



# Multi-taxon conservation in northern forest hot-spots: the role of forest characteristics and spatial scales

Simon Kärvemo · Mari Jönsson · Anne-Maarit Hekkala ·  
Jörgen Sjögren · Joachim Strengbom

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## Abstract

**Context** Biodiversity is highly affected by industrial forestry, which leads to the loss and fragmentation of natural habitats. To date, most conservation studies have evaluated associations among a single species group, forest type, or spatial scale.

**Objective** The objective was to evaluate the richness of multiple species groups across various forest types and characteristics at multiple scales.

**Methods** We used the occurrence data for 277 species of conservation interest from 455 stands of high conservation value, including four species groups and four forest types.

**Results** Local, landscape, and regional forest characteristics influenced biodiversity in a non-uniform

pattern among species groups and forest types. For example, an increased local spruce basal area in spruce forests was associated with higher vascular plant and bryophyte richness values, whereas macrofungi and lichen richness were positively correlated with dead-wood availability, but negatively correlated with the spruce volume in the landscape. Furthermore, landscapes with twice as much mature forest as the average, had more than 50% higher richness values for vascular plants, macrofungi, and lichens.

**Conclusion** Among sessile species groups in northern forests, a uniform conservation strategy across forest types and scales is suboptimal. A multi-faceted strategy that acknowledges differences among species groups and forest types with tailored measures to promote richness is likely to be more successful. Nevertheless, the single most common measure associated with high richness across the species groups and forest types was mature forest in the landscape, which suggests that increasing old forests in the landscape is a beneficial conservation strategy.

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S. Kärvemo (✉) · J. Strengbom  
Department of Ecology, Swedish University of  
Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden  
e-mail: simon.karvemo@slu.se

M. Jönsson  
Swedish Species Information Centre, Swedish University  
of Agricultural Sciences, Almas Allé 8E, Box 7007,  
750 07 Uppsala, Sweden

A.-M. Hekkala · J. Sjögren  
Department of Wildlife, Fish, and Environmental Studies,  
Swedish University of Agricultural Sciences,  
901 83 Umeå, Sweden

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## Introduction

Biodiversity is maintained by multiple interactions among biotic and abiotic factors that operate at multiple spatial scales. Differences in climate and land-use history generate large-scale species variation and this has been observed in many different biogeographical regions. However, the biotic interactions, including those related to habitat loss and fragmentation, determine variation at the landscape and local scale (e.g. Haddad et al. 2015; Newbold et al. 2016; Isbell et al. 2017). Thus, resources and processes operating at both the larger landscape scale (Poiani et al. 2000; With 2004; Thrush et al. 2013) and at local scales (e.g. Sverdrup-Thygeson et al. 2014; Nordén et al. 2018) will affect the occurrence and persistence of species. However, there is no consensus over the relative importance of local versus landscape processes as drivers of biodiversity (Hodgson et al. 2011; Fahrig 2013; Hanski 2015). Therefore, disentangling the importance of local and landscape effects would be highly beneficial to conservation management. Hence, there is a need to improve understanding about how different functional habitats (e.g. grasslands, wetlands, and old-growth forests) influence biodiversity and if such influence varies among species groups and over spatial scales (Poiani et al. 2000; Gonthier et al. 2014).

Anthropogenic land-use change mean that forest biodiversity is currently declining globally at an alarming rate (e.g. Bradshaw et al. 2009; Betts et al. 2017; Blowes et al. 2019). In many parts of the world, the introduction of industrial-scale forestry has fundamentally changed the forest landscape from multi-layered and diverse stands towards high domination by even aged and structurally homogeneous stands (Östlund et al. 1997; Carnus et al. 2006). These changes are accompanied by reduced biodiversity (Hedwall et al. 2019), especially for old-growth forest organisms that are dependent on high forest structural complexity and large amounts of dead wood (Siitonen et al. 2001; Paillet et al. 2010). Continuity of habitat, in both space and time, is a prerequisite for the long-term persistence of all species. Organisms differ in functional traits, such as range size, dispersal capacity, and sensitivity to forest activities, which means that the biodiversity of different species groups may respond differently to the various intensities and spatial scales used by forest management programmes (Paltto et al. 2006). For sessile organisms, such as bryophytes,

fungi, lichens, and vascular plants, variables associated with forest continuity is considered particularly important (e.g. Snäll et al. 2003; Jönsson et al. 2008; Johansson et al. 2012) and their dependence on this factor is commonly seen at rather small spatial scales (Sverdrup-Thygeson et al. 2014; Nordén et al. 2018). In addition, several studies indicate that the associated forest characteristics, such as mature forest, multi-layered tree stands and deadwood, are more important for species richness than forest continuity per se (e.g. Ohlson et al. 1997; Nordén and Appelqvist 2001; Löhmus and Löhmus 2011; Rudolphi and Gustafsson 2011).

Conservation strategies to mitigate forest biodiversity losses include increasing the number and size of conservation areas, maintaining or increasing habitat heterogeneity at both the local and landscape scales, and ensuring connectivity among forest conservation areas (Morecroft et al. 2012). Preserving biodiversity through a network of conservation areas that contain high-quality habitats is a prioritised international target (e.g. CBD-Aichi Target 11; <https://www.cbd.int/sp/targets/rationale/target-11/>). The objectives for areas subjected to such conservation strategies generally focus on maximising biodiversity (Nicholson and Possingham 2006), even though conservation measures favouring some taxonomic groups may disfavour others. Thus, identifying forest characteristics that promote high species diversity, such as deadwood, older trees, and variable tree species composition, is considered important when attempting to meet conservation objectives and develop sustainable forest management programmes. Inherent in this process is that conservation managers will strive for a multi-scale approach in the spatial planning process (Poiani et al. 2000). Such plans, when restricted to an individual forest stand, or a conservation area, may be too small for the efficient management of certain species (Block et al. 1995; Poiani et al. 2000, but see Wintle et al. 2019). If forest conservation is to be improved, the guidelines that detail outcomes across different species groups and forest characteristics need to be produced at both local and landscape scales.

