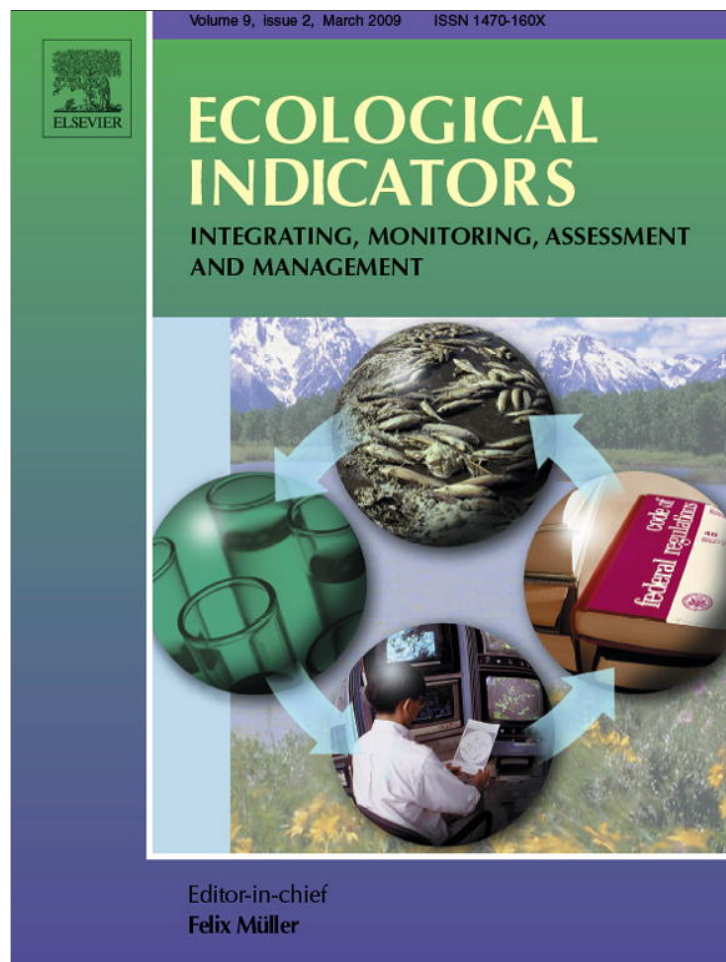


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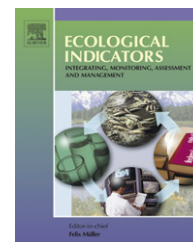


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## Perennial polypores as indicators of annual and red-listed polypores

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### ABSTRACT

Many polypores are specialized in their requirements for substrate and environment, and they have been suggested to indicate the continuity of coarse woody debris or naturalness of a forest stand. However, the use of polypores as indicators of conservation value is restricted by the temporally limited appearance of annual fruit bodies. We studied whether the species richness of perennial polypores (perennials) can be used to predict the species richness of annual or annual red-listed polypores (annuals). Our data included 1471 separate datasets (sample plots or larger inventoried areas) in different parts of Finland and Russian Karelia, ranging from the southern to northern boreal zone. At the large scale (the whole area) the number of perennials explained about 70% of the variation in the number of annuals, and about 67% in the number of red-listed annuals. A minimum set of 40–60 perennial occurrences gave a reliable estimate on the species richness of annuals, and 60–80 occurrences on the species richness of red-listed annuals. The richness of perennials predicted the richness of annuals and, in particular, richness of red-listed annuals, better than the size of inventoried area. According to our results, perennial polypores can be used as a surrogate for overall polypore species richness in natural and seminatural boreal forests, but the predictive power is weaker in managed forests. In addition, the relationship between the perennial and annual species seems to differ in different vegetation zones, management types and forest types. Due to this variation direct application of the indicator values derived from different vegetation zones and management or forest types are not recommended. Since perennials are easier to identify than annuals, detectable throughout the year, and have much smaller year-to-year variation, their use as an indicator group seems to offer advantages regarding the timing and cost-efficiency of inventories.

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## 1. Introduction

Long-term conservation of biological diversity in boreal forests is a major challenge for modern forestry, which has traditionally concentrated on producing timber for industry. The emphasis in the research of forest management and forest ecology has recently shifted towards the questions of ecosystem management and protection of important habitats (Angelstam et al., 2004). Conservation activity has grown, and conservation programmes and networks of protected areas are developed to reduce further losses of biodiversity (Parviainen et al., 2000). More focus is also turned to the cost-efficiency of conservation measures (Juutinen and Mönkkönen, 2004). Well-substantiated conservation efforts require data on ecological characters and species composition of the proposed conservation areas. However, complete species inventories of most taxa are impossible or expensive even in very small areas (Kaiser, 1997; Lawton et al., 1998). Rapid and reliable assessment methods are thus needed to evaluate the composition of species assemblages, and to survey and prioritize the conservation value of different forest areas.

Considering species assemblages, the use of indicator species or species groups has been suggested to fulfill the need for rapid biodiversity assessment (e.g. Pearson, 1994; Jonsson and Jonsell, 1999; Manne and Williams, 2003; Similä et al., 2006). The results of studies in different biogeographical regions and on different species groups have been somewhat contradictory. Several studies have shown that the covariation in species richness of different taxa is often low (Prendergast and Eversham, 1997; Jonsson and Jonsell, 1999; Berglund and Jonsson, 2001; Hopkinson et al., 2001; Similä et al., 2006), while fewer studies have found useful indicator species or species groups (Kerr et al., 2000; Jonsell and Nordlander, 2002; Lawler et al., 2003). The potential ability of some taxa to serve as indicators of the overall biodiversity (Faith and Walker, 1996; Jonsson and Jonsell, 1999; Hopkinson et al., 2001), or of the ecological integrity of an area (Carignan and Villard, 2002) has also been studied, with the conclusion that a single species group rarely functions as a general indicator of conservation aspects.

