








## Habitat diversity as a taxon-dependent tool for predicting red-listed forest species

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### ABSTRACT

Habitat features associated with species niches are commonly used as biodiversity proxies. Such proxies usually describe habitat diversity and have seldom been evaluated in a forestry context. As demands on forests to mitigate climate change and biodiversity loss increase, Conservation Value Assessments (CVAs) based on habitat diversity are increasingly utilised to guide conservation and resource extraction decisions. In central Sweden, we investigated the effectiveness of two widely used CVA protocols that assess forest habitat diversity to determine their ability to predict the occurrence of red-listed species for conservation prioritisation. We found that the tested CVAs effectively predicted the occurrence of red-listed wood-inhabiting bryophytes and fungi but were less effective for epiphytic and epixylic lichens or for predicting the occurrence of red-listed species across these three taxo-ecological groups. For red-listed bryophytes and fungi, we were able to identify ecological transition points where the probability of species occurrence had its most rapid increase. In addition, we identified threshold values above which the probability of finding one red-listed species was higher than not finding any red-listed species. These findings define conservation priority zones, which can guide prioritisation and restoration targets. Moreover, our study clearly shows that sites occupied by red-listed species had higher local species richness of non red-listed species in the same organism group. In conclusion, CVAs based on habitat diversity are valuable for identifying and prioritising areas for conservation of certain taxo-ecological groups, broader biodiversity assessments require complementary approaches to encompass the full taxo-ecological diversity in forests.

### 1. Introduction

The majority of terrestrial biodiversity on Earth is found in forest ecosystems. Anthropogenic pressure has over time greatly impoverished these ecosystems through habitat destruction, fragmentation and degradation, posing a significant threat to forest biodiversity (Pimm et al., 2014; Watson et al., 2018). Today forests face mounting societal demands to simultaneously support both socioeconomic development and maintain ecological integrity, often leading to tensions between production and conservation goals (Högbom et al., 2021; Svensson et al., 2020). To balance these competing demands on forests, and to halt

biodiversity loss, robust assessments are needed to identify which forests should be prioritised for biodiversity conservation.

The theoretical foundation for setting conservation goals is closely linked to the concept of ecological thresholds. Environmental drivers can exceed critical thresholds, triggering abrupt shifts in ecosystem structure and function (Graham et al., 2015; Hughes et al., 2013). In forest ecosystems, for example, species richness or the likelihood of occurrence for a certain species may increase once habitat heterogeneity surpasses a critical threshold, whereas low heterogeneity often supports fewer species (Hekkala et al., 2023; Müller and Bütler, 2010). These dynamics reflect ecological discontinuities, meaning that there are

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non-linear transitions between ecosystem states, rather than simple, linear species-habitat relationships (Ben-Hur and Kadmon, 2020; Holling, 1973). Specific resources, such as particular deadwood types, can shape community composition by enabling the persistence of highly specialised species that depend on them. However, further increase in an already existing resource may have diminishing effects, showing a saturation pattern with limited additional influence on community structure. Studying ecological discontinuities is valuable not only for identifying thresholds that signal risks of undesired shifts or collapses, but also for recognizing transitions towards positive shifts, insights that are instrumental for guiding conservation strategies (Angeler et al., 2016).

To maintain biodiversity both at the regional and local scale, practitioners around the world use a wide array of indicators or proxies to identify forests of high biodiversity, something we in this study refer to as Conservation Value Assessments (CVAs). CVAs assume that an increasing amount and diversity of resources and niches within a habitat lead to an increase in the number of species (Stein et al., 2014). Although the basic assumptions of CVAs derive from species-habitat relationships in intact habitats (Fahrig, 2013; Stein et al., 2014), they are still implemented in settings of altered habitat (such as forest managed for timber and pulp production). In Europe, proxies of forest habitat diversity, including both habitat amount and variation are widely used to measure biodiversity despite lacking scientific evaluation (Gao et al., 2015). As one example, the Index of Biodiversity Potential (IBP), a widely used CVA in Europe developed to identify forests of high conservation value by combining stand structures of known importance to biodiversity, can act as a proxy for biodiversity potential, but may require complementary species-based inventories for more detailed inference (Zeller et al., 2022). In one study, a commonly used CVA designed to capture habitat diversity and richness effectively predicted species richness and the abundance of sessile species of conservation concern in boreal forests (Hekkala et al., 2023). However, the same CVA failed to explain variation in soil fungal communities (Kyaschenko et al., 2025), highlighting potential limitations in how well such assessments capture less visible or belowground biodiversity. Despite these limitations, many CVA methods are used to prioritise areas for conservation, where sites with the highest habitat diversity score is interpreted as being the most diverse and thus have the highest likelihood of supporting species of conservation concern. Typically, CVAs are applied at the scale of entire forest stands (usually 2–20 ha), with the goal of identifying areas to set aside for maintaining viable populations of rare and red-listed species. Yet, because these species rarely occupy entire stands uniformly, this raises a key question: can CVAs be adapted to work at finer spatial scales, allowing not only the identification of which stands to protect, but also pinpointing the specific areas within the stands that hold the greatest conservation concern?

Species occurrences are not the only elements that show a patchy distribution in forest landscapes; the forests themselves are often highly fragmented by forestry operations. In Sweden, for example, the landscape is dominated by intensively managed forests, with scattered patches of protected or voluntarily set-aside stands. This has led to a situation where today, around 30 percent of all species on Sweden's national red list are strongly, negatively affected by forestry (SLU Art-databanken, 2020). To mitigate the negative impacts of forestry on biodiversity, a multi-scale conservation approach is commonly applied within the managed landscape. This includes measures such as retaining trees (both individually and in groups) during final felling and setting aside small stands for conservation (Felton et al., 2020). It could be argued that the multi-scale approach to forest management in Sweden has resulted in segregated forest types along a gradient of forest degradation, with young managed forests, retention patches and set-asides. Such fragmentation can cause aggregations of species groups of varied habitat specialisations in these three forest types. In the context of forest degradation, this means that we can expect that generalist species, which are less affected by forestry, may thrive in both degraded

and intact stands whereas specialist species that are negatively affected by forestry would be confined to intact forest stands, e.g., Nordén et al., (2013).

Most species communities consist of a few dominant generalist species and numerous rare species with narrow ranges, small population sizes and specific habitat preferences (Magurran and Henderson, 2003; Rabinowitz, 1981). Because rare species are more prone to extinction, habitat destruction and simplification caused by anthropogenic pressures – such as forestry – pose a significant threat (Harnik et al., 2012; IUCN, 2024). This is evident in the large amount of forest dwelling species that are threatened due to lack of specific habitat such as various types of deadwood (Hyvärinen et al., 2019; IUCN, 2024; SLU Art-databanken, 2020). Therefore, increasing habitat diversity may enhance the occurrence probability of species with narrow habitat range or requirements.

Habitat diversity in forests describes the number of ecological niches and structures found in a given area. Structures such as canopy structure, affect light availability and microclimatic conditions on a site (De Frenne et al., 2021), which in turn affect understory vegetation (Esseen and Ekström, 2023; Mestre et al., 2017; Van Couwenberghe et al., 2011). Furthermore, the occurrence of old trees is important for many epiphytic species (Brunialti et al., 2010; Fritz et al., 2009). Old trees are also more likely than young trees to develop tree-related microhabitats (TReMs) (Asbeck et al., 2021), an indicator of biodiversity that has been increasingly implemented in Europe (Larrieu et al., 2018). Especially old and large habitat trees, including TReM-bearing habitat trees, have been found to hold special significance for threatened biodiversity (Bütler et al., 2013). In Sweden, habitat trees are defined as meeting any number of the following criteria: be old and large living trees, have specific bark or canopy structures, or have occurrence of cavities, polyporous fungi or bird nests (Swedish Forest Agency, 2020). Additionally, deadwood amount and diversity are important for deadwood-dependent beetles and fungi (Blasi et al., 2010) whereas lichens and bryophytes found on deadwood are also affected by the quality of the substrate (Caruso and Rudolphi, 2009; Larsson Ekström et al., 2023). Forests with a high diversity of such habitats are typically located in more natural, unmanaged forests where we also find species that are not found in managed forests to the same degree, like red-listed species (Rudolphi et al., 2014, Hekkala et al., 2023).

