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Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood

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Using data from expert assessments, we classified the habitat and resource requirements of red-listed boreal forest species in Finland. All major taxa were included and represented by 466 species. Of the four major groups studied, red-listed Plantae & Fungi and Aphyllophorales were mainly inhabitants of shady coniferous forests, whereas the habitats used by Animalia and Coleoptera were more diverse. Of the boreal tree species, *Picea abies* harbours the greatest number of red-listed species, but *Pinus sylvestris* and *Populus tremula* host almost as many. The proportion of critically endangered species is highest on *Populus*. Our results emphasise the importance of dead wood and the conservation value of natural early successional forest habitats in addition to old-growth natural forests. Red-listed forest species are a highly heterogeneous group in their habitat and resource requirements, and this has to be taken into consideration in conservation and when seeking for cost-efficient conservation measures.

Introduction

Human activities have radically changed the boreal landscape, although transformation of forests to other biomes has not been an ecological problem (Esseen *et al*. 1997). In fact, the area of forested land increased during the 20th century (Anon. 2003, 2004). At the same time, however, forestry has been intensified and extended over vast areas which resulted in dramatic changes in the ecological properties of the Fennoscandian boreal forests. For example, the age distribution of forest stands and the tree species composition of the canopy have changed and the amount of dead wood has greatly diminished (Linder & Östlund 1998, Siitonen *et al*. 2000, Siitonen 2001, Rouvinen *et al*. 2002, Kouki *et al*. 2004).

In the 1970s and early 1980s, ecologists in Finland and Sweden started to become worried about the effect of industrial forestry on species diversity (e.g. Järvinen *et al*. 1977, Palm 1982, Söderström 1983, Heliövaara & Väisänen 1984), and national and international concerns spawned in 1985 the first official red list of endangered species in Finland (Rassi *et al*. 1986). In Sweden, the first red-list assessments for vertebrates had already been completed in the 1970s, to be followed by assessments of invertebrates, plants, and fungi in the mid-1980s (discussed in Gärdenfors 2000). In Norway, the first comprehensive red list was published in 1992 (Direktoratet for Naturforvaltning 1999). The latest assessments carried out in Fennoscandia estimate that almost half of all red-listed species are forest species, the exact figures being 38% in Finland (1042 species excluding the category DD), 46% in Norway (1405 species including the category DD), and 51% in Sweden (2101 species including the category DD) (Direktoratet for Naturforvaltning 1999, Gärdenfors 2000, Rassi *et al*. 2001).

The herb-rich forests of the hemiboreal and temperate zones, and especially the broadleaved forests, harbour roughly half of the red-listed forest species in Fennoscandia. In contrast to the boreal heath forests, these more southerly habitats experienced major changes centuries ago, when they were extensively cleared for agricultural land. Therefore, the factors that currently threaten the species inhabiting these habitats are likely to be different from those prevailing in the more northerly areas that are still largely forested. The species of the herb-rich and broadleaved forests are currently threatened mainly because of habitat restrictions, whereas the species of the boreal heath forests are threatened because of changes in the quality of their environment (*see* Angelstam 1992, Berg *et al*. 1994, Esseen *et al*. 1997). Moreover, the structure, dynamics, and tree species composition of broadleaved forests differ from those of boreal heath forests in many ways, for example in the fact that conifers are the dominant tree species in the latter and fire plays a profound role in shaping their structure (Esseen *et al*. 1997).

In order to obtain a better understanding of the mechanisms that cause species to decline and become threatened, we require a detailed knowledge of the habitat associations of these species. Such information about the habitat and resource requirements of Fennoscandian boreal forest species has not been published, although it is badly needed for effective conservation planning. Such information can be used to identify weak spots in current conservation policy, for example, and to further develop biodiversity-oriented forest management practices. A few reports have been compiled on the red-listed forest species of Sweden, but unfortunately none of them treat the boreal forest and broadleaf forest species separately, and two of them consider only species depended on dead wood (Berg *et al*. 1994, Jonsell *et al*. 1998, Dahlberg & Stokland 2004).

