiversity of fungi or even correlate negatively with fungal diversity (Kiesewetter & Afkhami, 2021) because habitat diversity is rather maintained by dynamic processes (Bradshaw et al., 2015; Groven et al., 2002; Nordén & Appelqvist, 2001; Sverdrup-Thygeson & Lindenmayer, 2003).

Fungal conservation is challenging due to high species diversity, multiple ecological strategies, a large number of rare or poorly known species, and the limited understanding of fungal habitat requirements. Although aboveground diversity of a subset of macrofungi of conservation concern could be predicted well based on conservation value (Hekkala et al., 2023), our results highlight the limitations of such measures when it comes to the highly diverse, belowground, cryptic biodiversity. Among all fungal guilds, only the richness and relative abundance of wood-dependent saprotrophs were positively associated with the conservation value assessment scores across the entire set of 74 investigated forests. Instead, all 12 taxonomic and ecological groups were more related to soil fertility and spruce basal area, particularly in the northern region.

Further, we observed contrasting community composition of all fungal groups in the 2 regions, and the assessed conservation value was clearly associated with the variation in community composition of all fungal groups in the southern but not in the northern region. Thus, our results draw a complex picture of how well assessed conservation values represent soil fungi. The complexity may depend on differences in soil fertility, host tree dominance, regional differences in management history and climate, and the particular fungal groups of interest. Our findings highlight the need for a better understanding of the interactions among edaphic factors, stand- and landscape-level continuity, host specificity, and plant effects on root-associated fungi beyond classification into broad ecological groups that provide limited resolution for the responses of individual taxa (Kia et al., 2017; Maciá-Vicente et al., 2023; Semchenko et al., 2022). Furthermore, that we found species in our study through DNA metabarcoding does not guarantee that they are reproductively successful. If the goal is to comprehensively assess and preserve the abundance and diversity of fungal communities in boreal forest, it is crucial that current conservation assessment tools be broadened to also consider other factors, such as soil fertility and tree species identity.

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## REFERENCES

Ahti, T., Hämet-Ahti, L., & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, *5*, 169–211.

Asamoah, E. F., Beaumont, L. J., & Maina, J. M. (2021). Climate and land-use changes reduce the benefits of terrestrial protected areas. *Nature Climate Change*, *11*, 1105–1110.

Bengtsson, J., Nilsson, S. G., Franc, A., & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*, *132*, 39–50.

Berglund, H., & Kuuluvainen, T. (2021). Representative boreal forest habitats in northern Europe, and a revised model for ecosystem management and biodiversity conservation. *Ambio*, *50*, 1003–1017.

Botnen, S. S., Davey, M. L., Halvorsen, R., & Kauserud, H. (2018). Sequence clustering threshold has little effect on the recovery of microbial community structure. *Molecular Ecology Resources*, *18*, 1064–1076.

Brabcová, V., Štursová, M., & Baldrian, P. (2018). Nutrient content affects the turnover of fungal biomass in forest topsoil and the composition of associated microbial communities. *Soil Biology and Biochemistry*, *118*, 187–198.

Bradshaw, R. H., Jones, C. S., Edwards, S., & Hannon, G. E. (2015). Forest continuity and conservation value in Western Europe. *The Holocene*, *25*, 194–202.

Brudvig, L. A., Damschen, E. I., Tewksbury, J. J., Haddad, N. M., & Levey, D. J. (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 9328–9332.

Bunce, R. G. H., Bogers, M. M. B., Evans, D., Halada, L., Jongman, R. H. G., Mucher, C. A., Bauch, B., de Blust, G., Parr, T. W., & Olsvig-Whittaker, L. (2013). The significance of habitats as indicators of biodiversity and their link to species. *Ecological Indicators*, *333*, 19–25.

Castaño, C., Berlin, A., Brandström Durling, M., Ihrmark, K., Lindahl, B. D., Stenlid, J., Clemmensen, K. E., & Olson, Å. (2020). Optimized metabarcoding with Pacific biosciences enables semi-quantitative analysis of fungal communities. *New Phytologist*, *228*, 1149–1158.

Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A., & Lindahl, B. D. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science*, *339*, 1615–1618.

Clemmensen, K. E., Finlay, R. D., Dahlberg, A., Stenlid, J., Wardle, D. A., & Lindahl, B. D. (2015). Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. *New Phytologist*, *205*, 1525–1536.

Clemmensen, K. E., Ihrmark, K., Durling, M. B., & Lindahl, B. D. (2023). Sample preparation for fungal community analysis by high-throughput sequencing of barcode amplicons. In F. Martin & S. Uroz (Eds.), *Microbial environmental genomics (MEG). Methods in molecular biology* (Vol. 2605, pp. 37–64). Humana Press.

Convention on Biological Diversity (CBD). (2022). *Report of the open-ended working group on the post-2020 global biodiversity framework on its third meeting (Part II)*. Secretariat of the Convention on Biological Diversity. https://www.cbd.int/doc/c/50c9/a685/3844e4030802e9325bc5e0b4/wg2020-03-07-en.pdf

Drakenberg, B., & Lindhe, A. (1999). Indirekt naturvärdesbedömning på beståndsnivå en praktiskt tillämpbar metod. *Skog & Forskning*, *99*, 60–66. (In Swedish).

Edgar, R. C., Haas, B. J., Clemente, J. C., Quince, C., & Knight, R. (2011). UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics*, *27*, 2194–2200.

Esseen, P.-A., Ehnström, B., Ericson, L., & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins*, *46*, 16–47.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 487–515.

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage.

Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. *Annual Review of Ecology, Evolution, and Systematics*, *50*, 237–259.

Frøslev, T. G., Kjøller, R., Bruun, H. H., Ejrnæs, R., Hansen, A. J., Læssøe, T., & Heilmann-Clausen, J. (2019). Man against machine: Do fungal fruitbodies and eDNA give similar biodiversity assessments across broad environmental gradients? *Biological Conservation*, *233*, 201–212.

Gao, T., Nielsen, A. B., & Hedblom, M. (2015). Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecological Indicators*, *57*, 420–434.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, *349*(6250), 819–822.

Grau, O., Geml, J., Pérez-Haase, A., Ninot, J. M., Semenova-Nelsen, T. A., & Peñuelas, J. (2017). Abrupt changes in the composition and function of fungal communities along an environmental gradient in the high Arctic. *Molecular Ecology*, *26*, 4798–4810.

Groven, R., Rolstad, J., Olaf, K., & Rolstad, E. (2002). Using forest stand reconstructions to assess the role of structural continuity for late-successional species. *Forest Ecology and Management*, *164*, 39–55.

Guo, J., Ling, N., Chen, Z., Xue, C., Li, L., Liu, L., Gao, L., Wang, M., Ruan, J., Guo, S., Vandenkoornhuyse, P., & Shen, Q. (2020). Soil fungal assemblage complexity is dependent on soil fertility and dominated by deterministic processes. *New Phytologist*, *226*, 232–243.

Gustafsson, L. (2000). Red-listed species and indicators: Vascular plants in woodland key habitats and surrounding production forests in Sweden. *Biological Conservation*, *92*, 35–43.

Hagenbo, A., Alday, J. G., Martínez de Aragón, J., Castaño, C., de-Miguel, S., & Bonet, J. A. (2022). Variations in biomass of fungal guilds are primarily driven by factors related to soil conditions in Mediterranean *Pinus pinaster* forests. *Biology and Fertility of Soils*, *58*, 487–501.

Hansson, L. (2001). Key habitats in Swedish managed forests. *Scandinavian Journal of Forest Research*, *3*, 52–61.

Heilmann-Clausen, J., Adamcík, S., Bässler, C., Halme, P., Krisai-Greilhuber, I., & Holec, J. (2017). State of the art and future directions for mycological research in old-growth forests. *Fungal Ecology*, *27*(Part B), 141–144.

