Breeding bird distribution in fragmented coniferous taiga in southern Finland

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We censused breeding birds in 35 fragments of old coniferous taiga (area range 0.4–101 ha), surrounded by clear-cuts and young managed forests, in southern Finland. The data are analyzed both at the community and at the species population level. Habitats in the fragments comprised fairly barren and uniform pine-spruce forests; the influence of habitat variation on the fragments' breeding communities was slight. The fragments were divided into four size classes. Species richness, analyzed by rarefaction, is highest in 6–16 ha fragments; individual small (<16 ha) fragments tend to have higher species numbers than predicted by rarefying the pooled sample of the large (50 ha) fragments. Distribution of breeding pairs in the fragments agrees with the random placement model. No "area effects" *sensu* the MacArthur–Wilson equilibrium hypothesis were detected. However, the communities in small fragments differ from those in large fragments, the most important difference being a high proportion and density of edge species in the former.

Scarce species tend to be sparse in small (<6 ha) fragments, but they occur in the size class 6–16 ha as frequently as expected on the basis of their occurrence in the largest (50 ha) fragments. When the observed population sizes in small fragments were compared with expectations based on densities in the largest fragments, the dominating patterns were found to be (1) agreement between observations and expectations, and (2) increased density of edge species in small fragments. Woodpeckers tend to be scarce in the small (<6 ha) fragments, and two hole-nesting passerines (*Phoenicurus phoenicurus* and *Parus major*) seem to avoid small fragments as well, presumably owing to a scarcity of suitable nest-holes. The density of hole-nesters shows a positive correlation with snag density in the fragments, but not with the fragment area.

We conclude that abundant taiga birds maintain breeding populations in a mosaically fragmented forest-management area where the size of old forest fragments is some tens of hectares, but crucial research problems for conservation ecology in the long run are (1) effects of forest management through changing proportions of different successional stages on the regional scale, and (2) dynamics of individual bird populations, particularly scarce habitat specialists, in human-made fragment archipelagoes.

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Introduction

Fragmentation of formerly continuous natural habitats has considerable importance for nature conservation (e.g. Burgess & Sharpe 1981, Harris 1984, Soulé 1986, Usher 1986). Fragmentation means that the average area of natural habitat patches decreases and, as the spatial configuration of the remaining fragments is different from the contiguous distribution in the past, the conditions for subsistence of populations in the area may change as well. Fragmentation thus calls attention to two particular ecological research problems: First, how do new habitats, created by human activities, differ from old, natural ones? And how numerous are species that can survive only in the original environmental types? Second, what is the effect of fragmentation *per se* on the probable future of those populations that are entirely dependent on natural habitats?

A widely applied conceptual frame in studies on consequences of habitat fragmentation was provided by MacArthur & Wilson (1967) in their theory of island biogeography. The application is based on the analogue of regarding habitat fragments as islands that are surrounded by a hostile "sea" of human-modified environments. However, the analogue between islands and habitat fragments is not necessarily valid (Niemelä & Haila 1986, Wilcove et al. 1986). Many terrestrial organisms that mainly reside in natural habitats can survive and reproduce in human-modified environments, which makes immigration and extinction rates in habitat fragments very different from those in real island situations.

The problem is accentuated if the equilibrium hypothesis is applied to communities of migratory birds. As they leave the islands each autumn and "recolonize" in the spring, immigration and extinction cannot be interpreted as population processes, and the equilibrium hypothesis is ecologically meaningless (Haila et al. 1982, Haila 1983a, 1986).

In this paper we summarize the results of breeding bird censuses conducted in fragments of coniferous *taiga* forests in southern Finland. The study was designed as a survey (as in Haila & Hanski 1984), namely, our aim was to investigate the distribution of breeding birds in this habitat archipelago to detect the possible consequences of habitat fragmentation. We analyze the data both on the level of species assemblages and individual populations, and discuss the significance of the results for nature conservation.

Materials and methods

Study area

Our study area is situated in the Seitseminen National Park and its surroundings in southern Finland (61° 55' N, 23° 30' E). Phytogeographically the area lies slightly south of the border between the south-boreal and mid-boreal zones of Ahti et al. (1968). Relatively barren mixed coniferous (*Pinus sylvestris* and *Picea abies*) forests of the Cajanderian Myrtillus - forest type abound, and deciduous forests are very sparse. In the ornithogeographic zonation of Järvinen & Väisänen (1980) our study area belongs to the south-boreal zone. In other words, it shares with the rest of southern Finland a common species pool from which the breeding community is derived. However, the composition of the actual communities is decisively constrained by habitats, and in the Seitseminen area species of deciduous and cultural habitats are scarce.

On a regional scale there is a clear difference between habitats and landscapes of the Seitseminen area and areas some tens of kilometers to the south. The Seitseminen area is both climatically and edaphically less suitable for agriculture and, consequently, cultural influence has been slight. The area has traditionally been the southernmost tip of a peninsular "wilderness" stretching from the north toward old agricultural areas of northern Häme.

Intensive forest management began in the region in the 1950s, and nowadays the forests comprise a mosaic of relatively uniform stands of varying age, created by clear-cuts. The proportion of old forests (>140 yrs) is 0.5%, and that of young forests (<60 yrs) is 50% of the total forest land (Yearbook of forest statistics 1984). The Seitseminen National Park (total area 31.6 km^2) is a mosaic of managed forests as well, due to intensive forestry in the area during the 1970s before the park was established in 1982, but in the central parts of the park there are several woods of primeval taiga.

For our census work we selected 35 forest "islands", called "fragments" below, with an area range of 0.4–101 ha, so that they would be as distinct from surrounding successional habitats as possible. Areas of the fragments were calculated from topographic maps (1:20 000) and aerial photographs. Twenty of the fragments are situated within the national park, and the rest lie within 10 km from the central parts of the park.

We grouped the forest fragments into four size classes: less than 3 ha (18 fragments, total area 28.5 ha), 3–6 ha (7 fragments, total area 27.5 ha), 6–16 ha (7 fragments, total area 89.9 ha) and large fragments (49.2, 55.8 and 101 ha). The fragments and their surroundings are characterized in Appendix 1; as forest fragments do not bear names on topographic maps, we refer to them in the following by codes that also indicate the size class in which they belong (i.e., XS1–XS18, S19–S25, M26–M32, and L33–L35).

Census methods

Each forest fragment was censused as a study plot by searching through the whole area during each census visit, with two observers participating in the censuses in the large fragments. All three of us participated in censuses in all four fragment size classes. The time spent per area unit was approximately constant during all census visits, about 1 hr/5 ha in fragments larger than 3 ha and somewhat longer in the smallest fragments (minimum time spent in the smallest fragments was 10–15 minutes per visit). L35 (101 ha) was the only exception; due to its large area, it was censused by 4.3 km of line transects. Fifteen of the smallest fragments were visited four times, and the rest of the fragments twice (see Appendix 1). All fragments except XS1 and XS4 were visited before the first census, and the larger ones were marked with coordinates to facilitate exact location of observed pairs.

During each visit observations were marked on maps, and particular attention was paid to getting simultaneous records of conspecific birds. Final estimates of numbers of breeding pairs were reached by inspecting the maps similarly to a mapping census (but for the two-visit fragments the higher of the two figures was in practice accepted). The efficiency of our censuses is, however, certainly lower than in a standard mapping census. In the two-visit fragments it is close to the efficiency of one-visit censuses on small real islands (i.e., about 70%, Haila & Kuusela 1982). One-visit censuses make distinguishing "transients", non-breeding visitors, from territorial pairs impossible. The main reason we made four census visits to the small fragments was to exclude transients from the data; only pairs observed in at least two censuses were accepted on the list of the four-visit fragments. We compared pooled lists of the four-visit fragments as estimated by (1) using all the visits (Appendix 2), and (2) using only two of the visits. The first list includes 115 pairs of 20 species, and the second 141 pairs of 26 species. Transients seem to be fairly common in the fragments. The methodological difference in our censuses in small and large fragments makes their comparisons conservative as regards impoverishment; data from large fragments include more transients than those from small fragments.

