Received: 23 September 2025 | Accepted: 6 February 2026

DOI: 10.1111/1365-2745.70296

Journal of Ecology

RESEARCH ARTICLE

Distinct diversity trajectories of boreal wood-inhabiting fungi following fire versus clear-cutting

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Funding information
Svenska Forskningsrådet Formas, Grant/Award Number: 2021-02116

Handling Editor: Anny Chung

Abstract

1. Two contrasting disturbance regimes—wildfire and clear-cutting—are common in boreal forests and create fundamentally different conditions for succession of wood-inhabiting fungi. We investigated (i) how species richness and community composition change after these two disturbances and (ii) which stand-level characteristics drive diversity trajectories.
2. In two chronosequences—managed clear-cut (1–109 years since clear-cut; $n = 18$) and unmanaged fire (4–375 years since fire; $n = 18$)—we combined fruiting-body surveys with DNA metabarcoding to quantify species richness of wood-inhabiting fungi, including total number of species, Agaricomycete and red-listed species. To identify drivers, we measured deadwood attributes and forest structural complexity using terrestrial laser scanning.
3. Species richness, including red-listed species, was highest in unmanaged fire stands. Unmanaged fire stands had ~55 more total species than managed clear-cut stands at comparable time since disturbance (≤109 years), and ~156 more species in stands >109 years. Communities differed markedly between chronosequence types. Managed clear-cut stands harboured a subset of species found in unmanaged fire stands, and nearly all red-listed and indicator species were exclusive to unmanaged fire stands. Total and Agaricomycete species richness increased with time in both chronosequences without saturating. Red-listed species richness remained low and did not increase with time in managed clear-cut stands, but was higher and increased with time in unmanaged fire stands. Conditional random forest models identified spruce deadwood percentage, deadwood volume, and forest structural complexity as dominant diversity drivers, with deadwood quality replacing forest structure as the best predictor for red-listed species. Species richness rose steadily with deadwood volume, levelling at ~50 $m^3 ha^{-1}$ for total species and >100 $m^3 ha^{-1}$ for red-listed species.
4. *Synthesis*. Clear-cutting altered fungal recovery trajectories differently from fire. While fires leave standing and fallen dead trees that host fungal communities

for centuries, clear-cutting removes these legacies and simplifies forest structure, resulting in a lack of recovery of red-listed species. These contrasting disturbance pathways shape boreal fungal communities through their effects on deadwood and structural continuity. Retaining high deadwood volumes and structural complexity can help maintain fungal diversity in managed forests; however, maintaining old-growth stands is essential for conserving highly diverse communities and red-listed species.

KEYWORDS
biodiversity, boreal forests, chronosequence, coarse woody debris, forest management, global change, wildfire, wood-decaying fungi

1 | INTRODUCTION

Boreal forests are experiencing unprecedented land-use intensification and shifts in disturbance regimes (Seidl et al., 2017; IPCC, 2023), which may profoundly impact biodiversity across boreal regions (Gauthier et al., 2015). Yet, how these changes affect wood-inhabiting fungal communities remains poorly understood. Wood-inhabiting fungi deliver essential ecosystem functions through deadwood decomposition and nutrient cycling, by forming key interactions with other organisms (Thorn et al., 2020), and as indicator species of forest continuity and complexity (Junninen et al., 2006; Majdanová et al., 2023; Taylor et al., 2014). Since wood-inhabiting fungi entirely depend on deadwood for their establishment, growth, and reproduction (Stokland et al., 2012), disrupted deadwood continuity could have large consequences for these fungal communities and their diversity (Siitonen, 2001). Forest management practices like clear-cutting, shortening rotation periods, and deadwood removal are thought to reduce substrate availability and simplify habitat structure (Abrego et al., 2017; Berch et al., 2011; Juutilainen et al., 2014; Krikken et al., 2019). At the same time, changes in fire frequency and severity (Flannigan et al., 2009; Remy et al., 2023; Seidl et al., 2014) could affect the successional window required for some fungal communities to establish. It remains poorly understood how disturbance type (fire versus clear-cutting) and changes in habitat structure through successional time shape wood-inhabiting fungal richness and community composition.

Historically, deadwood dynamics in boreal forests, particularly variation in deadwood quantity and quality, are believed to have been shaped by forest fires. These fires produced a large amount of substrate for pioneer wood-inhabiting fungal species through fire-induced tree mortality immediately post-fire (Siitonen, 2001). As forests mature, species composition shifts towards late-successional specialist fungi with narrow substrate or microclimatic requirements (Junninen et al., 2006). Old-growth boreal forests are believed to serve as key refuges for diverse wood-decaying fungal communities, including specialized and red-listed species, particularly among Agaricomycetes (Penttilä et al., 2004; Purhonen et al., 2021; Siitonen, 2001; Ylisirniö et al., 2012). The quantity, quality, and diversity of deadwood that builds up over decades to centuries is believed to be a major factor in the habitat conditions of old-growth forests (Baber et al., 2016; Hottola et al., 2009; Junninen & Komonen, 2011; Lassauce et al., 2011; Penttilä et al., 2004). Furthermore, forest structural complexity may enhance biodiversity through a variety of microclimatic conditions (Brabcová et al., 2022; Seidel et al., 2021). However, the role of forest structural complexity in shaping wood-inhabiting fungal diversity remains uncertain, as most evidence so far concerns other organism groups (Ehbrecht et al., 2021).

In managed forests, rotation lengths (time between successive clear-cuts) are often relatively short (60–100 years) compared with wildfire return intervals (time between successive fires historically between 50 and 200 years; Zackrisson, 1977), which can reduce both the quantity and quality of the deadwood (Djupström et al., 2008; Jonsell et al., 1998; Siitonen et al., 2000) and further disrupt the continuity of deadwood input and decay stages (Hottola et al., 2009; Penttilä et al., 2004; Ylisirniö et al., 2012). Therefore, it is crucial to understand how clear-cutting affects fungal communities to predict boreal forest diversity over extended time periods, and to guide national and international management efforts (Dinerstein et al., 2020; European Commission, 2022; United Nations Environment Programme, 2021).

Most knowledge on boreal wood-inhabiting fungi comes from fruiting-body surveys, which can miss cryptic species, as well as species without obvious fruiting bodies, and therefore may underestimate diversity (Boddy et al., 2014; Halme & Kotiaho, 2012). Although a growing number of studies have used DNA metabarcoding to supplement fruiting-body data, they have either focused on individual logs rather than stand-scale diversity (Lindner et al., 2011; Ottosson et al., 2015; Ovaskainen et al., 2013; Rajala et al., 2012; Runnel et al., 2015; Saine et al., 2020), studied temperate forests rather than boreal forests (Rieker et al., 2024), or targeted soil fungi rather than wood-inhabiting fungi (Heine et al., 2021). Importantly, no study has yet combined molecular and fruiting-body data to cover the entire post-fire and post-clear-cut successional gradient in boreal forests. The only comparable chronosequence study (Junninen et al., 2006) relied solely on fruiting-body surveys, potentially missing important diversity patterns captured by DNA-based methods. Here, we combined DNA metabarcoding with fruiting-body surveys to assess how fungal diversity responds to (i) deadwood characteristics and (ii) forest structural characteristics in Northern Swedish boreal forests.

To assess how fungal communities changed with time since forest fire and clear-cutting, we employed a chronosequence approach representing two contrasting trajectories: an unmanaged fire chronosequence (not managed for timber production; 4–375 years since forest fire) and a managed clear-cut chronosequence (1–109 years since clear-cut). We explored whether DNA metabarcoding and traditional fruiting-body surveys capture the same temporal patterns and tested the following hypotheses:

1. We predict wood-inhabiting fungal species richness (total, Agaricomycete, and red-listed species) is higher in unmanaged fire than managed clear-cut stands, and increases with time since disturbance, peaking in unmanaged old-growth forests. We anticipate these differences will correspond to a markedly different community composition between managed clear-cut and unmanaged fire stands, characterized by a greater number of specialized and rare species in unmanaged and older stands.
2. Fungal diversity patterns are explained by habitat features across two hierarchical levels. First, we predict deadwood characteristics (quantity, quality, and diversity) to explain species richness for total, Agaricomycete, and red-listed fungi. Second, we predict horizontal and vertical forest structural complexity to explain additional variation.