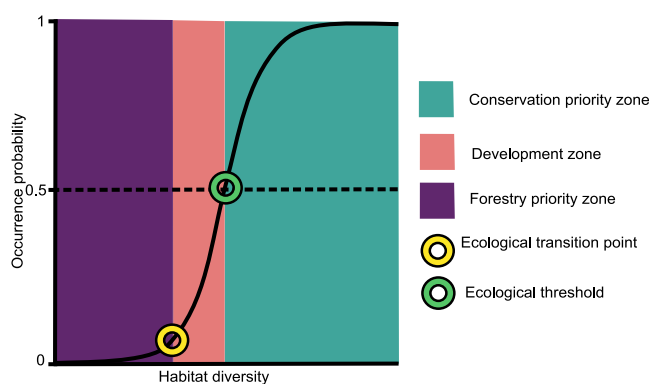
In a comprehensive multi-taxon species survey in boreal Fennoscandia, encompassing managed forests along a gradient of ecological degradation and intactness (young forests, retention patches and set-asides), we aim to evaluate the effectiveness of two commonly used Conservation Value Assessments (CVA) to identify small-scale habitats within forest stands occupied by red-listed species. We investigate cryptogam species belonging to three taxo-ecological groupings: wood-inhabiting fungi, epiphytic and epixylic lichens and epixylic bryophytes. Cryptogams represent essential components of forest biodiversity and function and serve as important indicators for conservation efforts (Hylander and Jonsson, 2007). These CVAs are based on systematic searches for forest structural components and stand characteristics describing diversity of habitats important for biodiversity. The presence of each feature (such as amounts and types of deadwood, habitat trees etc.) in the CVAs are recorded giving a score of habitat diversity. As these CVAs could be subjectively biased, we evaluate them in parallel to more conventional, detailed measurements of forest habitat diversity, so-called Conservation Value Measurements (CVMs) where we measure features such as deadwood amounts and types, habitat trees etc. We also seek to identify ecological conservation priority zones to guide practical conservation using CVAs. We hypothesise that: CVAs will be effective in predicting the occurrence and absence of red-listed species, as indicated by good model fits (H1). This is because CVAs are expected to capture information about both ecologically important resources and their diversity, while simultaneously reflecting aspects of forest continuity, factors known to be critical for the habitat requirements of red-listed species (SLU Art-databanken, 2020). We also expect CVAs to perform

equally as well as detailed CVMs in predicting the occurrence of red-listed species. Further, we hypothesise: (H2) A conservation priority zone (Fig. 1), categorised by a higher than 50 % occurrence probability of red-listed species, can be identified. However, where this zone lies in terms of CVA score may vary across taxo-ecological groups due to differences in ecological requirements. We also hypothesise (H3) that a transition point can be identified along the CVA scale, marking where habitat enhancement measures for species conservation could be effectively initiated. This transition point is expected to correspond to where the curve steepness increases most in the likelihood of detecting red-listed species with each incremental step on the CVA scale. Forests below this point along the CVA scale could then be considered to have lower conservation value, with a correspondingly low probability of red-listed species occurrence. In such areas, forestry operations would therefore be associated with a lower risk of negatively impacting habitats critical for these species. To investigate the relationship between single occurrences of red-listed species and overall richness, we also hypothesised that (H4): Plots with a single occurrence of red-listed species will be characterised by overall higher species richness.

## 2. Material & methods

### 2.1. Study area

This study was conducted in the southern boreal zone of central Sweden (Ahti et al., 1968) in the provinces of Hälsingland and Värmland (Fig. 2). The study areas are located in conventionally managed landscapes dominated by production stands planted with Norway spruce (*Picea abies* (L.) H. Karst) and Scots pine (*Pinus sylvestris* L.) with some elements of Birch (*Betula pendula* Roth. or *B. pubescens* Ehrh.) on mesic and moist soil types. Through remote sensing and stand data derived from the forest company Stora Enso AB, we identified multiple stands that underwent final felling 20–30 years ago while also implementing retention forestry, sensu Fedrowitz et al., (2014). Stands were selected based on a combination of stand data screening and field visits. In both regions, we identified three stand types: (1) Young forests: stands that



**Fig. 1.** Conceptual figure of H1, H2 and H3, visualising the occurrence probability of red-listed species along a gradient of habitat diversity. With an effective CVA, sites lacking red-listed species will be H1) aggregated at the lower end and sites occupied by red-listed species at the higher end of the habitat diversity gradient producing a distinctive s-shaped curve. The green circle indicates H2) the 50 % threshold above which forests have a higher chance to be of high conservation value. The yellow circle indicates H3) an ecological transition point where a certain habitat diversity score marks where the curve steepness increases most corresponding to the occurrence probability of red-listed species. The purple zone is a priority zone for forestry, characterised by lower conservation values. The orange zone make up the development zone where the occurrence probability of red-listed species rapidly increase with habitat diversity. The turquoise zone is the conservation priority zone representing forests with high habitat diversity exhibiting high occurrence probabilities of red-listed species.

were clear-felled 20–30 years ago and subsequently regenerated through soil scarification followed by planting of coniferous seedlings; (2) Retention patches: groups of trees retained during final felling within the now young forest stands. These patches had to be large enough to accommodate a circular sample plot with a 20 m radius; and (3) Set-asides: voluntary conservation areas exempt from conventional forestry, either to preserve existing values or allow the development of future ones (Gustafsson and Perhans, 2010). Set-asides were preferably located within 500–2000 m of the young stands, though in some cases suitable areas had to be identified outside this range. To ensure an even distribution of tree species composition across stand types within each region, we selected sites accordingly. An initial assessment of species composition was made using forest company databases, but final site selection was based on interpretation of aerial photographs. Study plots were selected to ensure that, within each forest type and region, there was a comparable gradient in conifer dominance, spanning from Norway spruce- to Scots pine-dominated stands.

We included 40 young forest plots, 40 retention plots within the same stand as the young forest plots, and 40 set-aside plots, totalling 120 plots. Twenty plots of each forest type were located in Hälsingland and 20 in Värmland (Fig. 2).

### 2.2. Species inventories

We set up a 20-m radius circular sample plot in the centre of each of the 120 plots.

Within each sample plot, we surveyed wood-inhabiting polyporous and a selection of corticioid fungi, hereafter fungi; epiphytic and epixylic lichens, hereafter lichens; and epixylic bryophytes, hereafter bryophytes.

Fungi were inventoried on standing and lying deadwood using the following methodology. We inventoried three small diameter (5–15 cm) lying dead trees and three small diameter (5–15 cm at breast height (DBH)) of standing dead trees for each common tree species (Norway spruce, Scots pine and Birch). Thereafter, we inventoried all standing dead trees with a DBH  $\geq 15$  cm and all lying dead trees with a DBH  $\geq 15$  cm and a length  $\geq 1.3$  m. If fewer than three lying dead trees  $\geq 15$  cm were found within the core 20-m radius plot, additional lying dead trees were sought for within the entire plot to reach a total of three lying dead trees. All standing dead trees were inventoried up to two metres height for occurrences of fungi.

For lichens, the surface of a subset of living trees and all dead standing trees with a minimum height of 1.3 m were inventoried up to two metres in height. First, we inventoried three living trees with a DBH of 5–15 cm for each common tree species (Norway spruce, Scots pine and Birch). Secondly, we inventoried seven trees with a DBH  $\geq 15$  cm for each common tree species. If less than three living trees with a DBH of 5–15 cm were present within the plot, larger trees were chosen, and if less than seven trees with a DBH  $\geq 15$  cm occurred, smaller trees were chosen, always aiming for a minimum of ten living trees per plot.

Bryophytes were inventoried on a subset of lying dead trees, only including species utilising lying deadwood as substrate. All lying dead trees with a diameter  $\geq 15$  cm were inventoried and at least five trees with a diameter  $< 15$  cm per common tree species (Norway spruce, Scots pine and Birch) were randomly sought after for bryophytes.

All species inventories were performed by taxonomic experts within a specific organism group.

### 2.3. Conservation value assessments

We performed two different CVA methods, which will be referred to as Conservation value assessments (CVA) 1 and 2, and one Conservation value measurement (CVM) within each plot. Both CVA methods are commonly used within commercial forestry in assessments of a forest's habitat diversity and conservation value (see below).

#### Conservation Value assessment 1 (CVA 1)

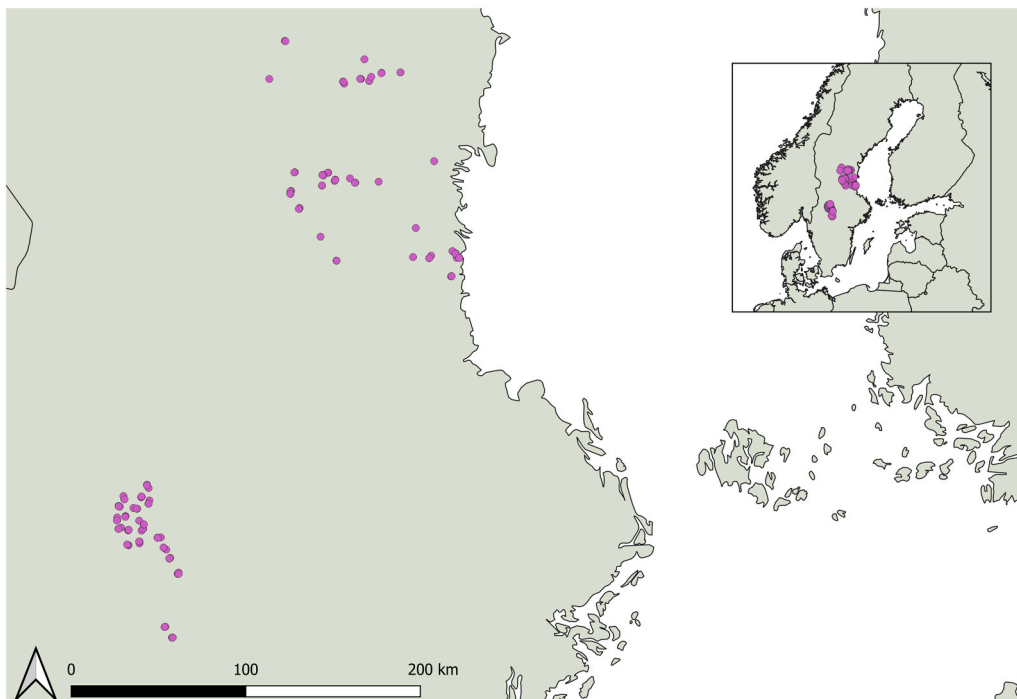


Fig. 2. Map showing the locations of the plot centres in Sweden.

