Geographical variation in bird communities of old, intact forests in northern Finland

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Regional variation in the structure of bird communities in northern Finnish primeval forests was studied using line transects. Birds were censused both in spruce- and pine-dominated forests in five areas of Lapland from 1982–86. The habitat structure of the census areas was defined by using habitat variables of silvicultural maps.

The northward decrease in the bird density of pine forests correlated positively with the latitudinal decrease in the cubic volume of the stand. There were no clear regional trends in the bird density of spruce forests, presumably, owing to the northward increase in the proportion of birch in these forests. This increase in the proportion of birch is probably advantageous to migratory foliage insectivores and seed eaters, such as *Carduelis flammea*. Species numbers decreased significantly to the north in spruce forests, which can partly be explained by the northward decrease in the number and density of southern bird species favouring spruce forests.

Within-habitat regional variation in the structure of bird communities agreed with an ornithogeographic zonation that is also affected by the regionally varying proportions of different habitats. The main reason for the agreement was that the density variation of forest habitat generalists (*Fringilla montifringilla*, *Phylloscopus trochilus*, *C. flammea*, *Anthus trivialis*, *Muscicapa striata*) in old forests seemed to be similar to the overall regional density trends of these species in northern Finland. Species preferring old forests are probably more affected by differences in local factors between the study areas, such as size of the primeval forest area (e.g. *Parus cinctus*) and hunting (*Tetrao urogallus*).

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Introduction

Regional trends in the structure of bird communities, such as the latitudinal decrease in species diversity (MacArthur 1965, Tramer 1974) are generally known. In Finland the regionality of the whole breeding land bird fauna has been studied (qualitative data: Lehtonen 1951, quantitative data: Järvinen & Väisänen 1980). In this paper regional variation in the bird communities of old, virgin forests will be studied on a smaller scale, in a 300 km wide area of northern Finland (Lapland). I also compare variation within homogeneous forests with the zonation of Järvinen & Väisänen (1980) that is affected not only by within-habitat variation but also by variation in the proportions of different habitats among regions.

Regional variation in the structure of bird communities within a given habitat type have been studied both in North America and Europe (Cody 1975, Järvinen & Sammalisto 1976, Rabenold 1979, Short 1979, Tiainen 1980, Wiens & Rotenberry 1981, Järvinen et al. 1987). Variation in habitat structure is an important factor explaining variation among bird communities. Latitudinal changes in the diversity of habitat structure affect bird communities, as do also specific local features, such as the size of the forest area (for raised bogs, see Boström & Nilsson 1983). It has been observed that a change in the adjacent forest habitats (e.g. clear-cuts) will influence bird populations in virgin forests (Väisänen et al. 1986).

Many southern species of spruce forests do not reach the northern spruce forest margin. This can be caused, not only by variation in the habitat structure, but also by other environmental factors, such as adverse climatic conditions in the northern forests. Tiainen et al. (1983) have suggested that differences in the insulation of three *Phylloscopus* warblers' nests (the Willow Warbler *Phylloscopus trochilus*, the Chiffchaff *Ph. collybita*, the Wood Warbler *Ph. sibilatrix*) might explain differences in their northern range boundaries in Finland. The northern distribution of a spruce forest specialist, the Goldcrest *Regulus regulus*, seems to be limited by the ambient temperature during the breeding season (Haftorn 1978).

In this study I explore variation in bird communities of spruce and pine forests in Lapland between latitudes 66–69° N. Regional trends are particularly interesting in spruce forests because the northern forest limit of the spruce passes between the northernmost study areas.

Material and methods

Study areas

The location of the study areas is shown in Fig. 1. Riisitunturi is mainly covered by spruce-dominated forests with small hillside swamps. In Maltio, Sompio and Pallas both spruce- and pine-dominated heath forests are common (Toivonen & Vuokko 1972). The Pomokaira census area consists only of spruce-dominated forests. The Menesjärvi census area is situated north of the spruce forest limit and consists of pine-dominated forests. Spruce-dominated forests in all the areas are mixed with birch *Betula pubescens*, and comprise moist heath forests of the *Hylocomium-Myrtillus* (HMT) type (according to Finnish forest classification, see Kalela 1961). Pine-dominated heath forests belong to the *Myrtillus-Calluna-Cladina* (MCClT) or *Empetrum-Myrtillus* (EMT) type. In the area of Pallas there are lush, deciduous forests owing to the bedrock properties (Toivonen & Vuokko 1972). The productivity of these forest types increases in the order: MCClT, EMT and HMT. All forests censused were primeval and the canopy trees more than 150 years old.

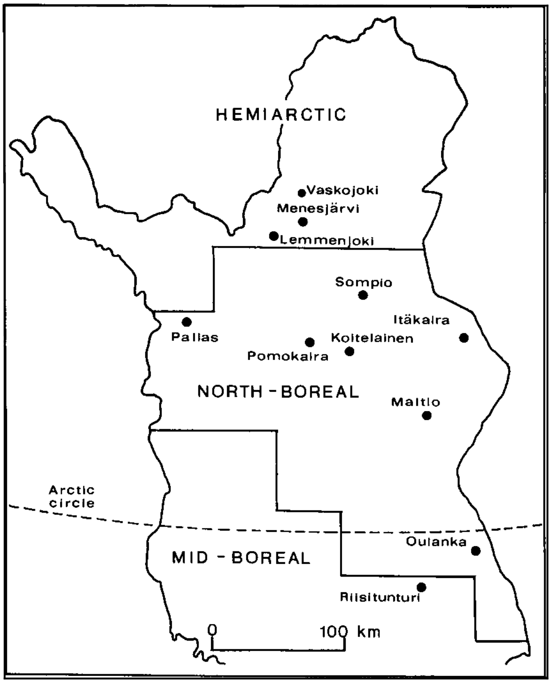

Fig. 1. Situation of the study areas in northern Finland. Ornithogeographic zonation presented by Järvinen & Väisänen (1980) is shown.