We collected data based on expert assessments concerning the habitats and resource requirements of the red-listed boreal forest species of Finland and explored the relative importance of forest characteristics such as the stage of succession, microclimate, tree species and quality of dead wood for these species. In addition, we examined the similarities and differences in habitat and resource requirements between the four major species groups. Our main aim was to analyse the overall habitat requirements of the red-listed species and to analyse whether taxonomically different groups exhibit the same patterns in relation to forest habitats. We suspect that such information may prove to be valuable when looking for umbrella or indicator groups or forest structure characteristics for use in biodiversity inventories. To our knowledge, this is the first attempt to summarise resource requirements of all red-listed species of boreal forests in Finland or elsewhere in northern Europe.

Methods

Compilation of the database

We first selected all those species classified as threatened or near-threatened (IUCN categories CR, EN, VU and NT) in "The 2000 Red List of Finnish species" (Rassi *et al*. 2001) whose primary habitat is given as forests in general (M), boreal heath forests (Mk, Mkk, Mkt) or spruce bog (Sk; for abbreviations, *see* Rassi *et al*. 2001: 388). These species are referred to below as *red-listed forest species*. Although some of the species classified as inhabitants of herb-rich forests (Ml, Mlt, Mlk) in the Finnish red list (Rassi *et al*. 2001) can also occur in boreal heath forests (e.g. in large aspen trees), we excluded all species of the herb-rich forest category in order to keep the criteria logical and simple. This deliberate choice may, however, lead to underestimates of the proportions of red-listed species in our data that are dependent on deciduous trees. Moreover, it is very probable that some less studied taxa, such as Diptera and Hymenoptera, are underrepresented in the current red list. Nevertheless, the state of the knowledge about fauna and flora of Finland is amongst the best in the world, thanks to the long tradition of taxonomic research. The total number of forest species included is 466, belonging to 16 mainly order-level taxa, although the list also includes some higher taxa such as Arachnida (Table 1). The taxonomical classification used here follows Rassi *et al*. (2001).

Next we defined seven attributes which describe the habitat and resource requirements of boreal forest species (Table 2). We emphasised characters describing the structure of forest stands and trees within stands, because these seem to be the key patterns for understanding the species occurrences and are also related to forest management operations. Experts in the various taxa then assessed the "habitat preferences" of the red-listed forest species in relation to these predefined attributes. A total of 24 experts participated in the assessment: for Aves, Timo Pakkala; Arachnida, Seppo Koponen; Heteroptera, Veikko Rinne; Lepidoptera, Jukka Kettunen and Mika Pajari; Diptera, Hans Bartch, Jevgeni Jakolev and Jere Kahanpää; Hymenoptera, Juho Paukkunen, Antti Pekkarinen, Pekka Punttila, Ilari E. Sääksjärvi, Matti Viitasaari and Veli Vikberg; Coleoptera, Esko Hyvärinen and Petri Martikainen; Tracheophyta, Sirkka Haka-

Table 1. Numbers of Finnish red-listed boreal forest species in taxa surveyed and proportions of them red-listed in Sweden as well (Gärdenfors 2000), calculated from the numbers of these species that exist in Sweden. The taxonomic grouping follows the 2000 red list of Finnish species (Rassi *et al.* 2001).

Taxon	Number of species in the current survey	Red-listed in Sweden (%)
Animalia		
Mammalia	6	100
Aves	14	42
Arachnida	5	50
Heteroptera	14	58
Homoptera	5	not evaluated
Lepidoptera	16	60
Diptera[1]	9	44
Hymenoptera	21	16
Coleoptera[2]	145	77
Plantae & Fungi		
Tracheophyta	11	56
Hepatophyta	15	53
Bryophyta	8	75
Agaricales, Boletales	25	50
Aphyllophorales	119	64
Ascomycota	11	50
Lichenales	42	64
Total	466	63

[1]Sufficient information on 8 species for further analysis.
[2]Sufficient information on 137 species for further analysis.

Table 2. Attributes describing the ecological requirements of forest species, and categories used in the enquiry among experts, who were asked to select a category that describes the primary requirement of each species. Thus association with a certain tree species does not necessarily mean that a species is absolutely monophagous. A species belongs only in one category per attribute.

