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RESEARCH ARTICLE

Red-listed species under threat: Unexpectedly high deadwood thresholds for their presence in managed boreal forests

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Abstract

1. Red-listed species form an important basis for conservation action, yet their specific habitat requirements often remain elusive due to their rarity and cryptic nature. We address this gap by testing whether commonly used indirect measures of forest biodiversity can also indicate the presence of red-listed species and yield informative threshold values.
2. We conducted a fieldwork campaign covering 120 plots along a gradient of structural availability and forest management intensity in Sweden. In these plots, we inventoried epixylic fungi and bryophytes, epixylic and epiphytic lichens, and tree-related attributes. Using logistic regression, we tested whether taxon-specific structural thresholds related to deadwood, broad-leaved trees, and large trees could be identified for the probability of presence of an increasing number of red-listed species.
3. We found that deadwood volume, which strongly correlated with deadwood diversity, indicated a significantly increased probability of presence of red-listed epixylic fungi and bryophytes. The threshold values, for a 50% probability of presence of one red-listed species ranged from 36 to 63 m^3/ha of total deadwood for fungi and 31 to 58 m^3/ha of lying deadwood for bryophytes. For lichens, we were unable to find significant predictors of their presence.
4. *Synthesis and applications*. We show that deadwood volume is a reliable, taxon-specific indicator of the presence of red-listed bryophytes and fungi but not lichens. By explicitly focusing on threatened species and deriving statistically defined thresholds from managed boreal forests, our study provides empirical benchmarks that go beyond commonly used biodiversity indicators. The threshold values identified here substantially exceed widely cited recommendations, demonstrating that deadwood requirements for red-listed species in contemporary managed landscapes are higher than previously assumed. This underscores the strong context dependence of structural thresholds and highlights a critical mismatch between current deadwood availability and the levels needed to sustain

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threatened epixylic species, reinforcing the importance of protecting deadwood-rich forests.

KEYWORDS
coarse woody debris, cryptogam conservation, ecological threshold, forest management, habitat–area relationship, logistic regression, sessile species, threatened species

1 | INTRODUCTION

Our largest forest biome, the boreal forest, covers roughly 30% of the global forest area (Brandt et al., 2013) and provides us with a wealth of wildlife, ecosystem services, and climate change mitigation potential (Bradshaw et al., 2009; Pan et al., 2011; Pohjanmies et al., 2017). The boreal forest has a long history of commercial exploitation that reaches into the present, with currently about two thirds of the area being managed (Gauthier et al., 2015). This management, while needed to meet the demand for wood, pulp, and paper products, has negative effects on the forest composition and its inhabitants (Esseen et al., 1997; Paillet et al., 2010; Siitonen, 2001; Wallenius et al., 2010) and has led to numerous species becoming red-listed. Across Fennoscandian boreal forests, nearly 2000 forest-dwelling species are currently nationally red-listed (Artsdatabanken, 2021; Hyvärinen et al., 2019; SLU Artdatabanken, 2020). Their red-list status is primarily attributed to industrial-scale forestry, which tends to create landscapes dominated by young forests with low availability of non-commercial wood and limited diversity in tree age and tree species (Jonsson et al., 2016; Määttänen et al., 2022; Östlund et al., 1997). Consequently, there is a notable scarcity of deadwood, large trees, and broad-leaved tree species (Halme et al., 2013; Kuuluvainen et al., 2012).

Conservation in managed boreal forests increasingly relies on structural indicators such as deadwood, large trees, and broadleaves to locate habitats that still support high degrees of biodiversity and threatened species (Gao et al., 2015; Hekkala et al., 2023; Lindenmayer & Laurance, 2017; Mikkonen et al., 2023; Zeller et al., 2023). Although indicators of biodiversity have been widely developed for whole species groups or single, non-threatened species, they remain poorly developed for red-listed species (Jonsson et al., 2016; c.f. Larsson Ekström et al., 2025). The scarcity of red-listed species demands extensive spatial datasets for reliable indicator identification—data that are frequently unavailable—while their often-cryptic nature hampers direct field surveys. These challenges highlight the need to find proxies that can, with reasonable confidence, predict the occurrence of red-listed species. With a targeted approach focusing explicitly on red-listed species and sufficient field data, it may yet be possible to define threshold values for commonly studied structural elements (described below) that indicate their presence. Such thresholds could then support cost-efficient biodiversity assessments and help guide conservation priorities in forest management.

With many deadwood-reliant species, deadwood amount and structural heterogeneity of deadwood items (which are often strongly correlated) are consistently important predictors of the species richness and abundance of several taxa (Gao et al., 2015; Hekkala et al., 2023; Zeller et al., 2023). To preserve forest biodiversity, it has subsequently been suggested that boreal forests at a minimum should contain 20–30 m^3/ha of deadwood (see Müller & Bütler, 2010). Even higher deadwood provision may then support additional species, but at a reduced rate, often following a curvilinear relationship (Hekkala et al., 2023; Martikainen et al., 2000). Deadwood provision at such peak values does not, however, seem to ensure the presence of all species in the wider landscape, particularly red-listed species, as many species have substantially higher deadwood requirements and are therefore often inextricably linked to old-growth forests (Bässler & Müller, 2010; Siitonen & Saaristo, 2000).