By using this approach, we aim to provide critical insights into how two major disturbance regimes in boreal forests—clear-cutting by rotational forestry and forest fire—shape wood-inhabiting fungal communities across boreal forest succession.

2 | MATERIALS AND METHODS

2.1 | Study sites and design

To test our hypotheses, we utilized an established study system of boreal Scots pine (*Pinus sylvestris*) stands in Northern Sweden, roughly spanning 64.8–66.5° N and 17.1–20.5° E, where understory vegetation diversity varies predictably with succession and resource availability (Buness et al., 2025). The study system consists of 36 1-ha stands (Table S1) representing different stages of forest development following disturbance. These are evenly divided into two chronosequences: 18 managed clear-cut stands and 18 unmanaged fire stands (Figure 1). The managed clear-cut stands have been subjected to the typical array of even-aged forestry practices, including clear-cutting (performed 1–109 years before our study), soil scarification, planting, and 2–3 thinning operations. In contrast, the unmanaged (i.e., not managed for timber production) fire stands experienced fires 4–375 years ago, with two of the 18 stands (5 and 28 years post-fire, respectively) instead subjected to prescribed fires. Fire severity varied from non-stand-replacing ground fires primarily affecting the organic surface layers to stand-replacing wildfires that regenerated

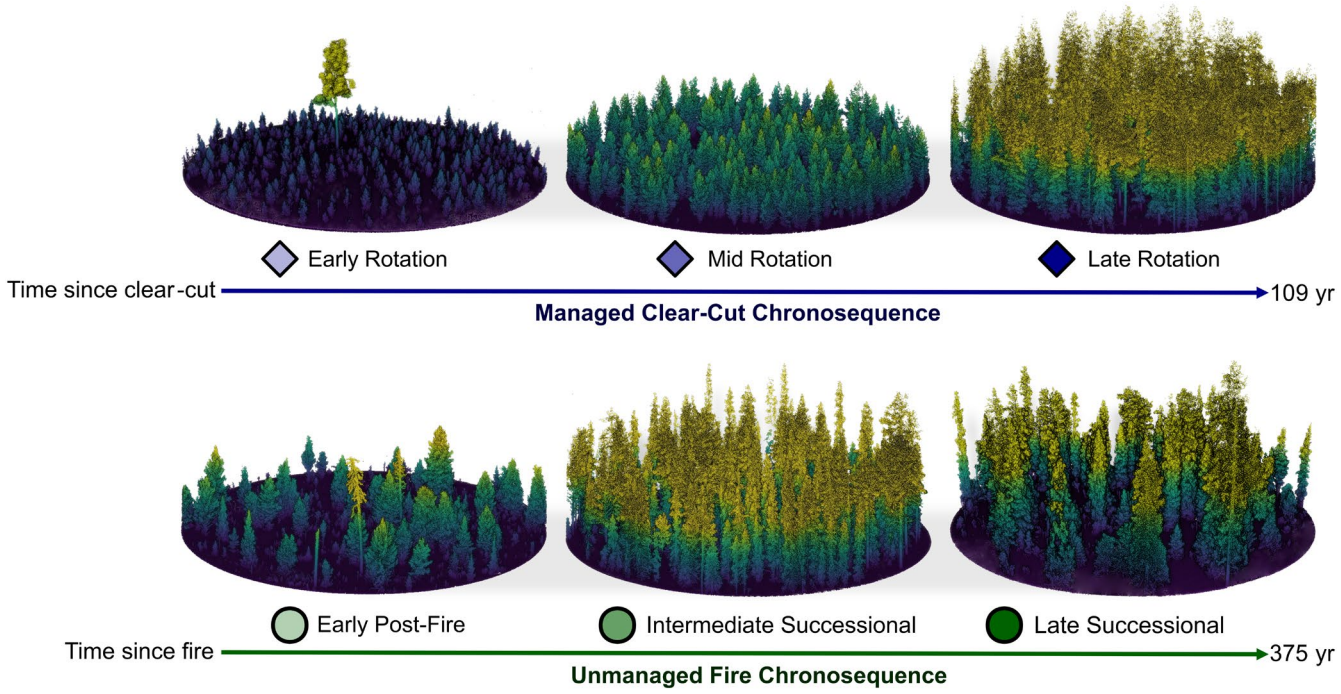

FIGURE 1 Overview of the study design, showing three stands within each of the two chronosequences: The managed clear-cut chronosequence (stands at the top row: 13, 42, and 100 years since clear-cutting) and the unmanaged fire chronosequence (stands at the bottom row: 56, 121, and 375 years since fire). The depicted stands represent key successional stages following disturbance and are visualized using terrestrial laser scanning (TLS) point clouds clipped to a 30 m radius around the plot centre. Point colours indicate height above ground.

entirely new stands (Eckdahl et al., 2022, 2023; Pérez-Izquierdo et al., 2023). Full details on the study system and stand selection are provided in Buness et al. (2025).

2.2 | Field sampling

Fieldwork was conducted in September 2023. Each stand comprised five predefined subplot locations: one central subplot and four subplots situated 35 m from the centre in each intercardinal direction. For deadwood assessment and fruiting-body inventories, subplots were circular with a 17.8 m radius (1000 m^2), while DNA sampling was conducted in smaller concentric subplots nested within these plots with a 10 m radius (314 m^2). This nested design reflects the practical constraints of each method: fruiting-body surveys can efficiently cover larger areas through visual inspection, while DNA sampling requires intensive work to acquire representative wood samples from each deadwood item. This approach follows standard practice where morphological surveys cover each sampling unit completely, whereas molecular assays rely on strategic subsamples (Rieker et al., 2024).

Deadwood was assessed in the 17.8 m radius circular subplots by measuring all pieces with a diameter of at least 10 cm on the larger end and a minimum length of 1 m, recording both diameters and the length of each piece. Only the portion of logs within the 17.8 m radius was measured. Tree species of deadwood were identified in the field when possible, and decay stages were classified into five categories following the Swedish National Forest Inventory protocol (Swedish University of Agricultural Sciences, 2023, please see Supporting Information, Section 1.2).

Fruiting-body inventories were carried out once over a 3-week period with stable weather conditions in September 2023, during the late-season period that consistently yields the highest fruit-body richness and detectability of wood-inhabiting fungi in boreal forests (Halme & Kotiaho, 2012). While repeated surveys across different periods or years can reveal additional species, a single monitoring during the primary fruiting-body season is consistent with established inventory timing in northern Fennoscandia (Berglund et al., 2005). The inclusion of DNA metabarcoding in our study provides a temporally more stable metric that captures species that may otherwise be missed by fruiting-body surveys. At the same time, DNA data should also be interpreted as the number of recorded species during a single sampling event. For the fruiting-body inventory, surveys were carried out within each of the five 17.8 m radius subplots (1000 m^2) across all 36 stands. Approximately, 30 min time was spent per subplot by two surveyors, systematically inspecting all deadwood items for reproductive structures. We recorded every species forming poroid fruiting bodies ("polypores") encountered on deadwood, including the genera *Odonticium*, *Asterodon*, and *Trichaptum*. Field identifications were made whenever possible; specimens that could not be identified in situ were collected and examined microscopically following standard microscopy procedures (details in Supporting Information, Section 1.3). Species nomenclature follows the Swedish Taxonomic Database (Artdatabanken, 2025), and red-list status for all species was obtained from the Swedish Red List database (Artdatabanken, 2020).