Because of stochastic variation inherent in the colonization of small habitat fragments by migratory birds (see Haila 1983a, 1986), we use in the analyses pooled data from groups of fragments, formed on *a priori* grounds.

The censuses were made between 15 May and 25 June 1985. The overall census results of the two census periods (17 two-visit fragments, total area 155.4 ha) were remarkably similar, as shown by the tabulation below:

	15–25 May	5–15 June
Number of pairs	494	485
Number of species	37	36
Fringilla coelebs	104	105
Carduelis spinus	69	51
Parus spp.	50	58
Phylloscopus spp.	44	46

The virtual identity of the two data sets supports our conclusion that the efficiency of our censuses is sufficient for comparisons and for analyses of pooled data.

In addition to the censuses in the forest fragments we censused 27 km of line transects within the Seitseminen National Park in early June.

The habitat space

In northern conditions at least, habitat structure of islands or insular habitat fragments has a decisive influence on the composition of bird communities breeding there (Haila 1983a, 1983b, Haila et al. 1983). We described habitats of the fragments by the 0.04 ha circle areal sampling method of James & Shugart (1970). One circle per hectare of fragment area was randomly placed in each fragment (with a minimum number of five circles in all fragments). In each circle we estimated the number of trees (four size classes: breast height diameter 3–8, 8–16, 16–48 and >48 cm, four groups of species); number of coniferous and deciduous saplings; canopy height (m) and foliage cover (%, based on 20 vertical point-sightings); cover of main vegetation types in the field layer (index values 0–5, logarithmic scale); and the horizontal thickness of the habitat by recording the visibility of a three-meter stick, erected in the middle of the circle, from four points on the circumference (index 0–5, logarithmic scale). In addition, we estimated snag densities along transects that were walked through the fragments or, in the small fragments up to 5 ha in size, by counting all snags.

Composition of breeding bird communities in small forest fragments may be influenced by surrounding habitats (Ambuel & Temple 1983, Helle 1984, 1985). We made descriptions of habitats in the immediate surroundings of all fragments up to 4.0 ha in area included in our study as follows: First we decided, by using aerial photographs, how many different environment types can be found in the immediate surrounding of each of the small fragments. This was relatively straightforward thanks to the uniformity of managed young forests; the numbers ranged from one to three. Descriptions were made in each of these types along a 200 m transect (5 m wide) that ran along the sides of a 50 m square, with each of the sides forming one description unit. Variables estimated were the number of trees (four size classes: height 3–8, 8–15, 15–25 and >25 m, four groups of species); canopy height (m) and foliage cover (%); thickness of the sapling and bush layer (by an index ranging from 0 to 3); dominating vegetation type in the field layer; and the number of snags.

For reasons of time economy the descriptions in the fragment surroundings were less detailed than those in the inner parts of the fragments. However, the averages differ greatly as shown in the following tabulation:

	Inner parts (380 points)	Surroundings (172 "units")
Number of trees/0.04 ha		
small	9.5	45.7
intermediate	10.5	6.6
large	10.8	1.6
"giants"	0.08	0
Proportion of birch (%)	12	21
Proportion of spruce (%)	70	6
Foliage height (m)	19.9	6.1
Foliage cover (%)	70	30

The surroundings mainly comprise young stages of secondary succession and young pine plantations.

We examined the pattern of variation in the habitat structure of the fragments by principal component analysis (PCA, using the standard procedure of the BMDP statistical package). We used PCA in a purely explorative fashion to compare habitat variation within individual fragments with variation over all the 35 fragments. We tried several combinations of the original variables and accepted as a basis for comparisons a two-axis model incorporating six variables: foliage height; foliage cover (in percentage); the total number of spruce trees; the percentage of spruce; the percentage of coniferous saplings; and horizontal thickness. For percentages we used the transformation $\log_{10}((x+1)/(101-x))$, suggested by James & Warner (1982). The first component in the ordination is correlated positively with the number of spruce trees and foliage cover, and the second component is correlated positively with thickness of the bush layer and negatively with foliage height.

Next we inspected the location of individual fragments in the PCA-ordination, and the result is shown in Fig. 1. Two conclusions emerge: First, the midpoints of the large fragments are very close to the midpoint of the ordination as a whole, but variance is smaller than in the whole habitat space. In other words, habitat structure tends to be more uniform in the large fragments than in the small ones. Second, the ordination helps to identify a few small fragments that deviate from the average habitat structure (note that at least five description points were made in each fragment). Three groups of small fragments situated "at some distance" from the midpoint of the ordination can be identified (see Fig. 1). We use the combined data of these fragments to check whether variation in habitats of the fragments influences the composition of their breeding assemblages.

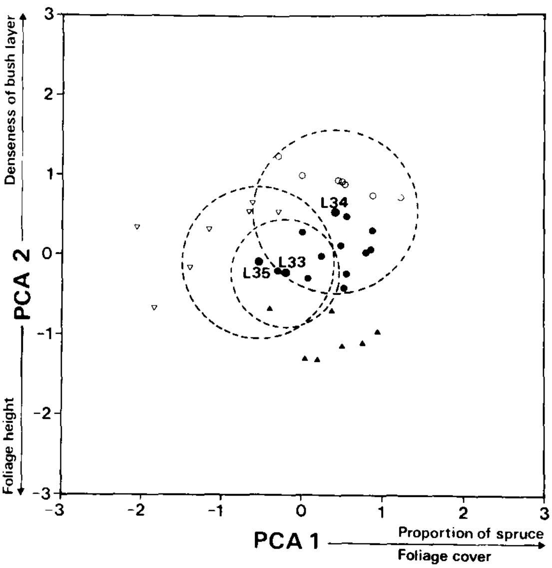

Fig. 1. The location of individual fragments in a PCA-ordination space, based on the habitat descriptions. The axes are scaled in SD-units, which indicates the dispersion of the normally distributed description points (n=186) in the ordination space. Each symbol indicates the average of the description points of individual fragments; an ellipsoid of one standard deviation is shown for the three largest fragments. Fragments with a "somewhat" deviating habitat structure are indicated by symbols: "bush fragments" (open circles), "pine fragments" (open triangles), and "spruce fragments" (black triangles).

The habitat description data from the fragment surroundings were subjected to principal component analysis as well. We accepted a three-axis solution incorporating seven variables; the first component is correlated positively with the frequency of birch, the second one with the frequency of pine, and the third one with foliage height and cover. We used both factor scores of these three components and the values of the original variables to trace such small fragments that have particularly dense habitats in their surroundings. These are characterized in Appendix 1.

Community characteristics

Fragment size classes

The census data are given in Appendix 2. In the 34 fragments censused as study plots we observed 930 pairs of 45 species. The total area of the fragments is 251 ha, which gives an average density of 370.7 pairs/km^2. In addition, 186 pairs of 29 species were observed in the 4.3 km of line transects in the fragment L35, and the line transect estimate of overall density was 237 pairs/km^2 (using the formulae of Järvinen & Väisänen 1983).

The numbers of pairs and species in individual fragments range from 0 (fragment XS2, 0.5 ha) to 172 pairs of 31 species (fragment L34, 55.8 ha). The data naturally show a strong positive correlation between fragment area and species number.

