Forest Ecology and Management 596 (2025) 123065

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Fragmented forests, isolated fungi: Saproxylic polypores in boreal woodland key habitats

Anita Atrena [a,*], Malin Undin [a], Mattias Edman [a], Fredrik Carlsson [a], Oskar Englund [a], Bengt-Gunnar Jonsson [a,b]

[a] Mid Sweden University, Faculty of Science, Technology and Media, Department of Natural Science, Design, and Sustainable Development, Holmgatan 10, Sundsvall 852 30, Sweden

[b] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

ARTICLE INFO

Keywords:
Fragmentation
Boreal forests
Saproxylic fungi
Landscape structure
Woodland key habitats

ABSTRACT

Forestry in boreal Sweden has significantly altered the landscape and reduced old-growth forests, promoting growth of younger, managed stands. Saproxylic polypores are in direct competition with forestry for resources and have declined significantly in diversity. These fungi play a crucial role in decomposing deadwood with their persistence reliant on habitat quality, connectivity, and continuous wood availability. We examined how log, stand, and landscape-level factors affect saproxylic polypore richness and community composition in 26 woodland key habitats (WKHs) in southern boreal Sweden. We recorded polypore fruitbodies on 1263 *Picea abies* deadwood units and assessed stand structure. GIS was used to quantify spruce forest amount and quality at 0.5, 5, and 15 km scales, including connections to larger high-quality habitats. Local-scale factors, especially deadwood volume and decay stage, strongly influenced fungal richness. Landscape effects were weaker, likely due to the homogenous and degraded surrounding forest matrix. However, polypore richness increased with high-quality forest cover at the 15 km scale, while medium-quality forest at 5 km had a negative effect. Red-listed species richness showed a strong eastward gradient, possibly reflecting historical forestry and extinction debt. Community composition patterns aligned with these trends, with further indirect effects from nearby forest amount and quality. We conclude that the landscape configuration matters but is context dependant. In our heavily managed study region, high-quality patches like WKHs are too isolated, leaving local conditions as the primary driver of fungal persistence. Effective conservation requires integrating landscape-scale measures, including identifying and protecting remaining forests with high natural values.

1. Introduction

In the context of the ongoing sixth global mass extinction (Ceballos et al., 2015; IPBES, 2019), habitat degradation and fragmentation are significant threats to boreal forest biodiversity (Hanski, 2011; Nordén et al., 2018). Traditionally, fragmentation refers to the division of large habitats into smaller patches. However, several processes contribute to fragmentation, e.g., overall habitat area reduction, loss of temporal and spatial connectivity, and deterioration in habitat quality (for instance, the conversion of old-growth forests to production forests) (Ahlström et al., 2022; Nordén et al., 2013). These processes negatively impact species diversity by increasing the distance between and size of habitat patches, thus reducing colonization probabilities, and limiting the resource availability and population sizes (Gu et al., 2002; Hanski, 2005; Nordén et al., 2018; Undin et al., 2024).

While forest fragmentation can occur due to natural processes such as fires or storms, the predominant driver is human activities, including urbanization, forestry, and agriculture (Ahlström et al., 2022; Andrén, 1994; IPBES, 2019). The majority of European forests have been subjected to extensive management over the past hundreds of years (Sabatini et al., 2018). This has affected, among others, forest disturbances, structural aspects and species compositions within and across stands, and overall landscape configuration (Angelstam and Kuuluvainen, 2004; Gu et al., 2002). In boreal regions, fragmentation is primarily linked to the loss of old-growth forests, increased areas of degraded forest, and deteriorated landscape structure (Nordén et al., 2013; Svensson et al., 2019). In Sweden, more than 90 % of the forest land has been altered over the past 150 years, leaving only remnants of

* Corresponding author.
E-mail address: anita.atrena@miun.se (A. Atrena).

https://doi.org/10.1016/j.foreco.2025.123065
Received 18 June 2025; Received in revised form 1 August 2025; Accepted 2 August 2025
Available online 9 August 2025

old-growth forests (Angelstam et al., 2020; Östlund et al., 1997). This fragmentation, combined with a general scarcity of deadwood, has created challenging conditions for wood-dependent organisms (Edman et al., 2004a; Nordén et al., 2013; Penttilä et al., 2006; Ruokolainen et al., 2018).

Conservation strategies to halt biodiversity loss often involve establishing single reserves or ideally connected networks of protected areas, i.e., functional green infrastructure (Angelstam et al., 2020; Svensson et al., 2019). Traditional approaches tend to focus on preserving old-growth and other high-quality forests as nature reserves and national parks (Timonen et al., 2010). Old-growth habitat patches typically support higher densities of saproxylic organisms due to high abundance and quality of deadwood. The rich biodiversity in these old forests can also lead to "spillover effects", promoting species presence in the surrounding managed forests (Angelstam and Kuuluvainen, 2004). In addition, a high proportion of mature forests on landscape scale can have significantly beneficial effects on many organism groups (Kärvemo et al., 2021), potentially reflecting the overall ecological naturalness and heterogeneity of such landscapes. However, the remaining old-growth forests in Fennoscandia are few and scattered (Angelstam et al., 2020; Kuuluvainen and Gauthier, 2018). Hence, effective conservation of forest biodiversity cannot rely solely on protecting remaining old forests, but must include interventions in managed forest as well (Felton et al., 2020; Kuuluvainen and Gauthier, 2018).

A common approach to maintaining biodiversity in managed landscapes is to identify and set-aside woodland key habitats (WKH) – small habitat patches, with a high likelihood of supporting red-listed species due to old-growth-like structural elements. In Sweden, all managed forest landscape have been subjected to WKH inventories since 1993 (Bjärstig et al., 2019; Nitare and Noren, 1992; Timonen et al., 2010). While there is no formal protection of the WKHs, they often serve as an essential conservation measure within managed forest landscapes (Jönsson et al., 2009). These habitats are typically embedded within a matrix of managed forests and are intended to serve as lifeboats for demanding species and source populations for species in the surrounding landscapes. Yet, the availability and heterogeneity of suitable substrates in the surrounding landscape are often limited, reducing the effectiveness of WKHs in maintaining species diversity and supporting viable populations (Stokland and Larsson, 2011; Undin et al., 2024).

Functional connectivity and stable patch dynamics are critical for successful dispersal, colonization and long-term persistence of forest-dependent species, in particular for sessile organisms such as saproxylic basidiomycetes (Angelstam et al., 2020; Hanski, 2011). Thus, saproxylic basidiomycetes, are among the most affected by forest fragmentation (Penttilä et al., 2006). These fungi are critical components of forest ecosystems as primary decomposers of wood, and together with other saproxylic organisms contribute to approximately 20–25 % of Scandinavian forest biodiversity (Siitonen, 2001). Saproxylic polypores are often long lived-organisms and in favourable conditions the lifespan of individual mycelia can be several decades old (Penttilä et al., 2006). It is well established that within-patch dynamics, such as the availability and quality of deadwood, are the primary drivers of saproxylic diversity (Atrena et al., 2020; Junninen and Komonen, 2011; Zibold et al., 2024). However, substantial evidence suggests that the surrounding landscape also plays a significant role in sustaining local as well as regional species diversity (Hottola and Siitonen, 2008; Lunde et al., 2025a; Undin et al., 2024). While some wood-inhabiting fungi can adapt to managed forests, many species require old-growth conditions with large volumes and diversity of deadwood of various size, decay and tree species. (Atrena et al., 2020; Edman et al., 2004a; Nordén et al., 2013; Ramiadantsoa et al., 2018). Generalist species may persist in fragmented landscapes due to their wide niche breath, whereas old-growth forest specialists require specific conditions such as high volumes of large-diameter deadwood to persist (Heilmann-Clausen and Christensen, 2004; Nordén et al., 2013). Consequently, while managed forests can act as buffers around higher quality forest patches, they do not necessarily facilitate connectivity between them.

