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## Global Ecology and Conservation

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## Original Research Article

## The potential to use documentation in national Red Lists to characterize red-listed forest species in Fennoscandia and to guide conservation

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## ARTICLE INFO

## Article history:

Received 20 February 2018

Received in revised form 30 June 2018

Accepted 30 June 2018

## ABSTRACT

Loss of biodiversity is a pressing global issue, hence it is vital to facilitate informed and effective conservation. As conservation mainly operates at the level of habitats, aiming for species of conservation interest, conservation and management require adequate ecological knowledge of prioritized species for the geographic and environmental setting considered.

Our aim was to investigate if ecological documentation in national Red Lists could be combined and used to identify important forest habitats and ecological variables for red-listed forest species in Fennoscandia, and whether this knowledge could be arranged at different geographical scales and for various selections of species of conservation interest. We compiled the national Red Lists of Finland, Norway and Sweden and extracted ecological information for all red-listed forest species ( $n = 4830$ ). We used a principal component analysis to investigate variation in distribution of species and their habitat associations and taxonomical groups, and to group species of similar associations. We further used the listed species in Sweden as an example, and compared the proportions of species associated to the ecological variables dead wood, living trees or merely the “forest floor and understory” a) at larger and smaller scale (Fennoscandia – county in Sweden), b) in regions with contrasting biomes (nemoral and boreal), and c) in two more limited selections of species of conservation interest; Fennoscandian and globally red-listed species also red-listed in Sweden.

Ecological information could be extracted for 96% of the species, albeit with a low resolution; i.e. overall forest habitats, associated tree species, lifeforms and six other ecological variables selected based on their frequent appearance in the Red List documentation. Using this information, we identified five large-scale patterns for Fennoscandian red-listed species; the majority of red-listed species is associated with coniferous forest. The number of red-listed species associated with specific tree species was poorly correlated with the amount of each tree species in Fennoscandia. Dead wood was one of the most important habitat features in terms of number of associated red-listed species, and the proportion of

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species associated to dead wood was similar in coniferous, boreal and nemoral broad-leaved forests types.

We demonstrate that ecological documentation in national Red Lists can be used to identify general ecological variables at varying geographical scales and for different selections of species, albeit not with sufficient resolution to provide detailed local conservation guidelines.

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## 1. Introduction

Biodiversity loss is one of the world's most pressing issues, and there is growing concern about the status of biological resources on which human life depends (CBD, 2006), and for the future for biodiversity (MEA, 2005; Isbell et al., 2017). Many species are declining to critical population levels, important habitats are being destroyed and fragmented, and ecosystems are being destabilized due to land transformation, pollution, invasive alien species, climate change and other human impacts (Steffen et al., 2015). Integrating biodiversity conservation measures into land use planning, as well as setting aside areas for conservation, is therefore urgent.

One comprehensive and widely used data source for species status and support for conservation decisions are Red Lists of threatened species. Red Lists are produced at national to global scale according to scientific based criteria set by the International Union for Conservation of Nature (IUCN) covering all multicellular taxonomic groups (IUCN, 2017). Red List assessments are based on estimations of extinction risk, but are by the IUCN not designed to set conservation priorities *per se* (Miller et al., 2007). Rather, Red Lists are meant as a tool to facilitate conservation priorities, i.e. to identify species of conservation interest or, based on such prioritized species, to select areas and habitats for conservation measures (Ricketts et al., 2005; Rodrigues et al., 2006; Eaton et al., 2005; Martín-López et al., 2011). Knowledge of red-listed species' habitat associations and other ecological variables important for red-listed species can therefore potentially be of great value for conservation. Specific knowledge for individual red-listed species are often presented in the documentation in national Red Lists, and may include key habitat types and important ecological variables (IUCN, 2017). The level of details in the documentations will vary with the knowledge of red-listed species and the efforts to compile such information for the Red List, but can in some cases be sufficient to identify species with similar habitat preferences. Red List documentation has been used to produce national Red List statistics from all Fennoscandian countries, (Henriksen and Hilmo, 2015b; Sandström et al., 2015; Rassi et al., 2010), and for national analyses of red-listed species (e.g. Berg et al., 1994; Tikkanen et al., 2006; Henriksen and Hilmo, 2015b; Sandström et al., 2015; Rassi et al., 2010). Surprisingly, it appears that this documentation is yet only rarely used to compile overviews to support conservation at smaller and larger geographical scales, and for various selections of species. Due to factors such as distributions of biomes and habitats, and land use history, the distribution of red-listed species differ geographically, e.g. from nemoral to boreal zones and locally among and within habitats. Thus, key habitats and ecological variables for red-listed species will depend on both the geographical context and the selection of species considered. Ecological information derived from Red Lists documentations could also be used to cover larger areas by compiling information from several national Red Lists for larger groups of species and for broader-scale regions, creating a potential also to extract information for various sub-groups of interest, independent of national borders. The set of selected species may have profound effect on identified key habitat and ecological variables, hence also on selected conservation measures.

Finland, Norway and Sweden, together forming the region Fennoscandia, all have up-to-date comparable national Red Lists following the IUCN criteria and where assessed species have rather extensive associated documentation. Furthermore, these national Red Lists encompass all groups of animals, fungi, and plants with sufficient knowledge to be assessed, and are published collectively for each country. Fennoscandia is therefore an ideal region for studying the content and potential usefulness of ecological documentation of red-listed species. Each country has between 4000 and 4500 red-listed species, of which 2000–2500 are forest species (Table 1) (Henriksen and Hilmo, 2015a; Artdatabanken, 2015; Rassi et al., 2010; Tiainen et al., 2016; Liukko et al., 2016). Forest is the most extensive land cover type across Fennoscandia, covering approximately 54% of the total land area (Forest.FI, 2016; NIBIO, 2016; Skogstyrelsen, 2016). Since late twentieth century, red-listed species are increasingly considered in Fennoscandian forest management and conservation; both when government agencies prioritize

**Table 1**  
Number of species red listed<sup>a</sup> in Finland, Norway and Sweden.

	Finland	Norway	Sweden	Fennoscandia
Estimated total no of multicellular species in each country	>45 000	>40 000	>50 000	
No of red-list assessed species	21 398	21 000	20 800	
Total no of red-listed species (2010/2015)	4960	4438	4273	
<b>Red-listed forest species (%)</b>	<b>2395 (48%)</b>	<b>2323 (48%)</b>	<b>2444(52%)</b>	<b>4830</b>
Threatened forest species (VU, EN, CR)	1117	1256	1195	

<sup>a</sup> As given in the three national Red Lists.

forest areas to be protected, and in forest owners forest management, e.g. in retention forestry and voluntary set-aside areas as required by forest certification schemes such as the Wood-land Key Habitats (Hottola and Siitonen, 2008; Baumann, 2002; Gustafsson et al., 1999; Gjerde et al., 2007; Timonen et al., 2010; Elbakidze et al., 2011).

During the last century, forestry has largely changed the forests in Fennoscandia, with resulting decline and impoverishment of biodiversity. The transition from historically extensive forest use to large scale intensive industrial forestry have caused a structural change from widely spread old-growth conditions to younger, more even-sized and even-aged forest stands with changing qualities and smaller amounts of dead wood (Östlund et al., 1997). Areas of forest with natural dynamics are strongly reduced and fragmented (Timonen et al., 2011). Following all these changes, the species diversity have been severely affected, and about 10% of the Fennoscandian forest species are nationally red-listed, often largely confined to remnant structures and habitats in which forestry has been less intense (Gustafsson, 2002; Mikusinski et al., 2007; Puumalainen et al., 2003; Timonen et al., 2011).

