

## Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests?

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### Abstract

Design and establishment of ecologically good networks of conservation areas often requires quick assessments of their biodiversity. Reliable indicators would be useful when doing such assessments. In order to explore the potential indicators for species richness in boreal forests, we studied (1) the co-variation of species richness and composition of species assemblages among beetles, polypores, birds and vascular plants, (2) the relationships between species richness and four boreal forest site types, (3) the relationship between species richness and forest physical structure and (4) the suitability of potential indicator groups within the four taxa to predict the species richness generally. The data show that there are probably not a single taxonomic or forest structural characteristic to be used as a general biodiversity indicator or surrogate for all the species. The correlations in species richness among the four taxa studied were low. However, group-specific indicators were obvious: forest site type was a good surrogate for vascular plant richness, and quantity and quality of dead wood predicted the species richness of polypores. The results support the view that different indicators shall be used for different forest types and taxonomic groups. These indicators should facilitate relatively rapid methods to assess biodiversity patterns at the forest stand level.

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## 1. Introduction

Large-scale habitat alterations during the past decades have caused worry about decreasing biodiversity worldwide (Pimm et al., 1995). There is no doubt that many ecosystems and species need conservation actions to alleviate the ecologically harmful consequences that habitat modifications are causing. This has led to major challenges because successful conservation requires, first of all, that species richness and composition of species assemblages in different habitats and in different taxa can be reliably assessed, often with limited resources available for such inventories (e.g. Oliver and Beattie, 1996; Uliczka and Angelstam, 2000). Biodiversity assessment methods that are efficient both ecologically and economically are rare but badly needed (Simberloff, 1998).

Several procedures have recently been suggested to make the biodiversity evaluation easier (e.g. Gaston and Williams, 1993; Pearson, 1995; Simberloff, 1998; Ferris and Humphrey, 1999; Sverdrup-Thygeson, 2001; Ranius, 2002; Kati et al., 2004). It is often suggested that instead of complete inventories of species in different taxa, one must rely on the diversity patterns observed or on rapidly measured indicators of species richness (Gaston and Williams, 1993; Margules and Pressey, 2000; Grelle, 2002). The site selection would be more effective if habitats that are rich in species for one taxon were also species-rich for other taxa and if also threatened species occurred in such species-rich habitats (Prendergast et al., 1993). Proper indicators or surrogates of overall species richness could ideally produce reliable and informative data about species richness with minimum effort (Hammond, 1995).

Studies on the co-variation of species richness between different taxa and on the overlap of species richness hot spots have mainly been carried out in national and regional scales (e.g. Prendergast et al., 1993; Gaston and David, 1994; Kerr, 1997; Prendergast and Eversham, 1997; van Jaarsveld et al., 1998; Myers et al., 2000; Summerville et al., 2004; Schmit et al., 2005) but less often in small-scale (Howard et al., 1998; Jonsson and Jonsell, 1999; Pharo et al., 1999; Berglund and Jonsson, 2001; Ranius, 2002; Kati et al., 2004). Large-scale inventories are helpful in identifying potential regions where con-

servation efforts should be concentrated but provide little insight to practical site selection problems that managers constantly face. Landscape-level studies on the co-variation among taxa in sites are needed to assist in management decisions. So far, studies have shown fairly little evidence for co-variation in biodiversity at either large or local scale (Prendergast et al., 1993; Gaston, 1996; Prendergast and Eversham, 1997; van Jaarsveld et al., 1998; Jonsson and Jonsell, 1999; Sverdrup-Thygeson, 2001; Kati et al., 2004; Schmit et al., 2005).

In this study, we focus on boreal forests, which cover large tracts in the northern hemisphere. Human-caused habitat changes are rapidly proceeding in many areas, both locally (e.g. Esseen et al., 1997; Uotila et al., 2002) and regionally (e.g. Kouki et al., 2001; Löfman and Kouki, 2001). For example, in Fennoscandian boreal forests many species are currently suffering from these habitat alterations (Esseen et al., 1992; Kouki et al., 2001; Rassi et al., 2001), and there is an urgent need to assess and protect forest habitats to facilitate future survival of these species. The selection of areas to be protected would be easier and more efficient if we knew to what extent the diversity of different taxa varies in parallel (e.g. Mönkkönen, 1999). So called key habitats are considered as important habitats for rare and threatened forest-dwelling species (Nitare and Norén, 1992; Meriluoto and Soinin, 1998; Hansson, 2001) even though little is known about their importance for various groups of species and about how the high species richness of vascular plants in fertile key biotopes reflects the species richness in general (Gustafsson, 2000, 2002; Ericsson et al., 2005).

Selecting indicator groups of species or structural surrogates for species diversity is a demanding task and it requires that the relationship between indicator group and species diversity patterns in general are well known. For example, in Finland alone about 20,000 forest-dwelling species represent a wide spectrum of taxonomic groups, life histories and habitat requirements, and the ecology of many species is still poorly known.

In Finland, certain indicator species groups have already been identified from relatively well studied taxa, e.g. from birds (Väisänen et al., 1998) and polypores (Kotiranta and Niemelä, 1996) to indicate old-growth and 'pristine' forests, and from plants to

indicate fertile forest key biotopes (Meriluoto and Soininen, 1998). Lindgren (2001) observed that number of non-threatened indicator polypores correlated with number of threatened polypore species, but little is known about the relationship between richness of indicator species and polypore species richness in general. Moreover, there is a lack of knowledge of the relationships between indicator polypores and other forest-dwelling species or other forest species associated with decaying wood.

Likewise, the relative importance of structural characteristics of forest stands and landscape in relation to diversity of common species or to the occurrence of endangered species is important to know (Mönkkönen, 1999; Kouki et al., 2001). The question here is whether we can use high structural diversity (tree species composition, abundance of living trees, volume of standing dead trees or downed logs, etc.) as a surrogate for taxonomic diversity. It has been already observed that many decaying wood features are reflected in the richness of species dependent on dead wood (saproxylic species; Speight, 1989) and composition of species assemblages (e.g. Bader et al., 1995; Økland et al., 1996; Martikainen et al., 2000; Similä et al., 2003; Ranius, 2002). However, so far the relationships between forest structure and different forest-dwelling species assemblages remain poorly known.