The CVA 1 method developed by Skogsbiologerna AB is tailored to measure the conservation value of any forest by capturing the forest's complexity and habitat diversity (Drakenberg and Lindhe, 1999). This method is widely used in Sweden but also in other European and North American countries (B. Drakenberg pers. comm.). Previous studies have shown this method to be effective at predicting conservation values connected to deadwood (Huo et al., 2023) and species of conservation concern (Hekkala et al., 2023). Across an entire forest stand, the assessor searches for the occurrence of 50 stand characteristics typical to different forest types such as boulders, steep inclination, signs of natural processes such as fire or tree succession and structures such as dead trees and habitat trees. The occurrence of each feature is then noted on a score sheet that gives a final score ranging from 0 to ca 30 (Table A.3), a so-called Habitat Heterogeneity Score (Hekkala et al., 2023).

#### **Conservation Value assessment 2 (CVA 2)**

We also performed the CVA used by the forest company Stora Enso AB which we will refer to as CVA 2. This method is based on assessing stand and structural characteristics and natural processes, like the CVA 1 method. Instead of scoring each individual feature, however, a score from 1 to 4 is given for a total of 14 categories of features on, for example, deadwood quality, with 4 indicating trivial or lacking said feature and 1 being the highest score possible. A certain number of 1's or 2's within selected categories then nominates the forest stand to be exempt from forestry, reaching Woodland Key Habitat (WKH) status (Table A.4). In our survey, we continued to assess each category even after the WKH threshold, resulting in a score similar to the CVA 1 (see above) although inverted, meaning that lower scores indicate a higher habitat diversity.

Both CVA methods were developed to be used across an entire stand, only using sample plots to calculate the number of structures, whereas we performed these assessments only within our 20-m radius plots. This limits the assessment of certain features, such as surrounding bodies of water. To control for this while retaining comparability between the methods, we omitted plots that were obviously affected by such features adjacent to the plots. For further details, see Tables A.3 and A.4.

The same assessor conducted the assessment in all plots.

#### **Conservation Value Measurement (Forest Structure)**

We included measurements of habitat features connected to species

for two reasons: because CVAs may be subjectively biased due to observer bias and because we also wanted to compare the outcomes of the CVAs to habitat availability for red-listed forest-dwelling species. To this end, we devised a Conservation Value Measurement, CVM; a habitat diversity metric using detailed measurements of forest substrate and environmental data, used to calculate a habitat diversity index. This CVM serves as a third alternative to the two CVAs.

All standing dead trees with a DBH  $\geq 5$  cm and a height  $\geq 1.3$  m, and all lying deadwood with a length  $\geq 1.3$  m and a diameter  $\geq 10$  cm at the thickest end, were inventoried within the 20-m radius plots. For standing deadwood, we recorded the DBH, height, and tree species. For lying deadwood, we measured the diameter, length, and tree species to estimate volume and decay stage following Siitonen (2001). Furthermore, all habitat trees within the 20-m radius plot were recorded following the classification of the Swedish Forest Agency (2020). The percentage of wet-to-moist ground cover (i.e., shallow groundwater, vegetation dominated by *Sphagnum* spp.) was estimated and the plot's inclination was assessed by measuring the elevation difference between the highest and lowest points within the plot using an inclinometer. For living trees, we placed a 7-m radius circular sample plot at the centre of each 20-m radius plot where we measured all trees with a height  $\geq 1.3$  m noting tree species and DBH.

In order to calculate the CVM index, we performed a Principal Component Analysis (PCA) using the `prcomp` function including plot-level total number of habitat trees (`nvtree`), number of unique habitat tree types (`nvtreediv`), total basal area (`ba`), basal area of deciduous (`Decba`) and coniferous (`Conba`) trees, total deadwood volume (`DW`), deciduous (`Decdw`) and coniferous (`Condw`) deadwood volumes, inclination (`incl`) and soil moisture (`moist`). We then extracted the first two axes of the PCA to serve as the CVM habitat diversity index (Fig A.1). However, during the analysis, we determined that the second PCA axis was not relevant since it produced poor models ( $p = > 0.3$ , Area-UndertheCurve (AUC)  $< 0.6$ ) and therefore excluded it from further analysis, thus only using the first PCA axis.

#### **2.4. Analysis**

All statistical analyses were done in R version 4.3.2 (R Core Team,

2021).

A commonly used method suitable for detecting ecological thresholds is logistic regression (Müller and Büttler, 2010). Ecological studies using logistic regression usually focus on the point where the probability of a given response variable is 50 percent or higher. Another cut-off point, commonly used in medicine, is the Youden Index, which is used to find an optimal point balancing sensitivity and specificity of the model and could be used to identify a transition point initiating a transition towards the threshold of high probability (Aoki et al., 1997; Fluss et al., 2005).

To address H1), we used logistic regression (glm, family=binomial, link=logit) to test for relationships between the occurrence of at least one threatened and red-listed species and our CVAs and CVM. We considered the within-plot occurrence of (at least one) species listed as red-listed (NT, VU, EN or CR) and threatened (VU, EN or CR according to the Swedish national red-list status) as the response variable (SLU Art-databanken, 2020). Due to the limited number of occurrences of threatened species, we did not distinguish between taxo-ecological groups. As we had sufficiently many occurrences of red-listed species, we conducted separate analyses for red-listed species of fungi, bryophytes and lichens. We found that the CVA 1 and CVA 2 methods and the CVM were highly correlated ( $\geq 0.7$ ), so we modelled them separately and compared Akaike Information Criterion (AIC) values to identify the best models. We also modelled plot type separately from the CVAs and the CVM. We omitted the model containing red-listed fungi and plot type due to rank-deficiency (young forests did not contain any red-listed fungi). We considered models with the lowest AIC and within 2 AIC units of that model to be the best, see Table 1. We also validated each model using McFadden's pseudo-R<sup>2</sup> value, package pscl (Jackman et al., 2015) and AUC value, package pROC (Robin et al., 2011). We considered models with McFadden's pseudo-R<sup>2</sup> values  $\geq 0.2$  and AUC values  $\geq 0.8$  to be of good fit and acceptable for threshold calculations (Hosmer et al., 2013; McFadden, 1979).

**Table 1**

Model results with the predictors CVA 1, CVA 2, CVM and Forest Type (Young forest, Retention and Set-aside). Response variables are: occurrence of at least one threatened species, red-listed species, red-listed lichens, red-listed fungi and red-listed bryophytes. For each model, we also show McFadden's pseudo-R<sup>2</sup> value for explained variance, Area Under the Curve (AUC) and OR = Odds ratio. Models of good fit (AUC  $\geq 0.8$  and McFadden's pseudo-R<sup>2</sup> value  $\geq 0.2$ ) are highlighted in grey.

Response variables	Predictors	OR	95 % CI	p-value	AIC	Pseudo-R <sup>2</sup>	AUC
All threatened species	CVA 1	1.2	1.08, 1.35	< 0.001	73.67	0.154	0.742
	CVA 2	0.86	0.77, 0.95	0.003	77.08	0.112	0.716
	CVM	0.66	0.50, 0.85	0.002	76.38	0.121	0.746
	Forest Type			0.002	76.22	0.147	0.759
	Young forest	—	—				
	Retention	2.05	0.19, 45.3				
All red-listed species	Set-aside	13	2.30, 245				
	CVA 1	1.17	1.08, 1.28	< 0.001	153.23	0.102	0.712
	CVA 2	0.86	0.79, 0.93	< 0.001	153.1	0.103	0.713
	CVM	0.6	0.45, 0.77	< 0.001	150.85	0.117	0.719
	Forest Type			< 0.001	132.27	0.240	0.800
	Young forest	—	—				
Red-listed lichens	Retention	5.13	1.85, 16.0				
	Set-aside	26.7	8.72, 96.3				
	CVA 1	1.11	1.04, 1.20	0.0039	159.59	0.055	0.658
	CVA 2	0.89	0.82, 0.95	0.001	156.88	0.072	0.674
	CVM	0.7	0.55, 0.87	0.002	157.34	0.069	0.673
	Forest Type			< 0.001	144.04	0.162	0.748
Red-listed fungi	Young forest	—	—				
	Retention	5.13	1.85, 16.0				
	Set-aside	13.2	4.66, 43.0				
	CVA 1	1.26	1.14, 1.42	< 0.001	84.93	0.228	0.838
	CVA 2	0.8	0.71, 0.88	< 0.001	85.81	0.22	0.837
	CVM	0.45	0.31, 0.61	< 0.001	74.39	0.329	0.910
Red-listed bryophytes	CVA 1	1.32	1.18, 1.52	< 0.001	70.89	0.290	0.853
	CVA 2	0.78	0.69, 0.87	< 0.001	75.13	0.245	0.829
	CVM	0.56	0.41, 0.73	< 0.001	78.60	0.208	0.825
	Forest Type			< 0.001	81.68	0.197	0.789
	Young forest	—	—				
	Retention	2.05	0.19, 45.3				
All threatened species	Set-aside	18.8	3.43, 351				

For H2), we set the cut-off value for the threshold at 50 percent probability, determined as the point where the curve reaches 50 percent, including the 95 % confidence interval (CI).