Forest structural characteristics were quantified using terrestrial laser scanning (TLS), conducted with a handheld mobile laser scanner (MLS, ZEB Horizon, GeoSLAM Ltd., UK) by circling the stand centre at radii of 12, 24 and 35 m before returning to the start. For detailed information, please see Supporting Information, Section 1.4.

2.3 | DNA-based community analysis

Within each 10 m radius subplot (314 m^2), wood substrate samples were taken by drilling into all deadwood items intercepted along four transects in cardinal and intercardinal directions. Three drill samples were taken per log, snag, or stump using a 30 cm increment drill (8 mm diameter) driven to the log centre, and pooled at the subplot level (full sampling details are provided in Supporting Information, Section 1.5). DNA was extracted using the NucleoSpin Soil kit (Macherey-Nagel, Germany). The ITS2–LSU region was amplified with primers gITS7 (Ihrmark et al., 2012) and TW13 (T. J. White; unpublished) and sequenced on the PacBio Revio platform (SciLifeLab NGI, Uppsala, Sweden). Sequence processing and taxonomic assignment followed the SCATA pipeline (Ihrmark et al., 2012) and taxonomy was assigned using the UNITE database. Further details on deadwood sampling, laboratory protocols, quality filtering, clustering, and data curation are provided in Supporting Information, Section 1.5. After filtering, samples retaining ≥2000 curated reads were rarefied to that depth for community analyses.

2.4 | Derived predictor variables

We calculated six stand-level habitat predictors from our field and laser scanning data to characterize deadwood resources and forest structure.

2.4.1 | Deadwood quantity

For each 17.8 m radius subplot (1000 m^2), we calculated the volume of every lying log as a truncated cone:

$$V = \frac{\pi \times L}{12}\left(D_1^2 + D_1 D_2 + D_2^2\right)$$

where L is length (m) and D_1, D_2 are the maximum and minimum diameters (m). For standing deadwood, we measured height and diameter at breast height (dbh) within the smaller, 10 m radius subplots, and estimated volume as a cylinder with a form factor of 0.5. We converted all volumes to $m^3 ha^{-1}$, added lying and standing deadwood, and averaged across the five subplots for each stand's total deadwood quantity (Figure S1).

2.4.2 | Deadwood quality

We characterized deadwood quality using the three metrics mean log diameter, percentage of logs ≥0.30 m diameter, and percentage of logs in late-decay classes (2–4; Swedish University of Agricultural Sciences, 2023). After standardizing these variables, we performed a principal component analysis that included all three metrics and extracted the first component (PC1), which explained 63.4% of the variance and increased with larger, more decayed logs to serve as our deadwood quality score in subsequent analyses.

2.4.3 | Percentage spruce deadwood and percentage deciduous deadwood

For each subplot, we calculated the average percentage of spruce deadwood and percentage of deciduous deadwood (*Betula pendula*, *Populus tremula*, *Sorbus aucuparia*, *Salix* spp.) of the total volume and used this to obtain stand-level values.

2.4.4 | Deadwood diversity

Within each subplot, we categorized logs by tree species × size class (small <0.15 m, medium 0.15–0.30 m, large ≥0.30 m) × decay class (1–5), creating a matrix of deadwood categories. For each category, we calculated the proportion of logs (p_i) relative to the total number of logs in that subplot. We then calculated Shannon's diversity index:

$$H = -\sum_{i}^{S} p_i \times \log(p_i)$$

where S is the total number of categories containing at least one log and p_i is the proportion of logs in category i. Subplot values were averaged to obtain stand-level deadwood diversity.

2.4.5 | Forest structural complexity

Based on TLS point clouds, we computed canopy rugosity (surface roughness of the canopy top) and the vertical Gini coefficient (evenness of vegetation distribution across height layers) (Atkins et al., 2018) at the stand level. These metrics capture horizontal and vertical forest heterogeneity. Their first principal component (PC1), explaining 80.0% of the variance, represented a forest structural complexity index (for details see Supporting Information, Section 1.6).

2.5 | Statistical analyses

All analyses were performed in R version 4.3.0 (R Core Team, 2020) using RStudio (RStudio Team, 2020). All data manipulation and visualization were performed using the *tidyverse* (Wickham et al., 2019) and *ggplot2* (Wickham, 2009) packages. We merged DNA-based species data with fruiting-body occurrences, both as stand-level presence/absence, and calculated three species richness metrics: total fungi, Agaricomycetes, and red-listed species. Total fungi and Agaricomycetes were dominated by DNA-based data (see Figure S5a,b). These metrics represent a gradient of niche breadth: Total fungi cover the whole community; Agaricomycetes constitute a narrower guild, commonly with a high capacity for wood decay due to a well-developed ligninolytic capacity; and red-listed species are mainly deadwood specialists.

2.5.1 | Chronosequence trajectories of species richness

To test how fungal richness changed with time since disturbance across different chronosequence types (Hypothesis 1), we fitted negative-binomial generalized additive models (GAMs) using the *mgcv* package (Wood, 2017). Each model included chronosequence type as a factor, separate smooths of time since disturbance for each chronosequence, and the square root of sequencing depth as a covariate. Further, we also compared richness among three stand groups—managed clear-cut (1–109 yeras; $n = 18$), unmanaged fire ≤109 years ($n = 9$), and unmanaged fire >109 years ($n = 9$)—using ANOVA followed by Tukey HSD contrasts (*multcomp* package; Hothorn et al., 2008).

P-values of the GAMs (hereafter called "GAM *p*") test initial differences at $t = 0$ (intercept) or temporal trends (smooth terms; Figure 2a–c; Tables S2–S4), while *p*-values of Tukey's tests (hereafter called "Tukey *p*") test pairwise differences between stand groups (Figure 2d–f, Tables S2–S4).

To compare trends in managed clear-cut forests with unmanaged fire forests for the same time span, we fitted additional GAMs to unmanaged fire forests restricted to 0–109 years ($n = 9$).

2.5.2 | Community composition, red-listed, and indicator species

To examine how fungal communities differed between chronosequence types and over successional stages (Hypothesis 1), we computed Jaccard dissimilarities and visualized community structure with non-metric multidimensional scaling (NMDS) using the *vegan* package (Oksanen et al., 2025). The effects of our predictor variables (Section 2.4) on community composition were tested using vector fitting (*envfit* function). We identified indicator species for six successional classes using the *indicspecies* package (De Cáceres & Legendre, 2009) and overlaid red-listed species positions to visualize species of conservation concern.

2.5.3 | Drivers of fungal species richness

To identify habitat features across stands that best predicted fungal richness (Hypothesis 2), we used conditional random forests (*party*