Northern European forests have been subjected to intensive forest management, which has resulted in the fragmentation of old-growth forests and deadwood (Kouki et al. 2001). Furthermore, it has been suggested that this fragmentation is the main cause of the ongoing decline in species richness (e.g. Dettki et al.

2000; Stokland and Siitonen 2012; Sverdrup-Thygeson et al. 2014). A common strategy to mitigate such adverse effects is to exempt areas of conservation concern from forestry. In several northern European countries, small (often 3–5 ha) forest habitat patches with high biodiversity value, the so-called woodland key habitats (hereafter, key habitats), are set aside for the preservation of forest biodiversity (Timonen et al. 2011b; Wijk 2017). These key habitats are considered to be biodiversity hot spots based on their management history and forest composition (presence of old trees, large amounts of dead wood at many different decay stages, etc.), and commonly harbour species of conservation interest, such as vascular plants, bryophytes, macrofungi, and lichens. Such species are selected by expert panels, and are commonly associated with the rare features that occurs in key habitat, such as calcareous ground, dead and old trees or stable moist microclimate (Timonen et al. 2011b).

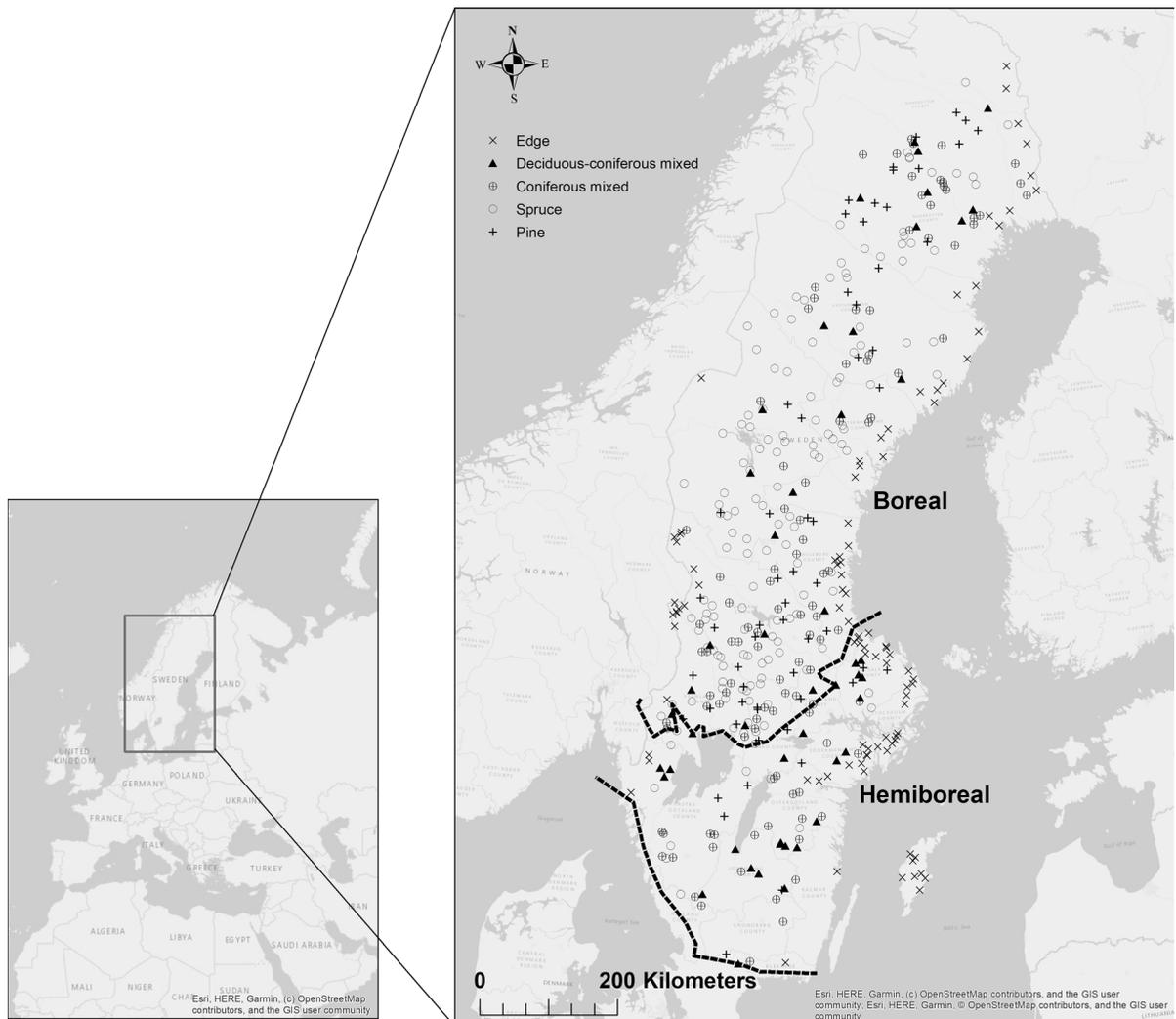
In this study, we utilised a unique data set from a national biodiversity survey conducted by the Swedish Forest Agency about the occurrence of several hundred species of conservation interest from vascular plants, bryophytes, macrofungi, and lichens (Wijk 2017). This data set enabled us to address how the biodiversity of multiple species groups varied among forest types and how the species groups were associated with tree species composition and the availability of key forest characteristics at the local and landscape scales. The main question for this study is: How is the species richness of different species groups associated with forest characteristics commonly considered in forest conservation planning? To answer this, we addressed how the species richness of vascular plants, bryophytes, macrofungi, and lichens of conservation interest differ in relation to the availability of forest characteristics at multiple scales. These characteristics are conservation areas, amount of dead wood, forest age, and tree-species composition. We considered their potential influence at the local and landscape scales. Furthermore, we addressed the importance of biogeographical regions (boreal vs. hemiboreal) and focal forest type, that is, whether the site was a deciduous-coniferous mixed, coniferous mixed, spruce-dominated, or pine-dominated forest type. As many of the studied species have a restricted dispersal capacity (Nordén and Appelqvist 2001), we hypothesised that key characteristics are more important at the local than at the landscape scale, and that the