To address H3), i.e., to test for transition points beyond which the probabilities of species occurrence rapidly increase, we calculated the Youden Index and identified the point with the greatest index value (Fluss et al., 2005).

To address H4), evaluating if the occurrence of a single, red-listed species could function as a surrogate for general biodiversity, we tested for differences in species richness between plots with or without the occurrence of a single, red-listed species, due to non-normality in the data, we used Mann-Whitney's *U* test. This analysis was conducted for all red-listed species combined, and for individual organism groups.

### 3. Results

In total, we found 456 species, of which 49 were classified as nationally red-listed (38 NT, 10 VU, 1 EN) in Sweden. For red-listed lichens, *Alectoria sarmentosa* and *Chaenotheca subroscida* constituted 48 % and 19 %, respectively, of the total number of occurrences of red-listed lichens in the study, respectively (Table A.1). For red-listed fungi, *Phellinidium ferrugineofuscum* and *Rhodofomes roseus* accounted for 45 % and 12 % of the total occurrences of red-listed fungi (Table A.1). *Crossocalyx hellerianus* and *Lophozia ascendens* constituted 64 % and 20 % of the total number of red-listed bryophyte occurrences in the study, respectively (Table A.1). Seventy-nine percent of the red-listed lichen occurrences were found on living trees and 21 % on dead trees.

Thirteen out of the 120 plots were occupied by one or more threatened (VU, EN, CR) species. Ten of these 13 plots were set-asides, two were retention patches and one was a young forest (Table A.2). Furthermore, 58 out of 120 plots hosted one or more red-listed (NT, VU, EN, CR) species (Table A.2). Among the 58 plots with red-listed species, 33 were set-asides, 19 were retention patches and 6 were young forests

(Table A.2). The average CVA 1 score was  $9.8 \pm 0.9$  in set-asides,  $7 \pm 0.7$  in retention patches and  $2 \pm 0.3$  in the young forests (Table A.2). For CVA 2, the respective scores were  $54 \pm 0.8$  for set-asides,  $57.8 \pm 0.8$  for retention patches and  $63 \pm 0.2$  for young forests (Table A.2). The average CVA 1 score was  $8.3 \pm 0.7$  for plots occupied by one or more red-listed species and  $4.4 \pm 0.5$  for plots unoccupied by red-listed species (Table A.2). For CVA 2, the respective scores were  $56.2 \pm 0.8$  and  $60.2 \pm 0.6$  (Table A.2).

### 3.1. H1 – suitability of CVAs

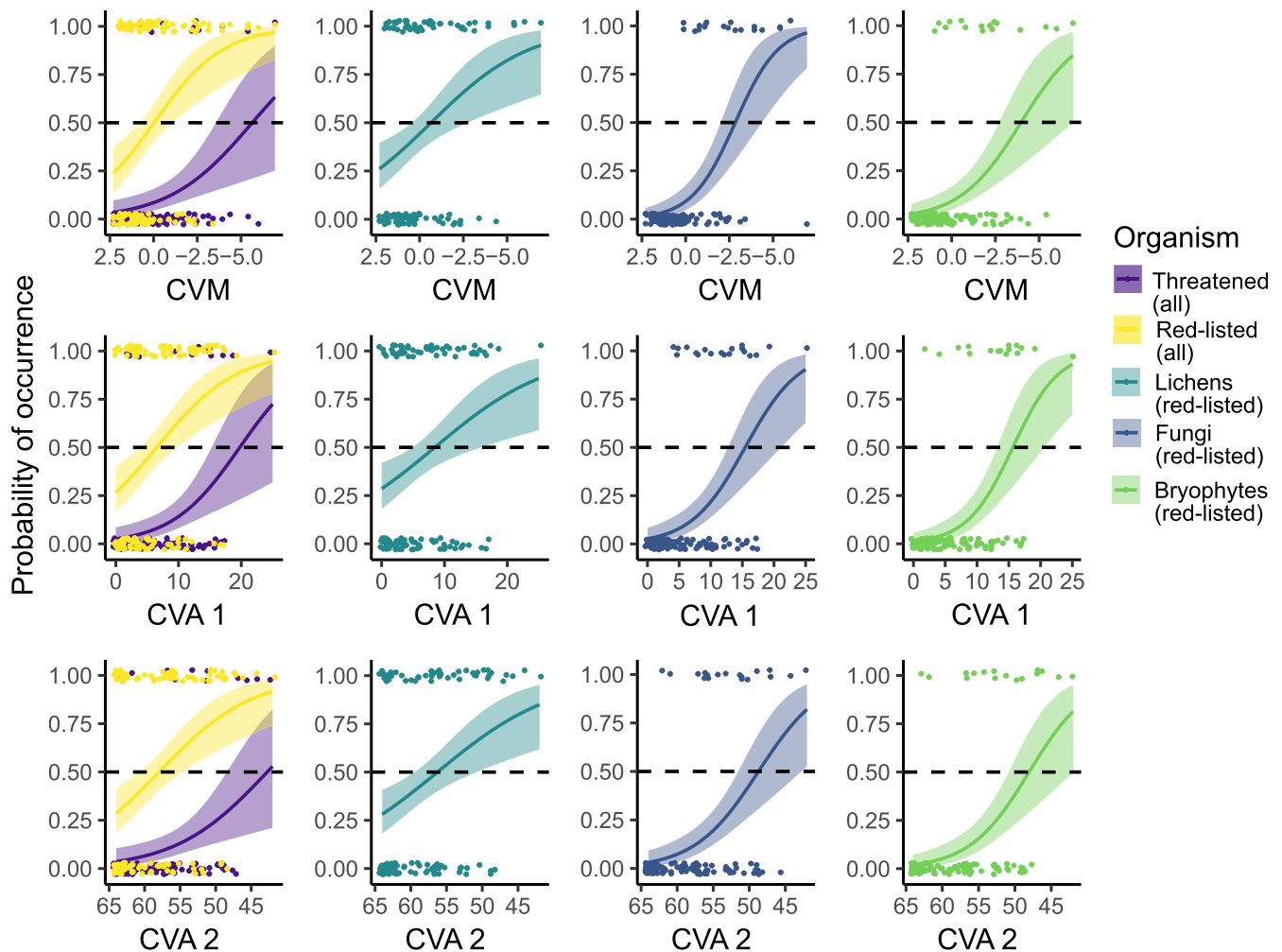
For red-listed fungi and bryophytes, both CVAs and the PCA-based CVM produced models of good fit ( $AUC \geq 0.8$ ,  $\text{pseudo-R}^2 \geq 0.2$ ), suggesting these tools are useful for identifying habitats with high conservation value. For red-listed lichens, neither the CVAs nor the PCA-based CVM produced models of good fit (Table 1). The PCA-based CVM was the strongest predictor for fungi ( $AUC=0.9$ ) and CVA 1 was the best for bryophytes ( $AUC=0.85$ ) (Fig. 3, Table 1). Although the models predicting the occurrence of all threatened species did not meet the criteria for good fit ( $AUC < 0.8$ ,  $\text{pseudo-R}^2 < 0.2$ ), CVA 1 was the best predictor for the occurrence of threatened species ( $AUC=0.74$ ) (Fig. 3, Table 1). Plot type was the best predictor for red-listed species overall ( $AUC=0.8$ ) and for red-listed lichens ( $AUC=0.75$ ), (Fig. 3, Table 1).