Table 1. The length of line transects (km) in different study areas and forest types in 1982–1986. The total area of the main belt is included (in parentheses, km^2). Survey belt data from pine forests of Riisitunturi in 1985 were not used. Areas are ordered from the south to the north.

Area	1982	1983	1984	1985	1986	Total	
Pine-dominated forests							
Riisitunturi	–	–	–	2.6	6.8	9.4	(0.47)
Maltio	–	–	–	23.0	–	23.0	(1.15)
Pallas	–	–	–	–	13.8	13.8	(0.69)
Sompio	10.0	11.8	8.1	8.1	8.1	46.1	(2.31)
Menesjärvi	–	5.7	4.1	5.4	–	15.2	(0.76)
Spruce-dominated forests							
Riisitunturi	–	–	–	–	36.8	36.8	(1.84)
Maltio	–	–	–	12.8	–	12.8	(0.64)
Pomokaira	–	7.8	8.8	6.5	6.0	29.1	(1.18)
Pallas	–	–	–	–	23.6	23.6	(1.18)
Sompio	14.8	14.8	15.9	15.5	10.1	71.1	(3.56)

Habitat variables

Habitat structure in the line transects (on the main belt, see next section) of the study areas was defined by using silvicultural maps, which contain homogeneous forest units. Each of these units is quantitatively described in explanatory files kept for forestry purposes. The following variables of homogeneous forest patches were taken into account (sample sizes in Table 2): 1) Cubic volume of the stand (m^3/hectare), 2) main stand height (m), 3) forest density (values 0 to 1), 4) proportion of birch (%) and 5) area of homogeneous forest patch (hectares).

Foliage volume, which is an important habitat variable for many bird species (e.g. foliage insectivores) was not measured, but it is reasonable to assume that the foliage and cubic volume of the stand have a close positive correlation within forest types.

The mean values of habitat variables in pine and spruce forests of different areas are presented in Table 1. Cubic volume and main stand height decrease evenly to the north reflecting the latitudinal gradient in forest habitats. In forest density the trend is not as clear. In spruce forests the proportion of birch is greater in the northern areas. The difference is statistically significant between, for example, Riisitunturi and both Pomokaira and Sompio (Mann-Whitney U-test, $P<0.001$). The northward decrease in the density of birch is probably connected with the decrease in the density of spruce. Similar trends are not found in barren pine forests because physical factors restrict the proportion of birch there (see, e.g., Kalliola 1973). There is considerable variation in the size of uniform forest patches, which probably has some effect on bird populations independent of regional density variation in bird species.

Bird censuses

Birds were censused in June 1982-86 using line transects (Järvinen & Väisänen 1976a). The average efficiency of one-visit censuses has often been estimated at 60–70% (e.g. Palmgren 1930, Järvinen 1978, Tiainen et al. 1980), although both lower and higher estimates have also been reported. The efficiency of the line transect census may increase to the north owing to the synchronised breeding season and openness of even wooded habitats (Järvinen et al. 1978, Helle 1986a).

The length of the transects are shown in Table 2. The birds were recorded separately on the 50 m wide main belt and outside the main belt (= the supplementary belt). Together they form the survey belt. Bird densities were calculated on the basis of both main and survey belt data. Densities were estimated from the survey belt data using the species-specific coefficients (K) of Järvinen & Väisänen (1983) from northern Finland. If the proportions of main and supplementary belt observations differed significantly from those of Järvinen & Väisänen (1983) (X^2-tests), a new species-specific correction coefficient (K) was calculated from the present data. The censuses of Riisitunturi were excluded from this comparison and were considered separately, because the censuses were carried out by other observers. In no species did the proportions of main and supplementary belt

Table 2. The mean values of habitat variables in pine and spruce forests of different areas. The forest density and proportion of birch in the stand were not measured in Pallas. N = number of homogeneous forest units.

Study area	Cubic volume of the stand (m^3/ha)	Main stand height (m)	Forest density	Proportion of birch (%)	Size of homogeneous forest (ha)	N
Pine forests						
Riisitunturi	93.5	16.2	0.84	12	33.9	10
Maltio	87.9	16.8	0.59	5	88.4	24
Pallas	71.8	14.5	–	–	121.2	20
Sompio	55.5	14.1	0.61	9	149.3	9
Menesjärvi	53.5	12.7	0.65	7	33.2	10
Spruce forests						
Riisitunturi	88.1	15.4	0.84	17	42.1	47
Maltio	80.0	14.9	0.60	18	88.4	7
Pomokaira	76.9	14.3	0.76	27	47.5	16
Pallas	65.0	13.5	–	–	129.2	20
Sompio	58.1	14.1	0.57	25	96.3	16

observations differ between Riisitunturi and the data of Järvinen & Väisänen (1983). In calculating the survey belt densities of Riisitunturi, all species-specific correction coefficients (K) were taken from Järvinen & Väisänen (1983), and density-dependent correction coefficients (y) were used.

For comparison of the communities of different areas and forest types, I also calculated the following parameters: species numbers were standardized using the method of rarefaction (Simberloff 1978); the bird communities in different study areas were compared using Renkonen's (1938) index of percentage similarity, $PS = \sum \min (p_{1i}, p_{2i})$, where p_{1i} and p_{2i} are the proportions of the *i* th species in samples 1 and 2; the dendrogram based on pairwise similarities was constructed according to Cody (1974); and the average weights of bird species were taken from von Haartman et al. (1963–72).

Results

Community parameters and structure

Total bird density in pine forests decreased northwards: the lowest densities were found in Sompio and Menesjärvi (Table 3), and the density difference between Sompio and Riisitunturi was statistically significant (main belt, $P<0.05$, X^2-test). In spruce-dominated forests there were no clear regional density trends. Both main and survey belt densities were almost similar in Riisitunturi (122 and 100 pairs/km^2, respectively), Pallas (111 and 95) and Sompio (113 and 108) in 1986. Locally there were differences in bird densities of spruce forests, because total density in Maltio was to some extent lower than in other areas for the same year (e.g. in Sompio 103 and 93 pairs/km^2).

