Available online at www.sciencedirect.com
SCIENCE DIRECT®
Biological Conservation 112 (2003) 319–328
BIOLOGICAL CONSERVATION
www.elsevier.com/locate/biocon

Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests

Håkan Berglund[a,*], Bengt Gunnar Jonsson[b,1]

[a]*Department of Natural and Environmental Sciences, Mid Sweden University, SE-851 70 Sundsvall, Sweden*
[b]*Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden*

Received 22 January 2002; received in revised form 16 October 2002; accepted 16 October 2002

Abstract

Knowledge of the distribution of rare species is crucial for species conservation in fragmented habitats. Species communities often exhibit nestedness, i.e. species in species-poor sites comprise a subset of richer ones. Thus, rare species are confined to species-rich sites. We evaluate whether plant and fungal communities in 46 old-growth spruce forest patches (0.17–12 ha) exhibit nestedness. The question whether a single large patch or several small patches capture most species (i.e. the SLOSS-issue) is evaluated in combination with species saturation analyses. All species groups exhibited significant nestedness. Area was generally related to nestedness, i.e. rare species were over-represented in the largest patches. Species saturation analysis indicated that large patches accumulated more Red-list species in patch interiors than small patches. Thus, rare and Red-list species were best captured in large patches. However, nestedness also emerged in equal sized sample plots, i.e. rare species were over-represented in high quality habitats. Thus, small habitats of high quality should not be neglected in a conservation perspective.

Keywords: Bryophytes; Lichens; Mosaic; Species–area relationship; Sweden

---

1. Introduction

During the last 150 years forestry has fragmented the majority of the Fennoscandian natural forest ecosystem and the forest landscape is now dominated by young even-aged stands (Östlund, 1993; Esseen et al., 1997; Axelsson, 2001; Kouki et al., 2001). In Sweden for instance, more than 95% of the forested land is used for production of timber and wood pulp (Bernes, 1994). The majority of the remnant old-growth forest is composed of small (a few ha) and isolated fragments (Anon., 1999). The relative amount of habitat edge has increased as an effect of fragmentation. Consequently, the influence of edges has increased which may affect habitat quality in forest patches (Murcia, 1995; Moen and Jonsson, in press). In addition, the complexity of stand structure in most remnant old-growth forests has been reduced through selective logging, which has been shown to deteriorate habitat quality (Bader et al., 1995; Sippola, 2001).

The fragmentation and degradation of old-growth forests have had negative effects on the persistence of many forest-dwelling species (Larsson, 1997; Hallingbäck, 1998; Thor and Arvidsson, 1999; Cederberg, 2001). Taking all taxa in the Red-list into consideration, some 115 forest inhabiting species have gone extinct and 1986 forest living species are currently classified as Red-list species in Sweden (Gärdenfors, 2000). To what extent these species may survive and reproduce in small-sized forest fragments is unclear. If extinction risks are strongly increased in small fragments, species may also risk going extinct at landscape and regional scale. At the larger scales this process may take time and thus there may be a time delay involved in the extinction of species following habitat loss and fragmentation (i.e. the ‘extinction debt’; sensu Tilman et al., 1994; Hanski,

---

* Corresponding author. Tel.: +46-6014-8402; fax: +46-6014-8802.

E-mail address: hakan.berglund@mh.se (Håkan Berglund).

[1] Present address: Department of Natural and Environmental Sciences, Mid Sweden University, SE-851 70 Sundsvall, Sweden.

PII: S0006-3207(02)00329-4

1999). In order to develop a conservation strategy for biodiversity in remnant old-growth forests, knowledge of the distribution pattern of rare and Red-list species becomes vital.

In many species groups a majority of species are rare (e.g. Hanski, 1982; Hanski, 1999). This poses practical problems on how to analyse the distribution of a large set of species. Increasingly popular in this respect has been to analyse to what extent species groups tend to form nested subsets (Wright et al., 1998; Jonsson, 2001). Nestedness occurs when species composition at species-poor sites is a subset of richer sites (Patterson and Atmar, 1986) and implies that rare species are statistically over-represented in species rich sites. Nestedness has been shown to be a common feature of insular biota (see review in Wright et al., 1998). Various processes have been put forward to account for nestedness, including differential extinction (Schoener and Schoener, 1983; Patterson and Atmar, 1986; Cutler, 1991; Atmar and Patterson, 1993), differential colonization (Patterson and Atmar, 1986; Kadmon, 1995; Lomolino, 1996), and nested habitat requirements (Simberloff and Martin, 1991; Honnay et al., 1999).

The analysis of nestedness provides important descriptive information about community structure and its relation to environmental variables (Worthen, 1996). For example, if nestedness occurs over a range of patches of varying size, it implies that small patches only contain a subset of the species in large patches. In such a case, rare species will be confined mainly to large, species rich patches. In this respect the degree of nestedness relates to the "Single Large Or Several Small" (SLOSS) discussion (Diamond, 1975; Simberloff and Abele, 1982; Soulé and Simberloff, 1986) where the question was whether a set of species is best captured by a single large site or by several small. However, insular biota is never perfectly nested which complicates the relationship between nestedness and SLOSS. In fact, empirical studies have found higher cumulative species richness in several small sites, even when the insular biota exhibits significant nestedness and species–area relationship (Cook, 1995; Boecklen, 1997). This comes from the fact that the nestedness analyses only account for overlap in species composition among sites. It does not incorporate the number of species per area unit in different sites. Cook (1995) concluded that nestedness analyses are important in that they indicate the degree to which rare species tend to be found in the largest sites. To obtain a more complete answer to the SLOSS issue, it has to be combined with analyses (e.g. analysis of species saturation; c.f. Cook, 1995) that explicitly incorporate the area of sites.

