Quantitative biogeography of Finnish land birds as compared with regionality in other taxa

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Quantitative distribution patterns of breeding land birds were studied in Finland and adjacent areas in 1973—77; about 120 000 pairs were observed in line transect censuses sampling a study area of 0.5 million km². The area was divided by numerical methods into six zones on the basis of the breeding bird faunas: arctic (probably comprising an arctic and an oroarctic zone), hemiarctic, north-boreal, mid-boreal, south-boreal and hemiboreal zones. The between-zone transitions generally resulted from differences in the area of the major habitats, but the boundary between the north-boreal and mid-boreal zones was due to a shift in bird species composition without equally striking differences in habitat. The zones seemed to be equivalent in the sense that each zone had 8—10 species with frequencies of at least 3 %, and adjacent zones differed mainly by 4—6 such species. The bird fauna of each zone is described, with special emphasis on quantitative aspects and differences between zones.

Regionality in breeding land birds is compared with various phytogeographical and zoogeographical zonations, including patterns of intraspecific variation in several animals. It is suggested that the different zonations reflect biologically significant differences among different taxa. Two main generalizations emerge. First, in areas north of the Arctic Circle, some species groups (plants, birds) show considerable regional heterogeneity, whereas others (ants) do not. Second, the bird fauna is fairly homogeneous in southern Finland, but other groups show more pronounced heterogeneity. Biological explanations for these generalizations are discussed.

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1. Introduction

In commenting on the history of biogeography, Nelson (1978) stressed the central position of "Buffon's law": different areas have different species. Biogeographers have shown the validity of this concept in comparing biota in different parts of the world, but no causal explanation for Buffon's law has been unanimously accepted; the major alternatives offer either tectonic change or improbability of dispersal as main causative actors. But biogeographical problems also arise on a smaller scale. Comparisons between the faunas and floras of different parts of the same biogeographic "realm" show that clear differences and biogeographically important transitions may occur within relatively narrow zones. Some of these differences may clearly be related to physical discontinuities in the environment, and faunal transitions may simply reflect sharp differences in vegetation. Thus "common sense" tells us that steep faunal gradients should occur near the northern forest limit in Fennoscandia, forest species disappearing, and species of alpine/ arctic habitats appearing. On the other hand, "common sense" would also lead us to expect sharply differing bird communities in forests dominated by different species of trees, but actually the forest bird communities of northern regions tend to be fairly similar (Järvinen & Väisänen 1976a, Haila et al. 1980).

In this study we used censuses of breeding land birds as our data. We have studied quantifiable ornithogeographical patterns in an area (Fig. 1) extending from southernmost Finland (about 60°N) to northernmost Norway (north of 70°N)

and from northern Sweden and westernmost Finland (west of 20°E) to the Leningrad area, easternmost Finland and easternmost Norway (east of 30°E). The area sampled covers about 0.5 million km².

The strategy adopted in this paper is largely descriptive. Where does the breeding bird fauna show the greatest quantitative differences? If sharp transitions exist, do they always coincide with differences in vegetation? How can Finland (and the adjacent areas covered) be divided into zones on the basis of bird census data? How do the bird faunas of the different zones differ? The ultimate purpose of these questions is to provide adequate quantitative information for a causal explanation of the distribution of breeding birds. For this purpose, we have compared our zonation with regionality in other well-studied taxa.

In comparison with an earlier study (Järvinen & Väisänen 1973), this paper shows many improvements. 1) We had about 40 000 pairs as our data base in 1973, but now we have over 120 000. 2) Areas adjacent to Finland were not covered in 1973, and our data from SW Finland were scanty. 3) Our analytic techniques have been substantially improved (Järvinen & Väisänen 1975 and later methodological papers). 4) Our present data are based on censuses made in 1973—77, especially in 1976—77, whereas the previous data covered three decades and were affected by long-term changes in Finnish bird populations.

For readers not acquainted with Finland, a brief description is necessary. Most of the country lies in the northern coniferous zone (taiga), and peatlands are abundant (though largely ditched in southern Finland). The whole country was covered by the ice sheet during the Würm glaciation, and has been recolonized during the past 10 000 years. There are no endemics in the avifauna. From the ornithological viewpoint, Finland has been vividly described by Palmgren (1960). According to von Haartman (1973), there are 233 breeding species; we have excluded waterbirds, such as waterfowl and gulls (but included waders). For the species included, see Järvinen & Väisänen (1977a).

In this paper we have used censuses of the bird fauna to compare different *areas*. In a further study we hope to compare bird *species* on the basis of their quantitative distribution patterns.

2. Material and methods

Breeding birds were censused by the line transect method (Järvinen & Väisänen 1977b) in 1973—77, particularly in 1976—77. Every pair observed was recorded, those recorded within 25 m of the transect separately. The transects were so planned that they included different major habitats, as distinguishable from available 1:20 000 or 1:50 000 maps, in approximately correct proportions, and checks made on data from Åland, southern Finland (Häme), central Finland (Oulu area and Kainuu), northern Finland (areas near Sodankylä) and northern Norway indicated that this requirement was met by the observers participating. For the habitats distinguished during the censuses, see Haila et al. (1980), Järvinen & Väisänen (1978a) and Sect. 4.

It is difficult to estimate the effect of interobserver variation, but all larger areas were covered by more than one observer. The results of each transect were analysed separately, and we could thus confirm that different observers reported similar densities from the same region if the habitats encountered along the transects were comparable. We discarded a small percentage of the censuses: these censuses had been made in poor weather or failed to meet the required standard in some other way.

The transects number 689, with a total length of 3190 km; 121 888 pairs of breeding land birds were observed. The study area and the geographical distribution of the censuses is shown in Fig. 1. Most of Finland was covered in several years, but almost all censuses on the Åland Islands were made in 1975. The Leningrad area was censused in 1975, northern Norway mostly in 1975—76, and northern Sweden almost exclusively in 1977. We regarded 25 km per 100-km square as an acceptable minimum (see Järvinen & Väisänen 1973). In most squares this limit was far exceeded, but regrettably three squares with land areas of at least 5000 km² each (67:6, 71:1, 76:4) had not more than 11—22 km of transects (Fig. 1).

The methods used in analysing the data have been described by Järvinen & Väisänen (1975, 1977a) and Järvinen et al. (1978b). The most essential point is that the observations made in the censuses can be transformed to estimates of relative density, expressed as pairs/km², with the aid of species-specific correction coefficients derived from the census data (Järvinen & Väisänen 1975, Järvinen 1976). As a check, the data of each transect were reanalysed by two other methods: using the main belt data only and using the survey belt data without the correction method of Järvinen & Väisänen 1977a). Although the main belt and the survey belt generally gave consistent results, there were two main types of discrepancy. 1) Certain observers (none of the most experienced) reported average results from the survey belt, but their main belt data indicated substantially higher densities. We attributed such discrepancies to errors in estimating main belt width, and in such cases the main belt data were ignored. 2) The survey belt data were consistent with the main belt data only if the correction method of Järvinen & Väisänen (1976c) was not applied. As suggested in the original methodological paper, discrepancies of this kind seem to arise in very patchy habitats. In other censuses the main cause of such discrepancies was probably unusually favourable weather (audibility of bird song exceptionally good in spite of relatively high densities). In these cases no correction was applied. A third kind of discrepancy must also be mentioned. About 1 per cent of the censuses were rejected, because the observer reported densities about 2 times higher than were reported by other
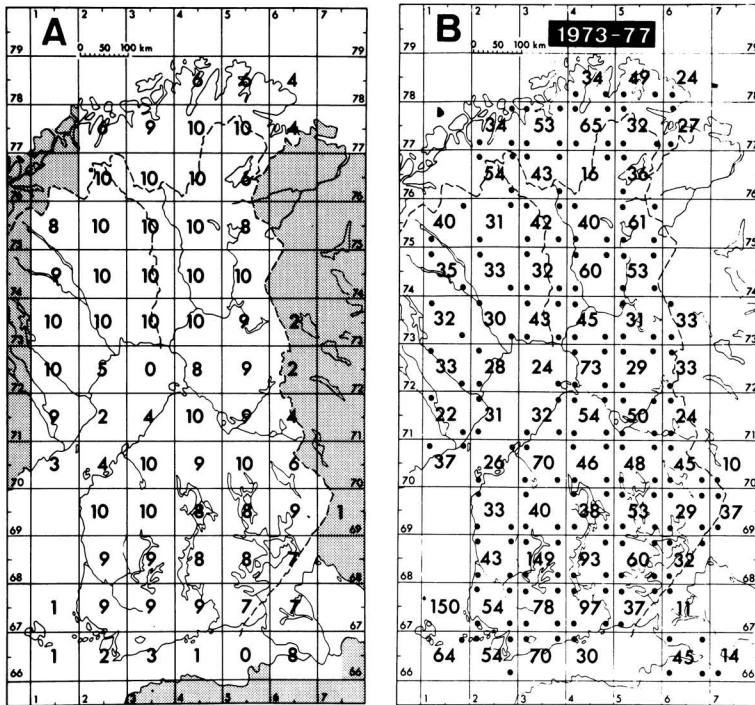
Fig. 1. A. The study area. Each square was weighted according to its approximate land area; the weights used (0—10) are indicated (1 = 1000 km² etc.). B. The distribution of the censuses in 1973 —77. Number = transect lengths (in km). In each square small dots indicate the quarter in which the censuses were made. In comparison with Fig. 1A, note that we have extrapolated the scanty data of 67:6 and 76:4 to the whole land areas of those squares. The importance of one observation in the final results can be deduced from Fig. 1: the importance was directly proportional to land area and inversely proportional to sample size (transect length).

observers in comparable habitats in the same region.