In this study, we focused on the co-variation of four taxa along the fertility gradient of boreal forests. We addressed the following questions:

1. Is the forest site type a good surrogate for species richness in the forest stand level? If species richness is strongly centered in certain forest site types, concentrating conservation efforts in these key-areas would be reasonable.
2. Are the structural characteristics of forests useful surrogate for species richness? This would be of practical importance because structural characteristics are relatively easy to measure.
3. Does the richness of species co-vary between the different taxa? If so, inventories could be limited to the taxonomic group easiest to sample and identify.
4. Are there subgroups of species that would indicate the overall species richness within their own taxon, or richness of other taxonomic groups? Focusing surveys to such indicator groups would be cost-efficient.

## 2. Material and methods

### 2.1. Sites studied

The study area was located in Pudasjärvi (Fig. 1), at the transition zone of the middle and northern boreal zones in northern Finland (center of the study area: 65°17'N, 27°51'E). We sampled four forest types based on Cajander (1949) forest type classification: (1) Scots pine (*Pinus sylvestris*) dominated *Vaccinium-Myrtillus/Empetrum-Vaccinium* type, labeled sub-xeric forest here (SX), (2) Norway spruce (*Picea abies*) dominated *Vaccinium-Myrtillus* type, labeled mesic forest (M), (3) Norway spruce dominated *Geranium-Dryopteris* or *Vaccinium-Myrtillus/Geranium-Dryopteris* type, labeled herb rich forest here (HR) and (4) heterogeneous group of Norway spruce dominated moist site types, labeled spruce mire (SM).

To locate suitable study sites we used the stand inventory data of the Finnish Forest and Park Service. We randomly selected as natural and large old forest stands as possible. The stands in the area can be considered as semi-natural. All sites had been selectively logged in the late 19th or early 20th century (some sub-xeric stands also later), but the intensity of these loggings was generally low. The shape of sampling area within a study site was a square or a rectangle, depending on the shape of stand studied.

From each forest type class we had eight replicates, making a total of 32 sites. The minimum distance between the sites was 500 m (when distance between two study sites was 500 m, sites represented different forest types).

We measured the relative amount and quality of dead wood in five circles (radius 10 m) on each study site (1570 m<sup>2</sup>/site) and counted the number of living trees in 5 cm diameter classes from <5 to >45 cm of each tree species. We classified the dead wood into four classes according to the stage of decay: (1) wood hard and all bark remaining, (2) wood soft on surface, bark partly or completely loose, (3) wood soft throughout and (4) wood dried and very hard (in conifers). Downed and standing logs and snags were kept separate. We calculated the diversity of dead wood as a number of combinations formed by tree species, position (snag and log), decay class (1–4) and 5 cm diameter classes, from 5.1 to 10, 10.1 to 15 cm and so on, present on each site (see Siitonen et al.,