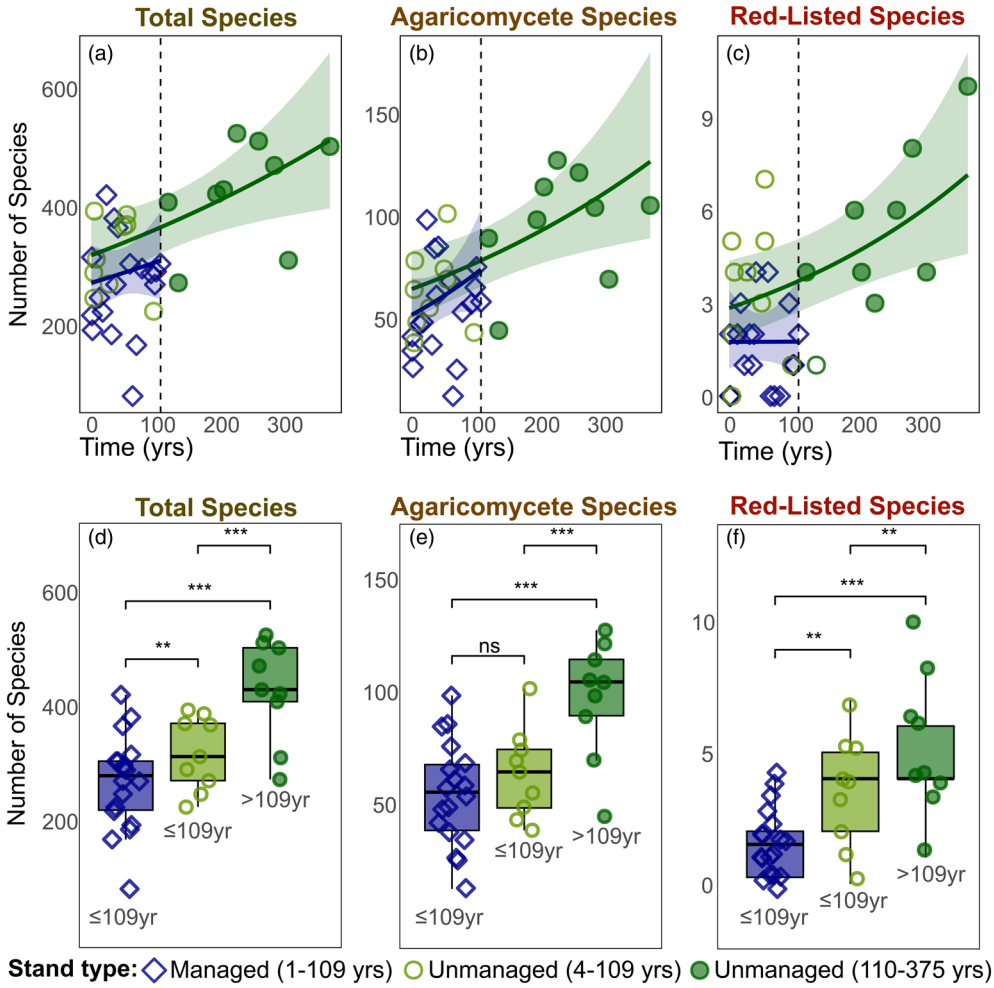

FIGURE 2 Species richness trajectories and group comparisons for total, Agaricomycete and red-listed fungi. Panels (a–c) show fitted GAM curves (±95% CI) of species richness against time since disturbance for the managed clear-cut chronosequence (blue diamonds) and the unmanaged fire chronosequence (green circles), with a dashed vertical line at 109 years marking the rotation length of the managed clear-cut chronosequence. Panels (d–f) display boxplots of fitted values from each group—managed clear-cut (M; $n = 18$), unmanaged fire ≤109 years ($F \leq 109$; $n = 9$), and unmanaged fire >109 years ($F > 109$; $n = 9$)—for (d) total species, (e) Agaricomycetes, and (f) red-listed species. Pairwise comparisons (Tukey-adjusted) are annotated with *** ($p < 0.001$), ** ($p < 0.01$) and ns ($p > 0.05$). GAMs explained 58.4% (total species), 53.2% (Agaricomycetes), and 54.6% (red-listed species) of deviance.

package; Hothorn et al., 2006; Strobl et al., 2007), which is a machine learning approach that handles complex predictor interactions while avoiding limitations of traditional regression with correlated variables and small sample sizes (Strobl et al., 2008). We chose this over a more traditional linear modelling approach (such as generalized linear models), because our habitat variables showed moderate collinearity (VIF ~2, |r| ~0.5), particularly between deadwood quantity and diversity (Seibold et al., 2016) and between deadwood quantity and percent of spruce deadwood. Such collinearity can bias generalized linear models, causing the exclusion of ecologically important predictors (Graham, 2003). Before analysis, we removed sampling effort effects (i.e. variation in sequencing depth among samples) by regressing richness against the square root of sequencing depth and analysing residuals.

Each random forest included 500 trees with the following six habitat predictors: deadwood quantity, quality, spruce percentage, deciduous percentage, diversity, and forest structural complexity. The algorithm randomly selected two predictors at each split, preventing dominant variables from masking others' effects. We assessed performance using 50 repeats of 10-fold cross-validation and calculated conditional permutation importance scores that account for correlations (Strobl et al., 2008). To identify the most important predictors, we used backward elimination (Povak et al., 2020), sequentially removing variables with the lowest median importance until model performance dropped below 95% of the full model's cross-validated R^2.

2.5.4 | Threshold identification

To explore and identify habitat thresholds where fungal diversity changes from approximately constant to increasing (onset) or from increasing to approximately constant (offset), we fitted GAMs (*mgcv* package), examining response curve shapes (Ficetola & Denoël, 2009).

Models included single habitat predictors (Section 2.4) with the square root of sequencing depth as an offset. Thresholds marked transitions in the rate of richness change, with uncertainty quantified via parametric bootstrap (for details see Supporting Information, Section 1.5.1).

2.5.5 | Method comparison: Fruiting-body survey versus DNA metabarcoding

To test whether DNA metabarcoding and fruiting-body surveys captured similar successional patterns, we compared their richness trajectories using parallel GAMs (*mgcv* package), following the same modelling framework described above. We normalized both datasets to directly compare temporal patterns independent of absolute richness values (for details see Supporting Information, Section 1.6.2). We also compared identities of red-listed species using a Venn diagram.

3 | RESULTS

3.1 | Sequencing output and fungal community overview

Following quality filtering, 4,905,900 high-quality sequences (68%) were retained and clustered into 7311 "species hypotheses" (SHs). After removal of chimeras, tag-switching artefacts, daughter OTUs, non-fungal reads, and rarefaction, 1800 SHs were identified as fungal, with sequencing depth ranging from 6 to 1923 reads per sample (mean = 1394). From the fungal sequences, 475 (26%) SHs were assigned to our fungal categories of interest: Agaricomycetes (461) and red-listed fungi (14). The five most abundant Agaricomycete species were: *Sistotremastrum suecicum* (18%), *Russula decolorans* (9%), *Trichaptum fuscoviolaceum* (4%), *Sistotrema* sp. (4%), and *Lactarius rufus* (3%).

3.2 | Species richness over time and by chronosequence type

When exploring if fungal species richness increased with time since disturbance and differed between chronosequence types (Hypothesis 1), we found that fungal species richness was generally higher in unmanaged fire than managed clear-cut forests, increased with time since disturbance, and reached its highest values in stands >200 years post-disturbance (Figure 2; Tables S2–S4). However, these patterns varied between fungal categories.

Specifically, total species richness of wood-inhabiting fungi was only slightly higher in unmanaged fire than managed clear-cut stands immediately after disturbance ($t = 0$), and this difference was not significant (GAM $p = 0.143$, Figure 2a, Table S2). Species richness increased significantly with time since disturbance in unmanaged forests (GAM $p = 0.009$), while the increasing trend in managed forests was not significant (GAM $p = 0.469$). Restricting unmanaged forests to 0–109 years ($n = 9$) still yielded a significant trend (GAM $p = 0.016$). Further, unmanaged stands ≤109 years harboured on average 55 more species per stand than managed stands within the same age category (Tukey $p = 0.007$, Figure 2d). Unmanaged stands >109 years had 156 more species per stand than managed stands ≤109 years (Tukey $p < 0.001$) and 101 more species per stand than unmanaged stands ≤109 years (Tukey $p < 0.001$).

Similarly, Agaricomycete richness did not differ between chronosequence types immediately after disturbance ($t = 0$; GAM $p = 0.605$, Figure 2b, Table S3). Agaricomycete richness increased over time in unmanaged forests (GAM $p = 0.007$), while the increasing trend in managed forests was not significant (GAM $p = 0.161$). Restricting unmanaged forests to 0–109 years yielded a significant trend (GAM $p = 0.044$). Unmanaged stands ≤109 years hosted 10 more Agaricomycete species than managed stands of the same time since disturbance category, but the difference was not significant (Figure 2e, Tukey $p = 0.103$). However, unmanaged stands >109 years hosted 31 more Agaricomycete species per stand than unmanaged stands ≤109 years (Tukey $p < 0.001$) and 42 more species per stand than managed stands ≤109 years (Tukey $p < 0.001$).