First we investigate variation in species numbers in the four fragment size classes introduced above (fragments XS1–XS18, area range 0.4–3.0 ha; S19–S25, range 3.1–5.4 ha; M26–M32, range 8.4–15.8 ha; and L33–L34, range 49.2–55.8 ha). These pooled data sets are shown in Table 1.

There is variation in average density in the four fragment size classes, the density in the largest size class being lower than in the others. This difference is highly significant (M vs. L, G-test, P<0.001). The high estimate for the size class XS may be partly due to an unrealistically small denominator in the density calculations. We calculated average densities relative to the area of the fragments, but territories of the breeding pairs may partly include fragment surroundings and, consequently, the estimates may be inflated.

Rarefaction is a statistical method that facilitates comparing species numbers in samples of varying size; it gives expected species numbers in subsamples drawn randomly from the original samples. By drawing successively smaller subsamples, rarefaction curves can be constructed (see Simberloff 1978, James & Rathbun 1981).

Rarefaction curves of the pooled communities of the four fragment size classes are shown in Fig. 2. The highest curve (class M) is the only one that differs significantly from the others (t-test, P<0.01; tested at the end points of the other curves). The two smallest size classes are virtually identical in terms of species numbers. The largest size class shows a tendency to higher species numbers than the smallest classes, but the difference is not statistically significant.

We checked the pattern by comparing the observed species number of each fragment in the three smaller size classes with an expectation estimated by rarefaction from the sample of the largest size class. The comparison is shown in Fig. 3. Four of the differences are statistically significant (P<0.05); of these four fragments, three had a higher species number than expected, and one had a lower one. For the fragment XS2 (no breeding pairs observed) the comparison is meaningless, but for the

Table 1. Pooled samples of the fragment size classes (fragment L35 is excluded).

Species	XS (<3 ha)	S (3–6 ha)	M (6–16 ha)	L (50 ha)
Accipiter gentilis	0	0	0	1
A. nisus	0	0	1	0
Bonasa bonasia	2	0	3	7
Tetrao tetrix	1	0	3	0
T. urogallus	1	0	1	1
Tringa ochropus	0	0	1	1
Scolopax rusticola	0	0	2	0
Columba palumbus	0	1	3	1
Cuculus canorus	0	1	2	5
Aegolius funereus	0	0	0	1
Strix uralensis	0	0	1	0
Apus apus	0	0	1	2
Jynx torquilla	0	1	1	0
Picoides tridactylus	0	0	1	2
Dendrocopos major	0	1	5	7
Dryocopus martius	0	0	2	3
Anthus trivialis	4	2	11	4
Motacilla alba	0	0	0	1
Prunella modularis	3	2	8	8
Erithacus rubecula	6	4	19	15
Phoenicurus phoenicurus	2	0	4	13
Turdus philomelos	4	2	1	8
T. iliacus	0	0	3	2
T. viscivorus	1	0	1	3
Sylvia curruca	0	0	1	0
S. borin	0	0	2	1
Phylloscopus sibilatrix	1	0	5	0
Ph. collybita	4	4	5	3
Ph. trochilus	13	8	20	13
Regulus regulus	11	9	29	24
Muscicapa striata	6	8	20	30
Ficedula hypoleuca	4	1	14	19
Parus montanus	8	5	13	5
P. cristatus	3	6	11	8
P. major	1	2	17	17
Certhia familiaris	3	2	12	11
Garrulus glandarius	1	1	2	1
Corvus corax	0	0	0	1
Fringilla coelebs	27	20	65	59
F. montifringilla	1	0	12	0
Carduelis spinus	29	23	37	33
Loxia spp.	0	1	1	3
Pyrrhula pyrrhula	2	4	10	8
Emberiza citrinella	0	0	1	0
E. rustica	0	0	3	0
Number of pairs	138	108	363	321
Number of species	24	22	41	35
Density (pairs/km^2)	488	484	393	306

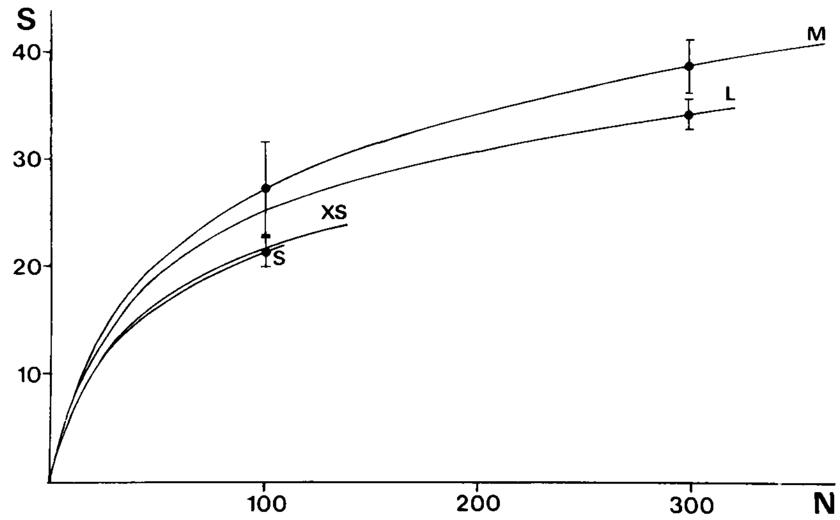

Fig. 2. Rarefaction curves derived from the pooled data sets of the four fragment size classes (area ranges: XS 0.4–3.0 ha; S 3.1–5.4 ha; M 8.4–15.8 ha; L 49.2–55.8 ha, L35 excluded). The vertical bars indicate ± 2 SD.

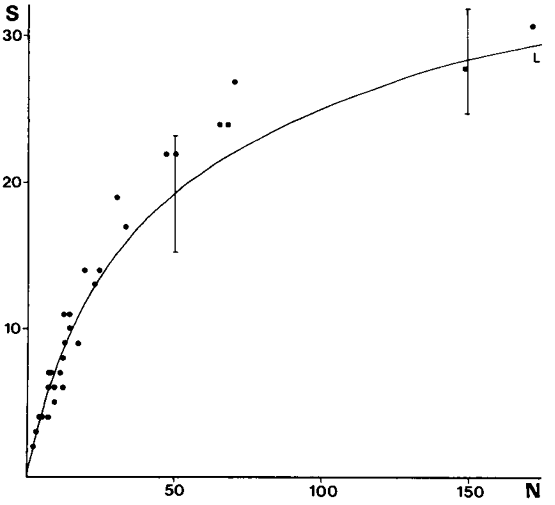

Fig. 3. A comparison of the observed species number in individual small fragments (size classes XS, S and M) with the rarefaction curve of the large fragments, L33 and L34. The vertical bar indicates ± 2 SD.

remaining 31 fragments there is a slight tendency toward a higher observed species richness than expected (22 positive deviations vs. 9 negative ones, $P<0.05$, G-test). The tendency is similar, but statistically not significant, for the smallest size class (17 comparisons with XS2 excluded: 11 positive deviations vs. 6 negative ones).

To summarize, species richness in any single fragment tends to be higher than expected in a similar sized random sample from the pooled data of the size class L. However, when the pooled data sets of the four size classes are compared, the relationship is reversed for the two smallest size classes, as shown by the rarefaction curves in Fig. 2.

Coleman (1981, see also Coleman et al. 1982) proposed a stochastic model of "random placement" for calculating expected species richness on small islands in an archipelago where abundances of all species are known. The most important biological assumption of the model — relative similarity of habitats of different islands — is fulfilled by the fragments included in our study. We compared the theoretical expectations of Coleman's model with our data. The comparison is shown in Fig. 4. Our census results are not absolute as demanded by the model (Coleman 1981); consequently, we use the model as an approximation and use $P<0.01$ as the confidence level. Four of the 34 fragments show statistically significant deviations from the expectations.