Attribute	Category
Successional stage	Early successional, Mid-successional, Old-growth, Indifferent
Fire	Obligate fire specialist, Prefers burned forests, Indifferent
Microclimate	Needs shady microclimate, Favours sun-exposed (sunny) sites, Indifferent
Tree species	*Alnus*, *Betula*, *Picea*, *Pinus*, *Populus*, *Salix*, Some other deciduous species, Deciduous generalists, Coniferous generalists, No association
Decay stage of dead wood	1 = recent dead tree, decay process not started, 2 = early decay stage, knife penetrates 1–2 cm into wood, bark relatively intact, 3 = middle decay stage, knife penetrates 3–5 cm into wood, bark mostly lost, 4 = late decay stage, whole knife penetrates easily into wood, bark lost, 5 = very soft trunk totally covered by epiphytes, kelo = wood dry and hard, knife penetrates < 2 cm, bark lost
Position of dead wood	Standing, Fallen, Hollow[1], Branch, Indifferent
Diameter of dead wood[2]	< 10 cm, > 10 cm, > 30 cm, Indifferent

[1] Includes living trees which have decaying parts but no open cavities in the trunk.
[2] Wood debris with diameter < 10 cm is of low commercial value and, therefore, abundant as logging residue; wood debris with diameter > 30 cm is rarely generated in managed boreal forests of Finland as stands are usually harvested before trees reach this diameter.

listo and Päivi Hokkanen; Hepatophyta & Bryophyta, Kimmo Syrjänen; Agaricales, Boletales & Ascomycota, Pertti Salo; Aphyllophorales, Kaisa Junninen, Heikki Kotiranta and Pertti Renvall; Lichenales, Kimmo Jääskeläinen. For Mammalia and Homoptera we used sources in the literature (Siivonen 1972, Heie 1982, 1986, 1992). One species of Diptera and eight species of Coleoptera were omitted from further analyses due to insufficient information, and some data were missing for a number of animal species. We consider this a minor problem, however, because the defects in the data are non-systematic. The only exception was the attribute *microclimate*, information on which was lacking for 27 species of Coleoptera, which were consequently added into the category *indifferent* (species with no specific microclimatical requirements).

Analysis of the data

Because of the small number of red-listed forest species in the kingdom of Plantae and in most order-level taxa of the other kingdoms (Table 1), we distinguished only four major groups for statistical analysis: the kingdom of Animalia (1), excluding its most numerous order, Coleoptera (2), and the combined kingdoms of Plantae & Fungi (3), excluding its most numerous order, Aphyllophorales (4). The numbers of species in these four groups were 90, 145, 112 and 119, respectively. We tested the independence of the frequency distributions of the attribute categories between the groups using the exact Goodman-Kruskal Tau test (G-$K\tau$, Bishop *et al.* 1975) with Monte Carlo estimation of the P value as provided by StatXact 4 for Windows (Measures of association for nominal data; CYTEL 2000). Because the expected frequencies in several group-category combinations were very low, the standard chi-square or log-likelihood tests used in contingency tables were not reliable and exact statistical procedures provided better solutions.

The distributions are presented as percentages in the figures, which should make comparisons between the species groups easier. For reference, we also present the distributions of *all species* among the attribute categories (not included in statistical tests). In addition, we analysed possible differences in the frequency distributions of the IUCN classes between the attribute categories with the same statistical procedure.

The Finnish Red List assessment was carried out concurrently with the Swedish assessment, using similar methods. This allowed us to check the proportion of the relevant species in the Red List for Sweden, in order to estimate how the results describe the characteristics of red-listed species in Fennoscandia as a whole (Table 1).

Results

Successional stage, fire, and microclimate

Half of the red-listed forest species lived in old-growth forests, whereas fewer than 10% lived in mid-successional forests (Fig. 1A). A considerable proportion, 20%, lived in early successional forests, and another 20% were indifferent (i.e. habitat generalists) with respect to the successional status of the forests. There was a conspicuous difference between Animalia and Plantae & Fungi in this respect, and even more so between the Coleoptera and Aphyllophorales, in that the proportions of the Animalia and Coleoptera groups living in early successional forests, 28% and 34%, were much larger than those of Plantae & Fungi or Aphyllophorales, only 18% and 5% (Fig. 1A).

The importance of forest fires for the red-listed forest species also differed between the major taxonomical groups. In general, only 10% of the species preferred sites affected by fire and 3% were dependent on fires. These proportions were the highest for Coleoptera (20% and 5%) and the smallest for Aphyllophorales (7% and 2%, Fig. 1B).

