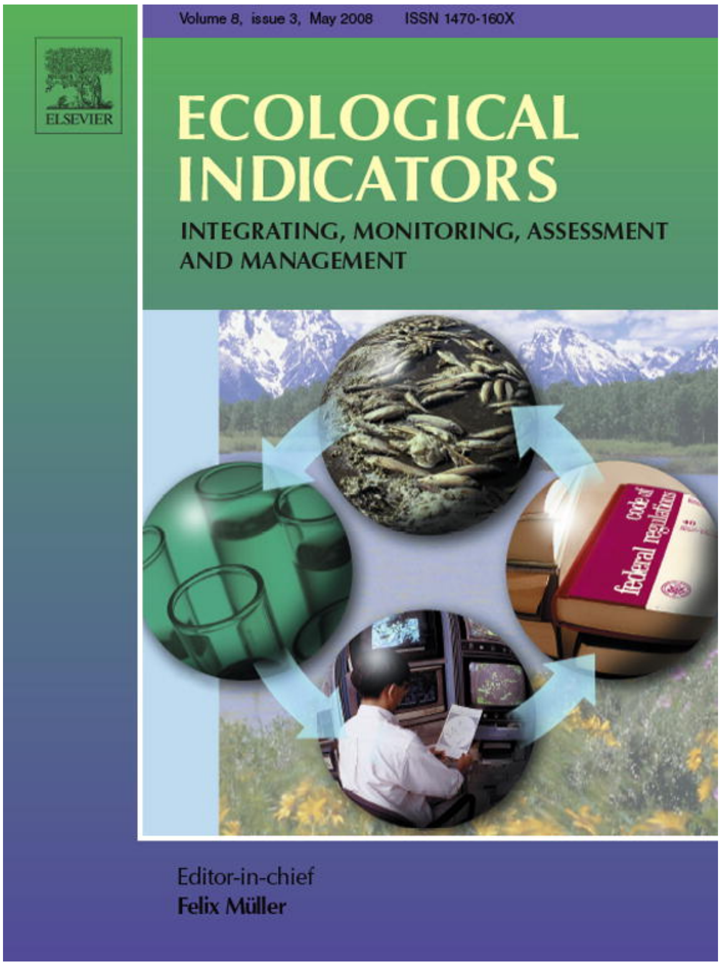
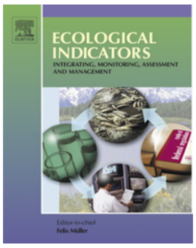

Volume 8, issue 3, May 2008 ISSN 1470-160X
ELSEVIER
ECOLOGICAL INDICATORS
INTEGRATING, MONITORING, ASSESSMENT AND MANAGEMENT
code of federal regulations
Editor-in-chief
Felix Müller

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/ecolind



Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests

Eija Hurme[a,*], *Mikko Mönkkönen*[b], *Anna-Liisa Sippola*[c],
Hanna Ylinen[a], *Mikko Pentinsaari*[a]

[a] *Department of Biology, P.O. Box 3000, University of Oulu, FIN-90014 Oulu, Finland*
[b] *Department of Biological and Environmental Science, P.O. Box 35, University of Jyväskylä, FIN-40014, Finland*
[c] *Arctic Centre, University of Lapland, P.O. Box 122, FIN-96101 Rovaniemi, Finland*

ARTICLE INFO

Article history:
Received 19 September 2006
Received in revised form
30 January 2007
Accepted 2 February 2007

Keywords:
Beetles
Coarse woody debris (CWD)
Lichens
management
Polypores
Site selection

ABSTRACT

One of the potentially useful indirect shortcut methods in biodiversity conservation is the umbrella species concept. An umbrella species can be seen relatively demanding for the size of the area and probably also for certain habitat types: conservation management for the umbrella species would thus encompass other species preferring similar habitats but with smaller area requirements. As such, it has a comprehensive spatial aspect for landscape planning. We tested the role of the Siberian flying squirrel (*Pteromys volans*) as an umbrella species for wood dependent species among red-listed and old-growth forest associated polypores, epiphytic lichens and beetles. Flying squirrels inhabit home ranges of several to tens of hectares, and prefer mature spruce-dominated (*Picea abies*) mixed forests, which often have high amounts of dead wood. We carried out species surveys and trappings during 1 year from 20 mature spruce-dominated forest stands (altogether 162 ha), of which 12 were occupied by the flying squirrel. The amount of dead wood was higher in occupied stands than in unoccupied stands. We also found a tendency for a higher number of species and number of records in occupied stands, a relationship mostly due to the polypore species. The presence of the flying squirrel may reflect the habitat availability for species depending on dead and living wood, and assist in site selection of conservation areas. We suggest that the flying squirrel has potential as an umbrella species to partly enhance maintenance of biodiversity in northern boreal forests in Finland.

1. Introduction

Several indirect shortcut methods have been introduced to describe biodiversity values and the occurrence of species to support landscape management planning (e.g., Noss, 1990; Ricketts et al., 1999; Andelman and Fagan, 2000; MacNally et al., 2002). Some of the commonly used indirect cues for the occurrence of a certain species or species groups are flagship, indicator, and umbrella species concepts. Public concern can be directed on a charismatic flagship species as a symbol of nature, which may increase funding for conservation (Caro and O'Doherty, 1999; Sergio et al., 2005). An indicator species reflects the quality of a certain habitat, or changes in populations of other species (Landres et al., 1988). An umbrella species is relatively demanding on the size of the area and probably also on certain habitat types (Roberge and Angelstam, 2004), and as such has the most comprehensive spatial aspect for landscape planning. Therefore, conservation areas planned for the umbrella species would include other species preferring similar habitats, but with smaller

---

[*] *Corresponding author*. Tel.: +358 8 553 1215; fax: +358 8 553 1061.
E-mail address: Eija.Hurme@oulu.fi (E. Hurme).

1470-160X/$ – see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.ecolind.2007.02.001

area requirements (Simberloff, 1998; Caro and O'Doherty, 1999; Fleishman et al., 2000; Suter et al., 2002). The umbrella species concept as an indirect shortcut method for conservation is thus tempting. However, it is not so straightforward in practice.

The umbrella species concept is suggested to improve the effectiveness of biodiversity conservation and field surveys (e.g., Simberloff, 1998; Caro and O'Doherty, 1999; Andelman and Fagan, 2000). It certainly would be faster and cheaper to survey the area for an easily recognizable species instead of conducting a survey for the majority of biota. Furthermore, population persistence is a positive function of population size (Hanski, 1999). From the long-term management perspective populations of an umbrella species should be viable (Berger, 1997; Martikainen et al., 1998; Caro and O'Doherty, 1999; Andelman and Fagan, 2000), when the population persistence of an umbrella species could assure also the population viability of the species under the umbrella. It has been argued that a single species can seldom be a surrogate for a variety of species, and thus the conservation areas based only on one umbrella species would create gaps in conservation (Kerr, 1997; Simberloff, 1998; Lindenmayer et al., 2002). Therefore, a concept of focal species (Lambeck, 1997) relies on many umbrella species: a taxon-based surrogate group of the most demanding species, each of which could be used to define different attributes of a landscape.