Species-abundance distributions in our total data set and in the pooled data sets of the four fragment size classes are shown in Fig. 5. They agree with theoretical expectations derived from Fisher's logseries model (Fisher et al. 1943; the expectations were calculated using an algorithm given by Birch 1963; G-test, $P>0.5$). Williams (in Fisher et al. 1943) originally suggested that the parameter of Fisher's logseries, α, can be used as a diversity index (see Taylor 1978, Engen 1978, Wolda 1983). The α's in the four fragment size classes are included in Fig. 5.

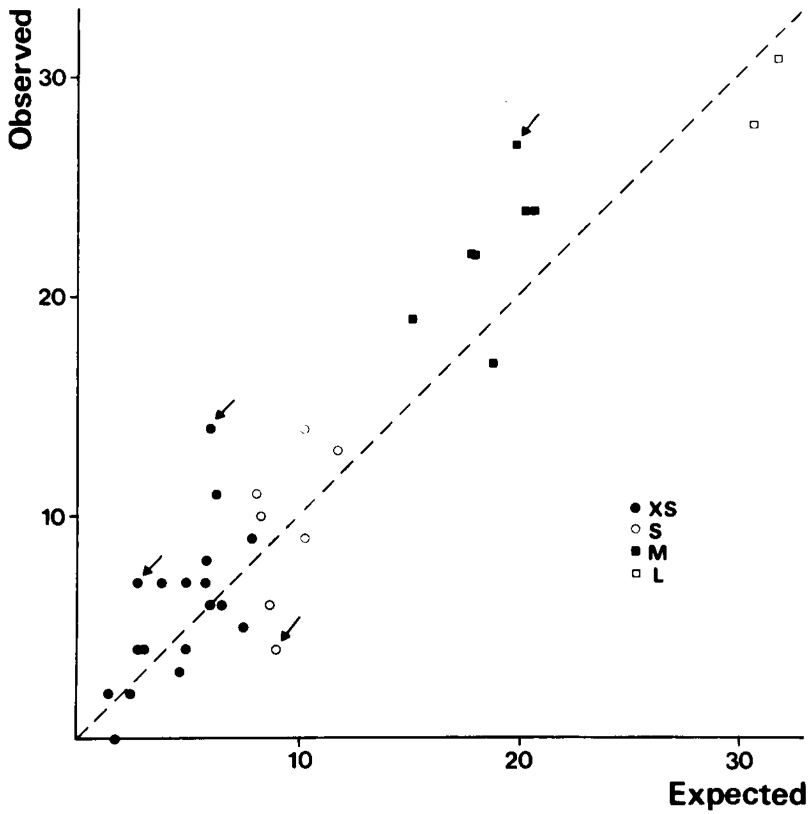

Fig. 4. Observed species numbers in individual fragments plotted against expectations derived using the random placement model (the size classes are shown by symbols; L35 excluded). The fragments with a significant difference (XS5, XS14, S22, M30; P<0.01) are indicated by arrows.

Fisher's α is mainly influenced by species numbers in intermediate abundance classes. By this criterion, then, the pooled communities of the two smallest fragment size classes are less diverse than the communities in the larger fragment size classes although the proportion of species present with only one or a few pairs is high in all of the four data sets (which is a basic characteristic of Fisher's logseries distribution). The comparison yields a similar result to the rarefaction analysis (Fig. 2).

We compared the pooled communities of the fragment size classes with each other by using the Czekanowski-Sørensen index of percentage similarity:

$$I_{CS} = \sum_i \min(p_{ij}, p_{ik}),$$

where p_{ij} and p_{ik} are the proportions of species i in samples j and k, respectively. Similarity indices can be used to estimate the amount of "beta diversity" (Whittaker 1960), namely, compositional variation between communities in different sites (or habitats; Wolda 1983). In choosing the index we followed the recommendation of Pesenko (1982). The index values range from 0.71 (XS vs. L) to 0.83 (M vs. L) and 0.84 (XS vs. S). The communities of the two smallest and the two largest fragment size classes show similar levels of similarity, whereas the other comparisons show larger differences, i.e., there is an element of "beta diversity" in the comparison of XS and S with M and L.

Habitat effects

Another natural *a priori* criterion for grouping the fragments would be habitat composition. The forest structure is fairly uniform in our fragments. However, by using the habitat ordination shown in Fig. 1, three groups of fragments that have a "somewhat" different habitat structure from the other ones can be discerned (indicated in Appendix 1); they comprise (1) seven fragments with low canopy and thick bush layer (area range 0.8–4.4 ha, called "bush fragments" below); (2) seven fragments with pine as the dominating tree (area range 0.7–3.4 ha, called

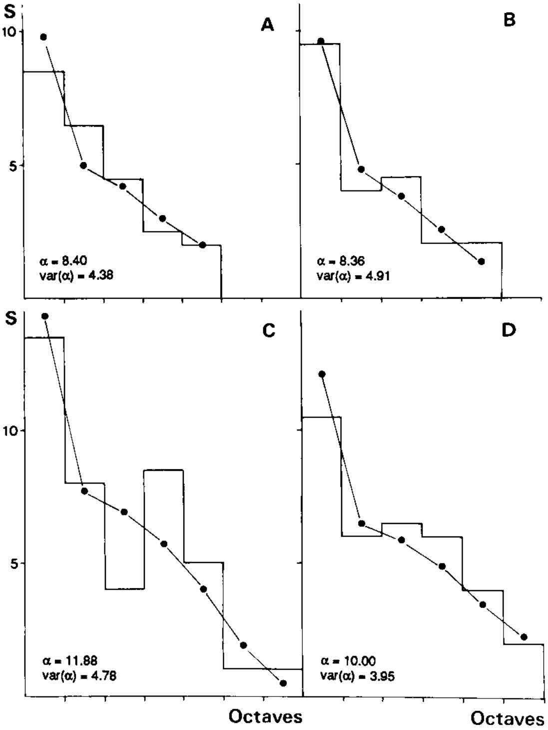

Fig. 5. Species-abundance distributions in the pooled data sets of the four fragment size classes (4A, class XS; 4B, class S; 4C, class M; 4D, class L). Dots indicate expectations derived from Fisher's logseries model. The species are arranged into abundance "octaves" n=1–2, 2–4, 4–8, ...; species with exactly 2^n individuals were divided between two neighbouring classes. Fisher's α and its variance are included.

"pine fragments" below); and (3) seven fragments with spruce-dominated, relatively high and open old forests (area range 0.4–15.8 ha, called "spruce fragments" below). One relatively large fragment is included among "spruce fragments" (M32, 15.8 ha), the area range of the others being 0.4–5.4 ha — comparable to the range in the other two groups. Therefore we checked the results of the analyses below with the fragment M32 excluded.

The general characteristics of the pooled communities of these three groups are as follows:

Fragment group	"Bush"	"Pine"	"Spruce"	(M32 excl.)
Total area (ha)	16.7	13.5	33.8	(18.0)
Number of pairs	89	54	144	(76)
Number of species	20	16	28	(23)
Species richness$_{(50)}$	16.9	15.5	19.1	(18.1)
Density (pairs/km^2)	533	400	426	(422)

Density differences among the groups are not statistically significant (G-test). We investigated variation in species richness over the groups by rarefying the pooled samples to 50 pairs. The difference between spruce fragments and the other two groups is statistically significant ($P<0.05$), whereas the other two groups are similar to each other in terms of species richness. The exclusion of M32 from the group of spruce fragments does not influence the results of these comparisons.

We also compared the communities of the three habitat groups with each other using the Czekanowski-Sørensen index of percentage similarity. The index values range from 0.64 ("pine" vs. "spruce") to 0.75 ("pine" vs. "bush").