The microclimatic associations of the red-listed forest species were similar to their successional requirements (i.e. difference in distribution pattern between Animalia-Coleoptera groups and Plantae-Aphyllophorales groups). Most species of Plantae & Fungi and Aphyllophorales (52% and 63%) needed a shady habitat, whereas the proportions of the Animalia and Coleoptera species in this microclimatic category were smaller (16% and 9%; Fig. 1C). In contrast, relatively large proportions of the Animalia and Coleoptera

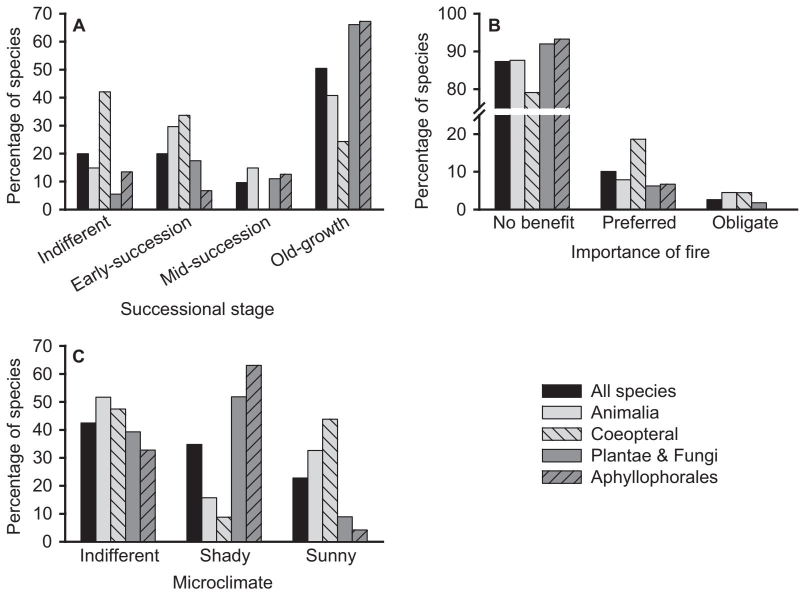

Fig. 1. Association of red-listed boreal forest species with (**A**) successional stages (n = 416, $G\text{-}K\tau$ = 0.105, P < 0.0001), (**B**) importance of forest fires (n = 454, $G\text{-}K\tau$ = 0.034, P = 0.0003), and (**C**) their microclimatic requirements (n = 457, $G\text{-}K\tau$ = 0.107, P < 0.0001).

species (33% and 44%) preferred sunny habitats, but only very small proportions of Plantae & Fungi and Aphyllophorales (9% and 4%; Fig. 1C). The differences among the species groups were not as distinct in the category *indifferent* as in the other two *microclimate* categories.

Association with tree species

The majority of the species studied (78%), were associated with trees in general, 18% with living trees and 60% with dead trees, and of these "dendrophilous" species, 61% were associated with conifers and 39% with deciduous trees. *Picea abies* Karst. harboured the largest number of species (Table 3), dominated by the Aphyllophorales, whereas high numbers of species were also reported to thrive on *Pinus sylvestris* L. and *Populus tremula* L. The numbers on the remaining three genera, *Betula*, *Alnus* and *Salix*, were smaller. Coleoptera and Lichenales differed from the rest of the taxa by being more species-rich on deciduous than on coniferous trees.

Type of dead wood

The majority of the species studied, 60%, were saproxylic (i.e. dependent on dead wood, *sensu*

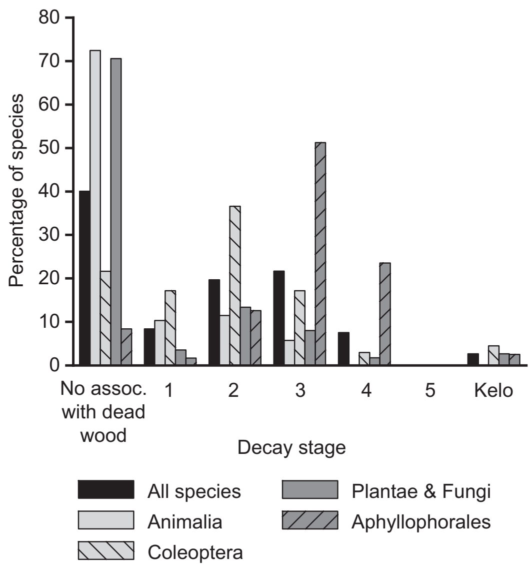

Fig. 2. Association of red-listed boreal forest species with decaying wood (n = 271, $G\text{-}K\tau$ = 0.107, P < 0.0001). For definitions of decay stages, *see* Table 2.