Diversity of tree species is also identified as an important driver of forest biodiversity (Cavard et al., 2011; Felton et al., 2010; Zeller et al., 2023). In the context of Fennoscandian boreal forest, this mainly means the increased admixture of broad-leaved species in conifer-dominated stands. Broad-leaved trees, both dead and living, harbour a variety of species, many of which are red-listed (Hyvärinen et al., 2019; SLU Artdatabanken, 2020), and even low shares of broadleaves may be important for biodiversity (e.g. Klein et al., 2021). While clear threshold values for broad-leaved trees have not been identified, various broadleaf-dependent species have been predicted to become extinct without intervention (e.g. Snäll et al., 2005). As the number of broad-leaved trees is considerably higher in old-growth forests compared with intensively managed forests, many species are considered dependent on the remaining old-growth forests (Kouki et al., 2004; Oldén et al., 2014) despite the number of broad-leaved trees therein rapidly declining (Hardenbol et al., 2020).

Finally, large trees appear crucial for biodiversity, both in general and specifically for certain species groups (Lindenmayer & Laurance, 2017). Larger diameter trees often present a higher quantity and diversity of tree-related microhabitats (Bütler et al., 2024; Kozák et al., 2023; Vuidot et al., 2011), which is in part related to larger trees typically being older, allowing time for colonisation of species requiring such microhabitats. As such, forests with a higher density of large trees can be expected to present higher overall species richness, particularly if these trees are also relatively old. Specifically for certain species groups, particularly lichens, species richness can increase considerably with increasing tree diameter (Nascimbene et al., 2009; Thor et al., 2010). Although the number of large trees in Fennoscandian boreal managed forests has been increasing in recent decades, following a prolonged decline, these trees are still considerably more abundant in old-growth forests (Henttonen et al., 2019; Jacobsson et al., 2025). Like for broad-leaved trees, clear threshold values for large trees have not been previously identified.

Despite forestry in boreal forests reducing the availability and diversity of the aforementioned structural elements, which in turn significantly drive biodiversity loss, we lack knowledge on the specific levels of structural complexity needed to support and sustain red-listed species. For deadwood, threshold values have been suggested (e.g. Hekkala et al., 2023; Müller & Bütler, 2010), but these are case-specific recommendations that do not sufficiently cover red-listed species (Jonsson et al., 2016). For the other structural elements mentioned, threshold values have not been established at all, except when included as parts of habitat diversity scores (Larsson Ekström et al., 2025). To accurately assess the requirements of red-listed species, species that are inherently rare, great effort is required to collect sufficient data. In this study, we focused on red-listed epixylic fungi, epixylic bryophytes, epixylic lichens, and epiphytic lichens, as these taxa play important ecological roles and serve as indicators of forest ecosystem integrity. Epixylic fungi are essential for nutrient cycling through decomposition, bryophytes contribute to nutrient cycling and to microclimatic buffering via moisture retention, while lichens provide primary production and nutrient inputs via nitrogen fixation (Cornelissen et al., 2007; Lustenhouwer et al., 2020). Most crucially, the sensitivity of these taxa to environmental change makes them valuable for assessing forest conservation status and management needs (e.g. Hofmeister et al., 2015). Through an intensive fieldwork campaign, we therefore aim to answer the following questions (conceptualised in Figure 1):

1. Do commonly studied structural elements (deadwood, broad-leaved trees, and large trees) indicate the presence of red-listed fungal, bryophyte, and lichen species across Swedish boreal forests?
2. What quantitative thresholds in these structural indicators are associated with the presence of different numbers of red-listed fungal, bryophyte, and lichen species? Specifically:
   a. At what indicator levels does the probability of presence reach 50%?
   b. Where are the transition points at which additional structural elements yield the largest increases in probability of presence?

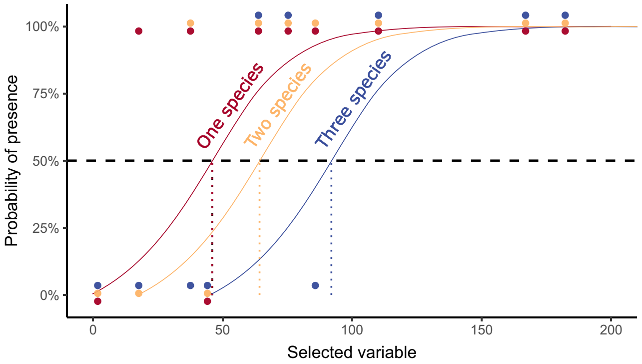

FIGURE 1 Conceptual figure showcasing the effect of an indicator variable on the probability that at least one or more species of a specific species group are present in a plot. The response variable is binary (0 = absence, 1 = presence) and the points denote plot-derived presences and absences at different values of the predictor (here in red for at least one species, orange for at least two species, and blue for at least three species). The horizontal dashed line shows the 50% threshold while the dotted vertical line depicts the predictor value at the 50% threshold mark.

2 | MATERIALS AND METHODS

2.1 | Study areas and plots

We conducted the study in two regions of Sweden: Hälsingland (east-central Sweden) and Värmland (south-western Sweden; Figure 2). We selected these regions, primarily in the southern and partly in the middle boreal zones (Sjörs, 1999), to achieve broad geographic coverage and variation in forest management history. These regions are characterised by distinct forest management histories: Hälsingland by less, and Värmland by more intensive historical forestry impact (Josefsson & Östlund, 2011; Lundmark et al., 2013; Östlund & Norstedt, 2021). Most forests in the two study areas are presently intensively managed for timber production (Roberge et al., 2024), with a small percentage of forests set aside for biodiversity as, for example, Natura 2000 sites or woodland key habitats (Nitare & Noren, 1992). In these forests, the dominant tree species are typically Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*). Silver birch (*Betula pendula*) and downy birch (*B. pubescens*) are rather common, while species such as European aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and grey alder (*Alnus incana*) have more scattered occurrences.