Red-listed species showed the most pronounced differences between chronosequence types. Unmanaged fire forests hosted significantly more red-listed species than managed clear-cut forests immediately after disturbance ($t = 0$; GAM $p = 0.037$, Figure 2c, Table S4). Red-listed species richness increased with time since disturbance in unmanaged forests (GAM $p = 0.007$) but not in managed forests (GAM $p = 0.994$). Further, unmanaged stands ≤109 years hosted 1.7 species more than managed stands (Tukey $p = 0.002$), while unmanaged stands >109 years had 2.0 species more than unmanaged stands ≤109 years (Tukey $p = 0.003$) and 3.7 species more than managed stands (Tukey $p < 0.001$, Figure 2f).

3.3 | Community composition and red-listed species

Examining how wood-inhabiting Agaricomycete species composition differed between chronosequence types and successional stages (Hypothesis 1), the unconstrained NMDS ordination showed that communities differed markedly between managed clear-cut and unmanaged fire forests by occupying different regions of the ordination space (primarily separated vertically in Figure 3, Table S5). Generally, there was no clear separation with time since disturbance along NMDS axes 1 or 2. However, late-successional unmanaged stands (>200 years) formed a cluster in the upper-left quadrant, clearly separated from both younger unmanaged stands and all managed stands. Additionally, four managed stands (M1b, M2, M65, M71) formed distinct outlier communities far along NMDS1, characterized by particularly species-poor communities.

Differences in fungal community composition were tightly associated with substrate characteristics among stands (Figure 3, Table S6). Deadwood quantity (envfit $r^2 = 0.58$, $p = 0.001$), deadwood diversity ($r^2 = 0.45$, $p = 0.001$), percentage of spruce deadwood ($r^2 = 0.39$, $p = 0.003$), and deadwood quality ($r^2 = 0.17$, $p = 0.047$) were

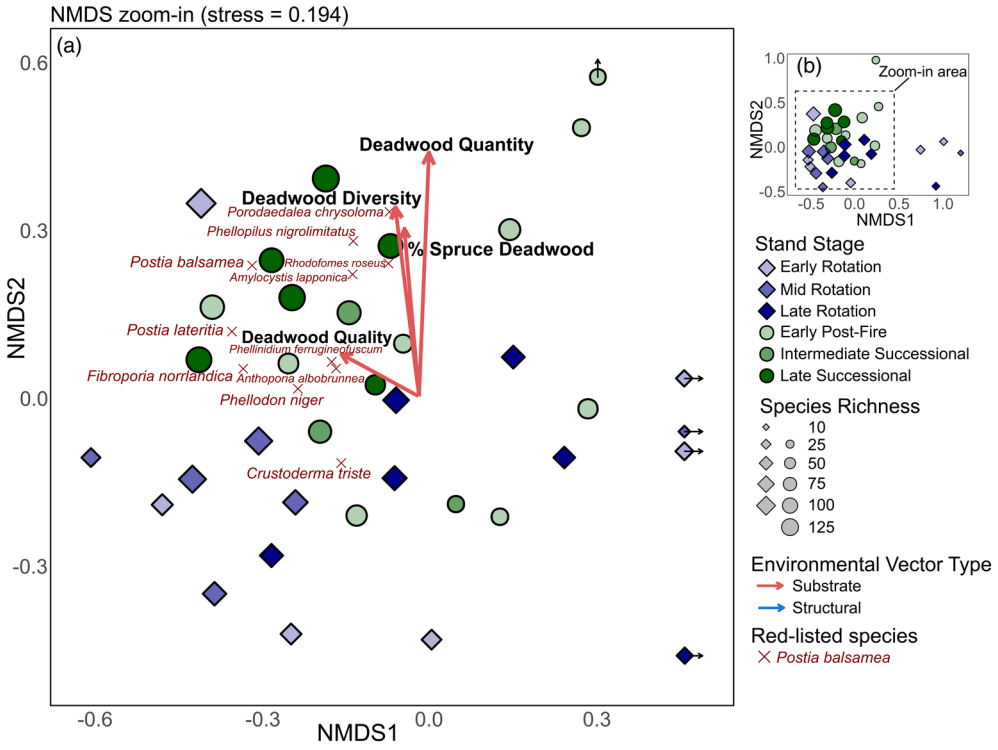

FIGURE 3 Community composition of wood-inhabiting Agaricomycetes. (a) Zoom-in on the two-dimensional NMDS ordination of all 36 stands (Jaccard, presence/absence; stress = 0.194). Symbol area scales with Agaricomycete richness (♦ managed clear-cut, ○ unmanaged fire chronosequence; colour shades trace time since disturbance within each chronosequence—see legend). Dark-red crosses give weighted-average positions of red-listed species. Arrows are envfit vectors: Red = substrate, blue = structural; solid lines denote $p < 0.05$, dashed lines $p \geq 0.05$. Indicator species for the six stand stages are shown separately in Figure S2. (b) Overview of all sites, zoom-in area marked with a dashed rectangle.

all significantly associated with fungal communities mostly found in older unmanaged stands. Forest structural complexity was positively associated with unmanaged stands along NMDS2, although not significantly ($r^2 = 0.12$, $p = 0.123$; Table S6).

Red-listed species were largely concentrated among unmanaged stands (Figure 3a, Table S7). Specifically, of 35 red-listed species detected across all stands (Table S7), those found in more than one stand were associated with old-growth conditions, where both deadwood quantity and quality were high (Figure 3a). Seven species (*Amylocystis lapponica*, *Anthoporia albobrunnea*, *Phellopilus nigrolimitatus*, *Phellinidium ferrugineofuscum*, *Fibroporia norrlandica*, *Postia balsamea*, *Postia lateritia*) were associated with old-growth forests and closely tracked the deadwood quality vector. *Porodaedalea chrysoloma* and *Rhodofomes roseus* were associated with deadwood quantity and spruce proportion, while *Crustoderma triste* was not closely associated with the management regime. Similarly, 15 of 17 significant indicator species represented unmanaged stands, predominantly in late-successional stages >200 years (Table S8, Figure S2).

3.4 | Relative importance of habitat predictors for species richness

To explicitly identify which habitat features best predicted fungal species richness across stands (Hypothesis 2) we used conditional random forest models (Figure 4). These models explained 21% of variance in total species richness, 12% in Agaricomycetes richness, and 41% in red-listed species richness (cross-validated pseudo-R^2; Figure 4a,d,g; Table S10).

Substrate characteristics dominated as predictors across all fungal categories, though the specific drivers differed between total fungal, Agaricomycete, and red-listed species richness (Figure 4a,d,g). For total species richness (Figure 4a), percentage of spruce deadwood was the most important predictor with a scaled importance of 1.00 (meaning it had the highest variable importance) and appeared among the top 3 predictors in 100% of our 50 model runs (Figure 4b). Forest structural complexity followed with moderate importance (scaled importance = 0.48) and high consistency (appearing in top 3 predictors in 100% of runs). In comparison, deadwood quantity had lower importance (0.24) and consistency (38% of runs). Only percentage of spruce deadwood and forest structural complexity were retained by our 95% model performance criterion, which keeps only predictors whose removal would reduce model performance by more than 5% (Figure 4b).

The pattern was almost identical for Agaricomycetes (Figure 4d), with percentage of spruce deadwood (importance = 1.00, frequency = 100%) and forest structural complexity (importance = 0.69, frequency = 100%) as the only retained predictors (Figure 4e).