richness, in accordance with the latitudinal species gradient (Pianka 1966), will be higher in the southern hemiboreal region than in the northern boreal region. However, regional variations of important substrates, such as deadwood and mature forest may influence this pattern (Fridman et al. 2000).

## Material and methods

### Field survey

We examined data from 277 species consisting of vascular plants (58), bryophytes (52), macrofungi (99), and lichens (68) that are of conservation interest (see Online resource 1. for species identification). These species groups were selected primarily for this study because they are considered to signal forests of high conservation value, not too rare, and are generally easy to identify in the field. The data was obtained from a biodiversity monitoring program conducted by the Swedish Forest Agency, and were sampled by trained experts who were skilled in species identification (Wijk 2017; Nitare 2019). The samples were taken from 455 forested key habitats across a long latitudinal range (1300 km/latitude) that covered both boreal and hemiboreal biogeographical regions (Fig. 1). The Swedish boreal forest is highly dominated by Norway spruce (*Picea abies* L., Karst.) and Scots pine (*Pinus sylvestris* L.). Birch species (*Betula* spp.) are quite common, but scattered groves of ash (*Fraxinus excelsior* L.) and aspen (*Populus tremula* L.), and locally elm (*Ulmus glabra* Huds.), pedunculate oak (*Quercus robur* L.), and linden (*Tilia cordata* Mill.) occur in the southern hemiboreal region. Although Norway spruce and Scots pine are the dominant species in the hemiboreal (or boreo-nemoral) region, the above listed deciduous trees in this region are more widespread than they are in the boreal region. Landscape and local forest characteristics were extracted from satellite and field data, respectively. Species of conservation interest are commonly positively correlated with the number of red-listed species or overall high biodiversity (Gustafsson et al. 2004; Perhans et al. 2007; Timonen et al. 2011b; Mežaka et al. 2012). This was generally the case also in our study, where the number of species of conservation interest correlated significantly with the number of observations of red-listed species for all



**Fig. 1** Studied woodland types in Sweden, including edge sites (removed from the main models) and different biogeographical regions

species groups (Online resource 2). The same was true for the bryophyte and lichen species groups associated with deadwood and other substrates (Online resource 3). Exceptions were found for the macrofungal species group, where the number of species on deadwood and the number on other substrates were not positively correlated in three of four forest types. However, for these models, a relatively higher percentage of fungal species, was found on deadwood (73–83%, dependent on the forest type), resulting in strongly biased data, and thus low model fits. Therefore, we expect that red-listed and deadwood species in general will respond similarly, and consequently we did not separate species of conservation interest and red-listed species,

or species found on different substrates, in the subsequent analyses. The species surveys were conducted in areas up to 2 ha in size by dividing the area into subplots (for key habitats < 2 ha, the entire key habitat was surveyed and for key habitats > 2 ha, a representative 2 ha area was surveyed). The number of subplots surveyed varied between one and 20. Local forest characteristics were surveyed using 20 m long transects (4 m wide) and the number of transects varied between one and 18. The number of subplots and transects was strongly related to the size of the key habitat. A summary table of the species groups, variables, surveyed areas and forest types is shown in Online resource 4.

## Explanatory variables

The importance of forest characteristics at the landscape scale was analysed across  $40 \times 40$  km squares surrounding each key habitat. Mean volumes  $\text{ha}^{-1}$  of spruce, pine, deciduous trees, birch, and the area of mature forest (ha of forest with an age  $> 120$  years) were extracted from satellite images (Landsat EMT; Reese et al. 2003) taken in 2010 and validated from the ground by the Swedish National Forest Inventory (<https://www.slu.se/nfi>). These data were in the form of grid cell layers (rasters) with  $25 \times 25$  m resolution. Since these data do not include logging operations that occurred after 2010, we created an additional layer containing information on all final felling that occurred during the period 2011–2018 (based on registrations at the Swedish Forest Agency). To further test the association between species richness and conservation areas in the landscape, we converged polygon data to raster data ( $100 \times 100$  m) and used the summed area of forested reserves and woodland key habitats (based on data from the Swedish Forest Agency) in the surrounding  $40 \times 40$  km squares. Finally, we used data from the Swedish National Forest Inventory for the period 2014–2018 to evaluate deadwood volumes at the landscape scale. The deadwood data were converged to raster data ( $100 \times 100$  m) from large squared polygons of different sizes ( $\sim 10,000$ – $100,000$  ha, including deadwood volumes  $\text{ha}^{-1}$ ), which were summed within the surrounding  $40 \times 40$  km squares. All landscape data were aggregated to  $1 \times 1$  km raster data by averaging tree species and deadwood volumes, and the conservation areas and areas of mature forest classified as older than 120 years were summed. This resulted in landscape data of 16,000 pixels surrounding each focal key habitat.