Heilmann-Clausen, J., Barron, E. S., Boddy, L., Dahlberg, A., Griffith, G. W., Nordén, J., Ovaskainen, O., Perini, C., Senn-Irlet, B., & Halme, P. (2015). A fungal perspective on conservation biology. *Conservation Biology*, *29*, 61–68.

Heilmann-Clausen, J., & Vesterholt, J. (2008). Conservation: Selection criteria and approaches. In L. Boddy, J. C. Frankland, & P. van West (Eds.), *Ecology of saprotrophic basidiomycetes* (pp. 325–347). Academic Press.

Hekkala, A.-M., Jönsson, M., Kärvemo, S., Strengbom, J., & Sjögren, J. (2023). Habitat heterogeneity is a good predictor of boreal forest biodiversity. *Ecological Indicators*, *148*, Article 110069.

Högberg, M. N., Bååth, E., Nordgren, A., Arnebrant, K., & Högberg, P. (2003). Contrasting effects of nitrogen availability on plant carbon supply to mycorrhizal fungi and saprotrophs—A hypothesis based on field observations in boreal forest. *New Phytologist*, *160*, 225–238.

Hoppe, B., Purahong, W., Wubet, T., Kahl, T., Bauhus, J., Arnstadt, T., Hofrichter, M., Buscot, F., & Krüger, D. (2016). Linking molecular deadwood-inhabiting fungal diversity and community dynamics to ecosystem functions and processes in Central European forests. *Fungal Diversity*, *77*, 367–379.

Jonsson, B., & Siitonen, J. (2012). Dead wood and sustainable forest management. In J. Stokland, J. Siitonen, & B. Jonsson (Eds.), *Biodiversity in dead wood (Ecology, biodiversity and conservation)* (pp. 302–337). Cambridge University Press.

Josefsson, T., & Östlund, L. (2011). Increased production and depletion: The impact of forestry on northern Sweden's forest landscape. In H. Antonsson & U. Jansson (Eds.), *Agriculture and forestry in Sweden since 1900: Geographical and historical studies* (pp. 338–353). The Royal Swedish Academy of Agriculture and Forestry.

Kärvemo, S., Jönsson, M., Hekkala, A.-M., Sjögren, J., & Strengbom, J. (2021). Multi-taxon conservation in northern forest hot-spots: The role of forest characteristics and spatial scales. *Landscape Ecology*, *36*, 989–1002.

Kia, S. H., Glynou, K., Nau, T., Thines, M., Piepenbring, M., & Maciá-Vicente, J. G. (2017). Influence of phylogenetic conservatism and trait convergence on the interactions between fungal root endophytes and plants. *The ISME Journal*, *11*(3), 777–790.

Kiesewetter, K. N., & Afkhami, M. E. (2021). Microbiome-mediated effects of habitat fragmentation on native plant performance. *New Phytologist*, *232*, 1823–1838.

Kimberley, A., Hooftman, D., Bullock, J. M., Honnay, O., Krickl, P., Lindgren, J., Plue, j., Poschlod, P., Traveset, A., & Cousins, S. A. O. (2021). Functional rather than structural connectivity explains grassland plant diversity patterns following landscape scale habitat loss. *Landscape Ecology*, *36*, 265–280.

Kivlin, S. N., Winston, G. C., Goulden, M. L., & Treseder, K. K. (2014). Environmental filtering affects soil fungal community composition more than dispersal limitation at regional scales. *Fungal Ecology*, *12*, 14–25.

Kõljalg, U., Nilsson, R. H., Abarenkov, K., Tedersoo, L., Taylor, A. F. S., Bahram, M., Bates, S. T., Bruns, T. D., Bengtsson-Palme, J., Callaghan, T. M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G. W., Hartmann, M., Kirk, P. M., Kohout, P., … Larsson, K.-H. (2013). Towards a unified paradigm for sequence-based identification of fungi. *Molecular Ecology*, *22*, 5271–5277.

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.

Kyaschenko, J., Clemmensen, K. E., Hagenbo, A., Karltun, E., & Lindahl, B. D. (2017). Shift in fungal communities and associated enzyme activities along an age gradient of managed *Pinus sylvestris* stands. *The ISME Journal*, *11*, 863–874.