We set up 120 sampling plots in Sweden, equally split into three forest types with distinct levels of management intensity to cover a gradient in the availability of structural features. These forest types were high-intensity old clearcuts (harvested 25–30 years ago), medium-intensity retention patches (tree groups left unharvested within the old clearcut stands), and low-intensity set-asides (mature forests left unmanaged in recent decades). Half the plots of each forest type were placed in the region of Hälsingland and the other half in the region of Värmland. Notably, the set-aside plots were located in voluntarily protected woodland key habitats.

We selected the stands for plots based on four criteria: (1) for all three forest types, stands needed to be conifer-dominated (i.e. at least 70% of the trees belonged to a conifer species). Half of the stands were dominated by Norway spruce and the other half by Scots pine, (2) non-conifer tree species composition had to be similar across stands, (3) the stands had to be located on mesic to moist soil types, avoiding the wettest and driest forests, and (4) exceedingly steep slopes were avoided, in part to facilitate data collection. Permission to access these sampling plots was granted by Stora Enso AB.

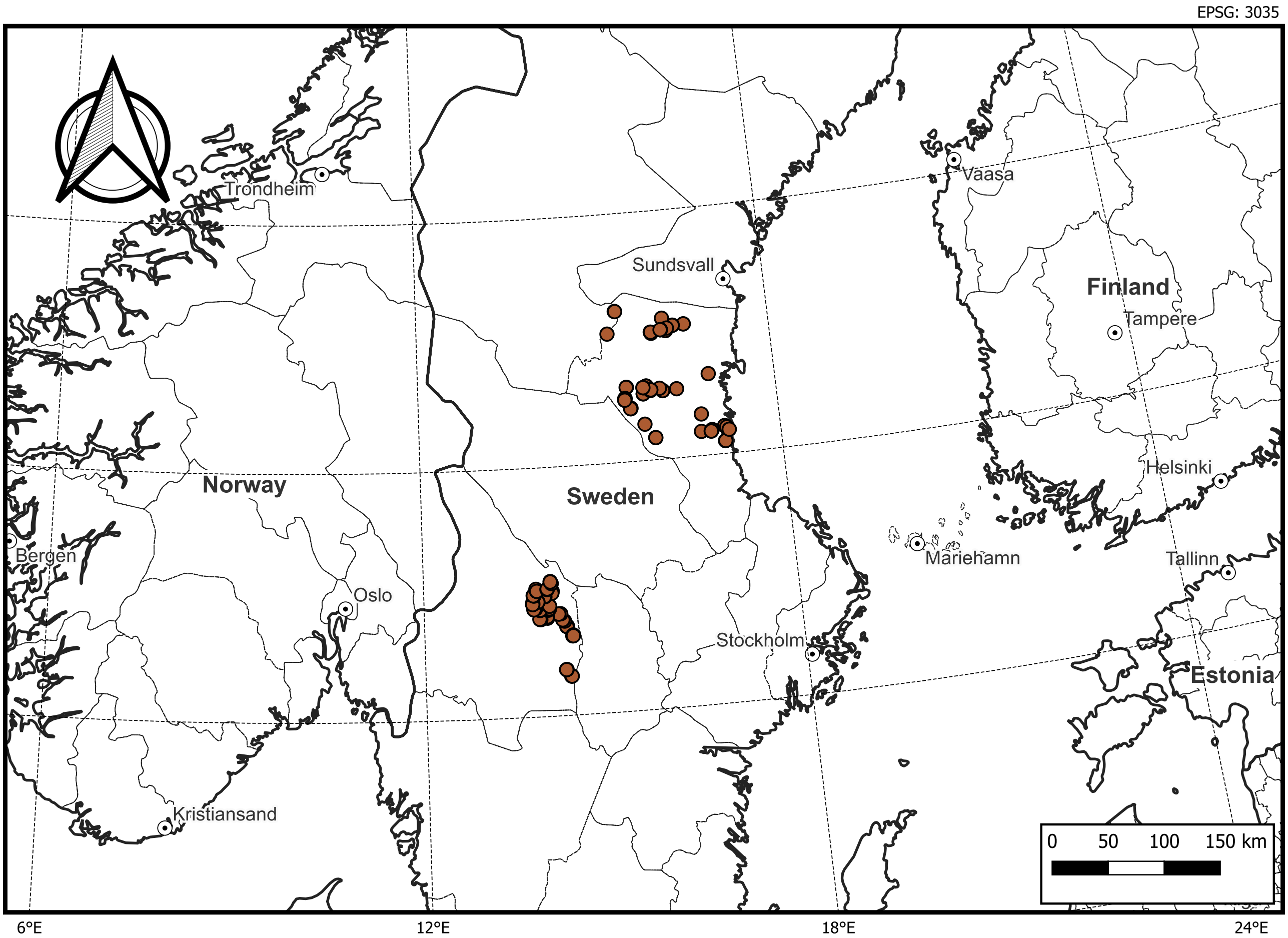

FIGURE 2 The locations of our 120 plots in Sweden (shown as brown circles). The northernmost plots are in the region of Hälsingland and the southernmost plots in the region of Värmland.