In this study, the aims were to 1) investigate the usefulness of ecological documentation from the national Red Lists of Finland, Norway, and Sweden to select information on the red-listed species habitats at different geographical scales and for various selections of species of conservation interest, 2) to provide an overview of the key habitats and ecological variables important for red-listed forest species in Fennoscandia, and 3) to discuss the potential for using such compiled ecological documentation from Red Lists to assist conservation planning and facilitate guidelines.

## 2. Materials and methods

### 2.1. Compilation of the database

We used the National Red Lists of Finland, Norway and Sweden, and extracted information from the documentations for each red-listed forest species (Henriksen and Hilmo, 2015a; Artdatabanken, 2015; Rassi et al., 2010; Liukko et al., 2016; Tiainen et al., 2016). This ecological information was used to complement the dataset of all red-listed forest species in Fennoscandia previously compiled by Tingstad et al. (2017). The term red-listed includes species within the Red List categories RE (Regionally Extinct), CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened) and DD (Data Deficient). This dataset consists of all nationally red-listed species classified with forest as their primary or secondary habitat type in at least one country. Forest is defined as primary habitat type when species primarily occur in forests, and secondary habitat type when forests are not the main habitat of the species, but the species may occur in forests (Gårdenfors, 2010). In total, the dataset contain 4830 red-listed forest species (Table 1, Supplementary material Table S1).

Besides Red List category, Red List criteria, and taxonomical group, the following information was available for most species: lifeform (e.g. herbivores, autotrophs), forest type associations (coniferous, boreal broadleaved, nemoral broadleaved, or mixed forest) and tree species associations (Table 2). In addition, the following ecological variables were extracted if present; associations with dead wood, old-growth forest, calcareous soils, post-fire conditions, hollow trees and/or swamp forest (Table 2). These six ecological variables were chosen because of their frequent appearance in the Red List documentations from all three countries.

Species were grouped in 11 taxonomical groups; beetles, birds, fungi, lichens, mammals, mosses, molluscs, reptiles, spiders and vascular plants. The few species of Hemiptera, Mecoptera, Neuroptera, Orthoptera, Psocoptera, Siphonaptera, Strepsiptera and Thysanoptera were treated as one group named "Insects", and Chilopoda, Hexapoda, Malacostraca, Myriapoda, Paurapoda and Tricladida as one group named "others" (Table 2).

Three main forest types were distinguished: coniferous forest was assigned for species reported as present in coniferous forest and/or associated to conifers (Norway spruce, Scots pine, and/or larch); boreal broadleaved forest was assigned for species associated to aspen, alder, birch, rowan or willow; nemoral broadleaved forest was assigned to species associated with or present in forests of ash, beech, elm, hazel, lime, maple or oak (Table 2). These were the only three key forest types in the

**Table 2**  
Ecological variables included in describing the ecological features of the red-listed forest species.

Variables	Elements
Forest type	coniferous, boreal broadleaved, nemoral broadleaved, mixed forest, no classified association
Associated tree species	Norway spruce ( <i>Picea abies</i> ), Scots pine ( <i>Pinus sylvestris</i> ) alder ( <i>Alnus</i> sp), birch ( <i>Betula pubescens/pendula</i> ), aspen ( <i>Populus tremula</i> ), willow ( <i>Salix caprea</i> ), rowan ( <i>Sorbus aucuparia</i> ), ash, ( <i>Fraxinus excelsior</i> ), beech ( <i>Fagus sylvatica</i> ), elm ( <i>Ulmus glabra</i> ), hazel ( <i>Coryllus avellana</i> ), maple ( <i>Acer</i> spp.), oak ( <i>Quercus robur/petraea</i> ), lime ( <i>Tilia cordata</i> )
Lifeform	Autotroph saprotroph/saproxyllic herbivore, nectar/pollen feeder, fungivore, mycorrhiza, carnivores, parasite, omnivore
Organism groups	Beetles ( <i>Coleoptera</i> ), birds, fungi, mammals, mosses, molluscs, lichens, reptiles, spiders ( <i>Arachnida</i> ), vascular plants, and other insects ( <i>Hemiptera</i> , <i>Mecoptera</i> , <i>Neuroptera</i> , <i>Orthoptera</i> , <i>Psocoptera</i> , <i>Siphonaptera</i> , <i>Strepsiptera</i> , <i>Thysanoptera</i> ), and "other" (arthropods: <i>Chilopoda</i> , <i>Hexapoda</i> , <i>Malacostraca</i> , <i>Myriapoda</i> , <i>Paurapoda</i> and <i>Tricladida</i> )
Other ecological variables	calcareous soils, dead wood, hollow trees, old growth forest, post-fire conditions, swamp forest

documentation that were comparable between all three countries. Among the species in the dataset, 47% were associated with more than one key forest type. These species were counted for each forest type it was associated with, and in addition, these species were registered as associated with “mixed forest”, accounting for any combination of the three key forest types. Information of species associations to dead wood was complemented with information from the Nordic saproxylic database (Stokland et al., 2006). Species associated to dead wood included all species documented as saproxylic (dependent on dead wood). All other species that were not saproxylic but had a specific tree species association, were assigned as species associated to “living trees”. The remaining species was categorized as “forest floor and understory” species.

When different scientific names were used for the same taxon in the different countries, species names were synonymized with the help of species specialists at Swedish Species Information Centre, the Norwegian Biodiversity Information Centre, and specialists associated with the Finnish Red List assessments. We also used the help of these specialists to complement information for species lacking assessment in their respective national Red List assessment. These species were nationally assigned to either NA (Not Applicable, i.e. species not resident), NE (Not Evaluated), or LC (Least Concern).

For the Swedish red-listed species, information on their presence in the northernmost and southernmost counties, Norrbotten and Skåne respectively, was added from the Swedish Red List documentation. These two counties were selected to represent different sub-national regions and different vegetation zones; boreal and nemoral. For the Swedish species, we also added information on global Red List status when present, to get a selection of species representing a different conservation interest.

The number of species associated to the various forest type and tree species were extracted from the dataset, together with the number of species associated to the six ecological variables. The growing stock (mill of m<sup>3</sup>) of tree species in Fennoscandia were attained from the national forest inventories and from country reports within the Global Forest Resource, but only for the tree species that have more than 50 associated red-listed species in Fennoscandia (FAO, 2015; Fransson, 2017; Larsson and Hylen, 2007; Forest.FI, 2016).

We assumed the ecology of species to be the same throughout Fennoscandia and used the summary classifications in the analysis. The complete dataset is included as a supplementary excel-file (Supplementary material Table S1).

## 2.2. Data analyses

To investigate how red-listed species habitat associations may be affected by geographical location and scale, we compared the proportion of red-listed species associated with dead wood, living trees and the forest floor and understory within each key forest type at three geographic scales; the Fennoscandian scale ( $n = 4830$ ), the national scale of Sweden ( $n = 2444$ ), and sub-national scale within Sweden. For the latter, we selected two distant counties in Sweden; the northernmost county, Norrbotten, in the boreal zone ( $n = 621$ ) and the southernmost county, Skåne, in the nemoral zone ( $n = 1129$ ).

