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Bird assemblages in silvicultural habitat mosaics in southern Finland during the breeding season

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We studied the significance of successional forest mosaics, created by modern forestry, for forest birds by censusing breeding birds during three summers in 12 study areas with variable habitat composition and configurations and in a reference area of old forest.

The number of bird species relative to sample size did not differ significantly between the silvicultural mosaics and old forest. However, in the silvicultural mosaics the total bird abundance was only about one third of that in the reference area. The relative abundances of different species also differed considerably. We divided the bird species into five groups on the basis of their observation frequencies and the way in which they used the silvicultural mosaics. The mosaics provided nesting habitats for the most common forest birds and for species favouring open habitats and forest edges. All other forest species visited the mosaics more or less irregularly. The total bird abundance in the silvicultural mosaics increased with habitat diversity, habitat productivity and the proportion of forested habitats. The effects of management practices on birds are discussed.

1. Introduction

Habitat relationships of birds have mainly been studied in homogeneous environments, although it is well known that natural habitats are mosaics of different habitat types (Wiens 1976, 1985, 1989). Incorporating the effects of small-scale heterogeneity gives rise to at least the following two questions:

1) How sensitive are different species to variation in habitat characteristics (Sherry & Holmes 1985, Wiens 1985, 1986)?
2) How do different species cope with small-scale mosaics, where "pure" habitats cover only small patches (Haila & Hanski 1987)?

Modern forestry has created a new type of habitat mosaics by dramatically reducing the proportion of old forests in the landscape. Studies of forest fragmentation (e.g. Askins et al. 1987, Robbins et al. 1989) have mainly dealt with the significance of these remaining forest patches for birds. Forest birds, however, do not necessarily live in a single patch of forest; they can include several different habitat types in their territories (e.g. Howe 1984, Haila & Hanski 1987, Hanski & Haila 1988, Haila et al. 1989). To predict the effects of modern forest management on the bird fauna, we ought to know how much different species use these silvicultural habitats.

This paper is a general survey (sensu Haila et al. 1987) of the forest bird assemblages in mosaics of different successional stages. We compare the relative abundances of birds observed in these habitat mosaics with an area of old forest, using observation frequencies of different species as a criterion. We evaluate the significance of silvicultural habitat mosaics for forest birds (see also Haila et al. 1989) and discuss the influence of environmental characteristics, such as habitat diversity and productivity, on spatial variation in bird abundances.

2. Material and methods

Our study area is situated in the Seitseminen National Park and its surroundings in southern Finland (61°55'N, 23°30'E). The forests in the region are rather barren, consisting mostly of pine (*Pinus sylvestris*) and spruce (*Picea abies*). Besides a few fragments of old forest, the area includes a mosaic of managed forests less than 100 years of age. A large proportion of the area is drained peatland. For a more detailed description of the study area, see Haila et al. (1987).

We censused silvicultural habitat mosaics in the surroundings of 12 mature forest fragments (Haila et al. unpubl.) by locating the observations of all birds on field maps, where the borders of different habitats were drawn on the basis of aerial photographs. The censused area was limited to the land lying within a radius of 100 m around each forest fragment (except in one case in which the radius was extended to 150 m, as the low vegetation easily allowed larger coverage), 107.7 ha in total. The same 12 study areas were censused five times each year from 1986 through 1988 between 11 May and 22 June.

The habitat types of the study area were described in 1985 and the data analysed with Principal Component Analysis (for details, see Haila et al. 1987). The first three principal components in the ordination were related to thickness of the bush layer, proportion of birch vs. pine, and canopy height. On the basis of the ordination we distinguished 10 different habitat types in the field; some characteristics of the habitats as well as their total areas are presented in Table 1. The areas of single habitat patches ranged from 0.13 to 19.3 ha. All the habitats surrounding the fragments are called collectively "silvicultural mosaics" below.

Our reference data originate from a 36-ha area of coniferous forest in Seitseminen, presented in Haila et al. (1989). For this comparison, data from the oldest stands (>100 years) with canopy height >25 m (17.5 ha in total), called "old forest" below, were used. This reference area was censused five times each year between 7 May and 21 June from 1986 through 1988 by the same method used for the silvicultural mosaics.

Here, by old forests we mean forests over 100 years of age and more or less in primeval condition, while mature forests refer to old silvicultural stands, usually less than 100 years old. Thus we compare forest bird assemblages in silvicultural mosaics (managed stands of varying age in the 12 study plots) with old virgin forest.