Although the effects of landscape fragmentation on saproxylic polypores have been documented, studies have shown mixed and inconclusive results (Undin et al., 2024). Some studies show that specialized saproxylic polypores may persist for years on suitable logs and for decades in isolated old-growth forest patches, resulting in a delayed response to landscape changes (Komonen et al., 2021; Penttilä et al., 2006). This delayed response, known as extinction debt, in combination with patch dynamics and the stochasticity in species occurrence, makes the task of untangling the relationship between saproxylic organism distributions and landscape factors affecting their long-term diversity an even more challenging task. Understanding how species respond to long-term landscape changes is a necessity for the effective planning of future forest reserves and restoration in managed forest landscapes. Hence, more empirical studies are needed that are considering both the dynamic nature of landscapes, including spatial and temporal aspects of landscape fragmentation to investigate the intricate connections between species diversity and landscape structure.

In this study, we analysed how the diversity of saproxylic polypores is affected by landscape composition across multiple spatial scales and varying forest quality thresholds (total, medium and high-quality spruce forests), as described in landscape variable section under high conservation value forests (HCVF). In addition, we assessed the quality of WKHs and deadwood as habitats in fragmented landscape. Specifically, our study addressed the following key questions:

1. How does landscape configuration influence the occurrence of saproxylic polypores on individual logs within woodland key habitats? We hypothesize that decreasing amounts of medium to good quality forests will lead to decreasing number of species, particularly for conservation relevant species.
2. What is the relative effect of substrate, stand and landscape factors in explaining the occurrence and richness of saproxylic polypores? We hypothesize that the effect of landscape fragmentation will be present even after accounting for deadwood and stand level factors.
3. At what spatial scales should forest management strategies be focused to most effectively conserve diversity of saproxylic polypores? We hypothesize that conservation efforts will be most effective when targeted at local to intermediate spatial scales, where WKHs embedded in high-quality forest matrices can maintain higher fungal diversity and support red-listed species.

2. Methods

2.1. Study sites

The study was conducted in the boreal zone of central Sweden, where 26 woodland key habitats (WKHs) were selected in the counties of Västernorrland and Jämtland (Fig. 1). Sites were chosen based on their canopy composition, with at least 70 % Norway spruce (*Picea abies*). We selected *P. abies* due to its regional dominance, the presence of larger areas of natural forest patches in the landscape, and its general role as a host to rich communities of saproxylic polypores.

In northern Sweden, clear-cutting has been the dominant forest management practice since the mid-20th century, resulting in gradual loss of old-growth and continuity forests. To maximize the variation in WKH isolation, site selection was guided by changes in the relative amount of continuity forest (forests that have not been clearcut for at least 80 years (Ahlkrona et al., 2017)) in the landscape over time, using aerial photos and, when available, satellite scenes (Landsat). This was done within a 15 km radius from the WKH considering five historical time periods: the 1940s, 1960s, 1980s, 2000s, and 2020 s. Despite our efforts to maximize the variation in isolation, many of the landscape variables had limited variation across scales and were strongly dominated by low quality forests (Table 1). This also led to high correlation across variables (Appendix Table A1 and Figure A1), indicating the high

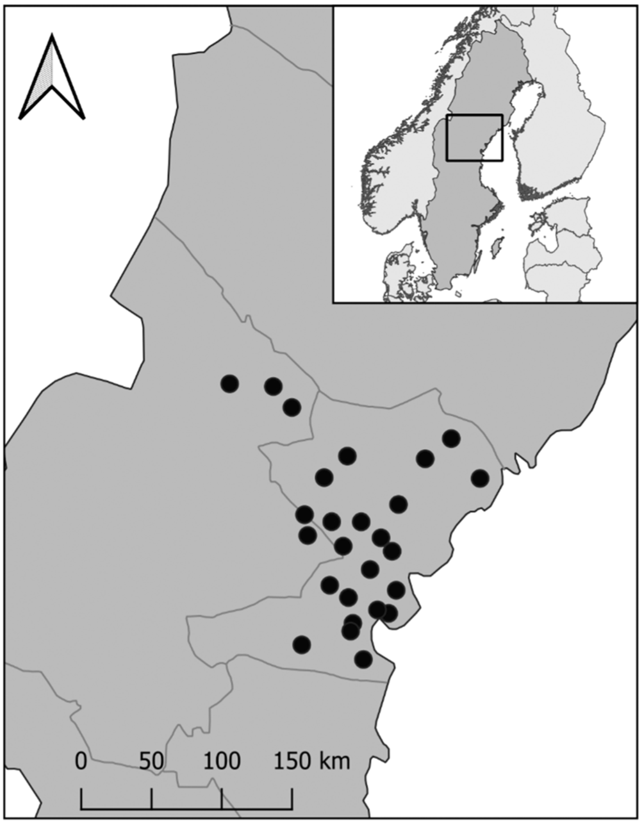

Fig. 1. Map of the study area showing the locations of 26 study sites.

homogeneity of quantity and quality of forests.

2.2. Inventory of saproxylic polypores and stand structural attributes

In each stand we established three randomly placed, non-overlapping transects, each measuring 100 m in length and 10 m in width. In smaller sites, where random non-overlapping placement of transects was unfeasible, we adjusted the transect placement to avoid inventorying the same wood item twice.

We surveyed all dead *P. abies* logs with a minimum basal diameter of 10 cm for the presence of polypore fruitbodies. The presence of one or more fruiting bodies of single species on a single log unit was recorded as an occurrence. In total, 1263 substrate units were examined within the transects. The species inventory was conducted during the fruiting season of polypores in northern Sweden, between August and October in 2020 and 2021. Most fruitbodies were identified in the field and those requiring further analysis were collected for microscopic identification. The conservation status of each species was based on the IUCN red-list categories (near-threatened [NT], vulnerable [VU], endangered [EN], critically endangered [CR]) (SLU Artdatabanken, 2020).

For each WKH, we measured environmental variables at both the tree and stand levels. To estimate wood item volume, we recorded length and diameter at three points (maximum, 4 m from the maximum, and minimum). Volume was then calculated using the conic-paraboloid formula (Fraver et al., 2007). Individual tree volumes were also aggregated at the stand level (m^3/ha). Additionally, we assessed the decay stage of each log using a four-level scale on wood hardness (Swedish University of Agricultural Sciences, 2020). At the stand level we recorded stand size, stand age, and the number of cut stumps. Stand size was obtained from the Swedish Forest Agency (Skogens pärlor). Stand age was determined by tree-ring analysis using wood cores, sampled from the largest trees at three points (0 m, 50 m, 100 m) along each transect. The number of annual rings was analysed using WinDendro (Regent Instruments Inc., 2014). If the pith of the core sample was missing, the number of missing rings was estimated based on the curvature of the innermost tree rings (Duncan, 1989). Cut stumps were counted along each transect and estimated as number of stumps per hectare per stand, as a proxy for historic management intensity.

2.3. Landscape variables

All landscape variables and calculations were prepared in QGIS (QGIS Association, n.d.) and GRASS GIS (GRASS Development Team, 2024). Landscape parameters were quantified at three spatial scales, using buffer zones with radii of 0.5 km, 5 km, and 15 km from the centre of each WKH, respectively. Below, the three buffers are referred to as “landscapes”.

To assess habitat suitability for spruce-specialist saproxylic polypores, we examined whether these fungi require spruce-dominated forest in general, medium- or high-quality spruce forests, or whether they can persist in any forest with the presence of spruce. Based on a tree species composition map from the Swedish University of Agricultural Sciences (2010) and the national land-use and land-cover (LULC) map of Sweden (Swedish EPA, 2019) we calculated two habitat availability variables with 10 m resolution at the landscape scale, using raster calculator and zonal statistics: (i) *the mean proportion of spruce cover* in all forests, and (ii) *the share of spruce forest*, defined as forest cells with at least 50 % spruce cover.

For habitat quality, we used the High Conservation Value Forest (HCVF) map of south boreal region (Bubnicki et al., 2024), which assess naturalness of Swedish forest landscape (forest cover > 50 %). The map provides a relative probability score (from 0 % to 100 %) with 1 ha resolution, indicating the probability of an area being of high conservation value. The HCVF models incorporates a variety of environmental, structural, and land-use variables, with some of the key factors influencing HCVF designation in the south boreal region being forest height, historical and current management intensity, and terrain slope.

