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SOCIETAS PRO FAUNA ET FLORA FENNICA

ACTA ZOOLOGICA FENNICA

145

Olli Järvinen and **Risto A. Väisänen**

Species diversity of Finnish birds,
II: Biotopes at the transition between taiga and tundra

HELSINKI—HELSINGFORS
1976

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ACTA ZOOLOGICA FENNICA 145
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SOCIETAS PRO FAUNA ET FLORA FENNICA

SPECIES DIVERSITY OF FINNISH BIRDS, II: BIOTOPES AT THE TRANSITION BETWEEN TAIGA AND TUNDRA

Olli Järvinen and Risto A. Väisänen

HELSINKI—HELSINGFORS
Oct. 1976

ISBN 951-661-015-3
ISSN 0001—7299

Abstract

Järvinen, Olli & Väisänen, Risto A. (Department of Genetics, University of Helsinki): Species diversity of Finnish birds, II: Biotopes at the transition between taiga and tundra. — Acta Zool. Fennica 145:1—35. 1976.

A method of classification developed from the Shannon index of diversity has been used to examine both the species composition and the densities of species. A biotope classification is presented that is applicable to the northern boreal and hemiarctic zoogeographical zones of Finland (the transition between taiga and tundra). Eleven biotopes are distinguished on the basis of ornithological data from 32 censuses of breeding land birds, performed in the study area in the period 1937—74.

The classification is found to be applicable to new censuses and, with the aid of the extensive line transect material available from Finland, it is shown that it can be used to predict the structure of the total bird fauna in the northernmost parts of the country.

The eleven biotopes are ordered in a vertical series of eight open biotopes (from stony ground on fell tops down to peatlands and burned areas surrounded by coniferous taiga forests), and three forest biotopes (from mountain birch forests to coniferous taiga forests). The bird communities of the biotopes are described, with densities, frequencies, and diversities.

There is considerable heterogeneity among the open biotopes, but the bird communities vary little between the forest biotopes. The difference can be explained by the facts that (1) waders divide the environment in terms of wetness, but other species (in effect passerines) divide it in terms of openness; (2) the importance of horizontal separation may decrease in vertically divisible biotopes; (3) the northern forests have impoverished bird communities, which facilitates habitat expansion of the species, while the open biotopes show no signs of species impoverishment; and (4) there is less geographical variation among the forest censuses than among the censuses of open biotopes. None of these factors can alone explain the results.

The number of biotopes occupied differs with the species. The most successful species are (1) behaviourally flexible with respect to habitat tolerance (especially the phylogenetically young passerines), (2) able to utilize resources that are common (i.e. abundant in at least one of the biotopes), or (3) not marginal in northern Finland.

The proportions of non-migrant species and individuals are correlated with the seasonal stability of the biotopes. Several non-migrant species occurred in the forests, but only two (*Lagopus mutus* and *L. lagopus*) in the open biotopes. The non-migrants are less abundant both in single biotopes and in larger regions than the migrants. The difference appears to be due to the larger size of the non-migrants.

Scandinavian censuses performed in subalpine and alpine biotopes are discussed. The bird communities in the more continental Finnish Lapland are poorer in individuals and species than the communities in the more maritime Scandinavian mountains.

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Contents

I. INTRODUCTION

The purposes of the present study are the following:

(1) To summarize the results of breeding bird censuses performed in the northern boreal and hemiarctic zoogeographic zones of Finland (see Järvinen & Väisänen 1973: Fig. 11);

(2) To develop a biotope classification based solely on ornithological data that is applicable to the two zoogeographical zones, and to describe the bird communities of those biotopes;

(3) To investigate the suitability of the classification; and

(4) To discuss the findings, with special reference to the bird community structure.

II. STUDY AREA

Our study area (Fig. 1) does not include the Norwegian coast, but is restricted to biotopes where seashore species do not usually occur. The northernmost corners of the area touch the arctic region (e.g. Salomonsen 1972: Fig. 1). Tundra or similar vegetation is present in the northern parts, though it is not clear whether any of the vegetation can properly be called arctic (Ahti et al. 1968). The boreal coniferous forests have their northern boundary roughly along the line Enontekiö—Inari (Fig. 1). In most of the area, the thermal growing period (days with average daily temperature of at least +5°C) does not exceed 125 days. The average annual temperature is mostly between —2°C and 0°C (Kolkki 1966).

A vegetational zonation scheme, based on the vegetation of mineral soils, has been presented and discussed, with abundant references to the botanical literature, by Ahti et al. (1968). A similar scheme, based on peatland vegetation, is given by Eurola (1968). Detailed information on the different plant communities is available in three botanical monographs, by Kalliola (1939), Ruuhijärvi (1960), and Hämet-Ahti (1963).

Extensive line transect data are available on the numbers of land birds breeding in Finland (see Järvinen & Väisänen 1973, for details of about 2/3 of the material used here). The so-called survey belt data can be transformed to densities (pairs per km^2; see Järvinen & Väisänen 1975 and Järvinen 1976). Certain basic parameters describing the structure of the avifauna in the study area are given in Table 1, and a list with more detailed information is available from the authors. We have classified the waders and *Stercorarius longicaudus* as land birds, in contrast to most authors (see Järvinen & Väisänen 1976b).

Comparisons between the census results of the

Table 1. Certain parameters of the structure of the avifauna in the northern boreal and hemiarctic zoogeographical zones of Finland (Forest and Fell Lapland, respectively). The data come from line transect studies, and the estimates are based on the linear model of Järvinen & Väisänen (1975).

	Northern boreal zone	Hemiarctic zone
Line transect km	172.7	216.3
Density of land birds	73.3 p/km^2	84.8 p/km^2
Species observed	75	71
Diversity (H')	3.15	2.99

northern boreal and the hemiarctic zones reveal a relatively sharp change at the transition from taiga to tundra. (Note that the northern boreal zone is not 'pure' taiga, and the hemiarctic zone is not 'pure' tundra; the terminology used by us in JÄRVINEN & VÄISÄNEN 1973 for the zones differs slightly from that used by botanists, e.g. AHTI et al. 1968.) As one passes from the northern boreal to the hemiarctic zone, a marked decrease is evident in the densities of species typical of coniferous forests: *Tetrao urogallus, Tetrastes bonasia,* several woodpeckers, *Perisoreus infaustus,* several *Parus* species, *Phoenicurus phoenicurus, Turdus philomelos, Muscicapa striata, Anthus trivialis, Loxia* spp., and *Emberiza rustica.* At the same time, several species become much more abundant: a number of *Charadrius* species, *Calidris temminckii, Philomachus pugnax, Phalaropus lobatus, Stercorarius longicaudus, Luscinia svecica, Oenanthe oenanthe, Anthus pratensis, Motacilla flava,* and *Calcarius lapponicus.* All of these inhabit open biotopes.

Changes also occur in the basic groups of the avifauna. KLOPFER & MACARTHUR (1960, KLOPFER 1973) found that the proportion of nonpasserines in the avifauna decreases towards the north in the northern hemisphere. Typical values in the northern parts of the U. S. and southern Canada are somewhat under 10 per cent. The values here are 6.6 per cent in the northern boreal zone (or Forest Lapland) and 2.2 per cent in the hemiarctic zone (or Fell Lapland). Charadriiformes have been excluded here, as in KLOPFER & MACARTHUR (1960). They also found that, on average, the number of individuals per unit area decreases towards the tropics in passerine species, while latitudinal gradients are not evident in non-passerines. Thus the ratio of the mean abundance of passerines to the mean abundance of non-passerines increases northwards. The median around 18°N is less than 1.5, and three values from censuses around 58°N range from 3 to 6 (KLOPFER & MACARTHUR 1960). For Forest Lapland (68—69°N) the ratio is 7.3, and for Fell Lapland (69—70°N) 11.4. The gradient is thus very steep at the transition from taiga to tundra. In contrast to KLOPFER & MACARTHUR (1960), we find that the change is not caused by a pronounced increase in the mean abundance of passerines, but by a decrease in the mean abundance of non-passerines (0.21 to 0.14 pairs per km^2 per species).

The location of the study area may also be examined with respect to gradients in species richness. Using data from the U.S.S.R., TERENTJEV (1963) provides two formulae which predict the number of bird species in rectangles of 10° lat. x 10° long. Calculations based on the average July temperature (+14°C, for the Enontekiö—Inari area), give almost 180 species in a rectangle extending from 64°N to 74°N, but the formula based on latitude (69°N), gives the number of species in the same rectangle as slightly above 130. The former prediction is superior, for the study area alone (with coasts), spanning less than 5 degrees of latitude, supports more than 140 species (counted from BRUUN & SINGER 1972).

Population fluctuations are generally assumed to be most pronounced in the north, but this view has recently been challenged by VON HAARTMAN (1971) with respect to birds, and by KREBS & MYERS (1974) with respect to small rodents. These authors claim that the data available do not allow definite conclusions. Yearly, more or less random fluctuations in the bird communities can be neglected in many studies of community structure (JÄRVINEN & VÄISÄNEN 1976a), at least in southern Finland, but unpublished data obtained by us indicate that northern communities fluctuate more than southern communities. Several arctic biologists (DUNBAR 1968, 1973, SALOMONSEN 1972) emphasize the importance of climatic disasters in the arctic. A survey of reports from northern Fennoscandia shows that several authors have observed large year-to-year fluctuations in the density of *Fringilla montifringilla* (SIIVONEN 1952, ENEMAR et al. 1965, HOGSTAD 1969, MOKSNES 1973), *Turdus pilaris* (YTREBERG 1972, MOKSNES 1973), *Phyllocopus trochilus* (HOGSTAD 1969, *cf.* also SIIVONEN 1950), and *Carduelis flammea* (ENEMAR 1969, ENEMAR & SJÖSTRAND 1970, MOKSNES 1973). Densities of *C. flammea* have been observed to increase 8- to 10-fold in one year (ENEMAR 1969). Population fluctuations in species of alpine and subalpine biotopes in North Europe have been attributed to several causes: variations in the abundance of the birch seed crop (e.g. ENEMAR 1960), mass occurrences of *Oporinia autumnata* larvae (e.g. SILVOLA 1967a, HOGSTAD 1969, YTREBERG 1972), late springs

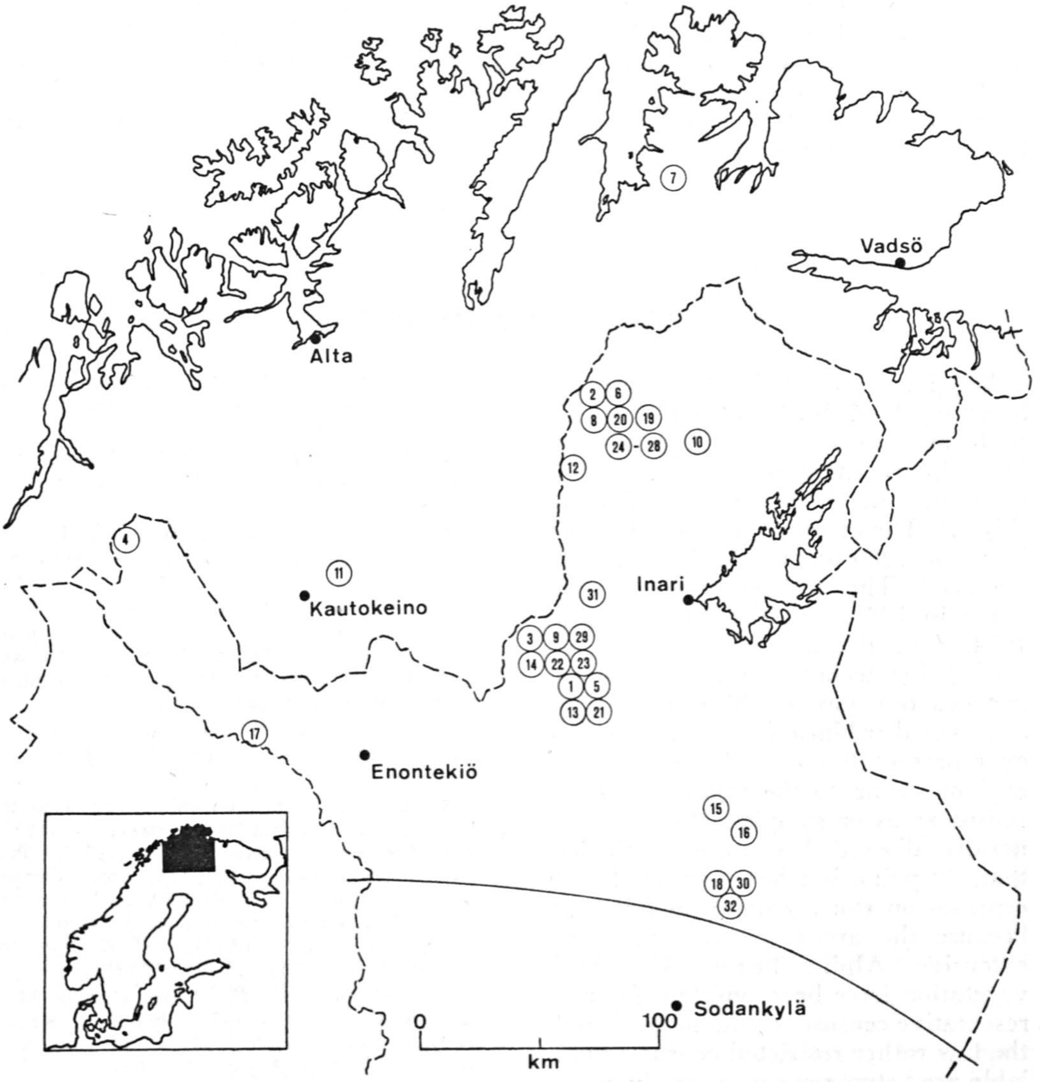


FIG. 1. Location of census areas (A1-A32; see Table 2 for further data on the censuses). The line between Sodankylä and Enontekiö shows the southern border of the northern boreal zone. Insert: location of the study area in North Europe.