To conclude, differences in habitat composition among some of the fragments seem to influence both the species richness and the composition of the pooled data sets. However, as most of the "bush", "pine" and "spruce" fragments belong to the smallest fragment size class (Appendix 1), the differences do not influence comparisons among fragment size classes.

By using habitat ordination of the fragment surroundings we could identify six such fragments that had particularly dense surrounding habitats (XS3, XS7, XS9, XS14, XS15 and S19, Appendix 1). All of them had higher species numbers than expected in the rarefaction and/or random placement analysis above (although all the differences are not statistically significant). The only fragment showing lower than expected species number in the comparison based on random placement, S22 (Fig. 4), is surrounded by peatland. The overall pattern thus suggests that the deviations are due to differences in the structure of habitats surrounding the fragments, but the data are too few for conclusive tests.

Distribution of individual species

Fragment size classes

We continue the analysis on the species population level by using the fragment size classes (data in Table 1). Haila et al. (1983, see also Haila & Järvinen 1981) developed a method of "prevalence functions" for studying the occurrence of single species in insular environments. Prevalence of a species in an island size class equals the observed population size divided by the expected population size, where expectations are calculated from reference data of mainland areas with similar habitats as the islands.

Table 2. Comparison of population numbers observed (Obs) in the three smallest fragment size classes with expectations (Exp) based on densities in L33 and L34. We compared the distribution of the observed pairs with the distribution of the size class areas using the G-test and pooling the data of several small size classes when needed; df gives degrees of freedom; statistical significances (sign): °=0.1>P>0.05, *=P<0.05, **=P<0.01, ***=P<0.001. Species with a total sample size of more than 10 pairs are included.

	XS	S	M	L	G-test	
	Obs/Exp	Obs/Exp	Obs/Exp	Obs	df	(sign)
Species abundant in large fragments						
Phoenicurus phoenicurus	2/3.5	0/3.4	4/11.1	13	1	(*)
Parus major	1/4.6	2/4.4	17/14.6	17	2	(°)
Species abundant in small fragments						
Anthus trivialis	4/1.1	2/1.0	11/3.4	4	1	(°)
Phylloscopus collybita	4/0.8	4/0.8	5/2.6	3	1	(°)
Ph. trochilus	13/3.5	8/3.4	20/11.1	13	3	(*)
Parus montanus	8/1.4	5/1.3	13/4.3	5	2	(**)
Fringilla coelebs	27/16.0	20/15.4	65/50.5	59	3	(ns)
Carduelis spinus	29/9.0	23/8.6	37/28.2	33	3	(***)
Species with uniform (or erratic) distribution						
Bonasa bonasia	2/1.9	0/1.8	3/6.0	7	1	(ns)
Dendrocopos major	0/1.9	1/1.8	5/6.0	7	1	(ns)
Prunella modularis	3/2.2	2/2.1	8/6.8	8	1	(ns)
Erithacus rubecula	6/4.1	4/3.9	19/12.8	15	3	(ns)
Turdus philomelos	4/2.2	2/2.1	1/6.8	8	1	(ns)
Regulus regulus	11/6.5	9/6.3	29/20.5	24	3	(ns)
Muscicapa striata	6/8.1	8/7.8	20/25.7	30	3	(ns)
Ficedula hypoleuca	4/5.2	1/5.0	14/16.3	19	2	(ns)
Parus cristatus	3/2.2	6/2.1	11/6.8	8	2	(ns)
Certhia familiaris	3/3.0	2/2.3	12/9.4	11	2	(ns)
Fringilla montifringilla	1/0	0/0	12/0	0	2	(***)
Pyrrhula pyrrhula	2/2.2	4/2.1	10/6.8	8	2	(ns)

A separate "mainland" does not exist for our forest "archipelago". However, in Table 2 we show prevalences for abundant species in our data (total of samples is at least ten pairs; 20 spp.) using the data from the largest fragments (L33 and L34) as a reference for the other size classes. We tested distributions of the species among the size classes against expectations based on the areas of the size classes (G-test; see Table 2).

The species are divided into three groups in Table 2 according to their distributional centre over the fragment size classes. Sample size is small for many of the species, and the patterns should not be overinterpreted. In the following we give detailed comments on the groups:

(1) Only two species seem to prefer large fragments: *Phoenicurus phoenicurus* and *Parus major*. Both of them are hole-nesting species, and they will be discussed below.

(2) The list of species with a clear preference for small fragments comprises six species. In small fragments the proportion of edges in the total area is higher than in large ones; these species in our data, then, might be favoured by the "edge effect". The two dominants of our data, included in this group, *Phylloscopus trochilus* and *Fringilla coelebs* were regarded as edge species by Hansson (1983), Vickholm (1983) and Helle (1985), and *Anthus trivialis* by Hansson (1983) and Helle (1985). *Parus montanus* was recorded several times in clear-cuts by Hansson (1985), which also agrees with the pattern in our data.

The status of the other two species in this group in our data, *Phylloscopus collybita* and *Carduelis spinus*, is uncertain because of the following methodological problems.

Ph. collybita often has large territories with several singing posts located at a distance of even more than a hundred meters away from each other (as observed also during our censuses). Consequently, males recorded singing in the small fragments may use them only as a part of their territory and our estimates for the small fragments may thus be inflated. The data show, though, that the species is definitely not restricted to the forest interior in our study area.

Censusing *Carduelis spinus* by the study plot method is unreliable because *C. spinus* males are continuously flying around at the tree-canopy height, often in small groups (2–3 ind.). The species was very abundant in our study area in 1985. It was recorded in virtually all small fragments (Appendix 2). Recording 1–3 males singing in a small fragment is straightforward, but our standard for distinguishing between different males in larger fragments may have been more conservative. Consequently, population estimates for the large fragments may be too low.

(3) The twelve remaining species have a uniform or unclear distribution pattern in our study area. Species that show a particularly good agreement with the expectation include *Prunella modularis*, *Erithacus rubecula*, *Muscicapa striata*, *Certhia familiaris*, and *Pyrrhula pyrrhula*. Most of the others are scarce, or show an erratic distribution (e.g. *Fringilla montifringilla* — but this is an artefact of the small data; several singing males of *F. montifringilla* were observed in the line transects in L35). *Regulus regulus* and *Parus cristatus* show prevalences higher than one in the size classes XS, S and M, which agrees with the conclusions of Hansson (1983) regarding their preference for forest edges.

Next we investigate the distribution of scarce species in the fragment size classes. To compile an ecologically realistic list of scarce species we used handbook information on habitat preferences and abundances of individual species (von Haartman et al. 1963–72, Solonen 1985). We included species that prefer (old) coniferous forests and that are relatively scarce in southern Finland; the species are indicated in Appendix 2. It is not possible to draw conclusions on the distribution of individual scarce species because data are limited. The distribution of the group as a whole (11 spp., 27 pairs) is shown in the tabulation below:

Size class	XS	S	M	L
Number of pairs	2	0	11	14
Number of species	2	0	8	8

Table 3. The pooled communities of the three fragment habitat groups. Species with a sample size of more than 10 pairs.

	"Bush"	"Pine"	"Spruce"
Erithacus rubecula	5	0	6
Ph. trochilus	10	6	8
Regulus regulus	8	2	9
Muscicapa striata	4	2	10
Parus montanus	5	6	4
P. cristatus	3	3	5
Fringilla coelebs	14	9	32
Carduelis spinus	14	14	21

The scarce species are underrepresented in the two smallest size classes compared with the two largest ones in terms of pair numbers (compared with the distibution expected on the basis of area proportions, G-test, $P<0.05$).