The bulk of the censuses were made in June. Small proportions of the data relate to late May (May 26 or later) or early July; the last day accepted for row 66 in the Finnish uniform grid (see Fig. 1) was July 1, and one day was added to this date for each row northwards (i.e. for each 100 km northwards). On average, census dates were somewhat later in the north than in the south, corresponding to phenological differences.

As relevant methodological problems have been examined in detail in other publications, we shall not review them here. For general points on methodology, see Järvinen & Väisänen (1973, 1975) and Järvinen (1976). For estimating diversity from bird census data, see Järvinen & Sammalisto (1973), Järvinen & Väisänen (1973), Järvinen et al. (1977, 1978a, 1978b) and Järvinen & Lokki (1978). For the effect of annual population fluctuations on estimates of diversity, see Järvinen & Väisänen (1976b). For census efficiency in line transects, see Haukioja (1968; cf. Järvinen & Väisänen 1975), Järvinen et al. (1978a, 1978b), Järvinen (1978a) and Tiainen et al. (1980 and pers. comm.). Notice that absolute (100 %) efficiency was not needed in the analysis of this paper. Of course, lack of absolute efficiency implies that the density estimates presented are underestimates, probably 50—75 % of absolute densities in most of the common species (Tiainen et al. 1980; see also Järvinen 1978a).

In comparing the composition of the bird faunas of different areas, we used as our basis the Finnish uniform grid (27°E) and three modifications: the original grid was transferred 50 km either 1) southwards or 2) west-

wards or 3) southwards and westwards. This procedure was also used by Järvinen & Väisänen (1973). *As the squares of the grid are 100 km by 100 km, this analysis is sufficient to show the general regional structure of the avifauna, but detailed patterns requiring greater resolving power cannot be observed.*

3. Ornithogeographical zonation

3.1. Principles

An ornithogeographical zonation could be based on vegetational zones, e.g. those of Ahti et al. (1968) or Kalliola (1973). We prefer zonations based on birds, as they may then be compared with vegetational zonations without any danger of arguing in a circle. The same argument, in our opinion, applies to zoological zonations based on soil fertility (Kalela 1944, Merikallio 1955).

Bird data can also be used in various ways. Lehtonen (1951) based his zonation on range boundaries, but they are uncertain for rare species and show wide annual fluctuations. As Lehtonen (1951) had no advanced quantitative methods at his disposal, his zones with unusually numerous range boundaries were identified subjectively. It is then difficult to be certain of the degree of equivalence of the zones. A similar method by

Salomonsen (1963) has been discussed by Järvinen & Väisänen (1973:115).

Baroni Urbani & Collingwood (1977), studying North European ants, adopted the principle that zones can be distinguished numerically on the basis of species composition. It does make a difference if two areas differ by 10 species but share 100, in comparison with two areas which differ by 10 species but share none. As before (Järvinen & Väisänen 1973), we have therefore taken species composition as our starting point, but we were able to utilize quantitative data, viz. the frequencies (%) of the bird species in the areas compared. In other words, we have given more weight to common species than to rarities, a decision justified by the fact that in our study area rare species show relatively less stable populations than the more common species (Järvinen & Väisänen 1977c), and the data for the common species are also more reliable.

All comparisons were between 100-km squares. In comparing two squares, the diversity values for the squares were first calculated. We used Shannon's diversity function

$$H' = -\Sigma p_i \ln p_i + f(N),$$

where p_i = frequency of the ith species in the square and $f(N)$ is a correction made for sample size (Hutcheson 1970). An estimate for the amount of diversity due to the differences in species composition between two squares (A and B) can be computed as

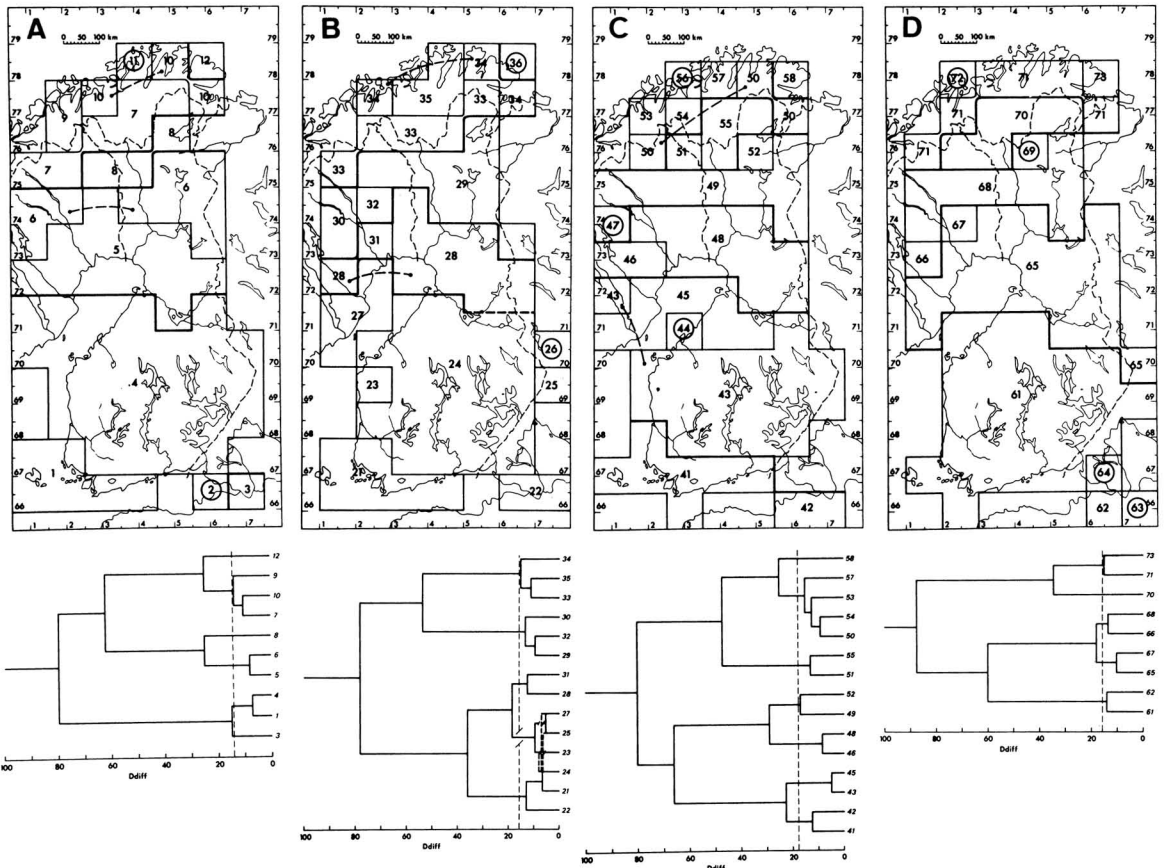$$DIV_{diff} = H'_{A+B} - 0.5(H'_A + H'_B).$$

Fig. 2. The final stages of the dendrogram analyses based on the four grid systems (A: 50 km westwards, B: standard, C: 50 km southwards and westwards, D: 50 km southwards). Encircled figures in the maps indicate that data for these squares were too scanty (< 25 km). Thick boundaries show the zones distinguished when areas differing by less than about 15 *Ddiff* units are combined; though not indicated in the dendrograms, the squares censused poorly were also examined (square 36 in Fig. 2B differs greatly from all others, but other poorly censused squares show fairly strong similarities with adjacent areas).

In this formula, H'_A and H'_B are the diversity values for the two squares and H'_{A+B} is the diversity value obtained by pooling the squares. In pooling, equal weight was given to each square, that is,

$$p_{A+B} = 0.5(p_A + p_B)$$

for any species encountered in A or B. As DIV_{diff} ranges from 0 to ln2, we scaled it by defining

$$Ddiff = 100 \; DIV_{diff}/\ln 2,$$

which ranges from 0 to 100. (For discussion, see Järvinen & Väisänen 1977a). In the following, we shall express differences between areas in units of $Ddiff$.

In comparing adjacent squares, we used procedures adopted by Järvinen & Väisänen (1973), and in analysing matrices of $Ddiff$ values we constructed dendrograms by a simple method (Cody 1974:92). However, dendrograms were analysed in a stepwise manner. We first combined the data for the squares that were most similar according to the original dendrogram, then calculated a new matrix and derived a new dendrogram, and so on.

3.2. Analysis

Each grid system was used as the basis of dendrogram analysis. At the first step all squares

Table 1. Characteristics of the "nuclear areas" in Fig. 3. S = number of species observed, H' = Shannon's diversity index, J' = evenness index ($= H'/\ln S$), D = total density (pairs/km²). In calculating these data, all squares were weighted according to their land area (Fig. 1A).