2.2 | Species surveys

Species surveys were conducted from 2021 to 2023 by expert consultants (see acknowledgements). Species were surveyed on dead (= epixylic) and living (= epiphytic) trees, covering four groups: epixylic fungi, epixylic bryophytes, epixylic lichens, and epiphytic lichens. For all species inventories, the typical plot was circular and had a 20 m radius (0.125 ha), but retention patches were sometimes smaller than this and were then inventoried in their entirety.

For epixylic fungi, all fruit bodies of polypores and a subset of corticioid fungi that are possible to identify in the field (Appendix S1 in Supporting Information) were inventoried. These fungi were surveyed on both standing and lying deadwood, with the base of the trunk within the plot. First, three lying trees with a base diameter of 5–14 cm and three dead standing trees with a diameter at breast height (dbh) of 5–14 cm per common tree species (Scots pine, Norway spruce, and birch [*Betula* spp.]) were surveyed, if available, starting from the plot centre outward, clockwise. Next, all standing deadwood with a dbh ≥15 cm and lying deadwood with a minimum length of 1.3 m and a base diameter ≥15 cm were surveyed. If fewer than three lying deadwood items with a base diameter ≥15 cm were found within the plot, the whole stand was searched for the remaining logs to survey. For standing trees, surfaces were surveyed up to 2 m in height.

For epixylic bryophytes, only lying deadwood was inventoried, with the base of the trunk within the plot. All lying deadwood items with a base diameter ≥15 cm were surveyed, along with five trees with a base diameter of 5–14 cm per common tree species, starting from the plot centre outward, clockwise.

Epixylic and epiphytic lichens were surveyed on standing dead and living trees, respectively, up to 2 m in height, including the trunk and branches. Lichen species were split into epixylic and epiphytic based on the condition (dead or living) of every tree on which a lichen sample was found. As such, the same lichen species could be classified as either epixylic or epiphytic on a tree-by-tree basis. For epixylic lichens, all standing dead trees ≥1.3 m in height were surveyed. For epiphytic lichens, living trees were subsampled. Three small (5–14 cm dbh) and seven large (dbh ≥15 cm) living trees of each common tree species were surveyed, starting from the plot centre outward, clockwise. If these numbers were not met, additional trees independent of size category were surveyed, always aiming for a total of 10 trees per common tree species.

2.3 | Tree inventories

Two different tree inventories took place during which dead and living trees were surveyed separately. The first inventory, for dead trees, was conducted in conjunction with the species inventories and followed the same plot parameters. The second inventory, for living trees, was conducted in circular plots with a radius of 7 m.

For dead trees, species, decay stage (see Siitonen et al., 2000), orientation (standing or lying), intactness (whole or broken), and size were recorded. Size measurements were taken differently depending on the orientation and intactness of a tree. For whole standing dead trees, only dbh was measured. For broken standing dead trees (≥1.3 m in height), dbh and stump height were measured. For whole lying dead trees, dbh as if the tree was standing was measured. For broken lying dead trees (≥1.3 m in length), their length and diameters either at the thinnest and thickest ends or at the centre point of the logs were measured. Note that for lying deadwood, only logs with a base diameter ≥10 cm were surveyed, requiring that their bases were located within the plot. For living trees, species and dbh for trees ≥1.3 m in height were recorded.

2.4 | Plot-level variables

From the species surveys, we extracted the number of unique nationally red-listed species (classified as Critically Endangered [CR], Endangered [EN], Vulnerable [VU], Near Threatened [NT], or Data Deficient [DD] as per the definition for red-listed species in Sweden) per species group per plot (SLU Artdatabanken, 2020).

From the tree inventories, we calculated several ecologically relevant plot-level variables relating to deadwood (volumes), broad-leaved trees (diversity index), and large trees (basal area and number of large trees), which we used as variables to predict the presence of species (Table 1). We calculated different variables for the four species groups based on the characteristics of the trees a particular species group was surveyed on. For example, because bryophytes were inventoried on lying deadwood, we specifically calculated the deadwood volume variable for lying dead trees. Descriptive statistics of all variables are shown in Appendix S2.

2.5 | Data analysis

We first assessed the possible correlation between total deadwood volume and deadwood diversity, considering that previous studies have found a strong correlation between these two variables (e.g. Müller & Bütler, 2010; Siitonen et al., 2000). Such a correlation provides justification for using only deadwood volume as a predictor. Deadwood diversity was calculated following Siitonen et al. (2000) based on the number of unique combinations of several categories. These categories were: tree species, decay stage (1 + 2, 3, and 4 + 5), diameter class (5–9, 10–19, …, 60–69 cm), and quality, which combines orientation with intactness (whole standing, broken standing, or lying tree). The deadwood diversity score for each plot was calculated by counting the number of detected distinct combinations of these categories. The correlation between total volume and diversity of deadwood was assessed through Spearman's rank-order correlation. We found a significant positive relationship between deadwood volume and deadwood diversity (rho = 0.87, $p < 0.001$; Appendix S4). This includes all deadwood, standing and lying, and led us to only use deadwood volume in subsequent analyses as the easier-to-measure variable.

We used logistic regression with the *glm*-function found in base R, version 4.2.1 (R Core Team, 2022), to investigate whether structural thresholds can be ascertained for the presence of an increasing number of red-listed species, separately for each of the four focal species groups, following the approach by Larsson Ekström et al. (2025). We tested plot-level variables from Table 1 to identify values exceeding a 50% probability of presence, an objective statistical threshold value. We first checked possible correlations between the explanatory variables with Pearson's correlation coefficient. For epiphytic lichens, there was a strong correlation (Pearson's $r \geq 0.7$; Schober et al., 2018) of the variable "living trees with a dbh ≥30 cm/ha" with "living trees with a dbh ≥40 cm/ha" (Pearson's $r = 0.79$) and "basal area of living

TABLE 1 The plot-level variables calculated for the four species groups we surveyed based on the conducted tree inventories.