Analysis of species distribution patterns in recently isolated old-growth forest stands is complicated by transient dynamics. Current distribution patterns may change with time and results obtained in recently isolated old-growth stands may be misleading. In this paper we examine ancient old-growth patches in a forest-wetland mosaic. The forested patches consist of moraine hills that rise above a wetland matrix and are covered by old-growth Norway spruce [*Picea abies ssp. obovata* (Ledeb.) Domin]. Extensive disturbances such as forest fire have been absent for several hundred of years and the forests have not been managed (Lövgren, 1986). Extinction and colonization should have reached a dynamic equilibrium during the approximately 3000 years (c.f. Tallantire, 1972) since spruce colonized the area. Thus, we can avoid temporary phases and the long-term effect of stand size and habitat quality should be detectable in the species distribution. In this study, we examine if the species distribution among six plant and fungal groups show nestedness in this insular old-growth system. We also intend to explore to what extent area and habitat quality relates to nestedness. The assumption is that patch area could create nestedness through differential extinction (Lomolino, 1996; Wright et al., 1998), and if important habitat characteristics occur in a nested way (Wright et al., 1998), nestedness could also emerge in plots (or patches) of equal size. To further investigate the SLOSS issue, the nestedness analysis is complemented with the analysis of the saturation index (SI; Quinn and Harrison, 1988), which explicitly incorporates the area of different sites.

Thus, the main questions of this study are: (1) Do plant and fungal species composition exhibit a non-random nested structure, (2) to what extent are patch area and habitat quality related to nestedness, and finally (3) is a set of species best captured by a single large site or by several small?

2. Material and methods

2.1. Site selection, stand variables and species registration

The study area, Granlandet nature reserve, is located in the north-boreal zone of Sweden (sensu Ahti et al., 1968). It is composed of isolated forest patches situated in a wetland matrix. In total Granlandet contains almost 1000 such patches of varying size and shape. We examined 46 patches that ranged in size from 0.17 to 12 ha, though the majority of the studied patches ($n = 34$) were less then 1 ha. The small patches were surveyed during 1997 while the 12 larger patches were inventoried during 1998. All fieldwork was performed during August and September when most annual wood-fungi produce fruiting bodies.

Separate recording of species occurrences were done on two spatial levels; (1) 'plot level', representing a 0.1 ha circular plot in the centre of each patch and (2) 'patch level', representing the whole patch. Three plant species groups; vascular plants, mosses and liverworts, and three fungal species groups; crustose lichens and corticoid and polyporous wood-living fungi (hereafter called 'corticoids' and 'polypores') were included in the study. Red-list species (according to Gärdenfors, 2000) were recorded and treated as a subgroup of species. The included species were all restricted to forests and did not occur in the surrounding wetland matrix. A list of the recorded species has been published elsewhere (Appendix 1 in Berglund and Jonsson, 2001, available at the electronic archive http://www.opuluspress.se). For further details on sampling procedure and study area see Berglund and Jonsson (2001).

The presence of basidiocarps was used to detect wood-fungi species. To control for the effect of between-year variations in basidiocarp production among wood-fungi, five plots from 1997 were re-inventoried 1998. The mean between year differences in observed species richness per plot (i.e. species richness in 1998 subtracted from that of 1997) was -1.0 ± 2.3 among corticoids, 0.4 ± 0.9 among polypores and 0.0 ± 0.7 among Red-list wood-fungi. Thus, species richness did not differ significantly between 1997 and 1998. The cumulative number of species was 6.1 ± 1.9 higher for the corticoids, 1 ± 1.4 for the polypores and 0.4 ± 0.9 for Red-list wood-fungi when comparing two years of inventory (1997+1998) with a single year (1997). Despite the fact that the corticoids exhibited notable between year variations, we have chosen to retain the data on the corticoids in the study. This is done under the assumption that the rate of basidiocarp turnover is fairly similar among corticoid wood-fungi species of different frequency (i.e. the turnover of species includes both rare and common species). Thus, the species occurrences in patches inventoried on two consecutive years are comparable.

2.2. Statistical analyses

To test if the species distribution exhibited nestedness, species and sites were ordered in a site-by-species matrix with sites in columns and species in rows. The species were always ranked by frequency from the most abundant species to the least abundant. However, in a first step of analysis sites were ranked by species richness from richest to poorest. In a second step of analysis we ranked the sites by area according Lomolino (1996). This was done to test whether area was related to the nested subset pattern.

For each ordered matrix we computed the discrepancy (*d*; Brualdi and Sanderson, 1999), which is the number of occurrences that needs to be shifted to produce a perfectly nested matrix from the observed matrix. The perfectly nested matrix is unique and the occurrences in each row are as far to the left as possible and the occurrences in each column are as far to the top as possible. We applied a Monte-Carlo test with 1000 random matrices to test if observed distribution exhibited significant deviation from randomness. We generated random null matrices through the RANDNEST procedure described by Jonsson (2001) where the species are randomly dispersed in the species–site matrix purely based on the observed species frequencies. The basic assumptions for this test procedure are that (1) the observed species frequency is an estimate of the probability of occurrence for the particular species and (2) all sites should be regarded as being equal. The observed species–site matrices were considered to agree with the nestedness hypothesis only when the observed discrepancy was significantly *lower* than the mean discrepancy of random matrices. Thus, only a one sided test was used. For matrices ordered by area, the observed index was in some cases larger than predicted by the RANDNEST procedure. Such instances are however statistical artefacts of a non-nested matrix sorted by other site variables than species richness and thus considered of no biological importance.