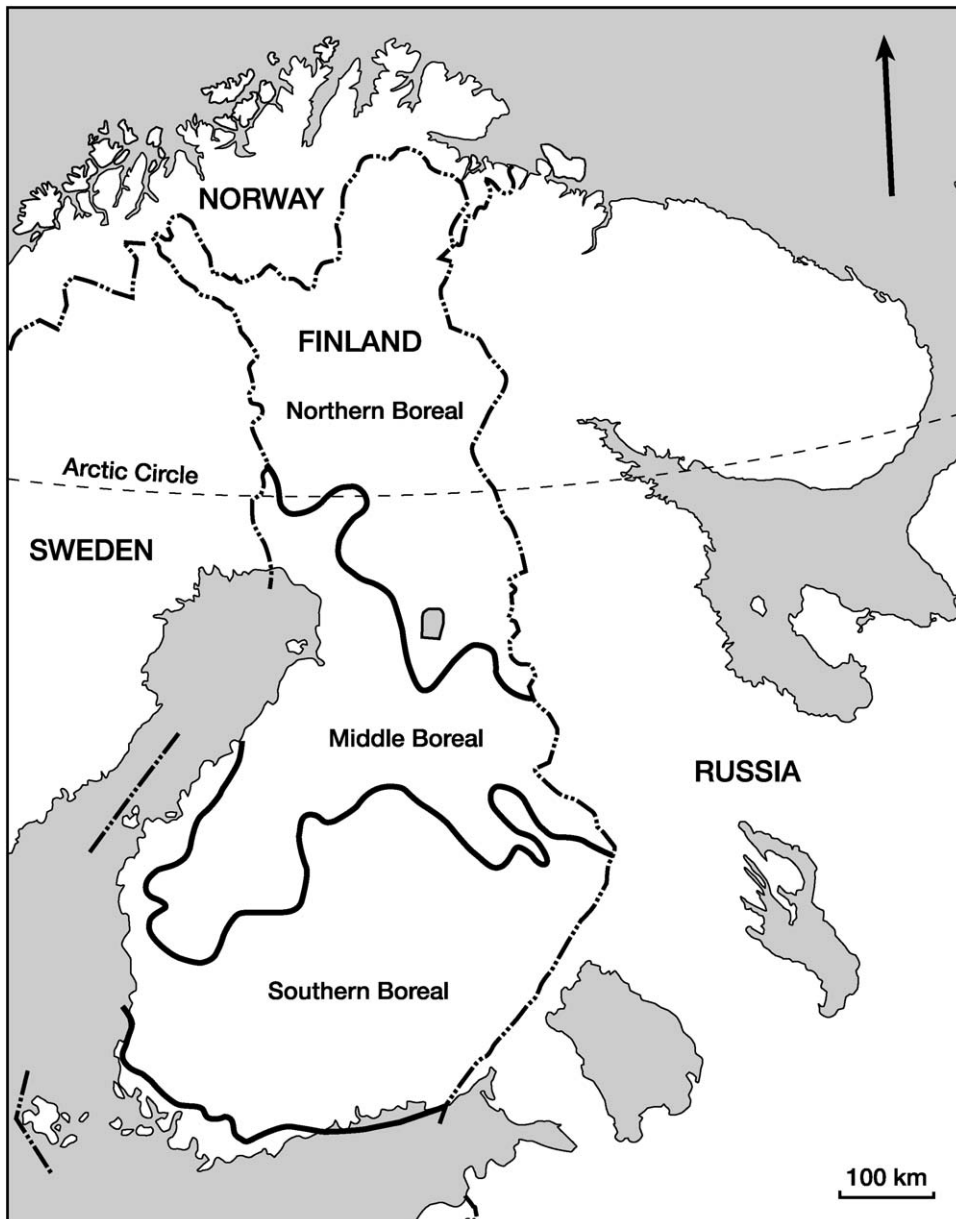


Fig. 1. Location of the study area (see also Similä et al., 2002). Vegetation zones are after Kalliola (1973).

2000). The mean timber volume varied from 170 to 292 m<sup>3</sup> ha<sup>-1</sup> among the forest types, and the mean volume was significantly lower in the sub-xeric than in the other forest types. The mean volume of dead wood was 40–50 m<sup>3</sup> ha<sup>-1</sup> depending on the forest type. Detailed stand characteristics of different forest types are presented in Similä et al. (2002).

## 2.2. Taxa studied

We sampled four taxa: beetles (Coleoptera), polypores (Basidiomycetes), birds (Aves) and vascular plants (Tracheophyta) on each study site. We selected these taxa to cover a wide array of dispersal potential and life forms in order to yield ecologically more

general results. Red-listed species are after Rassi et al. (2001). Both vulnerable and near-threatened species are called threatened species below (18 species in total).

Beetles were sampled using window and pitfall traps. There were five window traps on each study site, making 160 traps in total. Two pitfall traps were located within a 5 m radius around each window trap. Each pair of pitfalls was taken as one sample. The trapping period lasted from the end of May to the beginning of September in 1997. The traps were emptied with regular intervals five times during the period (for details of beetle sampling see Similä et al., 2002).

All the beetle specimens were identified to the species level and divided into saproxylic and non-saproxylic species. The grouping is similar to that used in Martikainen et al. (2000). The nomenclature of beetles follows Silfverberg (1992). The rarity class of each species was obtained from the frequency score list of the Finnish Coleoptera (Rassi, 1993). The rarity is based on the frequency of known occurrences of each species in Finland. We divided species into common (more than 50 observations or estimated occurrences in Finland during 1 January 1960–1 January 1990) and rare (50 observations at the most). We studied if the richness of rare saproxylic species (a potential indicator group) would indicate valuable forest sites in terms of beetle and overall species richness. Of all beetles 61 species (14%) were rare and 25 of them were saproxylic (6% of all beetle species). Five of the rare saproxylic beetle species were also threatened or near-threatened species. In addition, two vulnerable beetle species and one near-threatened species were found.

On each study site we surveyed five circles (radius 10 m; in total 0.16 ha/study site) for polyporous fungi assemblages. The inventories were done between mid-August and mid-September 1998. Site SX1 was cut in 1998 so it was not possible to collect polypore data from that study site. The nomenclature of the species follows Niemelä (2001). We recorded fruit bodies of polypores from all living trees and decaying wood with minimum length of 1 m and minimum basal diameter of 5 cm. We considered one species observed in a wood unit as one record, regardless of the number of fruit bodies. The species were either identified in situ or collected for the microscopic identification. Of

substratum tree species we recorded the stage of decay, basal diameter and position of tree. Kotiranta and Niemelä (1996) have listed polypore species that can be considered indicators of old-growth or pristine forest conditions. We used this information to study if these indicators are useful also in identifying valuable forest sites in terms of polypore and overall species richness (a potential indicator group). In total, 15 indicator species (25% of all polypore species) were observed, 11 of them were indicators for old-growth forests and four for 'pristine' forests. Of the indicator polypores, six species were classified also as threatened species or near-threatened. In addition, one vulnerable and one near-threatened polypore species were found.

Birds we censused with the point count method (Hilden et al., 1991) in June 1997. Each study site contained one point count station. Each station was visited three times (5 min per visit), between early and late June. All bird species seen or heard during the censuses were recorded regardless of the observation distance. We included only forest-dwelling species in the analyses. We separated species preferring old-growth forests using information in Väisänen et al. (1998). Birds nesting in Finland have been assigned a nominal value (NV) (Väisänen, 1996), which reflects the abundance, conservation status and reproductive potential of species. The formula of calculation is  $NV = (U \times S/K) \times 202\text{€}$ , where U is the species' ability to reproduce, S the need for the species' conservation and K is the size of species' population based on nationwide bird censuses. The constant (202€) has been set to proportion values to the reasonable scale; these values are applied in the Finnish court to judge the penalties for illegal killing and hunting of animals. Individuals of rare and threatened species with low reproductive potential have a higher value than individuals of common species with high fecundity. We used these data to divide species into 'expensive' (nominal value at least 84€) and 'cheap' (nominal value less than 84€) and tested if these values reflect the indicator property of species (a potential indicator group). Six bird species (17.6% of all bird species observed) were 'expensive' and four of them were also classified as indicators of old-growth forests, as well as one 'cheap' bird species, *Certhia familiaris* L. Both of the threatened bird species observed (vulnerable *Tarsiger cyanurus*



(Pallas) and near-threatened *Ficedula parva* (Bechstein)) were 'expensive' species.

Vascular plants were surveyed from 10 1 m<sup>2</sup> squares on each study site, located in a line where the distance between the squares was 5 m. We estimated the abundance of species as percentage coverage in each square. Inventories were conducted between mid-July and early August in 1998. We used the average of 10 squares as an indicator of species richness in each study site. Meriluoto and Soininen (1998) listed vascular plants whose presence indicates the high conservation value of forest biotopes. We analysed this species group as a potential indicator group for vascular plant and overall species diversity. In all, 30 vascular plant species (33%) of the present data were classified as species expressing forest key-biotopes important for conservation. Among vascular plants no red-listed species were found.