Roberge and Angelstam (2004) divided umbrella species to three groups: (1) area-demanding species, (2) species that are used in site selection, and (3) an extended umbrella species concept. Because the area requirements tend to be positively related to the body size of a species, the first group addresses mainly large vertebrates: mammalian carnivores (e.g., Noss et al., 1996; Carroll et al., 2001) or herbivores (Berger, 1997). In boreal forest environments, white-backed woodpecker (*Dendrocopos leucotos*) (Martikainen et al., 1998) and capercaillie (*Tetrao urogallus*) (Suter et al., 2002; Pakkala et al., 2003) have been studied for the umbrella effects to other forest species based on both their area and habitat type demands. The basis for the second group is especially the habitat type requirements of species. Studies on umbrella species assisting the site selection have focused mainly on bird (Fleishman et al., 2001; Poiani et al., 2001; Rubinoff, 2001; Sergio et al., 2005), butterfly (Launer and Murphy, 1994; Fleishman et al., 2000, 2001) and beetle species' (Bonn and Schröder, 2001) ability to provide umbrella for the larger species communities in the same habitats. Encouraging examples for the usage of umbrella species in the reserve site selection within large areas come from Africa, based on game reserves for large mammals (Caro, 2003), and on habitat suitability models for amphibians and mammals (Rondinini and Boitani, 2006).

The third group, an extended umbrella concept, emphasizes habitat connectivity, occurrence of certain ecosystem processes or the distribution of scarce resources at the landscape scale (Roberge and Angelstam, 2004). It has mainly been related to focal species. For example, Watson et al. (2001) used information on two focal species to identify the minimum patch size, habitat structural complexity and landscape connectivity to support the other 70 existing woodland bird species, and Bani et al. (2002) used several focal species to plan a habitat network to accommodate a larger community of forest birds and mammalian carnivores.

However, rigorous tests for the umbrella species concept are scarce (Andelman and Fagan, 2000; Roberge and Angelstam, 2004), and among the existing studies the effectiveness of the umbrella species has often been found limited (Roberge and Angelstam, 2004). The problems are related for example to the lack of intensive surveys of other species, or the study includes species that have ill-assorted habitat and area demands (Simberloff, 1999; Andelman and Fagan, 2000; Lindenmayer et al., 2002). Even several umbrella species (e.g., sensu Lambeck, 1997) do not necessarily remove the difficulties of identifying the most demanding species or the risks of excluding some important areas from conservation (Lindenmayer et al., 2002).

We address the site selection concept and test a possible role of an arboreal Siberian flying squirrel (*Pteromys volans*) as an umbrella for species dependent on dead and living wood in northern Finland. Flying squirrels prefer mature Norway spruce (*Picea abies*) dominated mixed boreal forests (Mönkkönen et al., 1997; Hanski, 1998), and the occupied forests are typically older and often characterized by higher amount of coarse woody debris (CWD) than unoccupied forests (Reunanen et al., 2002). Approximately one fourth of the forest associated species in Finland are dependent on CWD (Siitonen, 2001). In Fennoscandian boreal forests, these species have faced considerable habitat loss due to forestry practices, now being prominent among red-listed species (Rassi et al., 2001). Species associated with CWD are particularly common among polypores and beetles. We focus especially on red-listed and old-growth forest associated species in polypores (Basidiomycetes), epiphytic lichens (Lichenes) and beetles (Coleoptera).

The spatial patterns in the ecology of the flying squirrel matches with the rough spatial definition of an umbrella species: individual home ranges are rather large in size, on average 8 ha for females and 60 ha for males (Hanski et al., 2000). In addition, the breeding sites of the flying squirrel are protected since the species is categorised as a vulnerable species in Finland due to population decline and habitat loss (Rassi et al., 2001). Its occurrence is thus already taken into account in forestry planning, and the conservation effort would be even more effective if other species of concern were located at the same sites.

We surveyed mature spruce-dominated forest stands occupied and unoccupied by the flying squirrel, and compared the stands in terms of the number of species and records. From the practical perspective, the occurrence of the nocturnal flying squirrel in a forest stand is relatively easy to determine based on distinctive fecal pellets (e.g., Reunanen et al., 2000), compared with laborious surveys and identification of many polypores, lichens and beetles. Therefore, we evaluate the utility of the flying squirrel in the site selection for conservation, when the objective is to maximize species coverage in a hypothetical reserve network. In addition, since flying squirrels seem to be dependent on landscape connectivity (e.g., Reunanen et al., 2000, 2002) we discuss the extended umbrella species concept from the landscape planning perspective.

2. Material and methods

2.1. Study area

Our study area locates in northeastern Finland (65°30′N, 28°15′ E), and belongs to the northern boreal vegetation zone (Ahti et al., 1968). The topography varies between 220 and 370 m a.s.l. The study area is dominated by hills covered with boreal coniferous forests with bogs and open fens typically in the lowlands. Recent clear cuts and forest roads are common. About 28% of the forests are relatively old (>100 years) and mainly dominated by Norway spruce, while ca. 65% are under 60 years old, and mostly dominated by Scots pine (*Pinus sylvestris*). The most common deciduous trees are birches (*Betula pubescens*, *B. pendula*) and aspen (*Populus tremula*), mixed with some alder (*Alnus incana*) in more moist sites.

We selected 20 mature spruce-dominated forest stands (age 84–180 years, size 2.2–21 ha) with deciduous trees in a mixture, reflecting the typical habitat preferences of the flying squirrel (Mönkkönen et al., 1997; Hanski, 1998; Reunanen et al., 2002; Hurme et al., 2005). The stands can be considered semi-natural due to selective cuttings done ca. 80 years ago. The occupancy status of the Siberian flying squirrel in the stands was based on intensive field work done in 2002 (Hurme et al., 2005), and confirmed in spring 2003 before starting this study. Twelve stands were observed to be occupied by the flying squirrel based on the presence of the yellowish fecal pellets under the largest spruces and aspens, which indicate the sites where individuals spend most of their time (e.g., Reunanen et al., 2000). The selected stands covered altogether 162 ha, and were located within 2500 ha. We selected as homogeneous set of stands as possible to this study, based on the basic descriptions of stand characteristics by Metsähallitus (a state owned enterprise governing public land and waters), but some differences between occupied and unoccupied stands by the flying squirrel remained (Table 1).

