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Habitat heterogeneity is a good predictor of boreal forest biodiversity

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ABSTRACT

Reliable assessment measures are crucial for tracking changes in biodiversity and for evaluating the state of biodiversity. Two of the main drivers of biodiversity are habitat heterogeneity and resource amount. These drivers are used as proxies of biodiversity but assessing both is costly, limiting their practical use. To test which of the drivers best predicts the number and abundance of sessile species of conservation concern (including macrofungi, lichens, bryophytes, and vascular plants), we assessed forest stand heterogeneity using a method developed in Sweden ('Habitat Heterogeneity Score HHS'), and quantified the resource amount and quality of ecologically important structural variables (deadwood volume, basal area of living trees, proportion of broad-leaved trees, and the age of the oldest tree in the stand). We conducted the assessments in 77 boreal conifer-dominated forest stands in two regions of Sweden. Despite some group-specific organism differences, HHS was the best predictor of both number and abundance of all species of conservation concern, regardless of the region. Further, HHS was the best predictor of red-listed species number and abundance in the southern region, while a model including the volume of deadwood and the age of the oldest tree performed best in the northern region. Deadwood (CWD) volume was the single best resource amount predictor of the number and abundance of species of conservation concern, emphasizing the critical role that dead trees have for biodiversity. In addition, we calculated threshold values for deadwood volume and HHS depicting the level above which the number of red-listed species is significantly higher, and found this value to be higher in the southern region (22.4 m^3 ha^{-1} deadwood and a HSS value of 17) than in the north (20.0 m^3 ha^{-1} and 16). These values can be used as guidance when identifying coniferous forests with high enough qualities to support red-listed species. To conclude, the method of assessing habitat heterogeneity presented in this study is a practical and reliable way to identify forests of high biological diversity, and can therefore be part of the toolbox for sustainable forestry in boreal forests.

1. Introduction

Ensuring areas of high biological diversity are exempted from exploitation is a cornerstone in developing sustainable forestry. Knowledge on how biodiversity and conservation values are distributed across the landscape is, thus, a vital element of both forest management and conservation planning. Biodiversity assessment remains a challenge for practical conservation and forestry (Lindenmayer and Likens, 2010) because obtaining comprehensive and reliable data on biodiversity is extremely time consuming and expensive, and subsequently rarely possible. Nevertheless, with the escalating global concern about biodiversity loss, there is an urgent need for accurate measures to assess and report the status and direction of changes in biodiversity in different ecosystems (Brondizio et al., 2019; Independent Group of Scientists appointed by the Secretary-General, 2019).

The amount of resources (habitat amount) and the habitat heterogeneity (number of niches) are key components explaining positive species-area relationships (Schuler et al., 2015; Srivastava and Lawton, 1998; Wright, 1983), where resource-rich and heterogeneous habitats commonly harbour high species richness. Habitat heterogeneity, which

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is an umbrella term for habitat complexity/variability, including the quantity, quality, and breadth of resources and niche spaces, is positively correlated with biodiversity (Stein et al., 2014). At the same time, determining the main drivers of biodiversity is complicated as habitat heterogeneity commonly increases with an increasing amount of resources and habitat area (Kallimanis et al., 2008; Whittaker et al., 2001; Wright, 1983). Furthermore, species richness may show a unimodal or even more complicated responses to increasing habitat heterogeneity (Ben-Hur and Kadmon, 2020). The few studies that have examined the effect of one factor while keeping the other constant report either divergent (Báldi, 2008; Blakely and Didham, 2010) or context-dependent effects (Heidrich et al., 2020; Seibold et al., 2017). This suggests that an accurate practical method for assessing biodiversity should combine habitat heterogeneity with resource availability and amount. Ideally, such a method should include a number of ecologically important variables measured with a precision high enough to capture differences in amounts of a diverse set of resources (Heidrich et al., 2020; Kessler et al., 2011). One option is thus to assess forest biodiversity indirectly by quantifying the occurrence or amount of habitat structures that are associated with a high diversity of species of conservation concern. Such easily identifiable structural variables, indicator species or higher taxa/guilds are commonly used as proxies for biodiversity (Ćosović et al., 2020; Lindenmayer et al., 2000; Lindenmayer and Likens, 2010; McElhinny et al., 2005; Noss, 1990). Unfortunately, the empirical support for the reliability of such indirect methods is often poor (Gao et al., 2015; Vereecken et al., 2021) or based on subjective experiences or common knowledge from traditional management practices (Pullin et al., 2004; Sutherland et al., 2004).

Deadwood (CWD, coarse woody debris) is today a widely used indirect proxy for forest biodiversity (Gao et al., 2015; Lassauce et al., 2011). Deadwood volume and diversity have both been shown to be fairly good indicators of richness of deadwood-decaying fungi and saproxylic beetles (Similä et al., 2006; Brin et al,. 2009; Blasi et al., 2010; Djupström et al., 2010; Abrego and Salcedo, 2013; Seibold et al., 2015; Ylisirniö et al., 2016) or forest "naturalness" (Angelstam and Dönz-Breuss 2004; Kunttu et al., 2015). There is, however, a much weaker scientific consensus of the relationship between other forest structural features and non-saproxylic taxa, such as bryophytes and vascular plants (Gao et al., 2015), which may limit the applicability of deadwood as a general proxy of biodiversity.

Tree canopy cover and tree species mixtures in coniferous forests can have direct or indirect effects on species richness through their impact on microclimate and sun-exposure, growth and phenology of understory and, consequently, species that depend on understory vegetation (Coote et al., 2013; Felton et al., 2016; Willems et al., 2021). In very dense stands, the understory vegetation is hampered due to lack of light (Coote et al., 2013), but may through a stable microclimate favour cryptogams (Djupström et al., 2010; Madžule et al., 2012), leading to group-specific organism responses to canopy cover (Klein et al., 2020). In comparison to monocultures, forests with higher tree species diversity also support a greater biodiversity of other organism groups due to e.g., greater diversity of microhabitats (Cavard et al., 2011; Felton et al., 2016; Frisch et al., 2015; Klein et al., 2021). For this reason, forests with increasing proportion of broadleaved trees are assumed to generally support higher species richness of forest-dwelling species. In addition, tree age is often positively correlated with forest naturalness (Angelstam and Dönz-Breuss, 2004), and diversity of vascular plants (Coote et al., 2013; Gao et al., 2014), and there is evidence for a positive relationship between lichen species richness or abundance and tree age (Brunialti et al., 2010; Gao et al., 2015; Johansson, 2008). Forests with old trees may have longer continuity of microhabitats, which facilitates establishment of ecologically demanding and slow-growing mosses, lichens, and fungi.

The downside of using many of these ecologically important structural variables is that they require detailed information and calculations on volumes, proportions and diversity. To tackle the problems that appear in using single structure measures, a variety of so called composite measures have been developed for different ecosystems (e.g., Drakenberg and Lindhe 1999; Geburek et al., 2010; Oliver et al., 2014; Sabatini et al., 2016; Zeller et al., 2022). The common denominator among these measures is the ambition to describe the state of forest biodiversity in a simple way, preferably as a single index value. One of the most widespread indirect methods to assess the conservation value of forests in Sweden was developed by Drakenberg and Lindhe (1999). The method is also applied in other countries (e.g., in Denmark, Latvia, Armenia, Chile, China, USA, and Poland (B. Drakenberg, pers. comm.)) and is developed to function in several types of mature boreal forests. The method, hereafter referred to as "Habitat Heterogeneity Score" or "HHS", builds on forest disturbance dynamics and emphasises identifying natural forests through assessing forest complexity or heterogeneity. Similar principles are applied in the Index of Biodiversity Potential (see Larrieu et al., 2019) which is a method developed and tested for application in temperate forests (Zeller et al., 2022). Both methods aim to assess the biodiversity potential of a forest stand based on the presence of various habitat characteristics or structures, e.g., senescent trees, deadwood, and disturbance processes such as signs of natural disturbance dynamics, water etc. (Drakenberg and Lindhe, 1999; Zeller et al., 2022). However, despite the long history in forest biodiversity assessments in Sweden and other Nordic countries, no scientific evaluations of this or any other composite method to assess the biodiversity in boreal forests exists.