Epixylic fungi	Epixylic bryophytes	Epixylic lichens	Epiphytic lichens
Total deadwood volume (m^3/ha)	Lying deadwood volume (m^3/ha)	Standing deadwood volume (m^3/ha)	Basal area of living trees (m^2/ha)
Basal area of living trees (m^2/ha)	Basal area of living trees (m^2/ha)	Basal area of living trees (m^2/ha)	Living tree diversity index
Living tree diversity index	Living tree diversity index	Living tree diversity index	Living trees with a dbh ≥30 cm (No./ha)
		Dead standing trees with a dbh ≥30 cm (No./ha)	Living trees with a dbh ≥40 cm (No./ha)
		Dead standing trees with a dbh ≥40 cm (No./ha)	

Note: The deadwood volumes were calculated from the obtained tree size measurements (see Appendix S3 for deadwood volume calculations). Basal area was calculated as the cross-sectional area at breast height ($\pi \times (\text{dbh}/2)^2$) summed per hectare. The diversity of tree species was estimated using the Shannon–Wiener index (Shannon, 1948).

trees/ha" (Pearson's r = 0.75). As such, we excluded the variable "living trees with a dbh ≥30 cm/ha".

We used Akaike's Information Criterion (AIC; Akaike, 1974) to select the best model for each species group and number of species, initially excluding interactions. Importantly, the number of species is not the exact number, but refers to at least that number (e.g. at least one species). We chose the model with the lowest AIC value or the simplest model within 2 AIC units of the lowest value (Anderson & Burnham, 2002). We then added interactions between the remaining variables and reused AIC to select the final model. We investigated the fit of each best model with McFadden's pseudo R^2 value from the *pscl* package (Jackman, 2024) and the area under the curve (AUC) value from the *pROC* package (Robin et al., 2011). We considered models with a McFadden's pseudo $R^2 > 0.2$ and an AUC value >0.7 to be of acceptable fit and appropriate for threshold calculations (Hosmer et al., 2013; McFadden, 1979). Next, we determined transition points at which the probability of presence increased most rapidly using the Youden index, selecting the point of maximum sensitivity and specificity (Fluss et al., 2005) with the *pROC* package (Robin et al., 2011). Note that the maximum number of species we considered for each species group was dependent on exceeding the 50% probability-of-presence threshold for at least one of the selected predictors, including the upper confidence interval. Possible outliers that affected the threshold values were removed and results with and without presented.

3 | RESULTS

We detected at least one red-listed species in 24 out of the 120 plots for epixylic fungi, that is in 20% of the plots. The corresponding numbers were 13% for epixylic bryophytes, 18% for epixylic lichens, and 41% for epiphytic lichens. We found at least two red-listed species in 7% of the plots for epixylic fungi, 7% for epixylic bryophytes, 7% for epixylic lichens, and 22% for epiphytic lichens. Detailed information on the number of species in the different red-list categories and on the number of plots in which we found an increasing number of red-listed species, both split by species group, can be found in Appendices S5 and S6, respectively.

For epixylic fungi, the presence of at least one red-listed species was best predicted by total deadwood volume, showing a positive and strong association ($p < 0.001$; Table 2, Figure 3a). For every 1 m^3/ha increase in deadwood volume, the log odds of probability of presence increased by 0.066 (SE = 0.014). Deadwood volume reached the 50% threshold at 46 m^3/ha (95% CI: 36–63 m^3/ha). We were unable to establish thresholds for the presence of more than one fungal species based on our analyses. For epixylic bryophytes, the presence of at least one red-listed species was best predicted by lying deadwood volume, showing a positive and strong association ($p < 0.001$; Table 2, Figure 3b). For every 1 m^3/ha increase in lying deadwood volume, the log odds of probability of presence increased by 0.085 (SE = 0.019). Deadwood volume reached the 50% threshold

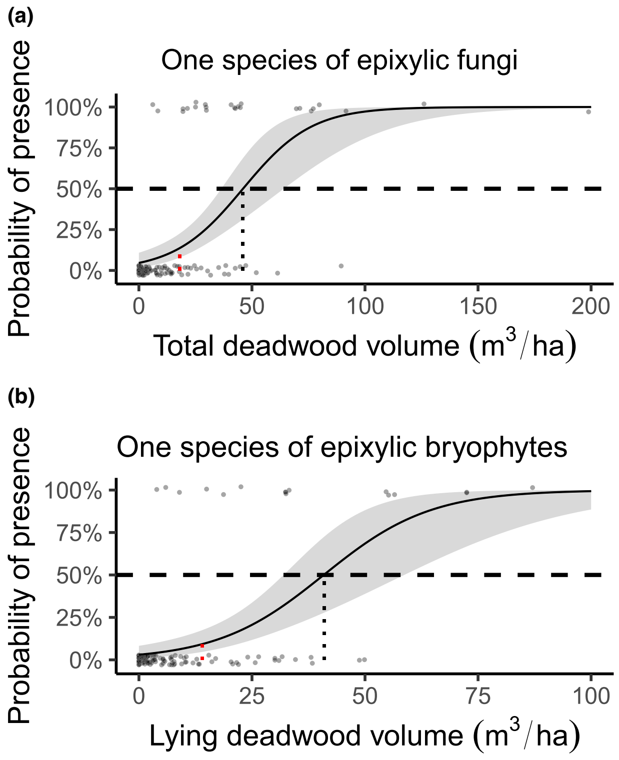

FIGURE 3 Regression curves for red-listed (a) epixylic fungi and (b) epixylic bryophytes showing the relationships between the probability of presence and the selected predictors in the best models for at least one red-listed species. The response variable is binary (0 = absence, 1 = presence) and the points denote plot-derived presences and absences at different values of the predictors (jittered for visualisation). The horizontal dashed lines show the 50% threshold while the dotted vertical lines depict the predictor values at the transition points (red) and the 50% threshold marks (black).