(Alm et al. 1966), and rigorous conditions in the winter quarters (Bengtson 1970). Late springs have consequences which are difficult to examine in long-term censuses of fixed census areas, because the populations may prefer different areas in different years (see Hogstad 1969, Lien et al. 1970). In addition, the numbers of several birds of prey fluctuate with the cycles of small rodents, and other bird species may also be affected. Moksnes (1973) observed that the breeding success of *Turdus pilaris,* and partly also that of *Fringilla montifringilla,* was seriously impaired after the decimation of the lemming populations, as *Corvus corone cornix* and *Mustela erminea* began to prey on bird nests. Small rodents may also influence bird population dynamics directly, for Arheimer & Enemar (1974) suggest that the density of small mammal populations is correlated with the choice of nest sites. Fortunately, only a small proportion of our results is based on single-season censuses.

Most recent faunal changes have been related to human activities (e.g. DORST 1972, VON HAARTMAN 1973), but human influence is very restricted in the study area. Two recent large-scale ventures may eventually have widespread effects: the construction of two big artificial lakes, and extensive clearcutting of the coniferous forests. Both of these will affect the southern parts of the study area.

III. MATERIALS AND METHODS

We have collected 32 censuses of breeding land birds, coded A1-A32, performed in northern Lapland and located, according to the census descriptions, in homogeneous biotopes (Fig. 1). The censused area totals 44.32 km^2, and 4269 pairs of birds have been observed. The earliest censuses were made in 1937, and the latest ones in 1974. Several censuses have been discarded for technical reasons (heterogeneous biotopes, doubt expressed by census-maker himself regarding quality or representativeness of his censuses, etc.) or owing to the smallness of the census areas or samples. We have generally discarded censuses with less than 20 pairs, but have accepted such censuses on stony ground on fell tops, because the areas censused are very extensive. Alpine heaths with bush vegetation have been omitted, for representative censuses could not be found; the few rather restricted censuses available are heterogeneous, possibly owing to inconsistency in biotope definitions.

The censuses are listed in Table 2. The dates and methods are given below; the sources are numbered as in Table 2.

1. GRANIT (1938). Viipustunturit fell area, Inari, 1937-06-26 - - 07-09. Line transect method, belt width 100 m (A1, A5) or 50 m (A13, A21).

2. KAREILA (1958). Urtasvaarri fell, Enontekiö, 1956-07-02 - - 08-03. Methods not known, the study area has presumably been censused once.

3. BAGGE et al. (1963). A long transect between Inari and Enontekiö (mainly Maarestunturit fell area), 1961-06-27 - - 07-10. Line transect method, three census-makers in front, belt width 50 m per census-maker.

4. HAAPĄNEN et al. (1966). Koitilaiskaira, Sodankylä, 1965-06-14 - - 21. Line transect method, belt width 60 m.

5. SILVOLA (1966b). Paistunturit, Utsjoki, 1960-07-05 - - 06 and 1964-06-27 - - 30. Line transect method.

6. SILVOLA (1966a, 1967b). Kevojoki river canyon, Utsjoki, end of June and beginning of July, ten seasons, 1955 to 1964. Line transect method (A19, A24-A27) or 'study area' method with transects 40 m apart (A28).

7. HILDÉN (1967). Pikkusuo, Karigasniemi, Utsjoki, 1967-06-09 - - 07-15. Mapping method (ENEMAR 1959).

8. L. Sammalisto (unpubl.). Bog censuses by methods described in SAMMALISTO (1955) and JÄRVINEN & SAMMALISTO (1976). Petsikko, Utsjoki, 1963-06-12 (A10); Isosaarenaapa, Vuotso, Sodankylä, 1957-06-10 (A15); Naarasaapa (0.8 km^2) and Kaita-aapa (0.6 km^2), Sompio, Sodankylä, June 1958 (A16); and Karesuvanto, Enontekiö, June 1956 and 1957 (A17).

9. Our own data. Ifjordfellet, Gamvik, Norway, 1974-06-28 (A7), and Labboluobbal, Kautokeino, Norway, 1974-06-30. Line transect method, belt width 100 m (A7) or 50 m (A11).

The density estimates can only be tentative, because of the length of the study period and the considerable variation in census techniques. In most cases census efficiency has presumably been about 60 per cent (PALMGREN 1930, ENEMAR 1959, 1963, HILDÉN 1967). As censuses based on one visit only include the so-called 'floating part of the population' of non-stationary individuals (ENEMAR 1959, CEDERHOLM et al. 1974), census efficiencies are higher

TABLE 2. The basic censuses: code number, area (km²), number of species (*S*), number of pairs (*N*), biotope characterization, and source. For more details of sources, see text.

Census	Area	S	N	Biotope characterization 1)	Source
A1	0.38	1	8	Stony ground on fell tops	1
A2	0.57	2	5	—»—	5
A3	0.19	4	9	—»—	3
A4	1.20	6	42	—»—	2
A5	1.60	6	17	Alpine meadow	1
A6	1.54	8	23	—»—	5
A7	0.70	15	43	Late-melting alpine meadow	9
A8	0.34	16	42	Alpine peatland	5
A9	0.62	12	57	—»—	3
A10	0.50	14	90	*Palsa* peatland	8
A11	0.25	14	68	—»—	9
A12	0.55	19	182	Subalpine open peatland	7
A13	0.19	9	36	—»—	1
A14	1.21	17	121	—»—	3
A15	0.63	8	35	R. sylvatica open peatland	8
A16	1.40	14	105	—»—	8
A17	0.25	8	38	Subalpine open peatland	8
A18	0.49	9	24	Burned open area	4
A19	2.85	17	126	*ECl* (b) birch forest	6
A20	0.82	12	61	± Dry birch forest	5
A21	0.31	9	24	*Myrtillus* birch forest	1
A22	5.44	20	262	Dry birch forest	3
A23	1.39	15	119	*Myrtillus* birch forest	3
A24	2.68	22	192	*ECl* (p) mixed birch forest	6
A25	4.16	24	438	*EV* (p) mixed birch forest	6
A26	5.72	25	523	*EV* (b) birch forest	6
A27	3.09	27	590	*EM* (b) birch forest	6
A28	1.52	25	733	*G* (b) birch forest	6
A29	0.54	17	46	Mixed forest (pine, birch)	3
A30	1.05	14	113	HMT mixed forest	4
A31	1.50	16	65	Pine forest	3
A32	0.64	12	32	EMT pine forest	4

1) Abbreviations: Cl = *Cladina*, E = *Empetrum*, G = *Geranium*, H = *Hylocomium*, M = *Myrtillus*, T = type, V = *Vaccinium*, b = birch, and p = pine.

than the estimated efficiencies in mapping studies, provided such birds exist and are counted. (In general, mapping estimates of efficiencies are slight overestimates, Mysterud 1968).

In contrast to densities, the composition of the bird fauna has been reported by many authors to be similar in mapping studies and studies involving one (line transect) census only (Enemar & Sjöstrand 1967, 1970, Hogstad 1969, Moksnes 1971, 1972, 1973). Actually, most authors consider that line transect censuses are better than mapping for elucidating the composition and fluctuations of the total breeding bird fauna of a larger area. Variation between different census-makers has been observed to be relatively small, so that different ornithologists obtain relatively consistent results concerning the total structure of the avifauna (Enemar 1962, Hogstad 1967). However, the use of very broad census belts may cause large inter-observer differences (Enemar & Sjöstrand 1967; cf. Järvinen & Väisänen 1975).

It should be remembered that the

breeding period is short in northern regions (data: Ricklefs 1966). This makes single censuses — and also evaluation of mapping results — far more trustworthy than in more southern communities (cf. e.g. Slagsvold 1973).

Diversity has been measured by the Shannon function, using $\log_e$:

$$H' = -\Sigma p_i \log_e p_i,$$

where p_i = the proportion of the *i*th species.

Incompleteness of the censuses does not cause too much bias when diversities are estimated in this way (Järvinen & Sammalisto 1973). Most of the samples are so large that we decided to omit Basharin's correction term $(S-1) / 2N$, where S = the number of species and N = the number of individuals.

The census areas have been compared with a modification of the index DIV_{diff}, used in the previous paper of this series (Järvinen & Väisänen 1973). The new index ranges from 0 to 100, and it is defined (Järvinen & Väisänen 1976a) as

$$rD = 100 \, [\exp(DIV_{\text{diff}}) - 1].$$

DIV_{diff} is defined as

$$DIV_{\text{diff}} = H'_{A+B} - 1/2\,(H'_A + H'_B),$$

where subscripts A and B refer to regions. When this definition is substituted for DIV_{diff} in the formula of rD, it can be seen that rD is independent of the logarithm system chosen for the calculations of diversity values, provided that DIV_{diff} is used as the exponent of the base of the particular logarithm system employed. Further, it can be shown by simple algebra that

$$rD = 100 \left(\frac{\exp(H'_{A+B})}{[\exp(H'_A)\,\exp(H'_B)]^{1/2}} - 1 \right)$$

Since exp (H') can be interpreted as the number of 'equally common species', the square root in the denominator is the geometric mean of the numbers of equally common species in the two regions. This is compared with the number of such species in region $A+B$.

Other relevant methodological questions are discussed elsewhere (Järvinen & Sammalisto 1973, Järvinen & Väisänen 1973, 1975, 1976a, Väisänen & Järvinen 1974).

IV. BIOTOPE CLASSIFICATION

We have grouped the 32 censuses on the basis of similarities in the composition of the bird communities. The comparisons were made with the index rD, and the resulting matrix was used to draw a dendrogram (Fig. 2), according to the rules given by, e.g., Cody (1974: 92). The three main branches in this dendrogram are (1) more or less dry, alpine biotopes on fells, (2) wet open biotopes, ranging from peatlands surrounded by coniferous forests to elevated alpine peatlands, and (3) forests. The forest group is most compact, while the open areas, especially the dry alpine biotopes, are often loosely connected.

Eleven biotopes have been distinguished on the basis of Fig. 2. Index values of the order of 10—20 have generally been regarded as critical. However, we also studied the complete matrix, of which the dendrogram is only a two-dimensional representation (the matrix could be accurately represented, as a dendrogram, in a 32-dimensional hyperspace). This has resulted in one change (explained below);

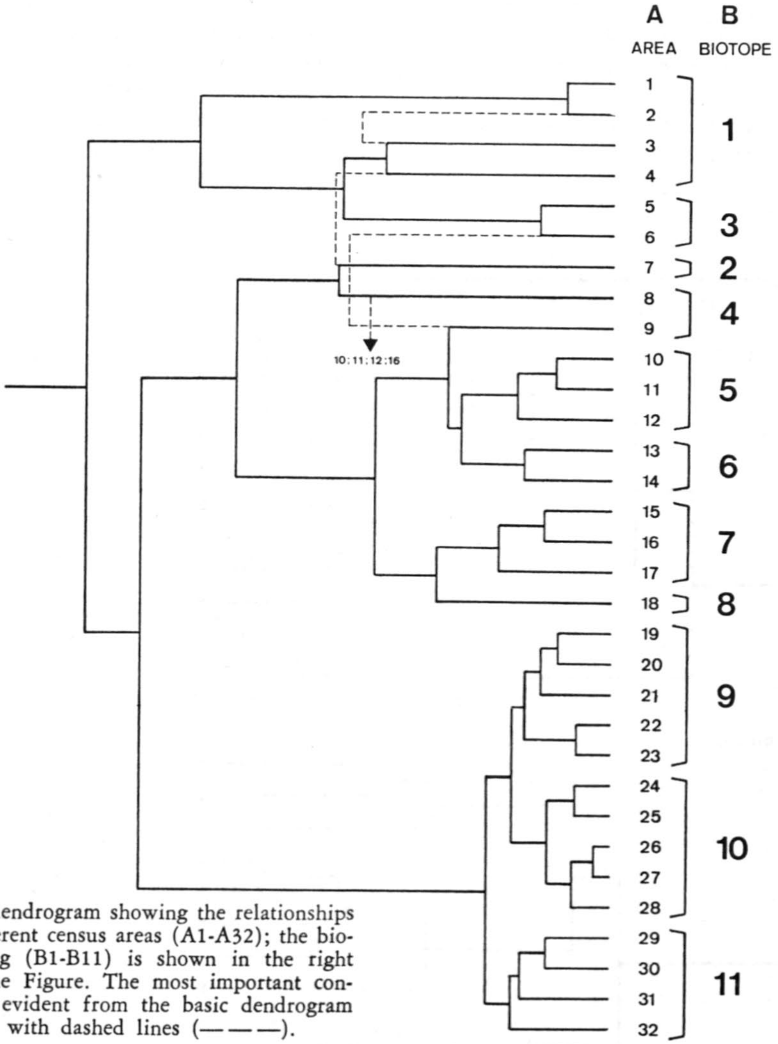


FIG. 2. A dendrogram showing the relationships between different census areas (A1-A32); the biotope grouping (B1-B11) is shown in the right margin of the Figure. The most important connections not evident from the basic dendrogram are indicated with dashed lines (— — —).

the most important 'hidden' connections between the study areas (A1-A32) have also been indicated in the dendrogram in Fig. 2. Modifications were also necessary with respect to stony ground areas on fell tops, which are represented by relatively few individuals (see below).