Density estimates (pairs/km^2) of breeding birds cannot be used when the territories include several habitat patches. Average densities per patch type are also unrealistic (Haila 1988, Haila et al. 1989). Instead, we calculated for each species an index called "observation frequency". The index gives the total number of individual observations of each species per hectare during five censuses in the three years. This gives an indication of the relative importance of different patch types for the birds. A similar method has been used by Fuller & Whittington (1987) in censusing woodland birds in England (see also Osborne 1984).

To decrease the probability of including the same individual twice in our calculations, we used only observations made at least 50 m apart in each census, except when a singing male was accompanied by another vocalizing individual, most probably a female. A nest or a group of fledglings were technically regarded as two records to avoid overestimation of abundances, e.g. of *Parus* species with early broods.

As the detectability and activity of the species affect the index values, the indices of different species are not directly comparable. However, the reference data from the old forest provide a means for pairwise comparison of observation frequencies of each species. Because the vegetation of the habitat mosaics is considerably lower than in the reference area, the audibility of the birds is presumably better in the mosaics. Thus the comparisons are conservative as regards impoverishment of the bird assemblages in the habitat mosaics.

The procedure did not allow a detailed evaluation of the exact status of the observed birds. A part of the observations presumably concerns individuals only visiting the silvicultural mosaics occasionally. However, in evaluating the significance of different habitat types for bird species, occasional visits should also be considered. Not only the actual breeding territory, but the whole home range is important. Furthermore, an index based on individual observations seems the only possibility in small-scale habitat mosaics, where single patches are considerably smaller than single territories.

We used three features to characterize each study area:

1) habitat diversity calculated as the inverse of Simpson's index $D = 1/\Sigma p_i^2$, where p_i is the proportion of habitat i,
2) the proportion of the most productive habitats, namely birch saplings, birch forest, mixed forest, spruce saplings and mature spruce-dominated forest, and
3) the proportion of forested habitats (birch forest, pine forest, mixed forest and mature spruce-dominated forest).

3. Results

The lists of observed species were rather similar in the silvicultural mosaics and old forest, but the relative abundances of the species differed con-

Table 1. Some characteristics of the habitat types of the silvicultural mosaics.

	Habitat type	Total area (ha)	Horizontal structure	Vertical structure	Dominant trees	Height (m)
1	Birch saplings	19.34	Dense, >1500 stems/ha	Even-aged, no large trees	Birch	1.5–3
2	Birch forest	0.13	Open	Dense shrub layer	Birch	15–20
3	Open stands of pine saplings	8.91	Open, ca. 500 stems/ha	Even-aged, few large trees	Pine	5
4	Dense stands of pine saplings	3.83	Dense, >1000 stems/ha	Even-aged, few large trees	Pine	5
5	Pine bog	46.13	Open, ca. 400 stems/ha	Sphagnum mosses, few shrubs and large trees	Pine, (birch)	3–5
6	Pine forest	2.78	Fairly open, ca. 500 trees/ha	Abundant saplings	Pine	10–15
7	Mixed saplings	16.40	Dense, ca. 1500 stems/ha	Occasional large trees	Birch, pine	5–7
8	Mixed forest	6.37	Fairly dense, >500 trees/ha with spatial variation	Trees of variable age, dense shrub layer	Pine, birch	10–15
9	Spruce saplings	2.17	Dense, >1000 stems/ha	Even-aged, few large trees	Spruce, birch	5–7
10	Spruce-dominated mature forest	1.61	Closed canopy	Trees of variable age, sparse shrub layer	Spruce, pine	15–25

Table 2. Number of observations (n) and observation frequencies (f) of species in the ten habitat types (see Table 1 for explanations) distinguished in the silvicultural mosaics and in the reference data from old forest.