2.2. Dead wood measurements

We measured the CWD using a plot size of 50 m × 4 m (200 m^2) in autumn 2003. One plot was surveyed per every 200 m of a species survey transect (see Section 2.3). All standing and downed dead wood pieces were tallied and the tree species identified. We measured the diameter at the breast height (1.3 m) for standing dead trees, and at the middle of a piece of downed wood with a precision of 0.5 cm and the length with a precision of 5 cm. The volume (cubic meters per hectare) for trees less than 3 m long was calculated using a formula of a cylinder, and for trees longer than 3 m we used tree species specific tables for volume estimates (Laasasenaho and Snellman, 1983) (Table 1).

2.3. Polypore and lichen survey

We surveyed polypore and lichen species using 8 m wide line transect. Sampling effort per unit area was held constant by surveying 100 m of line per each hectare of a stand (Table 1). Survey transects were placed evenly to a stand, with at least 50 m distance from the stand edges and from other survey transects. Among wood-decomposing polypores (Aphyllophorales) we searched for red-listed (Rassi et al., 2001) and old-growth forest associated species (Kotiranta and Niemelä, 1996), and among lichens, five easily recognizable epiphytic old-growth associated species were selected for the study (Appendix A). All visible specimens of the target species were surveyed from standing and downed trees, and on living trees up to the height of three metres. The nomenclature of polypores follows Niemelä (2005) and that of lichens is according to Jahns (1996). If necessary, a sample of a species was taken and dried for further examination. The survey was carried out from the middle of August to the beginning of October 2003. The weather conditions between May and October 2003 closely followed the average of the period 1971–2000 (Ilmatieteenlaitos, 2003).

2.4. Beetle survey

We used both active search and passive trapping in exploring the beetle species composition of the stands. We searched for the red-listed and rare beetles and their larvae (Silfverberg, 2004) by walking through each 20 forest stand during dry weather

Table 1 – The basic stand characteristics of the forest stands occupied (*n* = 12) and unoccupied (*n* = 8) by the Siberian flying squirrel

	Occupied		Unoccupied		U (*p*)
	Mean	95% CI	Mean	95% CI	
Stand size	9.6	6.0–13.2	5.8	2.9–8.7	26.0 (0.090)
Age	166.3	152.5–178.0	138.6	108.0–169.3	20.0 (0.029)
Growing stock total	125.5	102.7–148.3	96.9	70.6–123.2	25.0 (0.076)
Spruce	76.5	57.0–96.0	56.1	40.6–71.7	29.0 (0.142)
Pine	25.9	10.2–41.7	16.5	0–33.1	36.0 (0.353)
Birch	23.1	12.9–33.3	15.9	5.9–25.8	33.0 (0.245)
Deciduous trees	23.1	12.9–33.3	24.3	4.9–43.6	46.5 (0.908)
Total CWD	58.9	40.9–76.9	29.9	11.7–48.1	19.0 (0.025)
Downed wood	28.0	20.3–35.8	21.4	8.6–43.2	29.0 (0.143)
Downed spruce	14	4.3–23.8	12.9	0–26.7	41.0 (0.589)

Stand size (ha), age (years) of the stand and the volumes ($m^3\,ha^{-1}$) for living trees are from forest files of Metsähallitus, whereas volumes for coarse woody debris, CWD ($m^3\,ha^{-1}$), were measured in our study using plots of 200 m^2. Results of Mann–Whitney *U*-tests (statistical significance *p* in parenthesis) are shown.

from late June to early July 2003. The search focused on dead or almost dead aspens and spruces, which were standing or lying. Individuals found under the bark, inside the wood, on fruit bodies of polypores or in flight were caught. We also checked the bark of logs for the signs of egg laying, holes of emergence or eating, and peeled the bark to find the beetle larvae.

For the passive survey, we put up five trunk window traps and five cylinder traps per stand. Trunk window traps collect especially rare and threatened beetles more efficiently than free hanging window flight traps (Kaila, 1993; Martikainen, 2000). The traps were attached about 2 m height above ground level against the trunks of large-diameter dead or dying trees. Three traps were hung on spruces and two on aspens per stand. In two stands no aspens were found; in them only three window traps were attached on spruces. A cylinder trap (Fig. 1; design by Dr. J. Forsman) was designed to enclose a fruit body of polypore species. A cylinder of thin metal (aluminium) was adjusted by cutting the edge to match a trunk size and form of a standing or lying tree. A foamed plastic filling was set between the cylinder and the trunk as a gasket, and a trap was tied to the tree. The diameter of a cylinder (10, 20 or 30 cm) closely matched to the size of a fruiting body of a polypore. The outer end of the cylinder was covered with a dark cloth, and a transparent plastic tube (2.5 cm in diameter, 8 cm in length) was attached under a cylinder: insects coming out from the fruiting body were attracted by light. Three red-belted polypores (*Fomitopsis pinicola*), mainly on spruces, and two tinder fungi (*Fomes fomentarius*), mainly on birches, per stand were enclosed within a cylinder trap.

The trapping period was from mid May until the end of September, the total catching period being 19 weeks. The containers and tubes were half filled with salt water with a drop of detergent to break the water tension to drown the individuals fast. The containers of the trunk window traps were emptied five times and of the cylinder traps three times at regular intervals during the catching period. From the containers of the 96 trunk window traps we got altogether 470 samples. Ten samples were lost in late July: two were due to fallen trees and eight due to reindeers, which had reached the containers with salty water. These traps were hung on another tree in a stand or hung up again but higher for the rest of the catching period.

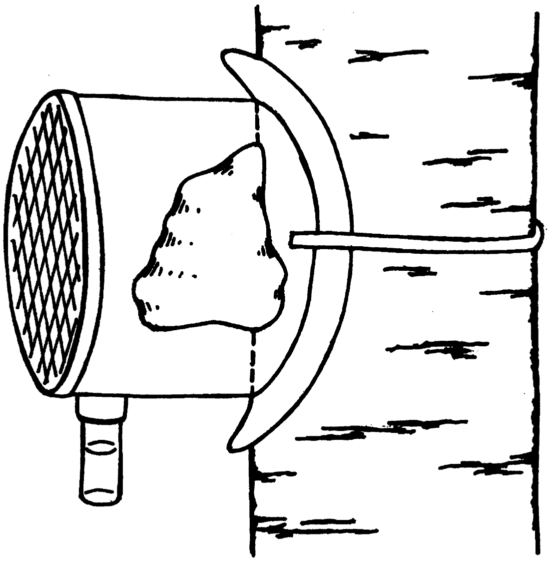


Fig. 1 – A cylinder trap adjusted to cover a fruit body of a polypore (design by Dr. J. Forsman). The front of an aluminium cylinder was covered with a dark cloth, so that the daylight through a transparent plastic tube below attracted the emerging insects into the tube.