The relationships of the 11 biotopes are depicted in Fig. 3. Information on their bird communities is presented in Tables 3 and 4 and Figs. 4 and 5. The matrix on which Fig. 3A is based is given in Table 5. The observations made in the rest of this section are based on these figures and tables, unless specific references are given.

B1. Stony ground on fell tops (rakka). Most of the ground is covered with stones and is almost devoid of vegetation, but occasional strips of alpine meadow occur, which have an important influence on the structure of the bird community, for *rakka* proper supports very low numbers of birds.

Census areas A1 and A2 are the most extreme ones: 80 to 100 per cent of all the birds are *Plectrophenax nivalis.* Area A3 is only slightly more similar to A4 than to A2 (Fig. 2); A3 is characterized by high frequencies of *Lagopus mutus* and *Oenanthe oenanthe.* Area A4 includes occasional willows, which attract *Phylloscopus trochilus* and *Luscinia svecica.* Surprisingly, owing to these scattered willows, the bird community of A4 is not completely dissimilar to that of the most barren mountain birch forests: the *rD* between A4 and A19 is only 48.4, which is comparatively low compared with the other values in Fig. 2. On the whole, the stony ground census areas are rather heterogeneous, but, in our view, this is

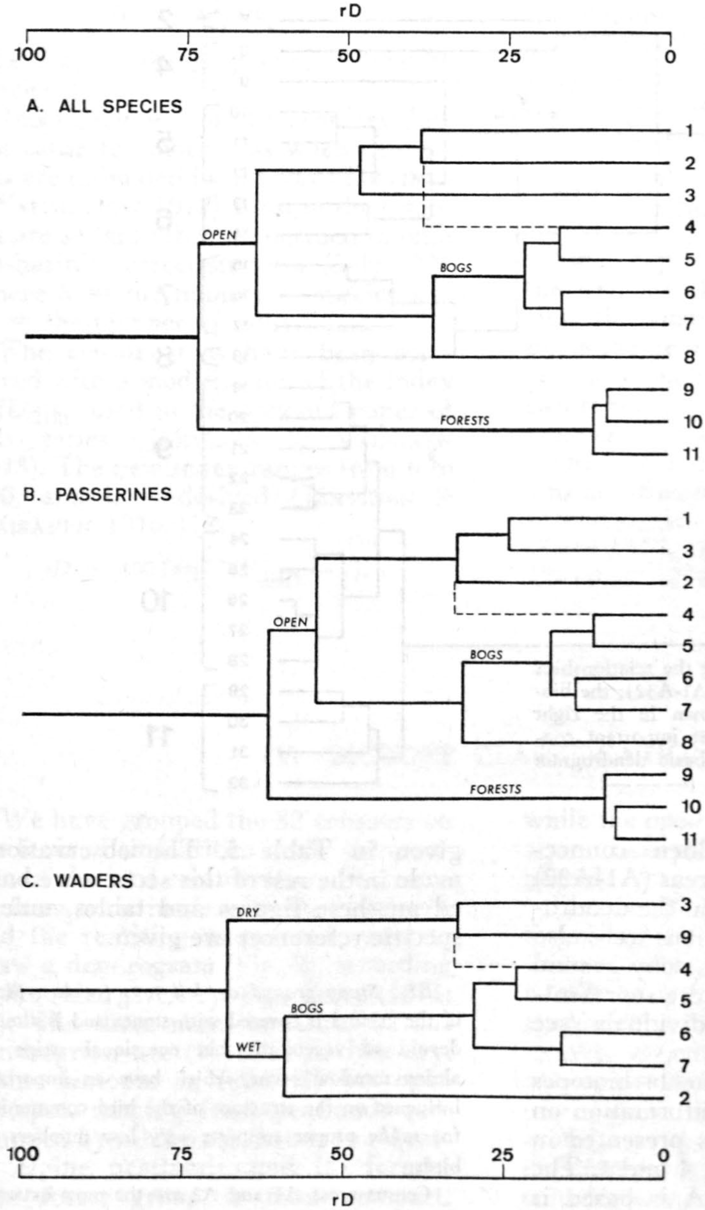


FIG. 3. A dendrogram showing the relationships between the different biotopes (B1-B11). *A.* Based on all land birds. *B.* Based on passerines. *C.* Based on waders (B1, B8, B10, and B11 excluded owing to the very small numbers of wader observations).

TABLE 3. Frequencies of species with optimal habitats among the open biotopes (B1-B8). The species are ordered rather roughly according to their maximum frequencies. An asterisk before the scientific name indicates that the species is a non-migrant, and "m" after the name indicates marginality (for definitions, see pp. 28 and 23). Density is equal to frequency multiplied by total density (Fig. 4) and divided by 100.

Species	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11
Buteo lagopus	1.6	—	—	—	—	—	—	—	—	—	—
Plectrophenax nivalis	32.8	16.3	5.0	—	—	—	—	—	—	—	—
**Lagopus mutus*	6.3	4.7	—	—	—	—	—	—	—	—	—
Arenaria interpres	—	2.3	—	—	—	—	—	—	—	—	—
Charadrius morinellus	1.6	—	25.0	—	—	—	—	—	—	—	—
Charadrius hiaticula	—	11.6	—	1.0	0.9	—	—	—	—	—	—
Eremophila alpestris	—	—	15.0	—	—	—	—	—	—	—	—
Oenanthe oenanthe	29.7	9.3	15.0	2.0	0.6	—	—	4.2	3.4	0.9	0.4
Calidris temminckii	—	14.0	—	3.0	0.3	1.9	2.8	—	—	—	—
Charadrius apricarius	—	4.7	22.5	10.1	2.6	0.6	—	—	1.9	0.0	—
Tringa totanus m	—	—	—	1.0	—	—	—	—	—	—	—
Limosa lapponica	—	—	—	1.0	—	—	—	—	—	—	—
Numenius phaeopus	—	—	2.5	3.0	—	0.6	—	—	1.4	0.0	—
Stercorarius longicaudus	—	—	—	2.0	0.3	—	—	—	0.5	—	—
Phalaropus lobatus	—	2.3	—	5.1	2.1	—	0.6	—	—	—	—
Anthus cervinus	—	4.7	—	4.0	2.6	—	3.4	—	0.2	0.0	—
Luscinia svecica	10.9	—	—	3.0	3.5	3.2	1.7	—	1.4	0.7	—
Calcarius lapponicus	—	7.0	—	13.1	22.6	1.9	1.1	—	0.3	0.0	—
Limicola falcinellus	—	—	—	—	2.9	—	—	—	—	—	—
Alauda arvensis m	—	—	—	—	0.3	—	—	—	—	—	—
Anthus pratensis	14.1	7.0	12.5	30.3	17.9	43.9	25.3	16.7	10.1	1.5	0.8
Lymnocryptes minimus	—	—	—	2.0	0.6	0.6	2.2	—	—	—	—
Capella gallinago	—	—	—	4.0	0.6	—	5.1	—	—	—	—
Emberiza schoeniclus	—	2.3	—	3.0	4.4	10.8	5.1	—	0.5	1.8	—
Philomachus pugnax	—	—	—	2.0	7.4	1.3	9.6	—	—	—	—
Tringa glareola	—	—	—	7.1	2.4	5.7	7.9	4.2	0.2	—	—
Saxicola rubetra m	—	—	—	—	—	0.6	—	—	—	—	—
Motacilla flava	—	—	—	1.0	15.3	11.5	31.5	33.3	4.1	0.9	1.2
Tringa erythropus	—	—	—	—	0.3	3.2	3.4	4.2	0.2	—	—
Grus grus m	—	—	—	—	—	—	0.6	—	—	—	—
Motacilla alba m	—	—	2.5	—	0.3	—	—	16.7	0.3	—	—
Tringa nebularia	—	—	—	—	—	—	—	4.2	—	—	—

largely due to variation in the occurrence of strips of alpine meadow and patches of bush vegetation, and we have therefore combined areas A1-A4.

The resulting biotope B1 is largely weighted by A4 (two-thirds of observations). So the descpription applies best to stony biotopes with occasional willows, etc. The density of the avifauna is low (27 p/km^2) and the diversity very low (H' = 1.66). Waders are almost absent (the only species is *Charadrius morinellus* with 0.4 p/km^2). No tetraonid reaches a higher frequency in our data than *Lagopus mutus* in B1: slightly over 6 per cent. The two dominant passerines are *Oenanthe oenanthe* (8 p/km^2, 30 %) and *Plectrophenax nivalis* (9 p/km^2, 33 %). These two species reach their maximum frequency in this biotope. Biotopes B2 and B3 are most similar to B1, while the other biotopes differ very much.

B2. Late-melting alpine meadow (alpine heath). Area A7, the single representative of this biotope, is situated only about 300 m above sea level, but is very northern. The area was characterized by abundant late snow-drifts on the census day (June 28, 1974), and numerous small meltwater pools and brooklets. Owing to the wetness and fairly low altitude of this area, and presumably also to the thickness of the snow cover in the winter (protection from cold and winds), the vegetation was often rather rich compared with that of the nearby *rakka.* Strips of *rakka* were not uncommon in A7, however. This kind of biotope is rare in Finnish Lapland, but is commoner on the Norwegian mountains, where there is a thicker snow cover and more suitable mineral soil (L. Hämet-Ahti, pers. comm.).

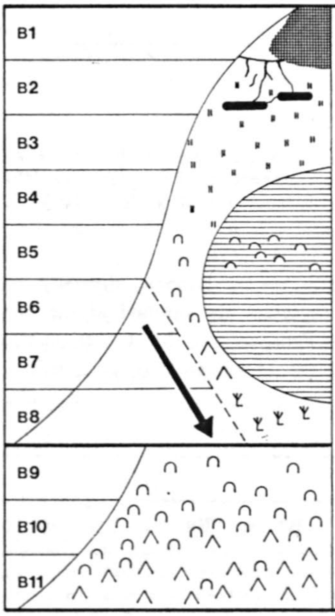
The number of species (S) in this biotope is high (15) compared with the numbers in B1 and B3 (8 species each, though similar numbers of pairs were observed). Density is remarkably high (61 p/km^2). Diversity is higher than in any of the other biotopes ($H' = 2.53$), the contribution of J', the evenness component of diversity (see e.g. Järvinen & Sammalisto 1973), being especially high: $J' = H'/\log_e S = 0.94$. The nearly maximal value for evenness is due to the absence of strongly dominating species in the community of type B2. The most frequent species are *Plectrophenax nivalis* (10 p/km^2, 16 %), *Calidris temminckii* (9 p/km^2, 14 %), and *Charadrius hiaticula* (7 p/km^2, 12 %). Traces of several other biotopes can be discerned in B2. Typical *rakka* species (B1) are *Lagopus mutus* (5 %), *Oenanthe oenanthe*

Table 4. Frequencies of species with optimal habitats among the forest biotopes (B9-B11); *Carduelis flammea* could possibly also be classified as a species of open biotopes. The species are given in two groups. The first 18 were encountered in only 1—2 forest biotopes. The other 13 were found in all of the forest biotopes. The species are ordered rather roughly according to their maximum frequencies within these two groups. An asterisk before the scientific name indicates that the species is a non-migrant, and "m" after the name indicates marginality (for definitions, see pp. 28 and 23).

Species	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11
**Parus montanus* m	—	—	—	—	—	—	—	—	0.3	0.4	—
Lanius excubitor	—	—	—	—	—	—	—	—	0.2	0.5	—
Pinicola enucleator	—	—	—	—	—	—	—	—	0.2	0.8	—
Sylvia borin m	—	—	—	—	—	—	—	—	—	0.7	—
Prunella modularis m	—	—	—	—	—	—	—	—	—	0.4	—
Phylloscopus borealis	—	—	—	—	—	—	—	—	—	0.4	—
**Dendrocopos minor* m	—	—	—	—	—	—	—	—	—	0.2	—
Pandion haliaetus	—	—	—	—	—	—	—	—	—	0.2	—
**Aegolius funereus* m	—	—	—	—	—	—	—	—	—	0.0	—
Falco columbarius	—	—	—	—	—	—	—	—	—	0.4	0.4
Bombycilla garrulus	—	—	—	—	—	—	—	—	—	0.7	1.2
Ficedula hypoleuca m	—	—	—	—	—	—	—	—	—	1.6	2.7
Turdus viscivorus m	—	—	—	—	—	—	—	—	0.2	—	0.4
**Picoides tridactylus*	—	—	—	—	—	—	—	—	—	0.1	0.4
**Tetrao urogallus* m	—	—	—	—	—	—	—	—	—	0.1	2.3
Apus apus m	—	—	—	—	—	—	—	—	—	—	0.4
**Loxia curvirostra m*	—	—	—	—	—	—	—	—	—	—	0.8
**Tetrastes bonasia* m	—	—	—	—	—	—	—	—	—	—	0.4
**Lagopus lagopus*	—	—	—	—	—	0.6	—	—	2.2	1.1	1.2
Phylloscopus trochilus	3.1	—	—	1.0	6.8	7.6	—	4.2	27.4	28.9	23.8
Turdus iliacus	—	4.7	—	—	1.5	0.6	—	—	9.1	7.6	8.2
Fringilla montifringilla	—	—	—	—	0.3	0.6	—	—	20.1	33.3	19.9
Phoenicurus phoenicurus	—	—	—	—	—	—	—	—	4.9	6.7	6.3
**Parus cinctus*	—	—	—	—	—	—	—	—	0.2	2.3	0.8
Carduelis flammea	—	4.7	—	1.0	3.5	4.5	—	12.5	9.6	3.2	11.3
Turdus pilaris m	—	4.7	—	—	—	—	—	—	0.2	0.9	0.8
**Perisoreus infaustus*	—	—	—	—	—	—	—	—	0.2	1.1	1.2
Muscicapa striata m	—	—	—	—	—	—	—	—	0.7	1.8	5.5
Turdus philomelos m	—	—	—	—	—	—	—	—	0.5	0.4	2.3
Cuculus canorus	—	—	—	—	—	—	—	—	0.2	0.1	2.3
Anthus trivialis	—	—	—	—	—	—	—	—	0.3	0.2	5.1

(9 %), and *Plectrophenax nivalis.* Species characteristic of alpine meadows (B3) and different types of peatlands (B4-B7) are also present: *Charadrius apricarius* (5 %), *Phalaropus lobatus* (2 %), *Anthus cervinus* (5 %), *Carduelis flammea* (5 %), *Emberiza schoeniclus* (2 %), *Calcarius lapponicus* (7 %). The generalist species of open biotopes (B1-B8), *Anthus pratensis,* has a fairly low frequency (7 %, compared with 18 to 44 % on peatlands).