All six different species groups as well as the subgroup of Red-list species (according to Gärdenfors, 2000) were tested separately on the two spatial levels of species survey. The different analyses were assumed to test different ecological aspects depending on spatial level. When patches were ranked by species richness, it was assumed to represent a neutral test of nestedness. This test did not elucidate any relations between environmental variables and species distribution. However, as suggested by Lomolino (1996) sites can be ordered by patch area and isolation (not done in this study) in order to test if these can explain the observed nestedness. Thus, any direct relation between nestedness and area was explored on the patch level.

The size of sample plots was independent of patch size. Thus, differences between plots in species occurrences were assumed to reflect differences in important habitat characteristics (e.g. the occurrence of specific habitat elements or substrates and microclimate conditions). A nested subset pattern on the plot level that was related to species richness was therefore assumed to indicate that important habitat characteristics occurred in a nested way.

Nestedness relates to the "Single Large Or Several Small" (SLOSS) discussion. It has been suggested that strong nestedness and species–area relationships indicate that a single large site will harbour more species than any combination of several small sites (Wright and Reeves, 1992; Worthen, 1996). To further explore this hypothesis, the nestedness analysis was combined with the analysis of a "saturation index" (SI; Quinn and Harrison, 1988). SI was calculated as the ratio between the integrals of the cumulative species–area curves (1) for sites sampled in order of the smallest to the largest and (2) for sites sampled from the largest to the smallest. Both curves pass through the origin and a point representing the total number of species at the total area of studied sites. SI-values smaller than 1 indicate that large sites contain more species than several small sites with the same total area. SI-values larger than 1 indicate the opposite. However, if the two cumulative species–area curves intersect between the extremes the importance of patch size cannot readily be interpreted. The SI was calculated on both patch and plot level. The area of the patches was used to order sites on the plot level too. However, 0.1 ha (i.e. plot size) was added for each plot to the cumulative area when the species–area curves on the plot level were constructed.

3. Results

Data on patch area and species richness are presented in Table 1.

Most species were infrequent in the studied landscape (Fig. 1) and as much as 50% of all species were noted in nine or less patches. Only 5% of the species were noted in all 46 patches and slightly less than 30% of all species were recorded in more than 50% of the patches. The species frequency distribution of Red-list respectively non Red-list species did not differ significantly from each other (Kolomogorov Smirnov two sample test, $P>0.05$), and they were both dominated by rare species.

The species-by-site matrices for all six species groups as well as Red-list species were significantly ($P<0.05$) nested on the patch level when patches were ranked by species richness (Table 2). The same was true for all species groups as well as the Red-list species except vascular plants and crustose lichens when patches were ranked by area (Table 2). The species-by-site matrix for Red-list species on the patch level is shown in Fig. 2. All species–site matrices on the plot level, except those of vascular plants and mosses, showed a significantly nested structure, when plots were ranked by species richness (Table 2). Area was not related to the nested structure at plot level in any case (Table 2).

Table 1
The range (min- and maximum values), median, mean and standard deviation (SD) of area and species richness values used to rank sites ($N=46$) during nestedness analyses of the plant and fungal species distribution patterns in the nature reserve Granlandet, northern Sweden

Ranking variable		Min.	Max.	Median	Mean	SD
Area (ha)		0.17	12	0.82	2.2	3.1
Species richness						
Patch level	Vascular plants	7	26	12.5	13	4.3
	Mosses	16	41	23	25	6.0
	Liverworts	10	32	18	20	6.0
	Crustose lichens	16	31	21	22	3.8
	Corticoids	6	57	18.5	24	16
	Polypores	5	30	13	15	6.7
	Red-list	2	24	8	9.7	5.9
Plot level	Vascular plants	4	20	8	8.0	2.7
	Mosses	13	23	18	18	2.4
	Liverworts	5	26	12.5	13	3.7
	Crustose lichens	0	26	20	19	4.2
	Corticoids	3	25	13	13	5.8
	Polypores	1	16	8	7.8	3.5
	Red-list	1	11	4	4.6	2.9