Further, to investigate various selections of species and corresponding habitat associations, we compared the proportions of species associated to dead wood, living trees and the forest floor and understory within each forest type for three selections of red-listed species; 1) all nationally red-listed forest species in Sweden ( $n = 2444$ ), 2) those red-listed in all three countries Finland, Norway and Sweden ( $n = 546$ ), and 3) species red-listed in Sweden and on the global Red List ( $n = 40$ ). These selections were chosen to represent three selections of species of different conservation interest; a national, a regional (Fennoscandian), and a global perspective.

To get an overview of the red-listed species in Fennoscandia and their habitat associations and ecology, we used a principal component analysis (PCA) to investigate the variation in distribution of species and their habitat associations and taxonomical groups (Legendre and Legendre, 2012). In these analyses, we used the different species as “sampling units” and the different habitat associations as “species”. The lifeforms and taxonomical groups were added as passive variables to investigate their variation with ecological variables along the two first axes without affecting the structure of the PCA. This will result in a diagram illustrating how the different ecological variables are connected on the same species and how the life forms and taxonomical groups are associated with the different ecological variables. In this way, we got four PCAs; one for the combined data set of all 4830 red-listed species, and additional three PCAs for Finland, Norway and Sweden separately.

In order to limit the number of variables in the final PCA plot, variables with less than 50 associated species were not included in the analysis. The following tree species were omitted: fir (*Abies* spp.), chestnut (*Aesculus* sp.), common hornbeam (*Carpinus betulus*), juniper (*Juniper communis*), larch (*Larix decidua*), crabapple (*Malus* sp.), haggberry (*Prunus padus*) and elderberry (*Sambucus* sp). In addition, the lifeforms “clepto-parasite” and “parasitoid”, and the taxonomic groups birds, mammals, molluscs and reptiles were omitted.

The statistics and figures were performed using RStudio Version 3.4.2 with the packages Vegan (Oksanen et al., 2017), ggplot2 (Wickham, 2009), dplyr (Wickham et al., 2017), and ggrepel (Slowikowski, 2017).

## 3. Results

The red-list documentation from Finland, Norway and Sweden provided information on forest types for 96% of the species (4522/4830 species). Of these, 70% contained additional information on tree species association and ecological variables (Table 2, Supplementary material S1).

### 3.1. Quantities of forest type and tree species associations

Most red-listed species were associated with coniferous forest (68%), and this forest type accounts for ca. 84% of the growing forest stock in Fennoscandia (Fig. 1). Further, 40% of the red-listed forest species were associated with boreal broadleaved forest, representing ca. 16% of the total growing stock. Finally, 35% of the species were associated with nemoral broadleaved forest, which represents less than 1% of the total forest stock in Fennoscandia (Fig. 1). Of the red-listed species in coniferous forest, 54% were classified as obligate to this forest type. The corresponding proportions in boreal and nemoral broadleaved forest were 14% and 27%, respectively (Fig. 2, upper row).

Oak was the tree with the highest number of associated red-listed species (768), followed by Norway spruce (666), Scots pine (539), beech (527), aspen (368), and birch (369) (Fig. 1). Fungi, beetles and lichens were in general the most numerous taxonomic groups, and beetles and fungi dominated among those associated with oak (Fig. 1). Fungi represented the dominant proportion of red-listed species in conifers and hazel, and beetles in the boreal broadleaved trees alder, aspen, birch and willow, and in the nemoral broadleaved trees ash, beech elm and oak. Lichens constituted a large portion of the red-listed species on ash and rowan (Fig. 1).

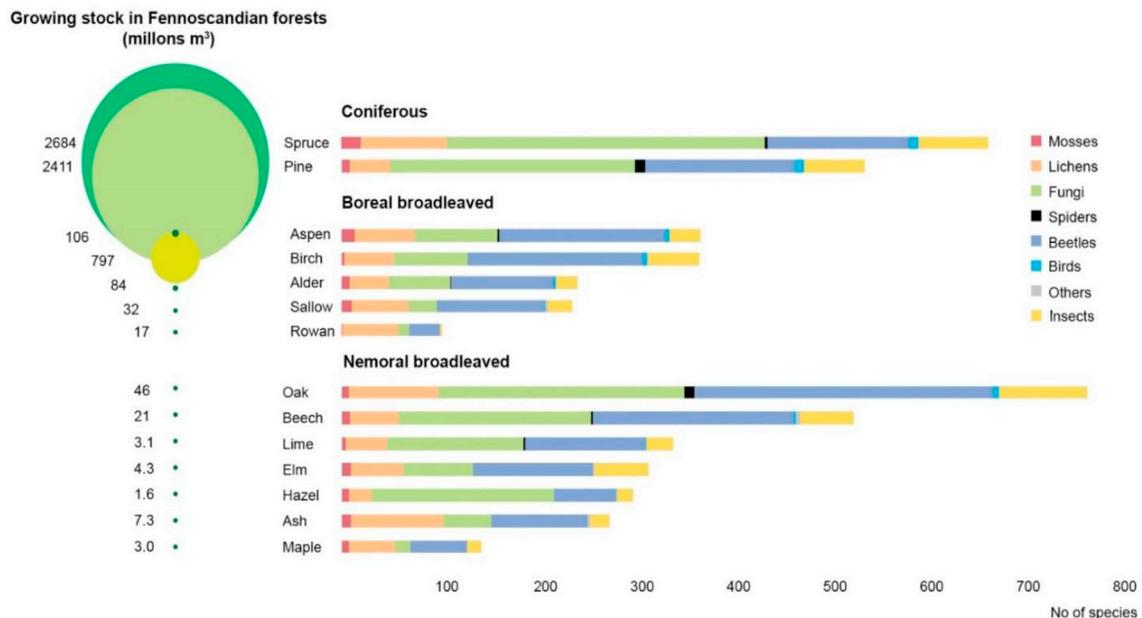
Equal proportions of red-listed species were associated to living trees, dead wood and the forest floor and understory in coniferous and broadleaved forest, while forest floor and understory species constituted a smaller share in nemoral broadleaved forest (25%) (Fig. 2, upper row).