The bird community of this biotope most resembles those of stony ground (B1, especially census area A4) and alpine peatlands (B4). This emphasizes its intermediate position between the barren stony areas and alpine meadows on the one hand, and different types of peatlands on the other. Its intermediate position is further reflected in the absence of 'characteristic' species — only two waders, *Charadrius hiaticula* and *Calidris temminckii,* have notable peaks in their abundance and frequency in this biotope. A third wader deserves to be mentioned: *Arenaria interpres* is not known to be an inland breeder in Scandinavia (HAFTORN 1971), but an individual showing the alarm behaviour typical of individuals at their nests was encountered during the census made by K. and R. A. Väisänen, at a small lake, about 1 km south of the road passing Ifjordfellet. The distinctiveness of the wader community is very clearly seen in Fig. 3C, and was mainly responsible for the separation of B2 as a distinct biotope; the passerine community can be regarded as a mixture of those of biotopes B1 (about three quarters) and B4 and B5 (about one quarter). The general composition of the passerine community is most similar to those of the communities of stony ground (B1) and alpine peatlands (B4). *Turdus pilaris* and *T. iliacus*



	ALL SPECIES p/km²	ALL SPECIES S	ALL SPECIES H'	PASSERINES p/km²	PASSERINES S	PASSERINES H'	WADERS p/km²	WADERS S	WADERS H'
B1	27	8	1.66	25	5	1.39	0	1	0
B2	61	15	2.53	37	9	2.05	21	5	1.36
B3	13	8	1.84	6	5	1.45	6	3	0.86
B4	103	21	2.48	60	9	1.49	41	11	2.14
B5	262	24	2.44	208	13	1.94	52	10	1.87
B6	112	18	2.00	96	10	1.56	16	7	1.61
B7	78	14	2.03	53	6	1.23	25	7	1.72
B8	49	9	1.88	43	6	1.57	6	3	1.10
B9	55	30	2.31	51	23	2.11	2	4	1.00
B10	144	36	2.15	141	26	2.05	0	2	0.69
B11	69	25	2.45	64	18	2.23	0	0	-

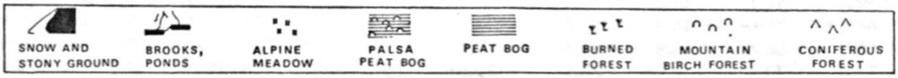
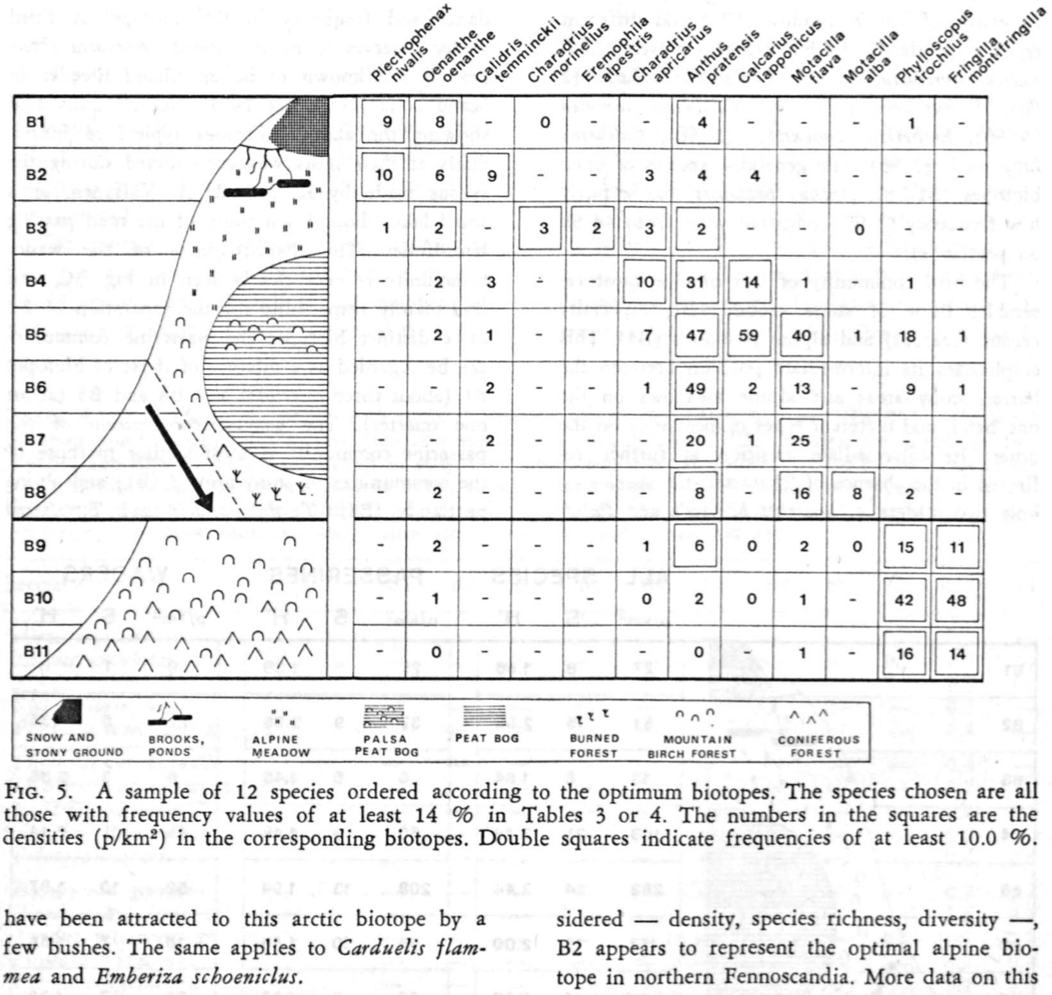


FIG. 4. *Left:* Diagram of an idealized fell, illustrating the different biotopes. Peat bog biotopes B4-B7 are so depicted that the character of the surrounding drier areas is also shown. *Right:* Density, species richness, and diversity (p/km², *S*, and *H'*, respectively) of the bird communities of the biotopes; data for passerines and waders are also given separately.



	Plectrophenax nivalis	Oenanthe oenanthe	Calidris temminckii	Charadrius morinellus	Eremophila alpestris	Charadrius apricarius	Anthus pratensis	Calcarius lapponicus	Motacilla flava	Motacilla alba	Phylloscopus trochilus	Fringilla montifringilla
B1	9	8	-	0	-	-	4	-	-	-	1	-
B2	10	6	9	-	-	3	4	4	-	-	-	-
B3	1	2	-	3	2	3	2	-	-	0	-	-
B4	-	2	3	-	-	10	31	14	1	-	1	-
B5	-	2	1	-	-	7	47	59	40	1	18	1
B6	-	-	2	-	-	1	49	2	13	-	9	1
B7	-	-	2	-	-	-	20	1	25	-	-	-
B8	-	2	-	-	-	-	8	-	16	8	2	-
B9	-	2	-	-	-	1	6	0	2	0	15	11
B10	-	1	-	-	-	0	2	0	1	-	42	48
B11	-	0	-	-	-	-	0	-	1	-	16	14

FIG. 5. A sample of 12 species ordered according to the optimum biotopes. The species chosen are all those with frequency values of at least 14 % in Tables 3 or 4. The numbers in the squares are the densities (p/km²) in the corresponding biotopes. Double squares indicate frequencies of at least 10.0 %.

have been attracted to this arctic biotope by a few bushes. The same applies to *Carduelis flammea* and *Emberiza schoeniclus.*

When all our community parameters are considered — density, species richness, diversity —, B2 appears to represent the optimal alpine biotope in northern Fennoscandia. More data on this kind of biotope should evidently be collected.¹

TABLE 5. *rD* matrix showing the similarities of the composition of the bird communities in the eleven biotopes. Fig. 3A is a dendrogram representation of this matrix.

	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
B2	42.6									
B3	38.6	53.5								
B4	59.8	51.1	38.2							
B5	64.5	70.0	45.4	17.0						
B6	58.8	68.4	58.0	23.4	17.6					
B7	71.6	77.4	64.4	26.9	20.6	16.6				
B8	64.7	65.9	69.8	53.8	35.0	27.3	30.1			
B9	62.4	68.4	60.1	53.5	39.5	35.1	63.3	44.0		
B10	79.4	91.5	75.2	79.3	60.7	57.5	85.0	70.3	9.5	
B11	85.7	95.3	77.0	86.5	65.3	62.9	91.6	65.5	13.8	9.5

B3. Dry alpine meadow (alpine heath). The vegetation consists mainly of dwarf shrubs and grasses, and the ground is partly stony. (The alpine areas with bush vegetation, omitted by us — see p. 6 —, are similar, but the commonest plant is *Betula nana,* which is interspersed with *Juniperus communis;* according to SILVOLA 1966b, the maximum height of the vegetation is 0.5 m).

Both the number of species (8) and the density of birds (13 p/km²) are low. The bird communities of the two alpine meadows (A5, A6) are similar, and it was obvious that they should be combined. Their densities and diversities are also similar. Two waders compose almost 50 per cent of the community: *Charadrius apricarius* (3 p/km², 22 %) and *Ch. morinellus* (3 p/km², 25 %). Three passerines are noteworthy: *Eremophila alpestris* (the only observations in our data, 2 p/km², 15 %), *Oenanthe oenanthe* (2 p/km², 15 %), and *Anthus pratensis* (2 p/km², 12 %). This biotope is apparently optimal for *Eremophila alpestris* and *Charadrius morinellus.*

B4. Alpine peatlands. The two alpine peatlands, A8 and A9, have been combined despite considerable dissimilarity. Neither of these areas is closely related to any of the other areas. A8 has abundant vegetation (wet ground with *Betula nana* and *Salix* reaching one metre in height) and most resembles a group of four peatland areas (A10—A12, A16; *rD* level about 40), owing to similarities in the rich wader fauna (the proportion of waders exceeds 50 % in A8). The drier A9 has affinities to the alpine meadows *(rD* level 46.3 in Fig. 2). In A9 waders constitute only about one quarter of the bird community. We justify our combination of these two census areas by the absence of better alternatives. The areas are hardly extensive enough to be treated as separate units. We suggest that they are members of a single continuum of alpine peatlands, i.e. that intermediate areas, fairly similar to both A8 and A9, can be found. More censuses of alpine peatlands are evidently necessary.

Of the alpine biotopes (B1—B4), the alpine peatlands have most species (21; the number of pairs observed is also largest), and most pairs per unit area (103 p/km²). Diversity is high ($H' = 2.48$). Roughly 40 per cent of the birds are waders (41 p/km²); their diversity is higher in this biotope than in any other one. The alpine peatlands most resemble the palsa peatbogs (B5) as regards the total bird community, the wader community, and the passerine community. It may be noted that the *rD* value between alpine peatlands and palsa peatlands in Fig. 3 is much lower than that in Fig. 2. This supports our view that the two census areas A8 and A9 represent different extremes of B4. The similarities apparent in Fig. 3A between B4 and the even more elevated, or alpine, wet biotope B2, late-melting alpine meadows, include several shared species *(Charadrius apricarius, Ch. hiaticula, Calidris temminckii, Phalaropus lobatus, Oenanthe oenanthe,* etc.), but none of these species is exclusively alpine. All the species common to B2 and B4 have also been able to invade less alpine peatlands. On the other hand, several species have not been able to invade other alpine biotopes than the alpine peatlands: *Tringa glareola, Capella gallinago, Lymnocryptes minimus, Philomachus pugnax,* and *Motacilla flava thunbergi,* among others. All of these species are common peatland birds whose range extends far to the south (JÄRVINEN & SAMMALISTO 1976). The following species have frequencies exceeding 5 per cent on the alpine bogs: *Charadrius apricarius* (10), *Tringa glareola* (7), *Phalaropus lobatus* (5), *Anthus pratensis* (31 p/km², 30 %), *Calcarius lapponicus* (13). Two species, *Limosa lapponica* and *Tringa totanus,* have not been observed in other biotopes. A number of waders (e.g. *Charadrius apricarius* and *Numenius phaeopus)* and *Stercorarius longicaudus* reach their peaks of abundance in B4. All the passerines have other optimal biotopes.