The aim of this study is to test and compare the precision of biodiversity assessments in boreal coniferous forests based on two different approaches, using either the Habitat Heterogeneity Score (HHS) (Drakenberg and Lindhe 1999) or the amount and quality of key resources known to be important for boreal forest biodiversity (i. e., deadwood volume, total basal area of living trees, proportion of broadleaved trees and the age of the oldest tree in a stand (e.g., Thorn et al., 2020)). We ask the following main questions: 1) how well do the HHS and habitat amount and quality variables predict the number of species of conservation concern?, and 2) does the result depend on type of organism group and region? We hypothesize that 1) the number and abundance of species of conservation concern are positively related with HHS and resource amount variables, 2) there are group-specific differences in the responses, 3) the relationships between biodiversity and HHS and resource amount and quality variables do not differ between North and South regions. In addition, we tested for the threshold values for the different measures for detecting significantly higher number of red-listed species, to guide the practical end-users of these measures. We use sessile species of conservation concern as a direct measure of biodiversity, because we argue that they reflect the state of biodiversity better than a random sample of common forest species. Further, sessile and specialist species can be more sensitive to changes in their environments than mobile and generalist species.

2. Methods

2.1. Study areas

The study was done in northern and south-central Sweden (Fig. 1), located in the boreal vegetation zone (Ahti et al., 1968). These two study regions were selected as they differ in management history, e.g., in terms of when the large-scale industrialised forestry was introduced (Angelstam, 1997) and the proportion of old forest in the landscape (Kärvemo et al., 2021). The northern region is less affected by forestry than the southern region, both in terms of a shorter history in forestry and greater amounts of old forests in the surroundings.

Within each region, we selected 40 mature (>65 years old in the southern region and >75 years old in the northern region) coniferous-dominated forest stands (Appendix A). Stand selection was based on the management class in forest owners' databases and the known tree species distribution. The forest stands ranged from structurally simple production forests with no known conservation values, to potential

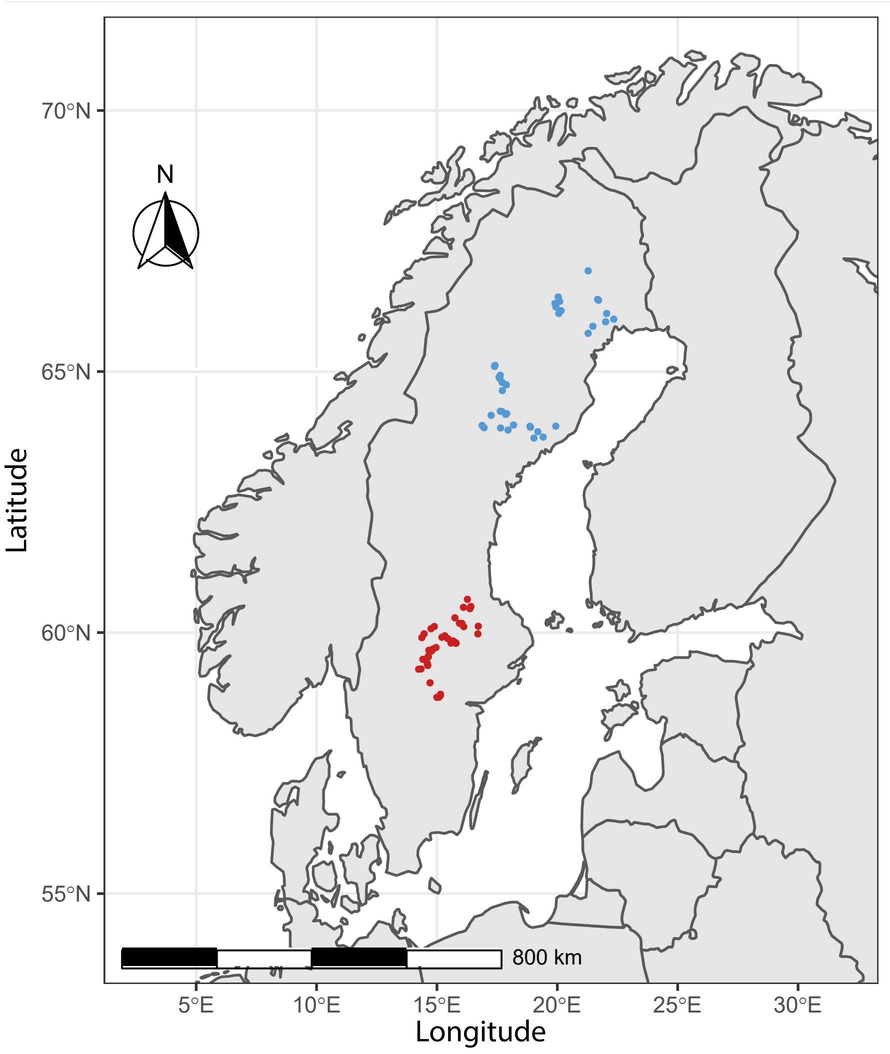

Fig. 1. The location of study sites in Sweden. Each dot represents a forest stand of at least 2 ha in size. N = 77 stands. The stands represented with blue belong to the northern region and stands with red to the southern region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Woodland Key Habitats (defined as an area with high conservation value in which red-listed species occur or are likely to occur (Nitare and Norén, 1992)). Most stands were classified as Western Taiga forests of mesic and moist bilberry (*Vaccinium myrtillus* L.) type (Natura 2000 habitat type 9010 (Anonymous, 2007)), with a few dryer and wetter stands (Appendix A). The stands were, according to the information in forest owners' databases, dominated by Norway spruce (*Picea abies* (L.) Karst) (>65 % spruce), or Scots pine (*Pinus sylvestris* L.) (>65 % pine), or were mixed coniferous (>65% spruce and pine), or mixed forests, with 35–41 % broadleaved trees, 29–61 % spruce and 2–30 % pine. Mixed coniferous and mixed forests were pooled in the analyses. One stand was dominated by broadleaved trees (>70 % of standing volume) and was consequently removed from analyses. Furthermore, two stands were omitted because they were harvested before all inventories were conducted. Finally, we ended up having 38 forest stands in the northern Sweden and 39 in southern Sweden, resulting in a total of 77 forest stands (21 spruce, 27 pine, 39 mixed). All three forest types occurred in both regions and there was no substantial difference in the richness (in all comparisons $p > 0.09$) or composition of species of conservation concern ($p > 0.08$) between forest types (Appendix B). A 2-ha study site was placed at the centre of each forest stand, and all the surveys (section 2.2.) were limited to this 2-ha study site even though some stands were substantially larger. By systematically placing the survey plot we ensured that the size of the stand does not affect the results, and that the structural measurements and species surveys were done in the same area.