"Nuclear area"	S	H'	J'	D
A	61	2.91	0.71	86.4
B	63	2.81	0.68	108.5
C	75	2.89	0.67	111.1
D	82	3.12	0.71	135.1
E	90	3.27	0.73	204.5
F	88	3.42	0.76	321.0

differing by less than about 5 units were combined, at the second step the limit was about 8 units, and at the third step about 10 units. At the final step, depicted in Fig. 2, the critical limit was about 15 units. Six main zones can be distinguished as a result of each analysis, but the four variants (Fig. 2A-D) differ considerably, partly owing to the effects of early combinations in the dendrograms. However, Fig. 2 was used to identify six "nuclear areas". Each of these included three 100-km squares, was fairly homogeneous as regards bird data, was distinguishable in most dendrogram analyses from other nuclear areas, and provided a sufficient data base for comparisons with other squares. As a result, the drawing of boundaries between zones was greatly facilitated. The "nuclear areas" were (see Fig. 3):

A. Northernmost Norway. Varangerhalvøya in the east seems somewhat different from the other squares of this area, and in two analyses it was separated as an area of its own.

B. Continental "tundra" Lapland. This area tended to be separated in all analyses, though in different shapes.

C. Northern Finland ("Peräpohjola"). Distinct in all analyses (though northern in Fig. 2A).

D. Areas between the Arctic Circle and Oulu. Observed in all analyses except Fig. 2A.

E. Lake Finland. Clearly seen in all analyses.

F. Leningrad area. Not very distinct from E, but separated here tentatively because F represents the southern extreme of our study area. As shown in Fig. 3, the differences between D and E and between E and F are roughly equal.

The "nuclear areas" differ not only in species composition, but also in other characteristics of the avifauna (Table 1). Diversity increases southwards from B to F (all differences between adjacent "nuclear areas" significant, $P < 0.01$). Diversity is significantly higher in A than in B, but this is an artefact caused by the heterogeneity among the squares in A (cf. above). From A to D, densities increase slowly (from 86 to 135 pairs/
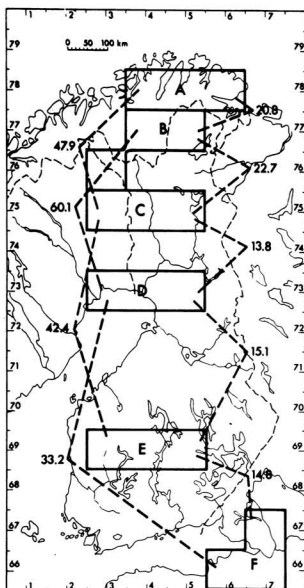

Fig. 3. The "nuclear areas" A—F distinguished on the basis of Fig. 2. $Ddiff$ values between adjacent areas (right) and between every second area (left) indicate that the "nuclear areas" are somewhat more similar in the south than in the north, mainly because B is more distinct from adjacent areas than C—E.

km²), but in the south the increase is steep (204 and 321 pairs/km² in E and F, respectively). As a broad rule we may generalize that in the south it is total density which changes most, and in the north species composition. Diversity tends to change more or less everywhere.

Comparisons between the "nuclear areas" and all squares outside them resulted in the zonation given in Fig. 4. We simply joined each of the remaining squares to that nuclear area which showed the greatest similarity to it, though, of course, we encountered many boundary cases. Final decisions upon them were based on Figs. 2 and 5. The boundaries of Fig. 4 are best thought of as blurred zones; we have emphasized this interpretation by giving the boundaries as lines following the square boundaries in our various grids. The differences between adjacent zones shown in the dendrogram of Fig. 4 are fairly similar to the differences between adjacent zones in Fig. 3, except that there is a very small difference between the two southernmost zones in Fig. 4. In Fig. 3, southern Finland was represented by nuclear area E, but in Fig. 4 we have distinguished two subzones, 6A and 6B. These subzones do not differ sharply with respect to species composition, but there is a steep gradient in total density: subzone 6A is similar to E, but subzone 6B is similar to F in total density. Our decision to combine 6B and 7 in our presentation thus decreases the difference in species composition between 6A and 6B+7, but the differences in total density are preserved. In addition, we justify our decision by the fact that zone 7 was represented by only a small number of censuses.

Another fundamental difference should be noted between the nuclear areas of Fig. 3 and the zones of Fig. 4. We have divided the northernmost areas, represented by A in Fig. 3, into two zones, for Varangerhalvøya with the other parts of northernmorst Norway seems to form a zone of its own (see Fig. 2A and 2C).

A comparison between Tables 1 and 2 shows that some of the zones are more heterogeneous than others. Diversity is considerably higher in zones 4, 5 and 6B+7 than in the corresponding nuclear areas (C, D and F, respectively), implying that in these zones we have combined areas that differ in species composition. According to the primary data and Fig. 5, this heterogeneity can be traced to differences between the Finnish and Swedish areas in zones 4 and 5, and between 6B and 7 in 6B+7. As total density tends to be lower in the Swedish parts of zones 4 and 5 than in the Finnish parts, the total densities in 4 and 5 are
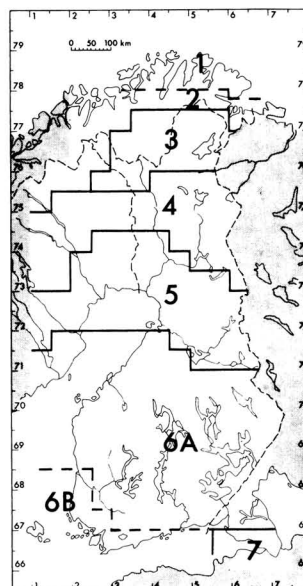
	1+2	3	4	5	6A	6B+7
1+2	—					
3	18.5	—				
4	41.8	21.0	—			
5	51.4	40.2	12.4	—		
6A	65.0	63.0	38.7	12.1	—	
6B+7	70.4	71.9	51.1	24.8	7.1	—

Fig. 4. The zoogeographical zones distinguished and the _Ddiff_ matrix of their interrelations. 1+2 = arctic, 3 = hemiarctic, 4 = north-boreal, 5 = mid-boreal, 6A = south-boreal and 6B+7 = hemiboreal.

lower than in the corresponding nuclear areas. A similar decrease in 1+2 in comparison with nuclear area A is due to the fairly low bird densities in the western, relatively mountainous parts of 1+2.

Table 2. Characteristics of the ornithogeographical zones in Fig. 4. For abbreviations, see Table 1. Each square included in a zone was weighted according to its land area (Fig. 1A). The figures in parentheses after the name of the zone indicate the percentage of the total land area falling within this zone.

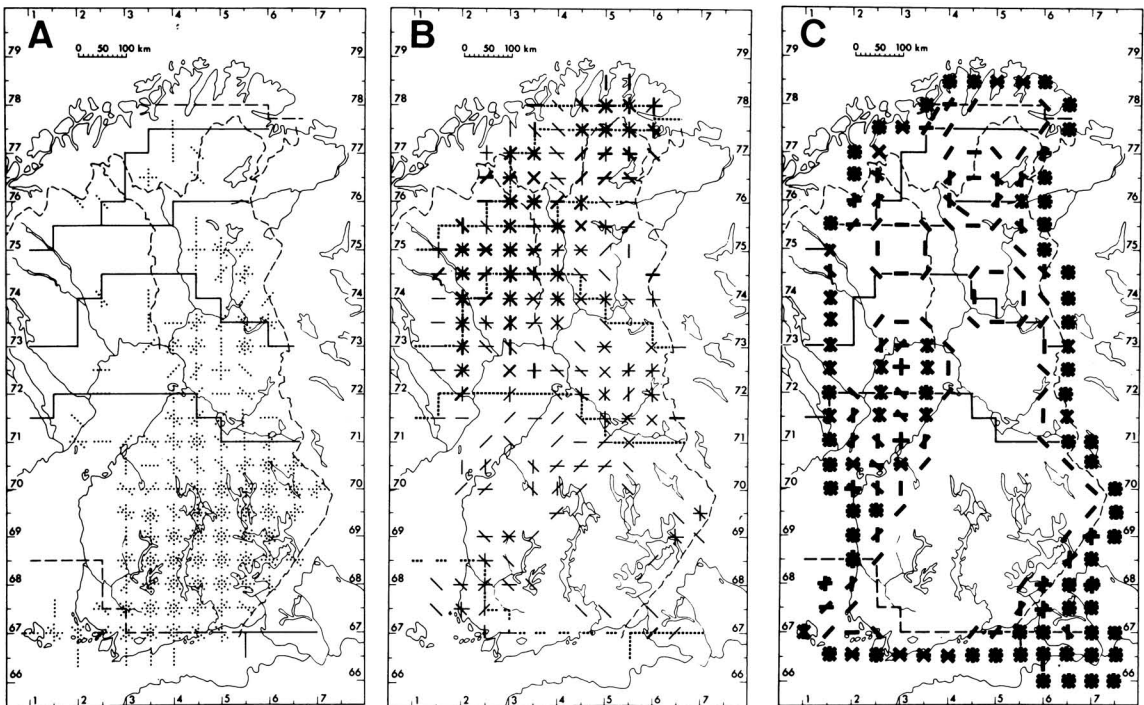| Zone (%)		_S_	_H'_	_J'_	_D_
1+2	Arctic (11.7)	75	2.92	0.68	66.8
3	Hemiarctic (9.7)	69	2.82	0.67	105.1
4	North-Boreal (17.4)	99	2.99	0.65	90.1
5	Mid-Boreal (19.6)	105	3.30	0.71	119.8
6A	South-Boreal (36.4)	129	3.30	0.68	208.5
6B+7	Hemiboreal (5.2)	126	3.64	0.75	324.2

Fig. 5. Comparisons between neighbouring squares of the four grid systems used. The symbols are placed between the two squares compared; e.g., a vertical symbol compares two horizontally adjacent 100 km squares. A. $Ddiff < 6.6$. Notice that neighbouring squares are usually similar throughout southern Finland. B. $Ddiff \geq 6.6$. Thin lines: $6.6 \leq Ddiff < 15.0$, thick lines: $Ddiff \geq 15.0$. Areal differences are particularly great in the north. C. Symbols indicate $Ddiff$ values that were omitted or not calculated owing to scarcity of data.