	1		2		3		4		5		6	
	n	f	n	f	n	f	n	f	n	f	n	f
Bonasa bonasia	–	–	–	–	–	–	–	–	–	–	–	–
Tetrao tetrix	1	0.0	–	–	1	0.1	1	0.3	15	0.3	–	–
T. urogallus	–	–	–	–	–	–	–	–	2	0.0	–	–
Grus grus	–	–	–	–	–	–	–	–	2	0.0	–	–
Pluvialis apricaria	–	–	–	–	–	–	–	–	8	0.2	–	–
Scolopoax rusticola	–	–	–	–	–	–	–	–	–	–	–	–
Tringa ochropus	3	0.2	–	–	1	0.1	–	–	–	–	–	–
T. glareola	–	–	–	–	–	–	–	–	17	0.4	–	–
Cuculus canorus	–	–	–	–	–	–	1	0.3	3	0.1	–	–
Jynx torquilla	1	0.0	–	–	–	–	–	–	–	–	–	–
Dryocopus martius	–	–	–	–	–	–	–	–	–	–	–	–
Dendrocopos major	2	0.1	–	–	–	–	1	0.3	1	0.0	1	0.4
Picoides tridactylus	–	–	–	–	–	–	–	–	–	–	–	–
Anthus trivialis	55	2.8	1	7.7	47	5.3	9	2.3	116	2.5	8	2.9
A. pratensis	–	–	–	–	–	–	–	–	4	0.1	–	–
Motacilla flava	–	–	–	–	–	–	–	–	32	0.7	–	–
M. alba	7	0.4	–	–	–	–	1	0.3	1	0.0	–	–
Prunella modularis	–	–	1	7.7	1	0.1	–	–	–	–	–	–
Erithacus rubecula	4	0.2	1	7.7	3	0.3	4	1.0	5	0.1	2	0.7
Phoenicurus phoenicurus	–	–	–	–	3	0.3	1	0.3	1	0.0	–	–
Saxicola rubetra	2	0.1	–	–	–	–	–	–	2	0.0	–	–
Turdus pilaris	1	0.0	–	–	1	0.1	–	–	–	–	–	–
T. philomelos	–	–	–	–	3	0.3	2	0.5	–	–	1	0.4
T. iliacus	–	–	–	–	–	–	–	–	–	–	–	–
T. viscivorus	–	–	–	–	–	–	–	–	–	–	–	–
Sylvia curruca	5	0.2	–	–	6	0.7	4	1.0	1	0.0	–	–
S. borin	–	–	–	–	–	–	–	–	1	0.0	–	–
Phylloscopus sibilatrix	–	–	–	–	–	–	–	–	–	–	–	–
Ph. collybita	–	–	–	–	–	–	–	–	–	–	–	–
Ph. trochilus	57	2.9	11	84.6	60	6.7	47	12.3	57	1.2	18	6.5
Regulus regulus	–	–	–	–	1	0.1	–	–	–	–	2	0.7
Muscicapa striata	1	0.0	–	–	1	0.1	–	–	5	0.1	2	0.7
Ficedula parva	–	–	–	–	–	–	–	–	–	–	–	–
F. hypoleuca	–	–	–	–	–	–	–	–	1	0.0	–	–
Parus montanus	–	–	–	–	6	0.7	5	1.3	1	0.0	2	0.7
P. cristatus	–	–	–	–	–	–	1	0.3	4	0.1	–	–
P. major	–	–	–	–	1	0.1	1	0.3	2	0.0	–	–
Certhia familiaris	–	–	–	–	–	–	–	–	–	–	–	–
Lanius collurio	6	0.3	–	–	1	0.1	–	–	–	–	–	–
Garrulus glandarius	–	–	–	–	–	–	–	–	–	–	–	–
Fringilla coelebs	2	0.1	3	23.1	15	1.7	2	0.5	12	0.3	10	3.6
F. montifringilla	–	–	–	–	2	0.2	–	–	5	0.1	4	1.4
Carduelis spinus	1	0.0	–	–	3	0.3	1	0.3	2	0.0	2	0.7
Loxia curvirostra/pytyopsittacus	–	–	–	–	1	0.1	–	–	–	–	–	–
Pyrrhula pyrrhula	–	–	1	7.7	–	–	1	0.3	–	–	2	0.7
Emberiza citrinella	5	0.2	–	–	–	–	–	–	–	–	–	–
E. rustica	1	0.0	–	–	5	0.6	5	1.3	14	0.3	7	2.5
Total	154	8.0	18	138.5	162	18.2	87	22.7	314	6.8	61	21.9

Table 2. (continued)