Red-listed species richness was predicted exclusively by substrate attributes, with no contribution from forest structural complexity (Figure 4h). Percentage of spruce deadwood was again the most important predictor (importance = 1.00, frequency = 100%;

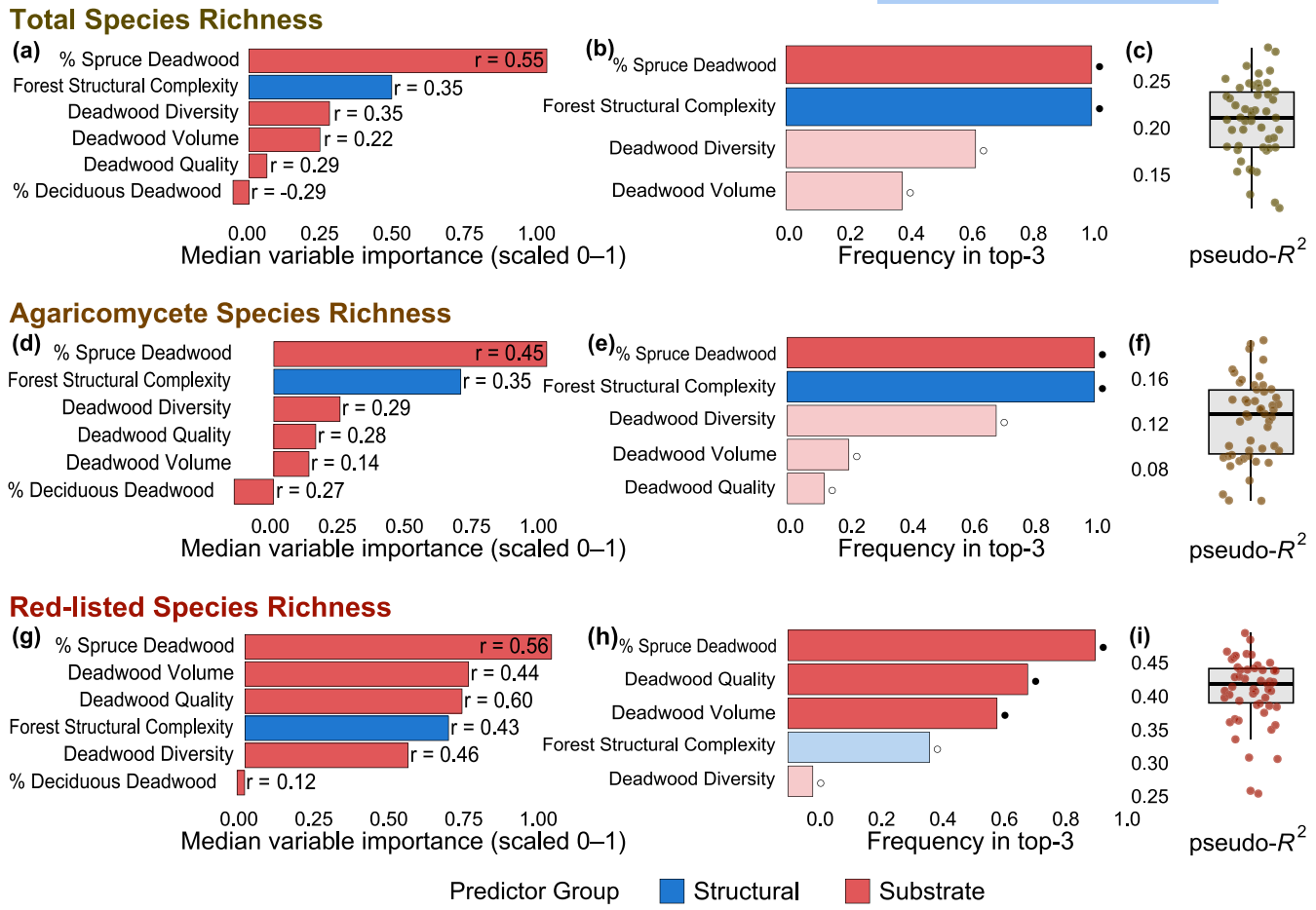

FIGURE 4 Conditional random forest model diagnostics for three fungal diversity responses to predictor variables (Section 2.4). Total species richness (a–c): (a) Median variable importance scaled 0–1, with Pearson correlation coefficients (*r*) between each predictor and fungal diversity; (b) Frequency of predictors appearing among the top 3 most important variables across 50 cross-validation runs; (c) Distribution of cross-validated pseudo-R^2 values from 50 independent model runs, showing the consistency of model predictive performance. Agaricomycete species richness (d–f): Panels as above. Red-listed species richness (g–i): Panels as above. In panels (a, d, g), predictors are coloured by group: Substrate (red) and structural (blue). In panels (b, e, h), filled circles (●) indicate predictors retained after backward elimination using the 95% performance threshold, while open circles (○) indicate eliminated predictors. The pseudo-R^2 distributions show how well models predict fungal diversity on unseen data, with higher values indicating better predictive ability and narrow distributions indicating consistent performance across different data subsets. Variables retained in final models explained 21%, 12%, and 41% of cross-validated variance for total, Agaricomycete, and red-listed species richness, respectively.

Figure 4g), followed by deadwood quality—specifically the presence of large, late-decay logs (importance = 0.71, frequency = 78%)—and deadwood quantity (importance = 0.73, frequency = 68%). All three substrate variables were retained as important predictors (Figure 4h).

3.5 | Thresholds for fungal richness

When exploring whether wood-inhabiting fungal species richness showed threshold responses to the key deadwood variables, we found that deadwood quantity showed clear offset thresholds across all fungal categories (Figure 5). Specifically, total species richness and Agaricomycete species richness increased from 0 $m^3 ha^{-1}$ and plateaued near 55 $m^3 ha^{-1}$ and 51 $m^3 ha^{-1}$ of total deadwood, respectively (Figure 5a,c). Red-listed species richness showed a higher offset threshold at 108 $m^3 ha^{-1}$ (Figure 5e).

Further, total species richness and Agaricomycete species richness also increased up to thresholds of approximately 49% and 48% spruce deadwood, respectively (Figure 5b,d), while red-listed species showed a consistent positive response to increasing spruce proportion (Figure 5f). However, deadwood quality (a composite measure of diameter, proportion of large logs, and late-decay stages) was positively associated with species richness throughout the entire gradient for all fungal categories (Figure 5c,f,i).

3.6 | Method comparison: Fruiting-body survey versus DNA metabarcoding

While the above analyses were performed on a composite dataset combining fungi detected through fruiting-body surveys and DNA metabarcoding, we also evaluated whether the two approaches