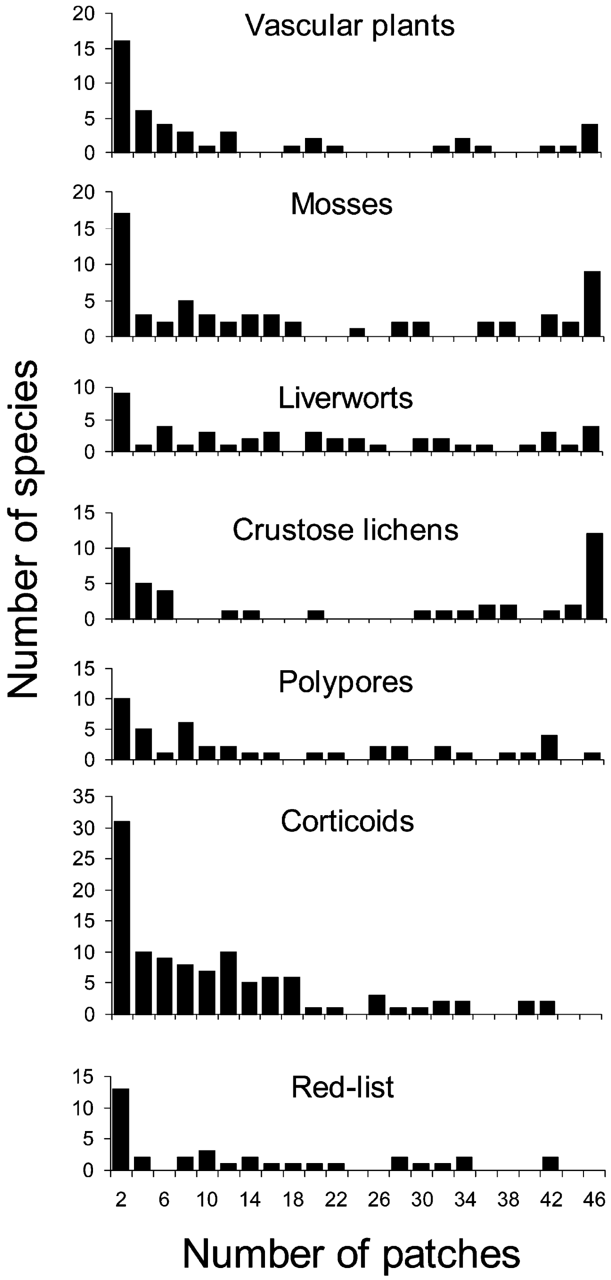

Fig. 1. The frequency distribution of six different plant and fungal species groups as well as the subgroup of Red-list species in 46 old-growth forest patches in the Granlandet nature reserve, northern Sweden.

Table 2
Results from the nestedness analysis of the different species–site matrices in the nature reserve Granlandet, northern Sweden[a]

Spatial scale	Ranking variable		Species groups						
			Vascular plants	Mosses	Liverworts	Crustose lichens	Corticoids	Polypores	Red-list
Patch	S	*d*	131	205	193	90	354	136	92
		z	3.7***	4.4***	5.6***	3.8***	13.0***	6.9***	8.2***
	A	*d*	159	222	211	124	385	169	110
		z	0.6	2.8**	3.7***	−0.3	10.9***	3.7***	6.1***
	Random	*d*	164.4	252.6	247.0	121.5	552.9	207.9	162.6
		SD	9.1	10.8	9.7	8.3	15.3	10.4	8.6
Plot	S	*d*	92	177	179	91	298	130	82
		z	1.0	−0.3	1.9*	2.1**	2.4**	2.4**	2.7**
	A	*d*	139	204	214	124	351	175	103
		z	−5.6	−3.1	−1.8	−1.7	−1.7	−3.1	−0.3
	Random	*d*	99.2	174.4	197.3	111.0	329.3	149.7	101.1
		SD	7.1	9.7	9.5	7.6	13.1	8.1	7.0

[a] Each of the six species groups as well as Red-list species was tested on the two spatial scales of species survey; patch and plot. The discrepancy (*d*) from perfect nestedness when sites were ranked with respect to species richness (S) and area (A) are presented. The observed discrepancy was compared with the mean discrepancy of 1000 random simulations on each species–site matrix. The *z*-values are the number of standard deviations (SD) that the observed discrepancy differed from the mean discrepancy of the simulated matrices.

* One sided *P*-values: $0.01 \leqslant P < 0.05$

** One sided *P*-values: $0.001 \leqslant P < 0.01$

*** One sided *P*-values: $P < 0.001$

In most cases the saturation indices (SI) were larger than 1 on patch level (Fig. 3), indicating that small patches accumulate species faster than large patches. However, only the species richness among plant species groups and corticoids was clearly increased by habitat subdivision since the small-to-large curve remained consistently above the large-to-small curve. The curves intersected among crustose lichens, polypores and Red-list species (Fig. 3). These three species groups as well as the liverworts exhibited an effect of area on plot level, despite a general trend of SI < 1 (Fig. 3). In these cases, the large-to-small curve remained consistently above the small-to-large curve (Fig. 3), indicating a faster accumulation of species in large patches than in small.

4. Discussion

The study clearly shows that both plants and fungi in old growth forests occur as nested subsets. This represents a non-random situation and implies that some important processes regulate the occurrence of rare species and make them over-represented in species rich sites.

4.1. Nestedness and area

The fact that five of six species groups as well as Red-list species exhibited nestedness in relation to area on the patch level indicates that area was an important factor for species distribution on the stand scale. Two main mechanisms have been proposed to explain a strong relation between area and nestedness. Wright et al. (1998) argued that it could be explained by the fact that species with large area requirements will tend to be found in large habitat patches, while species that can survive even in the smallest patches are likely to be found everywhere. In addition, Worthen (1996) stated that nested habitats could also create this pattern if habitat diversity was related to area. The importance of area in the studied landscape is further supported by Edenius and Sjöberg (1997) who found that some bird species avoid small patches while patches larger than 10 ha have more species then expected by random.

The distribution of vascular plants as well as crustose lichens diverges from the general pattern of a relation between nestedness and area on patch level. Other factors beside area seem to be decisive for these groups. In general, the distribution of vascular plants and crustose lichens seem to be more affected by random factors than the other groups. The observed matrices of these species groups diverged least from randomness (i.e. small *z*-values; c.f. Table 2) in the neutral test of nestedness (i.e. when sites were ranked by species number).