Species numbers were compared between the areas using t-tests, so that the selected risk level (0.05) was divided by the number of pairwise comparisons (10). Differences in species numbers were significant ($P<0.005$) only in spruce forests between Riisitunturi and Pomokaira and between Riisitunturi and Sompio. Owing to smaller sample sizes in pine forests of Riisitunturi the differences in species numbers between this and other areas are not significant.

The biomass of bird pairs in spruce forests was clearly highest in Sompio and Maltio, which was mainly due to the high density of the Capercaillie *Tetrao urogallus* (see Table 5) in these areas. Because *T. urogallus* was also recorded in the pine forests of Riisitunturi, the biomass there was higher than in other pine forests.

Table 3. Parameters of bird communities in pine- and spruce-dominated forests. All years are combined. Densities (pairs/km^2) were calculated separately for the main belt (MB) and survey belt (SB). Other community parameters are based on survey belt observations. The expected number of species is presented in a random sample of 150 pairs ($E(S_{150})$). The smallest sample is from pine forests of Riisitunturi (n = 196). Standard deviation of species is shown. The biomass (kg/km^2) without *Tetrao urogallus* is in parentheses.

Study area	Density MB	Density SB	$E(S_{150})\pm SD$	Biomass	
Pine forests					
Riisitunturi	93.6	77.0	20.7±1.3	15.9	(3.0)
Maltio	75.7	71.4	19.1±2.0	3.6	(3.6)
Pallas	78.3	80.4	16.4±1.5	3.5	(3.5)
Sompio	57.3	62.1	17.7±1.8	6.5	(6.5)
Menesjärvi	55.3	57.3	17.3±1.4	5.1	(5.1)
Spruce forests					
Riisitunturi	121.7	100.4	19.7±2.1	12.7	(5.1)
Maltio	75.0	72.1	18.5±1.6	23.4	(4.1)
Pomokaira	88.0	90.8	16.2±1.9	5.4	(5.4)
Pallas	111.0	95.1	18.4±1.8	5.1	(5.1)
Sompio	92.0	90.8	15.8±1.9	22.9	(6.0)

There were three significant correlations between habitat variables and community parameters. In pine forests the total bird density correlated positively with the cubic volume ($r = 0.924$, $P<0.05$, $n = 5$) and biomass with forest density ($r= 0.970$, $P<0.05$, $n=4$). In spruce forests there was a negative correlation between the proportion of birch and species numbers ($r = -0.954$, $P<0.05$, $n = 4$).

The cluster analysis of both pine and spruce forests revealed four groups at the similarity level of 0.7 (level chosen arbitrarily): the northernmost census area Menesjärvi, the southernmost Riisitunturi and spruce and pine forests in other census areas (Fig. 2).

Dominant species

Tables 4–5 show the densities and proportions of species comprising more than 3% in at least two areas in the same forest type (survey belt data). The Brambling *Fringillla montifringilla* was the most abundant species in all areas, except in Riisitunturi, where *Ph. trochilus* was the dominant. The density of *Ph. trochilus* was highest in Riisitunturi, whereas *F. montifringilla* reached its highest densities in more northern areas: in the spruce forests of Sompio and in the pine forests of Maltio and Pallas.

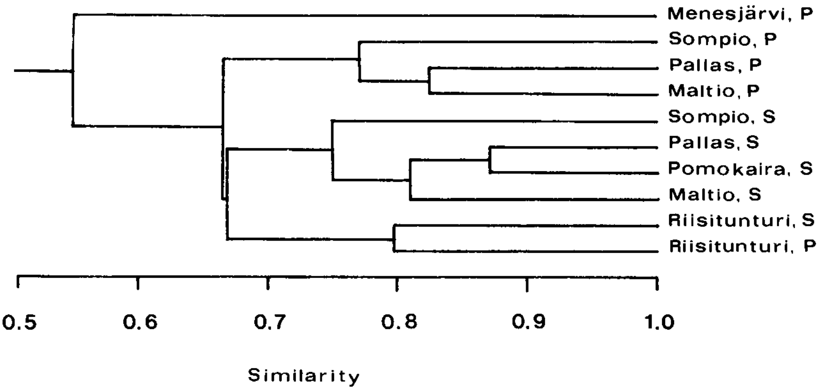

Fig. 2. Dendrogram based on percentage similarities of bird communities in pine (P) and spruce (S) forests of different areas.

The Redstart *Phoenicurus phoenicurus* prefers light pine forests, where it seemed to be equally common in all areas. The density of *Ph. phoenicurus* was clearly lower in spruce forests, except in Riisitunturi. The number of Redwing *Turdus iliacus* increased to the north both in pine and spruce forests. The Tree Pipit *Anthus trivialis* and the Spotted Flycatcher *Muscicapa striata* were scarcest in the northernmost study areas — Sompio and Menesjärvi.

Year-to-year variation in the densities of bird species may have an effect on the observed regional density variation, because censuses of some study areas were distributed over many years (e.g. in Sompio), whereas in Maltio censuses were carried out in 1985 and in Pallas and Riisitunturi (mainly) in 1986. In the virgin forests of Sompio in 1982–1986 the density of *F. montifringilla* was at its lowest in 1986 (Virkkala, unpubl.), but nevertheless was more

Table 4. Densities (pairs/km^2) and proportions of most common species (proportion 3% in at least two study areas) in pine forests according to survey belt observations. The irregularly fluctuating *Carduelis flammea* has been excluded due to having had a peak year in 1986.