2.5. *Statistical analysis*

The statistical unit in our analysis was a forest stand. The survey efforts for CWD, polypore and lichen species, and the active search for beetles, were adjusted according to the stand size. The number of traps for beetles was constant within stands, and thus the survey effort per unit area by the traps was higher in small stands than in larger stands. Difference in species richness and the number of records between occupied and unoccupied stands were compared using standard non-parametric statistics (Mann–Whitney *U*-test).

General linear modelling (GLM, e.g., Quinn and Keough, 2002) was used to model factors affecting species richness. Species richness is typically a positive function of area, and this relationship is linear on log-log scale: $\log(S) = \log(c) + z \times \log(A)$ where S is number of species, A the size of area surveyed, and c and z are constants (Rosenzweig, 1995). We used the length of a survey transect in a stand as the measure of the size of the area searched (*A*). The $\log_{10}$-transformed transect length was included in every model for the number of species to control for the area. Next, we entered CWD variables ($\log_{10}(x)$-transformed) in the model one by one, and the most significant term was retained. We used three variables: volumes ($m^3\ ha^{-1}$) of total CWD, downed wood and downed spruce. We tested also other CWD variables, but these selected three explained most of the variation. Their selection is also based on previous knowledge on habitat preferences of the polypore species (see e.g., Sippola et al., 2001, 2004). We entered each CWD variable into the model one by one. The most significant term was retained. Finally, we included the occurrence of the flying squirrel as a fixed factor into the model to check if it improved the model.

General linear models for the number of records were otherwise similar except that we entered untransformed transect length into the models: the expectation is a linear relationship between the area of a stand and the number of records. All models were done by SPSS for Windows (Version 12.0.1). Only the simplest significant models are shown. The contribution of each variable to the overall coefficient of determination of the model was examined using partial regression analyses (Legendre and Legendre, 1998).

If a set of stands where flying squirrels occur accommodates more species and individuals than an equally large set of stands selected randomly, information on flying squirrel presence is useful when assigning a stand for conservation versus harvesting. To address this site selection problem we resampled the data (Blank et al., 2001). We picked up randomly 1–12 stands 1000 times from the whole data of 20 stands, and calculated the mean for the number of species (with 95% confidence interval, CI) in each set. For comparison the 12 stands occupied by the flying squirrel were resampled to estimate the average species richness in a set of 1–11 occupied stands. If the average number

Table 2 – The number of species and records in the stands occupied ($n = 12$) and unoccupied ($n = 8$) by the Siberian flying squirrel

Number	Occupied		Unoccupied		U (p)
	Mean	95% CI	Mean	95% CI	
All species	11.3	9.1–13.5	7.6	5.1–10.2	19.5 (0.027)
Polypore species	6.4	4.9–7.9	3.1	1.4–4.9	14.0 (0.008)
Lichen species	1.9	1.0–2.8	1.6	0.7–2.5	42.5 (0.663)
Beetle species	3.0	1.7–4.3	2.9	1.7–4.0	43.5 (0.721)
All records	47.2	31.6–62.9	24.9	31.1–36.7	20.5 (0.034)
Polypore records	32.5	19.3–45.7	13.6	4.6–22.6	15.0 (0.011)
Lichen records	10.1	2.7–17.4	5.4	0.5–10.3	39.5 (0.509)
Beetle records	4.7	1.6–7.7	5.9	2.3–9.4	40.5 (0.556)

Results of Mann–Whitney U-tests (statistical significance p in parenthesis) are shown.

of species or records in the flying squirrel stands was above the 95% CI of the equally large set of randomly selected stands, the difference was statistically significant.

Finally, linear optimization analyses were used to examine the combination of stands that covers the maximum number of species for a given level of protection (e.g., Andelman and Fagan, 2000). The optimization analyses were carried out for all species found within the 20 stands. We varied the number of protected stands, and at each level searched an optimal set of stands that maximized the number of species. We examined how many stands in the optimal set contained flying squirrels. If the majority of selected stands included the flying squirrel, it is likely to be a useful umbrella species for the other red-listed and old-growth forest associated species when selecting stands for protection. We also studied how many stands at the minimum were needed to include all the other species, and to what extent this minimum set of stands overlapped with the flying squirrel occurrence. Targeting at the optimal set of sites with only a single occurrence for each species may not be reasonable from species persistence point of view (Cabeza and Moilanen, 2001). Therefore, we also repeated the optimizations to cover at least two or three occurrences for each species (single and double records as such).

3. Results

3.1. *The number of species and records in occupied and unoccupied stands*

The total volume of CWD was higher in occupied than in unoccupied stands (Table 1). A total of 42 red-listed or old-growth forest associated species were found (Appendix A): 21 polypore species, 5 lichen species and 16 beetle species. The number of polypore records was 499, of lichens 164, and the total number of beetle individuals found was 103 (Appendix A). Of the beetles, the majority of the individuals were caught by trunk window traps, five by cylinder traps and four by active search. For all the species together and polypores, a higher number of species and records were observed in occupied stands than in unoccupied stands (Table 2). However, the number of species and records of lichens and beetles did not differ between the flying squirrel occupancy (Table 2).

Downed spruce was the most important CWD variable explaining the numbers of species and records (Table 3). GLM explained 58% of the number of all species and 88% of the number of all records (Table 3). The corresponding numbers for polypores were 69 and 76%, respectively. Partial regression showed that the occurrence of the flying squirrel alone explained 12% of the variation in the number of polypore species, while the transect length, downed spruce and interactions explained 58%. The estimated marginal means for the number of polypore species, when the size of a stand and the volume of downed spruce were held constant, were on average 5.2 and 3.1 polypore species in an occupied and an unoccupied stand, respectively. None of the variables was significantly associated with the number of beetles species or records. The number of lichen species was too small for any analyses separately.

3.2. *Site selection*

Resampling revealed that the number of species was consistently higher in the flying squirrel stands than in

Table 3 – The results of general linear models for the number of species ($\log_{10}$-transformed variables) and records (no transformation)

Number	R^2	Length of a transect	Downed spruce	Flying squirrel
All species ($n = 42$)	0.584 df = 2	23.367 (0.000)	7.565 (0.014)	NS
Polypore species ($n = 21$)	0.694 df = 3	14.084 (0.002)	6.908 (0.018)	6.014 (0.026)
Beetle species ($n = 16$)	0.165 df = 2	1.623 (0.220)	3.052 (0.099)	NS
All records ($n = 766$)	0.879 df = 2	112.203 (0.000)	17.659 (0.001)	NS
Polypore records ($n = 499$)	0.760 df = 2	51.821 (0.000)	13.631 (0.002)	NS
Beetle records ($n = 103$)	0.071 df = 2	0.112 (0.742)	1.291 (0.272)	NS

R^2 denotes the proportion of variation explained by the model, and F statistics with p in parenthesis show the significance for explanatory variables.