Finally, we analysed the data by the methods of Järvinen & Väisänen (1973), comparing all adjacent squares with each other (including diagonal comparisons). The results (Fig. 5) indicate areas where species composition shows negligible (Fig. 5A) or relatively sharp (Fig. 5B) local gradients. Unfortunately, the patterns are none too clear; it is hardly possible to draw boundaries on the basis of Fig. 5 without introducing considerable elements of subjectivity. However, the zones distinguished above show similarities to the occurrence of local differences (e.g. the homogeneity of the south-boreal zone is also evident from Fig. 5). Of special interest is the region called Suomenselkä in the western parts of the south-boreal zone in Finland (see e.g. Merikallio 1958). Suomenselkä cannot be distinguished in Fig. 4, but Fig. 5 does reveal differences between Suomenselkä and adjacent areas. The point is, however, that quantitatively these differences are fairly small; Suomenselkä does not deserve the status of a separate (sub)zone. It is true that, on the one hand, a number of northern bird species attain relatively high densities in Suomenselkä, but nowhere else in the south-boreal zone, and, on the other hand, some southern species do not occur in Suomenselkä although they breed in low densities in Lake Finland and along the coast of the Gulf of Bothnia, i.e. in areas east and west of Suomenselkä. The total effect of these species is nevertheless quantitatively small. However, if Suomenselkä is defined as a narrow (pen)insular extension of the mid-boreal zone, the squares used here are simply too large.

4. Land bird fauna in the zones distinguished

In the following we shall describe the land bird fauna in the zones distinguished in Sect. 3.2 (see Fig. 4). Our emphasis will be on the common species of the zones (cf. Sect. 3.1). Densities and frequencies of all species reaching frequencies of at least 3 % are given in Table 3. Species whose

Table 3. The densities (pairs/km²) and frequencies (%, in parentheses) of all species reaching frequencies of at least 3 % in any of the zoogeographical zones distinguished. The species are arranged roughly according to their geographical distribution, from northern to southern species. *D* and *F* as explained in the text.

	Arctic			Hemiarctic			North-boreal			Mid-boreal			South-boreal			Hemiboreal		
Plectrophenax nivalis	3.4	(5.2)	DF	—			—			—			—			—		
Oenanthe oenanthe	5.4	(8.1)	DF	2.3	(2.2)		1.0	(1.2)		0.6	(0.5)		0.9	(0.4)		1.3	(0.4)	
Anthus pratensis	15.4	(23.0)	F	9.2	(8.8)	DF	1.6	(1.8)		2.0	(1.7)		0.9	(0.4)		1.9	(0.6)	
Pluvialis apricaria	3.8	(5.7)		4.0	(3.8)	DF	0.4	(0.4)		0.1	(0.1)		0.1	(0.1)		—		
Calcarius lapponicus	5.0	(7.4)	DF	11.7	(11.2)	DF	—			—			—			—		
Luscinia svecica	2.1	(3.1)		4.0	(3.8)	DF	0.5	(0.5)		—			—			—		
Motacilla flava	0.4	(0.6)	DF	11.9	(11.3)	, F	7.2	(8.0)	F	5.3	(4.4)	DF	1.8	(0.8)		2.8	(0.9)	
Carduelis flammea	3.0	(4.4)		5.2	(4.9)		3.7	(4.1)		2.1	(1.7)		0.2	(0.1)		—		
Fringilla montifringilla	3.9	(5.8)	DF	10.6	(10.1)	F	15.1	(16.7)	DF	7.5	(6.2)	DF	0.8	(0.4)		—		
Tringa glareola	0.2	(0.2)	D	3.1	(3.0)		·2.9	(3.2)		1.6	(1.3)		0.5	(0.2)		0.1	(0.0)	
Turdus iliacus	3.8	(5.7)	D	8.2	(7.8)		9.5	(10.5)	F	8.8	(7.4)		10.1	(4.8)		8.6	(2.6)	
Phylloscopus trochilus	6.6	(9.9)	DF	18.6	(17.7)		17.6	(19.6)		22.5	(18.8)	F	33.0	(15.8)	F	30.7	(9.5)	
Emberiza rustica	—			—			1.8	(2.0)	D	3.9	(3.3)	D	1.3	(0.6)		0.0	(0.0)	
Anthus trivialis	—			0.1	(0.1)	DF	3.4	(3.7)		6.1	(5.1)		9.9	(4.8)		10.3	(3.2)	
Muscicapa striata	—			0.2	(0.2)	DF	4.2	(4.6)		6.9	(5.7)		6.2	(3.0)		10.0	(3.1)	
Regulus regulus	—			—			0.2	(0.2)		2.3	(2.0)	D	6.8	(3.3)		8.4	(2.6)	
Fringilla coelebs	0.0	(0.0)		—			1.4	(1.6)	DF	12.8	(10.6)	DF	41.4	(19.9)	F	51.8	(16.0)	
Turdus pilaris	1.8	(2.8)		0.4	(0.4)		0.8	(1.0)		2.5	(2.1)	D	8.2	(4.0)		13.8	(4.2)	
Erithacus rubecula	—			—			0.3	(0.3)		1.8	(1.5)	D	7.8	(3.7)		11.0	(3.4)	
Parus major	0.1	(0.1)		—			0.1	(0.2)		1.2	(1.0)	D	4.4	(2.1)	D	13.9	(4.3)	
Emberiza citrinella	—			—			0.1	(0.2)		0.9	(0.8)	D	5.0	(2.4)	D	10.6	(3.3)	
Alauda arvensis	0.1	(0.1)		0.0	(0.0)		0.1	(0.1)		0.6	(0.4)		2.5	(1.2)	D	9.6	(3.0)	
Passer domesticus	0.1	(0.1)		—			—			0.2	(0.2)		1.5	(0.7)	D	12.0	(3.7)	

frequencies exceed 5 % will be called dominant in the zone in question. We have drawn attention to quantitatively noteworthy differences in density and frequency between two adjacent zones by the symbols *D* and *F* in Table 3. *D* indicates that the density of the species is at least 100 % higher in one of the zones than in the other (species whose densities were below 3 pairs/km² in both zones are neglected). *F* indicates that the frequency of the species in the adjacent zones differs by at least 3 % units.

The percentages of the main habitats are given for each zone, as faunistic differences between the zones may be due to differences in the coverage of different habitats. Habitat data are not very accurate for the northern areas (the main sources were the Atlas of Finland 1960 and our own line transect data). The Atlas of Finland (1976) provides fairly accurate data for the north-boreal and mid-boreal zones, and the data for the southernmost zones are based largely on the most recent (1971—76) National Forest Survey, the results of which were re-analysed for the present purposes with the kind help of the Forest Research Institute in Finland.

Note that our terminology largely follows that of Ahti et al. (1968), but our zones are not identical. Regrettably, no generally accepted terminology has yet emerged (for a discussion, see Hustich 1979 and references there). We have not used the term "subarctic" here because of the widely differing definitions given by various authors.

4.1. Arctic zone (zones 1—2)

Habitats. Mountain heath 80 %, open peatland 10 %, mountain birch forest 10 %. "Oceanic" mountain heaths are prevalent; "continental" mountain heaths are more common in the southern part of this zone and in the hemiarctic zone (see Järvinen & Väisänen 1976a, 1978a). If a distinction is made between zones 1 and 2, we suggest the names *arctic* and *oroarctic* for them, respectively (see Sect. 5.1).

Bird fauna. Total density was 68 pairs/km², biomass (calculated from the weights compiled by Järvinen & Väisänen 1977a) being as low as 7.7 kg/km². The dominant species were *Anthus pratensis* (15 pairs/km²), *Phylloscopus trochilus* (7 pairs/km²), *Oenanthe oenanthe* (5 pairs/km²), *Calcarius lapponicus* (5 pairs/km²), *Fringilla montifringilla* (4 pairs/km²), *Pluvialis apricaria* (4 pairs/km²), *Turdus iliacus* (4 pairs/km²) and *Plectrophenax nivalis* (3 pairs/km²). Ten species had frequencies of at least 3 %, and in the whole land bird fauna these accounted for as many as 78 % of the pairs; this fact is reflected in the low diversity of the zone (*H'* = 2.92). In fact, marginally occurring species are more characteristic of northern than of southern areas in Fennoscandia

(Järvinen & Väisänen 1977d). A more detailed analysis of northern Norway has been published by Järvinen & Väisänen (1978a).