### 3.2. Sets of red-listed species at different geographical scales

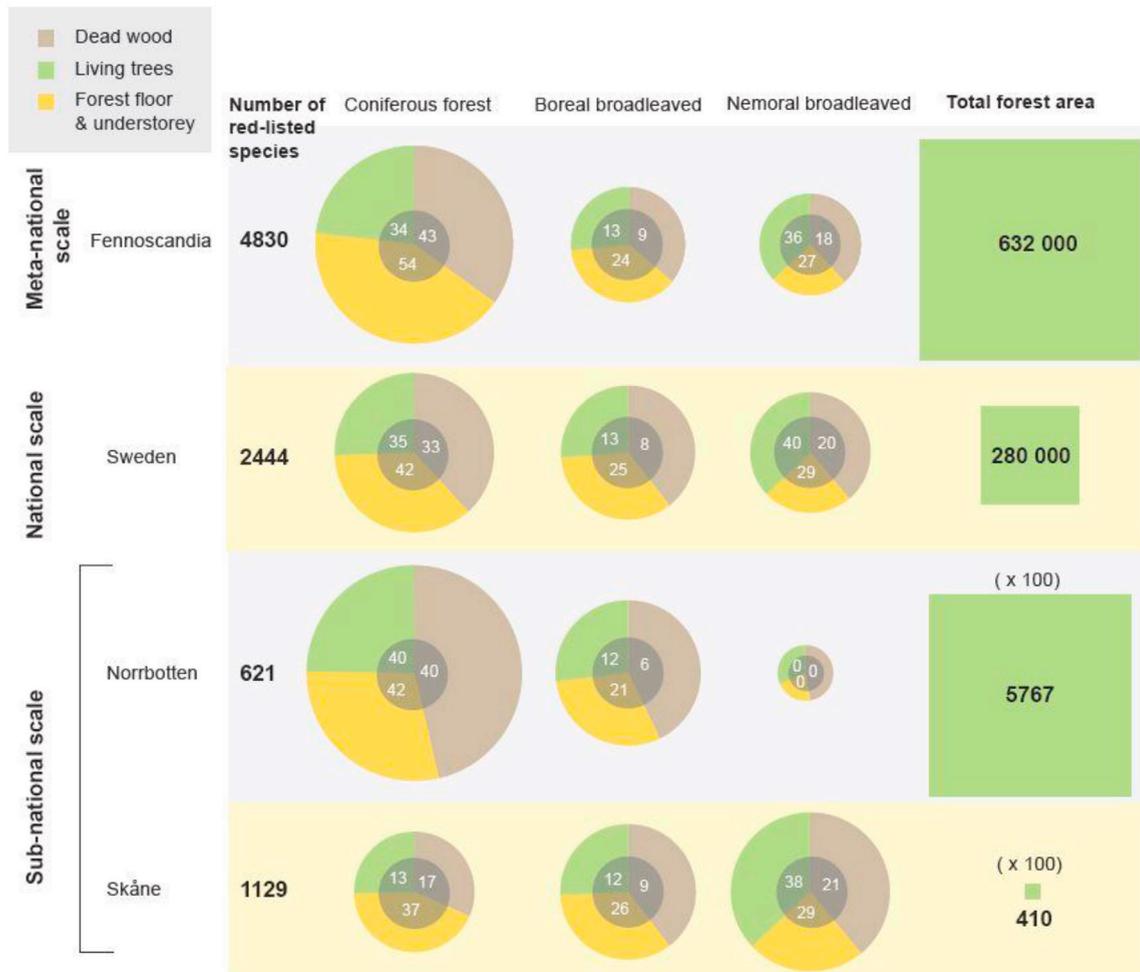
In coniferous forest at Fennoscandian level, 31% of the species were associated with dead wood, 37% with the forest floor and understory, and 20% with living trees (Fig. 2). Among the species associated to boreal broadleaved forest, 40% were associated with dead wood and 38% with the forest floor and understory, while in nemoral broadleaved forest, 39% were associated with dead wood and 26% with the forest floor and understory (Fig. 2, upper row).

At the national scale of Sweden, proportions of species associated with the three key forest types were similar as for the Fennoscandian level, albeit proportionally with some more species associated to boreal and nemoral broadleaved forest (Fig. 2). Nemoral forest had a higher proportion of species associated with living trees compared to the other forest types, and fewer species associated with the forest floor and understory. For the other variables, the national scale of Sweden resembled the Fennoscandian scale. For both Fennoscandian and national scale, the highest proportion of obligate species was found in coniferous forest (Fig. 2).

The distribution of red-listed species among the three key forest types in the northernmost county Norrbotten in Sweden resembled the Fennoscandian level with the largest portions of species associated with coniferous forest. Dead wood



**Fig. 1.** The number of red-listed forest species in Fennoscandia associated with different tree species. The contribution of different species groups are shown by the different colors (mammals, molluscs, reptiles and vascular plants are not shown due to few species or missing associations to specific tree species). The trees are grouped in coniferous, boreal and nemoral broadleaved forest types, and sorted according to the growing stock (millions of m<sup>3</sup>) of each tree species in Fennoscandia. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 2.** The proportion of red-listed forest species associated to different forest types considering the total number of present red-listed species at different spatial scales; in Fennoscandia, in Sweden and at the most northerly and southerly located counties in Sweden, Norrbotten and Skåne. To facilitate comparison between spatial scales, the three horizontally located pie-charts within each spatial scale sum up to 100%. The differently colored pie-charts shows the proportions of species associated to living trees, dead wood or the forest floor and understorey for each forest type. The figures in the inner grey circle shows the percentage of species obligate associated to living trees, dead wood or the forest floor and understorey, respectively, for each forest type. Total forest area at each spatial scale (km<sup>2</sup>) is given as a comparison. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

associated species constituted a larger share (47%) of the red-listed species in Norrbotten than at any other scale. In the southernmost located county Skåne, nemoral broadleaved forest had the highest proportion of the red-listed forest species (68%). Skåne had a higher number of red-listed species relative to forest area (Fig. 2). In Skåne, a high proportion of the nemoral species were obligate associated with nemoral broadleaved forest ranging from 21% for species associated with dead wood to 38% for those associated with living trees (Fig. 2).

### 3.3. Sets of red-listed species chosen by conservation interest

The national and global selection of species resulted in roughly the same proportions of species associated with each of the key forest types. The selection of species red-listed in all three countries resulted in a higher proportion of species associated to coniferous forest, fewer to nemoral broadleaved forest, and a higher proportion of species associated to dead wood in all three forest types. Independent of the selection of species, nemoral broadleaved forest had a lower proportion of species associated with the forest floor and understorey (Fig. 3).

### 3.4. Grouping of species with similar habitat associations

Based on the pattern of species and ecological variables in the PCA diagrams, we were able to distinguish groups of species clustered by associated ecologies (Fig. 4). The results of the PCAs showed that the total variation in the data for Fennoscandia



**Fig. 3.** The proportion of species of conservation interest in different forest types and their habitat association with three different sets of species; all red-listed species in Sweden, species red-listed in Sweden and in neighbouring countries Norway and Finland, and red-listed species in Sweden and in IUCN's Global Red List. To facilitate comparison between the three sets of selected red-listed species, the three horizontally located pie-charts scale sum up to 100%. Colors illustrate proportion of species associated to living trees, dead wood or forest floor and understorey within each forest type. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

is 2.22, Finland 1.89, Norway 1.95, whereas Sweden has the highest inertia of 3.5. The amount of variation captured by the two first PCA axes in Fig. 4 for the Fennoscandia are 22.8 and 12.7%, whereas for Finland, Norway and Sweden, the percentage variations are 31.04 and 11.4%, 20.5 and 16.7%, and 22.2 and 18.4%, respectively.

At the level of Fennoscandia, PCA separated species associated with mixed forests from those associated with coniferous forest (Fig. 4), and among the species associated with mixed forest, associations with nemoral and boreal broadleaved tree species dominated. Mixed forest species had representatives from many taxonomical groups, but fungi and various insects dominated. In coniferous forest, a high proportion of the species were fungi, lichens and beetles (Fig. 4).