B5. Palsa peatlands. These are wet open peatlands in the subalpine mountain birch region, in places where the climate and topography have

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[1] We revisited part of A7 on 1975-06-20. We did not observe any *Arenaria interpres,* but saw three *Calidris maritima,* showing territorial behaviour, and also feeding *Philomachus pugnax* 2 ♂♂ and 7 ♀♀). The lakes were 90 % ice-covered, and at least a third of the ground was covered by thick layers of snow. The results of censuses of other areas with similar bird communities in N Norway in 1975 suggest that B2 should perhaps be called *"oceanic"* instead of "late-melting" alpine meadow, though A7 is certainly also late-melting. The best designation of B3 would then be *"continental alpine meadow".*

allowed *palsa* mound formation (see RUUHIJÄRVI 1960). Census area A12, included in B5, lacks proper *palsa* mounds, possibly owing to its narrow shape, but large *Sphagnum* hummocks are abundant there, too.

The combination of areas A10—A12 is straightforward. No 'hidden' connections, suggesting a deviation from Fig. 2, can be found in the original matrix. The density of land birds is higher than in other biotopes of northern Fennoscandia, 262 p/km², though the most luxuriant forests may have even higher densities (see B10). However, caution is necessary in making comparisons: area A12 has been censused by the mapping method, and is largely responsible for the high densities (331 p/km² in A12). On the other hand, A11, which was censused by the line transect method, also has a very high density — 272 p/km²; this is noteworthy, for HILDÉN (1967) reports that the census efficiencies on A12 were generally under 50 per cent. Doubling the values for A11 yields very high estimates indeed.

More species (24) have been observed in this biotope than in other open biotopes (B1—B8). Diversity is high ($H' = 2.44$). Passerines are mainly responsible for the high densities in this biotope, having 208 p/km². Three passerines are very abundant: *Anthus pratensis* (47 p/km², 18 %), *Motacilla flava* (40 p/km², 15 %) and *Calcarius lapponicus* (59 p/km², 23 %). It would be interesting to make a long-term study of *C. lapponicus* on a *palsa* peatland. Its numbers have been reported to fluctuate very much (e.g. MERIKALLIO 1958), and a preliminary analysis of line transect data collected between 1938 and 1974, appears to justify this view, for its proportion in the total land bird fauna of Fell Lapland varies from about 1 per cent to over 10 per cent in three different periods, each 10—15 years long (our unpublished data).

The other dominants of *palsa* peatlands include *Philomachus pugnax* (7 %) and *Phylloscopus trochilus* (7 %). The former species has probably become more abundant during recent decades (JÄRVINEN & SAMMALISTO 1976). The fact that the records of *Limicola falcinellus* are restricted to *palsa* peatlands (A12) may reflect the careful censusing of HILDÉN (1967) rather than a biological reality (the species is more abundant in the northern boreal zone than in Fell Lapland). One *Alanda arvensis* was also observed on *palsa* peatlands (A11).

B6. Open subalpine peatland. The areas of subalpine peatland combined in B6 differ from B5 in the low frequency of very large *Sphagnum* hummocks or *palsa* mounds. These bogs support *Betula nana* and willows *(Salix* spp.), and include peatland on the slopes of fells (A14). The close affinity of areas A13 and A14 is evident from the dendrogram, and A14 is not very different from more southern peatlands (B7), either. This constitutes further evidence of a continuum of peatland biotopes, and its existence is very clearly revealed in Fig. 3, where the influence of small samples (especially A17—A18) is reduced.

Anthus pratensis is the top dominant in B6: 49 p/km², 44 %. Other dominants are *Tringa glareola* (6 %), *Phylloscopus trochilus* (8 %), *Motacilla flava* (12 %), and *Emberiza schoeniclus* (11 %). Densities, numbers of species and diversities are lower than in B5. Only three species present in B6 are absent from B5 (*Lagopus lagopus, Numenius phaeopus* and *Saxicola rubetra,* 0.6 % each), but many species present in B5 are absent from B6. The most important differences are the much lower abundances of several species in B6: *Calcarius lapponicus* (2 vs. 59 p/km², or 2 vs. 23 %), *Charadrius apricarius* (less than 1 vs. 7 p/km²), *Phalaropus lobatus* (0 vs. 5 p/km²), and *Philomachus pugnax* (about 1 vs. 19 p/km²). Thus B6 seems to be an 'impoverished' version of B5, lacking or almost lacking several typical '*palsa* species'.

B7. Aapa fen in the regio sylvatica. These fens are situated among the coniferous forests (A15—A16) or close to their northern boundary (A17). They are often large and wet peatlands.

The census areas A15—A17 have been combined according to the dendrogram in Fig. 2, though the small sample A15 does not differ much from A14, either. A17 is equally similar to A14 and A16, but differs very much from A13. Diversity is about equal in B6 and B7 ($H' = 2.00$ and 2.03, respectively), but density is lower in B7 (112 p/km² in B6, 78 p/km² in B7).

Motacilla flava is the most abundant (25 p/km², 32 %), and *Anthus pratensis* the next most abundant species (20 p/km², 25 %). The composition of the breeding bird fauna of this biotope most resembles that of B6, differing mainly in the dominant position of *Motacilla flava,* and in the changed abundances of *Philomachus pugnax, Phylloscopus trochilus, Carduelis flammea,* and *Emberiza schoeniclus.* The differences in the abundance of *P. pugnax* may be caused by long-term fluctuations in the numbers of this species (JÄRVINEN & SAMMALISTO 1976), but the differences in the three other species probably reflect the scarcity of willows on peatlands of type B7. There are four other dominants besides *Motacilla flava* and *Anthus pratensis: Tringa glareola* (8 %), *Capella gallinago* (5 %), *Philomachus pugnax* (10 %), and *Emberiza schoeniclus* (5 %).

B8. Open burned area. Clear-felled and burned land in the regio sylvatica is represented by a single census area (A18) with only 24 pairs. The area clearly has closer affinities to the peatlands than to any of the forest biotopes (B9—B11). Biotopes B6—B7 are most similar to B8. A18 is located 'among the peatlands' in Fig. 2, and B8 is connected with the compact group of peatlands obtained when the census areas are combined (Fig. 3).

Diversity is low in B8 ($H' = 1.88$), and density is among the lowest in our material (49 p/km²; only B1 and B3, which are alpine biotopes, have less birds per km²). The main difference from peatlands is the scarcity of waders, though three *Tringa* species have been encountered. The most abundant passerines belong to Motacillidae: *Motacilla flava* (16 p/km², 33 %), *M. alba,* and *Anthus pratensis* (the two latter species 8 p/km², 17 %, each). *Carduelis flammea* is also dominant (12 %).

B9. Mountain birch forest. Five census areas A19-A23 have been combined in accordance with Fig. 2. All of these forests are among the barren ones in our material; the highest birches reach about 5 m.

B9 is the only forest biotope with a number of records of waders: 21 observations of 4 species. The two more abundant waders are *Charadrius apricarius* (2 %) and *Numenius phaeopus* (1 %). (These two species have also been able to invade forests of type B10, though in minimal densities.) B9 is most closely related to alpine meadows (B3) with respect to the waders; this is due to the more or less gradual transition from dry alpine meadows to dry (barren) mountain birch forests on the slopes of the fells.

The density of birds in B9 is lower than on peatlands (B4-B7), 55 p/km². Though the number of species is high (30), diversity is no higher than $H' = 2.31$, the evenness component being small: $J' = 0.68$. Two species are top dominants in all the forests included here: *Phylloscopus trochilus* and *Fringilla montifringilla,* which have abundances of 15 p/km² (27 %) and 11 p/km² (20 %), respectively. Other dominant species are *Turdus iliacus* (9 %), *Anthus pratensis* (10 %; this high frequency is evidence that numerous relatively open patches occur in forests of type B9), and *Carduelis flammea* (9 %). The occurrence of open patches in these forests is further indicated by the presence of *Oenanthe oenanthe* and *Motacilla flava.*

B10. Mixed (mountain birch, pine) forest. All the census areas (A24-A28) are situated in the canyon of the River Kevo (Utsjoki); they are intermediate between the mountain birch forests (B9) and the coniferous forests (B11). Two census areas (A24-A25) are mixed forests: A24 is a mixed pine and mountain birch forest of *Empetrum-Cladina* type, and A25 is a pine-dominated *Empetrum-Vaccinium* forest. Areas A26-A28 are mountain birch forests, A26 being the most barren (birch height 3—5 m), and A28 the most luxuriant (birch height even exceeding 7 m, abundant willow bushes, a more or less closed crown canopy).

Density is relatively high (144 p/km²) owing to the large number of birds in the most luxuriant area A28 (482 p/km²). The highest densities of breeding birds in northern Lapland thus occur in certain forests (cf. also Discussion, Section 4), but most forests are inferior to *palsa* peatlands, and often to other peatlands (B4, B6), too. The composition of the bird fauna of B10 is rather similar to that of B9 and B11, though *Fringilla montifringilla* is more abundant than *Phylloscopus trochilus* in B10 (48 p/km² or 33 %, and 42 p/km² or 29 %, respectively). Other dominants are *Phoenicurus phoenicurus* (10 p/km², 7 %) and *Turdus iliacus* (11 p/km², 8 %). As the proportions of other species are mostly very low, diversity is only $H' = 2.15$, although 36 species were observed. In consequence, the evenness component of diversity is very low, $J' = 0.60$.

B11. Coniferous forests. Two of the census areas (A29-A30) are mixed (pine) forests, and the other two (A31-A32) are proper pine forests. Spruce forests are not included. Affinities exist between these forests and areas A24-A25, but do not necessitate a modification of the grouping in Fig. 2.

Northern coniferous (pine) forests have low bird densities: 69 p/km², or less birds per km² than in any of the peatland biotopes (B4-B7). However, diversity is high, $H' = 2.45$. A great number of species are dominant: *Phoenicurus phoenicurus* (6 %), *Turdus iliacus* (8 %), *Phylloscopus trochilus* (24 %), *Muscicapa striata* (6 %), *Anthus trivialis* (5 %), *Carduelis flammea* (11 %), *Fringilla montifringilla* (20 %). The densities of most species are lower than in B10.

V. CLASSIFICATION OF NEW CENSUSES

We have studied the applicability of the new biotope classification to the line transect data given by Lähdesmäki & Rautiokoski (1968) from censuses performed in the period 1967-06-12 - - 17 in the Paistunturit fell area (close to areas A2 and A8 in Fig. 1). Their transect was 37 km long, and the main belt covered 1.85 km² and yielded records of 255 pairs, which were classi-

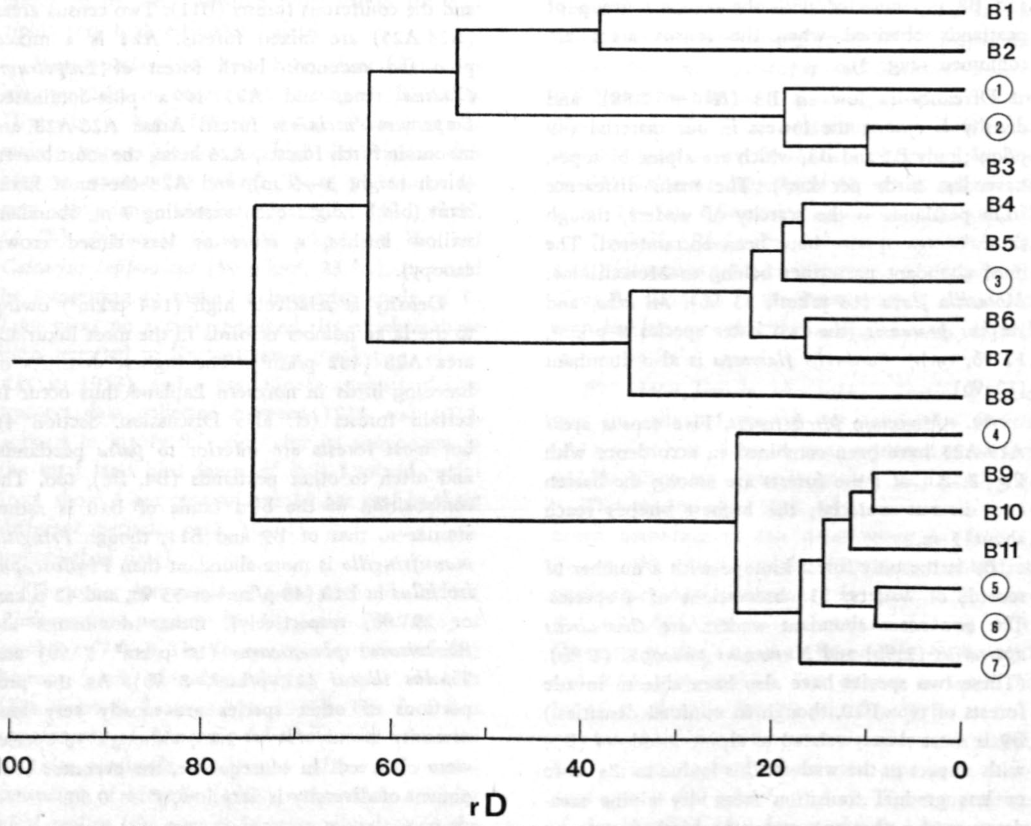

Fig. 6. Classification of new censuses. The relationship of the censuses of Lähdesmäki & Rautiokoski (numbered 1—7) to our biotopes (B1-B11).

fied by the census-makers as follows (descriptions in parentheses provided by P. Lähdesmäki):

1. Fell tops (alpine meadows on fell tops, no shrubs, numerous stony *rakka* areas), 8 pairs.
2. Open fell areas (treeless alpine meadows, shrubs), 30 pairs.
3. Open peatland (*palsa* mounds), 47 pairs.
4. Birch and willow zone along small rivers, 25 pairs.
5. Mountain birch forest, 47 pairs.
6. Birch-pine forest (resembling mountain birch forests more than coniferous forests), 50 pairs.
7. 'Man-made biotope' (fields, meadows, wooded areas around dwellings along the River Tenojoki), 50 pairs.