It can also be questioned whether species-oriented conservation is the most efficient avenue of conservation at all, or whether efforts should be concentrated on the preservation of whole ecosystems (Franklin, 1993; Simberloff, 1998). The extant species assemblages constitute, nevertheless, the most important criteria in a more detailed evaluation of the conservation value of different areas, and thus some information on species must be gathered even though the focus is in preserving ecosystems. Several criteria have been proposed for the selection of indicators (e.g. Noss, 1990; McGeoch, 1998; Juutinen and Mönkkönen, 2004). For instance, the data for the indicator should be relatively easy to sample, the indicator should be sufficiently sensitive to environmental changes, widely applicable, and relatively insensitive to sample size. No single indicator taxon is likely to fulfill all the properties of an ideal indicator; therefore, different indicators are needed for different purposes.

It indeed seems unlikely, that any species group could serve as a general indicator of the overall biodiversity, or of

other taxa with very different ecological requirements. Thus, we would argue, that the most promising avenue of using indicator species appears to be that the species richness of an ecological group is predicted with a subgroup of its own members, or with another taxonomic group sharing similar niche requirements. Ideally, an indicator group has higher detectability or some other attributes making it a more useful target for practical surveys and monitoring than the entire species group of interest.

Among stand structural features, the amount and quality of coarse woody debris (CWD) have been suggested as potential surrogates for evaluating the conservation value of forest areas (Humphrey et al., 2004; Stokland et al., 2004; Juutinen et al., 2006). Polypores have been proposed to function as good indicators of the CWD continuity and naturalness of a forest area (Bader et al., 1995; Kotiranta and Niemelä, 1996; Müller et al., 2007), and they are commonly used for those purposes in the Nordic countries (Karström, 1992; Kotiranta and Niemelä, 1996; Nitare, 2000; Stokland and Kausrud, 2004) even though some critique has also been presented (Nordén and Appelqvist, 2001). In addition, some studies indicate that polypores could work as indicators of the species diversity of other saproxylic taxa (Jonsson and Jonsell, 1999; Juutinen et al., 2006; Similä et al., 2006).

In Finland, about 25% of all polypore species form fruit bodies that live for several years (Niemelä, 1986). These species are called perennials in this paper. The rest of the species form mainly short-living fruit bodies living from few weeks or months to a maximum of 1 year. These species are called annuals in this paper. The majority of annual fruit bodies appears in boreal forests from August to November, and there are often large year-to-year fluctuation in their occurrence and abundance. In unfavourable years, some annual species may not form fruit bodies at all, and thus remain undetectable.

Polypores with perennial fruit bodies form a group of species which are easily detectable throughout the snow-free season, and have little year-to-year variation in their occurrence. In the boreal forests, there are only a few species groups which are possible to detect throughout most of the year with the same frequency and same perceptivity. These groups (including perennial polypores, woody plants, epiphytic lichens, etc.) are also the only species groups in boreal forests whose occurrence is not substantially influenced by the weather or other conditions that may vary within a year or between the years.

In this paper we studied the possibility to predict the species richness of annual polypores, and the species richness of annual red-listed polypores, based on the richness of perennial polypore species. The strength of the relationships between the occurrences of these species groups will reveal the utility of the perennials as indicators of the whole polypore diversity. Furthermore, we examined the effects of vegetation zone, dominant tree species and the management history to the correlations between the perennial and annual species diversity. We also focused on what is the size of the inventory area and sample size required for reliable conclusions based on the perennial species diversity.

To accomplish this, we compiled a comprehensive polypore species data collected by several Finnish polypore

researchers. The data includes the majority of all the polypore data collected in Finland during the last two decades. The data cover different geographical regions and forest site types as well as management histories, allowing observations of general patterns of co-occurrences that would be impossible to detect with smaller or more focused data. In Finland the polypore species assemblages and their ecology are among the best studied in the world, due to the long research tradition and the accumulated data and knowledge.

## 2. Material and methods

### 2.1. Study area

The study area includes Finland and adjacent Russian Karelia. The data includes datasets from southern boreal to northern boreal vegetation zones (Ahti et al., 1968). The studied forest stands or larger areas have been affected by varying levels of forest fragmentation and forestry history (more details given in e.g. Sippola and Renvall, 1999; Lindgren, 2001; Sippola et al., 2001, 2004, 2005; Penttilä et al., 2004, 2006; Junninen and Kouki, 2006; Junninen et al., 2006; Hottola and Siitonen, in press).

### 2.2. The polypore data

The majority of the datasets (1141 datasets out of 1471) was collected by the authors and was therefore available with all the recorded environmental information. The rest of the data were collected and published by other researchers, and were thus available for us only for the published parts. All the included datasets with their background information are given in Electronic Appendix A. The datasets were included only if all of the following conditions were fulfilled: (1) the data were collected of the whole polypore species assemblage, and species identifications were considered reliable. (2) The data were up-to-date regarding the present knowledge of the polypore taxonomy. Therefore, datasets older than 30 years were not included. (3) Each dataset had to include at least the following information: species list, location of sampling site, sampling year, sampling dates with at least the accuracy of 1 month, and methods of sampling. (4) The data were collected during the autumn (August–November).