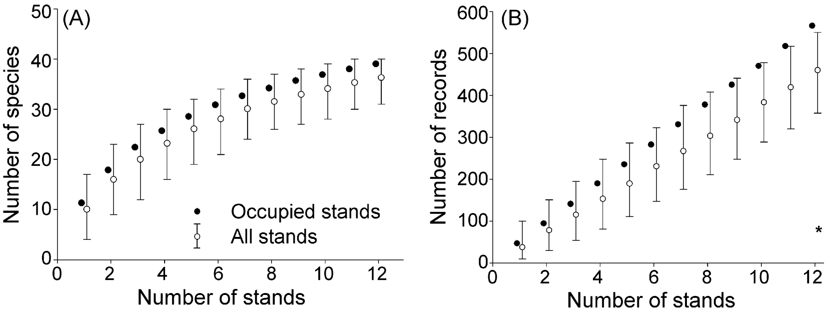


Fig. 2 – Resampling of the stands for the number of all species (A) and all records (B). Black circles show the mean of 1–11 stands randomly picked up from 12 stands occupied by the flying squirrel (the 12 occupied stands were not sampled), and open circles show the mean (with 95% CI bars) of 1–12 stands randomly picked up from the whole data of 20 stands. The number of records was significantly higher in 12 flying squirrel stands than in 12 sampled stands (*). Notice different Y-axes.

the equal number of randomly selected stands, but the difference was not statistically significant ($p = 0.163$) (Fig. 2A). Instead, the number of records was significantly higher in the occupied than in randomly sampled 12 stands (566 records versus 459.8 records, $p = 0.007$) (Fig. 2B).

According to the optimizations a minimum set of stands that included all species at least once included 10 stands and covered 90.2 ha (Fig. 3). With decreasing number of protected stands, also the number of species decreased. Most of the selected stands were occupied by the flying squirrel, particularly if only few stands were protected (Fig. 3). If we wish to include each of the 42 species at least twice (single observations as such) within the selected network of protected stands, a total of 112 ha would be needed, including 13 stands of which 8 were occupied by the flying squirrel. For a minimum of triple occurrences (single and double observations as such) the respective numbers are 138 ha including 15 stands, of which 10 were occupied by the flying squirrel.

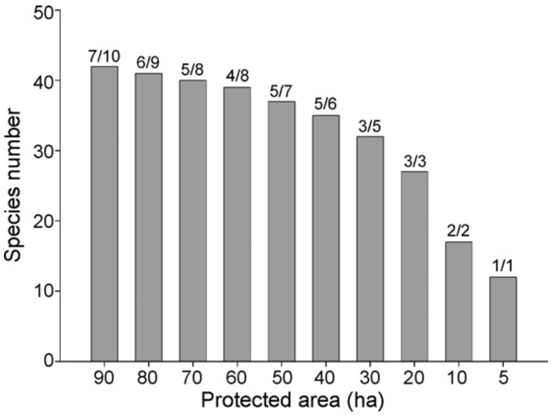


Fig. 3 – Results of the optimization analysis. The smaller the size of protected areas, fewer species will be included in it. All 42 species found in the study will be included to a protected area of 90 ha. The majority of the protected stands were occupied by the Siberian flying squirrel, see above bars: occupied stands/protected stands.

4. Discussion

The results showed that in our study area the flying squirrel may serve as an umbrella species for a group of red-listed and old-growth forest associated species. The volume of CWD was larger and the number of species and the number of records seemed to be higher in the forest stands occupied by the flying squirrel than in unoccupied stands. This relationship especially reflected the co-occurrence of the flying squirrel and polypore species. Even for a given amount of CWD the occurrence of the flying squirrel was associated with an increased likelihood of finding also other red-listed species. These patterns can be useful in forestry planning since nowadays total volume of CWD is routinely measured in forestry planning, and also the occurrence of the flying squirrel is usually noticed (the breeding sites of flying squirrels are protected, Rassi et al., 2001). These are intriguing findings because flying squirrels do not seem to need CWD as such: their diet mainly consists of leaves and catkins of deciduous trees as well as buds and green cones of conifers (Mäkelä, 1996), and the used cavities seem to be mainly in living aspens (Hanski, personal communication, 2006; Hurme, personal observations). Therefore, the occurrence of the flying squirrel most probably is an indirect cue for the forest structure: mature and especially older boreal forests often have both downed wood and cavity trees (Esseen et al., 1997).

A general phenomenon in our results was that the growing stock volume, the volume of CWD (Table 1) and the number of species (Table 2) tended to be higher in the stands occupied by the flying squirrel. We assumed that a tendency for higher growing stock volumes in the occupied stands, a source of dead wood in time, may be a sign of the productivity of the forest and as such have more general applications for forest management. However, it has to be remembered that substantial changes in productivity are also associated with changes in the tree species composition, which in turn affect to the composition of species assemblages (e.g., Sippola et al., 2004). Thus, the effect of productivity on the species diversity of a forest site should be assessed within the forest site type, not between them.

When focusing on different species groups, lichens and beetles did not show association with the occurrence of the flying squirrel, and the positive relationship in our study seemed to apply only to polypore species. In the case of lichens, the small number of target species may have influenced the results. Indeed, 69% of the variation in the number of polypore species was explained by the transect length, volume of downed spruce and by the occurrence of the flying squirrel, of which the flying squirrel alone explained 12%. While keeping the stand size and the volume of downed spruce in a stand constant, there were on average two polypore species (40%) more in an occupied stand than in an unoccupied stand. This indicates that the occurrence of flying squirrels most likely reflected an overall forest structure and thus the existing substrate for polypores, but may also be a sign of some other important features than only the volume of CWD.

From the site selection perspective our results suggested that if a set of protected stands was selected based on the presence of the flying squirrel, the network would encompass larger total populations (i.e., a larger number of records) of species dependent on CWD (Fig. 2B). Therefore, the flying squirrel could function as an umbrella for population viability of these species, since population size is a crucial determinant of the population persistence. Optimization analyses further suggested that if only a small number of stands can be selected for conservation due to limited resources, a useful strategy would be to select a stand occupied by the flying squirrel since that stand would probably include also more species in concern (Fig. 3). The utility of the umbrella species in the site selection hinges on the cross-taxon congruence, and co-variation in the species richness has been demonstrated among some taxa (e.g., MacNally and Fleishman, 2002; Moore et al., 2003; Su et al., 2004; Betrus et al., 2005; Similä et al., 2006). However, among the smaller vertebrates closest to our approach, the northern flying squirrel (*Glaucomys volans*) in southeastern Alaska did not qualify the criteria as an indicator species for other species in temperate rain forests (Smith et al., 2005).