Comprehensive landscape data surrounding each key habitat was produced after removing sites close to the national borders of Sweden (within 20 km, including sea and missing data from neighbouring countries), which left a total of 358 sites that used in our further analyses. The landscape data were interpolated into each site using a  $40 \text{ km}^2$  “moving window” approach (R package “raster”: Hijmans 2017). A distance-weight function was added to each landscape variable by applying a Gaussian kernel filter within the  $40 \times 40$  km “moving window” using the “focalWeight” function in the R package “raster”

(Hijmans 2017). A sigma value of 7000 was chosen to correspond to a typical normal-distribution curve within the  $40 \text{ km}^2$  window, and was based on information from previously reported landscape associations with forest plants ( $\sim 2$  km; Amici et al. 2015), macrofungi (1–3 km; Nordén and Larsson 2000; Edman et al. 2004b), and lichens (0.2–4.7 km; Ruete et al. 2014).

The landscape variables linked to each forest type were mirrored for the local variables, which meant that we could include field-surveyed local data about the basal area per hectare for spruce, pine, birch, and other deciduous trees when applicable. Local basal area per hectare for deadwood was included in all models. Data for these variables were sampled using transects (see “Field survey”).

## Statistical analyses

We analysed how the different biogeographical regions, landscapes, and local site factors (within key habitats) influenced the richness of the species of conservation interest within the four groups, which were vascular plants, bryophytes, macrofungi, and lichens. We ran separate analyses for each species group in four different forest type models: (i) *deciduous-coniferous mixed forest* (large numbers of deciduous trees), (ii) *coniferous dominated mixed forest* (dominated by spruce and pine), (iii) *spruce dominated*, and (iv) *pine dominated* (Table 1), which resulted in 16 different models. The species richness of the four species groups were additionally compared among the key habitat types and between sites located in the boreal and hemiboreal regions by applying sample-based rarefaction curves obtained using R package *vegan* (version 2.5-3; Oksanen et al. 2018). All 455 sites were included. A compilation of the species groups, model variables, and types of data are shown in Online resource 4.

All models included landscape data for the conservation areas and mature forests, whereas deadwood and tree species data were analysed at both the landscape and local scales. The conservation area, mature forest, deciduous, birch, and deadwood variables were  $\log + 1$  transformed to mitigate the effect of multiple outliers in the landscape data. The choice of tree species variables for each model was linked to the forest type in question (see Online resource 4). This resulted in nine variables for the deciduous-

**Table 1** Definitions of the four forest types surveyed

| Forest types                      | Deciduous | Conifers | Spruce | Pine  |
|-----------------------------------|-----------|----------|--------|-------|
| Deciduous–coniferous mixed forest | 40–60%    | 40–60%   | < 60%  | < 60% |
| Coniferous–dominated mixed forest | < 30%     | > 70%    | < 70%  | < 70% |
| Spruce-dominated forest           | < 30%     | 70–100%  | > 70%  | < 30% |
| Pine-dominated forest             | < 30%     | 70–100%  | < 30%  | > 70% |

coniferous mixed (including living deciduous tree species variables) and coniferous mixed models (including living spruce and pine variables), and seven variables for the spruce (including living spruce variables) and pine models (including living pine variables).

We included site identity as a random effect in the generalised linear mixed models (GLMM) to reduce the effect of overdispersion and to control for possible variation associated with site-based spatial correlations. A Poisson distribution of errors was used to analyse the data because the response variables were species counts. Prior to each analysis, we checked the correlation matrices, including all continuous explanatory variables. None of the pairs had correlations > 0.7 so we kept all the variables in the models (Dormann et al. 2013). To control for biogeographical differences in species numbers and uneven sampling effort, we included regions (boreal/hemiboreal) as categories and the size of the inventoried area as an offset in the models, which resulted in a rate dependent response. All continuous explanatory variables were standardised with means of zero and standard deviations of one. All models were fitted by optimising the model algorithm via the `glmerControl` “bobyqa” optimiser to rectify convergence problems (Powell 2009). This procedure minimises the model function of variables subjected to bound optimisation by quadratic approximation (Bates et al. 2015). To account for model uncertainty (e.g. variables with low weight) and increase the robustness of the variable estimates, we performed an unconditional model averaging (MuMIn package in R; Barton 2018), i.e. we used a weighted average of the estimates derived from the multiple variable combinations produced by each model. All models with a  $\Delta AICc > 2$  compared to the best-fitted model were omitted to remove redundant and spurious models with very poor weights (Anderson and Burnham 2004; Grueber et al. 2011). Consequently, not all variables were included in all final models. Standard GLMM models were used to