TABLE 2 The best models after model selection for the different species groups and numbers of red-listed species within the groups with AUC, McFadden's pseudo R^2, and threshold values (at 50% probability of presence), as well as the transition point (highest Youden index value).

Taxon	Number of species	Predictor	AUC value	McFadden's pseudo R^2 value	Threshold value (CI)	Transition point (m^3/ha)
Epixylic fungi	≥1	Total deadwood volume/ha	0.90	0.33	46 m^3/ha (36–63)	18
Epixylic bryophytes	≥1	Lying deadwood volume/ha	0.89	0.34	41 m^3/ha (31–58)	14

Abbreviations: AIC, Akaike's information criterion; AUC, area under the curve; CI, confidence interval.

at 41 m^3/ha (95% CI: 31–58 m^3/ha). Note that we here removed an outlier plot with a lying deadwood volume of 187 m^3/ha. Inclusion of this outlier increased the threshold value to 62 m^3/ha (95% CI: 43–122 m^3/ha) of lying deadwood for the presence of at least one red-listed species. Like for fungi, we were unable to establish thresholds for the presence of more than one bryophyte species. We found no predictors for either epixylic or epiphytic lichens with which the 50% probability-of-presence threshold was exceeded, even for at least one red-listed species.

4 | DISCUSSION

In this study, we aimed to find suitable indicators of the presence of red-listed species from sessile taxa in Fennoscandian boreal forests. Our studied taxa are all sensitive to changes in forest conditions, but their responses to human activities in boreal forests vary (Kärvemo et al., 2021; Nirhamo et al., 2025). We found that deadwood volume was a strong indicator of the presence of red-listed epixylic fungi and bryophytes in Fennoscandian boreal forests, with clear threshold values emerging for both groups. Specifically, the 50% probability of encountering at least one red-listed species was at total deadwood volumes of 46 m^3/ha (95% CI: 36–63) for fungi and at lying deadwood volumes of 41 m^3/ha (95% CI: 31–58) for bryophytes. In contrast, we found no clear structural indicators for red-listed epiphytic or epixylic lichens. These results suggest that while deadwood volume can serve as a reliable indicator of conservation value for some sessile taxa, it is not universally applicable across groups. The absence of clear predictors for lichens likely reflects their broader ecological variability and complex microhabitat requirements (Caruso & Rudolphi, 2009). Given that our data were collected across a representative gradient of forest conditions in the managed Fennoscandian boreal landscape, these findings are likely widely applicable and can support evidence-based conservation planning focused on deadwood retention and restoration. Importantly, our approach differs from many earlier studies by explicitly modelling the probability of encountering red-listed species rather than overall species richness or general deadwood-associated taxa. By linking structural habitat variables directly to conservation-priority species, we provide empirically derived, conservation-relevant threshold estimates. Although our analyses are situated within a Fennoscandian boreal context, the general modelling framework is also readily transferable to other forest regions and taxonomic groups.

For two of the three deadwood-associated species groups in this study, our findings indicate that locally deadwood-rich forests greatly improve the likelihood of red-listed species presence. This finding supports previous studies and reviews, underlining the importance of deadwood for maintaining high species diversity in forested ecosystems (Hekkala et al., 2023; Junninen & Komonen, 2011; Müller & Bütler, 2010), although additional structural variables were considered during model selection. We pose three likely reasons for deadwood amount being a reliable indicator in our study area:

1) **Habitat-amount hypothesis** – Higher deadwood volumes, regardless of configuration, increase total habitat availability and deadwood surface area (Bässler et al., 2010), which can directly raise the likelihood of deadwood-dependent species presence at a specific site.
2) **Deadwood amount correlates with deadwood diversity** – Higher deadwood volumes are often associated with greater deadwood diversity, including variation in decay stages and tree species (Müller & Bütler, 2010; Siitonen et al., 2000), a pattern also observed in the present study (Appendix S4). This higher diversity increases the number of niches, which is generally assumed to support more species (Abrego & Salcedo, 2013; cf. Zibold et al., 2024), while also enabling the presence of red-listed species that are often restricted to specific decay stages, host trees, or microclimatic conditions (Nordén et al., 2013; Tikkanen et al., 2006) and may therefore be absent from sites with low deadwood availability.
3) **Deadwood volume as a proxy for habitat continuity** – High deadwood volumes may reflect long-term forest continuity (Kunttu et al., 2015). This continuity benefits species with slow colonisation and limited dispersal capabilities. However, we find no support for this explanation considering the lack of a detectable effect of deadwood volume on lichen presence—lichens, particularly red-listed ones, being strongly tied to forests with long-term continuity (e.g. Hofmeister et al., 2024).