Species	Riisitunturi		Maltio		Pallas		Sompio		Menesjärvi	
	p/km^2	%	p/km^2	%	p/km^2	%	p/km^2	%	p/km^2	%
Fringilla montifringilla	18.8	25.8	29.2	42.4	29.4	40.1	23.9	41.4	21.9	40.2
Phylloscopus trochilus	21.2	29.1	6.6	9.6	7.1	9.7	7.3	12.7	7.9	14.5
Phoenicurus phoenicurus	8.8	12.1	6.5	9.4	7.4	10.1	6.8	11.8	6.8	12.5
Muscicapa striata	9.9	13.6	7.0	10.2	13.7	18.7	0.9	1.6	–	–
Anthus trivialis	4.0	5.5	3.8	5.5	2.9	4.0	0.8	1.4	0.8	1.5
Parus cinctus	1.2	1.6	3.1	4.5	2.6	3.5	2.8	4.9	3.3	6.1
Turdus iliacus	0.5	0.7	0.5	0.7	1.5	2.0	2.6	4.5	3.5	6.4
Perisoreus infaustus	–	–	3.1	4.5	1.9	2.6	2.0	3.5	2.8	5.1
Oenanthe oenanthe	–	–	2.0	2.9	1.1	1.5	4.3	7.5	1.9	3.5

Table 5. Densities (pairs/km^2) and proportions of most common species in spruce forests. Explanations as in Table 4.

Species	Riisitunturi		Maltio		Pomokaira		Pallas		Sompio	
	p/km^2	%	p/km^2	%	p/km^2	%	p/km^2	%	p/km^2	%
Fringilla montifringilla	19.7	21.2	29.1	42.2	32.4	39.0	29.8	36.0	39.6	46.7
Phylloscopus trochilus	28.5	30.6	10.6	15.4	19.5	23.5	18.3	22.1	14.0	16.5
Muscicapa striata	10.3	11.1	5.3	7.7	8.3	10.0	10.3	12.5	2.7	3.2
Turdus iliacus	1.2	1.3	2.0	2.9	3.5	4.2	2.9	3.5	7.1	8.4
Anthus trivialis	4.4	4.7	2.3	3.3	2.0	2.4	1.1	1.3	1.0	1.2
Phoenicurus phoenicurus	7.5	8.1	3.6	5.2	4.0	4.8	3.0	3.6	2.4	2.8
Parus cinctus	0.3	0.3	3.4	4.9	0.3	0.4	2.0	2.4	3.2	3.8
Emberiza rustica	3.0	3.2	1.3	1.9	3.0	3.6	2.7	3.3	1.8	2.1
Tetrao urogallus	1.3	1.4	3.3	4.8	–	–	–	–	2.9	3.4

abundant in the spruce forests of Sompio in 1986 than elsewhere. The densities of *Ph. trochilus* and *Phoenicurus phoenicurus* in 1986 were on an average level, whereas *T. iliacus* was particularly abundant in Sompio in 1986 (Virkkala, unpubl.).

Variation in the densities of *Tetrao urogallus* and the Siberian Tit *Parus cinctus* seems not to have any geographical trend in my data. *T. urogallus* was common in spruce forests in Sompio and Maltio, but was lacking from Pomokaira and Pallas. *P. cinctus* clearly had the lowest densities in Riisitunturi and Pomokaira.

The Redpoll *Carduelis flammea* has been excluded from the above analysis, because it had a peak year in 1986. In 1986 the density of *C. flammea* was lowest in the southernmost census area, Riisitunturi.

Southern vs. northern species

Northern taiga species *Parus cinctus*, the Siberian Jay *Perisoreus infaustus*, Waxwing *Bombycilla garrulus*, Pine Grosbeak *Pinicola enucleator* and the Three-toed Woodpecker *Picoides tridactylus* prefer virgin, old forests, and most of the southern species observed (the Hazel Hen *Bonasa bonasia*, Green Sandpiper *Tringa ochropus*, Dunnock *Prunella modularis*, *Phylloscopus collybita*, *Ph. sibilatrix*, *Regulus regulus*, Robin *Erithacus rubecula*, Song Thrush *Turdus philomelos*, Crested Tit *Parus cristatus*, Great Tit *P. major*, Treecreeper *Certhia familiaris*, Bullfinch *Pyrrhula pyrrhula*, Chaffinch *Fringilla coelebs* and Siskin *Carduelis spinus*) prefer spruce-dominated forests. These groups have been selected mainly by using the classifications of Järvinen & Väisänen (1979a) and Väisänen et al. (1986). I tested whether there are regional trends in the combined densities of these groups (Table 6).

Table 6. Density (pairs/km^2) and frequency (%, in parentheses) of northern and southern species (see text) according to main (MB) and survey belt (SB) observations in spruce forests of different areas.

Area	Southern species		Northern species	
	MB	SB	MB	SB
Riisitunturi	11.4 (10.7)	7.6 (8.2)	2.7 (2.5)	3.5 (3.8)
Maltio	– –	2.8 (4.1)	4.7 (6.4)	4.1 (5.9)
Pomokaira	0.7 (0.9)	3.1 (3.7)	3.4 (4.3)	3.5 (4.2)
Pallas	6.8 (7.4)	6.2 (7.5)	5.9 (6.5)	4.0 (4.8)
Sompio	4.2 (4.9)	3.9 (4.6)	5.3 (6.3)	6.5 (7.7)

The density of southern species was highest in Riisitunturi and second highest in Pallas, whereas northern species were most abundant in Pallas and Sompio. The densities of northern and southern species (survey belt) did not correlate significantly ($r = -0.275$, ns, $n = 5$).

Discussion

Comparison with earlier studies

Bird densities of pine and spruce forests obtained in this study agree moderately well with those of earlier studies (Table 7, the location of the study areas in Fig. 1). Bird densities in Vaskojoki and Lemmenjoki are in good accordance with the bird density of the adjacent Menesjärvi census area as are also densities in birch-spruce and pine forests of Koitelainen compared with the corresponding forests in Pomokaira and Sompio (see Table 3). However, the bird density in the spruce forests of Riisitunturi is to some extent higher than that of the adjacent Oulanka (Helle & Sulkava 1986, this study).