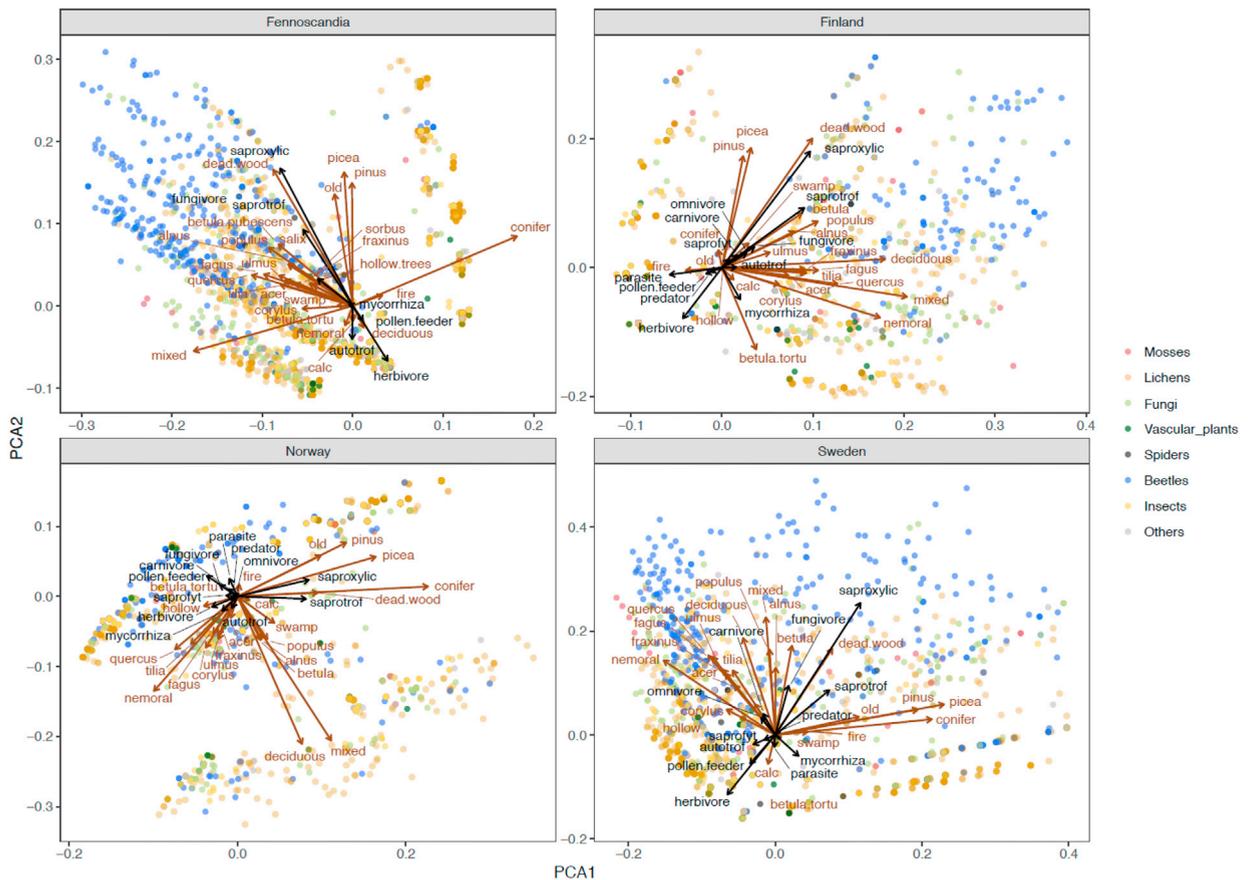
Dead wood and old-growth forest associated red-listed species were strongly correlated with Scots pine and Norway spruce. The species associated with dead wood were mainly beetles, lichens, fungi, and insects (Fig S1). About half of the species associated to specific tree species were saproxylic (Table S1).

Species associated to boreal broadleaved tree species appeared clustered with fungivores and saprotrophic species, mainly fungi and insects. The species associated to nemoral broadleaved tree species grouped together, and were separated from coniferous and old-growth forest.

Red-listed species associated to coniferous trees correlated both with post-fire conditions and mycorrhizal fungal species. In total, 6% (265) of red-listed forest species were classified as dependent on forest fire, dominated by insects and fungi (Fig S1).

Calcareous soils correlated with autotrophs, mostly vascular plants, while fungi is the most numerous taxonomical group (Fig S1).

The patterns at the national level were largely coherent with the Fennoscandian pattern e.g. the clustering of old-growth forest, coniferous tree species, and species associated to dead wood (Fig. 4). Mixed forest appear as a distinct ecological grouping also at national levels; in Finland and Norway associated with nemoral broadleaved trees, and dominated by fungi and lichens, in Sweden mainly associated to boreal broadleaved tree species and dominated by beetles and fungi.



**Fig. 4.** PCA for all red-listed forest species in Fennoscandia, and for nationally red-listed species in Finland, Norway and Sweden, separately. The brown arrows mark the response variables, black arrows mark passive variables. Note the scale differences between the plots. See legend for different symbols. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

## 4. Discussion

In this study, we show that species main forest type and general habitat associations are relatively well documented in the Red List documentations for most (96%) of the 4830 nationally red-listed forest species in Finland, Norway and Sweden. The documentations in these three national Red Lists together contain an extensive amount of species-specific classified ecological information, in total more than 51 000 records, of e.g. forest type and tree species associations, life-form, habitat preferences and ecological variables like association to dead wood, old-growth forest, calcareous soils, post-fire conditions, hollow trees and swamp forest. Access to such information on red-listed species can be important for identifying general patterns of red-listed species habitat and ecology. Information at the level of habitats for all or larger multi-taxa groups of red-listed species may also support conservation planning, as a supplement to information on single species (Flensted et al., 2016), as conservation prioritization of species can be arranged in different ways (Miller et al., 2006). Here we have investigated three possible approaches: (1) a selection based on all nationally red-listed species, with the potential option to focus on a selection of species or species confined to certain geographical regions or habitats, (2) as in option one but only considering species also assessed as red-listed in nearby countries or at the continental level (Red Lists is present for several species groups in Europe), and (3) as in two, but only selecting red-listed species that also are globally red-listed.

### 4.1. Overall characteristics of red-listed forest species in Fennoscandia

We identify five large scale patterns for red-listed forest species in Fennoscandia. First, most of these species (68%), are associated with coniferous forest, although approximately half of them also occur in boreal or nemoral broadleaved forest. Still, coniferous forest has the highest proportion of obligate species, i.e. confined to coniferous forests only. The corresponding figures for boreal and nemoral broadleaved forest are 40% and 35% associated species, of which 15% and 28% are obligate species, respectively. The high number of red-listed species in coniferous forest is probably largely due to the large conifer dominance in Fennoscandian forests; Norway spruce and Scots pine constitutes about 85% of the total tree volume

(Fig. 1) (FAO, 2015). A more detailed classification of the red-listed species' associated forest type could not be compiled for all species, although it is present for many species, and in particular the species red-listed in Sweden. The coarse classification of forest types presented still gives an overall perspective on the red-listed species main forest habitat associations, albeit with a low resolution.

Secondly, the number of red-listed species associated to different tree species poorly relate to the total volume of the trees in Fennoscandia. The broadleaved trees have strikingly high numbers of associated red-listed species in relation to volume in comparison to conifers. Oak is unparalleled in being associated with many red-listed species, despite oak's small contribution to the total volume of trees in Fennoscandia. Nemoral broadleaved trees are also paid much attention to in conservation, with many associated red-listed species, especially beetles (e.g. Berg et al., 1994; Ranius and Jansson, 2000). Among the boreal broadleaved trees, birch and aspen are the most important tree species in terms of number of associated red-listed species. As no estimations exists of the total number of species associated with different tree species, no further analyses of the differing portions of red-listed species between trees could be made to approach why and if so, underlying mechanisms.