Kyaschenko, J., Clemmensen, K. E., Karltun, E., & Lindahl, B. D. (2017). Below-ground organic matter accumulation along a boreal forest fertility gradient relates to guild interaction within fungal communities. *Ecology Letters*, *20*, 1546–1555.

Laita, A., Mönkkönen, M., & Kotiaho, J. S. (2010). Woodland key habitats evaluated as part of a functional reserve network. *Biological Conservation*, *143*(5), 1212–1227.

Larrieu, L., Cabanettes, A., Courbaud, B., Goulard, M., Heintz, W., Kozák, D., Kraus, D., Lachat, T., Ladet, S., Müller, J., Paillet, Y., Schuck, A., Stillhard, J., & Svoboda, M. (2021). Co-occurrence patterns of tree-related microhabitats: A method to simplify routine monitoring. *Ecological Indicators*, *127*, Article 107757.

Lawrence, A., O'Connor, K., Haroutounian, V., & Swei, A. (2018). Patterns of diversity along a habitat size gradient in a biodiversity hotspot. *Ecosphere*, *9*(4), Article e02183.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H. M., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., … Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, *585*(7826), 551–556.

Lindahl, B. D., Ihrmark, K., Boberg, J., Trumbore, S. E., Högberg, P., Stenlid, J., & Finlay, R. D. (2007). Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. *New Phytologist*, *173*, 611–620.

Lindahl, B. D., Kyaschenko, J., Varenius, K., Clemmensen, K. E., Dahlberg, A., Karltun, E., & Stendahl, J. (2021). A group of ectomycorrhizal fungi restricts organic matter accumulation in boreal forest. *Ecology Letters*, *24*, 1341–1351.

Linder, P., & Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. *Biological Conservation*, *85*, 9–19.

Luque, S., & Vainikainen, N. (2008). Habitat quality assessment and modelling for forest biodiversity and sustainability. In R. Lafortezza, G. Sanesi, L. Chen, & T. R. Crow (Eds.), *Patterns and processes in forest landscapes* (pp. 241–264). Springer.

Maciá-Vicente, J. G., Francioli, D., Weigelt, A., Albracht, C., Barry, K. E., Buscot, F., Ebeling, A., Eisenhauer, N., Hennecke, J., Heintz-Buschart, A., van Ruijven, J., & Mommer, L. (2023). The structure of root-associated

fungal communities is related to the long-term effects of plant diversity on productivity. *Molecular Ecology*, *32*, 3763–3777.

Mayer, M., Matthews, B., Sandén, H., Katzensteiner, K., Hagedorn, F., Gorfer, M., Berger, H., Berger, T. W., Godbold, D. L., & Rewald, B. (2023). Soil fertility determines whether ectomycorrhizal fungi accelerate or decelerate decomposition in a temperate forest. *New Phytologist*, *239*, 325–339.

Mazerolle, M. J. (2023). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3.2. https://cran.r-project.org/package=AICcmodavg

Molina, R., Horton, T. R., Trappe, J. M., & Marcot, B. G. (2011). Addressing uncertainty: How to conserve and manage rare or little-known fungi. *Fungal Ecology*, *4*, 134–146.

Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, L. S., & Kennedy, P. J. (2016). FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology*, *20*, 241–248.

Nilsson, R. H., Larsson, K. H., Taylor, A. F. S., Bengtsson-Palme, J., Jeppesen, T. S., Schigel, D., Kennedy, P., Picard, K., Glöckner, F. O., Tedersoo, L., Saar, I., Kõljalg, U., & Abarenkov, K. (2019). The UNITE database for molecular identification of fungi: Handling dark taxa and parallel taxonomic classifications. *Nucleic Acids Research*, *47*(D1), D259–D264.

Nilsson, S. G., Arup, U., Baranowski, R., & Ekman, S. (1995). Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology*, *9*(5), 1208–1215.