Table 7. Bird density according to other censuses carried out in the old coniferous forests of northern Finland. Size of the censused area is presented in parentheses. L = line transect, S = study plot method.

Study area (km^2)	Forest type	Year(s)	Method	Bird density (pairs/km^2)	Source
Riisitunturi (0.58)	spruce	1981	L	125.8	Helle & Sulkava 1986
Oulanka (1.56)	spruce	1968–71	L	92.9	Hakala & Sulkava 1978
Oulanka (1.36)	spruce	1980–82	L	79.0	Helle 1985a
Oulanka (1.20)	pine	1980–82	L	45.0	Helle 1985a
Koitelainen (0.64)	pine	1965	L	49.8	Haapanen et al. 1966
Koitelainen (1.05)	birch–spruce	1965	L	107.6	Haapanen et al 1966
Itäkaira (0.88)	pine	1971	S	82.0	Saari 1977
Vaskojoki (2.03)	pine	1961	S	53.7	Bagge et al. 1963
Lemmenjoki (0.90)	pine	1937	S	58.9	Granit 1938

Regional trends of bird communities

Why does bird density decrease northwards in pine forests, but not in spruce forests, even though the cubic volume (and probably also foliage volume) seems to have a similar latitudinal trend in these forest types? A plausible explanation is that the higher proportion of birch in spruce forests of the northern study areas increases the foliage diversity. This can be advantageous to foliage insectivores, which comprise 50–70% of the bird communities, as it can also be to some seed eaters (*Carduelis flammea*). For example, Alatalo (1982) observed that migratory foliage insectivores, such as *Fringilla montifringilla* and *Phylloscopus trochilus*, forage particularly in deciduous trees.

Also, foliage height diversity probably increases to the north in spruce forests due to the increase in the proportion of birch, because spruce tend to be 14–15 m, but birch only 6 m tall. MacArthur & MacArthur (1961) observed a close positive correlation between bird species diversity and foliage height diversity. This correlation has been confirmed in several later studies, although in many cases the relationship between bird species diversity and foliage height diversity has been ambiguous or non-existent (for references, see Wiens 1983). In the present study, increase in foliage height diversity seems not to increase species numbers. On the contrary, bird species numbers in spruce forests were lowest in the northern study areas, Pomokaira and Sompio.

The northward decrease in species numbers in spruce forests is probably a consequence of the fact that many southern species of spruce forests do not reach the spruce forest limit. This may be due to adverse climatic conditions rather than variation in habitat structure. Whether species numbers decrease to the north also in pine forests is ambiguous due to smaller sample sizes in my data. Tiainen (1980) did not find differences in bird species diversity in pine forests between Poland, central Finland and northern Finland, but he compared very heterogeneous census data (see Wiens 1983).

Effect of local environmental factors on bird populations

Local environmental factors, such as the area of homogeneous forest patches and the structure of surrounding habitats influence bird populations in virgin forests. Size of homogeneous forest blocks is not constant in the study areas. Although homogeneous forests are distinguished on the basis of both isolation and differences in habitat variables (e.g. tree species composition), variation in the size of homogeneous forest probably affects species preferring forest edges and small areas, (e.g., *Turdus iliacus* and *Ph. trochilus*; Helle 1984, Virkkala, unpubl.). There is also considerable variation in the structure of forest habitats surrounding virgin forests. For example, Riisitunturi is mainly enclosed by managed forests, whereas Sompio is connected to a large virgin forest area (UKK-Koilliskaira National Park).

Ph. trochilus was most abundant in Riisitunturi, but the small forest size may have a positive effect on the density of the species. The high density of *Phoenicurus phoenicurus* in the spruce forests of Riisitunturi can also be due to smaller forest patches in this area. In Sompio *Ph. phoenicurus* is more abundant in small spruce forest fragments than in large, uniform forests (Virkkala, unpubl.).

T. iliacus increased to the north in virgin forests, although regionally in northern Finland the density of the species varies little (Järvinen & Väisänen 1980). The greater proportion of birch in northern spruce forests can be advantageous to *T. iliacus*, but variation in the proportion of birch cannot explain the trend in pine forests. *T. iliacus* is more abundant in managed than in old forests (Helle 1986b, Virkkala, unpubl.). Around Riisitunturi and Maltio there are large forest regeneration areas, in which *T. iliacus* is relatively abundant (M. Vickholm, pers. comm.; own observations), whereas similar areas are not found near Sompio. It is possible that the low density of *T. iliacus* in Riisitunturi and Maltio is caused by the fact that these areas are surrounded by forest regeneration areas, which are more suitable to *T. iliacus* than large, old forests.

Parus cinctus prefers large, uniform forests (Virkkala 1985 and unpubl.), and the species has, therefore, declined during the last few decades due to large-scale clearcuttings, which were started in northern Finland in the 1950s (Järvinen & Väisänen 1979b, Järvinen et al. 1977). The influence of adjacent forest regeneration areas (see Väisänen et al. 1986) can be reflected in the low density of *P. cinctus* in Riisitunturi and Pomokaira.

The high density of *Tetrao urogallus* in spruce forests of Sompio and Maltio compared with other areas was probably caused by the fact that these areas are Nature Reserves, in which hunting is either forbidden (Sompio) or restricted (Maltio). In certain areas in Finland the protection of *T. urogallus* has had a positive effect on its numbers (Lindén 1981).

Southern species are usually found in the most productive habitats near the northern margin of their ranges. The abundance of southern species in the coniferous forests of Pallas (Table 6) may be due to the occurrence of lush, deciduous forests in close vicinity to coniferous forests. For example, the density of *Fringilla coelebs* in spruce forests of Pallas was 1.5 pairs/km² (survey belt, n = 12), whereas this species was not observed in censuses in Sompio, where many more censuses were made (Table 2).