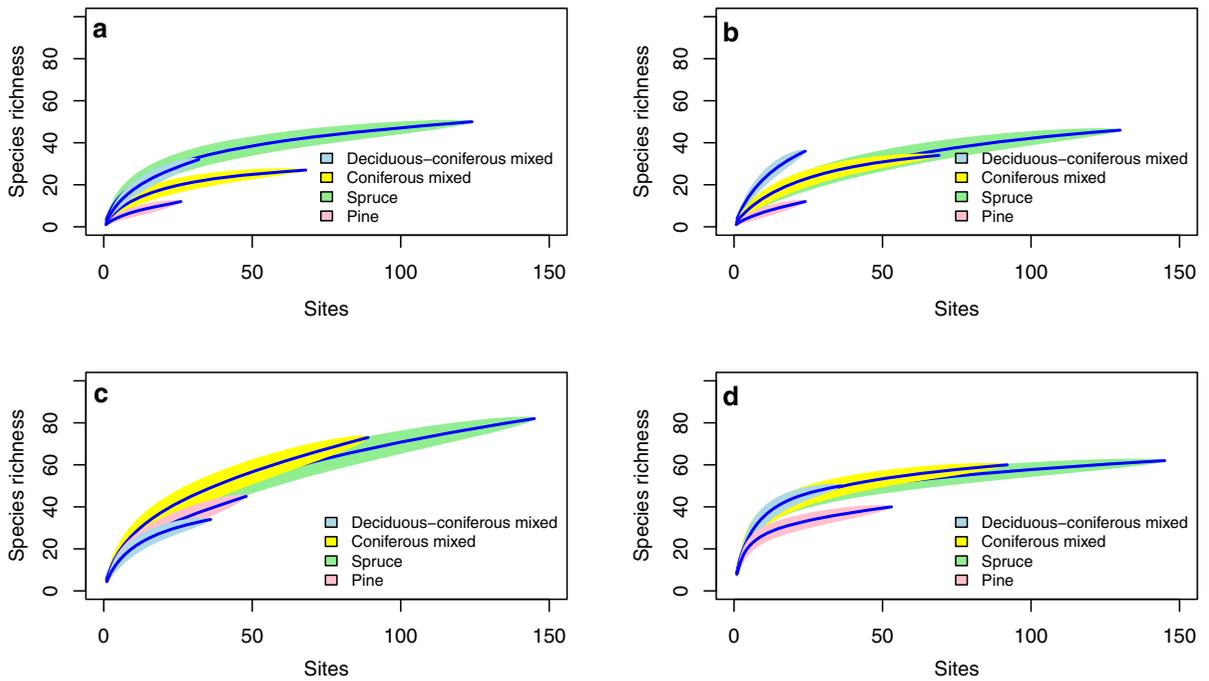
visualise predicted single variable effects by holding the other variables constant (function `allEffects` from the package “effects”; Fox 2003).

The data were processed and analysed in ArcMap 10.6 (ArcGIS, ESRI, Redlands, CA, USA) and R version 3.5.2 (R Development Core Team 2015).

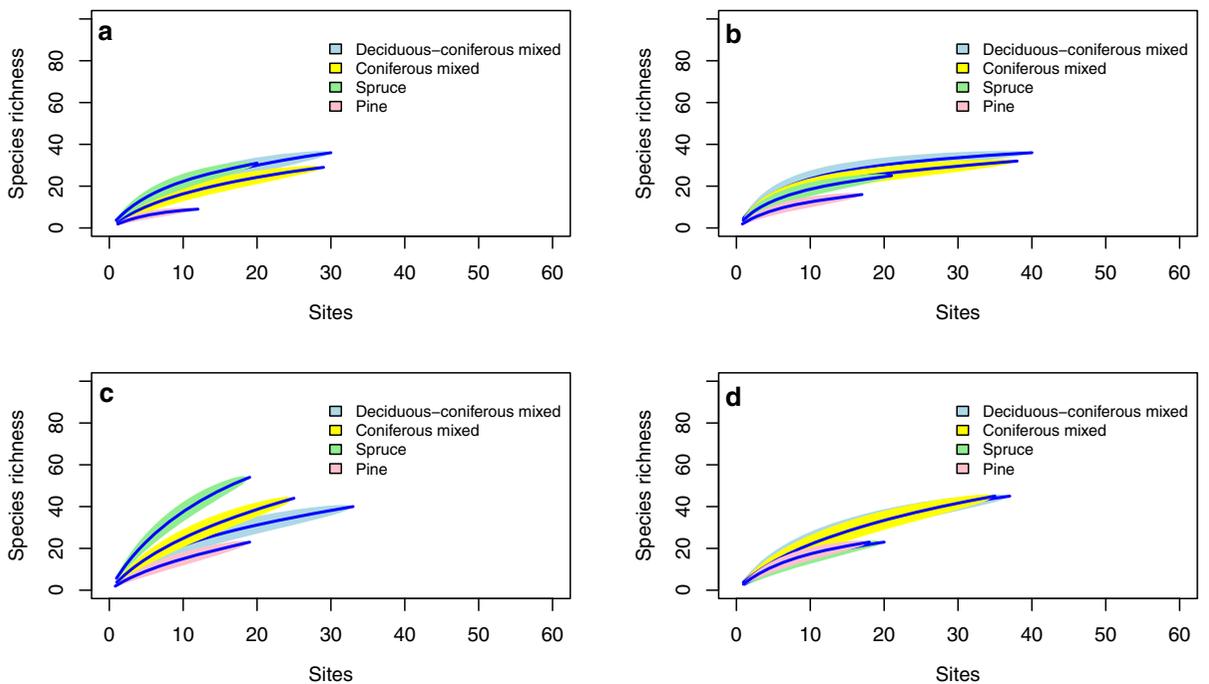
## Results

### Biogeographical regions

Generally, in both biogeographical regions, differences among forest types (deciduous-coniferous mixed, coniferous mixed, spruce, and pine) followed the same pattern across species groups. Species richness was highest in spruce and/or the mixed forest types and lowest in pine forests (Figs. 2, 3). However, in the boreal region, spruce forests had a similar species richness as coniferous mixed forest for all species groups except for vascular plants (Fig. 2). Bryophyte richness was greatest in the deciduous-coniferous mixed forests (Fig. 2b). In the hemiboreal region, the richness of macrofungi had the highest variation among forest types, being particularly high in spruce forests (Fig. 3c). Forests in the boreal region seemed to have a higher vascular plant, bryophyte, and lichen species richness than forests in the hemiboreal region. The macrofungi rarefaction curves never reached an asymptote in any of the regions, which suggested that increased sampling would generate higher species richness in the hemiboreal region. Differences among forest types were less distinct in the hemiboreal region than in the boreal region, which was probably due to the lower sample size and a relatively smaller geographic extent. Despite the sample size differences, the steeper accumulation curve at low sample sizes revealed a generally higher species richness in the boreal region compared to the hemiboreal region.