2.2. Field measurements and calculations

2.2.1. The habitat heterogeneity score 'HHS'

The habitat heterogeneity scoring method we refer to was developed in late 20th century by a consultant company AB Skogsbiologerna (Drakenberg and Lindhe, 1999). According to the developers, the method can be used in any type of forest to measure its conservation value, does not require special education besides a short introduction course that is given for surveyors, and can be used to compare different forest stands. The surveyor uses a score sheet with 50 features per forest type (Appendix C) and systematically searches for the presences of stand characteristics (e.g., springs, boulders, shallow soils), signs of ecological processes typical to each forest type (e.g., fire, beavers, natural regeneration), and structures such as age-distribution of the stand, dead trees, trees with holes or other microhabitats. The survey is normally conducted all over the forest stand (0.5–10 ha when the stand is uniform), but in our study the survey was done in the 2-ha study site within the forest stand (see section 2.1.).The presence of each feature in the score sheet that illustrate the history, dynamics and characteristics of the study site is registered in the field protocol. The more quantitative features (structures, trees, deadwood) are registered if the site on average fulfils the criteria. Finally, the sum of all registered features result in the score of the site, hereafter '*Habitat Heterogeneity Score*' or '*HHS*'. The score is an integer value ranging from 0 to 50, where a higher score indicates a higher habitat heterogeneity, but in practise the score rarely exceeds 30 (Drakenberg and Lindhe, 1999). The features differ according to forest main disturbance types and geographical zones, in our study we use the general boreal score template and the forest types mainly belonged to "sites with a history of strong fire disturbances dominated by pine with a mixture of broadleaves in later successional stages" and "sites with small-scale disturbances, dominated with spruce" (see Appendix C). In general, spruce forests reach slightly higher values than pine forests, which is due to absence of natural fires in most today's pine forests.

The consultant company Greensway AB conducted the Habitat Heterogeneity Score assessments during 2017–2018. The survey is normally conducted all over the forest stand when the stand is uniform, but in our study the survey was limited to a 2-ha study site within the forest stand (see section 2.1.). The method is described in more detail in Blicharska (2005), where it is called "The Swedish Assessment", and in Appendix C.

2.2.2. The resource amount and quality measures

Field surveyors from The Swedish Forest Agency conducted detailed measurements of the forest structural variables in the 77 forest stands between 2015 and 2018. The measurements were conducted from systematically arranged transects throughout the 2-ha study site. Each transect was divided into 20–30 sections of 20 m in length and 4 m in width (80 m^2 each). The area surveyed in each stand was approximately 0.2 ha (range 0.16–0.24 ha). All living trees with diameter at breast height (dbh) $>$ 4.5 cm were measured within each transect, and obtained data were used for the calculations of the basal area of each tree species within the stand (m^2/ha). The proportion of broadleaved trees was calculated using the basal areas. All down dead trees (logs) $\geq$ 10 cm in diameter were measured within the borders of the 20 m * 4 m sections by measuring the base and top diameter (minimum 10 cm) and the length of the log between these two points. The decay class (1–4) was estimated following Swedish National Forest Inventory instructions (1 being a hard, recently dead tree, and 4 being a soft, decayed tree). When shorter than 1.3 m, standing dead trees and stumps over 50 cm in height were surveyed by measuring dbh or stump top diameter and height. The dbh and standing height were measured or estimated for the stumps taller than 1.3 m and broken trees. Volume (V) of logs was calculated with the formula of a truncated cone : $V = (r^2 + r \times R + R^2)(\pi^* h)/3)$, where r is the top radius of the log, R is the base radius of the log and h is the length of the log. For the volume of standing dead trees, a simple secondary function $V = 0.12 \times dbh^{2.5}$, was used, because the height of the tree was not always measured. Volume of stumps and broken trees taller than 0.5 m was calculated with a help of a taper function $d_2 = d_1 - h \times (a \times d1 + b)$, where d_2 is the top diameter, d_1 is the dbh and h is the height of the stump, a and b are species-specific taper coefficients. The coefficients have been developed by Swedish Forest Agency (Wijk, 2017) from field data of logs (see Appendix B for the used coefficients). The base diameter of stumps and broken trees was systematically set to be 10 % greater than dbh. After obtaining the top and base diameters, the stump volume was calculated with the formula of a truncated cone. Volumes of logs, standing dead trees, and stumps were summed up to represent deadwood (CWD) volume, and standardized to m^3/ha by using the area of measured the transects. Two of the living pines and spruces that the surveyor estimated to be the oldest within the 2-ha stand were cored at dbh, and a microscope was then used to determine the age of the trees. The oldest of those four trees was used in analyses representing the longevity of the tree cover, and as a measure of habitat quality. Because different forest structural variables are highly correlated with each other, we focused on the four resource amount and quality measures that are shown to be important for boreal forest biodiversity for the analyses (deadwood volume, basal area of living trees, proportion of broadleaved trees and the age of the oldest tree), but present the correlation matrix of all variables as supporting information (Appendix B).

2.2.3. Species of conservation concern

In order to test the precision of the indirect methods, we used surveys of 'species of conservation concern'. The list of species of conservation concern is a well-defined group of species that are relatively common, easy to find and identify in the field, strongly associated with forests with high conservation value, and rarely occur in structurally deprived forests (e.g., homogenous even-aged stands) (Pearson, 1994; Swedish Forest Agency, 2014). The list includes 648 species acknowledged to signal occurrences of red-listed species or species that are especially demanding in their habitat requirements (Swedish Forest Agency, 2014). The list was developed in 1990′s and is today widely accepted and used in forest inventories across Sweden (Nitare, 2019; Swedish Forest Agency, 2014). Many of the species of conservation concern are positively correlated with the number of red-listed species or overall high biodiversity within the same stand (Fritz et al., 2008; Gustafsson et al., 2004; Mezaka et al., 2012; Perhans et al., 2007; Timonen et al., 2011).

Within the 2-ha study site in each of the 77 stands (see section 2.1), a pair of experienced professional species surveyors from Swedish Forest Agency systematically searched for the occurrences of vascular plants, bryophytes, macrofungi, and lichens of conservation concern. The surveyed 2-ha area was first divided into sections and marked in the field, and then each section was thoroughly surveyed by both experts. All species included in the survey can be observed during the summer and fall season, when the species survey was conducted. Some of the macrofungi fruiting bodies may be missed, as at the time of the survey they might not have developed fruiting bodies. However, as most species in the list are either perennial or can be identified from older fruiting bodies, this is likely of minor significance. Further, most surveys took place in August, which is the optimal time to notice most species.

The abundance of each species was assessed by counting the occurrences of the species; for ground- and/or rock-living species the abundance measure was the count of 1 dm^2 quadrates. For wood- or tree-living species, the abundance measure was based on the number of substrate items the species inhabited. The full species list with respective abundances and red-list classifications are given in Appendix B.