To match the LULC data, we resampled the HCVF data to 10 m resolution using the GRASS GIS algorithm r.resamp.interp (lanczos) and adjusted the resulting values to fall within [0, 100]. The forest quality within the landscape was then assessed by calculating the average HCVF value for all forests within each landscape. To account for the *overall landscape quality* rather than just the forested areas, we adjusted the HCVF probability scores by subtracting the proportion of non-forested land within each buffer and multiplying the adjusted score by the forested proportion of the landscape.

To distinguish between different habitat qualities, we classified *medium-quality forest* as spruce forests with HCVF probability > 40 % and *high-quality forest* as spruce forests with HCVF probability > 70 %. Jonsson et al. (2024) estimated that in south boreal region of Sweden, forests with HCVF probability > 40 % likely include forest patches without formal protection but with considerable conservation value, such as woodland key habitats and voluntary set-asides, while forests below this threshold was estimated to be conventionally managed forest land. In contrast, forests with HCVF probability > 70 % correspond to formally protected areas, such as national parks and nature reserves.

Finally, we assessed whether WKHs were connected *to medium-* and *high-quality habitat areas*. Such habitat areas were delineated by first identifying the share of medium and high-quality habitat cells (for each 10 m cell in the study area) relative to total forest within a 250 m radius, using the GRASSS GIS r.neighbours algorithm. Then we applied a threshold of 20 % to delineate connected habitat areas (Englund, 2024), polygonised them, and computed their respective areas. For each WKH, the size of the medium- and high-quality habitat area in which it is located was then identified (see appendix B1 for illustrations). Medium- to high-quality forests, such as WKHs and nature reserves, generally contain higher levels of deadwood than conventionally managed forests (Asplund et al., 2024; Häkkilä et al., 2021). Since deadwood availability is a key factor for saproxylic polypores (Atrena et al., 2020; Parajuli and

Table 1
Summary of variables used and considered for analysis in the study. Abbreviations for variable scale: DW – deadwood item level, S – stand scale, L – landscape scale. All variables were considered for GLMMs, used in NMDS as well as used for overall study area assessments.

Variable	Abbreviation used in plots	Definition	Scale		Range	Mean
Deadwood unit volume	dw_log	Volume of deadwood unit (m3).	DW		0001–5,29	0,28
Decay stage	decay	Summary of number of logs per decay stage on stand level[a].	DW	Decay 1	12–55	23
		Stage 1: < 10 % of wood decayed.				
		Stage 2: 10–25 % decayed wood.		Decay 2	3–45	16
		Stage 3: 26–75 % decayed wood.				
		Stage 4: 76–100 % decayed wood.		Decay 3	1–18	8
				Decay 4	0–7	3
Deadwood volume per stand	dw_stand	Deadwood volume as measured m^3 / ha.	S		12,81–198,69	44,59[b]
Stand age	age	Stand age as approximated to the oldest wood core from each stand indicating continuity of tree cover.	S		124–271	186
Stand size	size	Size of woodland key habitat (ha).	S		1,09–16,6	5,88
Stumps	stumps	Number of cut stumps per hectare indicating historic management intensity.	S		60 – 520	255
Mean spruce cover in the landscape	mean05	Average cover of spruce in all forests in the landscape, including mixed and deciduous forests (%).	L	0.5 km	29–63	44
	mean5			5 km	22–44	35
	mean15			15 km	25–41	34
Share of spruce forest	share05	Share of spruce forest (> 50 % cover) relative to total forest (%) in the surrounding landscape.	L	0.5 km	20–73	41
	share5			5 km	12–41	30
	share15			15 km	13–38	29
Share of medium- quality habitat	share40_05	Share of medium-quality (HCVF probability > 40 % - 100 %) spruce forest (spruce > 50 % cover) in the surrounding landscape.	L	0.5 km	0–73	19
	share40_5			5 km	3–17	7
	share40_15			15 km	2–14	7
Share of high-quality habitat	share70_05	Share of high-quality (HCVF probability > 70 %) spruce forest (spruce > 50 % cover) in the surrounding landscape.	L	0.5 km	0–59	6
	share70_5			5 km	0–5	1
	share70_15			15 km	0–4	1
Landscape quality	hcv05	The average probability of HCV forest (0 – 100 %) in the surrounding landscape.	L	0.5 km	1–55	15,15
	hcv5			5 km	3,56–13,9	7,11
	hcv15			15 km	3,68–11,9	7,01
Size of surrounding medium-quality habitat area	area40	Size of medium-quality habitat area in which the WKH is located (ha).	L		0–4730,61	268,18
Size of surrounding high-quality habitat area	area70	Size of high-quality habitat area in which the WKH is located (ha).	L		0–227,45	15,41
North - South	north	Northern coordinates (SWEREF 99).	S		6907542–7102828	-
East - West	east	Eastern coordinates (SWEREF 99).	S		519866–697678	-

[a] While in analysis decay stages were used at wood item level, here we aggregated them on stand level (number of deadwood units per decay stage per stand and the average across all stands) for summarization purposes.
[b] The deadwood volume was strongly affected by a single site with volume of 198,69 m3 /ha. Without this site the mean deadwood volume was 38,96 m3 /ha.

Markwith, 2023; Runnel and Lõhmus, 2017), we considered these areas as a proxy for suitable habitat.

2.4. Statistics

All analyses were performed in R version 4.4.3 (R Core Team, 2024). We applied generalized linear mixed-effects models (GLMMs) to evaluate the relative contributions of variables at log, stand, and landscape scales to fungal species richness and occurrence (log level species occurrence). Two separate GLMMs were constructed, namely a) a logistic model for red-listed species incidence per log (binary response) and b) a COM-poisson model for total fungal species richness per log (count response). For species richness, we initially used Poisson error distribution, but quantile residual diagnostics (DHARMa package (Hartig, 2022)) revealed under dispersion, hence we applied COM-Poisson error distribution, which allows for flexible dispersion modelling (Sellers and Shmueli, 2010). To account for the nested sampling design and potential spatial autocorrelation, we included stand and transect number as random effects for species richness and stand as a random effect for red-listed species incidence. Transect could not be included as a random factor in the red-listed species model due to convergence issues. Models were fitted using maximum likelihood estimation with Laplace approximation (Brooks et al., 2017) in the R package glmmTMB (Brooks et al., 2017).

Part of the predictor variables exhibited high right-skewness and strong collinearity, while correlations between species richness and landscape variables were weak. To improve model fit, residual distributions, and linear relationships between predictors and responses, we log-transformed selected variables before model fitting (full list of transformed variables in Appendix C1). All continuous predictors, except for geographical coordinates, were standardized (z-scored) to ensure comparability and model convergence.

Due to the large number of highly correlated predictor variables, we implemented a three-step variable selection procedure to avoid redundant variables and model overfitting. First, we computed a correlation matrix and removed variables with pairwise correlation > 0.9 (Appendix A1). Second, we applied Elastic Net regularization (R package glmnet (Tay et al., 2023)) with 10-fold cross-validation to identify the most relevant predictors for each response variable, with the optimal penalty parameter (lambda) chosen by minimizing cross-validated error. Third, after fitting the initial GLMMs with variables selected through Elastic Net, we calculated variance inflation factors (VIFs) (R package performance (Lüdecke et al., 2021)) and removed any predictor with VIF > 4 to mitigate remaining multicollinearity issues.

Model fit was assessed through quantile residual simulations, Q-Q plots, and dispersion diagnostics (R package DHARMa (Hartig, 2022)). For logistic GLMM, we evaluated predictive power using the area under the receiver operating characteristic (ROC) curve (AUC) (R package pROC (Robin et al., 2011)), along with sensitivity, specificity, precision, and recall. The final logistic model exhibited high sensitivity (0.98) but low specificity (0.08), reflecting the rarity and cryptic nature of red-listed fungi (present in only 19 % of samples). To improve specificity, we tested class weighting (presence = 1.5), but this adjustment did not significantly improve AUC-ROC, sensitivity, specificity, precision, or recall and was therefore removed for model simplicity. Despite low specificity, the model's high sensitivity and precision indicate strong performance in detecting rare species occurrences, making it valuable for the analysis.