	7		8		9		10		Total		Old forest	
	n	f	n	f	n	f	n	f	n	f	n	f
Bonasa bonasia	1	0.1	–	–	–	–	–	–	1	0.0	8	0.4
Tetrao tetrix	5	0.3	4	0.6	–	–	–	–	27	0.2	–	–
T. urogallus	–	–	1	0.2	–	–	–	–	3	0.0	5	0.3
Grus grus	–	–	–	–	–	–	–	–	2	0.0	–	–
Pluvialis apricaria	–	–	–	–	–	–	–	–	8	0.1	–	–
Scolopoax rusticola	1	0.1	–	–	–	–	–	–	1	0.0	1	0.1
Tringa ochropus	–	–	–	–	1	0.5	–	–	5	0.0	–	–
T. glareola	–	–	–	–	–	–	–	–	17	0.2	–	–
Cuculus canorus	–	–	–	–	–	–	–	–	4	0.0	–	–
Jynx torquilla	1	0.1	3	0.5	2	0.9	4	2.5	11	0.1	2	0.1
Dryocopus martius	–	–	–	–	–	–	–	–	–	–	2	0.1
Dendrocopos major	2	0.1	4	0.6	1	0.5	3	1.9	15	0.1	41	2.3
Picoides tridactylus	–	–	–	–	–	–	–	–	–	–	6	0.3
Anthus trivialis	54	3.3	28	4.4	8	3.7	4	2.5	330	3.1	34	1.9
A. pratensis	–	–	–	–	–	–	–	–	4	0.0	–	–
Motacilla flava	–	–	–	–	–	–	–	–	32	0.3	–	–
M. alba	1	0.1	–	–	–	–	–	–	10	0.1	–	–
Prunella modularis	2	0.1	4	0.6	7	3.2	9	5.6	24	0.2	2	0.1
Erithacus rubecula	10	0.6	17	2.7	7	3.2	3	1.9	56	0.5	44	2.5
Phoenicurus phoenicurus	1	0.1	2	0.3	–	–	–	–	8	0.1	15	0.8
Saxicola rubetra	1	0.1	–	–	–	–	–	–	5	0.0	–	–
Turdus pilaris	–	–	–	–	–	–	–	–	2	0.0	–	–
T. philomelos	8	0.5	2	0.3	3	1.4	2	1.2	21	0.2	20	1.1
T. iliacus	4	0.2	–	–	6	2.8	–	–	10	0.1	1	0.1
T. viscivorus	–	–	–	–	–	–	–	–	–	–	4	0.2
Sylvia curruca	5	0.3	7	1.1	2	0.9	2	1.2	32	0.3	–	–
S. borin	4	0.2	–	–	–	–	–	–	5	0.0	1	0.1
Phylloscopus sibilatrix	–	–	1	0.2	–	–	1	0.6	2	0.0	6	0.3
Ph. collybita	–	–	–	–	–	–	–	–	–	–	2	0.1
Ph. trochilus	173	10.5	91	14.3	28	12.9	18	11.2	560	5.2	46	2.6
Regulus regulus	1	0.1	2	0.3	1	0.5	2	1.2	9	0.1	38	2.2
Muscicapa striata	4	0.2	2	0.3	–	–	1	0.6	16	0.1	33	1.9
Ficedula parva	–	–	–	–	–	–	–	–	–	–	3	0.2
F. hypoleuca	–	–	2	0.3	–	–	4	2.5	7	0.1	46	2.6
Parus montanus	2	0.1	12	1.9	2	0.9	2	1.2	32	0.3	12	0.7
P. cristatus	3	0.2	1	0.2	–	–	–	–	9	0.1	25	1.4
P. major	4	0.2	–	–	1	0.5	2	1.2	11	0.1	49	2.8
Certhia familiaris	–	–	–	–	–	–	1	0.6	1	0.0	41	2.3
Lanius collurio	1	0.1	–	–	2	0.9	–	–	10	0.1	–	–
Garrulus glandarius	2	0.1	–	–	–	–	–	–	2	0.0	1	0.1
Fringilla coelebs	31	1.9	55	8.6	14	6.4	17	10.6	161	1.5	183	10.4
F. montifringilla	5	0.3	4	0.6	5	2.3	4	2.5	29	0.3	37	2.1
Carduelis spinus	10	0.6	12	1.9	6	2.8	4	2.5	41	0.4	49	2.8
Loxia curvirostra/pytyopsittacus	2	0.1	3	0.5	–	–	–	–	6	0.1	6	0.3
Pyrrhula pyrrhula	2	0.1	3	0.5	–	–	1	0.6	10	0.1	14	0.8
Emberiza citrinella	3	0.2	1	0.2	–	–	–	–	9	0.1	1	0.1
E. rustica	7	0.4	2	0.3	1	0.5	1	0.6	43	0.4	2	0.1
Total	350	21.3	263	41.3	97	44.7	85	52.8	1591	14.8	780	44.6