2.3. Data analyses

Statistical analyses were performed in R version 4.02 (R Development Core Team, 2020). We considered species richness and number of records and cover (abundance) as response variables, dividing them to organism groups: 1) lichens, 2) macrofungi, 3) bryophytes, and 4) vascular plants, and considering all species of conservation concern, or nationally red-listed species (IUCN categories EN, VU, NT (ArtDatabanken, 2015)). Because northern and southern study regions differ significantly in forest management history, we modelled the regions separately. The relationships between the predictors (resource amount and quality measures or HHS) and the response variables were modelled with Generalized Linear Models using negative binomial error distribution as it provided better fit for occasionally overdispersed data (function glm.nb in MASS-package (Venables and Ripley, 2002)). We created two models for each response variable and study region: 1) the habitat heterogeneity model, where the HHS was used as the predictor variable for the richness and abundance of species, and 2) the resource amount and quality model, where the four pre-selected non-correlating structural variables (deadwood volume, basal area of living trees, proportion of broadleaved trees and the age of the oldest tree) were used (see Appendix B for correlation matrix). Data on proportional scales were Arcsine square root transformed and deadwood volume was $\log_{10}$-

tranformed to achieve a normal distribution of the variables (Crawley, 2007). The full model, including all resource amount and quality predictors, was used as the baseline for model averaging, and the set of predictors significantly explaining the variation in the richness of species were selected by model averaging to represent the final resource amount model (conditional average, package MuMIn (Barton, 2020)). We quantified the variation explained by the two models (the habitat heterogeneity model and the resource amount and quality model) by calculating an adjusted coefficient of determination (Adjusted Nagelkerke's pseudo R^2) based on maximum likelihood as suggested by Zhang (2017) and Nagelkerke (1991) (R package rcompanion (Mangiafico, 2020)). The final models were compared with AIC, where the models with $\Delta AIC < 2$ were considered equally good. The model predictions were plotted using sjPlot-package (Lüdecke, 2021). The effect sizes (Incidence Rate Ratio IRR) and their 95% confidence intervals are reported for each explanatory variable.

Finally, we calculated threshold values for HHS and the resource amount and quality measures above which we have significantly ($\alpha = 0.01$) higher richness of red-listed species. We used the richness of red-listed species as response variable, because their richness can be seen as a proof of conservation value of the stands. The calculations were done with the R package party, function ctree (Hothorn et al., 2006). This function calculates conditional inference trees by binary recursive partitioning to find statistically significant split(s) for one or more critical thresholds. We used 5000 Monte Carlo permutations to obtain p-values for the splits.

3. Results

In total, we recorded 13,477 occurrences of 159 species of conservation concern. Over 40% of the species (68 species with 8868 occurrences) were red-listed according to ArtDatabanken (2015) (Appendix B). The total number of species of conservation concern was similar across the two study regions; 120 species in the southern region and 112 species in the northern region, but the average richness per stand was less than half in the south region in comparison to the north (Table 1). Red-listed species were considerably more numerous at stand scale in the northern region, with a four-fold higher average richness in comparison to the southern region. Regarding the forest structural measures, forests in the southern region were slightly denser (measured by the stand basal area), contained less broadleaved trees, and were younger in terms of the oldest tree in the stand (Table 1). The HHS and deadwood volume were similar between the regions (Table 1.)

Table 1
The richness and abundances (stand mean ± s.d.) of species of conservation concern and the model predictors in northern and southern study regions. The p-values are based Welch two-sample t-tests or non-parametric Wilcoxon tests (for species richness and abundances) between northern and southern regions. Significant differences ($p < 0.05$) are shown in bold. "Total" refers to all species of conservation concern. Number of stands (n) included were 77.

	Northern region	Southern region	p
Total richness	20.8 ± 9.2	9.6 ± 6.7	**<0.001**
Total abundance	274.4 ± 160.6	47.2 ± 46.2	**<0.001**
Red-listed richness	13 ± 6.3	3.1 ± 2.4	**<0.001**
Red-listed abundance	205.8 ± 128.5	10.0 ± 10.5	**<0.001**
Macrofungi richness	5.8 ± 3.7	2.6 ± 2.7	**<0.001**
Macrofungi abundance	38.8 ± 46.1	8.7 ± 10.7	**<0.001**
Lichen richness	11.6 ± 5.4	3.6 ± 2.9	**<0.001**
Lichen abundance	204.4 ± 119.9	18.4 ± 22.6	**<0.001**
Bryophyte richness	0.8 ± 1.2	2.3 ± 2.3	**0.002**
Bryophyte abundance	6.5 ± 12.9	11.3 ± 16.2	**0.027**
Vasc. plant richness	2.6 ± 1.9	1.2 ± 1.9	**<0.001**
Vasc. plant abundance	24.7 ± 42.6	8.8 ± 29	**<0.001**
Habitat Heterogeneity Score	16.6 ± 7.1	13.9 ± 5.8	0.07
Volume CWD m^3/ha	18.6 ± 16.3	17.3 ± 21.6	0.26
Basal area of living trees m^2/ha	23.6 ± 7.8	28.1 ± 7.9	**0.015**
Proportion of broadleaved trees	0.2 ± 0.1	0.1 ± 0.1	**<0.001**
Age of the oldest tree	189.2 ± 75.3	149.1 ± 53.4	**0.009**

3.1. *Relationship between species richness and HHS and resource amount and quality*

3.1.1. *All species of conservation concern and red-listed species*

There was a significant positive relationship between the HHS and the number of species of conservation concern in both study regions (Table 2, Fig. 2). The resource amount and quality model that best explained richness of all species of conservation concern included CWD volume, but was significantly weaker than the habitat heterogeneity model in both study regions (Table 2). Further, the HHS was the best predictor of the abundance of all species of conservation concern and red-listed species (Table 3.) Only richness of red-listed species in the northern region deviated from the pattern, being best explained by the resource amount and quality model that included CWD volume and the age of the oldest tree (Tables 2 and 3, Fig. 3).

3.1.2. *Organism group-specific responses*

In terms of abundance, lichens of conservation concern were by far the most dominant organism group in the study, with 50 species and 9096 records. The richness of lichen species in the southern region was on average less than half compared to the northern region (Table 1), ranging from 0 to 13 species per stand in the south (37 species in total) in comparison to 2 to 23 in the north (42 species in total). In the south, none of the structural variables could improve the resource amount and quality model and the HHS was a poor predictor of lichen species richness ($R^2 < 0.2$). In the northern region, lichen richness was best predicted by HHS (Table 4, Appendix B).

Macrofungi was the most species rich organism group in our dataset of species of conservation concern, with 54 species and 2046 records ranging between 0 and 11 species/stand in the south (37 in total) and 0–13 species/stand in the north (41 in total). Richness was best predicted by the HHS in the southern region, but CWD volume was slightly better predictor than the habitat heterogeneity score in the north (Table 4). Adjusted R^2 indicated a moderate model fit in the south, but was rather low in the north (Table 4, Appendix B).

In total, 30 bryophyte species of conservation concern were recorded, 27 species in the southern region (range 0 to 8 per stand) and 10 species in the northern region (0 to 5 per stand). The HHS and CWD volume were equally good in explaining the richness of bryophytes in the southern region, while in the northern region HHS predicted species richness significantly better (Table 4, Appendix B).

In total, 25 species of vascular plants of conservation concern were recorded in the south, ranging from 0 to 10 species per stand, and 16 species in the north (0 to 7 per stand). Their richness was best explained by CWD volume and the age of the oldest tree in a stand in the south, where age had a negative relationship with the richness. In the northern region the total basal area was selected as the only significant variable in the resource amount and quality model (Table 4). HHS had a positive but weak relationship with vascular plant richness in both regions (Table 4, Appendix B).

3.2. *Thresholds for high red-listed species richness*

In the southern region, the threshold value for HHS was 17, indicated by on average a 128% higher species richness of red-listed species in sites that scored 18 or higher than those, that scored 17 or less (mean richness increased from 2.8 to 5.2). In the north, the threshold value was 16, indicated by on average a 95% higher species richness of red-listed species in sites that scored 17 or higher than those, that scored 16 or less (mean richness increased from 9.3 to 18.1). For CWD volumes, the threshold values were 20 m^3 ha^{-1} in the northern region and 22.4 m^3 ha^{-1} in the southern region. The forest stands that contained more CWD

Table 2
The results of the two competing models explaining the richness of all species of conservation concern and red-listed species in forest stands. The proportion of explained variation by each model is given using Adjusted Nagelkerke R^2 ($R^2_{Adj.N}$). Models with $\Delta AIC < 2$ are considered equally good. The best model is shaded with grey; the darker the shade, the higher the R^2 value (cutting points for darker shades $R^2 \geq 0.2$; $R^2 \geq 0.4$; $R^2 \geq 0.6$). IRR = Incidence Rate Ratio, CI = Confidence intervals (0.95). N = 39 in the south and 38 in the north.