For interpretability, model coefficients were presented as incidence rate ratios (IRRs) for the COM-Poisson GLMM and odds ratios (ORs) for the logistic GLMM, indicating the expected relative change in species counts or red-listed species occurrence per unit increase in each predictor, while holding other predictors constant (Rita and Komonen, 2008). To aid interpretation, estimates were back-transformed from scaled and log-transformed values before being presented as IRRs and ORs.

To assess whether effects detected in the wood-item-level GLMMs remained significant at the stand level, we conducted permutation-based Spearman correlation tests (R package coin (Hothorn et al., 2008)) with 999 permutations for the predictor variables retained in the final model. To account for multiple testing, we applied Benjamini-Hochberg adjusted p-values, which reduced false positives while maintaining statistical power. This provided a robust, assumption-free check of stand-level associations given the limited sample size (n = 26 stands).

To explore patterns in species composition, we employed non-metric multidimensional scaling (NMDS) with Jaccard distance matrix (R package vegan (Oksane et al., 2022) to the species occurrence data. The ordination was performed with 999 iterations, and the number of dimensions was chosen with the stress value < 0.2. We removed species with less than two observations to ensure stability of the ordination. We then fitted the environmental variables onto the ordination to determine if any of the landscape variables were affecting the turnover in fungal communities. We used R package ggplot2 for visualizations (Wickham, 2016).

3. Results

In total, 1263 spruce logs were inventoried. Of these, 694 logs (55 %) hosted at least one polypore species, and 202 logs (19 %) had at least one red-listed species present. In total, 33 saproxylic polypore species were found, of which 12 were red-listed (Table 2 for red-listed species, appendix D1 for full list of species).

3.1. Species richness

The GLMM for total species richness (Table 3) revealed a strong relationship with substrate-level variables, namely, a strong positive

Table 3
GLMM for total species richness for wood item level and permutation tests for data aggregated on stand level for stand- and landscape scale variables. Asterisks for permutation tests indicate - ns: $p > 0.05$; *: $p < 0.05$; ***: $p < 0.001$.

Predictors	*Estimates*	*CI*	*p*	*Stand level perm. test*
(Intercept)	0.69	0.61 – 0.77	**< 0.001**	—
Deadwood log volume (m3)	1.84	1.71–1.97	**< 0.001**	—
Decay stage baseline: decay 1				—
Decay stage 2	1.40	1.24 – 1.58	**< 0.001**	—
Decay stage 3	1.07	0.91 – 1.27	0.410	—
Decay stage 4	0.64	0.47 – 0.89	**0.007**	—
Deadwood volume (m^3/ha)	0.99	0.89–1.09	0.772	+ ***
Age of dominant tree	0.99	0.89–1.09	0.836	ns
Share of medium-quality forest within 5 km	0.93	0.89–0.97	**0.002**	ns
Size of the high-quality connected forest area	1.17	1.01–1.35	**0.036**	ns
North gradient	1.00	1.00 – 1.00	0.609	ns
East gradient	1.00	1.00 – 1.00	0.189	ns
Random Effects				
Residual variance (σ^2)	0.76			
Variance explained by transects ($\tau_{00\ transect:site}$)	0.03			
Variance explained by site ($\tau_{00\ site}$)	0.02			
Intra-class correlation between individuals within groups (ICC)	0.05			
Number transects per site ($N_{transect}$)	3			
Number of sites (N_{site})	26			
Observations	1263			
Marginal R^2 / Conditional R^2	0.291 / 0.330			

Table 2
Red-listed species, abbreviations used, preferred substrate, status in the Swedish Red-list, and the number of observations (mean/SD and range per stand and the total number of observations).

Species (full name and abbreviation)	**Red-list status**	**Decay stage (dominant)**	**Preferred substrate**	**Mean observations per stand (+/- SD)**	**Range of observations per stand**	**Total observations**
Amylocystis lapponica (amylap)	VU	2	*Picea abies*	0.04 (±0.20)	0–1	1
Leptoporus mollis (lepmol)	NT	1	*P. abies, P. sylvestris*	0.12 (±0.33)	0–1	3
Neoantrodia infirma (neoinf)	EN	2	*Pinus sylvestris*, sometimes *P. abies*	0.04 (±0.20)	0–1	1
Osteina undosa (ostund)	VU	2	Prefers *P. abies*, but will use other substrates	0.04 (±0.20)	0–1	1
Phellinidium ferrugineofuscum (phefer)	NT	1–2	*P. abies*	3.04 (±2,93)	0–10	79
Phellopilus nigrolimitatus (phenig)	NT	2	*P. abies*, sometimes *P. sylvestris*	1.31 (±1,54)	0–6	34
Porodaedalea chrysoloma (porchr)	NT	2	*P. abies*	0.27 (±0,53)	0–2	7
Rhodofomes roseus (rhoros)	NT	1–3	*P. abies*, sometimes *P. sylvestris* and deciduous trees	3.54 (±4.69)	0–15	92
Skeletocutis kuehneri (skekue)	NT	1, 3	*P. abies* and *P. sylvestris*	0.08 (±0,27)	0–1	2
Skeletocutis odora (skeodo)	VU	1, 2	*P. abies*, sometimes *P. sylvestris* and *Populus tremula*	0.08 (±0,27)	0–1	2
Skeletocutis stellae (skeste)	VU	1	*P. abies*, sometimes *P. sylvestris*	0.04 (±0.20)	0–1	1
Steccherinum collabens (stecol)	VU	2–3	*P. abies*, sometimes *P. sylvestris*	0.38 (±0.85)	0–3	10

association with deadwood log volume ($p < 0.001$) and decay stage 2 ($p < 0.001$) and a negative association with decay stage 4 ($p < 0.001$). None of the stand level variables had a significant contribution to species richness. At the landscape scale, the model indicated a negative correlation between species richness and the share of medium-quality forests within 5 km (area40_5) and a positive correlation with the size of the high-quality forest area (area70) in which the WKH is located. The model explained 33 % of variation in total species richness. When aggregating the total species count on stand level and testing the stand- and landscape scale variables with permutation tests, only correlation between stand level deadwood volume remained significantly positively correlated with total species richness (Spearman $\rho = 0.60$, $p < 0.001$).

Focusing on the red-listed species model (Table 4), deadwood log volume again emerged as a key predictor ($p < 0.001$). Logs in intermediate decay stages (2 and 3) were significantly more likely to host red-listed species compared to fresh logs (stage 1) (both $p < 0.001$). At the broader spatial scale, a negative relationship ($p = 0.005$) was detected between red-listed species incidence and the share of medium-quality habitat within 5 km (share40_5), although the odds ratio was rather close to 1. By contrast, a strong positive relationship was found with the share of high-quality habitat within 15 km (share70_15). The GLMM model did not detect any effect of stand level variables. Permutation tests of the aggregated stand level red-listed species richness versus stand and landscape scale variables showed a different pattern with a highly positive correlation with stand level deadwood volume (Spearman $\rho = 0.56$, $p = 0.002$), and negative with east gradient (Spearman $\rho = -0.39$, $p = 0.040$).

Table 4
Red-listed species GLMM for wood item level and permutation tests for data aggregated on stand level for stand- and landscape scale variables. Asterisks for permutation tests indicate - ns: p > 0.05; *: p < 0.05; ***: p < 0.001.