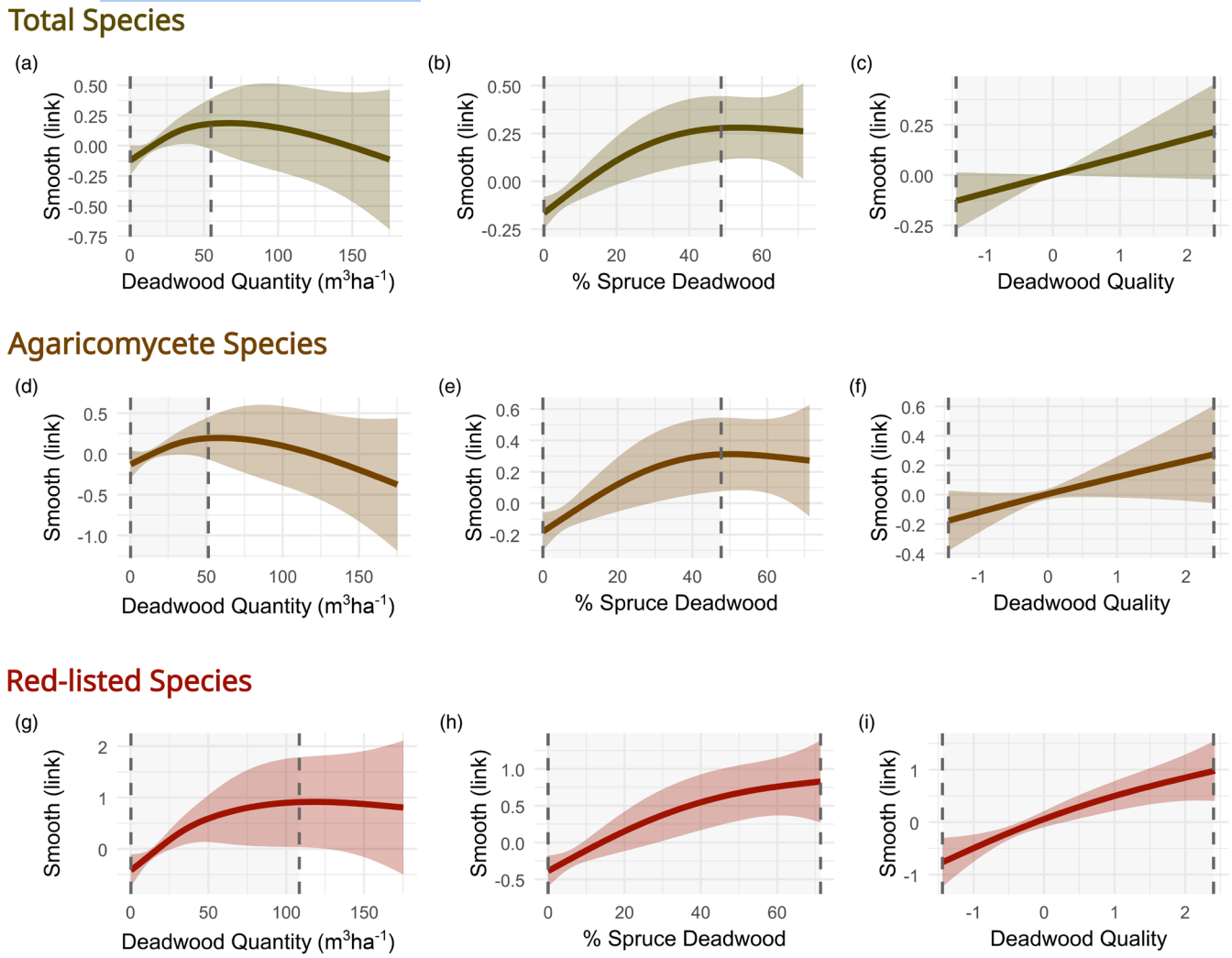

FIGURE 5 Key habitat thresholds from generalized additive models. Smooth curves (±95% CI) show how fungal richness responds to (a) deadwood quantity, (b) % spruce deadwood, and (c) deadwood quality for total species richness; (d) deadwood quantity, (e) % spruce deadwood, and (f) deadwood quality for Agaricomycetes; and (g) deadwood quantity, (h) % spruce deadwood, and (i) deadwood quality for red-listed species. Vertical dashed lines indicate identified thresholds; where no onset threshold was detected, lines appear at the start of the *x*-axis, and where no offset threshold was detected, lines appear at the end of the *x*-axis. Models were adjusted for sequencing depth differences between samples. See Table S11 for threshold estimates and 95% CIs.

revealed different ecological patterns when analysed separately. The two methods showed fundamentally different species richness trajectories along succession. Specifically, DNA-detected richness increased significantly with time since disturbance, while fruiting-body richness followed a U-shaped pattern, although this pattern was not significant (Figure S4, Tables S12 and S13). In the managed clear-cut chronosequence, fruiting-body surveys overestimated relative species richness during the first ~20 years after clear-cutting and again just before final harvest, while underestimating it in between (Figure S4e). In the unmanaged fire chronosequence, fruiting-body surveys overestimated richness for approximately the first 120 years post-fire, after which it underestimated it.

The methods showed minimal overlap in species detection across all fungal categories examined (Figure S5). Of 1879 total fungal species detected, DNA metabarcoding identified 1800 species, while fruiting-body surveys detected 60 species, and only 19 taxa were found by both methods. For Agaricomycetes, DNA metabarcoding detected 461 species and fruiting-body surveys detected 43 species, with 19 species shared between methods. For red-listed species, fruiting-body surveys detected 23 species while DNA metabarcoding detected 14, with only two species found by both methods (35 red-listed species total).

4 | DISCUSSION

4.1 | Disturbance type and time since disturbance govern wood-inhabiting fungal communities

By combining DNA and fruiting-body data for wood-inhabiting fungi in boreal forests, we found clear evidence that old unmanaged fire stands support greater species richness of total

wood-inhabiting fungi, Agaricomycetes, and red-listed species than managed clear-cut stands. Richness increased steadily with time since disturbance in unmanaged stands, while managed stands showed an increasing trend that was not statistically significant due to higher variability among stands. These findings support our first hypothesis, namely that diversity of all fungal groups would peak in unmanaged old-growth forests (Figure 2a–c), underscoring the key role of this forest type as habitat for a broad range of wood-inhabiting fungi (Junninen et al., 2006; Majdanová et al., 2023). Notably, while total and red-listed species richness differed significantly between managed and unmanaged stands of comparable time since disturbance (≤109 years), Agaricomycete richness did not. Here, the high variability among managed stands suggests that legacy effects from pre-harvest conditions—such as deadwood from seed trees left during historical, less intensive harvesting practices—may temporarily maintain Agaricomycete diversity in some managed forests.

Further in line with our first hypothesis, we found a markedly different community composition in managed and unmanaged forests, and over time. Specifically, late-successional unmanaged stands were clearly separated from managed forests, with nearly all red-listed species and indicator species exclusive to unmanaged stands. These results are in line with previous findings that managed stands harbour only a subset of the community found in unmanaged forests (Abrego & Salcedo, 2014; Bässler et al., 2010; Juutilainen et al., 2014), reflecting the importance of forest continuity for specialist species (Hottola & Siitonen, 2008; Nordén et al., 2018), while generalists are able to persist in managed landscapes (Nordén et al., 2013). Recovery was more consistent in unmanaged forests following fire, whereas managed forests showed highly variable recovery patterns, and specifically a lack of recovery for red-listed species.

4.2 | Substrate characteristics drive fungal diversity patterns

The distinct diversity patterns and community compositions between managed and unmanaged forests raise the question of which environmental factors drive these differences. We found clear support for our second hypothesis that deadwood characteristics were more important than overall forest structure in determining fungal diversity, though the relative importance of substrate-related drivers differed markedly between fungal categories. While both the share of spruce deadwood and forest structural complexity predicted total and Agaricomycete species richness (Figure 4), red-listed species depended solely on deadwood quantity, quality, and the share of spruce deadwood. Contrary to our expectation, deadwood diversity was not identified as a significant predictor of fungal diversity. Here we show that deadwood characteristics are the principal drivers of wood-inhabiting fungal diversity across the entire community, reinforcing earlier conclusions drawn from fruiting-body surveys alone (Heilmann-Clausen & Christensen, 2005; Junninen & Komonen, 2011). Our study also highlights the importance of spruce deadwood for maintaining higher fungal diversity (Kuuluvainen & Siitonen, 2013) in pine-dominated forests, reflecting how Norway spruce provides critical habitat for specialized fungi in European coniferous forests (Stokland et al., 2012) and how both individual log volume and tree species identity support red-listed species. Several red-listed species illustrate these substrate specializations: *Amylocystis lapponica* and *Rhodofomes roseus* are typically confined to large, late-decay spruce logs, whereas *Postia lateritia* occurs mainly on large, fallen pine. Our threshold analyses align with these patterns: total and Agaricomycete richness increased up to ~50–55 $m^3 ha^{-1}$ of deadwood, while red-listed species reached their highest richness only beyond ~100 $m^3 ha^{-1}$, and richness increased with the proportion of spruce deadwood up to ~48%–49%. However, deadwood quantity alone did not explain diversity patterns as young disturbed stands contained high deadwood volumes comparable to old-growth forests (Figure S1), yet harboured far fewer species. This demonstrates that substrate quality and diversity, rather than quantity alone, drive fungal richness. Forest structural complexity, quantified from TLS, influenced wood-inhabiting fungal communities by creating fine-scale variation in light, temperature, and humidity. Such microclimatic heterogeneity can promote coexistence among species with different environmental preferences (Bässler et al., 2010; Kovács et al., 2017; Máliš et al., 2023). Although structural complexity ranked below substrate variables in predicting total and Agaricomycete species richness, its effect remained significant, suggesting that physical stand structure complements substrate-driven diversity. The contrasting responses between fungal categories—with red-listed species depending entirely on substrate while other fungi also benefitted from structural complexity—likely reflect fundamental differences in ecological strategies between common and rare species (Hottola & Siitonen, 2008; Moor et al., 2021).