A third pattern is that groups of red-listed species can be distinguished around two ecological variables; dead wood and old growth forest. Both are since long identified as key features for many red-listed species in Fennoscandia (e.g. (Siitonen, 2001; Storaunet and Rolstad, 2015; Gustafsson, 2002; Timonen et al., 2011; Tikkanen et al., 2006; Berg et al., 1994), and habitat deterioration, loss and fragmentation of old growth forest is identified as one of the most important reasons for declines of many red-listed forest species (Kouki et al., 2001; Jonsson et al., 2016; Tikkanen et al., 2006). Natural forest dynamics with old-growth forests and forest formed by extensive forest use are to a large extent replaced by managed production forests. Hence, important ecological structures like old snags, logs and other types of dead wood are missing (Kouki et al., 2001). Beside maintaining dead wood formed by storm falls and fire, different retention forest management practices are therefore important features for supporting conservation of red-listed species also in managed forests (Fedrowitz et al., 2014).

Historically, forest fire has been the major disturbance to which many forest species have evolved in boreal forest ecosystems (Esseen et al., 1997). A significant portion of the red-listed forest species in Fennoscandia, approximately 6%, are classified as dependent on forest fires. The PCAs showed correlation between species dependant on forest fires and species associated to coniferous forest, and that the same species were associated with old-growth forest. Hence, forest fires might be most important for red-listed species in old-growth coniferous forest. In example, forest fires provide important early-succession areas with deciduous trees attractive for, e.g. birds, vascular plants, and beetle species. Especially aspen is a tree species with a high number of associated red-listed species that is largely dependent on forest fires, as aspen seedling establishment is facilitated by fire (Turner et al., 2003; Kouki et al., 2001; Tikkanen et al., 2006). Hence, protection of old-growth forest with high amounts of appropriate types of dead wood and the occurrence of forest fires are important factors for the persistence of many red-listed species.

A fourth pattern is that the proportions of red-listed species associated to living trees (e.g. herbivore insects, mycorrhizal fungi and lichens), dead wood of the trees (mainly beetles, fungi and other insects) or species merely associated to the forest habitat (occurring in the forest floor and understory) (e.g. mosses, vascular plants) are similar in coniferous, boreal and nemoral broadleaved forest. The divergent pattern, however, is that wood-inhabiting red-listed species and those living on forest floor and understory tend to be more frequent in coniferous and boreal broadleaved than in nemoral broadleaved forests. This imply the need for considering variation in habitat structures and tree species in forest management order to meet the ecological preferences for the different red-listed species. If all red-listed species hypothetically should be considered of equal conservation value, our results suggests conifer and boreal broad-leaved forests to be of higher/similar value for saproxylic species as nemoral broadleaved forests, although nemoral trees has been underpinned as of being of particular importance for the saproxylic biodiversity (Framstad et al., 2017; Jonsson et al., 2016).

#### 4.2. Effects of selecting species by geographic area and conservation interest

The proportions of red-listed species associated to different forest types, and to dead wood, living trees or the forest floor and understory within each forest type, were overall similar at the Fennoscandian scale and the national scale of Sweden. However, selecting the smaller geographical counties Norrbotten in northern and Skåne southern Sweden resulted in different ecological characteristics. Norrbotten resembles the pattern for Fennoscandia, due to the region being located within the boreal vegetation zone and dominated by coniferous forest. The northern parts of Sweden also lack nemoral broadleaved tree species. In contrast, Skåne which is located in the nemoral vegetation zone, has the highest number of associated red-listed species, and a high proportion of them are confined to nemoral trees only. This might seem trivial, but is included here to illustrate the importance of choosing the appropriate selection of species and scale for conservation planning to have relevant ecological information. The important ecological factors for the national scale of Sweden are appropriate for Norrbotten, but not for Skåne. Similarly, Fennoscandian level perspective is not always appropriate for the national level.

We also explored the effects on the ecological characteristics from different selections of species of conservation interest. The subsets included all nationally red-listed species in Sweden, those that additionally also were red-listed in Finland and Norway, and those that in addition also were red-listed globally. The outcomes provides different perspectives; considering forest species red-listed in all Fennoscandian countries with the same value of each species, the conservation emphasis should be put on coniferous forests. However, with a selection of species red-listed at a Swedish or global level, it would be more appropriate to equally put efforts to coniferous and broadleaved forests. The proportions of red-listed species associated

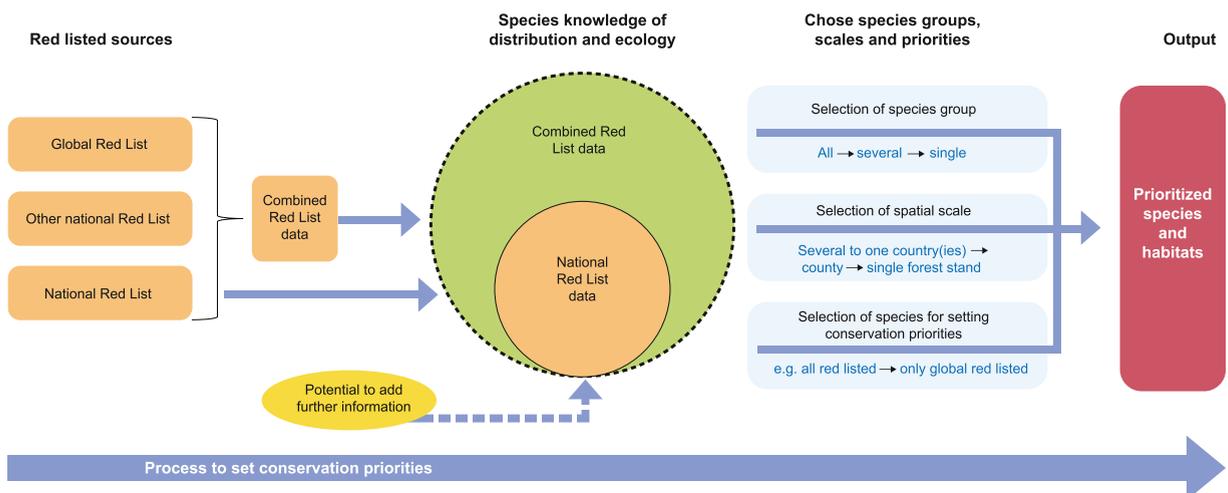
with living trees, dead wood or forest floor and understory within the forest types were not much affected by species selection. However, the proportion of species associated with living conifers is higher with a Swedish perspective than with the global perspective, which illustrates how selection of species and spatial scale may affect forest associations and ecological variables.

#### 4.3. Implications for conservation

Our study suggests that a combined and general description of red-listed forest species' habitats and ecologies based on the documentation in Red Lists can be informative if available, but will probably be rather coarse. The degree of details will depend on whether, and to which extent, the ecologies of the species have been classified and documented during assessments of Red Lists. This kind of information may therefore not be sufficiently detailed for conservation directed to individual or few red-listed species, but appropriate for an overview of general ecological patterns; and for selected areas or groups of species of conservation interest. Red List documentations may thereby provide a supporting tool to identify habitats, habitat structures or other ecological variables to consider in conservation. We show that overall ecological characteristics of red-listed species in Fennoscandia may vary at different scales, regions, and with selection of species. This underlines the importance of using contextually selected information.