Ornithogeographic zonation

In their ornithogeographic zonation, based on the proportions and abundances of bird species in different areas, Järvinen & Väisänen (1980) separated three zones in northern Finland: the mid-boreal, the north-boreal and the hemiarctic (see Fig. 1). Riisitunturi is situated at the border between the mid- and north-boreal zones, Menesjärvi in the southern part of the hemiarctic zone, while the other areas are located in the north-boreal zone. Differences in the bird community structure of old forests seem to agree with this zonation: bird communities were most similar to each other in old forests situated in the north-boreal zone (Fig. 2). The distinction between the hemiarctic and the north-boreal zone was partly due to the southwardly rising frequencies of *Anthus trivialis* and *Muscicapa striata* (Järvinen & Väisänen 1980). These trends can also be observed also in virgin forests (see Table 4). Regionally the density of *Fringilla montifringilla* was highest in the north-boreal zone, as it was in the forests situated in this zone.

Bird communities of virgin forests fit well with the observed regionality of the bird fauna: the overall regional density variation of the most common forest passerines (*F. montifringilla, Phylloscopus trochilus, Carduelis flammea, Turdus iliacus, A. trivialis, M. striata*; Järvinen & Väisänen 1980) is similar to the variation in virgin forests (except in *T. iliacus*). These species comprise about 80% of the bird community in spruce forests and about 70% in pine forests. They are all forest habitat generalists (Helle 1985b) and are thus not dependent on the distribution of virgin, climax forests.

Within-habitat regional density trends of species clearly preferring virgin forests (northern taiga species, *Ph. phoenicurus, T. urogallus*) are more affected by local environmental factors, such as the size of virgin forest and the proportion of these forests in a larger area. These species comprise, however, only a minor proportion of the bird community in terms of pair numbers (but not in terms of biomass, see Table 3).

Impoverishment of the bird fauna in northern forests

Because of the great similarity of bird communities in pine and birch forests Järvinen & Väisänen (1976b, 1980) suggested that the avifauna is impoverished in the forests of northernmost Lapland (northern part of the north-boreal zone and the hemiarctic zone). They assumed that the impoverishment is due to the fact that the forests of northern Lapland are the northwestern tip of the taiga (peninsular effect). In order to estimate whether the bird communities of pine and spruce forests become more similar towards the north, I compared their percentage similarities in four study areas (survey belt):

Riisitunturi	83.7
Maltio	75.6
Pallas	74.4
Sompio	76.1

The percentage similarity of pine and spruce forest bird communities does not increase towards the north in my data.

Haila (1983) compared bird communities in similar forest habitats in Finnish Lapland, northern Russia and western Siberia, and found that average densities and species numbers were almost identical in these three communities. He concluded that the decrease in the number of forest birds in the Finnish hemiarctic zone is probably due to the lack of spruce forests there and is not due to the peninsular effect.

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Selostus: **Pohjois-Suomen vanhojen havumetsien lintuyhteisöjen maantieteellinen vaihtelu**

Pohjois-Suomen vanhojen havumetsien lintuyhteisöjen rakennetta ja alueellisia eroja tutkittiin vuosina 1982–86. Lintuja

laskettiin linjalaskentamenetelmällä sekä mänty- että kuusivaltaisissa metsissä viidellä alueella Lapissa (taulukko 1, kuva 1). Laskentatuloksista tarkasteltiin seuraavia tunnuslukuja: linnuston tiheys, lajimäärä (standardoitu ns. rarefaktio-menetelmällä) ja biomassa (taulukko 3). Yhteisöjen rakennetta verrattiin Renkosen prosenttisella samankaltaisuudella. Laskenta-alueiden metsien rakennetta analysoitiin käyttäen hyväksi Metsähallituksen metsätalouskarttojen selitysten ympäristömuuttujia (kuutiomäärä/ha, metsän valtapituus, metsän tiheys, koivun osuus puustosta, metsäkuvion pinta-ala, taulukko 2).

Männiköissä lintutiheyden väheneminen pohjoiseen korreloi positiivisesti kuutiomäärän vähenemiseen. Kuusikoissa ei vastaavaa ollut havaittavissa. Tämän oletetaan johtuvan koivun osuuden lisääntymisestä pohjoiseen tutkituissa kuusivaltaisissa metsissä. Koivun osuuden kasvu todennäköisesti suosii muuttavia hyönteissyöjälajeja ja siemensyöjiä, kuten urpiaista. Lajimäärä väheni merkitsevästi pohjoiseen kuusivaltaisissa metsissä. Tämä johtui osaksi eteläisten kuusivaltaisia metsiä suosivien lajien lukumäärän ja tiheyden vähenemisestä pohjoiseen (taulukko 6).

Havumetsien lintuyhteisöjen rakenteessa havaittu alueellinen vaihtelu (kuva 2) vastasi varsin hyvin lintumaantieteellistä vyöhykejakoa, johon vaikuttaa kuitenkin myös eri biotooppien osuuden alueellinen vaihtelu. Tämä johtui todennäköisesti siitä, että metsien yleislajien (järripeippo, pajulintu, harmaasieppo, metsäkirvinen, urpiainen, taulukot 4 ja 5) tiheysvaihtelu vanhoissa havumetsissä oli samankaltainen kuin näiden lajien alueellinen tiheysvaihtelu koko Pohjois-Suomessa. Nämä lajit muodostavat 70-80% vanhojen metsien lintuyhteisöjen parimääristä. Paikalliset tekijät vaikuttavat enemmän vanhoja havumetsiä suosivien lajien esiintymiseen. Näihin lajeihin vaikuttavia paikallisia tekijöitä ovat esim. metsäalueen koko (lapintiainen) ja metsästys (metso).

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Appendix 1. Main/survey belt densities (pairs/km^2) and the corresponding number of observations (n) in pine forests of different areas. Only survey belt data from 1986 in Riisitunturi have been used (see Table 1).