Our findings on the relationship between the occurrence of the flying squirrel and other species, especially polypores, may also be related on the landscape connectivity since forest connections between suitable habitat patches enhance patch occupancy by the flying squirrel (Reunanen et al., 2002). As such, the presence of flying squirrels could indicate connected habitat networks also for other species that have limited dispersal abilities, a characteristic that may be difficult to measure directly from the landscape. For example, Komonen et al. (2000) found that the frequency of fruit bodies of a bracket fungus *Fomitopsis rosea*, an old-growth forest specialist, on suitable fallen spruce logs was lower in the forest fragments than in more continuous forests. Most of the spore deposition seem to fall close to the fruiting body (Nordén and Larsson, 2000; Edman et al., 2004a,b), even though spores of wood-decaying Basidiomycetes have been found to disperse for at least 3 km (e.g., Edman and Gustafsson, 2003). Information on beetle species dispersal is rather scanty but there is evidence of relatively good dispersal abilities among dead wood associated beetles (Nilssen, 1984; Jonsell et al., 2003; Jonsson, 2003).

van Langevelde et al. (2000) pointed out that a landscape sufficiently connected for the umbrella species should be functional for many other species (see also Bani et al., 2002). Since the knowledge of long-distance dispersal abilities of different species is scarce and we did not examine that aspect, we can only hypothesize that landscape configuration may affect on the distribution of species having limited dispersal abilities in a similar way as it does for flying squirrels. This would partly explain the positive association between polypores and the flying squirrel we observed. Further examination of an extended umbrella species concept (sensu Roberge and Angelstam, 2004) from the flying squirrel perspective for species, especially those demanding the connectivity of spruce-dominated forests due to relatively poor dispersal abilities, is needed.

General application of our results may be questioned because the positive relationship between the flying squirrel occurrence and the total number of species only applied to polypore species. However, polypores are an important part of the northern boreal forest ecosystem and compared with many other taxa also disproportionally threatened (Rassi et al., 2001). Consequently, the lack of association of the flying squirrel with lichens and beetles would not totally dismiss the potential role of the flying squirrel as an umbrella for biodiversity. One potential benefit of the umbrella species concept is related to the costs of surveying sites. In our study, surveying for the occurrence of the flying squirrel in 20 stands took about 2 working weeks whereas surveying and identifying the polypores, lichens and beetles took about 14 working months in total. The total survey costs for the flying squirrel occurrence were thus only a fraction of those for other taxa.

It is likely that no single species can function as an effective umbrella for overall biodiversity even at a regional scale. Several umbrella species should probably be considered simultaneously. Angelstam (1992) suggests that the existence of viable populations of three species, capercaillie, hazel grouse (*Bonasa bonasia*) and white-backed or three toed woodpecker (*Picoides tridactylus*), would indicate sufficient resources to accommodate a typical bird species community in a boreal forest landscape in Fennoscandia. In Finland, there is evidence to support the use of capercaillie (Pakkala et al., 2003) and white-backed woodpecker (Martikainen et al., 1998) as umbrella species. Capercaillie has large area requirements of closed canopy forests, especially pine-dominated older forests also essential for other old-growth forest bird species. The white-backed woodpecker prefers extensive birch forests with large amount of dead wood fostering a rich beetle community, particularly beetles dependent on dead birch. We suggest that this list could be supplemented by the flying squirrel, whose existence could be a surrogate at least for polypore species and relatively well connected mature spruce-dominated forests in the landscapes in northern Finland.

Our results cannot, however, be generalized to other regions without further study (see also Ricketts et al., 1999; Simberloff, 1999; Roberge and Angelstam, 2004). Even though flying squirrels seem to prefer similar habitat characteristics thorough out its range in Finland (Mönkkönen et al., 1997; Hanski, 1998; Selonen et al., 2001), particularly in southern parts of Finland, they may also inhabit middle-aged mixed forests and even relatively urban forests such as city parks. Therefore, careful generalization should be considered only to forests that have relatively similar forest management history than the forests in our study (see also Stockland, 2001).

To summarize, our results from northern Finland suggested a potential of the flying squirrel as an umbrella species for mature spruce-dominated forests and especially for polypore species, probably also for other wood-dependent species, within the study region. We also see two possible applications for landscape management planning. First, flying squirrels may assist in site selection, i.e., assigning stands for protection versus harvesting. Second, related to the extended umbrella species concept the presence of the flying squirrel may be used to assess the landscape connectivity needed to ensure species diversity, especially in terms of a habitat network. These applications need further research, but we suggest that the flying squirrel could supplement the effectiveness of a larger group of umbrella species and thereby enhance landscape management for general biodiversity in boreal forests.

Acknowledgments

We are grateful for Ulla Vuoti, Teppo Kuusela, Damien Cocatré, Minna Sankari, Jukka Forsman and Petri Kärkkäinen for their help in the field. The staff of Zoological Museum at University of Oulu is highly acknowledged for making the cylinder traps and preparing the beetle trap samples for further identification, and the Arctic Centre at the University of Lapland for borrowing the trunk window traps. We also received excellent help for some identification problems from Matti Kulju, Tuomo Niemelä and Petri Martikainen. Metsähallitus kindly provided the forest planning data, and the Ministry of Agriculture and Forestry of Finland financed the study (Project 25058).

Appendix A

Red-listed (EN = endangered, VU = vulnerable, NT = near threatened) and old-growth forest associated species found from the 20 stands, and the number of records in stands according to the occurrence of the Siberian flying squirrel.

	Red-list status	Number of records	
		Occupied	Unoccupied
Polypore species			
Amylocystis lapponica (Romell) Singer	VU	11	4
Antrodia albobrunnea (Romell) Ryvarden	NT	6	0
Antrodia pulvinascens (Pilát) Niemelä	VU	3	0
Antrodiella citrinella Niemelä & Ryvarden	VU	1	0
Cinereomyces lenis (<*Skeletocutis lenis*) (P. Karst.) Spirin	VU	5	1
Diplomitoporus crustulinus (Bres.) Domański	NT	3	0
Fomitopsis rosea (Alb. & Schwein.: Fr.) P. Karst.	NT	5	1
Junghuhnia collabens (Fr.) Ryvarden	VU	1	0
Junghuhnia luteoalba (P. Karst.) Ryvarden		1	0
Leptoporus mollis (Pers.: Fr.) Quél.		2	0
Oligoporus lateritius (<*Postia lateritia*) (Renvall) Ryvarden & Gilb.	VU	2	0
Oligoporus sericeomollis (Romell) Bondartseva		1	1
Phellinus chrysoloma (Fr.) Donk		36	9
Phellinus ferrugineofuscus (P. Karst.) Bourdot	NT	6	1
Phellinus lundellii Niemelä		16	2
Phellinus nigrolimitatus (Romell) Bourdot & Galzin		32	15
Phellinus pini (Brot.: Fr.) A. Ames		1	0
Phellinus viticola (Schwein.: Fr.) Donk		254	72
Skeletocutis brevispora Niemelä	VU	0	1
Skeletocutis odora (Sacc.) Ginns	NT	1	0
Skeletocutis stellae (Pilát) Jean Keller	VU	3	2
Lichen species			
Lobaria pulmonaria (L.) Hoffm.		1	0
Nephroma bellum (Spreng.) Tuck.		92	34
Nephroma parile (Ach.) Ach.		4	1
Nephroma resupinatum (L.) Ach.		12	5
Pannaria pezizoides (Weber) Trevisan		12	3
Beetle species			
Acmaeops septentrionis (Thomson)	VU	6	13
Agathidium pallidum (Gyllenhal)	NT	5	1
Atomaria abietina Reitter	NT	1	0
Atomaria elongatula Erichson	NT	3	0
Atrecus longiceps (Fauvel)	NT	4	1
Cercyon emarginatus Baranowski	NT	1	2
Cryptophagus lysholmi Munster	NT	15	2
Cyphea latiuscula Sjöberg	NT	4	12
Enicmus apicalis J.Sahlberg	NT	6	1
Euclilodes caucasicus (Reitter)	VU	3	1