### 3.2. H2 & H3 – transition points and thresholds

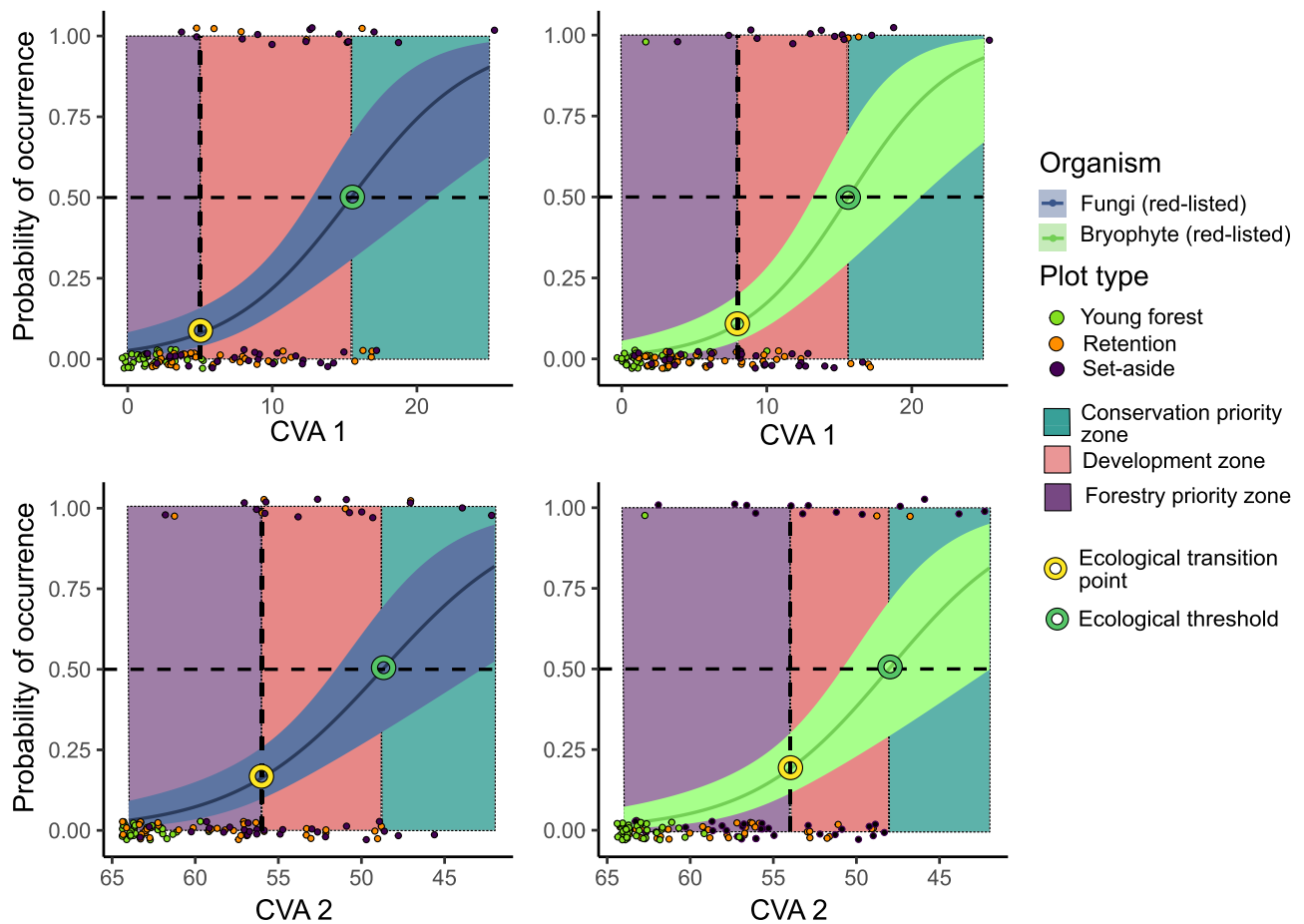
The transition point at which the development zone started and where it reached the threshold varied between organism groups. We found the transition point for CVA 1 to be between 4 and 5 for red-listed fungi and between 8 and 9 for red-listed bryophytes (Fig. 4). The 50 percent threshold for CVA 1 was reached between scores 15 and 16 with the 95 % CI reaching 50 percent between scores 13 and 21 for both red-listed fungi and bryophytes (Fig. 4). For the CVA 2 method, the transition point was between 56 and 57 for red-listed fungi and 54 and 55 for red-listed bryophytes (Fig. 4). The 50 percent threshold was reached between 48 and 49 for both red-listed fungi and bryophytes with the 95 % CI between 42 and 51 (Fig. 4).

### 3.3. H4 – relationship between red-listed species occurrence and species richness

Plots occupied by one or more red-listed species were characterised by significantly higher species richness, for all species combined and for each individual species group (Mann-Whitney  $U$  test, Fig. 5).



**Fig. 3.** Predicted conditional means and their 95 % confidence interval for CVM, CVA 1 and CVA 2 predicting the occurrence of at least one threatened species, red-listed species, epiphytic and epixylic red-listed lichens, wood-inhabiting red-listed fungi and epixylic red-listed bryophytes. All response variables are binary (0–1) but are visualised with added jitter for clarity. Horizontal dashed line = threshold at 50 % occurrence probability. Regression lines with a 95 % CI smoothed with the `geom_smooth` function of the `ggplot2` package for visualization only.



**Fig. 4.** Predicted conditional means and their 95 % confidence interval for the CVA 1 and CVA 2 methods predicting the occurrence of at least one red-listed fungi and bryophytes. The fifty percent threshold values are indicated by horizontal dashed lines and the green circle. Ecological transition points (highest Youden Index) are indicated by vertical dashed lines and by the yellow circle. All response variables are binary (0–1) but are visualised for each plot type as dots with different colours, with added jitter for clarity. Ecological priority zones (fields) are shown with different colours. Regression lines with a 95 % CI smoothed with the `geom_smooth` function of the `ggplot2` package for visualization only.

#### 4. Discussion

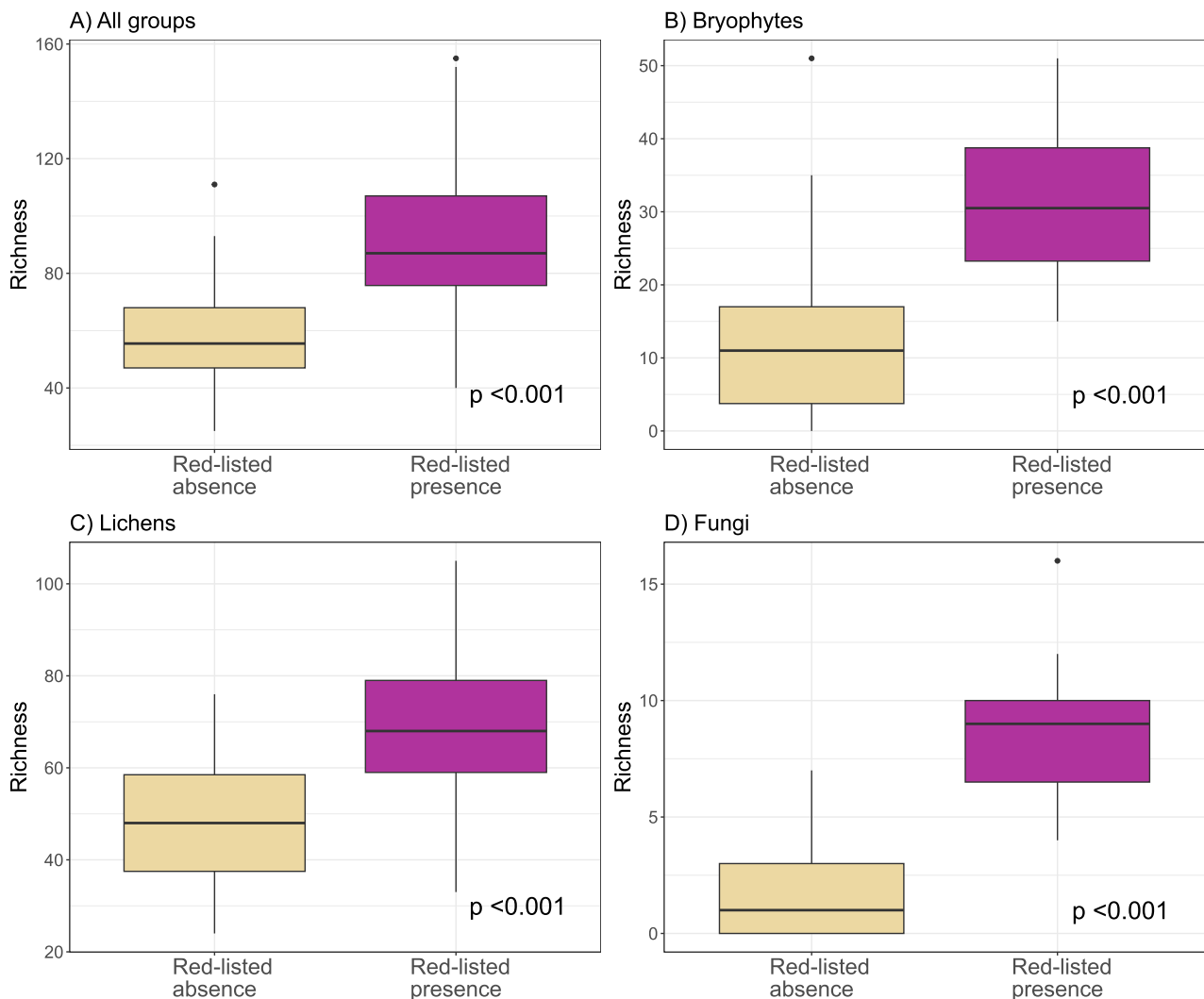
This study provides novel insights regarding the ability to assess local habitat diversity and the occurrence of red-listed forest species by providing further evidence for widely used CVA protocols lacking sufficient scientific evaluation (Gao et al., 2015).