4.2. Hemiarctic zone (zone 3)

Habitats. About 50 % fairly barren forests (about 30 % mountain birch, about 20 % pine), 30 % dry continental mountain heaths, 10 % wooded bogs and 10 % open peatlands. The northern forest limit runs through this zone (see Hustich 1979 and references there).

Bird fauna. Total density was 106 pairs/km^2 and biomass 10.0 kg/km^2, both figures being higher than in the arctic zone. The dominants were *Phylloscopus trochilus* (19 pairs/km^2), *Motacilla flava* (12 pairs/km^2), *Calcarius lapponicus* (12 pairs/km^2), *Fringilla montifringilla* (11 pairs/km^2), *Anthus pratensis* (9 pairs/km^2) and *Turdus iliacus* (8 pairs/km^2). Ten species had frequencies of at least 3 %, and these accounted for a higher percentage of the whole land bird fauna than in any other zone, 82 % of the pairs. In consequence, diversity was as low as $H' = 2.82$.

The hemiarctic zone differs from the arctic zone by as much as 18.5 *Ddiff* units. This is mainly due to five species of open habitats (*Plectrophenax nivalis*, *Oenanthe oenanthe*, *Anthus pratensis*, *Calcarius lapponicus* and *Motacilla flava*) and two forest species (*Fringilla montifringilla* and *Phylloscopus trochilus*). In addition, two further species, *Tringa glareola* and *Turdus iliacus*, were observed in considerably higher densities than in zones 1 and 2. The differences in density and frequency can probably be traced to differences in habitat: southwards the importance of forests increases and the importance of mountain habitats decreases. Similarly, the rarity of *Motacilla flava* and *Tringa glareola* on peatlands of the arctic zone (see also Järvinen & Väisänen 1978a) may at least partly be due to the absence of suitable perching trees in the north (see Sammalisto 1957), though this idea needs more study.

In an earlier paper (Järvinen & Väisänen 1976a) we have analysed this zone and the northern parts of the north-boreal zone on the basis of older data. We concluded that the northern forests have an impoverished bird fauna, which is reflected, for instance, in the remarkably close similarity between the bird communities of birch and pine forests. Impoverishment may be related to the fact that the north-boreal forests (including the forests of our hemiarctic zone) represent the western tip of a "taiga peninsula" (for a map, see Ahti et al. 1968). Furthermore,

east of Finland the White Sea breaks the continuity of this zone. It would be highly desirable to be able to compare Fennoscandian data with censuses made in equivalent areas near the transition between taiga and tundra in western Siberia or northern Russia west of the Ural Mts.

4.3. North-boreal zone (zone 4)

Habitats. About 55 % forests (pine 35 %, spruce 15 %, deciduous trees 5 %), 25 % wooded bogs, 20 % open peatlands.

Bird fauna. Total density was low, 90 pairs/km^2, and biomass was 11.0 kg/km^2. North Swedish parts of this zone are poorer than the Finnish parts, largely because peatlands are more extensive in northern Finland, and these support dense bird communities (e.g. Järvinen & Sammalisto 1976, Järvinen & Väisänen 1976a, 1978a). The dominant species were *Phylloscopus trochilus* (18 pairs/km^2), *Fringilla montifringilla* (15 pairs/km^2), *Turdus iliacus* (10 pairs/km^2) and *Motacilla flava* (7 pairs/km^2). Eight species had frequencies of at least 3 %, their contribution to the whole land bird fauna being 70 %, much less than in the two northernmost zones. Diversity was accordingly higher than in the north ($H' = 2.99$).

The north-boreal zone differs from the hemiarctic zone by 21.0 *Ddiff* units, this being the greatest difference between any two adjacent zones. It is caused mainly by a southwardly decreasing gradient in the frequencies of *Anthus pratensis*, *Pluvialis apricaria*, *Calcarius lapponicus*, *Luscinia svecica* and *Motacilla flava* and rising frequencies of *Fringilla montifringilla*, *Anthus trivialis* and *Muscicapa striata*. As a rule, these species also showed considerable differences in densities. The differences between the two zones are clearly caused by a major habitat difference: mountain heaths are virtually absent from zone 4 but forests are a major type of vegetation. Here, we wish to call attention to the abrupt gradient in the numbers of *Calcarius lapponicus*. The species breeds only locally on open peatlands in the north-boreal zone (von Haartman et al. 1963—72, own observations), but in our hemiarctic zone it is one of the dominants of mountain heaths and open peatlands (see Järvinen & Sammalisto 1976, Järvinen & Väisänen 1976a, 1978a). The southern range boundary of this species certainly merits a detailed study. Another abrupt range boundary is that of *Luscinia svecica*, though the gradient is not so steep as in *C. lapponicus*. *L. s. svecica* is intriguingly absent from southern Fin-

land, although another subspecies, *L. s. cyanecula*, breeds in Central and Eastern Europe.

4.4. Mid-boreal zone (zone 5)

Habitats. About 50 % forests (pine 25 %, spruce 20 %, deciduous trees 5 %), 30 % wooded bogs (mainly ditched), and 20 % open peatlands.

Bird fauna. Total density (120 pairs/km^2) and biomass (13.8 kg/km^2) higher than in the more northern zones. North Swedish parts of this zone are also poor, owing to the scarcity of peatlands. The dominant species are *Phylloscopus trochilus* (22 pairs/km^2), *Fringilla coelebs* (13 pairs/km^2), *Turdus iliacus* (9 pairs/km^2), *Fringilla montifringilla* (8 pairs/km^2), *Muscicapa striata* (7 pairs/km^2) and *Anthus trivialis* (6 pairs/km^2). Eight species had frequencies of at least 3 %, but their contribution to the whole bird fauna was only 62 %. This implies that diversity is high; however, part of the high diversity ($H' = 3.30$) is due to the heterogeneity among the different areas within the zone (Sect. 3.2). There is a difference of 12.4 units between the north-boreal and mid-boreal zones, due chiefly to the sharp gradient in the relative proportions of *Fringilla coelebs* and its ecologically similar congener *F. montifringilla*; the frequency of *F. coelebs* is higher and that of *F. montifringilla* lower by about 10 % units in the mid-boreal zone than in the north-boreal zone. The complementary distribution pattern of the two *Fringilla* species is strong evidence for interspecific competition, but other dynamic phenomena are also involved (for details, see Järvinen & Väisänen 1979b). Other species showing steep gradients in frequency include *Motacilla flava* and *Turdus iliacus* (their densities differ only slightly), but the zone boundary is affected about as much by the two *Fringilla* species as by all the other land bird species together (but see Sect. 5). The density of *Emberiza rustica* doubles from the north-boreal to the mid-boreal zone.

It is questionable whether the 1:1 boundary between the two *Fringilla* species can be accounted for by habitats, for this boundary is highly dynamic (see Järvinen & Väisänen 1979b and references there). Suomenselkä (see Sect. 3.2) is often considered a southward extension of the mid-boreal zone, and it is of interest to find that this watershed area is not distinguishable in the map of Järvinen & Väisänen (1979b) showing the density ratios of the two congeners.

4.5. South-boreal zone (subzone 6A)

Habitats (in Finland). About 78 % forests (pine 42 %, spruce 31 %, deciduous trees 7 %), 5 % wooded bogs, 11 % ditched bogs, 1 % open peatlands, 14 % agricultural land, 2 % built-up areas.

Bird fauna. Total density was clearly higher than in the more northern zones, 208 pairs/km^2. Density increases southwards within the zone, from about 150 pairs/km^2 to about 250 pairs/km^2. Biomass was also relatively high, 20.4 kg/km^2. Only two species were dominants, *Fringilla coelebs* (41 pairs/km^2) and *Phylloscopus trochilus* (33 pairs/km^2). Eight species had frequencies of at least 3 %, and their contribution to the whole bird fauna was 59 %; therefore, diversity was high, $H' = 3.30$.

The south-boreal zone differs from the mid-boreal zone by 12.1 *Ddiff* units. Part of this difference is the result of southward decreases in frequency in *Motacilla flava*, *Fringilla montifringilla* and *Phylloscopus trochilus*, but the most important single difference is the southward increase in the frequency of *F. coelebs*. Differences in density do not coincide with differences in frequency, for there is a considerable southward increase in the density of a large group of southern forest species, especially *Regulus regulus*, *F. coelebs*, *Turdus pilaris*, *Erithacus rubecula*, *Parus major* and *Emberiza citrinella*. Habitat differences seem to be sufficient to explain the main differences between the zones, particularly because they reflect considerable differences in productivity. Productivity is closely correlated with bird density (e.g. Palmgren 1928, Nilsson 1979).

4.6. Hemiboreal zone (subzone 6B and zone 7)

Habitats (in Finland). About 63 % forests (pine 37 %, spruce 17 %, deciduous trees 5 %), 5 % wooded bogs (more than half ditched), 1 % open peatlands, 26 % agricultural land and 4 % built-up areas.

Bird fauna. Total density was far higher than in the other zones, 324 pairs/km^2. Subzone 6B (belonging rather to the south-boreal zone on the basis of species composition) and zone 7 (the hemiboreal zone proper) had similar densities, though their bird faunas differed somewhat. This heterogeneity partly accounts for the high diversity of the zone, $H' = 3.64$, but diversity was high even in small areas (e.g. $H' = 3.54$ in the Åland Islands). In accordance with high diversity, the ten species having frequencies of at least 3 % did not comprise more than 54 % of the pairs in the whole bird fauna of the zone.