Species	Riisitunturi		Maltio		Pallas		Sompio		Menesjärvi	
	p/km^2	n	p/km^2	n	p/km^2	n	p/km^2	n	p/km^2	n
Falco columbarius	–	–	–	–	–	–	–/0.1	–/2	–	–
Lagopus lagopus	–	–	–	–	–	–	2.2/2.4	5/11	1.3/1.3	1/2
Tetrao urogallus	2.1/2.2	1/1	–	–	–	–	–	–	–	–
Numenius phaeopus	–	–	–/0.1	–/2	–	–	0.9/0.5	2/22	1.3/0.5	1/8
Tringa ochropus	–/0.4	–/1	–/0.5	–/4	–/0.2	–/1	–	–	–	–
T. erythropus	–/0.5	–/1	0.9/0.2	1/1	–	–	–/0.1	–/1	–/0.4	–/2
T. nebularia	–/0.3	–/2	–/0.1	–/3	–	–	–/0.05	–/2	–/0.1	–/2
Cuculus canorus	–/0.4	–/4	–/0.8	–/29	–/0.6	–/12	–/0.5	–/37	–/0.5	–/11
Surnia ulula	–	–	–	–	–	–	0.4/0.1	1/1	–/0.3	–/1
Apus apus	–	–	–/0.1	–/2	–	–	–	–	–	–
Picoides tridactylus	–	–	0.9/0.3	1/1	–	–	0.4/0.1	1/1	–	–
Dryocopus martius	–	–	–/0.03	–/1	–/0.1	–/1	–/0.02	–/1	–	–
Anthus trivialis	2.1/4.0	1/11	3.5/3.8	4/56	–/2.9	–/26	0.4/0.8	1/23	–/0.8	–/8
Motacilla flava	–/0.6	–/2	–/0.5	–/6	–	–	–/0.2	–/4	–	–
M. alba	–	–	–	–	–	–	–/0.2	–/2	–	–
Bombycilla garrulus	–	–	–	–	–	–	–/0.05	–/1	1.3/0.6	1/4
Perisoreus infaustus	–	–	2.6/3.1	3/8	2.9/1.9	2/3	2.2/2.0	5/11	–/2.8	–/5
Corvus corone	–	–	–/0.1	–/1	–	–	–	–	–	–
C. corax	–	–	0.9/0.02	1/1	–/0.1	–/2	–/0.1	–/10	–	–
Prunella modularis	–/0.8	–/2	–	–	–	–	–/0.05	–/1	–	–
Phylloscopus trochilus	29.9/21.2	14/56	2.6/6.6	3/72	1.4/7.1	1/46	3.5/7.3	8/156	9.2/7.9	7/56
Ph. collybita	–/0.3	–/1	–	–	–	–	–	–	–	–
Ph. sibilatrix	–	–	–	–	–	–	–/0.05	–/1	–	–
Ph. borealis	–	–	–	–	–	–	–/0.1	–/1	–	–
Ficedula hypoleuca	2.1/1.6	1/3	1.7/1.7	2/19	2.9/1.9	2/13	0.4/0.3	1/6	1.3/0.4	1/3
Muscicapa striata	10.7/9.9	5/5	6.1/7.0	7/12	8.7/13.7	6/14	1.7/0.9	4/4	–	–
Oenanthe oenanthe	–	–	2.6/2.0	3/9	–/1.1	–/3	3.0/4.3	7/40	2.6/1.9	2/6
Phoenicurus phoenicurus	8.6/8.8	4/24	7.0/6.5	8/80	5.8/7.4	4/55	6.9/6.8	16/168	13.2/6.8	10/73
Luscinia svecica	–	–	–	–	–	–	–	–	–/0.8	–/3
Erithacus rubecula	–/0.5	–/1	–	–	–/0.3	–/1	–	–	–	–
Turdus iliacus	2.1/0.5	1/1	–/0.5	–/5	5.8/1.5	4/8	2.6/2.6	6/47	1.3/3.5	1/25
T. philomelos	2.1/1.1	1/5	0.9/0.6	1/15	–/0.1	–/2	–/0.5	–/24	1.3/0.8	1/13
T. viscivorus	–/0.3	–/1	–/0.3	–/3	–/0.2	–/1	–	–	–	–
T. pilaris	–	–	–	–	–	–	–/0.1	–/1	–	–
Parus cinctus	2.1/1.3	1/1	5.2/3.1	6/8	2.9/2.6	2/4	3.9/2.8	9/15	6.6/3.3	5/6
P. cristatus	2.1/1.2	1/1	–	–	–	–	–	–	–	–
Certhia familiaris	–	–	–/0.4	–/1	–	–	–	–	–	–
Fringilla coelebs	–	–	–	–	–/0.6	–/3	–	–	–	–
F. montifringilla	23.5/18.8	11/47	38.3/29.2	44/254	34.8/29.4	24/153	25.2/23.9	58/432	14.5/21.9	11/131
Carduelis spinus	–/1.4	–/5	–/0.2	–/3	–	–	–/0.04	–/1	–/0.1	–/1
C. flammea	4.3/4.1	2/12	1.7/2.6	2/27	11.6/7.0	8/43	3.5/4.4	8/95	1.3/2.8	1/20
Pinicola enucleator	–	–	0.9/0.6	1/2	1.4/1.1	1/2	–/0.3	–/2	–	–
Loxia sp.	–/1.5	–/9	–/0.1	–/3	–/0.6	–/8	–/0.4	–/16	–/0.1	–/1
Emberiza rustica	–	–	–	–	–	–	–/0.2	–/1	–	–

Appendix 2. Main/survey belt densities (pairs/km^2) and the corresponding number of observations (n) in spruce forests of different areas.