### 2.3. Statistical analyses

We compared the species richness (i.e. the number of species present on a study site) among the four forest types with one-way ANOVA (all species and species within each taxon). We used Spearman rank correlation coefficient to test if species richness co-varied among taxa, or if the species richness in the potential indicator groups correlated with the species richness in the main taxon, with the species richness in other taxa or with the overall species richness. Likewise, we studied if the species richness correlated with the variables describing stand characteristics (e.g. timber volume and amount of dead wood). In this connection, we adjusted the *P*-values within eight species groups with sequential Bonferroni correction (Rice, 1989) to avoid the group-wide type I error. Study site SX1 was excluded when all species and polypore data were analysed because of the missing data.

If a group of species is a reliable surrogate for overall species richness, sites rich in species for that particular group should overlap with sites rich in other groups (see Prendergast et al., 1993). In this study, we consider habitats with high species richness as hot spots (for other definitions for the term hot spot; see, e.g. Reid, 1998).

We measured the degree of the overlap in species richness hot spots among the four taxa by calculating

the number of shared sites among the 10 most species-rich sites. To test if the overlap significantly deviated from random overlap we performed a re-sampling analysis. We shuffled site ranks 1000 times to provide random samples. In each sample we calculated the amount of overlap among the top 10 sites between a pair of taxa. Across the whole sample we then counted the frequency of cases, which provided at least the observed overlap of top 10 hot spots between the two taxa. This gave the probability to get a result at least as extreme as the observed case by chance alone (i.e. one-tailed *p*-value).

To explore the composition of species assemblages in the four taxa we used the detrended correspondence analysis (DCA-ordination; Hill and Gauch, 1980). We used the log ( $x + 1$ ) transformation to normalize the distribution of species data in every taxon and rescaled axis with 26 segments (McCune and Mefford, 1999). We compared the ordination of sampling sites along Axis 1, produced for each taxon separately, with Pearson correlation coefficient. Significant (negative or positive) correlation indicates parallel variation in the species composition between taxa. Vascular plant gradient (the location of sampling sites on Axis 1 of DCA based on vascular plant data) correlated significantly with the gradients of other taxa. Therefore, parallel structural changes between beetles and birds, for example, may stem from both groups responding independently to variation in the composition of vascular plant species (to site fertility) rather than from 'true' structural co-variation. To see if species composition in different taxa genuinely co-varied we first run the regression models between vascular plant (constant variable) and other gradients. Then, we studied the correlation of residuals among beetles, polypores and birds with the Pearson correlation coefficient.

### 3. Results

Overall, 619 species were observed (Table 1). The total species richness was higher in the herb rich forests and spruce mires than particularly in the mesic site type (one-way ANOVA,  $F_{3,27} = 4.967$ ,  $p < 0.01$  with Turkey a posteriori test M-HR:  $p < 0.05$  and M-SM:  $p < 0.01$ ). This was due to one taxon: the richness of vascular plant species was higher in the herb rich

Table 1  
Number of species and individuals/observations of four taxa in different forest types

	SX		M		HR		SM		All
	Mean ± S.D.	Total	Mean ± S.D.	Total	Mean ± S.D.	Total	Mean ± S.D.	Total	
<b>Beetles</b>									
Species	112.4 ± 8.4	289	98.9 ± 10.3	255	107.4 ± 16.2	268	106.8 ± 11.4	291	435
Individuals	1852.4 ± 1207.3	14819	3284.1 ± 1367.5	26273	4633.9 ± 2226.3	37071	2771.3 ± 1515.4	22170	100333
Rare saproxylic species <sup>a</sup>	3.5 ± 1.6	14	3.0 ± 1.4	15	3.3 ± 2.4	12	2.3 ± 1.3	9	25
<b>Polypores</b>									
Species	11.3 ± 2.3	33	10.6 ± 4.14	33	14.0 ± 3.1	45	9.1 ± 3.5	28	60
No. of observations	18 ± 8.35	126	21.9 ± 10.7	175	33.8 ± 10.8	270	27 ± 14	216	787
Indicator species <sup>a</sup>	3.4 ± 1.6	10	1.9 ± 1.1	6	3.4 ± 1.9	12	1.9 ± 1.4	7	15
<b>Vascular plants</b>									
Species	9.3 ± 3.6	20	13.0 ± 4.3	31	22.8 ± 4.0	47	31 ± 9.5	81	90
Expressive species <sup>a</sup>	1.0 ± 1.1	3	2.0 ± 1.7	6	6.9 ± 2.4	15	11.4 ± 5.7	28	30
<b>Birds</b>									
Species	11.5 ± 1.6	21	11.4 ± 1.2	27	11.4 ± 2.5	29	11.1 ± 2.4	23	34
Individuals	17 ± 3.0	136	16 ± 2.4	128	15.0 ± 3.7	124	15.5 ± 3.8	120	508
Expensive species <sup>a</sup>	1.3 ± 0.7	3	1.6 ± 0.7	3	1.9 ± 0.8	5	1.8 ± 0.7	5	6
Total number of species	143.0 ± 11.3	362	133.9 ± 11.8	346	155.5 ± 17.7	389	158.0 ± 14.4	400	619

<sup>a</sup> Considered as potential indicator group, see Section 2.

forests and spruce mires than in the sub-xeric and mesic types (one-way ANOVA,  $F_{3,28} = 22.371$ ,  $p < 0.001$  with Dunnett T3 a posteriori test SX-HR:  $p < 0.001$ , SX-SM:  $p < 0.01$ , M-HR:  $p < 0.01$  and M-SM:  $p < 0.01$ ). In the other three taxa species richness did not differ between the forest types (one-way ANOVA, beetles  $F_{3,28} = 1.750$ ,  $p = 0.18$ ; polypores  $F_{3,27} = 2.954$ ,  $p = 0.05$  and birds  $F_{3,28} = 0.050$ ,  $p = 0.985$ ). Thus, the forest site type was a feasible surrogate for species richness in vascular plants but not in other taxa.