Speight 1989), including 92% of the Aphyllophorales and 79% of the Coleoptera (Fig. 2, Table 3), whereas the proportions in the other groups were much smaller (< 30%). Of the red-listed saproxylic forest species, the Coleoptera used mainly relatively fresh dead wood (decay stage 2), whereas the species of Aphyllophorales had a clear bias towards well-decayed wood

Table 3. Associations of red-listed boreal forest species with tree species and types of dead wood. Because of some missing data, the sums of the stages of decay or locations of dead wood do not equal the numbers in the respective cells in the Saproxylic column.

	Species				Stage of decay		Location of dead wood		
	Total	Threatened	Near threatened	Saproxylic	Recently dead	Advanced decay	Standing	Fallen	No importance
Total	457	246	211	276	122	140	49	143	76
No tree species association	99	50	49						
Deciduous trees	138	85	53	102	54	45	29	32	43
Deciduous generalists	50	28	22	36	15	21	7	12	19
Alnus	5	3	2	4	3	1			3
Betula	24	12	12	20	9	11	5	11	4
Populus	52	39	13	40	25	12	15	9	16
Salix	7	3	4	2	2	0	2	0	1
Coniferous trees	220	111	109	163	68	95	20	111	33
Coniferous generalists	58	26	32	50	16	34	3	33	15
Picea	95	47	48	65	28	37	5	56	5
Pinus	67	38	29	48	24	24	12	22	13

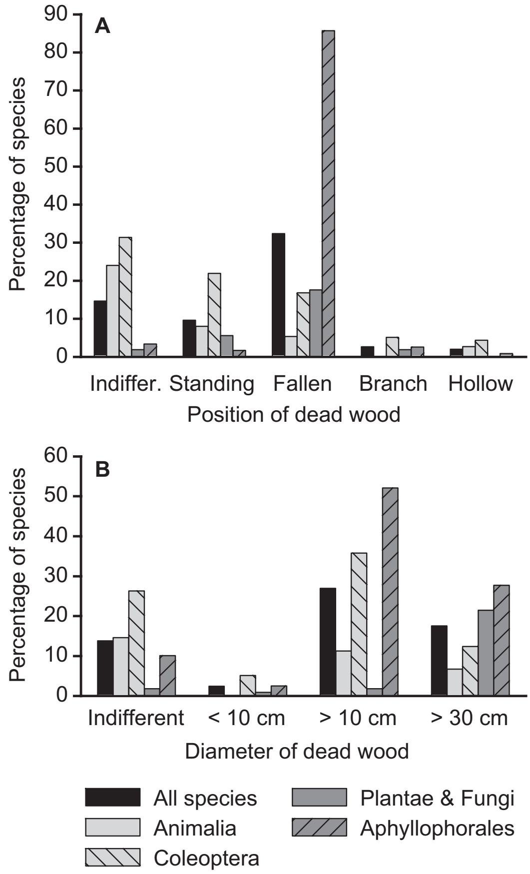

Fig. 3. Association of saproxylic red-listed boreal forest species with (**A**) position ($n = 280$, $G\text{-}K\tau = 0.273$, $P < 0.0001$), and (**B**) diameter of dead wood ($n = 277$, $G\text{-}K\tau = 0.116$, $P < 0.0001$). The histograms show proportions of the total group of red-listed species, including those which are not associated with dead wood at all.

(decay stages 3 and 4). No species used highly decomposed wood (decay stage 5) as its primary substrate, and only a few (< 3%) occurred on dead but dry, hard wood (the "kelo" trees).

The greatest proportion of saproxylic species were associated with fallen dead wood (i.e. logs; Fig 3A), with the Aphyllophorales as the most distinctive group in this category (86%). Of the Coleoptera species, 33% were indifferent with regard to the position of the dead wood, and approximately equally as many lived on standing dead trees or snags as on downed logs. Branches and hollow or damaged trees hosted a very small proportion of species (< 3%), mainly Coleoptera.