Of the total of 1471 datasets, 1105 were based on fixed-sized sample plots with the size varying between 0.02 and 1.1 ha. In these plot-based inventories, all the occurrences (one species with one or several fruiting bodies growing on one substrate unit) of all polypore species were recorded. All these sample-plot based inventories in the present material were carried out in circular or rectangular plots. There were also 58 partially inventoried sample plots with the size varying between 1.8 and 9 ha. On these plots, the inventory was limited by both time and area. The remaining 308 datasets were general inventories of larger forest areas with the size varying between approximately 1 ha up to several square kilometres. In these general inventories, all the species occurring within the studied area were inventoried and recorded as completely as possible, but the exact number of occurrences of each species was not recorded. Because the exact sizes of these general inventory areas were not available, they were

excluded from the analyses concerning the size of the study sites.

All the species that form fruit bodies which stay alive for several years were regarded as perennial. In addition, we treated as perennials also those species which form fruit bodies living from 2 to 3 years, and which are therefore detectable with the same frequency throughout the year. According to these criteria, there were 44 species considered as perennial in our data. The rest of the species were regarded as annual species which comprised 127 species in the data (Electronic Appendix B). The division was based on literature (Niemelä, 2005) and personal field experience of the authors. Furthermore, we divided the annual species into red-listed and others (see Electronic Appendix B). All the species classified as threatened or near threatened in Finland were regarded as red-listed (Rassi et al., 2001). Scientific species names are according to Niemelä (2005).

The datasets were divided according to the location of the sampling site into southern ( $n = 383$ ), middle ( $n = 436$ ) and northern ( $n = 558$ ) boreal subsets (Ahti et al., 1968). A few datasets from the northern fringe of the hemiboreal zone were included into the southern boreal datasets in the analyses. The rest ( $n = 94$ ) of the datasets were not divided into vegetation zones because they were located at the border of two zones. Almost all of the datasets collected by the authors included also information on the forest site type of the study sites. Based on this information we divided the data into three categories: spruce-dominated ( $n = 708$ ), pine-dominated ( $n = 231$ ), and others ( $n = 532$ ). We classified sites as spruce- or pine-dominated when the volume of the living spruce or pine trees constituted more than 50% of the volume of all living trees. All the cases with lacking information, or with some other tree species as dominant, were classified as others.

We assessed the effects of management history on the relationship between the annuals and perennials by dividing the datasets into three classes, based on the intensity of the past logging of the site: (1) natural forest: no signs of logging or other human influence that would have affected the amount of decaying wood or the age distribution of trees on the site ( $n = 264$ ), (2) seminatural forest: some signs of previous logging, in the form of scattered stumps or lack of trees older than the dominating cohort ( $n = 283$ ), (3) managed forest: cut stumps abundant and even age-distribution of the living trees brought about by intensive thinning ( $n = 272$ ). The sites that could not be classified into these categories were excluded from the analysis involving management history.

We also assessed how many occurrences of perennial species were sufficient for reliable predictions on the species richness of annual or red-listed annual species. In the inventories, one or several fruiting bodies of particular species per substrate unit were counted as one occurrence. We divided the data into classes based on the number of occurrences of the perennial species in each dataset. The cut points of the classes were evenly set to 10, 20, 30, etc., occurrences, i.e. the first class included all the datasets with 1–10 occurrences, the second class datasets with 11–20 occurrences of perennial species, etc. The number of datasets in each of the classes is given in Table 1. Similarly, we assessed how the size of the inventoried area affected the correlation between the perennial and annual species, by dividing the data into size

**Table 1 – The number of datasets in classes determined by either the number of occurrences of perennial species or the size of the inventoried area**

Number of occurrences of perennial species	Number of datasets	Size of inventoried area (ha)	Number of datasets
1–10	487	0.02–0.04	533
11–20	173	0.041–0.08	30
21–20	69	0.081–0.1	72
31–40	59	0.11–0.15	38
41–50	38	0.151–0.2	231
51–60	49	0.21–0.3	98
61–70	19	0.31–0.4	28
71–80	12	0.41–0.5	109
81–90	13	0.51–1.0	10
91–100	9	1.01–4.0	32
101–110	9	4.01–9	39
111–120	7		
121–130	7		
131–140	7		

classes. The cut points of the classes were set to 0.02, 0.04, 0.08, 0.1, 0.15, 0.2, 0.3, 0.4, 0.5, 1 and 4 ha. The number of datasets in each class is given in Table 1.

### 2.3. Statistical analyses

First, we tested the relationships between the perennials and annuals without taking the environmental factors into consideration. The number of annual species (either all or red-listed) constituted the dependent variable, whereas the number of perennial species was used as an explanatory variable in the analysis. These relationships were tested with both the linear and quadratic regression analysis. In both cases, the quadratic regression had more explanatory power, and therefore only the results of quadratic regressions are reported here. We also tested the relationship between the size of the inventoried area and number of annual species (either all or red-listed). These relationships were tested with linear regression and using log-transformed values of area.