Habitat effects

Table 3 shows the distribution of individual species in "bush", "pine" and "spruce" fragments (species with a pooled sample size of at least ten pairs; the original data are in Appendix 2). Using the G-test we tested the evenness of the distributions of species with an adequate sample size relative to the total areas of the groups; no statistically significant differences emerged.

Hole-nesting species

Hole-nesting species comprise an ecologically homogeneous group as regards their nest-site requirements. We divide hole-nesters occurring in our study area into three groups: (1) woodpeckers that make their own nest cavity; (2) species dependent on old woodpecker nests; and (3) tits that make their own nest cavity. The species in the third group (*Parus montanus* and *P. cristatus*) were discussed above. In the following we analyze the distribution of the other two groups relative to the density of snags in the fragments.

Fig. 6 shows the total densities of these two species groups in the fragments of size classes M and L against snag densities in the same fragments. The slope of regression is positive for both of the species groups ($P<0.05$), and both correlations are significant at the $P<0.05$ level. However, the relationship is decisively influenced by fragment M26

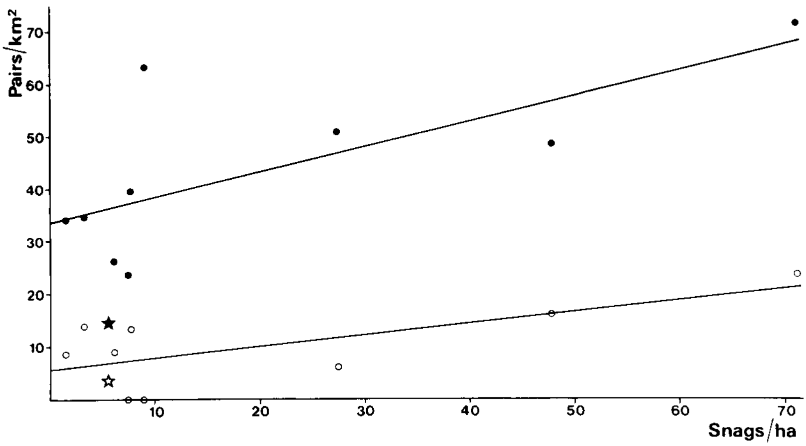

Fig. 6. Densities of hole-nesting species in individual fragments, size classes M and L (L35 excluded), plotted against snag density in each fragment. Open circles: woodpeckers; closed circles: species dependent on old woodpecker nests. The open star and the closed star indicate the density of birds against the density of snags in size class S (pooled data) for the two groups, respectively.

that has a very high snag density (71.3/ha); when it is removed, neither the positive slopes of regression nor the correlation coefficients are statistically significant. Unfortunately, M26 is the only relatively small fragment with a high snag density in our study area.

We checked this pattern by calculating correlations between the fragment area and hole-nester densities: woodpeckers: r=0.234, and species dependent on woodpecker nests: r=0.182. The correlation coefficients were far from being statistically significant. This implies that fragment area is of secondary importance for the occurrence of the hole-nesting species. The availability of suitable nest sites seems essential.

The two smallest size classes were excluded from Fig. 6 because of too small sample sizes (particularly for woodpeckers). However, we included points describing pooled data of the size class S (density of snags 5.0/ha — comparable to those found in the size class M; density of woodpeckers 3.6 pairs/km^2; pooled density of the hole-nesting species 14.5 pairs/km^2). In the case of woodpeckers the point is close to the regression line, but the samples are small. In contrast, the point for the other species lies at a considerable distance from the regression line (expected density about 35 pairs/km^2; the difference is statistically highly significant, $P<0.001$).

A possible *ad hoc* explanation for this detail is that the relative scarcity of woodpeckers in small fragments compared to the large ones is real. In the long run, this would result in there being fewer nest holes available in the small fragments although average snag density is similar to that in larger fragments.

Consequences of forest fragmentation for taiga birds

Area effects?

The equilibrium hypothesis of MacArthur & Wilson (1967) predicts that species numbers are lower on small than on large islands because of differences in immigration/extinction dynamics as a function of the island area; this would be an "area effect" on the species richness of the island community. However, the very concept of area effect is in need of clarification for several reasons.

First, the equilibrium explanation is not the only possible one for low species richness in small fragments; for a discussion of alternatives, see Connor & McCoy 1979. Second, there may be ecological mechanisms of other kinds operating in insular environments that are *area-mediated* (Ambuel & Temple 1983, Howe 1984, Rosenberg & Raphael 1986, Wilcove et al. 1986). These can be classified into two groups: (1) Habitat quality may be area-dependent due to systematic differences in habitat structure between smaller and larger fragments; for instance, the smaller the fragment, the relatively more important the edge effect. (2) The influence of fragment area may be mediated through minimum area requirements of individual populations that would preclude their successful reproduction on small islands or fragments (e.g., Ahlén & Nilsson 1982, Freemark & Merriam 1986).

We tested the reality of the "area effects" in the sense of the equilibrium hypothesis in our data by comparing observed community structure with expectations based on population sizes and found no traces of impoverishment due to "area effect".

However, we did detect *area-mediated differences* in the breeding bird communities of different-sized fragments. Edge effect clearly is an important factor in the Seitseminen forest "archipelago". Total densities calculated per fragment area are highest in the smallest fragments, possibly due to the species favouring edges having the ability of using areas outside the fragments as parts of their home range. Assuming that the breadth of an "edge" is 50 m and that total density is 50% higher at the edge than in the inner parts of the fragments (following Hansson 1983), we can calculate that total densities at the edges of our 15 ha fragments (fragment size class M) would be 484 pairs/km^2, which is close to our density estimates for the small fragments (Table 1).

The difference in average densities in the large fragments (size class L) and the other ones is too great to be attributed to edge effect alone, however. The line transect estimate from L35, 237 p/km^2, agrees roughly with the estimates from L33 and L34 (average 306 p/km^2), taking into account the lower census efficiency of the line transect method compared with the study plot method. We assume that this is a habitat effect. The large fragments mainly comprise uniform and fairly barren primeval forest, whereas the forests of the smaller fragments combined are more heterogeneous, but data on the exact location of individual territories relative to habitat structure would be needed to check this assumption.

Our data also suggest that minimum area requirements of individual species may bring about impoverishment in bird community structure in small fragments. Woodpeckers seem to be less abundant in small fragments than expected on the basis of their average densities. Home range sizes of woodpeckers are presumably on the order of 20 ha (*Dendrocopos major*, Pynnönen 1939) to >100 ha (*Dryocopus martius*, Pynnönen 1939, Blume 1966). However, *Dryocopus martius* often resides in fragmented areas, using different areas widely dispersed from each other for foraging (von Haartman et al. 1963–72, P. Pouttu, pers. comm. 1985, own observations). A decisive question is, how do woodpeckers establish home ranges in mosaic-like fragment archipelagoes?

Scarce species taken as a group appear less abundant in the small fragments than in the large ones. The list of regionally scarce species mainly includes nonpasserines (Appendix 2) that presumably have large territories and/or specialized habitat requirements. Their occurrence in very small fragments may thus be precluded by their minimum area requirements but, again, data on their spatial territory structure are needed. For example, large birds of prey have strict nest site requirements, but they often include very variable habitats in their hunting territories.

Prospects

Modern forestry, the main reason for forest fragmentation in the Finnish coniferous taiga, has brought about dramatic changes in the area proportions of different successional forest stages. It has been extensively documented that the composition of the taiga avifauna has changed as well (von Haartman 1973, 1978, Järvinen & Väisänen 1977, 1978, Järvinen et al. 1977, Haila et al. 1980, Helle & Järvinen 1986).