		Habitat heterogeneity model			Resource amount and quality model		
Response variable	**Predictors**	**IRR**	**CI**	**p**	**IRR**	**CI**	**p**
Richness of all species of conservation concern: South	(Intercept)	2.43	1.75 – 3.33	<0.001	3.10	1.98 – 4.81	<0.001
	Habitat Heterogeneity Score	1.09	1.07 – 1.11	<0.001			
	CWD volume				1.54	1.31 – 1.81	<0.001
	$R^2_{Adj.N}$		*0.91*			*0.43*	
	ΔAIC					*10.7*	
Richness of all species of conservation concern: North	(Intercept)	9.35	7.03 – 12.41	<0.001	8.76	6.00 – 12.76	<0.001
	Habitat heterogeneity Score	1.05	1.03 – 1.06	<0.001			
	CWD volume				1.37	1.20 – 1.57	<0.001
	$R^2_{Adj.N}$		*0.49*			*0.36*	
	ΔAIC					*8.0*	
Richness of red-listed species: South	(Intercept)	0.96	0.52 – 1.72	0.888	0.59	0.25 – 1.32	0.211
	Habitat heterogeneity Score	1.08	1.04 – 1.12	<0.001			
	CWD volume				1.41	1.16 – 1.72	0.001
	Age of the oldest tree				1.00	1.00 – 1.01	0.009
	$R^2_{Adj.N}$		*0.33*			*0.32*	
	ΔAIC					*2.1*	
Richness of red-listed species: North	(Intercept)	6.08	4.33 – 8.50	<0.001	3.49	2.28 – 5.28	<0.001
	Habitat Heterogeneity Score	1.04	1.03 – 1.06	<0.001			
	CWD volume				1.35	1.19 – 1.53	<0.001
	Age of the oldest tree				1.00	1.00 – 1.00	0.001
	$R^2_{Adj.N}$		*0.22*			*0.55*	
	ΔAIC		*8*				

than the threshold values hosted 86 % and 104 % more red-listed species in the north and south, respectively (Appendix B.)

4. Discussion

4.1. Habitat Heterogeneity Score as an indicator of conservation value

Despite resource (habitat) amount and habitat heterogeneity being known as the main drivers of biodiversity, it is still a challenge to find proxies that capture the causal relationship for a multitude of taxa, as illustrated recently in, e.g., Larrieu et al. (2019), Penone et al. (2019), Kärvemo et al. (2021) and Zeller et al. (2022). Nevertheless, our results lead us to conclude that the Habitat Heterogeneity Score (HHS) is a reliable proxy for both the total richness and abundance of sessile species of conservation concern, and even for the more demanding red-listed species. The HHS was especially good in predicting the richness of species in the southern study region ($R^2 = 0.91$). Most importantly, there was a consistent positive relationship between the HHS and species richness, regardless of organism group.

The most plausible explanation for the clear positive associations is that HHS accounts for the presences of the most important structural variables for boreal forest biodiversity. Apart from the strong relationship between deadwood, saproxylic insects and wood-decaying fungi, resource amount of single resources can rarely explain species richness, even less so for multitaxon richness (Gao et al., 2015; Larrieu et al., 2019; Lassauce et al., 2011; Seibold et al., 2015). Even when we simultaneously included several ecologically important forest structural measures that should encompass a wide range of available resources, the resource amount and quality model did not outperform the HHS, which was almost always the best predictor of both species richness and

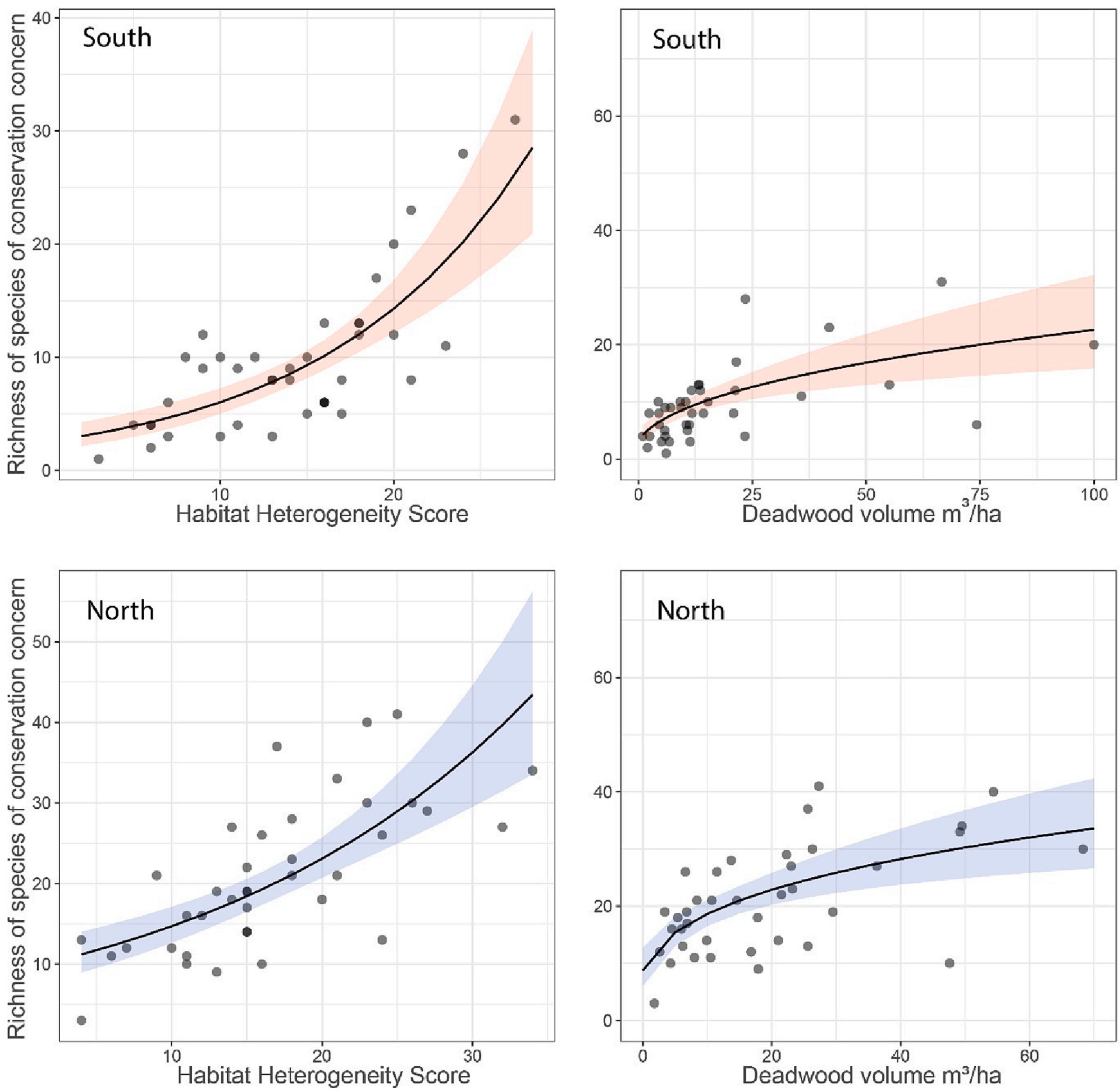

Fig. 2. Richness of species of conservation concern plotted against the Habitat Heterogeneity Score and the best predictors in resource amount model based on model averaging (see Table 2). Forest stands situated in the southern region are illustrated with red and forests in the northern areas with blue. The curves depict predicted means based on negative binomial GLMs and the ribbons depict the confidence intervals (0.95) of predicted values. Original data point values are shown as dots, where darker dots illustrate overlapping points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