Table 4. Relative densities of the various subgroups of the whole land bird fauna, with the density of the hemiboreal zone as 100 (the actual density, in pairs/km², in parentheses). The abbreviations are: A = arctic zone (zone 1+2), HA = hemiarctic (zone 3), NB = north-boreal (zone 4), MB = mid-boreal (zone 5), SB = south-boreal (zone 6A) and HB = hemiboreal (zone 6B+7).

	A	HA	NB	MB	SB	HB
All land birds	21	32	28	37	64	100 (324)
Migration strategies						
Sedentary	7	10	12	20	45	100 (75)
Migrants	25	39	32	42	70	100 (249)
Habitats						
Forest	10	22	30	43	76	100 (227)
Open	71	90	35	33	44	100 (60)
Other	3	4	4	9	27	100 (37)

Table 5. Differences (in units of *Ddiff*) between adjacent zones using data on various subgroups of the land bird fauna. For abbreviations, see Table 4. Question marks indicate insufficient data.

	A-HA	HA-NB	NB-MB	MB-SB	SB-HB
All land birds	18.5	21.0	12.4	12.1	7.1
Migration strategies					
Sedentary	41.3	30.6	22.7	8.9	13.0
Migrants	18.9	21.3	10.8	11.6	5.2
Habitats					
Forest	4.9	13.9	11.3	10.7	4.9
Open	26.4	22.2	11.9	18.7	4.8
Other	?	?	?	9.9	14.5

The zone differs relatively little from 6A (7.1 units) because of the great similarity between 6A and 6B (cf. Table 1). As seen from Table 3, the densities in 6B+7 tend to be at least as high as in 6A (the frequencies of *Phylloscopus trochilus* and *Fringilla coelebs* in the hemiboreal zone are lower only because of the higher densities of many other species, such as *Parus major*, *Emberiza citrinella*, and particularly *Alauda arvensis* and *Passer domesticus*). The boundary between the zones seems to be due mainly to the activities of man; the importance of agricultural land and forests near human habitation is strikingly greater in 6B+7. The densities of two *Phylloscopus* species are high in zone 7 as compared with subzone 6B; *Ph. trochilus* has a density of about 40 pairs/km² (nearly 13 %) and *Ph. sibilatrix* a density of over 15 pairs/km² (about 5 %) in zone 7. The Åland Islands, which form part of 6B, have been analysed in detail by Haila et al. (1980).

4.7. Distribution patterns of various subgroups

Detailed analyses based on various ecologically or taxonomically defined subgroups often require a different approach from that adopted in this paper, as the numbers of observations on most subgroups are too low. No taxa will be analysed separately here (for waders, see Järvinen & Väisänen 1978b), but the results for two ecological subgroups (defined mainly on the basis of data in von Haartman et al. 1963—72) are presented in Tables 4—5.

Migration strategies. We included both partial migrants and irruptive species among the sedentary species; our migrants are thus true migrants that winter in Central Europe, the Mediterranean countries, Africa or Asia (at most a small minority of their populations may winter in Finland). The densities of the migrants decrease northwards, but much more slowly than do those of the sedentary species. In the hemiboreal zone the percentage of sedentary species was about 23 % of the pairs, but in the arctic and hemiarctic zones it was not more than about 5 % (Table 4). This difference indicates that in these northern latitudes the scarcity of winter resources, accentuated by the severity of the winters, plays an important role in population regulation. This is supported by the dramatic decreases that have occurred in many of the sedentary birds, such as *Parus* spp., that winter in the northern coniferous forests, because these decreases seem to be due to intesified forestry (see Järvinen & Väisänen 1979a, 1979b); note that most birds wintering in the north are inhabitants of coniferous forests (Järvinen & Väisänen 1976a). The importance of winter conditions is also shown by the fact that the differences in species composition between adjacent zones tend to be greater for the sedentary species than for the migrants (Table 5). In other words, the sedentary species divide our study area into more distinct zones than the migrants do. As most Finnish bird species are migratory, our zonation is decisively affected by them, but considerable between-zone differences in the sedentary populations are thus masked. The characteristic sedentary species of the different zones are:

Arctic: *Lagopus mutus* (1.0 pairs/km²) and *L. lagopus* (0.6 pairs/km²);
Hemiarctic: *L. lagopus* (1.1 pairs/km²) and *Parus cinctus* (0.7 pairs/km²);
North-boreal: *L. lagopus* (1.0 pairs/km²) and *Perisoreus infaustus* (0.8 pairs/km²);
Mid-boreal: *Parus montanus* (2.9 pairs/km²) and *Regulus regulus* (2.3 pairs/km²);
South-boreal: *R. regulus* (6.8 pairs/km²), *Emberiza citrinella* (5.0 pairs/km²) and *Parus montanus* (4.9 pairs/km²);

Hemiboreal: *P. major* (13.9 pairs/km²), *Passer domesticus* (12.1 pairs/km²) and *E. citrinella* (10.6 pairs/km²).

In this analysis (Table 5) we omitted *Carduelis flammea*, as its frequencies (Table 3) would have led to completely different results for the three northernmost zones. We consider the omission justified by the fact that few individuals of *C. flammea* winter in the north. *Regulus regulus*, though a partial migrant, was included here because a high proportion of individuals nevertheless winter in Finland.

Habitats. The habitat preferences of the different species were classified into three groups: forests, open habitats (e.g. peatlands, mountain heaths or fields) and "other habitats" (urban habitats, rocks etc.). The densities of forest species parallel the general trend except, naturally, in the arctic zone. The high densities of birds in open habitats in the north are largely due to the extensive peatland habitats (Järvinen & Sammalisto 1976, Järvinen & Väisänen 1976a, 1978a).

Differences in species composition between the zones tend to be greater for species of open habitats than for those of forests, and the difference between the two groups is particularly great in the north. The ratio between the *Ddiff* values is 5.4 for the comparison between the arctic and hemiarctic zones and 1.6 for that between the hemiarctic and north-boreal zones, but almost exactly 1 for comparisons between areas further south. The comparison between the mid-boreal and south-boreal zones is exceptional because of man's activities: in the mid-boreal zone peatland species dominate, but in the south-boreal zone the commonest birds of open habitats are species of agricultural areas (Table 6).

Finally, we point out that the south-boreal and hemiboreal zones are distinguishable largely because of species of "other habitats", in this case mainly urban environments. As noted above (Sect. 4.6), this effect is partly due to the inclusion of the Finnish subzone 6B in zone 7 in the present analysis. In other words, the Finnish subzones 6A and 6B differ hardly at all with respect to species composition in "natural" habitats, such as forests or peatlands.

5. Comparisons to regionality in other taxa

In the following discussion we shall focus on comparisons between our zonation and other zonations based on phytogeographical or zoogeographical data. However, we first wish to point out a noteworthy pattern that emerges from

Table 6. The more common species of open habitats in the mid-boreal and south-boreal zones. All species exceeding 5 % of the pair numbers of open habitats in either zone were included.

	Mid-boreal	South-boreal
Motacilla flava	26.4 %	6.7 %
Anthus pratensis	10.2 %	3.3 %
Saxicola rubetra	9.6 %	7.1 %
Emberiza schoeniclus	8.0 %	4.5 %
Tringa glareola	7.8 %	1.8 %
Motacilla alba	6.4 %	12.4 %
Emberiza citrinella	4.6 %	18.8 %
Sturnus vulgaris	2.8 %	9.1 %
Alauda arvensis	2.7 %	9.4 %
Total density of species of open habitats (pairs/km²)	20.0	26.6

our quantitative analysis of the zones. The zones (Table 3) seem to be equivalent in the sense that each has 8—10 species with frequencies of at least 3 %, of which usually 4—6 are responsible for the main differences between adjacent zones. In the north these species account for about 80 % of the avifauna and in all zones their contribution exceeds 50 %. It is indeed remarkable that the 23 species listed in Table 3 are sufficient to characterize the basic features of the bird communities in such a large area as our study area, which extends from the arctic to the hemiboreal zone.

In a previous publication (Järvinen & Väisänen 1973) we raised the question of whether zoogeographical zones are due to a replacement of communities, the species substituting each other more or less coincidently, or whether the range boundaries of the different species are largely independent of each other. Our present data indicate that most of the ornithogeographic transitions in our study area result from changes in the coverage of the major habitats. The replacement zone of the two Finnish *Fringilla* species (Sect. 4.4 and Järvinen & Väisänen 1979b), however, is a striking exception. Similar replacements of congeners occur in other genera (e.g. *Buteo, Charadrius, Sterna, Parus, Carduelis*) in about the same region (Voipio 1956, Järvinen & Väisänen 1979b); notice that *Parus* spp. were previously more abundant (Järvinen & Väisänen 1979b) and these species would thus have made this zone boundary less dependent on the replacement zone of the two *Fringilla* species. So there is a fairly abrupt gradient in species composition near the boundary between the north-boreal and mid-boreal zones. This transition from northern to southern species in an area where habitat differences are not striking (Kujala 1936) reminds one of an idea of

MacArthur's (1972): he showed that transitions between alternative communities may be due to the poor invasibility of densely packed communities with the result that whole sets of species would replace each other. But the case discussed here is not of MacArthurian type; the Finnish replacements are no doubt one-to-one replacements between two congeners, one northern and the other southern, and no interactions need be invoked between the species of the northern or the southern set of species. Further, it is doubtful whether bird communities are densely packed at our latitudes (e.g. Järvinen 1978c, Järvinen & Väisänen 1979b, Järvinen & Ulfstrand 1980).