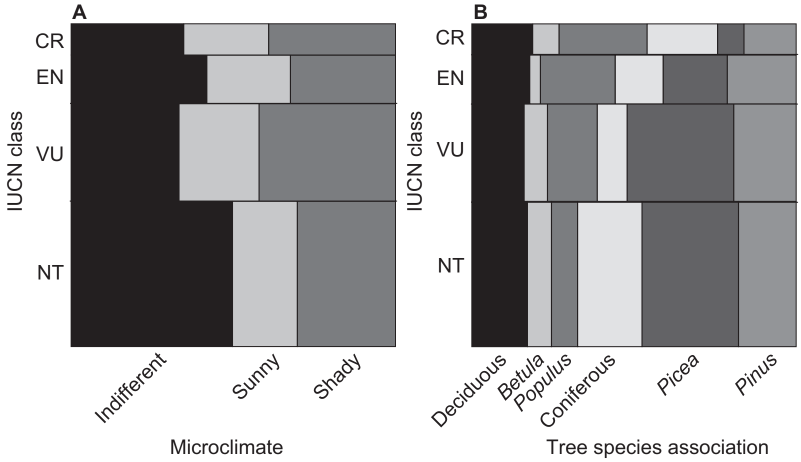

Fig. 4. Proportions of red-listed forest species of different IUCN classes by (**A**) microclimatic category (n = 457, $G\text{-}K\tau$ = 0.015, P = 0.0221), and (**B**) tree species association (n = 358, $G\text{-}K\tau$ = 0.025, P = 0.0357).

Most of the saproxylic species lived in coarse woody debris (diameter class > 10 cm; Fig. 3B) and a relatively large proportion were specialised in living in large-diameter trunks (> 30 cm; 18% of all red-listed forest species). The proportions of the Plant & Fungi and Aphyllophorales groups using large-diameter dead wood (21% and 28%) were considerably larger than those of Animalia and Coleoptera (7% and 12%). Less than 3% of all the red-listed forest species were specialised in living on small-diameter dead wood (< 10 cm).

Distribution of IUCN classes among the attribute categories

Of the seven attributes, the frequency distributions of the IUCN classes differed among the categories only in the case of *microclimate* and *tree species* ($P < 0.05$). Among the species in the near-threatened class (NT), the proportion that do not have any specific microclimatic requirements (the *indifferent* category) was conspicuously large compared with the proportions of shade-demanding or sun-preferring species, while the numbers of species in the other IUCN classes were distributed more evenly among the microclimatic categories (Fig. 4A).

The effect of *tree species* on the distribution of red-listed forest species among the IUCN classes and attribute categories was obvious, in that the proportion of critically endangered species (CR) was highest on *Populus* and small on *Picea*, whereas the proportion of near-threatened species was small on *Populus* and largest on *Picea* (Fig. 4B).

Discussion

Habitat requirements of the red-listed forest species

There are profound differences in habitat requirements among the red-listed forest species, and it would be an error to consider these species as a homogenous group. These differences must be acknowledged in the use of any indicator or umbrella species application for the selection of conservation areas (reviewed in Niemi & McDonald 2004). Of the four major taxonomic groups included in this study, the Plantae & Fungi and Aphyllophorales were mainly inhabitants of old-growth coniferous forests with a shady microclimate, while the habitats used by Animalia and Coleoptera were more diverse, most likely because many species in these groups are specialised on living on deciduous tree species and prefer a sunny microclimate. Furthermore, the proportion of species demanding or favouring forest fires is larger in the Animalia and Coleoptera groups than in the Plantae & Fungi and Aphyllophorales. Active mobility and sensor organs of animals enable rapid utilisation of emerging new habitats, such as new dead wood generated by forest fire. This may explain why pyrophily has evolved more often among forest animals than among plants and fungi which rely on passive and random dispersal mechanisms.

Intensive forestry has altered the boreal forests in many ways, each of which has different effects on particular groups of forest species. The fragmentation of the shady old-growth forests and the decline in their area has probably had the greatest impact on the Plantae & Fungi and Aphyllophorales, while the changes in tree species distribution due to the favouring of conifers in silviculture, the suppression of forest fires, and the disappearance of early-succession natural forests have had a larger impact on the Animalia and Coleoptera. All groups have suffered from the decline of dead wood, but the effect has been much stronger on the Coleoptera and Aphyllophorales than on the other taxa.