To investigate the SLOSS issue, the nestedness analysis was combined with the analysis of the saturation index (SI). Further, the relation between area and species composition patterns was explored on two spatial scales (patch and plot). Before examining the results from a SLOSS perspective, it is important to first review

	Patch																																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	Species frequency
Species *Fomitopsis rosea* P	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	1	42
Phellinus nigrolimitatus P	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	42
Anastrophyllum hellerianum L	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	0	1	0	1	1	1	0	0	0	1	0	0	0	1	0	34
Cyphelium karelicum CL	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	1	1	0	0	0	33
Amylocystis lapponica P	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	32
Lophozia longiflora L	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	29
Onnia leporina P	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	28
Skeletocutis odora P	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	1	0	1	1	1	0	1	1	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	27
Lophozia ascendens L	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22
Cystostereum murrayi C	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	19
Phlebia centrifuga C	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	18
Skeletocutis brevispora P	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
Asterodon ferruginosus C	1	1	1	1	1	1	0	1	0	1	1	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	14
Sclerophora coniophaea CL	1	1	0	0	1	1	1	1	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	13
Trichaptum laricinum P	1	1	1	1	1	0	1	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	12
Aleurodiscus lividocaeruleus C	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Steccherinum luteoalba P	1	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Skeletocutis chrysella P	0	0	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Skeletocutis kuehneri P	1	1	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Skeletocutis stellea P	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8
Byssocorticium molliculum P	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Postia balsamea P	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Arthonia incarnata CL	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Crustoderma dryinum C	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Laurilia sulcata C	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Postia hibernica P	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Perenniporia subacida P	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Anomoporia bombycina P	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Calopogeia suecica L	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chaenotheca laevigata CL	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Steccherinum collabens P	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Kavinia alboviridis C	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Postia placenta P	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Diplomitoporus lenis P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Tayloria tenuis M	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Species richness	24	21	21	20	20	19	19	17	15	15	14	14	13	12	11	10	10	10	9	9	9	8	8	8	8	8	7	7	7	6	6	6	6	6	6	6	5	4	4	4	4	3	3	2	2	2	
Area (ha)	12	7.8	5.4	10	9.8	6.6	5.9	8.9	4.9	3.8	2.6	1.4	0.96	0.53	0.81	0.45	0.49	0.96	0.79	0.96	0.64	0.89	0.89	0.63	0.75	0.82	0.82	0.33	0.84	0.90	0.38	0.43	0.51	0.58	0.43	0.21	0.17	0.48	0.90	0.83	0.48	0.25	0.22	0.96	0.50	0.17	

Fig. 2. Species–site matrix for 35 Red-list species recorded in 46 old-growth spruce forest patches in the Granlandet nature reserve, northern Sweden. Species presences are marked with 1 and species absences with 0. Patches (indicated by numbers 1–46) are ranked by species richness and species are ranked by frequency. The letters behind the species names indicate species group; C: Corticoids; CL: Crustose lichens; L: Liverworts; M: Mosses; P: Polypores.

the properties of the nestedness analysis respectively the analysis of the SI. It is clear that under perfect nestedness and strong species–area relationships, a single large site will contain more species than any combination of smaller sites. However, perfect nestedness is almost never attained in natural systems. Even if the relation between nestedness and area is statistically significant, it is possible that there are enough departures from perfect nestedness so that species richness might be maximized by collections of smaller sites (Cook, 1995; Boecklen, 1997). This observation comes from the fact that the nestedness analysis only account for how much sites overlap in species composition. It does not account for the number of species per area unit among sites of different size. The actual size of sites is only used to *rank* the sites during the nestedness analysis. The analysis of SI accounts both for the overlap in species composition between sites and the actual size of sites. Thus, the analysis of SI is complementary to nestedness investigating the SLOSS issue. The main merit of the nestedness indices, though, is that they indicate the degree to which *rare* species are confined to the most species rich sites, a compositional patterns not revealed by SI (Cook, 1995).

The fact that nestedness was related to area on patch level among most species groups indicates that large patches tend to harbor more rare species than small patches even having taken random sampling effects into account. In a SLOSS perspective this imply that a single large patch will generally contain more rare species than collections of smaller patches having the same total area. By contrast, the results from the analysis of SI on patch level showed that small patches generally accumulate species faster than large patches. However, among the Red-list species, the analysis of SI on patch level did not provide a clear answer to the SLOSS question. Thus, the combined result of both analyses indicates that large patches generally are more important for Red-list species than any collection of smaller patches.