Certain, but not all of these biotopes could presumably be correctly classified on the basis of the descriptions of the vegetation. Comparisons made with *rD* give the following results (Fig. 6). As might be expected, censuses 1—2 represent biotopes similar to B3, the alpine meadows, and are very unlike any of the other biotopes. Census 3 is most similar to B5, palsa peatlands. Census 4 falls outside the classification; none of census areas A1-A32 or biotopes B1-B11 fit the description. Biotopes B9-B10 (mountain birch forests and mixed pine-birch forests, respectively) and censuses 5 and 6 are most similar to census 4. Censuses 5 and 6 might be expected to be most similar to one of the forest biotopes (B9 or B10 is the most likely), but they form their own branch in the dendrogram in Fig. 6. However, the original matrix reveals close connections to B10 (*rD* level 9.6), and the result could have been changed by only a few observations. Not surprisingly, census 5 is most similar to B9, and census 6 to B11. Census 7, an apparent mixture of different elements, is most similar to B10, and next to censuses 5 and 6.

We conclude that our classification can be applied to other censuses and that both the results and the method can be used to distinguish possible 'new' biotopes from those already defined (census 4 above).

VI. COMPARISONS WITH LINE TRANSECT RESULTS

The biotope classification B1-B11 was used to 'predict' the structure of the total avifauna in the northern boreal and hemiarctic zones. The percentage representation of biotopes B1-B11 was crudely estimated as 0-0-15-0-0-5-10-5-15-5-45 and in the northern boreal zone 5-5-25-5-5-5-5-1-25-10-10 in the hemiarctic zone. These estimates were derived from the ATLAS OF FINLAND (1960), KALLIOLA (1973), and our own field experience.

The line transect censuses (Table 1) performed in the study area provide an acceptable basis for comparison, for they are practically independent of the present data. From the biotope data, we could expect densities of 65.9 p/km^2 in the northern boreal zone, and 70.8 p/km^2 in the hemiarctic zone. Both estimates are satisfactorily close to the values in Table 1 (the correction procedure used in Table 1 may be expected to give slightly higher estimates than ordinary single census results; see JÄRVINEN & VÄISÄNEN 1975). The value predicted for diversity in the hemiarctic zone was rather good, about 6 per cent too high, while that for the northern boreal zone was about 15 per cent too low. A simple reason for the inaccuracy of the latter value is that an ecologically distinct group, *Perisoreus infaustus, Parus cinctus, P. montanus, Anthus trivialis,* and *Emberiza rustica,* is underrepresented in the biotope data. When examining the frequencies of the species, we excluded all

$$\begin{tikzcd}[column sep=large]
\textit{Hemiarctic} & \text{observed} \arrow[rr, leftrightarrow, "0.0083"] \arrow[d, leftrightarrow, "0.0243"] \arrow[rrd, leftrightarrow, "0.0216"] & & \text{calculated} \arrow[d, leftrightarrow, "0.0094"] \\
\textit{N. boreal} & \text{observed} \arrow[rr, leftrightarrow, "0.0116"] \arrow[rru, leftrightarrow, "0.0240"] & & \text{calculated}
\end{tikzcd}$$

those whose predicted and observed frequencies were less than 1.0 per cent in both the zones. Thirty-four species remained. The species whose predicted frequencies were at least 1.0 per cent too high or too low numbered 12 in the northern boreal zone and 11 in the hemiarctic zone. A crude estimate of the accuracy of the calculated frequency distributions was made with the index (HEATWOLE & LEVINS 1972)

$$D_{ij} = \sum_{k}(p_{ik}-p_{jk})^2,$$

where p_{hk} = the relative frequency of the kth ($k = 1,\ldots, 34$) species in the hth ($h = 1,\ldots, 4$) set. Three decimals were used for p_{hk}. (The index rD could also have been used, but it is more laborious to calculate, should be calculated from exact data, and is affected by the poor prediction of diversity in the northern boreal zone.) The comparisons between the frequency distributions yield the D_{ij} values shown in the upper part of this side.

The following observations emerge:

(1) The observed distribution in the hemiarctic zone differs from the observed and calculated ones in the northern boreal zone by an almost equal amount (D over 0.02).

(2) The observed distribution in the northern boreal zone differs from the observed and calculated ones in the hemiarctic zone by an almost equal amount (D over 0.02).

(3) The observed distribution in the northern boreal zone differs least from the calculated one in the same zone, and the observed distribution in the hemiarctic zone differs least from the calculated one in the same zone (D about 0.01).

(4) The calculated distributions for the two regions converge (D about 0.01).

Our classification can thus be used to calculate some features of the avifauna of a given region, but has two weak points. First, the coniferous forests of the southernmost parts of the study area are not adequately represented. Second, the predictions show different regions to be more similar than in reality, because the same data are used all the time.

The frequencies of four species were wrongly 'predicted' in both zones; those for *Anthus pratensis, Motacilla flava,* and *Fringilla montifringilla* were gravely overestimated, and that of *Turdus iliacus* was underestimated. Long-term changes in the avifauna may have caused the poor predictions, though these changes influenced both the line transect and the biotope data. Predictions were usually poor, if large changes occurred in the density of the species within the study area. To elucidate this point, we classified the 34 species according to the following dichotomies: Is the predicted frequency at least 1.0 percentage unit off the mark in one or both of the regions? And: Does the frequency of the species change by at least 1.0 percentage unit between the northern boreal and hemiarctic zones? The results are as follows:

	Change in frequency	
	Yes	No
Prediction not accurate	16	3
Prediction accurate	5	10

The difference in the accuracy of prediction is significant ($\chi^2 = 9.19$, $P < 0.01$, d.f. = 1). We may therefore infer that large changes in the frequency of a species within the study area are an important cause of inaccurate predictions. This should be remembered if our classification is used to estimate the avifaunal composition of regions lying within the study area, e.g. for conservational purposes.

VII. DISCUSSION

1. Similarities in the bird communities of the biotopes

To use PIELOU's (1969) terminology, our method of classification is *hierarchical* and *agglomerative*. Methods based on the use of the presence and absence of indicator species or species groups are certainly inferior in studies of this kind (this is easily seen if indicator species are sought in Tables 3 and 4), though they may be appropriate for other purposes. *Quantitative* methods appear preferable to *qualitative* ones, as birds are a mobile group, and single individuals may thus occasionally be found in 'surprising' biotopes. In other groups of organisms this choice is not so obvious (see WILLIAMS et al. 1973).

All classifications incorporate arbitrary elements. As regards our classification, the following points should be noted. The forest biotopes (B9-B11) are exceptionally similar to each other (Table 5), while some of the open biotopes (B1-B3) differ rather widely from the others (in addition B1 is very heterogeneous in itself). Thus, the calculations based on the number of biotopes (below) are only tentative. To put it briefly, the fundamental variable in our classification is neither the number of biotopes, nor the difference between them, but the total heterogeneity provided by one biotope or a group of them. Another important point has already been made by PIELOU (1969:236) in respect of the study of vegetation: "The act of classification does not itself answer the question: does the vegetation consist of a number of distinct communities or do the communities merge imperceptibly into one another because the vegetation varies continuously."

The dendrograms (Figs. 2 and 3) raise a basic question: Why is there so much heterogeneity in the avifaunas of the open biotopes, compared with those of the forests? Fig. 3 provides part of the answer. In contrast to the other species, which divide the biotopes in terms of openness, waders (Fig. 3C) tend to divide the biotopes in terms of wetness, thus subdividing the open biotopes. This is certainly one of the causes, for all the connections in Fig. 3B are closer than in Fig. 3A, although the samples in 3B are smaller. On the other hand, additional explanations are necessary, because Fig. 3B reveals the same general pattern as Fig. 3A, heterogeneity being greater in the open biotopes.

Several authors have pointed out the significance of vertical stratification in forest bird communities (MACARTHUR & MACARTHUR 1961, MACARTHUR et al. 1962, RECHER 1971, BLONDEL et al. 1973, and several others). Horizontal habitat separation is an important "coexistence mechanism" in lower vegetation (CODY 1968, 1974). These ideas can perhaps be applied to our Figs. 2 and 3.

Vertical separation will be small in

the various open habitats, and they must therefore be partitioned among the different species on a horizontal basis or according to food and feeding specialization (CODY 1968: Fig. 15). Thus large differences in the bird communities of such biotopes will arise. Horizontal separation may well be less significant in forest bird populations, but it is not insignificant, since, for example, the deciduous and coniferous forests in southern Finland have rather different bird communities (e.g. SOVERI 1940, MERIKALLIO 1946). In a preliminary analysis of biotopes in SW Finland, we have found that forests do not form such a compact group as in this study, though there, too, they are not as heterogeneous as the open biotopes. It is perhaps only in certain regions that the increase in the similarity of the bird communities with increasing possibilities for vertical separation occurs to the extent observed in our study area.

The compactness of the forest branch of the dendrograms in Figs. 2 and 3 thus require additional explanation. We suggest that the dendrogram pattern is largely attributable to the impoverishment of the bird communities in the forest biotopes, *compared with the open biotopes;* owing to reduced competition, less habitat separation will be required than in richer forests. The main reason for the depauperate bird communities of the northern forests is presumably the combination of adverse climate and diminished resources (low maximum height of trees, thin forests, often poorly developed bush layer), which makes adaptation 'too costly' for a number of species, possibly excluding small populations in optimal patches.[1] The open biotopes do not show the same reduction of resources as the forests; in the case of peatlands, the northward increase of humidity in Finland is important (RUUHIJÄRVI 1960; for birds: JÄRVINEN & SAMMALISTO 1976). Our hypothesis is directly related to the compression hypothesis of MACARTHUR & WILSON (1967:108) that "on being freed from competition on an island, a species can be expected to alter and usually to enlarge its habitat, but not its range of diet."

Before applying two tests, we compared the species composition of B9-B11 with data from Scandinavian mapping bird censuses. Our forest data (A19-A32) comprise 3324 observations. We favoured a conservative comparison between the two geographical regions, and chose only subalpine birch and mixed pine-birch forests from the Scandinavian mountains, using the following censuses:

meadow birch forests I & II (ENEMAR 1963),
heath birch forests III & IV (ENEMAR 1963),
heath birch forests D2+D3 (ENEMAR 1964, ENEMAR et al. 1965),
meadow birch forests A4-A6 (ENEMAR 1964, ENEMAR et al. 1965),
mixed birch forests A2-A3 (ENEMAR 1964, ENEMAR et al. 1965),
mixed birch forest (HOGSTAD 1969),
heath birch forest (HOGSTAD 1969),
heath birch forest (ERIKSSON et al. 1971),
birch forest (YTREBERG 1972),
heath (meadow) birch forest (MOKSNES 1973, only B1+B2),
meadow birch forest (MOKSNES 1973), and
meadow birch forest (ENEMAR et al. 1973).

These censuses comprise 1705 observations, or about 51 per cent of the Finnish forest material. Owing to the much smaller number of observations and especially a narrower habitat range, we might except that there would be considerably fewer species in the Scan-

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[1] L. Hämet-Ahti has pointed out to us that the Fennoscandian forests have fewer bushes than other boreal forests, and that the development of the bush layer is poorest in the north. These differences in forest structure make comparative studies of avian diversity in boreal forests particularly attractive for it is thus possible to test MACARTHUR'S (e.g. MACARTHUR & MACARTHUR 1961) hypothesis of the correlation between bird species diversity and foliage height diversity.

dinavian than in the Finnish material, but the contrary appears to be true. The birch forest biotopes proper, B9-B10, have only three species which have not been observed in the Scandinavian censuses (all species with scattered occurrence, frequency under 1.0 % in both B9 and B10 excluded): *Charadrius apricarius, Numenius phaeopus,* and *Motacilla flava.* These are typical species of open biotopes (Table 3).

In the Scandinavian censuses, the total number of species is 35 and in Finland it is 44. Altogether 10 species lacking from B9-B11 were observed in the Scandinavian censuses. A number of them are rare, but several would probably be absent even from a much larger Finnish material: *Parus major* (1), *Troglodytes troglodytes* (1), *Turdus torquatus* (1), *Hippolais icterina* (3), *Sylvia atricapilla* (4), and *Pyrrhula pyrrhula* (1). These species were observed by HOGSTAD (1969) or YTREBERG (1972). The others are more common: *Erithacus rubecula* (15), *Turdus merula* (14), *Carduelis spinus* (8), and *Fringilla coelebs* (42). These were observed by ENEMAR (1964), ENEMAR et al. (1965, 1973), HOGSTAD (1969) and YTREBERG (1972). Most of the differences are thus to records from the Norwegian census areas. These forests are probably the most productive (very abundant annual precipitation, more southern location), and their bird populations may be considerably enriched by the proximity of 'more southern' biotopes at lower elevations. Comparisons between the Scandinavian and Finnish censuses also reveal several quantitative differences, which support our view that the northern Finnish forests are impoverished (see also Section 4 of Discussion): most Scandinavian census areas have dense populations of *Turdus pilaris* (200 observations), *Anthus trivialis* (56) and *Prunella modularis* (58).