On the other hand, the total number of threatened species per forest type seemed to be highest in the herb rich forest type and lowest in the sub-xeric type (Table 2) but the numbers of species were too low for the statistical tests. The number of individuals (observations in polypores) of threatened species differed among the forest types (Chi-square = 8.66, d.f. = 3,  $p = 0.034$  compared to even distribution), being highest in the herb rich sites and lowest in the mesic forests.

Correlations of the species richness among the four taxa were generally weak ( $r_s$  varied between  $-0.258$  and  $0.189$ , NS). Species richness of the two groups

associated with decaying wood, polypores and saproxylic beetles, were also only weakly correlated with each other ( $r_s = 0.266$ ,  $p = 0.148$ ).

Moreover, the hot spots of species richness did not overlap considerably among the taxa. More overlap than expected by chance alone existed only between the total richness of all species and all beetle species, as well as between the richness of all beetle species

Table 2  
Number of threatened species and individuals/observations in the four studied forest types

		Sub-xeric	Mesic	Herb rich	Spruce mire	Total
Beetles	Species	2	5	5	2	8
	Individuals	4	6	5	7	22
Polypores	Species	3	1	5	3	8
	Observations	6	1	11	3	21
Birds	Species	0	1	2	2	2
	Individuals	0	1	6	3	10
Total no. of species		5	7	12	7	18
Total no. of individuals/ observations		10	8	22	13	53

Table 3  
Overlap of species richness hot spots among four taxonomic groups and two subgroups of beetles

	Beetles			Polypores	Birds	Plants	All species
	All	Saproxylic	Non-saproxylic				
Beetles							
All	–	<b>8</b>	5	3	2	3	<b>7</b>
Saproxylic	<0.001	–	4	4	3	2	6
Non-saproxylic	0.120	0.361	–	3	3	5	6
Polypores	0.915	0.692	0.705	–	3	3	3
Birds	0.994	0.962	0.705	0.962	–	2	1
Vascular plants	0.689	0.903	0.120	0.915	0.994	–	6
All species	0.007	0.066	0.066	0.802	0.997	0.066	–

Numbers above diagonal indicate how many sites the two groups share in common among the 10 most species-rich sites. Significant overlaps are in boldface. Numbers below diagonal denote the probability to get the same result by chance only (based on the re-sampling analysis, see Section 2).

and saproxylic beetles (Table 3). Birds and polyporous fungi did not show a slightest tendency for hot spot overlap with any other taxa. Sites rich in all species tended to be the same as the sites rich in beetles and vascular plants. This is logical because beetles was the most species-rich group comprising 70% of the total species number, and vascular plants was the only taxa which remarkably increased the total number of species on the study sites in fertile forest types.

### 3.1. Indicator groups

In beetles, richness of rare saproxylic species, a potential indicator group, did not correlate with the richness of all beetle species (Table 4), with all saproxylic species ( $r_s = 0.292$ ,  $p = 0.110$ ), with non-saproxylic beetle species ( $r_s = 0.123$ ,

$p = 0.503$ ) or with the species richness of other taxa (Table 4).

By contrast, indicator polypore species seemed to be a useful tool in assessing the richness of polypore species in general. The number of indicator polypore species correlated strongly with the richness of all polypores (Table 4 when indicator species were included in the total polypore species richness, and  $r_s = 0.330$ ,  $p = 0.07$  when indicator species were excluded from the total species richness), and the number of non-threatened indicator polypore species correlated with the number of threatened polypores ( $r_s = 0.471$ ,  $p < 0.01$ ). Also, the correlation between the richness of indicator polypore species and beetle species was nearly significant among all (Table 4) and saproxylic ( $r_s = 0.320$ ,  $p = 0.079$ ) beetle species. Furthermore, the combined richness of both rare saproxylic beetle species and indicator polypore

Table 4  
Correlations between species richness of indicator groups and the main taxon/other three taxa (indicator species included in the total number of species in each taxa)

	Rare saproxylic beetles	Indicator polypores	Expensive birds	Expressive vascular plants
Beetles	0.206	0.328	<b>–0.517</b>	–0.049
	0.258	0.071	<b>&lt;0.01</b>	0.792
Polypores	0.198	<b>0.747</b>	–0.223	0.051
	0.285	<b>&lt;0.001</b>	0.228	0.785
Birds	0.079	–0.060	<b>0.435</b>	–0.127
	0.667	0.749	<b>&lt;0.05</b>	0.489
Vascular plants	–0.263	–0.192	0.204	<b>0.949</b>
	0.146	0.301	0.263	<b>&lt;0.001</b>

Upper number within each taxon is Spearman correlation coefficient and lower number is the significance value.



species correlated positively with the richness of saproxylic beetle species ( $r_s = 0.435$ ,  $p < 0.05$ ;  $r_s = 0.356$ ,  $p < 0.05$  when rare saproxylic species are excluded) and with the richness of polypore species ( $r_s = 0.622$ ,  $p < 0.001$ ) on each study site.

In birds, the richness of ‘expensive’ birds correlated (Table 4), but the richness of old-growth forest birds did not correlate ( $r_s = 0.073$ ,  $p = 0.691$ ) with the richness of bird species in general. Richness of ‘expensive’ birds correlated negatively with the richness of beetle species (Table 4, and for beetle subgroups:  $r_s = -0.421$ ,  $p < 0.05$  for saproxylic and  $r_s = -0.427$ ,  $p < 0.05$  for non-saproxylic species).

In vascular plants, the number of expressive species was positively correlated with overall plant species richness (Table 4). In all above-mentioned correlations considering potential indicator groups and their own taxon, the total richness of species included the indicator species as well. If indicator species were excluded from the total species richness in each taxon, vascular plants was the only group where the richness of indicator species correlated positively with the richness of the rest of the species of the same taxon ( $r_s = 0.807$ ,  $p < 0.001$ , indicator species excluded).