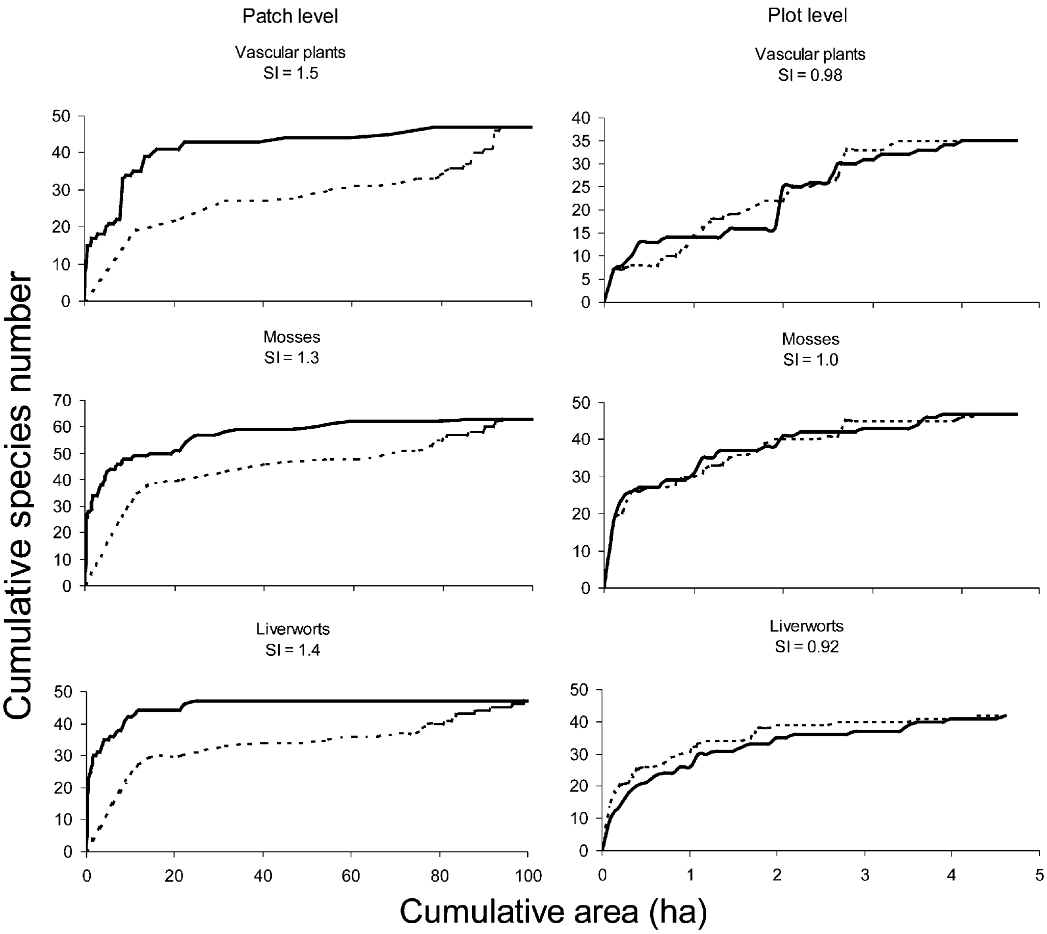

Fig. 3. Cumulative species–area curves used for the analysis of the saturation index (SI) for six plant and fungal species groups as well as the subgroup of Red-list species on two different spatial levels; patch and plot, in 46 old-growth spruce forest patches in the Granlandet nature reserve, northern Sweden. The area of the individual patches was used to rank sites on both spatial levels. On the plot level 0.1 ha (i.e. plot size) was added for each plot cumulatively (range 0–4.6 ha) in the species–area curve. The *Solid line* represents the situation when sites were ranked from small to large. The *Dashed line* represents the situation when sites were ranked from large to small.