The lack of a discernible influence of local deadwood and other studied variables on lichens may reflect the overriding importance of broader-scale or longer-term ecological processes. For instance, landscape composition—such as the amount and spatial configuration of suitable forest habitat (e.g. with long-term habitat continuity; Hofmeister et al., 2024) in the surrounding area—may play a greater role than local ecological characteristics in shaping lichen distributions (Hämäläinen et al., 2023), at least when the forest locally has been intensively managed (Gustafsson et al., 2025). This pattern may be driven by dispersal limitations common among many lichen species (Johansson et al., 2012), which depend on remnant patches of suitable habitat to act as dispersal sources (Gustafsson et al., 2025). Additionally, lichen communities can exhibit delayed responses to environmental change, meaning that historical habitat conditions may better explain present-day occurrences than current local conditions (Hämäläinen & Fahrig, 2024; Johansson et al., 2013).

Threshold values for deadwood amounts to support higher degrees of "biodiversity" (e.g. species richness) in Fennoscandian boreal forests have previously been reported around 20 m^3/ha (range 10–70 m^3/ha; e.g. Hekkala et al., 2023; Hottola et al., 2009; Junninen & Komonen, 2011; Müller & Bütler, 2010). Our study suggests higher threshold values for total deadwood, i.e. 46 m^3/ha for red-listed fungi. Several factors likely explain our higher threshold values: Some earlier studies used non-random sampling focused on sites with known species presence (e.g. Siitonen & Saaristo, 2000); many were conducted in more intact landscapes with greater forest connectivity (e.g. Ylisirniö et al., 2012); and most used larger plot sizes, which will increase species detection probabilities (e.g. Penttilä et al., 2004). Additionally, differences in the taxa studied and the frequent inclusion of generalist or non-red-listed species likely lowered thresholds in previous works (e.g. Martikainen et al., 2000; Økland et al., 1996). Moreover, many studies suggesting thresholds do not specifically test for such, that is, lacking robust statistical approaches to identify suggested thresholds (Müller & Bütler, 2010; Spake et al., 2022). With these arguments in mind, we compare our findings to studies that have previously outlined thresholds for relevant taxa in boreal forests (Appendix S7). Our findings contrast reviews (Junninen & Komonen, 2011; Müller & Bütler, 2010) and individual studies (e.g. Penttilä et al., 2004; Ylisirniö et al., 2012; Ylisirniö et al., 2016) that have conjectured deadwood threshold values of, as mentioned above, around 20 m^3/ha in boreal forests. Most of the studies mentioned in Appendix S7 present results from more pristine landscapes and stands than in the present study. The differences in threshold values between this study and previous research underscore their context dependence—shaped by spatial, temporal, and organisational factors (Spake et al., 2022), including disturbance history and landscape configuration—and caution against extrapolating them to other settings (van der Hoek et al., 2015). Nevertheless, the works by Junninen and Komonen (2011) and Müller and Bütler (2010) have still been used to broadly guide policy for forest conservation, restoration, and management (Framstad & Sverdrup-Thygeson, 2017; Nabuurs et al., 2024). Our data represent a more typical contemporary Fennoscandian boreal forest landscape that is managed with intensive silvicultural practices including soil scarification, planting, pre-commercial and commercial thinning and rotation times around 80 years. Our findings are thus more relevant for informing policy in these less pristine landscapes, where connectivity is likely much lower, and many deadwood-dependent species have probably already disappeared from most locations. In this context, beyond confirming the general importance of deadwood, our results refine deadwood threshold values for red-listed species, with direct implications for existing conservation targets in managed boreal forests.

Most forests in the wider landscape contain far less deadwood than the threshold values we identified, resulting in a lower probability of finding red-listed species. Derived from recent national forest inventory (NFI) data, productive managed forests in Sweden contain an average of 7.8 m^3/ha of deadwood, while the corresponding number for protected forests is 19.4 m^3/ha (NFI 2013–2017; Kyaschenko et al., 2022). At these levels, our discovered probabilities for finding at least one red-listed species of epixylic fungi and bryophytes lie between 5% and 15%. In contrast, natural and near-natural old-growth forests can contain deadwood amounts upwards of even 100 m^3/ha (Jonsson et al., 2016; Siitonen, 2001). Hence, if a causal relationship is assumed, the average volume of deadwood required to sustain red-listed species must be substantially higher than the levels currently found in Fennoscandian forests. The transition points in this study, which show the values at which we can find the steepest increase in probabilities of presence in relation to increasing amounts of deadwood, may serve as a possible target for restoration. However, due to the rather smooth regression curves and the lack of “critical” threshold values (i.e. values that drastically alter the likelihood of finding at least one red-listed species), restoration efforts may not be successful. Based on the high threshold values for deadwood-associated species reported here, a conservation strategy that focuses more on land sparing than land sharing might be preferable rather than vice versa. This inference is in accordance with earlier studies underlining the importance of preserving deadwood-rich sites (Müller & Bütler, 2010; Penttilä et al., 2004). Despite the EU's Nature Restoration Law having recently entered into force (European Commission, 2024), restoration should thus be exercised without overly high expectations, as restoration efforts do not guarantee the return of a species, especially in a depauperate landscape with a long-interrupted habitat continuity (Crouzeilles et al., 2016).