### 3.2. Co-variation of species assemblages

The ordination analysis of beetles (Fig. 2), polypores (Fig. 3), birds (Fig. 4) and vascular plants

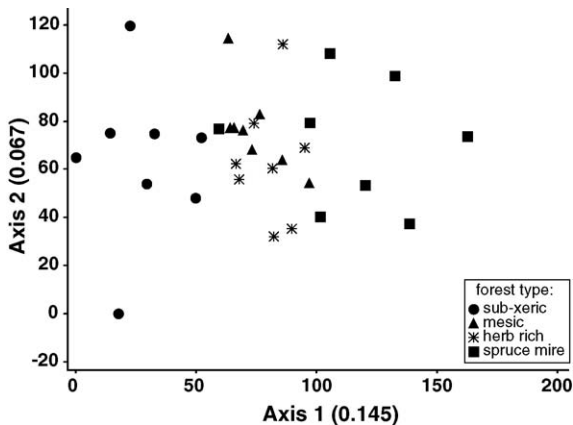


Fig. 2. The DCA ordination of beetles (total inertia of ordination is 1.688).

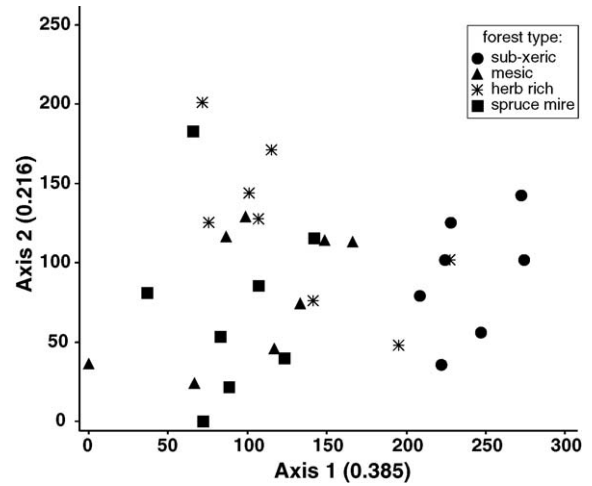


Fig. 3. The DCA ordination of polypores (total inertia of ordination is 3.416).

(Fig. 5) showed that species composition tended to change in a similar manner in every taxon. The position of the study sites along Axis 1 correlated among taxa (Table 5). The beetle and vascular plant species assemblages in sub-xeric forest type and in spruce mires were more or less separated from the assemblages in other forest types, whereas the assemblages in mesic and herb rich forests overlapped. In polypores, the species assemblages of sub-xeric forest type were separated from assemblages in other forest types. Bird species assemblages were

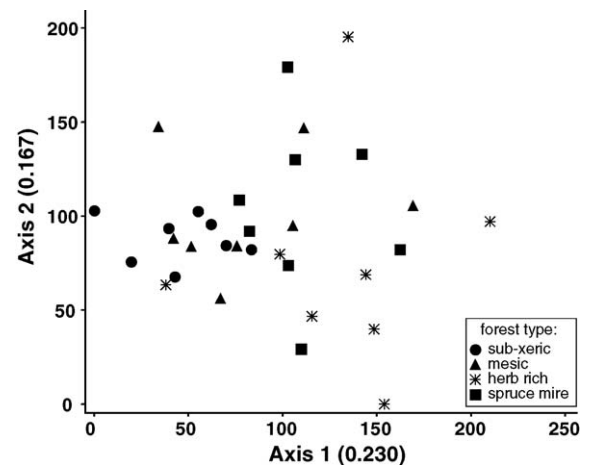


Fig. 4. The DCA ordination of birds (total inertia of ordination is 1.816).

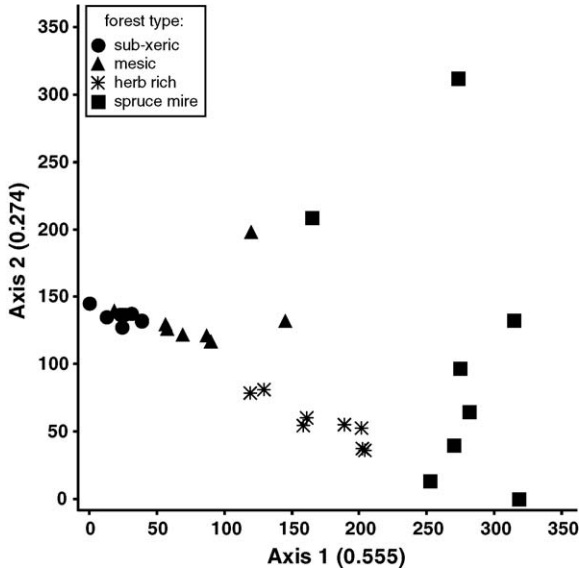


Fig. 5. The DCA ordination of vascular plants (total inertia of ordination is 2.886).

Table 5

Correlations between species assemblages in four taxa (the upper triangle), according to the Axis 1 of DCA-ordination of each taxon, and correlations of residuals between three taxa (the lower triangle; the effect of vegetation gradient excluded)

	Beetles	Polypores	Birds	Vascular plants
Beetles		-0.735***	0.532**	0.817***
Polypores	-0.503**		-0.510**	-0.622***
Birds	0.136	-0.256		0.573**

The significance levels are the same as in Table 6.

relatively homogeneous among four forest types, but still the pattern of change was parallel to that in other taxa (Table 5).

Vegetation gradient explained 66.7% of the variation in the beetle gradient ( $p < 0.001$ ), 38.7% of the variation in the polypore gradient ( $p < 0.001$ ) and 32.8% of the variation in the bird gradient ( $p < 0.01$ ). When the possibly common effect of vegetation gradient on other three taxa was excluded by exploring the correlation of residuals among them, the composition of beetle and polypore assemblages still changed in parallel along Axis 1 (Table 5).