Predictors	*Odds Ratios*	*CI*	*p*	*Stand level perm. test*
(Intercept)	0.07	0.05–0.10	**< 0.001**	—
Deadwood log volume (m3)	2.17	1.80–2.63	**< 0.001**	—
Decay stage baseline: decay 1				—
Decay stage 2	3.70	2.50 – 5.48	**< 0.001**	—
Decay stage 3	2.39	1.46 – 3.92	**0.001**	—
Decay stage 4	1.80	0.83 – 3.91	0.136	—
Deadwood volume (m3/ha)	1.03	0.78–1.37	0.086	+ ***
Age of dominant tree	1.00	0.81–1.23	0.925	ns
Stumps	0.94	0.74 – 1.19	0.587	ns
Share of medium-quality forests within 5 km	0.92	0.66–1.29	**0.003**	ns
Share of high-quality forests within 15 km	1.90	1.37–2.65	**< 0.001**	ns
Size of the high-quality connected forest area	0.92	0.74–1.15	0.298	ns
North gradient	1.03	0.79–1.35	0.847	ns
East gradient	1.03	0.74–1.15	0.807	- *
Random Effects				
Residual variance (σ^2)	3.29			
Variance explained by transect ($\tau_{00\ \mathrm{transect:site}}$)	0.16			
Variance explained by site ($\tau_{00\ \mathrm{site}}$)	0.00			
Intra-class correlation between individuals within groups (ICC)	0.05			
Number of site (N_{site})	26			
Observations	1263			
Marginal R^2 / Conditional R^2	0.228 / 0.245			

3.2. Species composition

The NMDS ordination space reflected several patterns in species composition, with environmental variables represented by vectors indicating the direction and strength of their correlation with species distribution (Fig. 2a, b). Both generalist and red-listed fungi varied gradually along Axis 1 (Fig. 2a, b), forming a strong gradient along eastward spatial gradient (east) and increasing share of high-quality forests at 15 km scale (share70_15). Few other of the substrate and landscape variables had significant correlations with the ordination space, primarily along Axis 2 and 3, suggesting an indirect role in shaping species distribution. Along Axis 2 (Fig. 2a), species distribution was most strongly associated with deadwood, both size of single logs (dw_log) and stand-level deadwood volume (dw_stand), as well as northward spatial gradient (north). Axis 3 was associated with landscape scale variables within 0.5 km radius of the stand, including share and quality of surrounding forests (share05, area70, share40_05 among others). Deadwood volume variables (dw_log and dw_stand) and share of high-quality forests within 15 km (share70_15) together with red-listed species were positioned in the negative half-space of Axis 3,

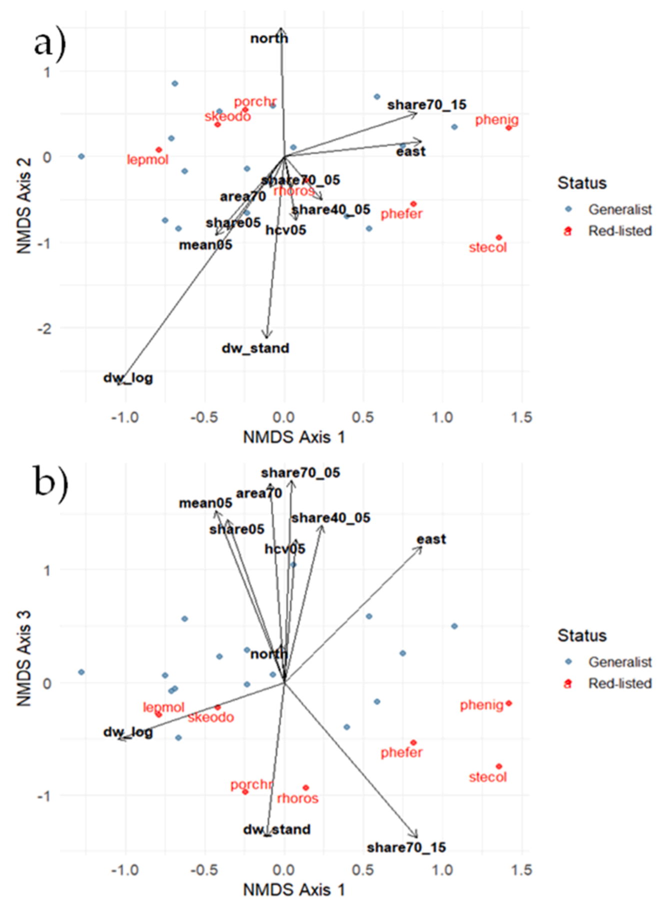

Fig. 2. NMDS plot for of species composition overlaid by environmental variables that significantly correlated with NMDS scores. Only significant variables were visualized. NMDS Stress = 0.046, k = 3. The main environmental gradients are: north – longitude, east – latitude, dw_log – deadwood log volume (m3), dw_stand – deadwood stand volume (m3/ha), mean05 – mean cover of spruce in landscape of 0.5 km from centre of site, share05 – share of spruce forests in landscape of 0.5 km from centre of site, share40_05 – share of medium quality forests in landscape of 0.5 km from centre of site, share70_05 – share of good quality forests in landscape of 0.5 km from centre of site, hcv_05 – quality of forests in landscape of 0.5 km from centre of site, share70_15 – share of good quality forests in landscape of 15 km from centre of site, area70 – size of the good quality forests connected with WKH. Red-listed species acronyms given in Table 2.

showing stronger connection of high-quality, substrate rich stands and red-listed species.

4. Discussion

4.1. Landscape structure

Our study revealed limited variation in landscape-scale variables across different spatial extents. Variables such as the average cover of spruce in all forests, share of spruce forests, and the proportion of medium- and high-quality spruce forests exhibited nearly identical mean values and ranges (Table 1) and were highly correlated across most landscape scales (Appendix A1). For instance, spruce cover at the 5 km scale was highly correlated ($r = 0.95$) with spruce cover at the 15 km. Similarly, landscape quality showed little variation between 5 km and 15 km scales. Notable differences were only observed between the immediate surroundings of the WKHs (0.5 km) and larger scales (>5 km), indicating a generally homogeneous forest landscape in the study region. While the overall share of spruce forest was high across different scales, the proportion of medium- and high-quality habitat was low (mean of 7 % and 1 % across scales, respectively), reflecting the large-scale loss of natural forests. Similar conclusions have been reached in other studies examining forest structure in managed landscapes (Angelstam et al., 2020; Bubnicki et al., 2024).

Our results indicate that landscape fragmentation has a significant influence on the abundance and occurrence of polypores, though not always in the expected ways. At the wood-item level, the GLMM for red-listed species (Table 4) revealed that an increasing share of high-quality forests within a 15 km radius positively affected the occurrence of polypores. This large-scale effect on red-listed and indicator species is in line with patterns also observed in similar studies (Nordén et al., 2013, 2018). Furthermore, WKHs connected to high-quality forest network had overall higher species richness (Table 3). These findings, in agreement with previous studies (Lunde et al., 2025a; Undin et al., 2024), emphasizes the importance of high-quality habitats that are well-connected, at both small and larger scales, and highlight the need for detailed landscape-level planning to support fungal biodiversity. Surprisingly, the share of medium-quality forests within a 5 km radius was negatively related to both total species richness and red-listed species incidence (Table 3 and Table 4), although with odds ratios close to one, indicating weak effects.

The long history of clear-cutting in boreal Sweden, has resulted in an even-aged, plantation-like landscape matrix, where even mature forest stands often lack structural heterogeneity (Asplund et al., 2024). Several studies (Penttilä et al., 2004; Runnel and Lõhmus, 2017) report that mature forests, considered of medium quality, have lower species richness than old-growth-like forests, such as WKHs. Unlike Nordén et al. (2018), we could not account for forest age in our landscape analysis, which may further contribute to discrepancies between our findings and those of other studies. Furthermore, our landscape assessment (Table 1) confirmed that overall habitat quality at all investigated scales was low, reflecting a high level of forestry impact and a predominance of younger forest stands resulting from rotation forestry.

4.2. Scale dependant processes in fungal diversity

In our study, patterns observed on wood item level GLMM did not match the permutation tests for data aggregated at stand level. Consistent with our second research question, the GLMMs showed that, while landscape scale processes were important, substratum-level variables were stronger predictors of species richness. A considerable proportion of the variation in fungal richness at substratum-level was explained by deadwood log volume and decay stage. Red-listed species differed only modestly from the total species pool at the substrate level, mostly in terms of resource utilisation (decay stages). Stand level variables, by contrast, did not significantly contribute to either overall or red-listed species richness in GLMMs. However, for data aggregated at stand level, permutation tests indicated deadwood volume at stand level as a significant factor for both total as well as red-listed species richness.