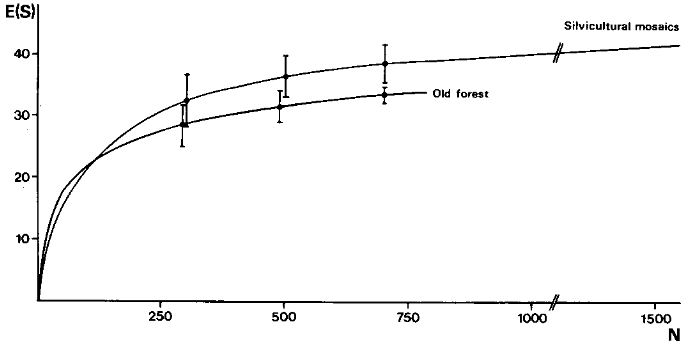

Fig. 1. Rarefaction estimates of expected species numbers E(S) as a function of sample size (N) in the silvicultural mosaics vs. old forest. Standard deviations shown for sample sizes of 300, 500 and 700 pairs. Ends of curves show total sample sizes.

siderably. The number of species observed was 42 in the silvicultural mosaics and 34 in the old forest. However, when assessed by rarefaction (e.g. Simberloff 1979, James & Rathbun 1981), the expected species numbers in samples of equal size did not differ significantly (Fig. 1). The steeper shape of the rarefaction curve in the old forest suggests that the evenness component of community diversity was slightly higher there than in the silvicultural mosaics (cf. Peet 1974, James & Rathbun 1981).

The total observation frequency of all species measured with our index was 14.8 in the silvicultural mosaics and 44.6 in the old forest — a three-fold difference. When the most abundant species in the silvicultural mosaics, the Willow Warbler (*Phylloscopus trochilus*; index 5.2 in the silvicultural mosaics, 2.6 in the old forest) and Tree Pipit (*Anthus trivialis*; 3.1, 1.9), were omitted, the difference was even more pronounced; the index value was 6.5 for the silvicultural mosaics and 40.1 for the reference area.

The index values seem biologically realistic also as regards the variation among different habitat types, the highest observation frequencies being obtained for birch forest (138.5), mature spruce-dominated forest (52.8), spruce saplings (44.7) and mixed forest (41.3). The value for birch forest is unreliable, however, because of the small sample size. The index was lowest in pine bogs (6.8), birch saplings (8.0) and open stands of pine saplings (18.2). The numbers of observations and abundance indices of different species in the ten habitat types in the mosaics, and in the reference area as well, are shown in Table 2.

Relative importance of the silvicultural mosaics and old forest

We divided the species into five groups (Table 3) according to their relative observation frequencies in the silvicultural mosaics vs. old forest, and to the way the species use these habitat mosaics. We did not use quantitative methods, but simply grouped species with roughly similar observation frequencies in the two data sets. We also checked the quality of the observations, viz. whether they suggested regular breeding territory or only occasional visits. Our purpose was to identify groups of species using the habitat mosaics in approximately the same way and thus ease conservation comparison. For scarce species the classification is tentative, but we decided to include them to give a preliminary assessment of their status. We omitted species which were recorded occasionally in our censuses and which occurred predominantly in different types of environments.

Mosaic generalists. The Willow Warbler and Tree Pipit were the most abundant species in the silvicultural mosaics, comprising 56% of the total number of observations. Both species apparently held territories in all ten habitat types distinguished in the mosaics. The Tree Pipit was most abundant in open stands of pine saplings (5.3). Both species were also common in our reference area of old forest, but occurred in lower frequencies there. In the old forest, the proportion of observations of these species together was about 10%.

Mosaic specialists. A group of species favouring open or bushy environments inhabited the sapling mosaics, but were absent or scarce in the old forest. As could be expected, the Black Grouse (*Tetrao tetrix*), Wood Sandpiper (*Tringa glareola*), Golden Plover (*Pluvialis apricaria*), Yellow Wagtail (*Motacilla flava*) and Red-backed Shrike (*Lanius collurio*) were not observed in the old forest at all. The Yellow Wagtail and the two waders were seen only in silvicultural mosaics comprising large peatland areas. On the other hand, the Rustic Bunting (*Emberiza rustica*), Dunnock (*Prunella modularis*), Lesser Whitethroat (*Sylvia curruca*), and Redwing (*Turdus iliacus*) represent species favouring open habitats, but also breeding in open forests and forest edges.

Table 3. Species groups and the observation frequencies of different species in the silvicultural mosaics vs. old forest.