Red List documentation may facilitate identification and semi-quantification of ecological information of conservation interest. With knowledge of the red-listed species distribution, this could be conducted and applied at any spatial scale, from smaller estates of private land owners to the full spatial extent of the Red list and for any selection of species of conservation interest. An option is also, as in this study, to combine the documentation from other appropriate sources of knowledge, e.g. adjacent countries national Red Lists documentations or databases such as the Nordic Saproxyl database, to complement the ecological knowledge, and increase the knowledge base to prioritize and to identify appropriate conservation measures among species. Conservation prioritization is certainly not a scientific matter as it is value-driven and subjective (Arponen, 2012). However, it is important that science can offer effective approaches for attaining what has been defined as conservation goals. In Fig. 5, we visualize the approach employed in this study aiming to efficiently integrate as much available and appropriate knowledge as possible to feed into the political process of prioritizing influenced by socio-political and other practical factors that determines what can be done.

In this study, we did this for Fennoscandia, but the same approach could easily be applicable in other regions in Europe where Red List information exist at a sufficiently detailed level. However, to our knowledge, no other European countries, except Denmark and to some extent Germany has similar extensive ecological documentation and concerted red-list assessment for many groups of organisms as Finland, Norway and Sweden. Compilation of ecologies from diverse groups taxonomically require large efforts. Even so, the approach of this type of study is flexible and can be used for single to several groups of red-listed species, using the information that is available within individual countries or combine this with information available in adjacent countries, or in e.g. European Red Lists which presently cover fifteen groups of species (European Red Lists, 2018) and species assessed globally (IUCN, 2017). There are also initiatives for assessing threatened habitats types (Janssen et al., 2016; Raunio et al., 2013; Artsdatabanken, 2017), but these tools base the assessments on habitat structures rather than species occurrences, and hence may rather be looked upon as a complement to species based Red Lists. It appears



**Fig. 5.** A conceptual framework for the process of identifying and setting conservation priorities using data from single national Red Lists or data from several (national to global) combined Red Lists. The potential to add additional appropriate ecological information is shown. The combined data may after appropriate selection of species groups, spatial scale and which red-listed species to select, be used to facilitate prioritizing of species and habitats of conservation interest. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

that the associated ecological documentation of species in national Red List assessments is an overlooked resource of ecological knowledge that could be compiled and analysed to a larger extent to advance an understanding of threatened species habitat affiliations and ecologies. Combining information from several national Red Lists may help to extract information and to reveal larger-scale patterns that are not easily revealed by a strict national perspective.

## Acknowledgements

We gratefully acknowledge the nearly 300 species experts that have been involved in the national Red List assessment of the species used in this study, from Finnish expert groups on different species, the Norwegian Biodiversity Information Centre (NBIC) and the Swedish Species Information Centre (SSIC). We also give a special thanks to Jonas Sandström (SSIC) and Snorre Henriksen (NBIC) for help to extract ecological data for the red-listed species, and Cajsa Lithell for figures. We thank colleagues for helpful comments. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.gecco.2018.e00410>.

## References

- Arponen, A., 2012. Prioritizing species for conservation planning. *Biodivers. Conserv.* 21, 875–893.
- Artdatabanken, 2015. Rödlistade Arter i Sverige 2015. SLU, Uppsala: Artdatabanken.
- Artsdatabanken, 2017. Red list for ecosystems and habitat types [online]. Norwegian biodiversity information Centre. Available. <https://www.artsdatabanken.no/Pages/135568>. (Accessed 10 January 2017).
- Baumann, C.G., 2002. Miljöregistrering i Skog - Biologisk Mangfold. Skogforsk - Norsk Institutt for Skogforskning.
- Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conserv. Biol.* 8, 718–731.
- CBD, 2006. Global biodiversity outlook 2. Montreal.
- Eaton, M., Gregory, R., Noble, D., Robinson, J., Hughes, J., Procter, D., Brown, A., Gibbons, D., 2005. Regional IUCN red listing: the process as applied to birds in the United Kingdom. *Conserv. Biol.* 19, 1557–1570.
- Elbakidze, M., Angelstam, P., Andersson, K., Nordberg, M., Pautov, Y., 2011. How does forest certification contribute to boreal biodiversity conservation? Standards and outcomes in Sweden and NW Russia. *For. Ecol. Manag.* 262, 1983–1995.
- Essen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. *Ecol. Bull.* 46, 16–47.
- European Red Lists, 2018. [Online]. European commission. <http://ec.europa.eu/environment/nature/conservation/species/redlist> [Accessed 2018-06-18 2018].
- FAO, 2015. Global Forest Resources Assessment 2015-Country Report. Rome.
- Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygesen, A., Gustafsson, L., 2014. REVIEW: can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol.* 51, 1669–1679.
- Flensted, K.K., Bruun, H.H., Ejrnæs, R., Eskildsen, A., Thomsen, P.F., Heilmann-Clausen, J., 2016. Red-listed species and forest continuity—A multi-taxon approach to conservation in temperate forests. *For. Ecol. Manag.* 378, 144–159.
- ForestFI, 2016. Finnish forest association [online]. <http://www.smy.fi/en/> [Accessed 31.10.2016 2016].
- Framstad, E., Blindheim, T., Granhus, A., Nowell, M., Sverdrup-Thygesen, A., 2017. Evaluering Av Norsk Skogvern i 2016. NINA Rapport 1352. NINA.
- Fransson, J., 2017. Forest statistics 2017—official statistics of Sweden/Skogsgata 2017. In: Fransson, J. (Ed.), Umeå. Swedish University of Agricultural Sciences.
- Gårdenfors, U., 2010. The 2010 red list of Swedish species. In: GÅRDENFORS, U. (Ed.), Artdatabanken. SLU, Uppsala.
- Gjerde, I., Sætersdal, M., Blom, H.H., 2007. Complementary Hotspot Inventory – a method for identification of important areas for biodiversity at the forest stand level. *Biol. Conserv.* 137, 549–557.
- Gustafsson, L., 2002. Presence and abundance of red-listed plant species in Swedish forests. *Conserv. Biol.* 16, 377–388.
- Gustafsson, L., De Jong, J., Noréng, M., 1999. Evaluation of Swedish woodland key habitats using red-listed bryophytes and lichens. *Biodivers. Conserv.* 8, 1101–1114.
- Henriksen, S., Hilmo, O., 2015a. Norsk Rødliste for Arter 2015. Artsdatabanken, Norge.
- Henriksen, S., Hilmo, O., 2015b. Norwegian Red List of Species - Methods and Results. Norwegian Biodiversity Information Facility.
- Hottola, J., Siitonen, J., 2008. Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. *Biodivers. Conserv.* 17, 2559–2577.
- Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A., O'connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L., LARIGAUDERIE, A., 2017. Linking the influence and dependence of people on biodiversity across scales. *Nature* 546, 65.
- IUCN, 2017. The IUCN Red List of Threatened Species Version 2017-1.
- Janssen, J.A.M., Rodwell, J.S., Garzía Criado, M., Gubbay, S., Haynes, T., Nieto, A., Sanders, N., Landucci, F., Loidi, J., Szymank, A., Tahvanainen, T., Valderrabano, M., Acosta, A., Aronsson, M., Arts, G., Attorre, F., Bergmeier, E., Blijnsma, R.-J., Bioret, F., Bita-Nicolae, C., Biurrin, L., Calix, M., Capelo, J., Carni, A., Chytrý, M., Dengler, J., Dimopoulos, P., Essl, F., Gardfjell, D., Gigante, D., 2016. European Red List of Habitats Luxembourg.
- Jonsson, B.G., Ekström, M., Esseen, P.-A., Grafström, A., Ståhl, G., Westerlund, B., 2016. Dead wood availability in managed Swedish forests – policy outcomes and implications for biodiversity. *For. Ecol. Manag.* 376, 174–182.
- Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S., Uotila, A., 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scand. J. For. Res.* 16, 27–37.
- Larsson, J.Y., Hylen, G., 2007. Statistics of Forest Conditions and Forest resources in Norway. Viten fra Skog og landskap 1/07. Norsk Institutt for Skog og landskap.
- Legendre, P., Legendre, L., 2012. Numerical Ecology. Elsevier, Amsterdam, The Netherlands.
- Liukko, U.-M., Henttonen, H., Hanski, I.K., Kauhala, K., Kojala, I., Kyheroinen, E.-M., Pitkanen, J., 2016. Suomen Nisakkaiden Uhanalaisuus- the 2015 Red List of Finnish Mammal Species.
- Martín-López, B., González, J.A., Montes, C., 2011. The pitfall-trap of species conservation priority setting. *Biodivers. Conserv.* 20, 663–682.
- MEA, 2005. Millennium Ecosystem Assessment. Ecosystems and human well-being, Synthesis Washington DC.
- Mikusinski, G., Pressey, R.L., Edenius, L., Kujala, H., Moilanen, A., Niemelä, J., Ranius, T., 2007. Conservation planning in forest landscapes of Fennoscandia and an approach to the challenge of countdown 2010. *Conserv. Biol.* 21, 1445–1454.
- Miller, R.M., Rodríguez, J.P., Aniskowicz-Fowler, T., Bambaradeniya, C., Boles, R., Eaton, M.A., Gårdenfors, U., Keller, V., Molur, S., Walker, S., Pollock, C., 2006. Extinction risk and conservation priorities. *Science* 313, 441–441.