**Fig. 2** Rarefaction curves for the species richness of **a** vascular plants, **b** bryophytes, **c** macrofungi, and **d** lichens in different forest types based on the number of sites sampled in the boreal biogeographical region

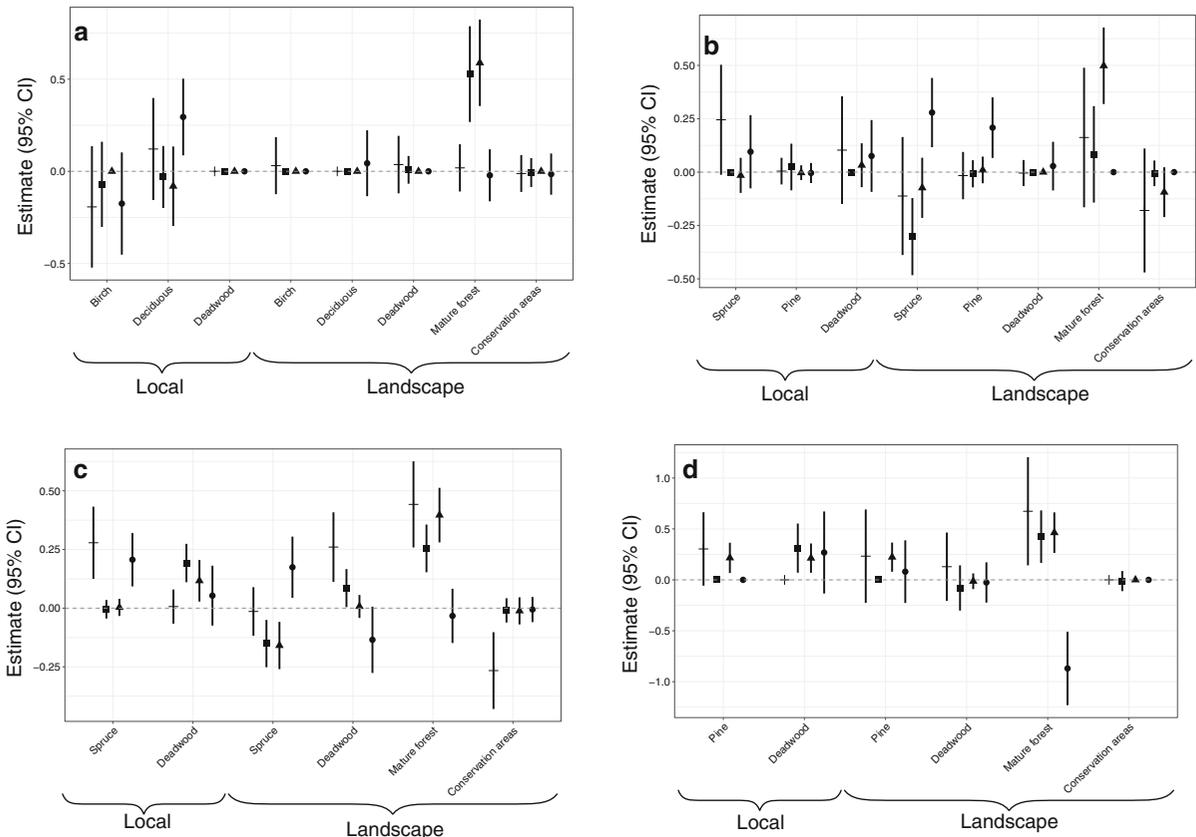


**Fig. 3** Rarefaction curves for the species richness of **a** vascular plants, **b** bryophytes, **c** macrofungi, and **d** lichens in different forest types based on the number of sites sampled in the hemiboreal biogeographical region

The results from the rarefaction curves corresponded somewhat with the results from the models. This can be exemplified by the significantly higher species richness of lichens and macrofungi in the boreal region compared to the hemiboreal region (based on three out of four forest type models for lichens and the coniferous-mixed forest type for macrofungi; Online resource 5). In contrast, bryophyte species richness in coniferous mixed forests was higher in the hemiboreal region than in the boreal region, but there were no significant differences in vascular plant richness among any of the forest types in either of the two regions.

Landscape factors

In general, the distribution of conservation areas in the surrounding landscape was a poor predictor of local species richness (Fig. 4a–c; detailed model results can be found in Online resource 5). One exception was in spruce-dominated forest types where vascular plant richness was negatively correlated with the extent of the conservation areas in the landscape (Fig. 4c). The area of mature forest (> 120 years) was a better predictor because the species richness of three out of four species groups, in at least one of the four forest types, was positively associated with the area of mature forest in the landscape. Specifically, lichen richness increased with increasing area of mature forests for all forest types (Fig. 4a–d). Richness of vascular plants and macrofungi in spruce and pine



**Fig. 4** Model estimates (95% confidence intervals) for the different species groups: dagger—vascular plants, filled square—macrofungi, filled triangle—lichens, and filled circle—bryophytes associated with local and landscape variables in **a** deciduous-coniferous mixed, **b** coniferous mixed, **c** spruce,

and **d** pine dominated forests. Variables with no effect and without error bars were not included in the final (averaging) models based on the criteria for deviation, which was more than two  $\Delta AIC_c$  from the best fitted model (see “[Statistical analyses](#)”)

forests was positively associated with the area of mature forests in the surrounding landscape (Fig. 4c–d). In addition, macrofungal richness in the deciduous-coniferous mixed forest type was also positively associated with the area of mature forest in the landscape (Fig. 4a). In contrast, bryophyte richness in pine forests showed no or even a strong negative association with the area of mature forest in the landscape (Fig. 4d).