Less than five percent of the red-listed species in our data were obligate fire specialists. Could this mean that the importance of fire for boreal biodiversity has been overstated? No, because fire is the element that is largely responsible for the dynamics of natural boreal forests, including the generation of early successional forests and especially deciduous trees (Hellberg *et al.* 2003). In addition to the diversity of species, the biodiversity of boreal forests also includes diversity of natural processes (Berg *et al.* 1994). Sexual reproduction in *Populus*, for example, may be largely dependent on forest fires, because the seedlings cannot establish themselves easily in unburned soil (Turner *et al.* 2003). Moreover, severe fires generate patches with enormous amounts of dead wood that are bonanzas for threatened saproxylic species. Penttilä (2004) found that, after an initial decline caused by fire, the number of red-listed Aphyllophorales almost doubled from 12 species observed before the burning to 22 species observed 14 years later. A similar trend can be seen in the abundance of red-listed saproxylic Coleoptera, and the response can be even faster than in the case of the Aphyllophorales (Hyvärinen *et al.* 2005; *see* also Ahnlund & Lindhe 1992, Similä *et al.* 2002).

Although old-growth forests harbour the greatest number of red-listed species, deciduous trees and deciduous forests are also highly valuable for boreal biodiversity, as shown by the fact that the proportion of red-listed forest species harboured by deciduous trees is much larger than the proportion of deciduous trees in the Finnish forests (Anon. 2003, this study). As both coniferous and deciduous forests are important for boreal biodiversity, it is, not surprisingly, difficult to rank individual host tree species. *Pinus* and *Populus* host nearly as many species as *Picea*, and the proportions of saproxylic species are relatively equal among the tree genera, except for *Salix*, where only two of the seven red-listed species are saproxylic. The proportion of critically endangered (CR) species is highest on *Populus*, however (Fig. 4B), and their relatively low abundance and patchy distribution makes small groups of *Populus* trees biodiversity hotspots in boreal forests. Furthermore, the importance of *Populus* has probably been underestimated in our study, since many species inhabiting hollow *Populus* trees in the boreal forests are classified as species of the herb-rich forests in the Finnish red-list and were thus excluded from our data.

The impact of industrial forestry on *Populus* has been especially strong because of its low economic value and negative effects on pine saplings (it is an intermediate host for the pine rust fungus). This can be seen especially in forests owned by the state and by companies (Anon. 2003). The situation of red-listed species associated with *Populus* and generalists living on deciduous trees is unlikely to be any better in the boreal zone of Sweden where a large proportion of forest land is owned by companies. Apparently, the abundance of *Populus* is lower in central Sweden (1.3 m^3 ha^{-1}) than in southern Finland (2.3 m^3 ha^{-1}), based on the official forestry statistics for the two countries (regional results of the 9th National Forest Inventory presented in supplements to Metsätieteen aikakausikirja #B 1998–2001, Anon. 2004). Indeed, 86% of the species that we found to be associated with *Populus* and which are present in Sweden are also mentioned in the Swedish Red List (Gärdenfors *et al.* 2000).

Only a very few red-listed forest species were associated primarily with *Alnus* or *Salix* (Table 3). These figures differ from those given by Dahlberg and Stokland (2004), partly because these species are classified in the Finnish Red List (Rassi *et al.* 2001) as species of herb-rich forests and were thus excluded from our material. Other clear differences relative to the situation in Sweden (Berg *et al*. 1994, Dahlberg & Stokland 2004) are the greater importance of conifers as hosts in Finnish boreal forests and the tendency towards smaller host tree diameter classes in the preference for decaying wood, which is also largely caused by the exclusion of species preferring herb-rich forests in the present case. However, there are also many similarities. For example, most of the red-listed saproxylic Coleoptera in this study were either indifferent about their microclimate or favoured sunny sites and were associated to dead trunks (standing or fallen), as they were in Sweden (Jonsell *et al*. 1998). Despite some minor differences mentioned earlier, our results reflect the typical habitat patterns of red-listed boreal species in general, because 63% of the species in our analyses are also red-listed in Sweden (Table 1). Furthermore, our general findings are concurrent with the work of Berg *et al*. (1994), done 10 years ago: lack of old trees and dead wood is still a major threat to biodiversity of forests of northern Europe.