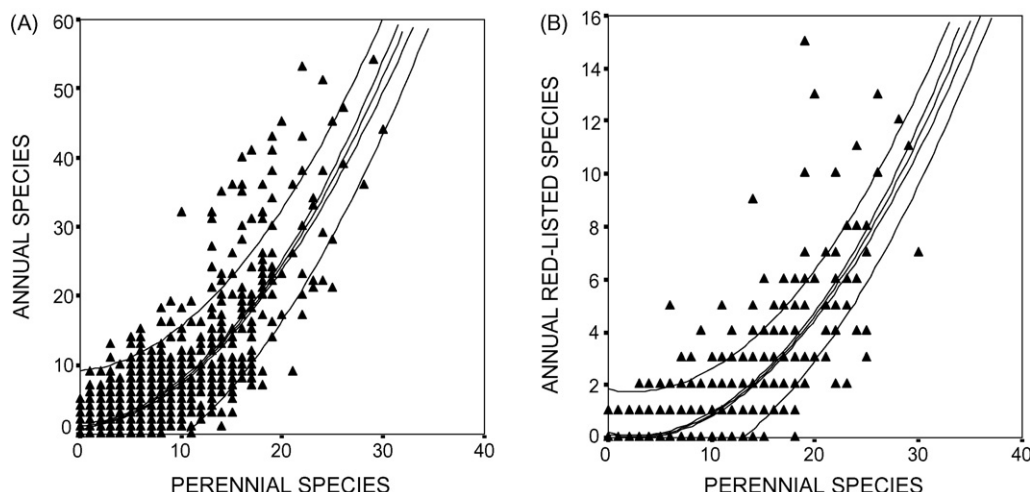
Second, we conducted an analysis of covariance (ANCOVA) to explore the interactions between different variables on the patterns of co-occurrences of perennial and annual species. In these analyses the number of annual species (either all or red-listed) was the dependent variable, the number of perennials and the size of the inventory area (log-transformed) were covariates, and the vegetation zone, management history and dominating tree species were factors. All of the two-way interactions between the factors and covariates were initially included in the models, but non-significant interactions were stepwise removed to produce the final model. Higher than two-way interactions were not included in the models. Higher order interactions were excluded because, despite of the large number of data sets, some factors would have included too few datasets for reliable conclusions, and the three-way interactions may be difficult to be interpreted empirically. Separate analyses including each dependent variable and each factor at a time were also conducted to reveal how large proportion of the variance in the richness of annual species could be explained by the richness of perennial species alone if the other factors possibly influencing the relationships were not taken into consideration.

Third, the correlations between the perennial species and annual species or red-listed annual species were tested separately in the classes that were constructed based on either the number of perennial species occurrences or the size of the inventoried area. Hence, we obtained correlation coefficients between perennial and annual species richness separately for datasets including 1–10, 11–20, 21–30, etc., occurrences of perennial species, and likewise for datasets with the inventoried area varying from  $\leq 0.02$  to 9 ha. These correlation coefficients were then compared between the classes to reveal what would be an adequate sample size for conclusions on the species richness of annual species.

## 3. Results

In the whole data, the number of perennial species was a good indicator of the number of annual species, explaining 69.7% of the total variation in their number ( $F_{2,1469} = 1692$ ,  $P < 0.001$ ) (Fig. 1A). The explanatory power was almost as good for the number of red-listed annual species, explaining 67.4% of their total variance ( $F_{2,1469} = 1519$ ,  $P < 0.001$ ) (Fig. 1B). In a respective analysis with a somewhat smaller data, where datasets with lacking information on the size of the inventory area were excluded, the size of the inventoried area explained 58.9% of the variation in the richness of the annual species ( $F_{1,1113} = 1592$ ,  $P < 0.001$ ), but only 35.8% of the variation in the richness of the red-listed annual species ( $F_{1,1113} = 622$ ,  $P < 0.001$ ).

The first analysis of covariance (Table 2) involving annual species as the dependent variable, and perennial species and the environmental factors as the explanatory variables, explained 87.6% of the total variance in the number of annuals ( $F_{21,667} = 217$ ,  $P < 0.001$ ). Five significant interactions were found, two of which involved the number of perennials. These two interactions showed that the relationship between the number of perennial and annual species depended on the vegetation zone and management history (Table 2). The second analysis of covariance (Table 3) explained 81.0% of the total variance in the number of red-listed annual species ( $F_{24,667} = 114$ ,  $P < 0.001$ ). Seven significant interaction effects



**Fig. 1** – The relationship between the number of perennial and annual species (A) and red-listed annual species (B). The central line represents the mean value, the middle lines represent the 95% confidence value of the mean value, and the outermost two lines represent the 95% confidence value of an individual observation.

**Table 2** – Analysis of covariance on the number of annual species

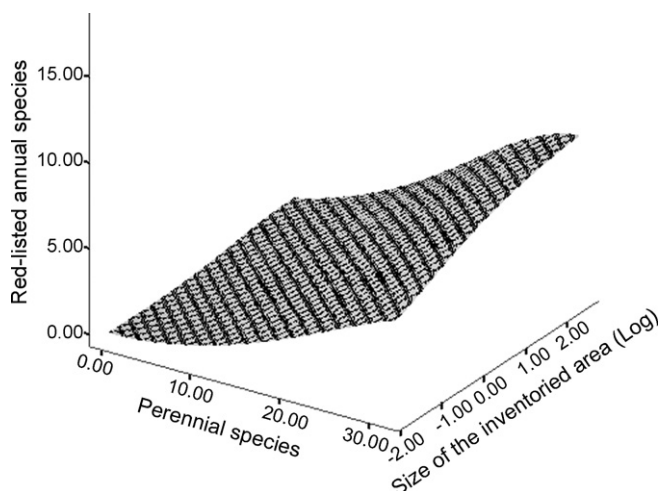
	MS	d.f.	F	P	eta <sup>2</sup>
Perennials	52.995	1	15.886	<0.001	0.024
Perennials <sup>2</sup>	184.923	1	55.432	<0.001	0.079
Area	194.707	1	58.365	<0.001	0.083
Zone	2.145	2	.643	0.526	0.002
Management	4.468	2	1.339	0.263	0.004
Dominant tree	32.874	1	9.854	0.002	0.015
Management × perennials × perennials <sup>2</sup>	34.825	2	10.439	<0.001	0.031
Zone × perennials × perennials <sup>2</sup>	50.785	2	15.223	<0.001	0.045
Zone × management	19.512	4	5.849	<0.001	0.035
Zone × dominant tree	27.719	2	8.309	<0.001	0.025
Management × area	14.068	2	4.217	0.015	0.013
Error	3.336	645	15.886	<0.001	0.024