The forests in our study represent a gradient of ecological forest degradation, detectable in their habitat diversity and occupancy by red-listed and threatened species in declining order from set-asides to retention patches to young forests. All the methods tested in our study efficiently predicted the occurrence of red-listed fungi and bryophytes, but not of red-listed lichens, overall red-listed species or threatened species. Despite slight differences, the CVA methods used in this study performed similarly well to the detailed CVM and thus likely manage to pinpoint similar structures of ecological importance, while failing at others. Although there may be observer bias in CVAs (Gosselin and Larrieu, 2020) which we did not account for in this study, the similar results between CVAs and the detailed CVM measurements suggest reliable assessments. We identified conservation priority zones using CVA scores, and that the development zone differed between red-listed bryophytes and fungi. The threshold for the conservation priority zone was reached at the same CVA score for both organism groups, without finding a zone where occurrence probability plateaus. This score of 15–16 is similar to the threshold found in Hekkala et al., (2023) of 16–17 for species richness, even though they used other methods to determine a threshold. Due to poor model fit, we did not proceed with identifying

conservation or forestry priority zones for threatened species or for combinations of red-listed taxa. For forest types, we found that young forest sites were characterised by low habitat diversity scores and a low number of plots occupied by red-listed species. In contrast, retention and set-asides were positioned along both the development and conservation priority zone of habitat diversity scores with increasing number of plots occupied by red-listed species. Further, we showed that CVAs efficiently capture the local habitat diversity important for certain species, but they may not be efficient in capturing habitat diversity important for all organism groups. Our results show that habitat diversity scores within certain priority zones can be useful for guiding conservation prioritisation efforts, but their application should be tailored to specific taxa and forest contexts. We also showed that sites occupied by red-listed species support a higher overall species richness than sites without these species, considering our study organism groups. Red-listed species can thus be used as surrogates for overall biodiversity, but this relationship may differ between taxa and location (Pearman and Weber, 2007; Sverdrup-Thygeson, 2001; Tälle et al., 2023).

##### 4.1. Local patches of conservation concern

Aligning with H1, we show that the CVAs effectively capture local habitat diversity for deadwood-inhabiting bryophytes and fungi but are less effective for lichens. This aligns with Gao et al. (2015), which showed evidence for a relationship between wood-living fungal richness and deadwood volume. Deadwood volume is also important for epixylic



**Fig. 5.** Box plots of species richness in forest plots with presence or absence of a red-listed species. A) Richness of all species groups on the y-axis and presence or absence of all red-listed species on the x-axis. B) Richness of epixylic bryophyte species and presence or absence of red-listed epixylic bryophyte species. C) Richness of epiphytic and epixylic lichen species and presence or absence of red-listed epiphytic and epixylic lichen species. D) Richness of wood-inhabiting fungi species and presence or absence of red-listed wood-inhabiting fungi species. The p-values are based on Mann-Whitney U tests.

bryophytes, although this can be counteracted by sensitivity to climatic factors (Kropik et al., 2021; Rudolphi and Gustafsson, 2011; Táborská et al., 2020). Based on these findings, we infer that the CVAs used in this study are efficient at capturing habitat diversity connected to deadwood structure. Both CVA methods proved to be reliable indicators for the occurrences of fungi and bryophytes. Yet the CVA 1 generally performed slightly better than the CVA 2 and the CVM only outperformed CVA 1 for red-listed fungi. Together with the results of Hekkala et al. (2023) which was done on a scale of 2 ha, this demonstrates that CVAs can effectively assess conservation values from local- to stand scales, particularly for those capturing conservation values associated with deadwood structure.

Although we found support for H1, CVAs were not effective predictors of habitat diversity important for red-listed species overall or for red-listed lichens. This contrasts with the findings of Hekkala et al. (2023), who found that CVA 1 performed well in predicting the richness of all red-listed species. This discrepancy may be due to a scarcity of threatened species present in our data. In addition, the patterns were driven by species with a Near Threatened (NT) status, meaning that our results do not represent threatened species. For threatened species, which are of greatest conservation concern, the fifty percent threshold may be too conservative and thus risk jeopardizing the survival of those

species at highest extinction risk. However, due to lack of threatened species in our data, we could not analyse variable threshold levels. Even though we recorded all species present, species inventories for fungi and bryophytes were limited to deadwood substrates, whereas lichens were inventoried on both dead and living trees, and an overwhelming majority of the lichens were recorded on living trees. The CVA methods we used may be biased towards deadwood and poor at capturing variation in other structural components. An example of this is in detailed descriptions of decay stages and microclimatic conditions for deadwood but the general lack of different TReMs for habitat trees. Nevertheless, the PCA-based CVM, which included several commonly measured structural variables, also performed poorly in predicting lichen occurrences. This emphasises the complexity of predicting biodiversity using indices or simplified metrics.

Tree age is an important structural feature for epiphytic lichens (Brunialti et al., 2010; Fritz et al., 2009; Gao et al., 2015). In Europe, research gaps have been found in the relationship between habitat trees bearing TReMs and the actual occurrence of certain species (Asbeck et al., 2021). In the CVAs used in our study, we used the Swedish definition of a habitat tree, encompassing trees with and without actual TReMs provided they meet a number of requirements for inclusion (see introduction; Swedish Forest Agency, 2020). Habitat trees in Sweden

have not been scientifically validated, and it could be that the requirements for inclusion are too low to indicate actual occurrence of, e.g., red-listed species. However, our results suggest that the inclusion of the broadly defined habitat trees may be inefficient at capturing the prevalence of age-related structures important for epiphytic lichens. The lack of predictability of our measured habitat diversity scores for lichens highlights the importance of identifying the driving factors of taxon-specific biodiversity. In contrast, [Hekkala et al. \(2023\)](#), found that richness of lichens of conservation value was rather well predicted by CVA 1, better than by tree age-related variables. This is probably due to the higher number of species included in their study, compared to our focus on red-listed species alone.

In this study, we did not consider the importance of the surrounding landscape in explaining local biodiversity patterns, which could have influenced our results ([Kärvelo et al., 2021](#)). The relative importance of local and landscape scales is a central question in biodiversity studies ([Tschamtko et al., 2012](#)). The amount and quality of available habitat in the surrounding landscape is important in explaining diversity patterns of deadwood-dependent lichens and fungi as well as red-listed lichens on living trees ([Hämäläinen et al., 2023](#); [Nordén et al., 2018](#); [Rudolphi and Gustafsson, 2011](#)). Hence, future research should evaluate the performance of CVAs across different landscape settings, including gradients of availability of potential source habitats for red-listed species. Assessing the reliability of CVAs in various forest landscape contexts could provide valuable insights regarding the habitat diversity and the thresholds that are necessary to support red-listed species in different forested landscapes. In addition, due to potentially scale-specific responses ([Angelstam et al., 2003](#); [Fahrig, 1998](#)), CVAs should also be evaluated at different spatial scales such as local-to-landscape scale. Regarding site-specific variation such as productivity, we assume that by selecting several plots of similar soil condition and tree species composition (within a gradient of moist-mesic and spruce-pine), we capture the potential differences in site-specific conditions.

#### 4.2. Priority zones

We found partial support for H2 and H3, as sites with low habitat diversity scores generally lack red-listed species, and beyond the development zone, the occurrence probability reached 50 percent for red-listed fungi and bryophytes. However, we did not identify areas where the occurrence probability of red-listed species plateaued. This could be due to, e.g., lacking old-growth forests, (set-asides are situated in landscapes with some history of management) or the scale of sampling. Young forest plots were clustered below the development zone and were characterised by low habitat diversity scores. In fact, only one young forest plot harboured threatened fungi or bryophyte species ([Fig. 4](#)). Retention and set-asides were scattered more evenly along the development and conservation priority zone. This means that the studied young forests were clearly poorer in terms of habitat diversity and red-listed species occupancy, whereas retention patches and set-asides represented both a development and conservation priority zone of increasing red-listed species occupancy, but below the plateau of consistent occurrence of red-listed species. Given the high proportion of young forests in today's forested areas in both Sweden ([Skogsdata, 2024](#)) and Finland ([Korhonen et al., 2021](#)), this emphasises the need for increasing habitat diversity, especially of such habitats or structures that are rare and of importance for red-listed species.