In addition to the landscape variables discussed above from GLMMs, the permutation tests on aggregated data also showed an eastward gradient in red-listed species richness. This pattern likely reflects historical land use, as intensive forestry in southern Boreal Sweden began in the Bothnian coastal region and gradually expanded inland. The modern forestry in Sweden started during early 1800's with minimal efforts in forest regeneration, which lead to a lack of standing wood volumes in the early 1900's (Östlund, 1993; Östlund et al., 1997). Hence, while our species richness analysis could not detect strong effects of current landscape structures, the results suggests that the landscape is now too fragmented to detect effects of the remnant high-quality forest patches, but with a potential effect of historical land use.

4.3. Species community patterns

NMDS ordination revealed two complimentary gradients in species composition. Axis 1 captured the main turnover: species that scored high on this axis were associated both with the eastern part of the study area and with sites embedded in landscapes that retain areas of high-quality forests within 15 km radius. In the raw data the two landscape attributes were moderately negatively correlated ($r = -0.44$), mirroring the historical pattern in which coastal (eastern) region was the first to be heavily logged. However, some of the eastern WKH still occur in landscape with old forests which apparently influence the community structure. Axis 3 separated these two predictors apart, with the east vector positively correlated with the axis and the high-quality forests within 15 km negatively correlated. Notably, the red-listed species were all confined to negative values on axis 3. This indicates that both generalist and red-listed species respond to landscape-scale gradients, potentially reflecting legacy effects of past management practices in addition to current stand and landscape conditions. This pattern is consistent with the concept of extinction debt, wherein slow-growing, cryptic organisms such as saproxylic polypores show delayed, yet pronounced responses to environmental change, so today's species composition still carries the imprint of historical logging rather than the present-day forest mosaic (Berglund and Jonsson, 2008; Komonen et al., 2021; Paltto et al., 2006; Penttilä et al., 2006). Accordingly, some red-listed fungi still occur in the coastal, historically intensively managed region, but their long-term viability there is uncertain.

Most of the additional variables that were significant on Axes 2 and 3 – notably deadwood availability at both log and stand scales, as well as the quantity and quality of habitat within 0.5 km – shaped finer-scale patterns of species distribution. While local habitat availability did not drive the main community gradient, its strong correlations with these secondary axes showed that microhabitat supply and short-range connectivity remain important for shaping polypore communities.

4.4. Woodland key habitats and saproxylic fungi conservation

WKHs are considered as an important conservation strategy tool in production forestry landscapes (Bjärstig et al., 2019). Yet, it remains a question if WKHs can provide suitable long-term conditions for all saproxylic fungi. Many WKHs are small in size (1–3 ha in our study, with a national median of 1.4 ha (Aune et al., 2005)) and are exposed to substantial edge effects which can alter microclimatic conditions up to 50 m into the forest patch (Ylisirniö et al., 2016). By definition, they should contain natural structures and red-listed species, but the amount of deadwood – the primary structure required by saproxylic fungi – varies significantly. The mean deadwood volume across WKHs in our study was 44.6 m^3 /ha, but excluding a single WKH that contained almost 200 m^3/ha of deadwood, resulted in a mean value of 38,4 m^3 /ha, with some stands containing as little as 12.8 m^3 /ha. This is higher than the average deadwood volume of 28,2 m^3/ha in protected forests in

Sweden (Sveriges lantbruksuniversitet, 2025) confirming that deadwood volumes in the study regions is generally high (Jönsson and Jonsson, 2007). However, a review by Timonen et al. (2011) estimated that the average deadwood volume in WKHs in Scandinavia is only around 19 m^3 /ha while in natural boreal forests the values vary between 28 – 170 m^3/ha (Aakala, 2010; Pastorelli et al., 2024; Sveriges lantbruksuniversitet, 2025).

Finally, Junninen and Komonen (2011) examined minimum thresholds for polypore conservation, suggesting a stand size of at least 20 ha and a deadwood volume of at least 20 m^3 /ha. Many WKHs do not meet these combined criteria. While WKHs in general contain more deadwood and thus support higher overall species richness than production forests (Häkkilä et al., 2021), they do not appear to sustain intact fungal communities according to our results and previous studies (Junninen and Kouki, 2006; Sippola et al., 2005; Ylisirniö et al., 2016). This raises concerns regarding the long-term conservation potential of saproxylic polypores in WKHs and suggests that additional conservation measures are necessary. Such measures include identifying and setting aside additional stands with natural values, enhancing landscape connectivity and increasing deadwood availability through active supplementation (Sandström et al., 2019).

4.5. Methodological considerations

The dominance of stand-level factors in our results should be interpreted with caution, as several methodological limitations may have reduced the potential to detect landscape effects. The studied WKHs were situated in similarly degraded and homogeneous landscapes, limiting variation in habitat quality and configuration across sites and thereby constraining the potential to identify broader-scale influences on fungal diversity. Additionally, the spatial scales used may not fully capture the ecological scales relevant to saproxylic polypores, which can respond at finer spatial scales due to limited dispersal (Edman et al., 2004b; Norros et al., 2015) and at broader scales through effective long-distance spore dispersal (Junninen and Komonen, 2011). Finally, our landscape metrics primarily reflected current forest conditions, without fully accounting for historical land use, despite indications that past habitat continuity and extinction debt continue to shape present-day species distributions. These limitations are likely to be common in many regions and highlight the challenge to explicitly consider historical landscape changes and a broader range of landscape conditions in understanding the multiscale drivers of saproxylic fungal diversity.

5. Conclusion

Despite these limitations, our study confirms the known relationship between substrate quality and abundance with occurrence of saproxylic polypores in individual stands. It further provides evidence that landscape factors offer additional insights into species distributions at the log-level. However, landscape effects were in general limited and partly contradictory (scale dependent), likely reflecting the homogeneity and degradation of the surrounding forest matrix. While these limitations constrained our ability to fully resolve landscape influences, our findings still indicate that habitat connectivity is important, although the spatial scales at which this connectivity should be prioritized remain uncertain. This highlights the complexity in identifying at which scale forest management should target to increase connectivity and establish functional green infrastructure. Our results suggest that the amount of high conservation value forest in the landscape is important and that preserving and connecting high-quality habitats can be beneficial, particularly in landscapes where such habitats are scarce. The role of landscape structure is multi-faceted and context-dependent, and although challenging, additional research is required to better understand its role.

While WKHs are a successful tool for nature conservation, the current homogeneity of forest landscapes with limited high-quality forests limits the conditions required for intact fungal communities. From this perspective, more extensive conservation measures are required, including identification and protection of remaining high-quality forests stands, establishment of buffer zones around known high-quality stands, supplementation of substrata, and creation of larger, connected habitat networks with stable microclimatic conditions.

CRediT authorship contribution statement

Anita Atrena: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Malin Undin:** Writing – review & editing, Investigation. **Mattias Edman:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Fredrik Carlsson:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Oskar Englund:** Writing – review & editing, Methodology, Investigation. **Bengt-Gunnar Jonsson:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Funding

This work was supported by Formas (2020–01225) and Skogssällskapet (2020–776-Steg 2 2019).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank SCA AB, Holmen Skog AB, and the County Administrative Board of Västernorrland for granting permission to conduct fieldwork. We are also grateful to Jon Andersson for assistance with GIS work during the pre-selection of woodland key habitats. Finally, we thank Formas and Skogssällskapet for funding this project.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123065.

Data availability

Data will be made available on request.

References

Aakala, T., 2010. Coarse woody debris in late-successional picea abies forests in Northern Europe: variability in quantities and models of decay class dynamics. For. Ecol. Manag 260, 770–779. https://doi.org/10.1016/j.foreco.2010.05.035.

Ahlkrona, E., Gilljam, C., Wennberg, S., 2017. Kartering av kontinuitetsskog i boreal region. Metria AB on commission from the Swedish Environmental Protection Agency. Stockholm, Sweden.