abundance. Similar findings were obtained by Zeller et al. (2022), who tested an Index of Biodiversity Potential against large variety of organism groups in temperate forests. They found several positive, and no negative, relationships between their composite measure and species richness, but the effect sizes were usually low. In this study, we were specifically interested in species of known conservation value, emphasising our goal of finding the hotspots using the biodiversity assessment. Using the subset of specialized species possibly reduces the variation in species richness between the different stands and enables stronger relationships. Furthermore, our study included a wide variation of forests in terms of presumed conservation value, ranging from biodiversity hotspots (highest score 34) to intensively managed production forest with presumed lower conservation value (lowest score 3), thus covering the whole range of the practical values of the method.

Repeatable and transparent methods to assess biodiversity are a prerequisite for safeguarding biodiversity and developing sustainable management strategies. The HHS is repeatable, but in comparison to quantitative measures of resource amount and quality (such as volume of deadwood per hectare or proportion of broadleaved trees) it is less transparent. In support for the HSS, however, the result is relatively simple to communicate since the value is intuitive and we have shown that a threshold value can be calculated from it. Although our threshold values (16 for the north and 17 for the south) suggest that the HSS scores can be used to identify forest with a high diversity of red-listed species, we stress that this type of surrogate measures should be seen as guidance, and that such values never can overtrump the actual occurrence of species of conservation concern. In addition, the great difference in species richness between the two study regions with similar HHS emphasises that the method cannot be used to compare conservation values across regions. Consequently, one should only use the values to compare the conservation values of forest stands within regions of similar forest management history. When used correctly, though, the threshold values can reliably guide the decision-making. The simplicity of the method also has potential for citizen science projects.

Table 3
The results of the two competing models explaining the abundance (number of records) of all species of conservation concern and red-listed species on forest stands. The proportion of explained variation by each model is given using Adjusted Nagelkerke R^2 ($R^2_{Adj.N}$). Models with $\Delta AIC < 2$ are considered equally good. The best model is shaded with grey; the darker the shade, the higher the R^2 value (cutting points for darker shades $R^2 \geq 0.2$; $R^2 \geq 0.4$; $R^2 \geq 0.6$). IRR = Incidence Rate Ratio, CI = Confidence intervals (0.95). N = 39 in the south, 38 in the north.

		Habitat heterogeneity model			Resource amount and quality model		
	Predictors	**IRR**	**CI**	**p**	**IRR**	**CI**	**p**
Abundance of Species of conservation concern:: South	(Intercept)	11.26	6.33 – 20.51	<0.001	16.45	8.80 – 32.27	<0.001
	Habitat Heterogeneity Score	1.10	1.06 – 1.14	<0.001			
	CWD volume				1.50	1.17 – 1.92	0.001
	$R^2_{Adj.N}$		*0.38*			*0.21*	
	ΔAIC					*9.4*	
Abundance of Species of conservation concern: North	(Intercept)	82.26	49.29 – 140.26	<0.001	44.83	18.94 – 111.76	<0.001
	Habitat Heterogeneity Score	1.07	1.04 – 1.10	<0.001			
	Age of the oldest tree				1.00	1.00 – 1.01	<0.001
	Basal area of living trees				1.04	1.01 – 1.06	0.004
	$R^2_{Adj.N}$		*0.36*			*0.29*	
	ΔAIC					6	
Abundance of Red-listed species: South	(Intercept)	1.96	0.74 – 5.41	0.132	2.69	0.75– 9.78	0.060
	Habitat Heterogeneity Score	1.11	1.04 – 1.19	<0.001			
	Age of the oldest tree				1.01	1.00 – 1.02	0.011
	$R^2_{Adj.N}$		*0.21*			*0.09*	
	ΔAIC					*5.3*	
Abundance Red-listed species: North	(Intercept)	64.17	36.84 – 115.15	<0.001	94.39	50.72 – 180.06	<0.001
	Habitat Heterogeneity Score	1.07	1.03 – 1.10	<0.001			
	Age of the oldest tree				1.00	1.00 – 1.01	0.008
	$R^2_{Adj.N}$		*0.30*			*0.14*	
	ΔAIC					7.9	

4.2. The importance of amount and quality of resources for species of conservation concern

Volume of deadwood is one of the EU-level indicators used to quantify the state of forests' biological diversity (Barbati et al., 2014; Bozzano and Oggioni, 2020), and our results clearly support the central role of dead trees in facilitating boreal forest biodiversity, especially red-listed species richness. Volume of deadwood turned out to be the single most important habitat amount variable explaining the overall richness of species of conservation concern. This is an important finding because the assembly of species included in this study is not limited to species directly dependent on dead trees as a substrate or resource. Our results are in accordance with studies demonstrating that volume of deadwood and tree age are good indicators of forest naturalness (Fritz et al., 2008; Kunttu et al., 2015). We therefore argue that in boreal coniferous forests (which are not affected by recent disturbances), the volume of CWD can be a proxy for the stability and "naturalness" of the stands, and can thus serve as a general proxy for the conservation value of a stands. The