The hypothesis that the forest biotopes are impoverished compared with the open biotopes in Finnish Lapland was tested in two ways. The first test is based on the idea that if the hypothesis is true, the forests should contain a large number of marginal species (see below). The second test utilizes the idea that in an impoverished biotope there will be comparatively little diffuse competition, and this will increase the possibilities for congeneric species to coexist.

(1). The densities of forest birds in southern Finland are roughly double those of northern Finland (NOWIKOW 1962, JÄRVINEN & VÄISÄNEN 1973). So it is not unreasonable to classify a species as 'marginal', if its average density in Forest and Fell Lapland is less than 20 per cent of the maximum density in Finland (we used Merikallio's zoogeographical areas and our own data). Such 'marginal' species can well be interpreted as species which fail to establish dense populations in other than occasional optimal biotope patches. Most of the differences in distribution appeared to be clear-cut, so that other choices than 20 per cent would have produced nearly identical results. Our hypothesis about the reduction in competition due to the impoverishment of the forest bird communities would be disproved, if there were more marginal species in the open biotopes than in the forests, since our hypothesis predicts the opposite result. Note that the comparison here is made with the open biotopes, and not with (a) Scandinavian mountain birch forests, or (b) forests in southern Finland. We obtained the following results:

	Forests	Open biotopes
Marginal	14	5
± Optimal	17	27

For the tabulation, $\chi^2 = 6.52$ ($P < 0.02$), so that our hypothesis is not disproved. The main weakness of the test is that the data do not include species which are very rare in or absent from the study area. However, this bias probably makes the test more conservative, for a number of forest species disappear towards the north, close to, but south of the study area, whereas the peatland avifauna becomes more diverse and dense northwards (HÄYRINEN 1970, JÄRVINEN & SAMMALISTO 1976).

(2). PIANKA (1974) has pointed out that the average amount of niche overlap between pairs of coexisting species is expected to decrease with increasing numbers of species. We did not apply any of the niche overlap measures presented in the literature, because they generally do not distinguish sufficiently clearly between the tendency of two species to occur in the same part of physical space and their possible competition (occurrence in the same part of ecological hyperspace). Instead, we measured occurrence of comparatively intense competition, using the frequency of congeneric species groups as an index, because there is plenty of evidence that precisely congeneric species relatively often show considerable overlapping in their ecologies (LACK 1971). If the forest biotopes are impoverished compared with the open biotopes, there should be less diffuse competition in the forests, and better possibilities for congeners to coexist. The calculations — made according to the careful exposition of WILLIAMS (1964, Ch. 9) — yield the following results:

Congeneric	Open biotopes Observed	 Expected	Forests Observed	 Expected
pairs	17/927	<13/703	27/1365	>13/946
groups of three	1/5185	< 5/8466	10/13500	> 5/13244
groups of four	0/21788	< 1/73815	2/98960	> 1/135751

The expected frequencies are calculated by assuming random occurrence of twos, threes and fours of each set of species observed in at least one of the open biotopes ($S = 38$) or one of the forests ($S = 44$). In all the comparisons, the open biotopes have fewer congeneric groups than expected on the basis of random occurrence, but the reverse is true of the forests. The difference is thus in the predicted direction.

Only 5 out of 24 observations (three comparisons per biotope) are larger than expected in the open biotopes, while the corresponding frequency is 6/9 for the forests. This difference is significant ($P<0.01$, Fisher's exact test, one-tailed). This provides additional support for the hypothesis that the similarity of the bird communities of the forest biotopes is due to reduced competition. The three deviating observations from the forests come from B10, where congeneric groups are less frequent than expected. Of course, this cannot be tested with the present material, but it might be expected that more productive forests would be the least impoverished; B10 is no doubt the most productive of our forest biotopes, at least as regards avian summer resources.

We conclude that the greater heterogeneity of the open biotopes as compared with the forests can be attributed to (1) the fact that waders subdivide the environment in a different way from the other land birds (almost exclusively passerines), (2) a possible decrease in the importance of horizontal separation in vertically divisible biotopes, such as the forests, and (3) the impoverishment of the northern forests compared with the northern open biotopes, which reduces the need for habitat separation in the forests.

A fourth factor should also be considered: the open biotope censuses are geographically more dispersed than the forest censuses. If the biotopes of a certain region tend to be inhabited by bird communities typical of the region, rather than of the particular biotope, our data for the forest biotopes should show greater similarity. There is evidence of this in Fig. 2 (B10) and in Fig. 6 (censuses 5 and 6), but the 'region effect' alone is clearly not sufficient to explain the basic pattern (e.g., Fig. 3 appears to be unaffected). Moreover, the 'region effect' can be explained by the fact that geographically close areas are (usually) censused during the same season or seasons and will therefore reflect the same fluctuations in the bird communities.

2. Successful species

An exponential function can be fitted to the data of Tables 3 and 4 to describe the number of species (S) occurring in at least B biotopes. Logarithms were used in the calculation of the least-squares regressions. For Table 3,

$$S = 60.0\ e^{-0.37B},$$

where $B = 1,...,11$, and for Table 4,

$$S = 43.4\ e^{-0.43B},$$

where $B = 1,..., 8$. The fit is good: the correlation coefficients are $r = -0.978$ and $r = -0.980$, respectively, and $\chi^2 = 6.44$ (d.f. $= 5$, $0.2<P<0.3$) for Table 3, and 1.70 (d.f. $= 3$, $0.5<P<0.7$) for Table 4. The result can be interpreted in an interesting way: the probability that a species inhabits at least $B+1$ biotopes, if it is known to inhabit B biotopes, is constant (69 % for open biotopes, 65 % for forests). In other words, species known to occupy a large number of K biotopes are not more or less likely to be represented in biotopes $K+1,...,B$ than the less successful species. This differs from the principle put forth by WILLIAMS (1964: 295) that "nothing succeeds like success."

A geometric series could as well have been fitted to the data, but this was avoided, since we did not wish to stress the concept that the different biotopes are strictly separate entities. Connections with MACARTHUR's (1957) 'broken-stick model' could probably be found on the basis of the above equations, if we measure niche size by the number of biotopes occupied. It will follow that niche sizes are exponentially distributed. Making some additional assumptions, we may possibly expect a 'broken-stick' distribution of abundances, for the 'broken-stick model' results (COHEN 1968) from the assumption that the abundances of the species are proportional to independent, identically and exponentially distributed random variates. However, this assumption is quite different from MACARTHUR's (1957) original one and invalidates the 'broken-stick model' as a useful tool in the study of niche relationships of different species (COHEN 1968, PIELOU 1969).

The above discussion relates to averages only. We suggest three hypotheses which may account for the differences between species: a successful species (that is, a species which has occupied a large number of biotopes) is (1) behaviourally flexible with respect to its habitat tolerance, (2) able to utilize resources that are commonly present, and (3) well adapted to northern conditions.

(*1*). Behavioural flexibility in habitat selection can be tested only indirectly from our data. As stated in the section on the study area, KLOPFER & MACARTHUR (1960) chose the proportion of passerines as an index to describe the bird fauna. They argued that, being phylogenetically young, passerines are behaviourally flexible (cf. also KLOPFER 1973), and thus tolerate environmental instability better than non-passerines. As environmental stability can be argued to be at a maximum in the tropics (KLOPFER & MACARTHUR 1961), the proportion of passerines in the avifauna should increase northwards (see p. 4). Similarily, passerines can be expected to be more successful in occupying a large number of biotopes than other groups. On average, each passerine species occupied 5.4 open biotopes ($S = 12$), while the average for the other species ($S = 20$) was 3.0. The forest passerines occupied 2.8 biotopes per species ($S = 20$) *Carduelis flammea,* whose classification is not obvious, is excluded, which makes the test more conservative), but the other forest species ($S = 10$) only 1.8. Both differences are significant (one-tailed Mann-Whitney U tests, $U<68.5$, $P<0.025$, and $U<60.5$, $P<0.05$, respectively), which supports the hypothesis that successful species are behaviourally flexible.

(2). The second hypothesis is that successful species can utilize resources that are of common occurrence. MCNAUGHTON & WOLF (1970) and RICKLEFS (1972) suggested that species with the greatest densities at optimal conditions occur most widely across ecological gradients, because they have specialized in using common resources, thought to be most pervasive and persistent.

The hypothesis was tested with the following classification: the critical abundance in the optimum biotope was chosen as 2.0 p/km², and species with peak densities not exceeding 2.0 p/km² were regarded as 'sparse'. Dispersion along ecological gradients was measured by the number of biotopes occupied by the species. The following results were obtained for *open biotope species:*

	Sparse	Abundant
1— 2 biotopes	17	1
3—11 biotopes	4	9

It is very improbable that this result would occur by chance; Fisher's exact test gives the probability $P< 3\times10^{-5}$.

Similarly, for *forest biotope species:*

	Sparse	Abundant
1— 2 biotopes	9	4
3—11 biotopes	0	19

The probability of this table is $P \approx 3 \times 10^{-4}$. Thus, it appears that abundant species do, indeed, tend to occupy a larger number of biotopes than sparse ones. It should be noted that abundance and sparsity here refer to occurrence in the optimal biotope. Though the results are very unlikely to occur by chance, caution is needed in their interpretation. First, as fluctuating species tend to occupy a large number of biotopes in their peak years (e.g. VON HAARTMAN 1971:431—432), the above result may be caused by masked peak-year effects in the data. It is impossible to check this with the present data; only a long-term study of many biotopes could elucidate this point. Second, the least abundant species are certainly often overlooked, so that the species classified as rare may in fact occur in a larger number of biotopes. However, the same source of error affects the suboptimal populations of the abundant species, and it is probably insufficient to explain the above results, especially in the forests, where the samples were large.

These ideas were developed further as follows. If a species is adapted to utilize resources which are likely to occur in one or a few biotopes only, we can expect that the distribution of its abundances in different biotopes will have a high, but narrow peak. We examined this by using the ratio between the abundance values in the optimum and the third best biotopes (species occurring in 1—2 biotopes only were excluded). A large ratio indicates a peaked distribution of abundance, and, as a corollary of the hypothesis of McNAUGHTON & WOLF (1970), we suggest that this ratio is negatively correlated with the number of biotopes inhabited by the species. We separated the 32 remaining species into two groups, those which inhabit 3—4 biotopes ($S=17$), and those which inhabit more than four biotopes ($S=15$). The difference in the ratios between the groups is highly significant (one-tailed Mann-Whitney U test, $U<48.5$, $P<0.001$). Combined with the preceding results, this suggests that a species is able to invade a large number of biotopes, if it has specialized in the use of resources that are abundant in a certain environment, for such resources are likely to be present to a considerable degree in other biotopes as well. There are obvious exceptions; *Calcarius lapponicus* has occupied more biotopes than the extreme peakedness of its abundance values suggests, but fewer biotopes than its highest density indicates. Thus, although the two tendencies often coexist, the one does not necessarily imply the other.

(*3*). Several authors (see HILDÉN 1965) have claimed that only optimal habitats are occupied by species living at the margins of their distribution. Our third hypothesis is that the successful species are well adapted to northern conditions, i.e. they are not marginal in the north. Of the 32 species of open biotopes, only 5 were classified as marginal (above), so that only forest data were used to test the hypothesis.

Again, the difference is as predicted. Marginal species occupy 1.8 biotopes per species (14), but the other species inhabit 3.4 biotopes per species (17). The difference is significant (one-tailed Mann-Whitney U test, $U<56.5$, $P<0.01$), but could be partly attributed to sample size. However, biologically meaningful absence/presence classifications should equate absence with low, but non-zero abundance, allowing especially for occasional sparse populations or even non-stationary 'floating' individuals. So the data should be considered to be biased only if it is probable that an increase in sample size would raise the average number of biotopes occupied by the marginal species more than the average of the non-marginal species. The validity of our result should be checked by more data, censusing especially in the open biotopes; if marginal species which have their optimal biotopes in the forests were shown to manage better in the open habitats than the non-marginal forest species, this would imply that our result is an artefact of small sample sizes.

It is not clear how the three hypotheses (1—3) discussed above are interrelated. The tests illuminate different aspects of the subject of successful species, which may partially overlap and have common causes. We have not implied any causal relationships. Several authors (e.g. DEN BOER 1968, 1971, REDDINGIUS & DEN BOER 1970, BIRCH 1971, BRYANT 1973) have recently pointed out that population stability is enhanced by "not-putting-all-eggs-in-the-same-basket" (MAY 1973: 7). To quote BRYANT (1973), "with increasing number of available habitats the probability of simultaneous downward trends in all habitats diminishes". Thus, for example, the correlation between high density in the optimal habitat of the species and the number of biotopes occupied may depend on flexibility in habitat selection, which is likely to be affected by the degree of environmental predictability.