The amount of dead wood was also important. The vascular plant and macrofungal richness in the spruce forest type was positively associated with the amount of dead wood in the surrounding landscape, but there was no association between deadwood and richness of lichens or bryophytes (Fig. 4). However, in the mixed-coniferous and pine forest types, the richness of bryophytes and lichens was positively associated with the volume of pine in the landscape (exclusively included in the coniferous mixed forest type and pine models) (Fig. 4b, d). Furthermore, associations between species richness and spruce volumes in the landscape (exclusively included in the coniferous mixed model and spruce models) also differed among species groups. Generally, bryophyte species richness was positively related to spruce volumes in the landscape (Fig. 4b, c), while macrofungal and lichen species richness were negatively related with this variable in the coniferous mixed and/or spruce forest types, respectively (Fig. 4b, c). The volumes of deciduous or birch trees in the landscape were not associated with the richness of any of the species groups assessed in the deciduous-coniferous mixed forest type (Fig. 4a).

#### Local factors

In spruce and pine forests, lichen and macrofungal species richness increased with local deadwood amount (Fig. 4c, d; detailed model results can be found in Online resource 5). Likewise, lichen species richness in pine forests increased with local pine volume (exclusively included in the coniferous mixed model and pine models; Fig. 4d). In spruce forests, species richness of vascular plants and bryophytes were higher in areas with higher basal areas of local spruce (exclusively included in the coniferous mixed model and spruce models; Fig. 4d). The bryophyte richness also increased with the basal area of local deciduous trees in deciduous-coniferous mixed forests

(Fig. 4a), whereas the basal area of local birch was not associated with any of the species groups in any forest type. The macrofungal species richness was not associated with any of the local live tree variables.

#### Discussion

This study demonstrates multifaceted biodiversity relationships among groups of species of conservation interest, and their associations with forest characteristics at multiple scales and different forest types. Our results concur with studies suggesting that both local and landscape factors can be drivers of diversity (e.g. Gonthier et al. 2014; Sverdrup-Thygeson et al. 2014). However, our results also highlight that there appears to be no simple general pattern for the local diversity of different species groups in various forest types in relation to local and landscape factors. This complicates conservation efforts because optimal conservation strategies must consider the biogeographical region in question, the target-specific forest type, and forest management regimes at different spatial scales to best support successful outcomes for biodiversity.

For example, species richness of bryophytes was higher in the coniferous-mixed forests in the southern hemiboreal region than in the northern boreal region. In contrast, the coniferous mixed, spruce, and pine dominated forest types in the boreal region had a higher richness of macrofungal and lichen species than forests in the hemiboreal region. This may seem counterintuitive to the latitudinal diversity gradient, where species richness is hypothesized to increase towards the south as a result of milder and more stable climate, increasing habitat, productivity and growth season (*sensu* Pianka 1966). However, the longer forest management history in the hemiboreal region has probably reduced the biodiversity of many species groups in that region of Sweden (Nilsson 1992). This highlights that even within a single biogeographic region, the preservation of biodiversity cannot rely on a common and uniform strategy that encompasses different species groups and forest types.

The availability and spatial distribution of habitat resources in the landscape may interact with the habitat resources at local scale, and affect species differently depending on their dispersal capability (e.g., Ranius et al. 2019). Species capable of long-distance movement, such as birds and insects, are

commonly affected by the availability of resources at both local and large spatial scales (Lindenmayer and Franklin 2002). A local increase in habitat, such as deadwood for saproxylic organisms, may generate greater increases in beetle species richness (Rubene et al. 2017) and red-listed wood fungi (Nordén et al. 2018) in landscapes with a lot of deadwood. The species included in our study were sessile species dependent on wind or vector-assisted dispersal of asexual and sexual propagules, with local species richness likely dependent on a combination of higher depositions of propagules from local sources and higher habitat amounts (e.g., Edman et al. 2004a, b). This meant that we, in accordance with other studies (Poiani et al. 2000; Aune et al. 2005; Paltto et al. 2006), expected local characteristics to have a stronger influence than landscape forest characteristics. Accordingly, bryophyte species richness was positively associated with the local basal area of deciduous trees, whereas deciduous volume at the landscape scale was a poor predictor of local bryophyte richness. However, spruce and pine in the mixed-coniferous forest were positively associated with bryophyte richness at the landscape, but not at the local scale. Furthermore, in the pine and spruce forest types, high species richness of macrofungi and lichens were associated with high amounts of dead wood at both the local and landscape scales, whereas vascular plant richness increased only with increasing amounts of dead wood at the landscape scale. Thus, we could not find a general support for a higher importance of forest characteristics at local scales compared to landscape scales. However, the results suggest that compared to bryophytes and vascular plants, macrofungi and lichens show stronger association with variables associated with forest continuity, such as deadwood and old trees (e.g. Dettki et al. 2000; Mežaka et al. 2012; Stokland and Siitonen 2012).