Species group	Mosaics	Old forest
Mosaic generalists		
Phylloscopus trochilus	5.2	2.6
Anthus trivialis	3.1	1.9
Mosaic specialists		
Motacilla flava	0.3	–
Tetrao tetrix	0.2	–
Tringa glareola	0.2	–
Pluvialis apricaria	0.1	–
Lanius collurio	0.1	–
Emberiza rustica	0.4	0.1
Sylvia curruca	0.3	–
Prunella modularis	0.2	0.1
Jynx torquilla	0.1	0.1
Turdus iliacus	0.1	0.1
Emberiza citrinella	0.1	0.1
Mature forest generalists		
Fringilla coelebs	1.5	10.4
Erithacus rubecula	0.5	2.5
Carduelis spinus	0.4	2.8
Parus montanus	0.3	0.7
Fringilla montifringilla	0.3	2.1
Turdus philomelos	0.2	1.1
Mature forest specialists		
Parus major	0.1	2.8
Dendrocopos major	0.1	2.3
Muscicapa striata	0.1	1.9
Pyrrhula pyrrhula	0.1	0.8
Ficedula hypoleuca	0.1	2.6
Regulus regulus	0.1	2.2
Parus cristatus	0.1	1.4
Phoenicurus phoenicurus	0.1	0.8
Certhia familiaris	0.0	2.3
Bonasa bonasia	0.0	0.4
Phylloscopus sibilatrix	0.0	0.3
Tetrao urogallus	0.0	0.3
Old forest specialists		
Picoides tridactylus	–	0.3
Turdus viscivorus	–	0.2
Ficedula parva	–	0.2
Phylloscopus collybita	–	0.1
Dryocopus martius	–	0.1

Mature forest generalists. Several species breeding predominantly in mature forests were frequently observed in the silvicultural mosaics and regularly included sapling habitats in their home ranges; e.g. the Chaffinch (*Fringilla coelebs*), Brambling (*F. montifringilla*), Robin (*Erithacus rubecula*), Willow Tit (*Parus montanus*), Song Thrush (*Turdus philomelos*) and Siskin (*Carduelis spinus*). Most probably the Robin and Song Thrush also bred there, although we did not find their nests in the study areas. As the Siskins regularly move around in large areas, assessing the status of the individuals is difficult. Nevertheless, the Siskin was among the most common forest birds observed in the silvicultural mosaics.

Mature forest specialists. Species clearly favouring forests which were observed regularly in silvicultural mosaics, but in low frequencies, include the Spotted Flycatcher (*Muscicapa striata*), Great Spotted Woodpecker (*Dendrocopos major*), Great Tit (*Parus major*) and Bullfinch (*Pyrrhula pyrrhula*). These species seem to use silvicultural mosaics predominantly for foraging. For instance, Great Spotted Woodpeckers were often seen searching for caterpillars in dense stands of pine saplings, especially if the trees were damaged by moose. Great Tits and Bullfinches often foraged among birch saplings.

The Goldcrest (*Regulus regulus*), Crested Tit (*Parus cristatus*), Redstart (*Phoenicurus phoenicurus*) and Pied Flycatcher (*Ficedula hypoleuca*) were observed in the silvicultural mosaics in similar frequencies, but sparsely: the number of observations for each species was less than ten. The Treecreeper (*Certhia familiaris*), Wood Warbler (*Phylloscopus sibilatrix*), Hazel Grouse (*Bonasa bonasia*) and Capercaillie (*Tetrao urogallus*) were among the rarest visitors in the silvicultural mosaics, each was observed only 1–3 times during the three study years.

Old forest specialists. The few species we did not observe in the silvicultural mosaics at all were the Three-toed Woodpecker (*Picoides tridactylus*), Mistle Trush (*Turdus viscivorus*), Red-breasted Flycatcher (*Ficedula parva*), Chiffchaff (*Phylloscopus collybita*) and Black Woodpecker (*Dryocopus martius*). However, these species are also scarce in old forest, and their absence from the silvicultural mosaics in our data may be accidental.

Significance of habitat characteristics

We studied the effects of habitat characteristics by regressing observation frequencies of birds against habitat diversity, habitat productivity and the proportion of forested habitats. From the analyses of habitat productivity an extreme outlier was omitted. All the 12 study areas are included in the other analyses.

Spatial heterogeneity as measured by the inverse of Simpson's diversity index increased the total observation frequency of birds ($r^2 = 0.534$, $P < 0.01$, Fig. 2A). Habitat productivity, that is the proportion of the most productive habitats, had an even stronger effect on total bird abundance ($r^2 = 0.640$, $P < 0.01$), when the outlier was omitted from the regression analysis (Fig. 2B). The outlier area consisted mostly of a uniform stand of low birch saplings, heavily browsed by moose, and the total observation frequency of birds was exceptionally low. It may be questioned whether a homogeneous birch sapling stand should be classified among "productive habitats".