5.1. Phytogeographical zonations

The following conclusions emerge from comparisons between our zonation and the phytogeographical zonations of Ahti et al. (1968, based on vegetation on mineral soil), Eurola (1968, mire vegetation) and Kalliola (1973, vegetation in general). The zonation of Abrahamsen et al. (1977; see also Kalliola 1979) is also discussed, although it is partly based on other than phytogeographical criteria (i.e. on general features of the landscape). Notice at the outset that there is a fundamental difference between the various phytogeographical zonations and our Fig. 4. We have studied actual bird distribution, but phytogeographical zonations refer to the climax communities in the different zones. Therefore, our zonation is affected by man-made modifications of habitats.

Arctic zone (zones 1-2). Our zones 1—2 correspond to the oroarctic zones of Ahti et al. (1968) and Eurola (1968) and the alpine zone of Abrahamsen et al. (1977). In the term oroarctic, the prefix *oro-* refers to altitudinal effects. Phytogeographically, our zones 1—2 (particularly zone 1) should be regarded as oroarctic, not arctic, owing to an interesting historical fact: the northernmost birchwoods of Scandinavia were much more extensive until the beginning of the last century, but most of them have been destroyed by man (Ahti et al. 1968 and references there). The "secondary tundra" (Ahti et al. 1968) of northernmost Norway may, however, be regarded as arctic from the avian point of view, since the decisive factor for birds is the general landscape — which is arctic. As Varangerhalvøya in the north-east is the most extreme part of our study area and as it was fairly well censused, the densities estimated for the commoner arctic species (1 pairs/km² or more) are given in

Table 7. Densities (pairs/km²) and frequencies (%) of land birds belonging to the arctic faunal type (Voous 1960) in Varangerhalvøya, N Norway, on the basis of 55.5 km of line transects censused in 1975. All species with a density of at least 1.0 pairs/km² are listed, but the total also includes the following species: *Buteo lagopus*, *Lagopus lagopus*, *Calidris temminckii*, *Stercorarius longicaudus* and *Nyctea scandiaca*.

	Density	Frequency
Lagopus mutus	1.9	1.8
Charadrius hiaticula	1.7	1.6
Eudromias morinellus	1.0	0.9
Pluvialis apricaria	5.8	5.5
Calidris alpina	5.2	4.9
Arenaria interpres	1.1	1.0
Phalaropus lobatus	1.0	0.9
Anthus cervinus	4.3	4.1
Calcarius lapponicus	7.1	6.8
Plectrophenax nivalis	16.5	15.6
All arctic species	47.0	44.4

Table 7 (Voous's faunal types of 1960 were used in defining arctic species). As more than 44 % of all land bird pairs observed in Varangerhalvøya were arctic, our hypothesis that zone 1 can be regarded as arctic is well supported. Specifically arctic aspects of the avifauna are the abundance of *Plectrophenax nivalis*, *Calcarius lapponicus*, *Anthus cervinus* and various waders (especially *Calidris* spp.). Another arctic feature is the inland breeding of *Arenaria interpres* (Götmark et al. 1978).

Hemiarctic zone (zone 3). Our zone 3 broadly coincides with two of the northern sections of the northern boreal zone of Ahti et al. (1968), overlaps extensively with the orohemiarctic zone and the Forest Lapland part of the north-boreal zone of Eurola (1968) and with Kalliola's (1973) Fell Lapland and the northern parts of his Forest Lapland. The northernmost parts of the northern boreal zone of Abrahamsen et al. (1977) are included in our hemiarctic zone.

North-boreal zone (zone 4). Our zone corresponds fairly well to a wide section of the northern boreal zone of Ahti et al. (1968), the more southern part of the north-boreal zone of Eurola (1968) and Peräpohjola of Kalliola (1973). However, our zone tends to lie about 100 km further north than its phytogeographical equivalents. The southern parts of the northern boreal zone of Abrahamsen et al. (1977) overlap extensively with our zone, except for a discrepancy in eastern Finland.

Mid-boreal zone (zone 5). Our zone is fundamentally different from the phytogeographical zonations; the mid-boreal zones of Ahti et al. (1968), Eurola (1968) and Abrahamsen et al. (1977) and Kalliola's Ostrobothnia-Kainuu all extend southwards to the Suomenselkä watershed region in western Finland and to northern

Karelia in the east (see also Solantie 1974). As pointed out in Sections 3.2 and 4.4, the present study does not lead us to regard Suomenselkä as part of the mid-boreal zone. It is interesting that Kujala's (1936) field studies of vegetation led him to distinguish a transition zone which is virtually identical with our mid-boreal zone. However, our squares were too large to allow detection of narrow (pen)insular southward extensions in Suomenselkä or in Northern Karelia.

South-boreal zone (zone 6A). Because of the discrepancy between our zone 5 and the phytogeographical zonations, there is an identical discrepancy here. Otherwise the zonations are largely similar, except that the hemiboreal zone of Eurola (1968) covers much larger parts of Finland than the other zonations.

Hemiboreal zone (zones 6B+7). Our zones 6B+7 correspond very closely to the hemiboreal zone of Ahti et al. (1968), to the oak zone of Kalliola (1973) and to the boreonemoral zone of Abrahamsen et al. (1977). Mire vegetation is characterized by a different hemiboreal zone (Eurola 1968).

In our zonation southwestern Finland forms a subzone of the south-boreal zone, but from a phytogeographic point of view it belongs to the hemiboreal zone. According to our data, the Leningrad area (where the effect of man on habitat structure is extensive) differs greatly from southwestern Finland with respect to the composition of the bird fauna, but there is also a pronounced difference in species richness (e.g. Järvinen & Väisänen 1978b, 1979a). Regrettably, comparable census data are not available from the Swedish parts of the hemiboreal zone. Swedish areas near Stockholm may differ quite extensively from the southwestern parts of Finland owing to differences in species composition (e.g. _Parus palustris_, _Sitta europaea_ and _Picus viridis_ breed commonly in Sweden but are absent from Finland) and probably in the abundances of the different species. The areas of southern Finland classified as hemiboreal by phytogeographers are actually insular, separated by the sea or by south-boreal areas from other parts of the hemiboreal zone.

Summarizing, we note that zonations based on plants and on birds show fundamental similarities in broad patterns, but numerous differences in details.

5.2. Zoogeographical zonations

Provinces based on soil fertility. Using data on soil fertility, Kalela (1944) and Merikallio (1955) presented a zonation for zoogeographical purposes. In northern Finland their zonations are similar to the phytogeographical zonations. In the south, our zone 6 (southern boreal zone) includes as many as 5 different zones in Kalela's and Merikallio's zonations. The zone comprising most of southwestern Finland coincides with maximum bird densities in Finland (over 250 pairs/km^2 according to our line transect data). This is not clear from Merikallio's (1958) censuses, largely because he made very few censuses in this province. His other zones in southern Finland also coincide with the density patterns of different bird species (see Merikallio 1958), but our present analysis shows that the composition of the bird fauna is not correctly reflected by zonations based on soil fertility.

Range boundaries of breeding birds. Despite our earlier reservations (Sect. 3.1), Lehtonen's (1951) zonation based on the range boundaries of breeding birds is interesting. His zonation bears a much closer resemblance to the phytogeographical zonations of Ahti et al. (1968) and Kalliola (1973) than to our zonation based on quantitative studies of breeding land birds. A point of special interest is that Lehtonen (1951) observed the great heterogeneity of the bird fauna in northern Finland (cf. Järvinen & Väisänen 1973). Moreover, he did attempt to use quantitative census data, but northern Finland was poorly covered in censuses published by 1951. As regards the areas included in our zones 5—6, he made the point that different species tend to have similar frequencies in different parts of this area and most species whose frequencies exceed 2 % are generally present in all areas. Lehtonen (1951, p. 48) stressed the need for quantitative data in future studies, because without such data it is impossible to decide whether transitions are stepwise or gradual. Our present quantitative data show that many range boundaries occur in areas characterized by very smooth gradients in the frequencies of the majority of species. Because marginal populations of birds tend to occupy optimal habitats (e.g. Hildén 1965), Lehtonen's zonation is affected not by the average habitats of different regions (as is our zonation), but by the patchy occurrence of the optimal habitats of different species.

Leafhoppers of oatfields. Raatikainen & Vasarainen (1976) studied leafhoppers (Homoptera, Auchenorrhyncha) in the southern half of Finland. Using three different methods, they obtained a zonation which is closely similar to the phytogeographical zonations proposed by Ahti et al. (1968) and Kalliola (1973), except that the

hemiboreal zone in the southwest (our subzone 6B) was not so distinct as in the phytogeographical zonations.