Ahlström, A., Canadell, J.G., Metcalfe, D.B., 2022. Widespread unquantified conversion of old boreal forests to plantations. Earths Future 10, e2022EF003221. https://doi.org/10.1029/2022EF003221.

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71, 355. https://doi.org/10.2307/3545823.

Angelstam, P., Kuuluvainen, T., 2004. Boreal forest disturbance regimes, successional dynamics and landscape structures: a european perspective. Ecol. Bull. 41, 117–136.

Angelstam, P., Manton, M., Green, M., Jonsson, B.-G., Mikusiński, G., Svensson, J., Maria Sabatini, F., 2020. Sweden does not meet agreed national and international forest biodiversity targets: a call for adaptive landscape planning. Landsc. Urban Plan 202, 103838. https://doi.org/10.1016/j.landurbplan.2020.103838.

Asplund, J., Nordén, J., Kjønaas, O.J., Madsen, R.L., Lunde, L.F., Birkemoe, T., Ronold, E. K., Norkute, M., Jansson, K.U., Karlsen, D.P., Sverdrup-Thygeson, A., Skrede, I., Methlie, I.-S.H., Maurice, S., Botten, U.G., Krok, R.J., Kauserud, H., Nybakken, L., 2024. Long term effects of forest management on forest structure and dead wood in mature boreal forests. For. Ecol. Manag 572, 122315. https://doi.org/10.1016/j.foreco.2024.122315.

Atrena, A., Banelytė, G.G., Læssøe, T., Riis-Hansen, R., Bruun, H.H., Rahbek, C., Heilmann-Clausen, J., 2020. Quality of substrate and forest structure determine macrofungal richness along a gradient of management intensity in beech forests. For. Ecol. Manag 478, 118512. https://doi.org/10.1016/j.foreco.2020.118512.

Aune, K., Jonsson, B.G., Moen, J., 2005. Isolation and edge effects among woodland key habitats in Sweden: is forest policy promoting fragmentation? Biol. Conserv 124, 89–95. https://doi.org/10.1016/j.biocon.2005.01.015.

Berglund, H., Jonsson, B.G., 2008. Assessing the extinction vulnerability of wood-inhabiting fungal species in fragmented Northern Swedish boreal forests. Biol. Conserv 141, 3029–3039. https://doi.org/10.1016/j.biocon.2008.09.007.

Bjärstig, T., Sandström, C., Sjögren, J., Soneson, J., Nordin, A., 2019. A struggling collaborative process – revisiting the woodland key habitat concept in Swedish forests. Scand. J. For. Res. 34, 699–708. https://doi.org/10.1080/02827581.2019.1674916.

Brooks, M., E., Kristensen, K., Benthem, K., J.. Van, Magnusson, A., Berg, C., W., Nielsen, A., Skaug, H., J, Mächler, M., Bolker, B., M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378. https://doi.org/10.32614/RJ-2017-066.

Bubnicki, J. W., Angelstam, P., Mikusiński, G., Svensson, J., Jonsson, B. G., 2024. The conservation value of forests can be predicted at the scale of 1 hectare. Commun. Earth Environ. 5, 196. https://doi.org/10.1038/s43247-024-01325-7.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253. https://doi.org/10.1126/sciadv.1400253.

Duncan, Ri, 1989. An evaluation of errors in tree age estimates based on increment cores in kahikatea (Dacrycarpus dacrydioides). N. Z. Nat. Sci. 16, 31–37.

Edman, M., Kruys, N., Jonsson, B.G., 2004b. Local dispersal sources strongly affect colonization patterns of wood-decaying fungi on spruce logs. Ecol. Appl. 14, 893–901. https://doi.org/10.1890/03-5103.

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B.G., Ericson, L., 2004a. Spore deposition of Wood-Decaying fungi: importance of landscape composition. Ecography 27, 103–111.

Englund, O., 2024. Delineating HCV forest areas using density analysis: it's not clear-cut. https://doi.org/10.31223/X5MM87.

Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindbladh, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämås, T., Brunet, J., Kalén, C., Kriström, B., Gemmel, P., Ranius, T., 2020. Keeping pace with forestry: multi-scale conservation in a changing production forest matrix. Ambio 49, 1050–1064. https://doi.org/10.1007/s13280-019-01248-0.

Fraver, S., Ringvall, A., Jonsson, B.G., 2007. Refining volume estimates of down woody debris. Can. J. For. Res. 37, 627–633. https://doi.org/10.1139/X06-269.

GRASS Development Team, 2024. Geographic Resources Analysis Support System (GRASS) Software.

Gu, W., Heikkilä, R., Hanski, I., 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landsc. Ecol. 17, 699–710. https://doi.org/10.1023/A:1022993317717.

Häkkilä, M., Johansson, A., Sandgren, T., Uusitalo, A., Mönkkönen, M., Puttonen, P., Savilaakso, S., 2021. Are small protected habitat patches within boreal production forests effective in conserving species richness, abundance and community composition? A systematic review. Environ. Evid. 10, 2. https://doi.org/10.1186/s13750-020-00216-6.

Hanski, I.., 2005. The shrinking world: Ecological consequences of habitat loss, Excellence in Ecology. International Ecology Institute, Oldendorf (Luhe).

Hanski, I., 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. AMBIO 40, 248–255. https://doi.org/10.1007/s13280-011-0147-3.

Hartig, F., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Heilmann-Clausen, J., Christensen, M., 2004. Does size matter? For. Ecol. Manag 201, 105–117. https://doi.org/10.1016/j.foreco.2004.07.010.

Hothorn, T., Hornik, K., Wiel, M.A. van de, Zeileis, A., 2008. Implementing a class of permutation tests: the coin package. J. Stat. Softw. 28, 1–23. https://doi.org/10.18637/jss.v028.i08.

Hottola, J., Siitonen, J., 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. Biodivers. Conserv 17, 2559–2577. https://doi.org/10.1007/s10531-008-9317-4.

IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Zenodo. https://doi.org/10.5281/ZENODO.3553579.

Jonsson, B.G., Angelstam, P., Bubnicki, J.W., Mikusiński, G., Svensson, J., Undin, M., 2024. Rapport 7136 – Naturvärdeskarta Skog: En sannolikhetsmodell för naturvärden på skogsmark (No. 7136). Naturvårdsverket, Stockholm.

Jönsson, M.T., Jonsson, B.G., 2007. Assessing coarse woody debris in Swedish woodland key habitats: implications for conservation and management. For. Ecol. Manag 242, 363–373. https://doi.org/10.1016/j.foreco.2007.01.054.

Jönsson, M.T., Fraver, S., Jonsson, B.G., 2009. Forest history and the development of old-growth characteristics in fragmented boreal forests. J. Veg. Sci. 20, 91–106. https://doi.org/10.1111/j.1654-1103.2009.05394.x.

Junninen, K., Komonen, A., 2011. Conservation ecology of boreal polypores: a review. Biol. Conserv 144, 11–20. https://doi.org/10.1016/j.biocon.2010.07.010.

Junninen, K., Kouki, J., 2006. Are woodland key habitats in Finland hotspots for polypores (Basidiomycota)? Scand. J. For. Res. 21, 32–40. https://doi.org/10.1080/02827580500530009.

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. Landsc. Ecol. 36, 989–1002. https://doi.org/10.1007/s10980-021-01205-x.

Komonen, A., Puumala, I., Varkonýi, G., Penttilä, R., 2021. Wood-decaying fungi in old-growth boreal forest fragments: extinctions and colonizations over 20 years. Silva Fenn. 55. https://doi.org/10.14214/sf.10491.

Kuuluvainen, T., Gauthier, S., 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. For. Ecosyst. 5, 26. https://doi.org/10.1186/s40663-018-0142-2.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an r package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6, 3139. https://doi.org/10.21105/joss.03139.