Table 6

Correlations between species richness and stand characteristics

	Beetles	Rare saproxylic species	Polypores	Indicator polypores	Birds	Expensive plants	Vascular birds	Indicator plants
<b>Living trees</b>								
Number of trunks ( $\varnothing > 0$ cm)	-0.203	-0.003	0.382	0.059	-0.162	-0.046	0.028	0.096
Total volume	-0.166	-0.206	<b>0.556*</b>	0.139	-0.140	0.144	0.419	<b>0.500*</b>
Volume of pine	0.264	0.309	0.038	0.152	0.012	<b>-0.478*</b>	<b>-0.725***</b>	<b>-0.656***</b>
Volume of spruce	-0.250	-0.253	0.274	-0.021	0.061	0.306	<b>0.645***</b>	<b>0.661***</b>
Volume of birch	-0.061	-0.111	0.274	0.035	-0.140	0.040	0.161	0.125
Proportion of deciduous trees <sup>a</sup>	0.005	-0.118	0.125	-0.091	-0.101	0.110	0.211	0.151
<b>Dead wood</b>								
Number of trunks ( $\varnothing > 10$ cm)	0.312	-0.250	0.192	0.071	-0.219	-0.004	0.228	0.227
Total volume	0.267	-0.030	<b>0.547*</b>	0.465	-0.186	-0.049	-0.035	0.059
Volume of snags	0.242	-0.121	0.390	0.192	-0.107	-0.101	0.065	0.118
Volume of logs	0.220	0.161	<b>0.589**</b>	<b>0.575**</b>	-0.280	-0.129	-0.240	-0.148
Volume of recently dead wood	-0.110	0.152	0.170	0.004	0.094	0.135	0.226	0.231
Volume of large dead wood	0.124	0.079	0.068	0.186	0.019	-0.124	-0.221	-0.118
Diversity of dead wood	0.076	0.040	<b>0.577**</b>	0.404	-0.201	-0.261	0.065	0.151
No. of cut stumps ( $\text{ha}^{-1}$ )	0.051	0.025	-0.275	-0.175	0.154	0.219	0.162	0.155

Volumes are  $\text{m}^3/\text{ha}$ . Significances are sequentially Bonferroni-corrected (Rice, 1989) within eight species groups.

<sup>a</sup> % of total volume.

\* Significance levels at  $p < 0.05$ .

\*\* Significance levels at  $p < 0.01$

\*\*\* Significance levels at  $p < 0.001$ .

### 3.3. Forest structure and species diversity

In vascular plants, species richness correlated with the composition of living trees (Table 6). This correlation is likely because of the parallel effects of forest site fertility both on vascular plant species assemblages and tree species composition. In birds, there may also be some direct effect of tree species composition as the ‘expensive’ species are generally considered being associated with existence of spruces (Table 6).

The richness of polypores correlated with the volume and composition of dead wood (Table 6). This suggests that high volume and diversity of dead wood in forest stand indicates a species-rich site for polypores. No correlations between beetle species richness and dead wood characteristics were found, but when the rare saproxylic beetle species and the indicator polypore species were combined, the species richness of that group correlated especially with the volume of downed logs (all logs:  $r_s = 0.488$ ,  $p < 0.01$ ; large logs:  $r_s = 0.458$ ,  $p < 0.01$ ).

Furthermore, the total richness of red-listed species correlated positively with the total volume of living trees ( $r_s = 0.377$ ,  $p < 0.05$ ) and with the volume of living spruce ( $r_s = 0.409$ ,  $p < 0.05$ ) indicating indirectly the importance of (unmanaged) fertile forest types for threatened species (see also Table 2). Of the dead wood variables, volume of recently dead wood (decay stage 1) correlated positively with the total richness of threatened species ( $r_s = 0.393$ ,  $p < 0.05$ ). The total volume of dead wood ( $r_s = 0.316$ ,  $p = 0.078$ ), volume of logs ( $r_s = 0.347$ ,  $p = 0.052$ ) as well as the diversity of dead wood ( $r_s = 0.333$ ,  $p = 0.063$ ) correlated nearly significantly with the richness of threatened species. This reflects the habitat requirements of the threatened species observed: 13 of the total 18 species were associated with dead wood.

## 4. Discussion

### 4.1. Forest site type and species richness

Our result that the forest site type was a good surrogate for vascular plant species richness was expected because the forest type classification (Cajander, 1949) is based on understorey vegetation,

including vascular plants, that reflects the site features. Vegetation in the field layer is directly dependent on the edaphic conditions, and therefore readily responds to the conditions in the soil.

In other taxa the forest site type was not a feasible surrogate for species richness, and the fertile forest did not self-evidently mean high species richness. Our beetle data suggested that rather than beetle species richness, the number of individuals increases with increasing fertility (Similä et al., 2002), but Sippola et al. (2002) observed increasing beetle species richness along the forest fertility gradient in Lapland. Bird species richness have been shown to be positively associated with forest fertility in boreal forests (e.g. Nilsson, 1979), but it seems that at the level of individual forest stands there is too much random variation in species numbers because of small sample size (low density) for any clear differences among the forest types to emerge. However, the negative correlation between the richness of ‘expensive’ birds and volume of living pines reflected indirectly the importance of fertile forests for the ‘expensive’ bird species as well.

The fertile forests seemed to be important habitats for threatened species (even bearing in mind that no one of the threatened species observed was a vascular plant), but that result must be interpreted with caution because the total number of threatened species observed was small.

### 4.2. Forest structure as a surrogate for species richness

In addition to expressive vascular plants, which prefer fertile and productive forests, the richness of polypore species correlated positively with the total volume of living trees, a pattern similar that was reported by Schmit et al. (2005). The latter correlation is reasonable because the substrate of polypores is dead wood, and in natural conditions volume of dead wood depends on volume of living trees (Sippola et al., 1998). The different habitat requirements of polypores may explain the apparent discrepancy that polypore species richness did not correlate with the other indicator of forest fertility, richness of vascular plant species.

Richness of polypore species correlated with the volume and diversity of dead wood, which is in agreement with earlier observations (e.g. Bader et al.,

1995; Renvall, 1995). Similar pattern has been observed also in saproxylic beetles (Økland et al., 1996; Martikainen et al., 1999, 2000; Similä et al., 2003), although in this study the positive tendency of correlation between beetle species richness and dead wood variables was not statistically significant (Table 6, see also Similä et al., 2002; Junninen et al., *in press*). The range in the volume of dead wood in this study was probably too narrow that significant correlations with beetles could be observed.