Niskanen, T., Douglas, B., Kirk, P., Crous, P., Lücking, R., Matheny, P. B., Cai, L., Hyde, K., Fah, M., & Cheek, M. (2018). New discoveries: Species of fungi described in 2017. In K. J. Willis (Ed.), *State of the world's fungi 2018* (pp. 18–23). Royal Botanic Gardens, Kew.

Nordén, B., & Appelqvist, T. (2001). Conceptual problems of ecological continuity and its bioindicators. *Biodiversity Conservation*, *10*, 779–791.

Nordén, B., Dahlberg, A., Brandrud, T. E., Fritz, Ö., Ejrnaes, R., & Ovaskainen, O. (2014). Effects of ecological continuity on species richness and composition in forests and woodlands: A review. *Ecoscience*, *21*(1), 34–45.

Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O., & Hermansson, L. (1997). Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation*, *81*(3), 221–231.

Östlund, L., Zackrisson, O., & Axelsson, A.-L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, *27*, 1198–1206.

Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., & Guilbert, E. (2018). The indicator side of tree microhabitats: A multi-taxon approach based on bats, birds and saproxylic beetles. *Journal of Applied Ecology*, *55*, 2147–2159.

Parker, S. S. (2010). Buried treasure: Soil biodiversity and conservation. *Biodiversity and Conservation*, *19*, 3743–3756.

Pearson, D. L. (1994). Selecting indicator taxa for the quantitative assessment of biodiversity. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, *345*(1311), 75–79.

Peay, K. G., & Bruns, T. D. (2014). Spore dispersal of basidiomycete fungi at the landscape scale is driven by stochastic and deterministic processes and generates variability in plant–fungal interactions. *New Phytologist*, *204*, 180–191.

Pohjanmies, T., Eyvindson, K., Triviño, M., Bengtsson, L., & Mönkkönen, M. (2021). Forest multifunctionality is not resilient to intensive forestry. *European Journal of Forest Research*, *140*, 537–549.

Purhonen, J., Abrego, N., Komonen, A., Huhtinen, S., Kotirana, H., Læssøe, T., & Halme, P. (2021). Wood-inhabiting fungal responses to forest naturalness vary among morpho-groups. *Scientific Reports*, *11*, Article 14585.

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Raimbault, A., Brin, A., Manzi, S., Savoie, J. M., Gandois, L., Olivia, P., Fogliani, O., Roy-Camille, C., Gratacap, L., & Roy, M. (2024). Influence of habitat fragmentation and habitat amount on soil fungi communities in ancient forests. *Landscape Ecology*, *39*, Article 19.

Ridding, L. E., Spake, R., Newton, A. C., Keith, S. A., Walls, R. M., Diaz, A., Eigenbrod, F., & Bullock, J. M. (2023). Historical data reveal contrasting habitat amount relationships with plant biodiversity. *Ecography*, *2023*(2), Article e06301.

Rudolphi, J., & Gustafsson, L. (2011). Forests regenerating after clear-cutting function as habitat for bryophyte and lichen species of conservation concern. *PLoS ONE*, *6*, Article e18639.

Saine, S., Aakala, T., Purhonen, J., Launis, A., Tuovila, H., Kosonen, T., & Halme, P. (2018). Effects of local forest continuity on the diversity of fungi on standing dead pines. *Forest Ecology and Management*, *409*, 757–765.

Semchenko, M., Barry, K. E., de Vries, F. T., Mommer, L., Moora, M., & Maciá-Vicente, J. G. (2022). Deciphering the role of specialist and generalist plant–microbial interactions as drivers of plant–soil feedback. *New Phytologist*, *234*(6), 1929–1944.

Siciliano, S. D., Palmer, A. S., Winsley, T., Lamb, E., Bissett, A., Brown, M. V., van Dorst, J., Ji, M., Ferrari, B. C., Grogan, P., Chu, H., & Snape, J. (2014). Soil fertility is associated with fungal and bacterial richness, whereas pH is associated with community composition in polar soil microbial communities. *Soil Biology and Biochemistry*, *78*, 10–20.

SLU Artdatabanken. (2020). *Rödlistade arter i Sverige 2020*. SLU.