Number of perennial species, quadratic term of the number of perennial species (perennials<sup>2</sup>) and the size of the inventoried area (log-transformed) (area) were included in the model as covariates, and management history (management), vegetation zone (zone) and dominant tree species (dominant tree) as fixed factors.

**Table 3** – Analysis of covariance on the number of red-listed annual species

	MS	d.f.	F	P	eta <sup>2</sup>
Perennials	8.565	1	33.831	<0.001	0.050
Perennials <sup>2</sup>	17.312	1	68.385	<0.001	0.096
Area	1.131	1	4.467	0.035	0.007
Zone	4.654	2	18.385	<0.001	0.054
Management	1.166	2	4.604	0.010	0.014
Dominant tree	4.074	1	16.092	<0.001	0.024
Area × perennials × perennials <sup>2</sup>	14.223	1	56.180	<0.001	0.080
Management × perennials × perennials <sup>2</sup>	5.579	2	22.036	<0.001	0.064
Zone × perennials × perennials <sup>2</sup>	3.688	2	14.570	<0.001	0.043
Zone × management	2.342	4	9.250	<0.001	0.054
Zone × dominant tree	2.652	2	10.474	<0.001	0.032
Zone × area	2.328	2	9.198	<0.001	0.028
Management × area	1.286	2	5.079	0.006	0.016
Error	0.253	642			

Number of perennial species, quadratic term of the number of perennial species (perennials<sup>2</sup>) and the size of the inventoried area (log-transformed) (area) were included in the model as covariates, and management history (management), vegetation zone (zone) and dominant tree species (dominant tree) as fixed factors.



**Fig. 2 – The relationships between the numbers of perennial and red-listed annual species and the size of the inventoried area.**

were found, three of which involved the number of perennials. The relationship between the perennial and red-listed annual species depended, in addition to the vegetation zone and management history, also on the size of the inventoried area (Table 3). The interaction with the size of the inventoried area and the species group relationship was such, that there were more red-listed annual species in relation to number of perennial species with growing size of the inventoried area (Fig. 2). To determine in more detail the effects of environmental variables, we analysed separately the relationships between the number of perennials and annuals or red-listed annuals with respect to the different vegetation zones and management-history classes.

**3.1. Effect of vegetation zone**

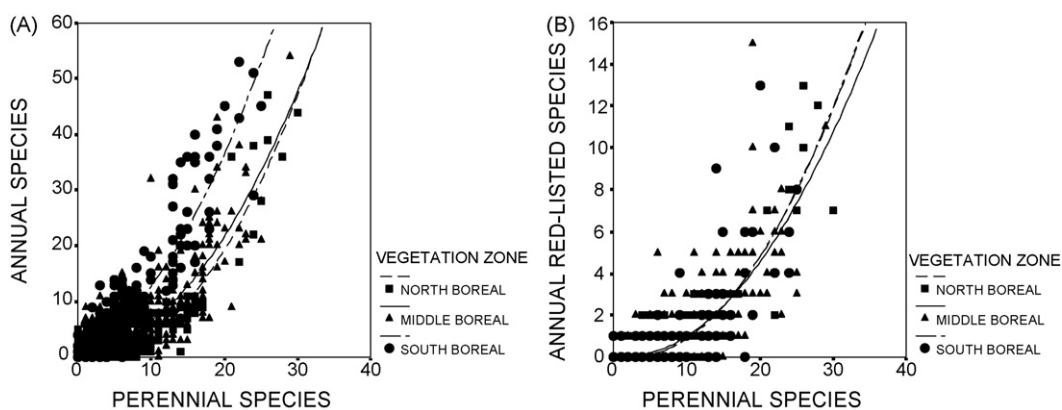
Vegetation zone affected significantly the relationships between the numbers of perennial and annual species, as well as perennial and red-listed annual species (Tables 2 and 3). In the southern, middle and northern boreal vegetation zones, the number of perennials explained 82.9% ( $F_{2,288} = 696, P < 0.001$ ), 61.7% ( $F_{2,410} = 330, P < 0.001$ ) and 87.5% ( $F_{2,555} = 1949, P < 0.001$ ) of the variation in the number of

annuals, respectively. For the red-listed annuals, the corresponding figures were 60.9% ( $F_{2,361} = 281, P < 0.001$ ), 60.8% ( $F_{2,433} = 335, P < 0.001$ ) and 80.7% ( $F_{2,555} = 1157, P < 0.001$ ), respectively.