Lunde, L.F., Birkemoe, T., Sverdrup-Thygeson, A., Asplund, J., Halvorsen, R., Kjønaas, O. J., Nordén, J., Maurice, S., Skrede, I., Nybakken, L., Kauserud, H., 2025a. Towards repeated clear-cutting of boreal forests – a tipping point for biodiversity? Biol. Rev., brv.13180 https://doi.org/10.1111/brv.13180.

Nitare, J., Noren, M., 1992. Woodland key-habitats mapped in a new project of the Swedish national board of forestry. Sven. Bot. Tidskr. 86, 219–226.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J. Ecol. 101, 701–712. https://doi.org/10.1111/1365-2745.12085.

Nordén, J., Åström, J., Josefsson, T., Blumentrath, S., Ovaskainen, O., Sverdrup-Thygeson, A., Nordén, B., 2018. At which spatial and temporal scales can fungi indicate habitat connectivity? Ecol. Indic. 91, 138–148. https://doi.org/10.1016/j.ecolind.2018.03.062.

Norros, V., Karhu, E., Nordén, J., Vähätalo, A.V., Ovaskainen, O., 2015. Spore sensitivity to sunlight and freezing can restrict dispersal in wood-decay fungi. Ecol. Evol. 5, 3312–3326. https://doi.org/10.1002/ece3.1589.

Oksane, J., Kindt, R., Blachet, F., Simpson, G., O'Hara, R., Minchin, P., Legendre, P., , 2022. vegan: Community Ecology Package.

Östlund, L., 1993. Exploitation and structural changes in the north Swedish boreal forest 1800-1992 (Doctoral thesis). Swedish Agricultural University, Umeå.

Östlund, L., Zackrisson, O., Axelsson, A.-L., 1997. The history and transformation of a scandinavian boreal forest landscape since the 19th century. Can. J. For. Res. 27, 1198–1206. https://doi.org/10.1139/x97-070.

Paltto, H., Nordén, B., Götmark, F., Franc, N., 2006. At which spatial and temporal scales does landscape context affect local density of red data book and indicator species? Biol. Conserv 133, 442–454. https://doi.org/10.1016/j.biocon.2006.07.006.

Parajuli, R., Markwith, S.H., 2023. Quantity is foremost but quality matters: a global meta-analysis of correlations of dead wood volume and biodiversity in forest ecosystems. Biol. Conserv 283, 110100. https://doi.org/10.1016/j.biocon.2023.110100.

Pastorelli, R., Vitali, F., Paletto, A., De Meo, I., 2024. Deadwood diversity of boreal and Sub-boreal Old-growth forests in Southern Finland. SouthEast Eur. For. 15, 141–150. https://doi.org/10.15177/seefor.24-18.

Penttilä, R., Siitonen, J., Kuusinen, M., 2004. Polypore diversity in managed and old-growth boreal picea abies forests in Southern Finland. Biol. Conserv 117, 271–283. https://doi.org/10.1016/j.biocon.2003.12.007.

Penttilä, R., Lindgren, M., Miettinen, O., Rita, H., Hanski, I., 2006. Consequences of forest fragmentation for polyporous fungi at two spatial scales. Oikos 114, 225–240. https://doi.org/10.1111/j.2006.0030-1299.14349.x.

QGIS Association, n.d. QGIS.org, %%Y. QGIS Geographic Information System.

R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramiadantsoa, T., Hanski, I., Ovaskainen, O., 2018. Responses of generalist and specialist species to fragmented landscapes. Theor. Popul. Biol. 124, 31–40. https://doi.org/10.1016/j.tpb.2018.08.001.

Regent Instruments Inc, 2014. WinDendro.

Rita, H., Komonen, A., 2008. Odds ratio: an ecologically sound tool to compare proportions. Ann. Zool. Fenn. 45, 66–72. https://doi.org/10.5735/086.045.0106.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., Müller, M., 2011. pROC: an open-source package for r and S+ to analyze and compare ROC curves. BMC Bioinforma. 12, 77.

Runnel, K., Lõhmus, A., 2017. Deadwood-rich managed forests provide insights into the old-forest association of wood-inhabiting fungi. Fungal Ecol. 27, 155–167. https://doi.org/10.1016/j.funeco.2016.09.006.

Ruokolainen, A., Shorohova, E., Penttilä, R., Kotkova, V., Kushnevskaya, H., 2018. A continuum of dead wood with various habitat elements maintains the diversity of wood-inhabiting fungi in an old-growth boreal forest. Eur. J. For. Res. 137, 707–718. https://doi.org/10.1007/s10342-018-1135-y.

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Marques Duarte, I., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe's last primary forests? Divers. Distrib. 24, 1426–1439. https://doi.org/10.1111/ddi.12778.

Sandström, J., Bernes, C., Junninen, K., Lõhmus, A., Macdonald, E., Müller, J., Jonsson, B.G., 2019. Impacts of dead wood manipulation on the biodiversity of temperate and boreal forests. A systematic review. J. Appl. Ecol. 56, 1770–1781. https://doi.org/10.1111/1365-2664.13395.

Sellers, K.F., Shmueli, G., 2010. A flexible regression model for count data. Ann. Appl. Stat. 4 (2). https://doi.org/10.1214/09-AOAS306.
Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41. https://doi.org/10.2307/20113262.
Sippola, A.-L., Mönkkönen, M., Renvall, P., 2005. Polypore diversity in the herb-rich woodland key habitats of koli national park in eastern Finland. Biol. Conserv 126, 260–269. https://doi.org/10.1016/j.biocon.2005.06.002.
Skogens pärlor [WWW Document], n.d. URL ⟨https://www.skogsstyrelsen.se/e-tjanster-och-kartor/karttjanster/skogens-parlor/⟩ (accessed 6.2.25).
SLU Artdatabanken, 2020. Rödlistade arter i Sverige. SLU, Uppsala.
Stokland, J.N., Larsson, K.-H., 2011. Legacies from natural forest dynamics: different effects of forest management on wood-inhabiting fungi in pine and spruce forests. For. Ecol. Manag 261, 1707–1721. https://doi.org/10.1016/j.foreco.2011.01.003.
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. Conserv. Biol. 33, 152–163. https://doi.org/10.1111/cobi.13148.
Sveriges lantbruksuniversitet, 2025. Forest statistics 2025. Sveriges lantbruksuniversitet, Umeå.
Swedish E.P.A., 2019. Nationella Marktäckedata.
Swedish University of Agricultural Sciences, 2010. SLU Forest map: tree species composition.
Swedish University of Agricultural Sciences, 2020. Fältinstruktion, Riksinventering av Skog.
Tay, J.K., Narasimhan, B., Hastie, T., 2023. Elastic net regularization paths for all generalized linear models. J. Stat. Softw. 106, 1–31. https://doi.org/10.18637/jss.v106.i01.
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. Scand. J. For. Res. 25, 309–324. https://doi.org/10.1080/02827581.2010.497160.
Timonen, J., Gustafsson, L., Kotiaho, J.S., Mönkkönen, M., 2011. Hotspots in cold climate: conservation value of woodland key habitats in boreal forests. Biol. Conserv 144, 2061–2067. https://doi.org/10.1016/j.biocon.2011.02.016.
Undin, M., Atrena, A., Carlsson, F., Edman, M., Jonsson, B.G., Sandström, J., 2024. To what extent does surrounding landscape explain stand-level occurrence of conservation-relevant species in fragmented boreal and hemi-boreal forest? – A systematic review. Environ. Evid. 13, 19. https://doi.org/10.1186/s13750-024-00346-1.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
Ylisirniö, A.-L., Mönkkönen, M., Hallikainen, V., Ranta-Maunus, T., Kouki, J., 2016. Woodland key habitats in preserving polypore diversity in boreal forests: effects of patch size, stand structure and microclimate. For. Ecol. Manag 373, 138–148. https://doi.org/10.1016/j.foreco.2016.04.042.
Zibold, M., Bässler, C., Hauck, M., Scherer-Lorenzen, M., 2024. Fungi and deadwood diversity: a test of the area-heterogeneity trade-off hypothesis. J. Ecol. 112, 1701–1718. https://doi.org/10.1111/1365-2745.14352.