Nonetheless, on the base of the correlations between the dead wood variables and the polypore species richness as well as the observations of other studies concerning saproxylic beetle species richness, we suggest that volume and diversity of dead wood (these characteristics are usually strongly inter-correlated) are valuable surrogates for the richness of dead wood associated species. Dead wood variables may also be a useful complementary part of the combination of a species richness indicator group (see also Berglund and Jonsson, 2001). As Noss (1990) states: “Monitoring both habitat and population variables seems to be essential in most cases”. We suppose that the diversity of dead wood indicates also the quality of species composition. When dead wood present in forest stand is diverse, it presents the wide variety of microhabitats for species to live in (Siitonen, 2001).

#### 4.3. Co-variation and indicator groups

There were no clear correlations in species richness or overlap in the species richness hot spots among the four taxa studied. This observation is in accordance with the results of several large-scale studies (Prendergast et al., 1993; Prendergast and Eversham, 1997; van Jaarsveld et al., 1998; Tardif and DesGranges, 1998). At the local scale Jonsson and Jonsell (1999) studied co-variation among five forest-dwelling taxa in northern Sweden, but found significant correlation at 1 ha level only between beetles and polypores and between bryophytes and vascular plants. The weak correlation between different taxa is rather evident because species represent a wide array of life histories (Reid, 1998; Jonsson and Jonsell, 1999; Sverdrup-Thygeson, 2001; Ranius, 2002; Kati et al., 2004).

Weak correlations among taxa and low overlap in the species richness hot spots in the four taxa studied imply that those taxa that are easy to survey, such as

birds or vascular plants, are not good surrogates for species richness hot spots (see Table 3). Birds have been considered potentially good indicators at the landscape level (Angelstam, 1992) but their usefulness in small-scale site selection cases is obviously limited. If the selection of conservation forest sites is based on the hot spots of beetle species richness, the overall species richness hot spots become selected. However, beetles comprised about 72% of the total number of species in the four taxa, and the hot spots may thus reflect more beetle species richness alone than the richness of other taxa. Beetles is a very time-consuming and expensive species group in terms of sampling costs for inventory (Martikainen and Kouki, 2003; Juutinen et al., 2004; Juutinen and Mönkkönen, 2004) which also limits its usefulness as a surrogate for species richness in general.

The richness of indicator polypores (as one of the potential indicator groups for species richness) represented well the richness of all polypores. The correlation was expected because in our polypore data relatively large proportions of species were indicator ones. However, the richness of indicator polypore species correlated nearly significantly also with the richness of the rest of the polypore species (i.e. indicators excluded from the total number of polypore species on each study site). Indicator polypores have been selected originally to indicate the naturalness of old-growth forest stands instead of the overall richness of the polypores (Kotiranta and Niemelä, 1996), but it seems that they are useful indicators for polypore species richness as well. Furthermore, indicator species include the information about the high quality of polypore species assemblage, e.g. the presence of threatened species (Lindgren, 2001), which is a necessary feature for a useful indicator group.

Rare saproxylic beetle species, as another potential indicator group, predicted neither the richness of all nor saproxylic beetles. However, the richness of indicator polypore species tended to correlate also with the richness of beetles, including saproxylic species, although the correlation was not statistically significant before the group of indicator polypore species was extended with the group of indicator beetle species, i.e. with rare saproxylic beetle species. Jonsson and Jonsell (1999) observed a straight correlation between the richness of saproxylic beetles and polypores in spruce forest. This suggests that the

relationships between saproxylic beetle species, polypores and dead wood variables may offer an interesting possibility to provide an indicator group for species richness of dead wood dependent species in general. To that possibility points also the parallel change of species assemblages of beetles and polypores through different forest types (Table 5). The selection of suitable and representative species for indicator group, however, requires the effective sampling of ‘all’ species living in different kinds of forests to make it possible to compile a group of indicator species that are easy to observe if present and that imply also the presence of rare and threatened species in surveyed forest stand.

‘Expensive’ birds were concentrated on fertile forest types, and it seemed that particularly the presence of those demanding ‘expensive’ species increased the total richness of birds on the study site. The richness of ‘expensive’ bird species correlated negatively with the richness of all beetle species. This emphasizes that the composition of species richness indicators should be compiled from species belonging to several different taxa, and that indicator groups must be different for different forest types.

#### 4.4. *Implications for forest conservation*

Our results suggest that the combination of carefully selected indicator beetle and polypore species group together with certain dead wood variables (e.g. volume and diversity of dead wood) may be a useful tool in selecting forest stands to be set aside for the conservation of dead wood dependent species (see also Sverdrup-Thygeson, 2001; Ranius, 2002; Kati et al., 2004; Schmit et al., 2005). However, it has been assessed that ‘only’ 20–25% of the forest-dwelling species are dependent on dead wood habitats (Siitonen, 2001). Our results showed that this kind of indicator group represents poorly the species richness of the other taxa. It seems evident that compiling one single indicator group is not likely to be a successful attempt. Instead of that, a more realistic alternative will be to compile different indicator groups for different forests and separately for different groups of species whose life histories resemble each other.

In addition to this study, the difference in the composition of species assemblages among the different boreal forest types has been demonstrated

in vascular plants (e.g. Tonteri et al., 1990; Lahti and Väisänen, 1987; Hokkanen, 2003) in birds (Mönkkönen, 1994; Kirk et al., 1996), in polypores (Junninen et al., in press) and in beetles (Similä et al., 2002; Sippola et al., 2002). This emphasizes the role of all forest types in the network of forest conservation areas because no single forest type can include all the (threatened) species (Kirk et al., 1996; see also Howard et al., 1998; Chase et al., 2000; Gustafsson et al., 2004). Focusing, for instance, only on the key biotopes in forest conservation excludes many rare and threatened species that are dependent on other types of forest habitats. Thus, the inclusion of different forest types in the conservation area network seems the only way to ensure the representativeness of all species within the network.

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