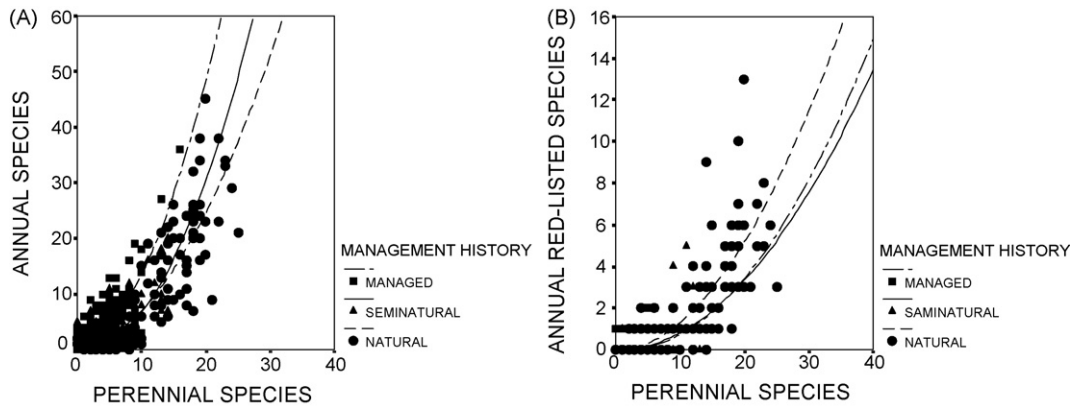
The number of annual species per unit number of perennial species was clearly higher in the southern boreal than in the middle and northern boreal zones (Fig. 3A), whereas the number of red-listed annual species per unit number of perennial species was strikingly similar in all the vegetation zones (Fig. 3B).

**3.2. Effect of management history**

Management history affected significantly the relationships between the numbers of perennial and annual species as well as between perennial and red-listed annual species (Tables 2 and 3). On the natural, seminatural and managed sites the number of perennials explained 81.0% ( $F_{2,261} = 556, P < 0.001$ ), 72.3% ( $F_{2,280} = 366, P < 0.001$ ), and 64.5% ( $F_{2,269} = 244, P < 0.001$ ) of the variation in the number of annuals. For the red-listed annuals, the corresponding figures were 72.7% ( $F_{2,261} = 347, P < 0.001$ ), 45.5% ( $F_{2,280} = 117, P < 0.001$ ), and 25.6% ( $F_{2,269} = 46, P < 0.001$ ), respectively.



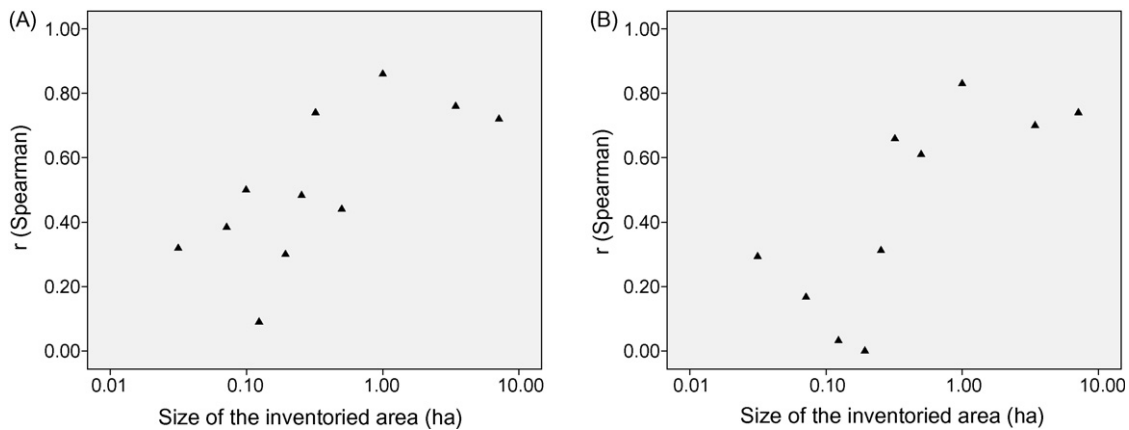
**Fig. 3 – The relationship between the number of perennial and annual species (A) and red-listed annual species (B) in the different vegetation zones. In panel (B) the lines of northern and southern boreal zones overlap.**



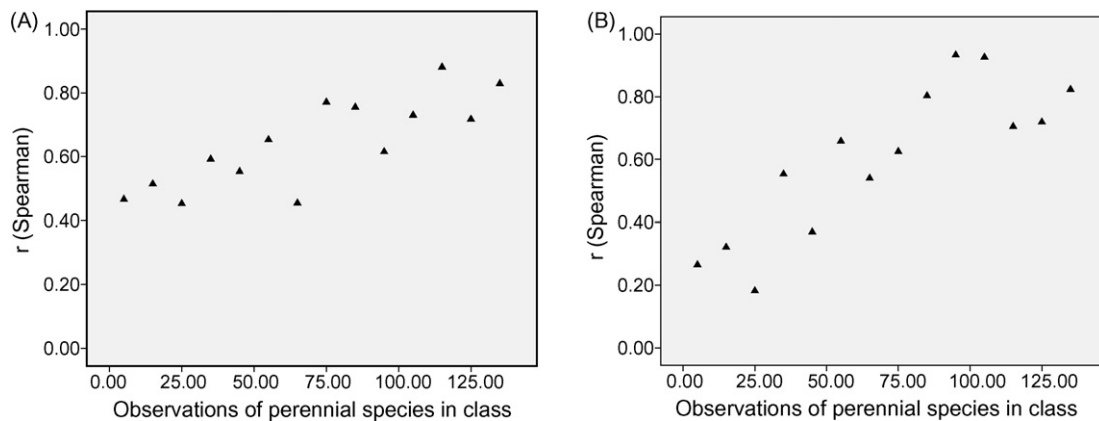
**Fig. 4 – The relationship between the number of perennial and annual species (A) and red-listed annual species (B) in different management history classes.**

The interaction with the management history and the species group relationship was such that the number of annual species in relation to the number of perennial species increased faster in managed forests than in

the natural forests (Fig. 4A). On the contrary, the number of red-listed annual species increased faster on natural sites than on seminatural or managed sites (Fig. 4B).