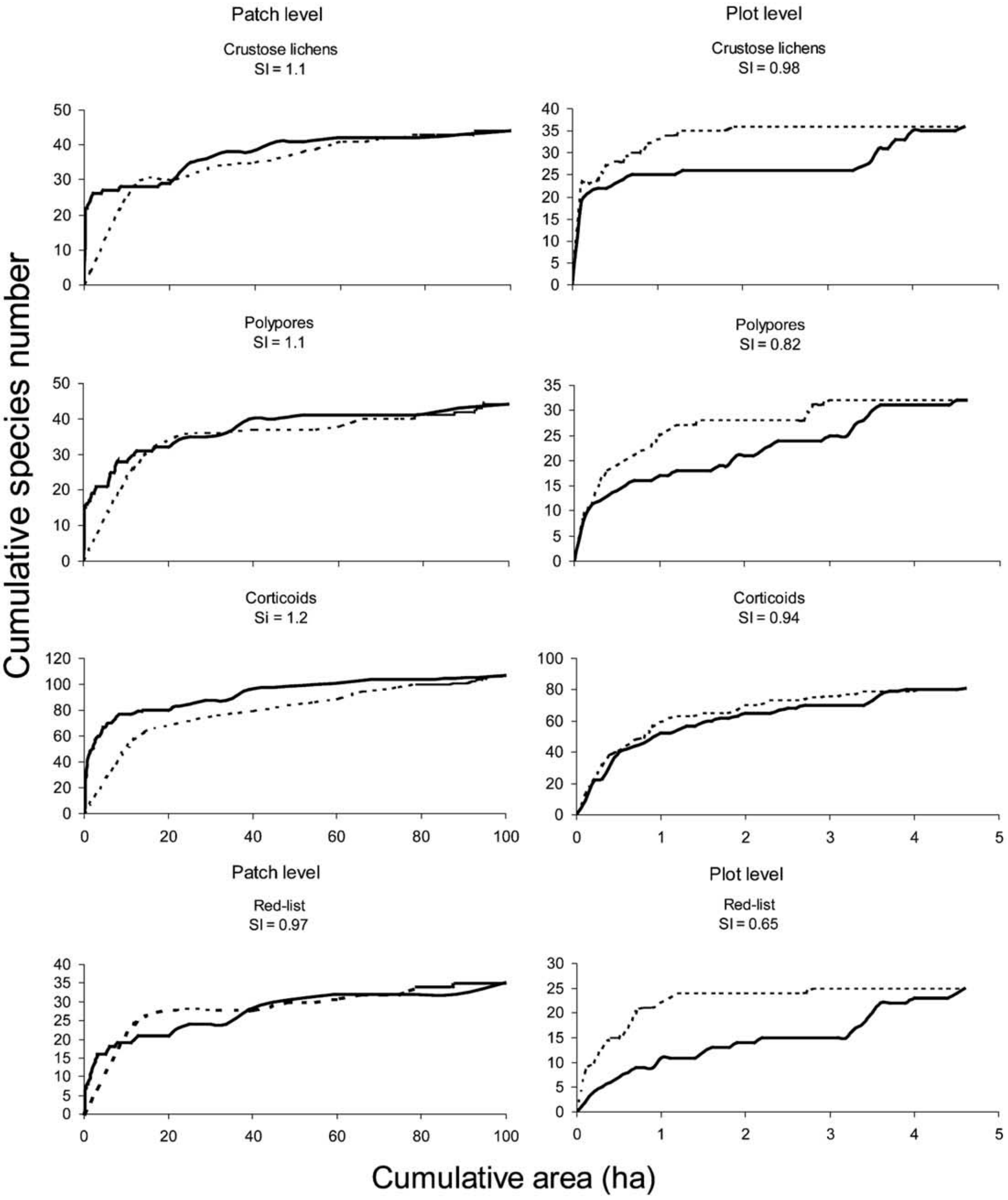

Fig. 3. Continued.

Area was not related to the nested structure on the plot level. This result indicates that the species occurrences in patch interiors were not affected by area. By contrast, the results from analysis of SI on plot level suggest that the interior habitat of large patches accumulated species faster than the interior habitat of smaller patches among liverworts, crustose lichens, polypores and Red-list species. A possible explanation for this result is that the interior habitat of large patches is less affected by edge effects than the interior habitat of small patches (Moen and Jonsson, in press). Edge effects could cause a harsher environment in the small patches that may negatively affect the species occurrences.

In summary, the results of this study indicate that the answer to the SLOSS issue is complex. Often the results from the nestedness analysis and the SI-analysis may appear contradictory. This is to some extent a result of the different emphases invoked in the analyses. However, it is notable that for Red-list species both nestedness analysis and SI suggest that large patches better capture the species pool. Based on other studies in Granlandet (Moen and Jonsson, in press; Kruys and Jonsson, 1997; Dettki et al., 1998) the probable causes are edge effects that create a harsher environment in the small patches. This observation is important since Red-list species make up the 'top' components of the old-growth spruce forest plant and fungal species diversity that we seek to conserve.

4.2. Nestedness and habitat quality

If important habitat characteristics occur in a nested way (Wright et al., 1998), nestedness could also emerge in plots (or patches) of equal size. Thus, nestedness on the plot level was assumed to indicate that habitat quality was important for species distribution. This was the case for five out of six species groups as well as the Red-list species. Such a pattern could arise if widespread species use most habitats while rare species have specific preferences that only occur in high quality habitats (Wright et al., 1998; Worthen, 1996). The relation between nestedness and habitat quality seem to be especially strong among the substrate-specific fungi and the Red-list species. The clear effect of habitat quality is somewhat surprising since the environmental gradients could be assumed to be relatively short in the present case (i.e. the forest patches are similar regarding forest vegetation type, stand structure and stand history).

The occurrence of specific habitat elements and microclimate conditions probably affect the quality of habitat. Downed logs and old living trees are critical for liverworts, crustose lichens and wood-fungi (Berg et al., 1994; Rydin et al., 1997; Söderström, 1988). In fact, the species richness within these species groups was strongly correlated to stand variables such as tree and downed log characteristics (Berglund and Jonsson, 2001). In addition, liverworts and epiphytic lichens are more abundant in interior parts of large patches than in small patches, probably as an effect of adverse climate at forest edges (Eriksson, 1999; Moen and Jonsson, in press).

4.3. Conclusions

The fact that most species are infrequent in insular old-growth spruce forest stands implies a major challenge to conservation management. Fortunately random processes do not seem to be decisive and species distributions exhibit predictable nested patterns.

The analysis of the relation between nestedness and area is not the same as a species–area correlation, since nestedness analysis takes random sampling effects into account (Worthen, 1996). Thus, our results suggest that rare species are over-represented in large and species rich patches even given a general species area correlation. In addition, large patches seem to host more Red-list species in patch interiors than in small patches. Besides area, the habitat quality of equal sized plots has been shown to be of great importance for the nested structure among the studied plant and fungi species as well as the Red-list species. Thus, small old-growth spruce forest habitats of high quality should not be neglected from a conservation perspective.

Acknowledgements

The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning, FORMAS, the Swedish Environmental Protection Agency and the Swedish Royal Academy of Science, KVA financially supported this work. The authors wish to thank A.-S. Duerden, A. Malmqvist, A. Skarstedt, F. Jonsson and M. Ekelund for field assistance and species surveys, and A. and B. Andersson for providing accommodation. We are grateful to S. Hultengren, K-H. Larsson, T. Niemelä and L. Ryvarden for the identification of difficult wood-fungi and crustose lichens.

References

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in north-western Europe. Annales Botanici Fennici 5, 169–211.

Anon., 1999. Nyckelbiotopsinventeringen 1993–1998. Slutrapport. Meddelande 1—1999. Skogsstyrelsen, Jönköping.

Atmar, W., Patterson, B.D., 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96, 373–382.

Axelsson, A-L., 2001. Forest landscape change in boreal Sweden 1850–2000—a multi-scale approach. Doctoral thesis, Swedish University of Agricultural Sciences, Umeå.

Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72, 355–362.

Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests—distribution and habitat associations. Conservation Biology 8, 718–731.

Berglund, H., Jonsson, B.G., 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. Journal of Vegetation Science 12, 857–866.

Bernes, C., 1994. Biologisk mångfald i Sverige, Monitor 14. Swedish Environmental Protection Agency, Solna.

Boecklen, W.J., 1997. Nestedness, biogeographical theory, and the design of nature reserves. Oecologia 112, 123–142.