When the total observation frequencies of mature forest specialists (Table 3) were regressed against habitat diversity and productivity, the trends were similar. However, in this case habitat diversity increased bird abundance more ($r^2 = 0.691$, $P < 0.001$) than did the habitat productivity ($r^2 = 0.470$, $P < 0.05$). The higher the proportion of forested habitats, the higher the total bird abundance ($r^2 = 0.610$, $P < 0.01$), and the abundance of mature forest specialists as well ($r^2 = 0.593$, $P < 0.01$).

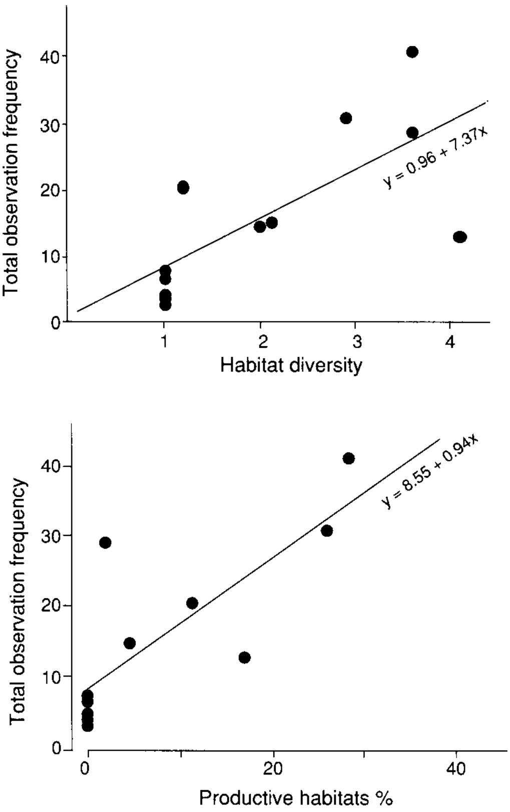

Fig. 2. Regressions of habitat diversity and habitat productivity against the total observation frequency of birds.

4. Discussion

Birds of the boreal forest often include several structurally different habitats in their home ranges when breeding in a patchy environment. Consequently, habitat mosaics have to be studied on a scale larger than that of single habitat patches. Our method based on the index of observation frequency showed that the relative abundances of forest bird species differed considerably in the silvicultural mosaics from those in the reference area of old forest, although the species lists were largely the same. The total abundance of birds in the silvicultural mosaics was one-third of that in the old forest. Small-scale spatial heterogeneity and habitat productivity clearly had a pronounced influence on bird abundances in the separate silvicultural mosaics censused.

However, our index values are valid only in this specific context. They cannot be compared with the actual densities of breeding pairs, as observations of non-resident birds are necessarily also included. Moreover, the observations in one census are not always independent, but can represent the same individual. When collecting the observations from our field maps, we tried to minimize the number of observations of the same individual, but the possibility still exists, as the birds may move around in large areas. The exact localization of different individuals would demand colour-ringing and radio tracking (cf. Hanski & Haila 1988), which are, of course, impossible in a study of this scale.

The fact that our study areas surrounded small forest fragments may have some influence on the bird species assemblages in the silvicultural mosaics. The observation frequency of forest birds in the immediate surroundings of a large forest fragment may be higher than around a small fragment. However, the size distribution of the forest fragments in our data did not allow us to test this aspect, as the sizes varied little. The effects of patch context will be studied in a further paper.

The silvicultural mosaics provided nesting habitats for the most common forest birds and for species favouring open habitats and forest edges. Mosaic generalists, the Willow Warbler and Tree Pipit, predominated in the bird communities in the silvicultural mosaics. In northern Finland, these species are the dominants in the "bush phase" of forest succession (Helle 1985). The mature forest generalists (Table 3) regularly included parts of silvicultural mosaics in their home ranges and some of them most probably also bred there. We lack direct evidence of breeding in these data, but further censuses made in 1988–1990 in the silvicultural mosaics of the Seitseminen area revealed that at least the Robin and Song Thrush and also the Redwing breed in almost pure stands of pine saplings.

All other forest species visited silvicultural mosaics more or less irregularly. For some species outbreaks of insects (aphids, pine sawflies) in sapling stands of birch and pine may provide an abundant temporary food source. For instance, in summer 1988 a mass outbreak of aphids on birch occurred in southern Finland, and Chaffinches and Willow Warblers were seen systematically gleaning aphids from birch saplings. Seedeaters, like the Bullfinch and Siskin, may benefit from the seed crop and leaf buds available in the silvicultural mosaics.