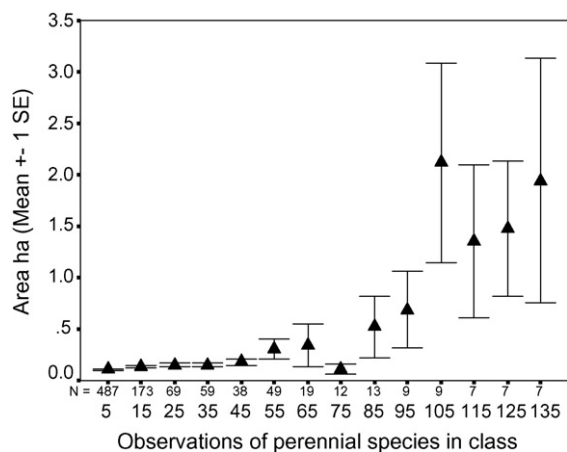


**Fig. 5 – The correlation between perennial and annual (A) and red-listed annual species richness (B) in relation to the size of the inventoried area. Subpart (B) represents one class less, because one of the classes (including sample plots from 0.081 to 0.1 ha) did not include any occurrences of red-listed species. The x-axis is on logarithmic scale.**



**Fig. 6 – The correlation between the species richness of perennial and annual species (A) and red-listed annual species (B) in relation to the number of observations of perennial species. Each dot in the figure represents the mean number of observations in each number-of-occurrences class. The number of cases in each of the classes are indicated in Fig. 7.**





**Fig. 7 – The mean size of the inventoried area in the number-of-occurrences classes in Fig. 6. The upper numbers in the x-axis show the number of datasets per each class, and the lower numbers the median number of perennial observations in each class.**

### 3.3. Estimation of an adequate sampling area

We compared datasets with sample plots of differing sizes to get an estimate of an adequate sampling area (Table 1 and Fig. 5). The correlation coefficients varied considerably between the classes including small sample areas (<0.3 ha), and especially in the case of red-listed annuals the correlation coefficients were low in sites under 0.4 ha in size.

### 3.4. Estimation of an adequate number of perennial observations

Relatively small numbers of perennial occurrences showed significant correlations with the numbers of annual species (Fig. 6). A sample including 40–70 perennial specimens seemed to be sufficient for conclusions about annual species richness, with most of the correlation coefficients being 0.55–0.65. Observations exceeding 70–80 perennials gave very reliable estimates of annual species richness (Fig. 6A). For the annual red-listed species richness a sample of 60–80 perennials seemed to be sufficient for considerably reliable assessment (Fig. 6B). We also determined the medium size of the inventoried area for each of the number-of-occurrences class of perennial species (1–10, 11–20, 21–30, etc., Table 1 and Fig. 7).

In our data, the sites of about 0.5 ha in size included on average as many as 80–90 observations of perennial species, indicating that this would be an adequate size of sampling area for reliable conclusions.

## 4. Discussion

Our results show that the species richness of perennial polypores correlated strongly with the species richness of both annual and red-listed annual polypores. The correlation remained strong through different vegetation zones, management history classes, and sites with different dominating tree species, except for red-listed annual species, which showed

weak correlation with perennials in managed and seminatural forests. The result is surprisingly strong if we take into account the fact that the between-year variation in the number of occurrences of annual species brings significant amount of noise into polypore data (Berglund et al., 2005).

It is a well-established fact that the number of species increases with an increasing area (Mac Arthur and Wilson, 1967). Accordingly, it could be argued that our results are mainly due to the fact that the larger the inventoried area, the more polypore species, both perennial and annual, are found. Indeed, the size of the inventoried area explained the species richness of annual species almost as well as the species richness of perennial species (58.9%). However, area failed to explain much variation in the richness of annual red-listed species, the variation explained being only 35.8%. In the analysis of covariance area had a significant interaction on the relationship between annual red-listed species and perennial species. However, this interaction was quite weak, and the number of perennial species explained a significant proportion of the variation of annual species even though the size of the inventoried area was included into analysis. Furthermore, the size of the site *per se* does not tell anything about the amount and quality of dead wood and occurrence of polypore species within a forest stand, whereas the occurrence of perennials seems to be a relatively good predictor of the species richness of annual species, especially since the proportion of variance explained stays high despite the broad variation in the data. Based on these facts, it seems that the species richness of perennials is a better predictor of the richness of annuals, and especially red-listed annuals, than the size of the inventoried area alone, at least in natural and seminatural forests.