Implications for biodiversity management

If biodiversity protection and silviculture are to coexist, it will prove very hard to meet the habitat demands of the Plantae & Fungi and Aphyllophorales in production forests. Many of these need a shady microclimate and old, large trees or dead wood of very large diameter (> 30 cm), properties that are not easily combined with efficient wood production (Kuusinen & Siitonen 1998, Pykälä 2004). Moreover, the need for an advanced stage of wood decay in the case of many Aphyllophorales species implies that there will be a long time lag before any artificial increase in dead wood as a habitat restoration measure can be effective. In contrast, Coleoptera have properties that may facilitate fast and successful restoration of habitats and even the combination of wood production with biodiversity protection in the same areas, since selective logging together with a sufficient number of retention trees might benefit many red-listed Coleoptera-species. For example, Lindhe *et al*. (Lindhe & Lindelöw 2004, Lindhe *et al*. 2004) found that cut logs and high stumps benefited red-listed coleopterans but had a very small effect on red-listed polypores. Deciduous tree species are especially valuable as retention trees (Martikainen 2001, Sverdrup-Thygeson & Ims 2002), although it is critical that a sufficient quantity of retention trees should be left during harvesting to sustain viable populations of the most demanding Coleoptera species (Martikainen *et al*. 2000, Similä *et al*. 2003), and the current forestry recommendations may be too low to meet these criteria (5–20 trees ha^{-1}; Metsähallitus 2004; also according to the Finnish Forest Certification System available on the internet at http://www.ffcs-finland.org and to the Swedish FSC standard for forest certification available on the internet at http://www.fsc-sverige.org).

This and earlier studies (e.g. Andersson & Hytteborn 1991, Kuusinen 1996, Martikainen 2001) all serve to stress the importance of *Populus tremula* as a keystone species in boreal forests. Therefore rapid action to ensure an increase in the *Populus* stock in the vicinity of known habitats of threatened "*Populus*-inhabiting species" is one of the most urgent biodiversity management issues in Finland (Martikainen 2001, Kouki *et al*. 2004), and probably in the boreal zone of Sweden. As *Populus* is the host for such a great number of red-listed species in several taxonomic groups (*Populus* + Deciduous generalists = 102 species, Table 3), this might be a cost-effective operation.

In addition, there is an apparent need for increasing the area of nature reserves to meet the habitat requirements of the most demanding species, especially in southern Finland, where only 0.6% of the forest land is protected (Hanski 2000, Virkkala *et al*. 2000, Anon. 2003). Unfortunately, the area of unprotected old-growth forests in southern Finland is very small (< 2% of the forest land, Virkkala *et al*. 2000), which places a limit on the possibilities for developing a conservation area network by protecting old-growth forests alone. Since this and previous studies (Kouki *et al*. 2001, Similä *et al*. 2002, 2003, Penttilä 2004) show that the conservation value of early successional habitats rich in dead wood and deciduous trees is also high, the burning of monotonous, managed forests adjacent to existing old-growth forests should be included in the conservation policy on a large scale (Hanski 2000, Kouki *et al*. 2001).

Conclusions

In analysis of the habitat requirements of red-listed boreal forest species, approximately 80% of the species could be linked to specific tree species or forest characteristics, and 60% of them were associated with dead wood. Together with reliable estimates of the critical amount of dead wood (e.g. Penttilä *et al*. 2004), the information gathered on the habitat requirements of red-listed forest species could be used to form general guidelines for the management of biodiversity in boreal forests at the stand level (e.g. recommendations on the nature, quantity and diversity of living and dead wood). Our results underline the great variability in the habitat requirements of forest-dwelling threatened species. For successful enhancement of the future viability of these species in forest landscapes, data on tree species composition and the amount and continuous availability of different types of dead wood are required. Some of the species need specific habitats that may not be able to be maintained simultaneously with timber production. We anticipate that the next step in attempting to maintain the biodiversity of boreal forests will be to evaluate the effectiveness of different combinations of biodiversity-oriented management with large enough protected areas.

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