- Miller, R.M., Rodríguez, J.P., Aniskowicz-Fowler, T., Bambaradeniya, C., Boles, R., Eaton, M.A., Gärdenfors, U., Keller, V., Molur, S., Walker, S., 2007. National threatened species listing based on IUCN criteria and regional guidelines: current status and future perspectives. *Conserv. Biol.* 21, 684–696.
- NIBIO, 2016. Skogfakta [online] [Accessed 31.10.2016 2016]. [http://www.skogoglandskap.no/temaer/skogfakta/subject\\_view](http://www.skogoglandskap.no/temaer/skogfakta/subject_view).
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, R., Mcglinn, D., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H., Szoecs, E., Wagner, H., 2017. *Vegan: Community Ecology Package*. R Package Version 2.4-5.
- Östlund, L., Zackrisson, O., Axelsson, A.-L., 1997. The history and transforamtion of a Scandinavian boreal forest landscape since the 19th century. *Can. J. For. Res.* 27, 11981206.
- Puimalainen, J., Kennedy, P., Folving, S., 2003. Monitoring forest biodiversity: a European perspective with reference to temperate and boreal forest zone. *J. Environ. Manag.* 67, 5–14.
- Ranius, T., Jansson, N., 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. *Biol. Conserv.* 95, 85–94.
- Rassi, P., Hyvärinen, E., Juslen, A., Mannerkoski, I., 2010. The 2010 Red List of Finnish Species Helsinki, Finland.
- Raunio, A., Schulman, A., Kontula, T., 2013. Finnish Red List of Threatened Habitats Finnish Environmental Institute.
- Ricketts, T.H., Dinerstein, E., Boucher, T., Brooks, T.M., Butchart, S.H.M., Hoffmann, M., Lamoreux, J.F., Morrison, J., Parr, M., Pilgrim, J.D., Rodrigues, A.S.L., Sechrest, W., Wallace, G.E., Berlin, K., Bielby, J., Burgess, N.D., Church, D.R., Cox, N., Knox, D., Loucks, C., Luck, G.W., Master, L.L., Moore, R., Naidoo, R., Ridgely, R., Schatz, G.E., Shire, G., Strand, H., Wettengel, W., Wikramanayake, E., 2005. Pinpointing and preventing imminent extinctions. *Proc. Natl. Acad. Sci. U.S.A.* 102, 18497–18501.
- Rodrigues, A.S., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., Brooks, T.M., 2006. The value of the IUCN Red List for conservation. *Trends Ecol. Evol.* 21, 71–76.
- Sandström, J., Bjelke, U., Carlberg, T., Sundberg, S., 2015. Tillstånd Och Trender För Arter Och Deras Livsmiljöer. *Artdatabanken Rapportar 17*. SLU, Uppsala: Artdatabanken.
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. *Ecol. Bull.* 11–41.
- Skogstyrelsen, 2016. Statistik [online]. Skogstyrelsen Available. <http://www.skogsstyrelsen.se/Myndigheten/Statistik/>. (Accessed 31 January 2016). <http://www.skogsstyrelsen.se/Myndigheten/Statistik/>.
- Slowikowski, K., 2017. Ggrepel: Repulsive Text and Label Geoms for "ggplot2". R Package Version 0.7.0.
- Steffen, W., Richardson, K., Rockström, J., Cornell, S.E., Fetzer, I., Bennett, E.M., Biggs, R., Carpenter, S.R., De Vries, W., De Wit, C.A., Folke, C., Gerten, D., Heinke, J., Mace, G.M., Persson, L.M., Ramanathan, V., Rayers, B., Sörlin, S., 2015. Planetary boundaries: guiding human development on a changing planet. *Science* 347.
- Stokland, J.N., Dahlberg, A., Meyke, E., Schigel, D., Siitonen, J., 2006. The Nordic saproxylic database - a comprehensive overview of the biological diversity in dead wood. In: 1st European Congress of Conservation Biology.
- Storaunet, K.O., Rolstad, J., 2015. Mengde og utvikling av død ved i produktv skog i Norge, med basis i data fra Landskogstakserings 7. og 10. takst Oppdragsrapport fra Skog og Landskap. Skog og Landskap.
- Tiainen, J., Mikkola-Roos, M., Below, A., Jukarainen, A., Lehtikoinen, A., Lehtiniemi, T., Pessa, J., Rajasarkka, A., Rintala, J., Sirkia, P., Valkama, J., 2016. Suomen Lintujen Uhanalaisuus -The 2015 Red List of Finnish Bird Species.
- Tikkanen, O.-P., Martikainen, P., Hyvärinen, E., Junninen, K., Kouki, J., 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Ann. Zool. Fenn.* 373–383. JSTOR.
- Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J.S., Stokland, J.N., Sverdrup-Thygeson, A., Mönkkönen, M., 2010. Woodland key habitats in northern Europe: concepts, inventory and protection. *Scand. J. For. Res.* 25, 309–324.
- Timonen, J., Gustafsson, L., Kotiaho, J.S., Mönkkönen, M., 2011. Hotspots in cold climate: conservation value of woodland key habitats in boreal forests. *Biol. Conserv.* 144, 2061–2067.
- Tingstad, L., Gjerde, I., Dahlberg, A., Grytnes, J.A., 2017. The influence of spatial scales on Red List composition: forest species in Fennoscandia. *Global Ecol. Cons.* 11, 247–297.
- Turner, M.G., Romme, W.H., Reed, R.A., Tuskan, G.A., 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) Landscape. *Landsc. Ecol.* 18, 127–140.
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wickham, H., Francois, R., Henry, L., Muller, K., 2017. *Dplyr: a Grammar of Data Manipulation*. R Package Version 0.7.4.