4.3 | Interpreting DNA and fruiting-body signals

Earlier studies using only fungal fruiting-body inventories have reported a U-shaped pattern of fungal richness following disturbance (Siitonen, 2001) or an early post-disturbance peak (Junninen et al., 2006). Our fruiting-body data also follow a U-shaped pattern in both chronosequences, whereas the DNA data consistently indicate a steady increase in richness with time since disturbance. These contrasting patterns arise because the two methods detect different components of the community, which also explains the relatively small overlap between taxa. Part of this limited overlap also reflects differences in taxonomic scope: the fruiting-body survey targeted polypores (and a few additional genera), whereas DNA metabarcoding detects all fungal groups present in the wood and bark. This is also reflected in the fact that only two of the 35 red-listed species we detected were identified by both methods, indicating clearly that each method captured a different subset of the fungal community. Fruiting-body surveys have clear strengths:

they record the more obvious reproducing individuals and detected more red-listed species in our study. However, they are biased toward taxa that form easily visible fruiting structures, and many wood-inhabiting fungi fruit infrequently or unpredictably (Halme & Kotiaho, 2012; Ovaskainen et al., 2013), which limits detectability.

On the other hand, metabarcoding from deadwood detects both living and recently dead mycelium, as well as spores, providing a powerful and inclusive tool to detect the presence of fungi. It can capture species that do not regularly fruit or have inconspicuous fruiting bodies, detect early recovery signals, and reveal hidden diversity. For example, it also detects fungi inhabiting the bark, and because bark can host up to three times as many species as the underlying wood, its inclusion can substantially increase community coverage (Naranjo-Orrico et al., 2025). Further, metabarcoding detected ectomycorrhizal taxa, such as *Russula* and *Lactarius*, which are known to colonize logs via fine-root in-growth in the later decay stages of wood (Mäkipää et al., 2017; Rajala et al., 2012). While DNA metabarcoding introduces some uncertainty regarding the amount of transient taxa and the active mycelial community, previous studies suggest that it captures the majority of wood-inhabiting fungal diversity (Lepinay et al., 2022; Rajala et al., 2012). Combining fruiting-body surveys and DNA metabarcoding therefore offers a more complete picture of how wood-inhabiting fungi respond to disturbance and long-term forest development.

4.4 | Implications

Our results highlight that following major disturbances in boreal forests, effective conservation of wood-inhabiting fungi depends on habitat attributes that accumulate only in late-successional forests, particularly the sustained presence of large, high-quality deadwood and the development of complex stand structure. The thresholds identified in our analyses reinforce this: total and Agaricomycete richness increased up to ~50 $m^3 ha^{-1}$ of deadwood, and red-listed species only approached their highest richness beyond ~100 $m^3 ha^{-1}$, far above the ~7 $m^3 ha^{-1}$ we found in managed stands. Hence, continuous recruitment and retention of large logs, mixed tree species composition, and high structural complexity are essential for supporting both generalist and specialist fungi in northern boreal pine forests. However, our results also suggest that even substantial increases in deadwood and heterogeneity cannot replace the ecological continuity provided by late-successional forests. Therefore, maintaining landscape-scale fungal diversity requires preservation of the ecological continuity that old-growth forests provide (Nordén et al., 2018).

AUTHOR CONTRIBUTIONS

Vincent Buness: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing—original draft (lead). **Michael J. Gundale**: Conceptualization (equal); Funding acquisition (lead); Project administration (lead); Methodology (equal); Supervision (equal); Writing—review and editing (lead). **Björn D. Lindahl**: Conceptualization (equal); Methodology (equal); Supervision (equal); Writing—review and editing (equal). **Tamlyn K. Gangiah**: Data curation (equal); Writing—review and editing (equal). **Peter Annighöfer**: Methodology (equal); Supervision (equal); Writing—review and editing (equal). **Torbjörn Josefsson**: Data curation (equal); Writing—review and editing (equal). **Noel Ingre Wieser**: Data curation (equal); Writing—review and editing (equal). **Daniel B. Metcalfe**: Funding acquisition (equal); Writing—review and editing (equal). **Isabelle Lanzrein**: Data curation (equal); Writing—review and editing (equal). **Syed Tuhin Ali**: Data curation (equal); Writing—review and editing (equal). **Marie-Charlotte Nilsson**: Funding acquisition (equal); Writing—review and editing (equal). **Maja K. Sundqvist**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (lead); Writing—review and editing (lead).

ACKNOWLEDGEMENTS

We thank Sveaskog AB for providing access to forest stands and their database. We extend our gratitude to Länsstyrelsen for allowing us to conduct research in protected areas. We acknowledge Morgan Karlsson, Per Schönning, and Carlos Miguel Aragon for their assistance with fieldwork, and Ilse van Duuren and Yasaman Najafi for laboratory work. The Centre for Statistics (SLU), particularly Magnus Ekström, provided valuable statistical advice. We also thank Mikael Brandström Durling for establishing and maintaining the bioinformatics pipeline. The data handling and processing was enabled by resources provided by the National Academic Infrastructure for Supercomputing in Sweden (NAISS), partially funded by the Swedish Research Council through grant agreement no. 2022-06725.

FUNDING INFORMATION

This study was supported by a grant from FORMAS (Swedish Research Council for Sustainable Development; Project Formas grant no. 2021-02116) awarded to M.J.G.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70296.

DATA AVAILABILITY STATEMENT

Data and analysis code that support the findings of this study are archived in Dryad (Buness et al., 2026) at https://doi.org/10.5061/dryad.tmpg4f5bs.

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SUPPORTING INFORMATION

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

Table S1. Stand name, time since disturbance (year), management regime, and disturbance type for all 36 study stands (1-ha plots).

Figure S1. Total deadwood volume trajectories.

Table S2. GAM results for total species richness of wood-associated fungi across two forest disturbance chronosequences (unmanaged fire versus rotational management stands).

Table S3. GAM results for Agaricomycete species richness of wood-associated fungi across two forest disturbance chonosequences (unmanaged fire versus rotational management stands).

Table S4. GAM results for red-listed species of wood-associated fungi across two forest disturbance chonosequences (unmanaged fire versus rotational management stands).

Table S5. NMDS site scores (stress = 0.194).

Table S6. Envfit vectors.

Table S7. Red-listed species occurrences and substrate requirements.

Figure S2. Community composition of wood-inhabiting Agaricomycetes.

Table S8. Significant indicator species (IndVal.g, $p < 0.05$).

Table S9. Explained variance of conditional-random-forest models.

Table S10. Predictor importance and stability across 500 CV fits.

Figure S3. Generalized additive model smooths and derivatives for fungal richness responses to seven habitat predictors.

Table S11. Estimated breakpoints (median $lower_{50}$ and $upper_{50}$) with 95 % CIs for seven habitat predictors across three richness metrics, as derived from GAM derivatives.

Figure S4. Comparison of the two survey methods.

Figure S5. Overlap between DNA metabarcoding (solid-outlined circles) and fruiting-body inventory (dashed-outlined circles) in detecting wood-inhabiting fungi.

Table S12. DNA-derived species richness.

Table S13. Sporocarp-derived species richness.

How to cite this article: Buness, V., Gundale, M. J., Lindahl, B. D., Gangiah, T. K., Annighöfer, P., Josefsson, T., Wieser, N. I., Metcalfe, D. B., Lanzrein, I., Ali, S. T., Nilsson, M.-C., & Sundqvist, M. K. (2026). Distinct diversity trajectories of boreal wood-inhabiting fungi following fire versus clear-cutting. *Journal of Ecology*, *114*, e70296. https://doi.org/10.1111/1365-2745.70296