Habitat diversity (e.g. MacArthur et al. 1962, Willson 1974, Freemark & Merriam 1986) and productivity (e.g. Nilsson 1979, Cody 1981) have often been found to increase local species diversity. However, as regards the habitat diversity, such studies concentrate on the within-habitat, and in most cases, vertical heterogeneity, while we measured between-habitat (horizontal) heterogeneity on the scale of habitat mosaics. In their simulation study, Urban & Smith (1989) suggested that among-stand variation may also contribute to the distribution of bird species and hence to the diversity. In Roth's (1976, 1979) studies horizontal habitat heterogeneity correlated significantly with bird species diversity within a habitat.

In our data, habitat diversity, habitat productivity and the proportion of forested habitats considerably increased the abundance of forest birds in the silvicultural mosaics. When studying bird species diversity in different successional stages, Willson (1974) did not find any correlation between habitat productivity and bird abundance, but the existence of a closed canopy had the most important effect on species number.

These results suggest that small-scale heterogeneity with high habitat diversity and productivity should be preferred in management practices, to increase the abundance of forest birds in silvicultural habitat mosaics. It would be especially favourable to forest birds to leave patches of mature forest in areas of saplings. Otherwise, these sapling mosaics provide an adequate nesting habitat only for the mosaic generalists and species specialized in open habitats. Data on the minimum sizes and spacing of such remnant patches will be published elsewhere. However, certain species, e.g. the Three-toed Woodpecker, Siberian Tit (*Parus cinctus*) and Siberian Jay (*Perisoreus infaustus*), will need intact forests to survive (cf. Virkkala 1987).

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Selostus: **Metsälintuyhteisöt eri sukkessiovaiheiden muodostamissa talousmetsämosaiikeissa**

Nykyaikainen metsätalous on pirstonut havumetsämme eri sukkessiovaiheiden muodostamiksi havumetsämosaiikeiksi. Koska metsälintujen reviiri voi tällaisessa elinympäristössä koostua useista eri biotooppilaikuista, pitää näitä alueita tutkia yksittäisiä laikkuja laajempina kokonaisuuksina.

Olemme tutkineet lintuyhteisöjen koostumusta ja lajien suhteellisisa runsauksia Seitsemisen kansallispuistossa ja sen lähiympäristössä Etelä-Suomessa kahdessatoista biotooppimosaiikissa, jotka sijaitsevat pienten metsäsaarekkeiden ympärillä. Vertailualueena oli lähes luonnontilainen vanhan metsän alue Seitsemisen kansallispuistossa. Jotta eri biotooppilaikkujen käytön vertailu olisi mahdollista, laskimme kullekin lintulajille indeksin, joka ilmoittaa havaintojen määrän hehtaaria kohden laskettuna koko kolmen vuoden aineistosta. Ryhmittelimme lajiston viiteen ryhmään niiden suhteellisten runsauksien perusteella ja sen mukaan kuinka ne käyttivät biotooppimosaiikkeja hyväkseen.

Tulosten mukaan lintujen lajimäärä talousmetsämosaiikeissa ja vanhan metsän alueella ei eronnut tilastollisesti merkitsevästi vertailtaessa samankokoisia näytteitä rarefaktion avulla. Sen sijaan lajien suhteelliset runsaudet erosivat huomattavasti tutkimusalueiden ja vertailualueen välillä. Linnuston kokonaistiheys oli talousmetsämosaiikeissa vain kolmannes vanhan metsän linnuston tiheydestä indeksillämme mitattuna. Biotooppien diversiteetti ja tuottavuus kullakin tutkimusalueella lisäsivät selvästi linnuston runsautta. Mitä suurempi metsäisten biotooppien osuus oli, sitä runsaampaa oli myös linnusto.

Tulosten perusteella talousmetsämosaiikit eivät tarjoa riittäviä lisääntymismahdollisuuksia muille kuin kaikkein runsaimmille metsälajeille ja avomaan lajeille. Metsätalouden toimenpiteiden mittakaava on selvästi tärkeä lintujen menestymiselle. Suosimalla pienipiirteistä ja monipuolista metsäkuviomosaiikkia voitaisiin metsälintujen elinolosuhteita parantaa huomattavasti nykyisissä talousmetsissämme, etenkin, jos taimikkoalueiden lomaan jätettäisiin metsäsaarekkeita.

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