Species	Riisitunturi		Maltio		Pomokaira		Pallas		Sompio	
	p/km^2	n	p/km^2	n	p/km^2	n	p/km^2	n	p/km^2	n
Buteo lagopus	–	–	–	–	–	–	0.8/0.3	1/1	–	–
Accipiter gentilis	–	–	–	–	–/0.2	–/1	–	–	–	–
Lagopus lagopus	–	–	1.6/0.8	1/1	0.7/0.4	1/1	0.8/0.5	1/1	0.6/1.2	2/8
Tetrao urogallus	1.1/1.3	2/3	4.7/3.3	3/3	–	–	–	–	2.8/2.9	10/14
T. tetrix	–/0.4	–/4	–	–	–/0.1	–/1	–	–	–/0.05	–/1
Bonasa bonasia	0.5/0.3	1/1	–	–	–	–	0.8/0.9	1/2	–	–
Tringa ochropus	–/0.2	–/2	–/0.2	–/1	–/0.1	–/1	–	–	0.3/0.1	1/2
T. erythropus	–/0.1	–/1	–	–	–	–	–	–	–	–
T. nebularia	–/0.1	–/3	–	–	–	–	–	–	–	–
Cuculus canorus	1.1/1.0	2/48	–/0.6	–/11	–/0.6	–/25	0.8/0.6	1/20	0.3/0.6	1/61
Surnia ulula	–	–	–/0.4	–/1	0.7/0.6	1/3	–	–	–/0.2	–/2
Apus apus	–/0.02	–/1	–	–	–	–	–	–	–	–
Picoides tridactylus	–/0.4	–/2	–	–	–	–	–	–	–	–
Dryocopus martius	–	–	–	–	–	–	–	–	–/0.01	–/1
Jynx torquilla	–/0.03	–/1	–	–	–/0.04	–/1	–	–	–	–
Anthus trivialis	3.8/4.4	7/62	1.6/2.3	1/19	2.1/2.0	3/38	3.4/1.1	4/17	1.7/1.0	6/48
Motacilla flava	1.1/1.8	2/9	1.6/0.8	1/5	–/0.1	–/2	–	–	–/0.1	–/4
Bombycilla garrulus	–	–	–	–	–	–	–/0.1	–/1	–	–
Perisoreus infaustus	1.1/1.3	2/5	1.6/0.7	1/1	2.1/1.6	3/5	1.7/1.2	2/3	0.8/1.5	3/12
Corvus corax	–	–	–/0.04	–/1	–/0.05	–/3	–	–	–/0.02	–/3
Troglodytes troglodytes	–	–	–	–	–	–	–/0.2	–/1	–	–
Prunella modularis	1.6/0.4	3/5	–	–	–	–	–/0.5	–/4	0.6/0.4	2/10
Phylloscopus trochilus	32.4/28.5	59/387	17.2/10.6	11/63	20.6/19.5	30/264	18.6/18.3	22/201	11.8/14.0	42/463
Ph. collybita	–/0.05	–/1	–	–	–	–	–/0.1	–/1	–/0.03	–/1
Ph. sibilatrix	–/0.1	–/1	–	–	–	–	–	–	–	–
Ph. borealis	–	–	–	–	–	–	–	–	–/0.05	–/1
Regulus regulus	0.5/1.1	1/6	–	–	–/0.4	–/2	–/0.3	–/1	–/0.5	–/6
Ficedula hypoleuca	2.7/1.2	5/12	–/1.4	–/9	1.4/1.4	2/21	–/1.4	–/17	0.3/0.2	1/5
Muscicapa striata	7.1/10.3	13/28	6.3/5.3	4/5	5.5/8.3	8/18	6.8/10.3	8/18	2.0/2.7	7/14
Oenanthe oenanthe	–	–	1.6/0.8	1/2	–	–	–	–	–	–
Phoenicurus phoenicurus	9.9/7.5	18/105	3.1/3.6	2/25	2.7/4.0	4/63	1.7/3.0	2/38	2.3/2.4	8/90
Luscinia svecica	–	–	–/0.3	–/1	–/0.3	–/2	–	–	–/0.2	–/3
Erithacus rubecula	0.5/0.5	1/5	–/0.5	–/2	–	–	1.7/0.6	2/4	0.3/0.2	1/3
Turdus iliacus	0.5/1.2	1/12	3.1/2.0	2/10	4.1/3.5	6/41	2.5/2.9	3/27	5.3/7.1	19/200
T. philomelos	2.7/1.8	5/42	–/1.2	–/16	0.7/1.9	1/58	0.8/1.3	1/32	3.1/2.2	11/166
T. viscivorus	0.5/0.3	1/4	–	–	–/0.2	–/2	–	–	–	–
Parus montanus	0.5/0.2	1/1	–	–	–/0.2	–/1	–/1.1	–/4	–	–
P. cinctus	–/0.3	–/1	3.1/3.4	2/5	0.7/0.3	1/1	3.4/2.0	4/5	3.9/3.2	14/25
P. major	0.5/0.1	1/1	–	–	–	–	–	–	–	–
Certhia familiaris	0.5/0.2	1/1	–	–	–	–	–	–	–	–
Fringilla coelebs	–/0.9	–/11	–	–	–/0.1	–/1	1.7/1.5	2/12	–	–
F. montifringilla	27.5/19.7	50/252	28.1/29.1	18/141	33.7/32.4	49/349	39.0/29.8	46/249	46.4/39.6	165/1033
Pyrrhula pyrrhula	–/0.1	–/1	–	–	–	–	–/0.4	–/4	–	–
Carduelis spinus	4.4/1.4	8/25	–/0.1	–/1	–/0.5	–/7	1.7/0.6	2/7	–/0.4	–/15
C. flammea	14.8/7.4	27/112	1.6/3.1	1/18	8.9/7.7	13/98	19.5/12.4	23/123	6.5/6.0	23/185
Pinicola enucleator	1.6/1.5	3/7	–	–	0.7/1.0	1/4	0.8/0.7	1/2	0.6/1.8	2/17
Loxia sp.	1.6/1.1	3/35	–/0.3	–/3	0.7/0.3	1/7	0.8/0.6	1/12	0.8/0.4	3/24
Emberiza rustica	3.8/3.0	7/12	–/1.3	–/2	2.7/3.0	4/10	3.4/2.7	4/7	1.7/1.8	6/15