Thresholds can be used to both identify tipping points defining the state beyond which a given ecological mechanism collapses or develops in an unfavourable trajectory, as well as points above which a system develops along a favourable path ([Angeler et al., 2016](#)). The transition point we identified in CVA scores, beyond which the development phase begins, can be used to identify and pinpoint locations where conservation may have the greatest relative effect. For example, an increase of the CVA 1 score from 0 to 4 increases the occurrence probability of red-listed fungi from 3 percent to 6 percent whereas an increase of the

score from 4, which is the transition point, to 8 increases the probability from 6 percent to 15 percent. The incremental gain thus becomes greater beyond the transition point, highlighting its potential importance for targeted conservation action. The 50 percent threshold value can be used to prioritise between moderate and high conservation value (below or above the threshold). These insights help identify zones where positive development starts and where it reaches a threshold of conservation importance. Conversely, the same principle could be applied to indicate zones where negative ecological development or deterioration starts, coinciding with low habitat diversity (or CVA scores) and low occurrence probabilities of red-listed species. We cannot discern these positive and negative feedback mechanisms, since studying the actual addition or removal of habitat diversity structures would be required, but this zoning can still be used to guide conservation efforts. Below the transition point, areas can be seen as priority zones for forestry operations with a lower risk of causing harm to red-listed biodiversity. Meanwhile, the development and conservation priority zones can guide conservation efforts. The development zone represents less habitat diverse forests where, e.g., restoration can have potentially positive effects, whereas the conservation priority zone may correspond to forests with existing conservation values that need maintaining.

#### 4.3. Red-listed species as indicators of overall species richness

We find support for H4; plots occupied by one or more red-listed species are also characterised by a greater total richness combined and separated for each organism group. This could be explained by the plots occupied by red-listed species also having greater habitat diversity scores, providing structures for a wide range of species, a relationship found in several previous studies, e.g., ([Hekkala et al., 2023](#); [Larrieu et al., 2019](#); [Zeller et al., 2022](#)). Our results thus provide support for the indicator value of red-listed cryptogams for overall cryptogam richness.

## 5. Conclusion

We show that conservation value assessments (CVAs) based on habitat diversity are effective at predicting the occurrence of red-listed fungi and bryophyte associated with deadwood. These assessments performed as well as, or even better than, a habitat diversity index derived from detailed measurements of forest structure. In addition, these assessments can effectively pinpoint conservation priority zones where the probability of species occurrence increases and reaches a threshold along a gradient of estimated conservation value or habitat diversity. Such priority zones represent critical points where changes in habitat diversity will significantly influence the occurrences of red-listed species. However, for threatened species that are poorly covered in our data, a higher threshold may be warranted. While promising, the CVAs presented here require further evaluation. Assessing and incorporating the influence of the surrounding landscape is highly important. Moreover, additional environmental variables or data points need to be included as the ones used here could not confidently explain the occurrence probability of lichens and threatened species. To better capture forest biodiversity, future studies should also include other organism groups not covered here.

#### CRedit authorship contribution statement

**Anne-Maarit Hekkala:** Writing – review & editing, Funding acquisition. **Faith A.M. Jones:** Writing – review & editing, Data curation, Conceptualization. **Alwin A. Hardenbol:** Writing – review & editing, Data curation, Conceptualization. **Albin Larsson Ekström:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Joachim Strengbom:** Writing – review & editing, Funding acquisition, Conceptualization. **Jörgen Sjögren:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Mari Jönsson:** Writing – review &

editing, Funding acquisition, Conceptualization. **Matti Koivula:** Writing – review & editing, Funding acquisition, Conceptualization.

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## 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.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122858](https://doi.org/10.1016/j.foreco.2025.122858).

## Data availability

Data will be made available on request.

## References

- Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. *Ann. Bot. Fenn.* 5, 169–211.
- Angeler, D.G., Allen, C.R., Barichev, C., Eason, T., Garmestani, A.S., Graham, N.A.J., Granholm, D., Gunderson, L.H., Knutson, M., Nash, K.L., Nelson, R.J., Nyström, M., Spanbauer, T.L., Stow, C.A., Sundstrom, S.M., 2016. Management applications of discontinuity theory. *J. Appl. Ecol.* 53, 688–698. <https://doi.org/10.1111/1365-2664.12494>.
- Angelstam, P.K., Bütler, R., Lazdinis, M., Mikusiński, G., Roberge, J.-M., 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation — dead wood as an example. *Ann. Zool. Fenn.* 40, 473–482.
- Aoki, K., Misumi, J., Kimura, T., Zhao, W., Xie, T., 1997. Evaluation of cutoff levels for screening of gastric cancer using serum pepsinogens and distributions of levels of serum pepsinogen I, II and of PG I / PG II ratios in a gastric cancer case-control study. *J. Epidemiol.* 7, 143–151. <https://doi.org/10.2188/jea.7.143>.
- Asbeck, T., Großmann, J., Paillet, Y., Winiger, N., Bauhus, J., 2021. The use of tree-related microhabitats as forest biodiversity indicators and to guide integrated forest management. *Curr. For. Rep.* 7, 59–68. <https://doi.org/10.1007/s40725-020-00132-5>.
- Ben-Hur, E., Kadmon, R., 2020. Heterogeneity–diversity relationships in sessile organisms: a unified framework. *Ecol. Lett.* 23, 193–207. <https://doi.org/10.1111/ele.13418>.
- Blasi, C., Marchetti, M., Chiavetta, U., Aleffi, M., Audisio, P., Azzella, M.M., Brunialti, G., Capotorti, G., Del Vico, E., Lattanzi, E., Persiani, A.M., Ravera, S., Tilia, A., Burrascano, S., 2010. Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. *Plant Biosyst. - Int. J. Deal. all Asp. Plant Biol.* 144, 160–170. <https://doi.org/10.1080/11263500903560538>.
- Brunialti, G., Frati, L., Aleffi, M., Marignani, M., Rosati, L., Burrascano, S., Ravera, S., 2010. Lichens and bryophytes as indicators of old-growth features in Mediterranean forests. *Plant Biosyst. - Int. J. Deal. all Asp. Plant Biol.* 144, 221–233. <https://doi.org/10.1080/11263500903560959>.
- Bütler, R., Lachat, T., Larrrieu, L., Paillet, Y., 2013. 2.1 Habitat trees: key elements for forest biodiversity. *Integr. Approaches Oppor. Conserv. For. Biodivers.* 84.
- Caruso, A., Rudolphi, J., 2009. Influence of substrate age and quality on species diversity of lichens and bryophytes on stumps. *Bryol.* 112, 520–531. <https://doi.org/10.1639/0007-2745-112.3.520>.
- R. Core Team, 2021. R: A language and environment for statistical computing.
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klings, D.H., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P., Hylander, K., 2021. Forest microclimates and climate change: importance, drivers and future research agenda. *Glob. Change Biol.* 27, 2279–2297. <https://doi.org/10.1111/gcb.15569>.
- Drakenberg, B., Lindhe, A., 1999. Indirekt naturvärdesbedömning på beståndsnivå—en praktiskt tillämpbar metod. *Skog Forsk.* 2, 60–66.
- Esseen, P.-A., Ekström, M., 2023. Influence of canopy structure and light on the three-dimensional distribution of the iconic lichen *Usnea longissima*. *For. Ecol. Manag.* 529, 120667. <https://doi.org/10.1016/j.foreco.2022.120667>.
- Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecol. Model.* 105, 273–292. [https://doi.org/10.1016/S0304-3800\(97\)00163-4](https://doi.org/10.1016/S0304-3800(97)00163-4).
- Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663. <https://doi.org/10.1111/jbi.12130>.
- Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., RoseCVAld, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. REVIEW: Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol.* 51, 1669–1679. <https://doi.org/10.1111/1365-2664.12289>.
- Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjäältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindblad, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämäs, 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>.
- Fluss, R., Faraggi, D., Reiser, B., 2005. Estimation of the youden index and its associated cutoff point. *Biom. J.* 47, 458–472. <https://doi.org/10.1002/bimj.200410135>.
- Fritz, Ö., Niklasson, M., Churski, M., 2009. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Appl. Veg. Sci.* 12, 93–106. <https://doi.org/10.1111/j.1654-109X.2009.01007.x>.
- Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecol. Indic.* 57, 420–434. <https://doi.org/10.1016/j.ecolind.2015.05.028>.
- Gosselin, F., Larrieu, L., 2020. Developing and using statistical tools to estimate observer effect for ordered class data: the case of the IBP (Index of Biodiversity Potential). *Ecol. Indic.* 110, 105884. <https://doi.org/10.1016/j.ecolind.2019.105884>.
- Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D., Wilson, S.K., 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518, 94–97. <https://doi.org/10.1038/nature14140>.
- Gustafsson, L., Perhans, K., 2010. Biodiversity Conservation in Swedish Forests: Ways Forward for a 30-Year-Old Multi-Scaled Approach. *AMBIO* 39, 546–554. <https://doi.org/10.1007/s13280-010-0071-y>.
- Hämäläinen, A., Fahrig, L., Strengbom, J., Ranius, T., 2023. Effective management for deadwood-dependent lichen diversity requires landscape-scale habitat protection. *J. Appl. Ecol.* N/a. <https://doi.org/10.1111/1365-2664.14429>.
- Harnik, P.G., Simpson, C., Payne, J.L., 2012. Long-term differences in extinction risk among the seven forms of rarity. *Proc. R. Soc. B Biol. Sci.* 279, 4969–4976. <https://doi.org/10.1098/rspb.2012.1902>.
- Hekkala, A.-M., Jönsson, M., Kärvelo, S., Strengbom, J., Sjögren, J., 2023. Habitat heterogeneity is a good predictor of boreal forest biodiversity. *Ecol. Indic.* 148, 110069. <https://doi.org/10.1016/j.ecolind.2023.110069>.
- Högbom, L., Abbas, D., Arnolaitis, K., Baders, E., Futter, M., Jansons, A., Jögeste, K., Lazdinis, A., Lukminė, D., Mustonen, M., Östiad, K., Poska, A., Rautio, P., Svensson, J., Vodde, F., Varnagirytė-Kabašinskiė, I., Weslien, J., Wilhelmsson, L., Zute, D., 2021. Trilemma of Nordic-Baltic Forestry—How to Implement UN Sustainable Development Goals. *Sustainability* 13, 5643. <https://doi.org/10.3390/su13105643>.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23. <https://doi.org/10.1146/annurev.es.04.110173.000245>.
- Hosmer Jr., D.W., Lemeshow, S., Sturdivant, R.X., 2013. *Applied Logistic Regression*. John Wiley & Sons, Incorporated, Newark, UNITED STATES.
- Hughes, T.P., Carpenter, S., Rockström, J., Scheffer, M., Walker, B., 2013. Multiscale regime shifts and planetary boundaries. *Trends Ecol. Evol.* 28, 389–395. <https://doi.org/10.1016/j.tree.2013.05.019>.
- Huo, L., Strengbom, J., Lundmark, T., Westerfelt, P., Lindberg, E., 2023. Estimating the conservation value of boreal forests using airborne laser scanning. *Ecol. Indic.* 147, 109946. <https://doi.org/10.1016/j.ecolind.2023.109946>.
- Hylander, K., Jonsson, B.G., 2007. The conservation ecology of cryptogams. *Biol. Conserv., Conserv. Ecol. Cryptogams* 135, 311–314. <https://doi.org/10.1016/j.biocon.2006.10.019>.
- Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., Liukko, U., 2019. Suomen lajien uhanalaisuus—Punainen kirja 2019. *Ymp. Suom. Ymp.*
- IUCN, 2024. The IUCN Red List of Threatened Species [WWW Document]. IUCN Red List Threat. Species. (URL <https://www.iucnredlist.org/en> (accessed 12.5.24)).
- Jackman, S., Tahk, A., Zeileis, A., Maimone, C., Fearon, J., Meers, Z., Jackman, M.S., Imports, M., 2015. Package ‘pscl’. *Political Sci. Comput. Lab.* 18.
- Kärvelo, 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>.
- Korhonen, K.T., Ahola, A., Heikkinen, J., Henttonen, H.M., Hotanen, J.-P., Ihalainen, A., Melin, M., Pitkänen, J., Rätty, M., Sirviö, M., Strandström, M., 2021. Forests of Finland 2014–2018 and their development 1921–2018. *Silva Fenn.* 55.
- Kropik, M., Zechmeister, H.G., Moser, D., Bernhardt, K.G., Dullinger, S., 2021. Deadwood volumes matter in epixylic bryophyte conservation, but precipitation limits the establishment of substrate-specific communities. *For. Ecol. Manag.* 493, 119285. <https://doi.org/10.1016/j.foreco.2021.119285>.
- Kyaschenko, J., Mielke, L., Jönsson, M., Hekkala, A.-M., Kärvelo, S., Sjögren, J., Clemmensen, K.E., Strengbom, J., 2025. Complex relationship between soil fungi and conservation value assessments in boreal forests. *Conserv. Biol.*, e70012 <https://doi.org/10.1111/cobi.70012>.