Red-listing assessments for many sessile forest species, including lichens, bryophytes, and fungi, are frequently based on inferred population trends from the decline or degradation of their habitats, rather than direct monitoring data, at least nationally (SLU Artdatabanken, 2020). While this approach is necessary due to data limitations resulting from the rarity and cryptic nature of such species (Hending, 2025), it introduces uncertainty regarding the actual conservation status of individual species, particularly when their microhabitat requirements or ecological plasticity are poorly understood. In this context, our results offer valuable empirical support for using threshold-level deadwood volume as a habitat-based proxy for predicting the occurrence of red-listed bryophytes and fungi. At the same time, our finding that no structural elements predicted the presence of red-listed lichens highlights the limitations of relying on coarse habitat proxies for certain taxa and underscores the need for finer scale ecological data to more accurately infer population trends and conservation status. The latter is also accentuated by the fact that our findings for fungi and bryophytes were limited to only one red-listed species per group, primarily those classified as NT or VU, with more threatened species being too rare to support robust threshold estimation (Appendix S4). Not finding thresholds for more than one red-listed species may be attributed to, for example, the general rarity of these species, limited co-occurrence within plots, and high variability in species-specific habitat requirements. This is also shown by our species surveys wherein, among the fungi, all but one species (*Phellinidium ferrugineofuscum*; 15 plot presences) occurred 1–4 times and, among the bryophytes, all but *Crossocalyx hellerianus* (13 plot presences) occurred 1–6 times (Appendix S5). Alternatively, this pattern may reflect severe deterioration of forest quality in intensively managed landscapes, as indicated by the substantially lower deadwood volumes in our plots compared with (near-)natural old-growth forests (Siitonen, 2001). Despite our inability to detect thresholds for more than one species, modelling the probability of encountering at least one red-listed species provides an estimate of whether ecological conditions meet the minimum requirements necessary to support taxa of recognised conservation concern. This approach does not aim to capture the full conservation value of a stand, nor the presence of the most habitat-demanding species, but rather to quantify the likelihood that conservation-priority taxa are present at all. Although red-listed species differ in specialisation and sensitivity, their presence reflects documented vulnerability at the national scale and therefore constitutes a meaningful applied conservation signal. Moreover, the presence of at least one red-listed species has been shown to correlate with higher within-taxon species richness (Larsson Ekström et al., 2025). Thus, for bryophytes and fungi, the higher probability of red-listed species presence with increasing deadwood amounts likely coincides with higher overall richness within each taxon.

To conclude, we found that structural elements, here specifically deadwood, may function well as indicators of the presence of red-listed species for some taxa but not all, underscoring the importance of taxon-specific evaluation when designing conservation indicators. Deadwood amount has previously been found to be a valuable single-variable indicator, and our results further strengthen this notion, even more so because we attempted to include other indicators, which turned out to be less informative. The associated threshold values we found for deadwood, however, are higher than previously reported, which highlights the importance of maintaining existing deadwood and establishing permanently set-aside forests. Our results also emphasise the context-dependent nature of threshold dynamics. Consequently, one of our key findings is that, to conserve epixylic species, higher deadwood volumes may be needed than previously suggested by studies conducted in uncommon pristine landscapes. To improve the usefulness of the type of thresholds we derived, we encourage future investigations to target habitat requirements at different spatial scales including the incorporation of environmental gradients and historical forest-use variables that were not available for the present analyses. Furthermore, exploring species-specific requirements, including those of other taxa, should be attempted, although the low frequency of most red-listed species and the limited overlap in their occurrences across plots make such species-specific modelling statistically unfeasible in typical empirical datasets. Pooling red-listed species therefore represents a pragmatic compromise that allows conservation-relevant inference while acknowledging that responses may vary among species. Despite the urgency, we suggest caution when it comes to using our results for setting restoration targets. Instead, our discovered high deadwood requirements accentuate the need for formal protection of forests that at present already contain high densities of ecologically valuable substrates like deadwood.

AUTHOR CONTRIBUTIONS

Alwin A. Hardenbol: conceptualisation, data curation, formal analysis, investigation, methodology, visualisation, writing—original draft. Faith A. M. Jones: conceptualisation, data curation, investigation, writing—review and editing. Jörgen Sjögren: conceptualisation, funding acquisition, project administration, writing—review and editing. Albin Larsson Ekström: conceptualisation, data curation, investigation, writing—review and editing. Anne-Maarit Hekkala: conceptualisation, funding acquisition, writing—review and editing. Mari Jönsson: conceptualisation, funding acquisition, writing—review and editing. Matti Koivula: conceptualisation, funding acquisition, writing—review and editing. Joachim Strengbom: conceptualisation, funding acquisition, project administration, supervision, writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

None of the authors have any conflicts of interest to report.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.ncjsxktb7 (Hardenbol et al., 2026).

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SUPPORTING INFORMATION

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

Appendix S1. Corticioid species that serve as old-growth forest indicators or that are of special conservation interest in boreal forests that were surveyed as part of the fungi surveys.

Appendix S2. Descriptive statistics of the calculated plot-level variables included in this study.

Appendix S3. Methodological details for calculating the volumes of dead trees.

Table S3.1. Equations used to estimate standing and lying whole dead tree heights.

Table S3.2. Equations used to estimate standing and lying whole dead tree volumes.

Appendix S4. Scatter plot showing the relationship between deadwood volume and deadwood diversity. The solid line shows a linear regression. Spearman's rank-order correlation coefficient is given. Deadwood diversity was calculated following the method suggested by Siitonen et al. (2000).

Appendix S5. The red-listed species we found, split by species group, with their Swedish national red-list status and the number of times they occurred in unique plots.

Appendix S6. The number of plots in which we found an increasing number of red-listed species split by species group.

Appendix S7. A list of original articles from Fennoscandian boreal forests that have found deadwood amount thresholds for the same red-listed species groups as we studied with comparisons to our study in chronological order.

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