Composition of the ant fauna. Baroni Urbani & Collingwood (1977) mapped the presence or absence of 67 indigenous ant species (Hymenoptera, Formicidae) of northern Europe in areas corresponding to the biological provinces of Finland. Several differences emerge when our zonation is compared with the areas distinguished by them in a cluster analysis (Baroni Urbani & Collingwood 1977, Figs. 71—72).

1) Northernmost Norway has unique bird communities (Sect. 4.1), but its ant fauna bears a great similarity to that of the Finnish areas between about 64°N and 67°N, especially that of Kuusamo. The reason for this is presumably that coniferous forests extend to the southernmost parts of northernmost Norway (as defined by province boundaries); this part of the province also supports birds characteristic of the taiga zone, such as *Mergus albellus* or *Emberiza pusilla* (Haftorn 1971).

2) In northern Finland and northern Sweden the ant fauna is poor and homogeneous, but in our ornithogeographic zonation this is a heterogeneous area. However, our mid-boreal zone has an almost identical equivalent in the zonation based on the ant fauna.

3) Southern Finland is fairly homogeneous with respect to the composition of the bird fauna, but two zones were distinguished on the basis of the ant fauna.

4) If our study area were divided into two parts on the basis of the ant fauna, one part would comprise the Finnish parts of our zones 6A-B, the other part all the rest. This is not so for birds (Figs. 2 and 4-5).

Intraspecific geographical variation. In an earlier study (Järvinen & Väisänen 1973) we pointed out that the northern boundary of our ornithologically determined south-boreal zone coincides with sharp transitions in the variation pattern of two conspicuously varying vertebrate species, the red squirrel *Sciurus vulgaris* and the grey-headed wagtail *Motacilla flava*. In the present zonation the coincidence is even closer. Another similarity between the composition of bird faunas and intraspecific variation in the two species is that the whole of southern Finland (our zone 6) is fairly homogeneous. The northern boundary of the south-boreal zone also shows an abrupt transition in the frontoclypeal colour polymorphism of *Philaenus spumarius* (Svala & Halkka 1974). A similar abrupt transition, this time of the pattern of the dorsal colour polymorphism of

Ph. spumarius, roughly parallels the border between our south-boreal and hemiboreal zones (6A and 7) in the southeast (Halkka et al. 1976). However, these coincidences are not perfect (e.g. the Åland Islands differ greatly from the Finnish mainland in *Philaenus* studies, but not in our ornithological data). A clear difference between the southwestern parts of Finland (6B) and the south-boreal zone (6A) was also observed by Saura et al. (1976) in their study of enzyme gene variation in the parthenogenetic weevil *Otiorhynchus scaber.* Interesting zoogeographic patterns would presumably emerge from studies of ecological genetics and the geography of genetic polymorphism, but too few detailed studies are as yet available (for further discussion, see Järvinen & Väisänen 1973:117—119).

5.3. Concluding remarks

In his review of zoogeography, Vuilleumier (1975) made a sceptical, but perspicacious remark: "The delimination of boundaries between subregions and of boundaries within each of the subregions, is evidently an endless exercise." Therefore, we do not propose our zonation (Fig. 4) as a basis of future studies of Finnish zoogeography. (This is especially so because most Finnish birds, in contrast to the majority of other Finnish animals, are migrants; see Sect. 4.7). To the contrary, other zonations are in many cases preferable to ours (for example, we ourselves use the Finnish uniform grid in analysing bird densities in Finland). Existing zonations may be useful in planning research programs, but strict adherence to previous zonations may give rise to misleading results. This is especially so because patterns of bird distribution are not static.

Our main aim in presenting the zonation shown in Fig. 4 is entirely different: we wish to work out broad patterns of bird distribution, in the hope that comparison with regionality in other taxa will lead to biologically meaningful interpretations of geographical distribution. In other words, we are not asking questions about Finland (which means different things to different taxa), but about the ways in which organisms can adapt to northern biota (as represented by Finland).

Before a comprehensive synthesis can be made, detailed evidence on regionality in several other taxa must still be gathered. Thus, the following discussion is largely tentative. We think that two fundamental conclusions emerge from the

comparisons made in Sections 5.1 and 5.2; one of them pertains to the transition between taiga and tundra, and the other to the extent of the south-boreal zone.

Transition between taiga and tundra. In areas north of the Arctic Circle, some groups (plants, birds) show major transitions, while others show no significant transitions (ants). We think that this observation has a simple interpretation. Ants have not adapted to arctic/alpine conditions, but plants and birds have. Therefore, ant species drop out one by one towards the north, whereas in plants and in birds there is a transition from arctic/alpine communities to taiga communities. (The available data thus suggest that arctic/alpine habitats and taiga habitats require fundamentally different adaptations. This is not necessarily true of all taxa.) In other words, we interpret the varying heterogeneity of distributional patterns in northern Finland as signs of the adaptability of the different taxa to arctic/alpine conditions. Why different taxa have or have not been able to adapt to arctic/alpine habitats is a different problem. As regards birds, their ability to migrate certainly makes it easier for them to adapt to extreme northern conditions. For example, few sedentary species occupy the open habitats characteristic of the arctic zone, while the northern forests support a higher density of sedentary birds (Järvinen & Väisänen 1976a). This is probably related to the pronounced seasonal changes of resource levels in the north (see also MacArthur 1959, Willson 1976, Herrera 1978).

South-boreal zone. In southern Finland (south of 64—65°N) birds, when analysed on a quantitative basis, show a basically homogeneous pattern, but in other groups regionality is more heterogeneous (the two problematic areas are SW Finland and Suomenselkä). We suggest that the essential question here is, Why do forest birds respond to differences in habitat productivity mainly (though not solely) by varying density, and not by varying species composition?

An explanation is that in birds habitat selection is based typically on the general structure of the vegetation or broad features of the landscape (e.g. Hildén 1965), whereas for plants the decisive factors are various small-scale phenomena, such as soil quality, availability of water and light, and microclimate (e.g. Kalliola 1973), and many insects are dependent on specific food plants. It is therefore understandable that forests of different kinds support similar (but not identical) bird communities, even though the composition of the plant communities varies widely (see also

MacArthur et al. 1962). Nilsson (1979), for example, studied eight forest plots in southern Sweden, and found that the bird communities in these plots were fairly similar as regards species composition, although the composition of the tree and shrub layers varied dramatically. However, different forests supported very different densities of birds. Another way of expressing our explanation is that in birds, as compared with more sedentary organisms, extreme mobility leads to much more "fine-grained" (Levins 1968) utilization of habitat; therefore, at any given locality birds are less dependent on specific conditions than more sedentary taxa. In this respect sedentary bird species are an intermediate group, and we may therefore expect between-zone differences to be more pronounced in sedentary birds than in migrants. In fact, this does seem to be the case (Table 5).

The above argument, when applied to SW Finland and Suomenselkä, explains the peculiarities of our zonation in these regions, as compared with other zonations. Southwestern Finland has very productive forests (at least as measured by bird density, which is the relevant criterion here), while Suomenselkä is more barren than its surroundings, but species composition in these regions is not radically different from that of other parts of southern Finland. We have not considered open habitats above, but in southern Finland most birds breed in forests (Table 4 and Sect. 4.7). On the other hand, it can be argued that hemiboreal vegetation in SW Finland is largely insular, while mid-boreal vegetation in Suomenselkä is peninsular. If the composition of bird communities is heavily affected by the adjacent bird communities in the surroundings, we would expect both SW Finland and Suomenselkä to be characterized by typical south-boreal elements. It has been suggested (Järvinen 1978b) that birds differ from plants in this respect; plant populations seem to persist well in areas that they have once succeeded in invading, whereas bird populations seem less persistent and so are affected by continuous immigration of new populations from the surroundings (for plants, see also McNeill & Cody 1978).

If the second hypothesis is true, we would expect insular communities of plants (and of ants, because in southern Finland their zonation coincides largely with that of plants) to be more distinctive than those of birds. This is certainly so. For example, the Åland Islands support a very rich flora as compared with the mainland of Finland (e.g. Kalliola 1973), while the land bird

fauna is clearly a subset of the Finnish bird fauna. Further, favourable soil conditions may facilitate the existence of plant communities which are sharply distinct from those of the surrounding areas (e.g. Eklund 1931, Kalliola 1973). As regards ants, insular faunas are highly distinctive, as amply documented by Baroni Urbani & Collingwood (1977). Our idea also emphasizes the important difference between insular patches and large coherent areas. The barren habitats of Suomenselkä are more or less (pen)insular and the "oak zone" habitats in southwestern Finland are strikingly insular (Jalas 1957). When similar habitats occur in larger, more coherent areas, such as northern Finland or the Leningrad area, the bird communities show considerable heterogeneity. One corollary of our hypothesis is that increased fragmentation should be highly detrimental for species requiring large forest tracts. This seems to hold true, as birds of old (and usually large) forests have decreased much more than the area of old forests in Finland (Järvinen & Väisänen 1979a).

The two hypotheses we have suggested are not mutually contradictory, and other explanations can probably be found. Studies of regional structure in other taxa would throw new light on our problems. Further, bird communities are not constant but dynamic (e.g. Kalela 1949, von Haartman 1973, Järvinen & Väisänen 1977c, Järvinen & Ulfstrand 1980). Therefore, new zonations are not "an endless exercise", but an attempt to reveal significant biological rules.

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