The data from our 27 km of line transects in the Seitseminen area corroborate this conclusion; estimates of regional densities of species observed in the transects are included in Appendix 2. The estimate of the total regional density (220 p/km^2) is even lower than the line transect estimate obtained in fragment LL35 (237 p/km^2). However, two species, *Anthus trivialis* and *Phylloscopus trochilus* got higher estimates in the line transects than in the fragment censuses (9.9 p/km^2 vs. 9.2 p/km^2, and 31.0 p/km^2 vs. 21.5 p/km^2, respectively). Both species are particularly abundant in recent clear-cuts and sapling stands. On the other hand, densities of forest birds preferring older successional forest stands are considerably lower on the regional level in our study area than in the fragments censused.

Väisänen et al. (1986) analyzed changes in bird community composition of a northern Finnish primeval taiga wood from the 1910s to the 1980s. They concluded that local bird population dynamics in this forest have been decisively influenced by regional population changes in surrounding areas that have presumably led to changes in colonization pressure. Helle (1986) reached similar conclusions in an analysis of population changes in a northern Finnish national park.

It thus seems that local bird community dynamics in fragments of coniferous taiga are closely connected with dynamics on the regional level. This implies that regional proportions of different forest types and forests of different age would be of greater importance to avifaunal composition of the taiga than spatial configuration of forests.

Our data suggest a similar conclusion. We found the highest species richness and diversity in size class M, with an area range of 8.4–15.2 ha. Similarly, on the level of species populations the possible effects of minimum area requirements are detectable only in the two smallest size classes (fragment area less than 5.4 ha). It seems that taiga birds are able to maintain populations in areas fragmented by forestry where fragment size is on the order of some tens of hectares.

Three points of caution must be added, however: First, we have no data on changes that have possibly already taken place. No birds of coniferous forests have become extinct in northern Europe since the mid-nineteenth century (Järvinen & Ulfstrand 1980), but the population size and range of some species have changed in ways that influence their prospects (e.g., Järvinen 1981). This is obvious in areas where modern forest management has created larger and more homogeneous clear-cut areas than in our study area (e.g., northern Finland, see Helle 1986, Helle & Järvinen 1986, Väisänen et al. 1986, Virkkala 1987).

Second, adequate quantitative data on scarce habitat specialists of the taiga are lacking. Data from northern Finland suggest that year-round residents of the taiga may be particularly vulnerable to fragmentation (Helle & Järvinen 1986, Virkkala 1987, see also Rosenberg & Raphael 1986).

Third, our conclusions are based on data on average densities, but densities may not adequately reflect underlying population dynamics (Van Horne 1984). In a habitat archipelago small fragments may represent a "sink" area where the local population is maintained by constant immigration from a "source" area somewhere else (Wiens & Rotenberry 1981). Ultimately we need detailed data on species population dynamics in different parts of habitat archipelagoes, but such data are rare indeed.

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Selostus: **Pesimälinnuston esiintyminen hakkuiden pirstomissa havumetsissä Pohjois-Hämeessä**

Suoritimme v. 1985 Seitsemisen kansallispuistossa ja sen lähiympäristössä 35 vanhan havumetsäsaarekkeen (0.4–101 ha) pesimälinnuston kartoituksia. Saarekkeiden ympäristö oli hakkuuaukeaa tai taimikkoa.

Ryhmittelimme metsäsaarekkeet neljään kokoluokkaan: <3 ha (XS1–18, 18 saareketta, yhteensä 28.5 ha), 3–6 ha (S19–25, 7/27.5 ha), 6–16 ha (M26–32, 7/89.9 ha) ja suuret saarekkeet (L33–35; 49.2, 55.8 ja 101 ha). Saarekkeet ja niiden ympäristö kuvataan liitteessä 1.

Kuvasimme saarekkeiden kasvillisuuden 0.04 ha:n ympyrän alueelta (menetelmä: ks. Haila & Hanski 1987), joita sijoitettiin satunnaisesti 2 kpl/ha, kuitenkin vähintään 5/ saareke. Lisäksi laskettiin saarekkeiden pökkelötiheys. Kuvasimme kasvillisuuden myös pienimpien saarekkeiden (<4 ha) ulkopuolelta.

Saarekkeiden kasvillisuuden vaihtelua tutkimme pääkomponenttianalyysillä (kuva 1.) Kolmen suurimman saarekkeen (L33–35) kasvillisuus näytti olevan yhtenäisempi kuin pienten.

Suurimpien saarekkeiden lintutiheys on alhaisempi kuin muiden (taulukko 1). Rarefaktiolla voidaan verrata eri kokoisten saarekkeiden lajimääriä. Suurimpien saarekkeiden lajimäärä näyttää olevan suurempi kuin pienempien (kuva 2), mutta ero ei ole tilastollisesti merkitsevä. Ainoastaan luokan M käyrä eroaa merkitsevästi muista.

Vertasimme myös yksittäisten saarekkeiden (kolme pienintä kokoluokkaa) lajimääriä suurimman kokoluokan aineistosta laskettuun rarefaktiokäyrään (kuva 3). Lajimäärä yksittäisissä pienissä saarekkeissa näyttää olevan suurempi kuin suurimmasta saarekeluokasta satunnaisesti otetun samankokoisen näytteen lajimäärä (enemmän käyrän yläpuolella olevia saarekkeita kuin alapuolella), mutta ainoastaan neljä saareketta eroaa tilastollisesti merkitsevästi (kolmessa suurempi ja yhdessä pienempi lajimäärä). Kun saarekkeet yhdistetään kokoluokittain, tilanne on päinvastainen. Tämä johtuu siitä, että pienten saarekkeiden lajit ovat pääosin samoja saarekkeesta toiseen.

Testasimme aineistomme avulla "satunnaisen sijoittumisen" mallia (Coleman 1981). Suurimmassa osassa saarekkeita lajimäärä ei eronnut merkitsevästi mallin ennustamasta (kuva 4).

Elinympäristön rakenteen vaikutusta tutkimme vertaamalla toisiinsa pensas-, mänty- ja kuusisaarekkeiden linnustoa (kuva 1). Kuusivaltaisten saarekkeiden lajimäärä oli merkitsevästi suurempi kuin muiden, mutta tiheydet eivät eronneet merkitsevästi (taulukko 3).

Ympäröivän alueen kasvillisuuden rakenteella näyttää olevan merkitystä saarekkeen linnustoon, sillä lajimäärä oli korkeampi kuudessa saarekkeessa, joiden ulkopuolinen kasvillisuus oli muita tiheämpää.

Harvinaiset lajit (ks. liite 2) näyttävät olevan harvalukuisia pienissä alle 6 ha:n saarekkeissa, mutta niiden paritiheys on 6–16 ha:n saarekkeissa yhtä suuri kuin suurimmissakin saarekkeissa.

Luokittelimme 20 runsainta lajia sen mukaan, missä saarekekokoluokassa niiden tiheys on suurin (taulukko 2). Vain leppälintu ja talitiainen tuntuvat suosivan suuria saarekkeita. Pienissä saarekkeissa runsaina esiintyvät kuusi lajia ovat reunaa suosivia (esim. pajulintu) tai saamamme tulos johtuu menetelmällisistä ongelmista (tiltaltti, vihervarpunen).

Kolopesijöiden tiheys on suurin saarekkeissa, joissa pökkelötiheys on korkein (kuva 6), mutta saarekkeen koolla sinänsä ei tunnu olevan merkitystä; leppälintu ja talitiainen ovat pienissä saarekkeissa vähälukuisia ilmeisesti pesäkolojen puutteen vuoksi.