Smith, J. E., Molina, R., Huso, M. M. P., Luoma, D. L., McKay, D., Castellano, M. A., Lebel, T., & Valachovic, Y. (2002). Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, U.S.A. *Canadian Journal of Botany*, *80*, 186–204.

Smith, S. E., & Read, D. J. (2008). *Mycorrhizal symbiosis*. Academic Press.

Solt, F., & Hu, Y. (2021). *dotwhisker: Dot-and-Whisker plots of regression results*. R package version 0.7.4.

Spake, R., Ezard, T. H., Martin, P. A., Newton, A. C., & Doncaster, C. P. (2015). A meta-analysis of functional group responses to forest recovery outside of the tropics. *Conservation Biology*, *29*, 1695–703.

Stenlid, J., Penttilä, R., & Dahlberg, A. (2008). Wood-decay basidiomycetes in boreal forests: Distribution and community development. In L. Boddy, J. C. Frankland, & P. van West, (Eds). *Ecology of saprotrophic basidiomycetes* (Vol. 28, pp. 239–262). Academic Press.

Sterkenburg, E., Bahr, A., Brandström Durling, M., Clemmensen, K. E., & Lindahl, B. D. (2015). Changes in fungal communities along a boreal forest soil fertility gradient. *New Phytologist*, *207*, 1145–1158.

Svensson, J., Andersson, J., Sandström, P., Mikusiński, G., & Jonsson, B. G. (2019). Landscape trajectory of natural boreal forest loss as an impediment to green infrastructure. *Conservation Biology*, *33*(1), 152–163.

Sverdrup-Thygeson, A., & Lindenmayer, D. B. (2003). Ecological continuity and assumed indicator fungi in boreal forest: The importance of the landscape matrix. *Forest Ecology and Management*, *174*, 35–363.

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., Ruiz, L. V., Vasco-Palacios, A. M., Thu, P. Q., Suija, A., Smith, M. E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., … Abarenko, K. (2014). Global diversity and geography of soil fungi. *Science*, *346*, Article 1256688.

Thakur, M. P., Phillips, H. R. P., Brose, U., De Vries, F. T., Lavelle, P., Loreau, M., Mathieu, J., Mulder, C., Van der Putten, W. H., Rillig, M. C., Wardle, D. A., Bach, E. M., Bartz, M. L. C., Bennett, J. M., Briones, M. J. I., Brown, G., Decaëns, T., Eisenhauer, N., Ferlian, O., … Cameron, E. K. (2020). Towards an integrative understanding of soil biodiversity. *Biological Reviews*, *95*, 350–364.

Thomson, B. C., Tisserant, E., Plassart, P., Uroz, S., Griffiths, R. I., Hannula, S. E., Buée, M., Mougel, C., Ranjard, L., Van Veen, J. A., Martin, F., Bailey, M. J., & Lemanceau, P. (2015). Soil conditions and land use intensification effects on soil microbial communities across a range of European field sites. *Soil Biology and Biochemistry*, *88*, 403–413.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J. S., Stokland, J. N., Sverdrup-Thygeson, A., & Mönkkönen, M. (2010). Woodland key habitats in northern Europe: Concepts, inventory and protection. *Scandinavian Journal of Forest Research*, *25*(4), 309–324.

Tomao, A., Bonet, J. A., Castaño, C., & de-Miguel, S. (2020). How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. *Forest Ecology and Management*, *457*, Article 117678.

Viljur, M.-L., Abella, S. R., Adámek, M., Alencar, J. B. R., Barber, N. A., Beudert, B., Burkle, L. A., Cagnolo, L., Campos, B. R., Chao, A., Chergui, B., Choi, C.-Y., Cleary, D. F. R., Davis, T. S., Dechnik-Vázquez, Y. A., Downing, W. M., Fuentes-Ramirez, A., Gandhi, K. J. K., … Thorn, S. (2022). The effect of natural disturbances on forest biodiversity: An ecological synthesis. *Biological Reviews*, *97*, 1930–1947.

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