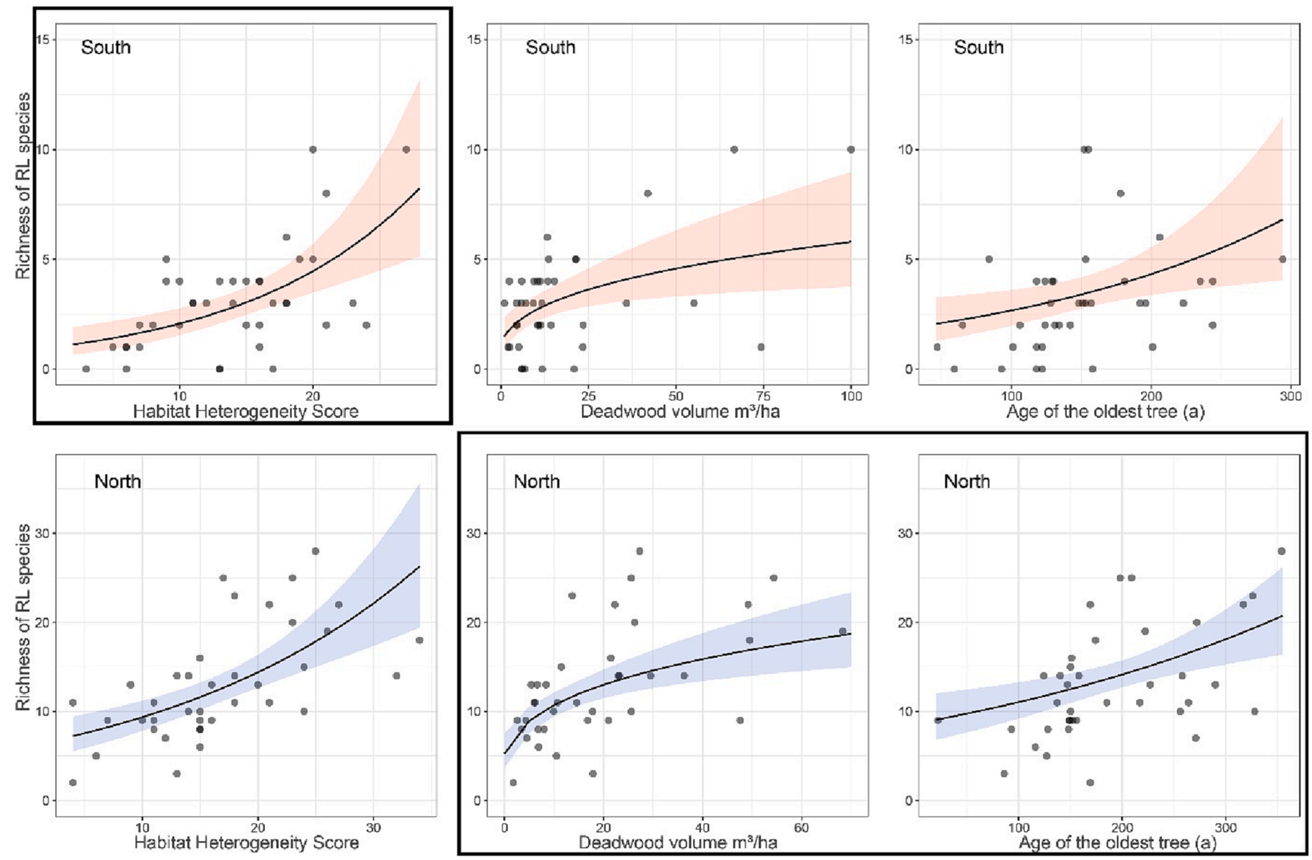

Fig. 3. Richness of red-listed species plotted against the Habitat Heterogeneity Score and the best predictors in resource amount and quality model based on model averaging. Forest situated in the southern region are illustrated with red and forests in the northern areas with blue. The best performing model for each region is framed (see Table 2). The curves depict predicted means based on negative binomial GLMs and ribbons depict the confidence intervals (0.95) of the predicted values. Original data point values are shown as dots, where darker dots illustrate overlapping points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

threshold value for CWD for a high probability of finding red-listed species was 20 m^3/ha in the north, and slightly higher in the south. This is in agreement with the deadwood threshold values suggested for the occurrences of threatened fungi in boreal forests, 20 m^3/ha (Penttilä et al., 2004). Even though some species require greater amounts of dead wood for survival (Müller and Bütler, 2010), we suggest that our threshold values for CWD can be used as a general guide for the amount of deadwood needed to support high richness of red-listed species in boreal forests. The CWD in our stands comprises various qualities, though, which is not accounted for in this analyses. Therefore, we must stress that the threshold is not an absolute value for "sufficient" amount of deadwood.

The age of the oldest tree in the forest stand was an important indicator for the abundance and richness of red-listed species, albeit the low explained variation. The reason may lie in the dominant red-listed species that share similar habitat requirements; lichen *Alectoria sarmentosa* (NT, 4309 obs.), fungi *Pseudographis pinicola* (NT, 1091 obs.) and lichen *Chaenotheca subroscida* (NT, 1089 obs.) all require old trees and a humid, stable microclimate (Nitare, 2019). Tree age can be a good proxy for tree cover continuity, and our results indeed show the importance of old trees for the populations of species of conservation concern. In certain conditions, for example if legacy elements such as old or decaying trees exist (Rudolphi et al., 2014; Rudolphi and Gustafsson, 2011), the species of conservation concern can survive even on clear-cuts, but very old stands (over 200 years) are often required for high species densities of, e.g., red-listed lichens (Larrieu et al., 2019; Moning and Müller, 2009). The species with low colonization rates can probably occur abundantly only on older trees or in stands with old trees and advanced decay classes (Moor et al., 2021; Nordén et al., 2018). Such stands, especially when spruce-dominated, have shady and cool microclimates, which probably explains the negative relationship between vascular plant richness and tree age. Further, the very old coniferous stands in boreal forests tend to be bryophyte- or lichen-covered, leaving little possibilities for the germination of vascular plants (e.g., Jalonen and Vanha-Majamaa, 2001).

The basal area of all living trees can indicate the canopy closure of a stand, which we expected to be negatively associated to the vascular plant richness. Indeed, the basal area turned out to be an important variable for vascular plants in the northern region, but in contrast to our expectations, the relationship was positive. We believe that the explanation for this lies in the generally positive correlation between productivity and species richness. A study from Minnesota, USA, shows that higher basal area can decrease understory vascular plant richness, but also that low light alleviates competitive exclusion from dominant understory species, indirectly leading to increased species richness (Reich et al., 2012). Without the explicit measurements of more components of the understory community, we however cannot be sure that this is also the mechanism in the northern stands of our study.

Surprisingly, tree species mixture in terms of proportion of broadleaved trees did not appear as an important variable in any of the models. We expected to see responses especially on vascular plants and lichens, as these and many other taxa have been shown to positively respond to increasing tree diversity (e.g., Cavard et al., 2011; Felton et al., 2016; Klein et al., 2021; Penone et al., 2019). We suggest the lack of relationship to result from high dominance of conifers in our stands. This is in accordance with Kärvemo et al (2021), who found that only

Table 4

The results of the two competing models explaining the richness of species of conservation concern, separated into organism groups. The proportion of explained variation by each model is given using Adjusted Nagelkerke R^2 (R^2_{AdjN}). Models with $\Delta AIC < 2$ are considered equally good. The best model is shaded with grey, where the darkness in grayscale indicates increasing R^2 (cutting points for darker shades $R^2 \geq 0.2$; $R^2 \geq 0.4$; $R^2 \geq 0.6$). IRR = Incidence Rate Ratio, CI = Confidence intervals (0.95). N = 39 in South, 38 in North.

		Habitat heterogeneity model			Resource amount and quality model		
	Predictors	**IRR**	**CI**	**p**	**IRR**	**CI**	**p**
Lichens: South	(Intercept)	1.60	0.82 – 3.04	0.167	3.56	2.75 – 4.61	<0.001
	Habitat Heterogeneity Score	1.06	1.01 – 1.10	0.011			
	$R^2_{Adj.N}$		*0.14*			*0.000*	
	ΔAIC					*4.2*	
Lichens: North	(Intercept)	5.48	3.91 – 7.65	<0.001	5.54	3.50 – 8.75	<0.001
	Habitat Heterogeneity Score	1.04	1.03 – 1.06	<0.001			
	CWD volume				1.31	1.12 – 1.54	0.001
	$R^2_{Adj.N}$		*0.37*			*0.22*	
	ΔAIC					*8.1*	
Macro-fungi: South	(Intercept)	0.47	0.22 – 0.98	0.051	0.60	0.27 – 1.24	0.180
	Habitat Heterogeneity score	1.11	1.07 – 1.17	<0.001			
	CWD volume				1.73	1.35 – 2.26	<0.001
	$R^2_{Adj.N}$		*0.41*			*0.33*	
	ΔAIC					*4.8*	
Macro-fungi: North	(Intercept)	2.60	1.57 – 4.26	<0.001	1.92	1.05 – 3.43	0.030
	Habitat Heterogeneity Score	1.05	1.02 – 1.07	<0.001			
	CWD volume				1.49	1.22 – 1.83	<0.001
	$R^2_{Adj.N}$		*0.24*			*0.29*	
	ΔAIC		*2.5*				
Bryophytes: South	(Intercept)	0.38	0.16 – 0.84	0.021	0.35	0.15 – 0.78	0.010
	Habitat Heterogeneity Score	1.12	1.07 – 1.17	<0.001			
	CWD volume				1.98	1.51 – 2.65	<0.001
	$R^2_{Adj.N}$		*0.42*			*0.40*	
	ΔAIC					*1.1*	
Bryophytes: North	(Intercept)	0.12	0.03 – 0.41	0.001	0.11	0.02 – 0.50	0.009
	Habitat Heterogeneity Score	1.11	1.04 – 1.18	0.001			
	CWD volume				2.02	1.22 – 3.52	0.011
	$R^2_{Adj.N}$		*0.25*			*0.18*	
	ΔAIC					*3.5*	
Vascular plants: South	(Intercept)	0.27	0.08 – 0.87	0.044	1.38	0.26 – 7.23	0.689
	Habitat Heterogeneity Score	1.10	1.02 – 1.18	0.019			
	CWD volume				1.63	1.07 – 2.55	0.022
	Age of the oldest tree				0.99	0.98 – 1.00	0.021
	$R^2_{Adj.N}$		*0.15*			*0.23*	
	ΔAIC		*1.6*				
Vascular plants: North	(Intercept)	1.44	0.76 – 2.66	0.245	1.01	0.51 – 1.95	0.980
	Habitat Heterogeneity Score	1.03	1.00 – 1.07	0.041			
	Basal area of living trees				1.04	1.01 – 1.06	0.003
	$R^2_{Adj.N}$		*0.10*			*0.18*	
	ΔAIC		*3.6*				