3. Migration patterns

MacArthur (1959) observed that generally more than half of the bird individuals breeding in the forested regions of North America are Neotropical migrants. He also found that, in the northern areas, Neotropical migrants constitute a greater proportion of the total number of individuals than of the total number of species, but that the trend is reversed in southern North America. MacArthur (1959) neglected winter populations, but they exhibit a multitude of alternatives, as is pointed out by Fretwell (1972:146—147). This is strikingly exemplified by three French studies. In Mediterranean *macchia,* the wintering community is dense and diverse, while the summer community consists of a few species only (Blondel 1969). This is explained by the food surpluses which become available in winter. At both early and climax stages of *Quercus robur (Q. pedunculata)* forests (Frochot 1971), bird populations are low in winter, but a considerable number of passing migrants visit the community in spring and autumn. In some of the forests censused by Eybert (1973), there is a winter peak and a summer peak, caused by different groups of migrant birds. Compared with these complex phenomena, the position in our study area is simple, for northern Finland is used as winter quarters only by species breeding there. We classified a species as migrant, if it does not reside in the study area in winter (using maps by Bruun & Singer 1972).

According to the line transect results, 31 per cent of the species are non-migrants in the northern boreal zone (coniferous forests abundant), and 20 per cent in the hemiarctic zone (forests mainly mountain birch). The proportions of non-migrant individuals are 15 and 3 per cent, respectively. According to MacArthur (1959), the difference between the zones can be interpreted as reflecting the instability of the biotopes, particularly the dominating types of forest, in respect of avian resources (summer vs. winter).

When our eleven biotopes are considered separately, it is found that there are several non-migrant species in the forests (B9: 13 %, B10: 22 %, B11: 28 %), whereas the only non-migrant species in the open biotopes, which have a thick snow cover in winter, are *Lagopus mutus* (B1, B2), and *L. lagopus* (B6). Even *L. mutus* is a migrant in disguise, for it 'migrates' downhill to the upper parts of the subalpine forests for the winter; real migrations of *L. mutus* occur in, e.g., Greenland. The percentages of the non-migrant individuals are 6 (B1), 5 (B2), 1 (B6), 3 (B9), 5 (B10), and 7 (B11). Both in the regions and in the separate biotopes, the non-migrant species are less abundant than migrating species (ratios of percentages of non-migrating individuals to those of non-migrating species all lower than 1). The difference is statistically significant (for the biotope data, P = 1/128, one-tailed test, for the trend is expected on the basis of MacArthur's results). Consideration of the species lists (Tables 3 and 4) gives a clue to one of the causes: it appears that, on average, the non-migrant species are larger than the migrants. This agrees with the observation made by Ulfstrand (1974) in Scania, southern Sweden, that the wintering avifauna includes a much larger proportion of heavy species than the breeding avifauna in summer. However, the wintering avifauna in Scania is not a subset of the summer avifauna, but includes many species which are only winter visitors.

4. Density, diversity

An adequate discussion of these basic parameters of the avifauna is not possible before comparable data become available from other parts of Finland. We shall mostly examine our results with reference to the Scandinavian subalpine and alpine censuses. Different aspects of these censuses have been treated by HOGSTAD (1969), YTREBERG (1972), and MOKSNES (1973).

The highest densities in our biotopes occur on palsa peatlands (B5), and only one forest area (A28) supports a denser bird fauna. Accordingly, one of the most important general conclusion drawn from bird census work, that breeding bird densities increase with increasing number of vegetation layers (OELKE 1966, MACARTHUR 1971), does not hold for the northernmost margins of the forests: in that region, bird densities are controlled by other factors besides the vertical structure of the environment.

The densities recorded for the peatland biotopes (B5-B7) accord with the geographical trend observed by HÄYRINEN (1970) and JÄRVINEN & SAMMALISTO (1976), but these authors do not discuss alpine peatlands (B4) separately. The forest densities are generally compatible with the estimates given by NOWIKOW (1962) in his survey of bird densities in European forests.

On the Scandinavian mountains, the rich mountain birch forests support 300—600 p/km^2 (ENEMAR 1963, ENEMAR et al. 1965, ENEMAR & SJÖSTRAND 1970, YTREBERG 1972, MOKSNES 1973), which agrees with the density recorded for the exceptionally rich Finnish mountain forest area A28.

Rich 'meadow birch forests' are rather scanty in Finnish Lapland, but the greater continentality of the Finnish mountain birch forests (HÄMET-AHTI 1963) is probably an even more important cause of differences in bird densities. The average annual precipitation in most of the Finnish parts of the study area is about 400 mm or less, but the Scandinavian maxima are fivefold this amount. In the 'heath birch forests', the mean bird densities fall between 120 and 210 (Table VI in HOGSTAD 1969), but are doubled if patches of meadow birch are intermixed (HOGSTAD 1969, ERIKSSON et al. 1971, MOKSNES 1973). As noted above, the census data show that Finnish mountain birch forests are poorer in species than the Scandinavian ones. The differences in bird densities are undoubtedly partly attributable to differences in methods, but, although this has not always been recognized, they are also partly real. This is evident from the fact that FREDRIKSSON et al. (1966) obtained rather high densities (110 to 290 p/km^2) in line transect censuses mostly performed in the mountain birch forests of Laisdalen, Swedish Lapland, although the transect belts were very broad (200—300 m; cf. VÄISÄNEN & JÄRVINEN 1974, JÄRVINEN & VÄISÄNEN 1975), and the censuses included areas above the tree line. Differences in the species composition also prove the existence of real differences between the mountain birch forests in Finland and in Scandinavia.

In general, the frequencies of *Fringilla montifringilla* in Sweden are much lower than in Finland or in Norway (HOGSTAD 1969, MOKSNES 1973). ENEMAR's (1963) results from the heath birch forests of Abisko, northernmost Sweden, appear to be most similar to Finnish results. This similarity is perhaps due to peak densities of *F. montifringilla* in Abisko in 1961 (A. Enemar, pers. comm.). On the other hand, botanically Abisko belongs to the same

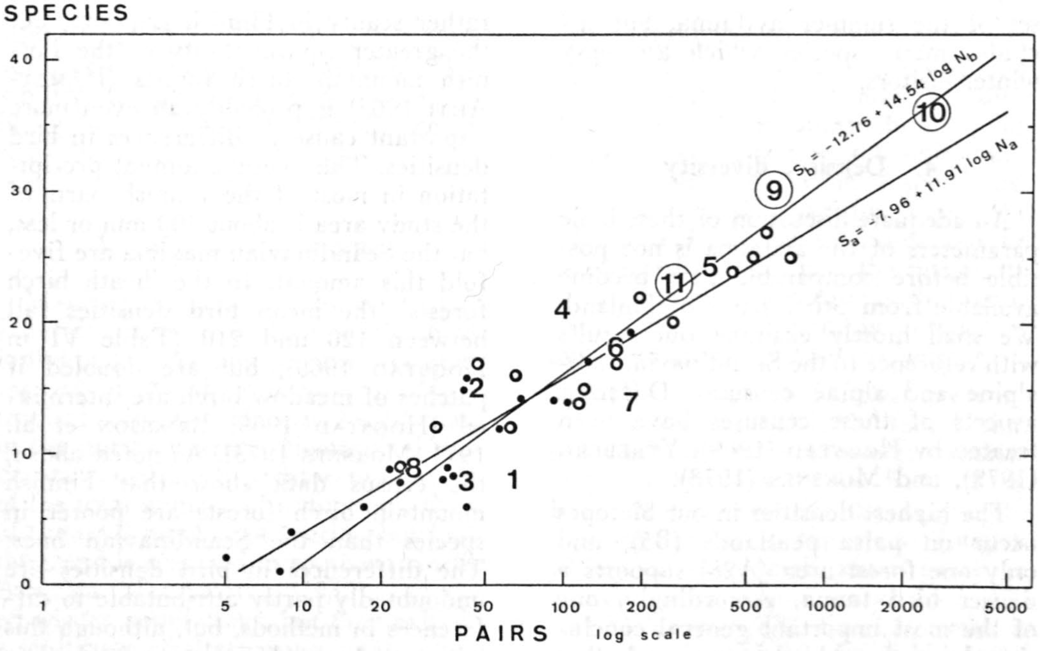

FIG. 7. Number of species (S_a) as a function of the number of pairs (N_a) observed in the censuses A1-A32; data from Table 2. ● = open area, O = forest area. Numbers 1—11 refer to the regression of S_b on N_b for biotopes B1-B11, forest biotopes encircled.

phytogeographical section as most Finnish mountain birch forests (L. Hämet-Ahti, pers. comm.).

SELBOE (1973) performed line transect censuses in the heath birch forests of Øvre Anarjokka (between Kautokeino and Inari, Fig. 1) in July 1973. Surprisingly, the most abundant species were *Calcarius lapponicus* and *Motacilla flava.* Whether this is due to the exceptionally late census period or to the fact that the censused areas were not pure biotopes (e.g., *Phalaropus lobatus* and *Philomachus pugnax* were observed) is difficult to judge.

Northern coniferous forests have been censused less intensively than mountain birch forests. ERIKSSON et al. (1971, also ANDERSSON et al. 1967) report densities of about 50 p/km² from a homogeneous pine forest, and 60—130 p/km² from a pine forest mixed with deciduous trees. ENEMAR et al. (1965) found that a primeval spruce forest, near the subalpine region, supported about 170 p/km², but mixed forests roughly 250 p/km². The low density of B11 is thus understandable, for it includes both pine forests (A31-A32) and mixed forests (A29-A30), and the result is an average.

Census data from open subalpine and alpine habitats are scanty. MOKSNES (1971, 1972, 1973) reports densities of 50 to 110 p/km² on subalpine peatlands. The surprisingly low values (mapping method and bird fauna fairly similar to B4) are possibly caused by the inclusion of heath patches.

In several of the alpine censuses reported, the samples are very small. The low-alpine zone in Nedal (MOKSNES 1973) is characterized by a high dominance of *Anthus pratensis,* while *Plectrophenax nivalis* composes about one half of the total bird community of the middle-alpine zone. Similar results were reported by LIEN et al. (1970), though *Oenanthe oenanthe* dominated between the two zones. These observations greatly resemble those made in B1-B2. In contrast to MOKSNES' results, two extensive study areas (K1, K2) in Ammarnäs were both found to be dominated by the meadow pipit (ALM et al. 1965, 1966). Definite conclusions can hardly be drawn, for the Ammarnäs areas include other habitats, e.g. peatlands. In summary, *Anthus pratensis* might be described as "a master-of-*all*-trades" in the Scandinavian mountains, but is not equally ubiquitous in Finland (or at the highest altitudes on the Scandinavian mountains). Further, results from later years (S. Svensson, pers. comm.) suggest that the frequencies of *Anthus pratensis* reported by ALM et al. (1965, 1966) were exceptional.

Bird species diversity in homogeneous forests is correlated with the diversity of vegetation layers (e.g. MACARTHUR & MACARTHUR 1961), but other controlling factors exist (e.g. Fig 4). Open biotopes support less than 15 species, on an average, but they reach an average diversity of $\overline{H}' = 2.11$. There are about 30 species per forest biotope, but the diversity is not much higher, $\overline{H}' = 2.30$. The difference in the relation between diversity and the number of species is clearly reflected in the average evenness values: $\overline{J}' = 0.81$ for the open biotopes (the highest value, $J' = H'/\log_e S = 0.94$, in B2, is rather exceptional; cf. TRAMER 1969, GŁOWACIŃSKI 1972, BEZZEL 1974, among others), and $\overline{J}' = 0.68$ for the forests. This difference, which is fairly significant, is difficult to interpret, for evenness values depend on sample size (e.g. JÄRVINEN & SAMMALISTO 1973). Indeed, if the numbers of species in the samples are plotted against the number of observations (Fig. 7), the difference between the forests and the open biotopes is seen to be heavily affected by sample size. For the 32 census areas (A1-A32), the coefficient of the correlation between the number of observations and the number of species is 0.943 *** (d.f. = 30) and for the biotopes (B1-B11), $r = 0.922$ *** (d.f. = 9). In the former case, 89.0 per cent of the variance in the numbers of species can be accounted for by sample size, and in the latter case, 85.0 per cent. In other words, the possible difference between the forests and the open biotopes cannot account for more than 11—15 per cent of the variance in the total numbers of species. This sheds a new light on the effect of the number of vegetation layers on bird communities: even the number of species (species richness) does not increase appreciably with the addition of the tree layer at the transition from tundra to taiga. Further, diversity varies with its evenness component, if the effect of sample size is eliminated. This is contrary to TRAMER's (1969) conclusions.

The dependence of evenness estimates on sample size can be overcome in at least two ways. First, sufficiently accurate numbers of species can be obtained from other sources, as was done in our estimates of the regional evenness values of Finnish waders (JÄRVINEN & VÄISÄNEN 1976b). Second, the effect can probably be rendered negligible by using very large samples, provided extinction and immigration do not occur on a large scale. If they do, real difficulties will be encountered in estimating the 'true' number of species in an area, as has already been pointed out by PALMGREN (1930, 1972).

Acknowledgements

During the preparation of the manuscript, Prof. Anders Enemar, the chief of the LUVRE project, kindly provided working facilities for O. J. at the Department of Zoology, University of Gothenburg. The stay in Gothenburg was financed by the Swedish Institute. ChLuvre A. Enemar read an earlier draft of the manuscript and his suggestions have much improved the text. Dr. Leena Hämet-Ahti, an expert in northern phytogeography, read the text and made many valuable comments. Dr. Lasse Sammalisto provided important unpublished census data and offered constructive criticism of the manuscript. Mrs. Anna Damström revised our English. We thank these persons, and all those who have assisted in this study, especially those who collected the field data in *Sameätnam,* the land of the Lapps.

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ISBN 951-661-015-3
ISSN 0001—7299
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