We also found the highest proportion of macrofungal and lichen species on deadwood, whereas e.g. bryophytes were commonly found on other substrates (see Online resource 3). Therefore, despite the complex nature of our results, they indicate that it is easier to find variables describing forest characteristics that predicts richness of macrofungi and lichens (12 and nine, respectively) than vascular plants and bryophytes (five and seven, respectively). This can be illustrated by a much higher proportion of macrofungal and lichen specialist species, compared to vascular

plants and bryophytes (Nordén et al. 2013; Staniaszek-Kik et al. 2019). This was also true for the spruce and pine forest types (14 and nine forest characteristic variables, respectively), but not to the same extent for the mixed tree species types (five for deciduous-coniferous mixed and seven for coniferous-mixed forests). This suggests that macrofungi and lichens are more affected by variables associated with forest loss and fragmentation (Arroyo-Rodríguez et al. 2020 and references therein), and that it is consequently easier to identify conservation strategies for these species groups than for bryophytes and vascular plants. On the contrary, bryophytes and vascular plants may be more dependent on soil characteristics and a stable humid microclimate to maintain high levels of richness (De Frenne et al. 2013; Fenton et al. 2015). Such environmental variables are typically not measured in forest biodiversity surveys, and were also not measured and tested in our study focusing on forest structural variables. Our results also suggest that, in general, it may be easier to promote species richness in spruce or pine dominated forests than in mixed forests.

Richness of all species groups, but bryophytes, increased as the proportion of mature forests in the surrounding landscape rose. This finding agrees with previous studies, which demonstrate that colonisation by epiphytic lichens (Dettki et al. 2000; Johansson et al. 2012), wood-decaying fungi (Edman et al. 2004a, b; Nordén et al. 2013), and vascular plants (Matlack 1994; Varela et al. 2018) is higher in landscapes with a high proportion of older forest, but failed to support the findings by Rudolphi and Gustafsson (2011), who found that species richness of bryophytes of conservation interest increased with larger areas of old forests in the surrounding landscape. The strong positive association between species richness and surrounding mature forest, and the observed negative relationship with high tree volumes of surrounding spruce stands were probably caused by a positive correlation between managed homogenous spruce forests and high volumes and stem densities of relatively young spruce trees (Table 7 in Anonymous (2018)). This result confirms the strong negative effects of intensive forest management on species diversity (Lassauce et al. 2011; Kouki et al. 2012). Our results also support the idea that maintaining or increasing forest age in the landscape can be an effective strategy to support richness of species of conservation interest. This is in accordance with

Roberge et al. (2018), suggesting that species requiring older forest would generally be positively affected by extended rotations. Although our results highlight the importance of older forests in the landscape, we found no support for the idea that a high proportion of conservation areas in the landscape promote local species richness. This might appear surprising as these conservation areas are known to have a higher-than-average biodiversity (Paillet et al. 2010; Timonen et al. 2011a; Hekkala et al. unpublished), and that aggregation of such areas into certain landscapes is a commonly recommended conservation strategy (Lindenmayer and Franklin 2002; Morecroft et al. 2012). The weak association between species richness and conservation areas in the surrounding landscape indicate that the landscape configuration for these species groups in conservation areas might be unimportant (Fahrig 2013) or, alternatively, that the fragmentation is so recent that the forest included in our study suffer from a large extinction debt (Berglund and Jonsson 2005; Paltto et al. 2006). A similar result will occur if there are too few conservation areas, or if they are too fragmented to maintain the patch networks needed to promote high richness levels for the studied species (Aune et al. 2005). The latter is in accordance with the clear positive effect of mature forests, where the mean percentage in the landscapes surrounding the different forest types studied was 15–24% whereas the corresponding percentage for conservation areas was 6–8%.

## Conclusions for practice

This study illustrates the challenges of adapting forest conservation measures to multiple species. Our results show that important forest characteristics at the local, landscape, and regional scales influence biodiversity in a non-uniform pattern among species groups and forest types. Although both local and landscape variables were associated with local richness, the forest characteristics important at the local scale often differed from those important at the landscape scale. This finding needs to be reflected in conservation strategies aiming at increasing structural diversity. Biodiversity, forest characteristics, and management history commonly differ among regions. Although it is a common recommendation that such factors should be considered when planning conservation strategies,

the empirical support to back such claims has so far been limited. Since our study include more species groups, a larger number of stands, and cover a larger geographical area than most other studies, our results add important empirical support for this claim. Despite that our data can not reveal the mechanistic explanations as to why these patterns occur, we conclude that the general productivity-diversity pattern observed for common species (e.g. Chase and Leibold 2002; Gillman and Wright 2006) also appears to be valid for the relationship between local productivity and diversity of species of conservation interest. Our finding that sites with higher spruce basal areas contain more bryophytes and vascular plants of conservation interest (Online resource 6a, 7a, 8a), suggests that if the goal is to safeguard diversity in the managed forest landscape, then it is important that high-productivity forests are well represented among the set asides. Currently, forests that are set aside for the preservation of biodiversity are commonly biased towards low productivity sites (Fridman 2000; Scott et al. 2001). In addition, our results suggest that a strategy that includes high productivity sites in conservation areas is not likely to favour the conservation of macrofungi and lichens. These groups (together with vascular plants) are more likely to respond positively to a landscape conservation approach that aims to set aside forests in areas with e.g. a high proportion of mature forest (Online resources 9d, and 10e). The finding that species groups were associated with different local and landscape variables highlights the importance of developing more differentiated conservation approaches that encompass species-specific demands at several spatial scales. In this context, our study recommends progressive landscape planning for biodiversity conservation, simultaneously considering both local and landscape goals for multiple species groups (Michanek et al. 2018). One must take into consideration that the results presented in this study may have multiple causal effects, and that variables such as productivity and historical land use may influence the result. Moreover, differences in forest structures may be associated with additional micro-climatic variables that were not included in this study, e.g. canopy cover, humidity, pH, soil characteristics, sun exposure and temperature (Esseen et al. 1997), which in turn may be associated with the species richness of the studied species groups (e.g. Frahm

2003; Zinko 2004; Pouska et al. 2016). In this context, our study needs to be followed by additional studies that clarify the importance of such factors.

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