Brualdi, R.A., Sanderson, J.G., 1999. Nested species subsets, gaps and discrepancy. Oecologia 119, 256–264.

Cederberg, B., 2001. Skogsbrukets effekter på rödlistade arter. ArtDatabanken Rapporterar 4. ArtDatabanken, SLU, Uppsala.

Cook, R.R., 1995. The relationship between nested subsets, habitat subdivision, and species diversity. Oecologia 101, 205–210.

Cutler, A., 1991. Nested faunas and extinction in fragmented habitats. Conservation Biology 5, 496–505.

Dettki, H., Edman, M., Esseen, P.-A., Hedenås, H., Jonsson, B.G., Kruys, N., Moen, J., Renhorn, K.-E., 1998. Screening for species sensitive to fragmentation. Ecography 21, 649–652.

Diamond, J.M., 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation 7, 129–146.

Edenius, L., Sjöberg, K., 1997. Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden, relations to habitat area and landscape context. Ecography 20, 425–431.

Eriksson, J., 1999. Edge effects on the epiphytic lichen Alectoria sarmentosa in a naturally heterogeneous forest landscape. Degree thesis, Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden.

Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. Ecological Bulletins 46, 16–47.

Gärdenfors, U. (Ed.), 2000. Rödlistade arter i Sverige 2000—The 2000 Red List of Swedish Species. ArtDatabanken, SLU, Uppsala.

Hallingbäck, T. (Ed.), 1998. Rödlistade mossor i Sverige—Artfakta [Swedish Red Data Book of Bryophytes]. ArtDatabanken, SLU, Uppsala.

Hanski, I., 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38, 210–221.

Hanski, I., 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Honnay, O., Hermy, M., Coppin, P., 1999. Nested plant communities in deciduous forest fragments: species relaxation or nested habitats? Oikos 84, 119–129.

Jonsson, B.G., 2001. Choosing a null-model for nested subset analysis. Oecologia 127, 309–313.

Kadmon, R., 1995. Nested species subsets and geographical isolation: a case study. Ecology 76, 458–465.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S., Uotila, A., 2001. Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat change. Scandinavian Journal of Forest Research Supplement 3, 27–37.

Kruys, N., Jonsson, B.G., 1997. Insular patters of calicoid lichens in a boreal old-growth forest-wetland mosaic. Ecography 20, 605–613.

Larsson, K.H. (Ed.), 1997. Rödlistade svampar i Sverige—Artfakta. [Swedish Red Data Book of Fungi 1997]. ArtDatabanken, SLU, Uppsala.

Lomolino, M.V., 1996. Investigating causality of nestedness of insular communities: selective immigrations or extinctions? Journal of Biogeography 23, 699–703.

Lövgren, R., 1986. Urskogar. Inventering av urskogsartade områden i Sverige. Del 3—Norra Sverige. Report 1509. Swedish Environmental Protection Agency, Stockholm.

Moen, J., Jonsson, B.G. Edge effects on hepatics and lichens in forest patches in a mosaic of boreal forest and wetland. Conservation Biology (in press).

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10, 58–62.

Östlund, L., 1993. Exploitation and structural changes in the north Swedish boreal forest 1800–1992. Dissertations in Forest Vegetation Ecology, 4. Swedish University of Agricultural Sciences, Department of Forest Vegetation Ecology, Umeå.

Patterson, B.D., Atmar, W., 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. Biological Journal of the Linnean Society 28, 65–82.

Quinn, J.F., Harrison, S.P., 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. Oecologia 75, 132–140.

Rydin, H., Diekmann, M., Hallingbäck, T., 1997. Biological characteristics, habitat associations, and distribution of macrofungi in Sweden. Conservation Biology 11, 628–640.

Schoener, T.W., Schoener, A., 1983. Distribution of vertebrates on some very small islands. 1. Occurrence sequences of individual species. Journal of Animal Ecology 52, 209–235.

Simberloff, D.S., Abele, L.G., 1982. Refuge design and island biogeographical theory: effects of fragmentation. American Naturalist 120, 41–50.

Simberloff, D.S., Martin, J.-M., 1991. Nestedness of insular avifaunas: simple summery statistics masking complex species patterns. Ornis Fennica 68, 178–192.

Sippola, A.-L., Lehesvirta, T., Renvall, P., 2001. Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. In: Jonsson, B.G., Kruys, N. (Eds.), Ecology of Wood Debris in Boreal Forests. Ecological Bulletins 49, 243-254.

Söderström, L., 1988. The occurrence of epixylic bryophytes and lichen species in an old natural and a managed forest stand in northeast Sweden. Biological Conservation 45, 169–178.

Soulé, M.E., Simberloff, D.S., 1986. What do genetics and ecology tell us about the design of nature reserves? Biological Conservation 35, 19–40.

Tallantire, P.A., 1972. The regional spread of spruce (*Picea abies* (L.) Karst.) within Fennoscandia: a reassessment. Norwegian Journal of Botany 19, 1–16.

Thor, G., Arvidsson, L. (Eds.), 1999. Rödlistade lavar i Sverige—Artfakta. [Swedish Red Data Book of Lichens]. ArtDatabanken, SLU, Uppsala.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Worthen, W.B., 1996. Community composition and nested-subset analyses: basic descriptors for community ecology. Oikos 76, 417–426.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A., Atmar, W., 1998. A comparative analysis of nested subsets patterns of species composition. Oecologia 113, 1–20.

Wright, D.H., Reeves, J.H., 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia 92, 416–428.