Ilmeisesti metsäsaarekkeiden koko ei ole kovinkaan merkityksellinen tekijä metsälinnuston menestymisen kannalta, kun saarekkeet ovat lähellä toisiaan kuten tutkimusalueellamme. Metsätalouden aiheuttamat linnuston muutokset johtunevat ennen muuta siitä, että eri-ikäisten metsien pinta-alasuhteet muuttuvat.

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Appendix 1. Characteristics of the forest fragments censused: area (A), the dominating forest type ("bush", "pine" and "spruce" refer to the fragment groups shown in Fig. 1), and the habitat type dominating in the fragment surrounding. * indicates fragments censused by four visits.

	A	Habitat	Surroundings
*XS1	0.4	spruce	mixed
*XS2	0.5	mixed	mixed
XS3	0.7	pine	young birch
*XS4	0.8	mixed	mixed
XS5	0.8	bush	mixed
*XS6	0.9	mixed	mixed
XS7	1.2	pine	young birch
*XS8	1.5	bush	mixed
XS9	1.6	bush	young birch
*XS10	1.6	pine	peatland
*XS11	2.0	spruce	peatland
*XS12	2.0	mixed	mixed
*XS13	2.1	pine	mixed
XS14	2.1	bush	dense coniferous
XS15	2.2	pine	dense coniferous
*XS16	2.3	pine	peatland
*XS17	2.8	spruce	mixed
*XS18	3.0	spruce	mixed
S19	3.1	bush	dense coniferous
S20	3.2	bush	mixed
*S21	3.4	pine	peatland
*S22	3.6	mixed	peatland
S23	4.4	bush	mixed
*S24	4.4	spruce	mixed
S25	5.4	spruce	mixed
M26	8.4	mixed	mixed
M27	11.5	mixed	mixed
M28	11.7	mixed	mixed
M29	12.8	mixed	mixed
M30	14.5	mixed	mixed
M31	15.2	mixed	mixed
M32	15.8	spruce	mixed
L33	49.2	mixed	mixed
L34	55.8	mixed	mixed
L35	101.0	mixed	mixed

Appendix 2. The primary data: Numbers of pairs in fragments XS1–XS18 (2a) and S19–L34 (2b); density estimates in fragments L35 and estimates of regional density, based on 27 km of line transects, are included in 2b. Regionally scarce species favouring coniferous forests are indicated by (s).

(2a)

	XS1	XS2	XS3	XS4	XS5	XS6	XS7	XS8	XS9	XS10	XS11	XS12	XS13	XS14	XS15	XS16	XS17	XS18
Bonasa bonasia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Tetrao tetrix	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
T. urogallus (s)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Anthus trivialis	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0
Prunella modularis	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0
Erithacus rubecula	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	2
Phoenicurus phoenicurus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Turdus philomelos	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0
T. viscivorus (s)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Phylloscopus sibilatrix	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ph. collybita	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0
Ph. trochilus	0	0	0	0	1	0	1	0	1	1	2	2	2	2	1	0	0	0
Regulus regulus	0	0	0	1	1	0	0	1	1	0	0	2	1	1	1	0	1	1
Muscicapa striata	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1
Ficedula hypoleuca	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Parus montanus	0	0	0	0	0	0	1	0	1	0	0	0	2	1	1	1	0	1
P. cristatus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0
P. major	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Certhia familiaris	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2
Garrulus glandarius	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Fringilla coelebs	1	0	0	1	1	1	1	1	1	1	3	2	3	3	1	1	4	2
F. montifringilla	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Carduelis spinus	1	0	1	1	1	1	2	1	2	1	2	2	3	2	2	2	2	2
Pyrrhula pyrrhula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

(2b)

	S19	S20	S21	S22	S23	S24	S25	M26	M27	M28	M29	M30	M31	M32	L33	L34	L35	Transect
Accipiter gentilis (s)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.0	0.00
A. nisus (s)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0.0	0.00
Bonasa bonasia	0	0	0	0	0	0	0	0	0	1	1	0	1	0	4	3	0.0	0.00
Tetrao tetrix	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0.0	0.50
T. urogallus (s)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	16.5	0.60
Scolopax rusticola	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0.0	0.60
Tringa ochropus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0.9	0.40
Columba palumbus	0	0	0	0	1	0	0	0	0	1	0	2	0	0	0	1	0.0	0.30
Cuculus canorus	0	0	0	0	1	0	0	1	0	0	0	0	1	0	2	3	0.5	1.00
Aegolius funereus (s)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.0	0.00
Strix uralensis (s)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0.0	0.00
Apus apus (s)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0.4	0.03
Jynx torquilla	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0.6	0.08
Dryocopus martius (s)	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	2	0.0	1.00
Dendrocopos major	0	0	0	0	0	1	0	1	1	1	0	1	1	0	2	5	9.5	1.40
Picoides tridactylus (s)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3.1	0.30
Anthus trivialis	1	0	0	0	0	1	0	1	1	1	2	3	1	2	2	2	5.6	9.90
Motacilla alba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0.0	1.20
Prunella modularis	1	0	0	0	0	0	1	0	1	0	1	4	1	1	5	3	0.0	0.90
Erithacus rubecula	1	2	0	0	1	0	0	2	1	5	2	2	5	2	5	10	10.5	13.70
Phoenicurus phoenicurus	0	0	0	0	0	0	0	1	0	1	0	0	0	2	7	6	6.7	2.10

(continues on p. 106)

(2b) cont.

	S19	S20	S21	S22	S23	S24	S25	M26	M27	M28	M29	M30	M31	M32	L33	L34	L35	Transect
Turdus philomelos	0	0	0	0	1	0	1	1	1	2	1	2	1	2	5	3	1.7	6.30
T. iliacus	0	0	0	0	0	0	0	0	1	0	0	2	0	0	1	1	1.1	1.70
T. viscivorus (s)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	1.5	0.20
Sylvia curruca	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0.0	0.40
S. borin	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1.0	2.10
Phylloscopus sibilatrix	0	0	0	0	0	0	0	0	0	1	0	2	0	2	0	0	0.0	2.70
Ph. collybita	1	1	0	0	1	0	1	1	0	1	0	1	1	1	1	2	0.0	2.10
Ph. trochilus	2	0	1	0	4	1	0	0	1	1	1	7	5	5	7	6	14.7	31.00
Regulus regulus	1	2	0	1	1	0	4	3	5	5	5	3	5	3	10	14	12.0	10.10
Muscicapa striata	0	1	1	0	2	3	1	2	3	2	0	4	5	4	16	14	23.2	16.20
Ficedula hypoleuca	0	1	0	0	0	0	0	2	1	2	1	2	3	3	10	9	11.0	3.50
Parus montanus	1	1	1	0	1	1	0	1	1	3	1	4	1	2	1	4	4.0	6.50
P. cristatus	1	1	1	1	1	0	1	1	1	2	1	1	2	3	4	4	9.6	8.20
P. major	0	0	0	0	1	0	1	3	2	1	2	2	2	5	8	9	6.4	5.90
Certhia familiaris	0	0	0	0	0	1	1	1	1	1	2	2	2	3	4	7	15.7	7.00
Garrulus glandarius	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	3.4	0.30
Corvus corax (s)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.0	0.04
Fringilla coelebs	2	2	2	2	4	4	4	3	10	9	6	9	14	14	28	31	52.2	54.20
F. montifringilla	0	0	0	0	0	0	0	0	6	0	1	2	1	2	0	0	3.1	1.50
Carduelis spinus	2	2	3	3	4	4	5	3	5	6	4	7	7	5	16	17	17.7	17.40
Loxia curvirostra	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2	1	1.2	1.80
Pyrrhula pyrrhula	1	1	0	0	1	0	1	1	1	2	1	1	2	2	3	5	1.1	1.00
Emberiza citrinella	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0.0	0.70
E. rustica (s)	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	2.4	2.50