bryophytes were positively associated with a high proportion of broadleaved trees. Further, the species of broadleaved trees were mostly birches (*P. pendula* and *P. pubescens*), only 25 the stands contained aspen (*P. tremula*), and even fewer alders, rowans or willows, showing that the stands are generally poor in tree species diversity which is typical for Fennoscandian boreal forests.

4.3. Differences between organism groups

Because biodiversity assessments should preferably cover as many species groups as possible (Burrascano et al., 2018; Kessler et al., 2011), proxies should in order to be functional, also predict diversity for several organism groups. In our study, the variation explained by HHS as a proxy was mostly rather low for individual organism groups (R^2-values ranging between 0.1 and 0.42). However, as all organism groups showed a positive association to the HHS, we argue that the score is a useful tool for assessing conservation value in boreal forests.

The variation explained by the habitat heterogeneity model was lowest for vascular plants. This confirms vascular plants as poor indicators of conservation value in boreal forests (Gustafsson, 2000) but contradicts many of the studies conducted in temperate zones (Burrascano et al., 2018; Coote et al., 2013) and emphasises that proxies for biodiversity may not be functional across biogeographical regions. However, as the exclusion of vascular plants from our models decreased the fit of the all-species model (results not shown), we suggest that it is still valuable to include vascular plants when assessing conservation values of boreal forests.

The bryophytes deviated from other organism groups by being more diverse in the southern region (see also Kärvemo et al., 2021). A low species richness in the north, where the majority of the occurrences constituted of two species representing only two distinct habitats: *Crossocalyx hellerianus* living on dead wood and *Hylocomiastrum umbratum* on the ground, could potentially explain why richness was poorly explained by HHS in this region. In contrast, HHS was a good predictor of bryophyte richness in the south, where the species found also represent a larger variation in habitat requirements from dead wood, trunks of living broadleaved trees, boulders, ground etc. that are better captured by HHS. Many bryophyte species grow on dead trees, and in accordance with other studies the volume of CWD was a good predictor of species richness (Djupström et al., 2010; Larrieu et al., 2019; Madžule et al., 2012; Rudolphi and Gustafsson, 2011).

Macrofungi and lichens were the most species rich and abundant organism groups in our study. Besides being rich in species, both groups demonstrate a great variation in life history traits by containing autotrophic, mycorrhizal, parasite and saprotrophic species, and include species classified as ground-living, epiphytes and saproxylic. Such variability is likely difficult to capture with a few structural variables, and it may thus not be that surprising that the resource amount and quality measures were poor predictors of the richness of macrofungi and lichens, and that HHS was most often the best predictor of their richness. Only volume of CWD was an important structural variable, but the explained variation was still rather low.

Future studies should assess whether the organism dependencies found in our study interact with the organisms' spatial scales (e.g., body size, dispersal, home range) in order to further disentangle if differences between organism groups relate to habitat heterogeneity or are interactively affected by dispersal constraints or fragmentation (Thomsen et al., 2022).

4.4. Regional differences in species richness and predictions

The relationship between species richness and the HHS was similar between southern and northern regions, demonstrating the measure's independency from region (given the similar forest type). Nevertheless, stands in the southern region harboured significantly fewer species of conservation concern, and the HSS and volume of CWD needed to reach higher threshold levels for significantly higher species richness of red-listed species in the south compared to the north. This demonstrates that forests in the south need to be more heterogeneous, and have larger amounts of dead wood to harbour the same number of species as a forest in the north. In turn, this indicates impoverished biodiversity in the south, or that the list of species of conservation concern may not be properly defined in southern region. Although the forests between regions differ in some aspects, such as younger mean tree age (149 vs. 189 years), higher basal area of living trees, and lower proportion of broadleaved trees in the south, these differences are likely not great enough to explain the pronounced differences in species richness. Instead, we suggest that the reason can probably be traced back to a longer history of industrial forest management in the southern parts of the country (Ericsson et al., 2005; Linder and Östlund, 1998; Östlund et al., 1997) which has caused habitat loss, fragmentation and local extinctions of species. Similar observations of the effect of longer history or more intensive forestry on red-listed deadwood-dependent species have been reported even elsewhere (Hottola and Siitonen, 2008; Kouki et al., 2012; Larsson Ekström et al., 2021; Penttilä et al., 2013).

5. Conclusions

The habitat heterogeneity score has a high potential to serve as a proxy for the conservation value of boreal coniferous forests. We show that a simple habitat heterogeneity measure describes the conservation value better than resource amount and quality variables, and that this measure can be used to provide threshold values for significantly higher richness of red-listed species. The volume of deadwood was the best resource amount and quality proxy for biodiversity, confirming its relevance as a biodiversity indicator. Our threshold analyses showed that diversity of red-listed species increased significantly when the volume of CWD exceeded 20.0 and 22.4 m^3 ha^{-1}, in north and south, respectively. We suggest that these thresholds can be used to identify coniferous boreal forest stands that likely harbour conservation qualities high enough to support red-listed species, and which should be prioritised when forest stands are exempted from forestry to safeguard biodiversity.

This study concentrated on boreal forests, which is the largest terrestrial biome in the world, and hosts unique species assemblages. Our results are directly applicable in the Fennoscandian countries (Finland, Sweden, Norway and parts of Russian Karelia). However, as forest heterogeneity and great amounts of CWD are factors of general importance for maintaining high biodiversity, the habitat heterogeneity score can likely be applied boreal forest in other regions as well, and perhaps as also in other types of forest such as temperate forests.

CRediT authorship contribution statement

Anne-Maarit Hekkala: Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Mari Jönsson:** Conceptualization, Funding acquisition, Writing – review & editing. **Simon Kärvemo:** Writing – review & editing. **Joachim Strengbom:** Conceptualization, Investigation, Data curation, Project administration, Funding acquisition, Writing – review & editing. **Jörgen Sjögren:** Conceptualization, Project administration, Funding acquisition, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data (Descriptive data on study areas (Appendix A), List of species and additional results (Appendix B), and Habitat Heterogeneity Score sheet (Appendix C) are available online. The authors are solely responsible for the content and functionality of these materials.) to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110069.

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