The species richness of polypores and especially the number of red-listed polypore species in a given area depends on the amount and quality of dead wood on the site (Bader et al., 1995; Sippola et al., 2001; Penttilä et al., 2004). Thus, it could be argued that it is more cost-efficient to simply survey dead wood in an area of interest than to survey perennial polypores. However, the amount and quality of dead wood cannot predict large-scale differences in species assemblages caused by biogeographical factors or differences in land-use history. There is evidence that the size of the potential source areas at the landscape, or even at the regional level, and the distance to the source areas affect the local polypore species assemblage (Siitonen et al., 2001; Penttilä et al., 2006). For example, in eastern Finland the polypore species assemblage is richer than in western Finland apparently due to forest fragmentation and longer history of forestry in the latter area. Thus, a given volume of dead wood in eastern Finland hosts more polypore species than the same volume in western Finland (Penttilä et al., 2006). Inventory of decaying wood might lead to the wrong assumption that sites with comparable dead-wood resources would host the same number of species. However, according to the present information, it seems that local-scale dispersal does not limit the occurrence of many polypore species (Edman and Jonsson, 2001; Rolstad et al., 2004; Komonen, 2005). This implies that, in order to survey and compare polypore assemblages among forest stands within the same region, an inventory based on randomly or systematically located sample-plots should be

sufficient. Based on our data, a sample including 60–80 observations of perennial species gives a reliable estimate on the richness of both annual and red-listed annual species within a stand. The area that needs to be inventoried to accumulate this number of observations varies considerably and is larger in managed than in natural forests. This is because the volume of dead wood is much lower in intensively managed than in seminatural or natural forests (e.g. Siitonen et al., 2000; Siitonen, 2001). Therefore, the sample size of 60–80 specimens of perennial polypores can be reached in an old-growth stand on a sample plot of 0.2–0.5 ha (Lindgren, 2001; Hottola, 2003; Ylisirniö, unpublished data), whereas several hectares may be needed for the same number of observations in managed forests (Halme et al., unpublished data).

In the analysis of covariance, several interactions between perennial species and environmental factors were significant. This means that the accumulation curves of annual and red-listed annual species relative to perennial species differed between vegetation zones and management history classes, and, in the case of annual red-listed species, also in relation to the size of the inventoried area. These results may partly be due to three-way interactions (e.g. vegetation zone  $\times$  management history  $\times$  perennial species) which, however, could not be analysed reliably because of the unbalanced data; despite of the large dataset, in some factor combinations there were too few samples to permit reliable analysis. There may be, however, also ecological explanations for these results. The results show that compared with middle and northern boreal zones, the number of annual species in southern boreal zone increases faster with the number of perennial species. The reason for this may be that the conditions in producing annual fruit bodies deteriorate towards north. During short and relatively cold summer it may be challenging to produce annual fruiting bodies every year compared with perennial species, which may distribute the growing effort on multiple seasons.

The results also indicate that the number of annual species in relation to perennials increase faster in managed than in natural forests. Perennial species include many common and dominating decomposer species; for example, in our data, seven out of the ten most common species were perennials (Electronix Appendix B). However, only few of them were common in managed forests of the study area (e.g. *Fomes fomentarius*, *Fomitopsis pinicola*, *Phellinus igniarius* s. lato, etc.). The rest of the perennials may not be able to occupy managed forests as easily as annuals. One potential explanation for this is that the smaller diameter decomposing wood in managed forests favours annual species, many of which can colonize small-diameter woody debris.

According to our data, the number of red-listed annual species in relation to number of perennial species was considerably higher in natural forests than in either seminatural or managed forests. This is a reflection of the fact that in managed forests the diversity of decaying wood is reduced, which favours common generalist species, whereas rare and red-listed species, which require specific substrate and/or specific environmental conditions, are more abundant in natural stands with more diverse CWD (e.g. Bader et al., 1995; Sippola and Renvall, 1999).

The practical use of perennial polypores as indicators of total polypore diversity would be relevant, for example, in

situations, where some basic information on the diversity of saproxylic species is needed. Furthermore, they could be useful for the rapid assessment and ranking of the conservation value of forest stands, at least as a complement to inventories including stand structure and other species groups. This kind of nature inventories are common when there is a need to allocate stands for conservation purposes or harvesting. Perennial polypores could also serve as a practical tool to evaluate the conservation value of large, poorly known areas when the resources for the inventories are limited.

Considering the practical use of perennial polypores as indicators of the conservation value, the results of our covariance analysis indicate that one should be careful not to compare very different habitats simultaneously (e.g. northern boreal pine-dominated forests and southern boreal spruce dominated forests). This is not necessarily a major drawback, since conservation-value inventories are usually compared and prioritized among forest stands that are relatively similar and located within the same region. However, the differences in the accumulation curves should be noted, to prevent the misuse of perennial species inventories. The results imply that inventories concentrating only to perennial species cannot serve all purposes, and their use as indicators does not abolish the need for the inventories of the total polypore species assemblage in the areas of special interest.

Research on indicator species has concentrated on the ability of different indicator groups to predict the species richness or composition of other taxa. Less effort has been concentrated on the cost-efficiency of indicators, and the easiness of inventory in relation to the identification of species (however, see, e.g. Juutinen et al., 2006). As annual polypore species can be successfully inventoried only in the autumn, it is difficult to connect the inventories with other biodiversity surveys. In contrast, perennial polypores are detectable throughout the year with same reliability, and are relatively easy to identify. This means that their inventory requires only a moderate effort, and the inventories can be easily connected to other fieldwork. As a conclusion we propose that perennial polypores is a good candidate group for rapid assessment of the conservation value of boreal forest stands, or at least to complement inventories of stand structure and other species groups.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.eco-lind.2008.04.005](https://doi.org/10.1016/j.eco-lind.2008.04.005).

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