Appendix A *(Continued)*

Lacon conspersus (Gyllenhal)	NT	0	1
Lacon fasciatus (Linnaeus)	NT	0	1
Peltis grossa (Linnaeus)	NT	1	1
Pseudeulgenes pentatomus (Thomson)	NT	1	0
Ptiliolum caledonicum (Sharp)	NT	4	8
Quedius lundbergi Palm	EN	2	3

REFERENCES

Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. Ann. Bot. Fenn. 5, 169–211.

Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proc. Natl. Acad. Sci. U.S.A. 97, 5954–5959.

Angelstam, P., 1992. Conservation of communities—the importance of edges, surroundings and landscape mosaic structure. In: Hansson, L. (Ed.), Ecological Principles of Nature Conservation, Applications in Temperate and Boreal Environments. Elsevier Science Publishers, UK, pp. 9–70.

Bani, L., Baietto, M., Bottoni, L., Massa, R., 2002. The use of focal species in designing a habitat network for a lowland area of Lombardy, Italy. Conserv. Biol. 16, 826–831.

Berger, J., 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. Conserv. Biol. 11, 69–78.

Betrus, C.J., Fleishman, E., Blair, R.B., 2005. Cross-taxonomic potential and spatial transferability of an umbrella species. J. Environ. Manage. 74, 79–87.

Blank, S., Seiter, C., Bruce, P., 2001. Resampling Stats Add-in for Excel. Resampling Stats, Inc., USA, 172 pp.

Bonn, A., Schröder, B., 2001. Habitat models and their transfer for single and multi species groups: a case study of carabids in an alluvial forest. Ecography 24, 483–496.

Cabeza, M., Moilanen, A., 2001. Design of reserve networks and the persistence of biodiversity. Trends. Ecol. Evol. 16, 242–248.

Caro, T.M., 2003. Umbrella species: critique and lessons from East Africa. Anim. Conserv. 6, 171–181.

Caro, T.M., O'Doherty, G., 1999. On the use of surrogate species in conservation biology. Conserv. Biol. 13, 805–814.

Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the Rocky Mountain Region. Ecol. Appl. 11, 961–980.

Edman, M., Gustafsson, M., 2003. Wood-disk traps provide a robust method for studying spore dispersal of wood-decaying basidiomycetes. Mycologia 95, 553–556.

Edman, M., Gustafsson, M., Stenlid, J., Ericson, L., 2004a. Abundance and viability of fungal spores along a forestry gradient—responses to habitat loss and isolation. Oikos 104, 35–42.

Edman, M., Gustafsson, M., Stenlid, J., Jonsson, B.G., Ericson, L., 2004b. Spore deposition of wood-decaying fungi: importance of landscape composition. Ecography 27, 103–111.

Esseen, P.-A., Ehrnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forest. Ecol. Bull. 46, 16–47.

Fleishman, E., Murphy, D.D., Brussard, P.F., 2000. A new method for selection of umbrella species for conservation planning. Ecol. Appl. 10, 569–579.

Fleishman, E., Blair, R.B., Murphy, D.D., 2001. Empirical validation of a method for umbrella species selection. Ecol. Appl. 11, 1489–1501.

Hanski, I., 1999. Metapopulation Ecology. Oxford University Press, UK, 313 pp.

Hanski, I.K., 1998. Home ranges and habitat use in the declining flying squirrel *Pteromys volans* in managed forests. Wildl. Biol. 4, 33–46.

Hanski, I.K., Stevens, P., Ihalempiä, P., Selonen, V., 2000. Home range size, movements and nest site use in the Siberian flying squirrel *Pteromys volans*. J. Mammal. 81, 798–809.

Hurme, E., Mönkkönen, M., Nikula, A., Nivala, V., Reunanen, P., Heikkinen, T., Ukkola, M., 2005. Building and evaluating predictive occupancy models for the Siberian flying squirrel using forest planning data. For. Ecol. Manage. 216, 241–256.

Ilmatieteenlaitos, 2003. Ilmastokatsaus. Ilmatieteen laitos, Helsinki, Finland (in Finnish).

Jahns, H.M., 1996. Sanikkaiset, sammalet ja jäkälät, third ed. Otava, Keuruu, Finland, 262 pp. (in Finnish).

Jonsell, M., Schroder, M., Larsson, T., 2003. The saproxylic beetle *Bolitophagus reticulates*: its frequency in managed forests, attraction to volatiles and flight period. Ecography 26, 421–428.

Jonsson, M., 2003. Colonisation ability of the threatened beetle *Oplocpehala haemorrhoidalis* and its common relative *Bolitophagus reticulates*. Ecol. Entomol. 28, 159–167.

Kaila, L., 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomol. Fenn. 4, 21–23.

Kerr, J.T., 1997. Species richness, endemism, and the choice of areas for conservation. Conserv. Biol. 11, 1094–1100.

Komonen, A., Penttilä, R., Lindgren, M., Hanski, I., 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. Oikos 90, 119–126.

Kotiranta, H., Niemelä, T., 1996. Uhanalaiset käävät Suomessa, second ed. Suomen ympäristökeskus, Edita, Helsinki, 184 pp. (in Finnish).

Laasasenaho, J., Snellman, C.-G., 1983. Männyn, kuusen ja koivun tilavuustaulukot. Metsäntutkimuslaitoksen tiedonantoja 113, Finland, 91 pp. (in Finnish).

Lambeck, R.J., 1997. Focal species: a multi-species umbrella for nature conservation. Conserv. Biol. 11, 849–856.