- Larrieu, L., Gosselin, F., Archaux, F., Chevalier, R., Corriol, G., Dauffy-Richard, E., Deconchat, M., Gosselin, M., Ladet, S., Savoie, J.-M., Tillon, L., Bouget, C., 2019. Assessing the potential of routine stand variables from multi-taxon data as habitat surrogates in European temperate forests. *Ecol. Indic.* 104, 116–126. <https://doi.org/10.1016/j.ecolind.2019.04.085>.
- Larrieu, L., Paillet, Y., Winter, S., Büttler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A. K., Regnery, B., Vandekerckhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecol. Indic.* 84, 194–207. <https://doi.org/10.1016/j.ecolind.2017.08.051>.
- Larsson Ekström, A., Sjögren, J., Djupström, L.B., Thor, G., Löfroth, T., 2023. Reinvention of permanent plots show that kelo lichens face an extinction debt. *Biol. Conserv.* 288, 110363. <https://doi.org/10.1016/j.biocon.2023.110363>.
- Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature* 422, 714–716. <https://doi.org/10.1038/nature01547>.
- McFadden, D., 1979. Quantitative Methods for Analysing Travel Behaviour of Individuals: Some Recent Developments. in: *Behavioural Travel Modelling*. Routledge.
- Mestre, L., Toro-Manríquez, M., Soler, R., Huertas-Herrera, A., Martínez-Pastur, G., Lencinas, M.V., 2017. The influence of canopy-layer composition on understory plant diversity in southern temperate forests. *For. Ecosyst.* 4, 6. <https://doi.org/10.1186/s40663-017-0093-z>.
- Müller, J., Büttler, R., 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *Eur. J. For. Res.* 129, 981–992. <https://doi.org/10.1007/s10342-010-0400-5>.
- 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>.
- 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>.
- Pearman, P.B., Weber, D., 2007. Common species determine richness patterns in biodiversity indicator taxa. *Biol. Conserv.* 138, 109–119. <https://doi.org/10.1016/j.biocon.2007.04.005>.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P. H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752. <https://doi.org/10.1126/science.1246752>.
- Rabinowitz, D., 1981. Seven forms of rarity in: Syngé, H., 1981. The biological aspects of rare plant conservation.
- 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 Bioinform.* 12, 77. <https://doi.org/10.1186/1471-2105-12-77>.
- Rudolph, J., Gustafsson, L., 2011. Forests regenerating after clear-cutting function as habitat for bryophyte and lichen species of conservation concern. *PLOS ONE* 6, e18639. <https://doi.org/10.1371/journal.pone.0018639>.
- Rudolph, J., Jönsson, M.T., Gustafsson, L., 2014. Biological legacies buffer local species extinction after logging. *J. Appl. Ecol.* 51, 53–62. <https://doi.org/10.1111/1365-2664.12187>.
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. *Ecol. Bull.* 11, 41.
- Skogsdata, 2024. Aktuella uppgifter om de svenska skogarna från SLU Riksskogstaxeringen.
- SLU Artdatabanken, 2020. Rödlistade arter i Sverige. Artdatabanken, SLU, Upps.
- Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* 17, 866–880. <https://doi.org/10.1111/ele.12277>.
- Svensson, J., Neumann, W., Bjärstig, T., Zachrisson, A., Thellbro, C., 2020. Landscape approaches to sustainability—aspects of conflict, integration, and synergy in national public land-use interests. *Sustainability* 12, 5113. <https://doi.org/10.3390/su12125113>.
- Sverdrup-Thygeson, A., 2001. Can “continuity indicator species” predict species richness or red-listed species of saproxylic beetles? *Biodivers. Conserv.* 10, 815–832. <https://doi.org/10.1023/A:1016679226554>.
- Swedish Forest Agency, 2020. Living trees and shrubs with nature values. *Lev. Tr. äd. och buskar Med natruvården*.
- Táborská, M., Kovács, B., Németh, C., Ódor, P., 2020. The relationship between epixylic bryophyte communities and microclimate. *J. Veg. Sci.* 31, 1168–1180. <https://doi.org/10.1111/jvs.12919>.
- Tälle, M., Ranius, T., Öckinger, E., 2023. The usefulness of surrogates in biodiversity conservation: a synthesis. *Biol. Conserv.* 288, 110384. <https://doi.org/10.1016/j.biocon.2023.110384>.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., Putten, W. H. van der, Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87, 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>.
- Van Couwenberghe, R., Collet, C., Lacombe, E., Gégout, J.-C., 2011. Abundance response of western European forest species along canopy openness and soil pH gradients. *For. Ecol. Manag.* 262, 1483–1490. <https://doi.org/10.1016/j.foreco.2011.06.049>.
- Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J., Lindenmayer, D., 2018. The exceptional value of intact forest ecosystems. *Nat. Ecol. Evol.* 2, 599–610. <https://doi.org/10.1038/s41559-018-0490-x>.
- Zeller, L., Baumann, C., Gonin, P., Heidrich, L., Keye, C., Konrad, F., Larrieu, L., Meyer, P., Sennhenn-Reulen, H., Müller, J., Schall, P., Ammer, C., 2022. Index of biodiversity potential (IBP) versus direct species monitoring in temperate forests. *Ecol. Indic.* 136, 108692. <https://doi.org/10.1016/j.ecolind.2022.108692>.