Landres, P.B., Verner, J., Thomas, J.W., 1988. Ecological uses of vertebrate indicator species: a critique. Conserv. Biol. 2, 316–325.

Launer, A.D., Murphy, D.D., 1994. Umbrella species and the conservation of habitat fragments: a case of a threatened butterfly and a vanishing grassland ecosystem. Biol. Conserv. 69, 145–153.

Legendre, P., Legendre, L., 1998. Numerical Ecology, second ed. Elsevier Science, Amsterdam, Netherlands, 353 pp.

Lindenmayer, D.B., Manning, A.D., Smith, P.L., Possingham, H.P., Fischer, J., Oliver, I., McCarthy, M.A., 2002. The focal-species approach and landscape restoration: a critique. Conserv. Biol. 16, 338–345.

MacNally, R., Fleishman, E., 2002. Using ''indicator'' species to model species richness: model development and predictions. Ecol. Appl. 12, 79–92.

MacNally, R., Bennett, A.F., Brown, G.W., Lumsden, L.F., Yen, A., Hinkley, S., Lillywhite, P., Ward, D., 2002. How well ecosystem-based planning units represent different components of biodiversity? Ecol. Appl. 12, 900–912.

Martikainen, P., Kaila, L., Haila, Y., 1998. Threatened beetles in white-backed woodpecker habitats. Conserv. Biol. 12, 293–301.

Martikainen, P., 2000. Effects of Forest Management on Beetle Diversity, With Implications for Species Conservation and Forest Protection. Dissertation. University of Joensuu, Finland.

Moore, J.L., Balmford, A., Brooks, T., Burgess, N.D., Hansen, L.A., Rahbek, C., Williams, P.H., 2003. Performance of sub-Saharan vertebrates as indicator groups for identifying priority areas for conservation. Conserv. Biol. 17, 207–218.

Mäkelä, A., 1996. Liito-oravan (Pteromys volans L.) ravintokohteet eri vuodenaikoina ulosteanalyysin perusteella. In: Liito-oravatyöryhmä (Eds.), Liito-orava Suomessa, vol. 8Maailman Luonnonsäätiö WWF:n raportti, Finland, pp. 54–58 (in Finnish).

Mönkkönen, M., Reunanen, P., Nikula, A., Inkeröinen, J., Forsman, J., 1997. Landscape characteristics associated with the occurrence if the flying squirrel *Pteromys volans* in old-growth forests of northern Finland. Ecography 20, 634–642.

Niemelä, T., 2005. Käävät—puiden sienet. Norrlinia 13, 1–320 (in Finnish with English summary Polypores, lignicolous fungi).

Nilssen, A.C., 1984. Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. Ann. Entomol. Fenn. 50, 37–42.

Nordén, B., Larsson, K.-H., 2000. Basidiospore dispersal in the old-growth forest fungus *Phlebia centrifuga* (Basidiomycetes). Nord. J. Bot. 20, 215–219.

Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conserv. Biol. 4, 355–364.

Noss, R.F., Quigley, H.B., Hornocker, M.G., Merrill, T., Paquet, P.C., 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conserv. Biol. 10, 949–963.

Pakkala, T., Pellikka, J., Lindén, H., 2003. Capercaillie *Tetrao urogallos*: a good candidate for an umbrella species in taiga forest. Wildl. Biol. 9, 309–316.

Poiani, K.A., Merrill, M.D., Chapman, K.A., 2001. Identifying conservation-priority areas in a fragmented Minnesota landscape based on the umbrella species concept and selection of large patches of natural vegetation. Conserv. Biol. 15, 513–522.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK, 537 pp.

Rassi, P., Alanen, A., Kanerva, T., Mannerkoski, I., 2001. Suomen lajien uhanalaisuus 2000. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, Finland, 432 pp. (in Finnish with English summary).

Reunanen, P., Mönkkönen, M., Nikula, A., 2000. Managing boreal forest landscapes for flying squirrels. Conserv. Biol. 14, 218–226.

Reunanen, P., Mönkkönen, M., Nikula, A., 2002. Habitat requirements of the Siberian flying squirrel in northern Finland: comparing field survey and remote sensing data. Ann. Zool. Fenn. 39, 7–20.

Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C., 1999. Who's where in North America? BioScience 49, 369–381.

Roberge, J.-M., Angelstam, P., 2004. Usefulness of umbrella species concept as a conservation tool. Conserv. Biol. 18, 76–85.

Rondinini, C., Boitani, L., 2006. Differences in the umbrella effects of African amphibians and mammals based on two estimators of the area of occupancy. Conserv. Biol. 20, 170–179.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK, 436 pp.

Rubinoff, D., 2001. Evaluation the California gnatcatcher as an umbrella species for conservation of southern California coastal sage scrub. Conserv. Biol. 15, 1373–1383.

Selonen, V., Hanski, I.K., Stevens, P., 2001. Space use of the Siberian flying squirrel *Pteromys volans* in fragmented landscapes. Ecography 24, 588–600.

Sergio, F., Newton, I., Marchesi, L., 2005. Top predators and biodiversity. Nature 436, 192.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol. Bull. 49, 11–41.

Silfverberg, H., 2004. Enumeratio nova Coleopterorum Fennoscandiae, Daniae et Baltiae. Sahlbergia 9, 1–111.

Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol. Conserv. 83, 247–257.

Simberloff, D., 1999. The role of science in the preservation of forest biodiversity. For. Ecol. Manage. 115, 101–111.

Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.-L., Huhta, E., 2006. Co-variation and indicators of species diversity: can richness of forest-dwelling species be predicted in northern boreal forests? Ecol. Indicat. 6, 686–700.

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. Ecol. Bull. 49, 243–254.

Sippola, A.-L., Similä, M., Mönkkönen, M., Jokimäki, J., 2004. Diversity of polyporous fungi (Polyporaceae) in Northern Boreal Forests: effects of forest site type and logging intensity. Scand. J. For. Res. 19, 152–163.

Smith, W.P., Gende, S.M., Nichols, J.V., 2005. The northern flying squirrel as an indicator species of temperate rain forest: test of a hypothesis. Ecol. Appl. 15, 689–700.

Stockland, J.N., 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecol. Bull. 49, 71–83.

Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conserv. Biol. 18, 167–173.

Suter, W., Graf, R.-F., Hess, R., 2002. Capercaillie (*Tetrao urogallos*) and avian biodiversity: testing umbrella-species concept. Conserv. Biol. 16, 778–788.

van Langevelde, F., Schotman, A., Claassen, F., Sparenburg, G., 2000. Competing land use in the reserve site selection. Landscape Ecol. 15, 243–256.

Watson, J., Freudenberger, D., Paull, D., 2001. An assessment of the focal-species approach for conserving birds in variegated landscapes in southeastern Australia. Conserv. Biol. 15, 1364–1373.