Species diversity of Finnish birds, I: Zoogeographical zonation based on land birds

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The regional species diversity (Shannon-Weaver function, H') of land birds breeding in Finland has been used in working out a zoogeographical zonation of Finland. Data of 307 line transect counts, made between 1941 and 1973, with a total length of 1 278 km, have been utilized.

H' is shown to be relatively independent of the distance from the census-taker, and the width of the census belt. For reliable results an area of 100 × 100 km^2 should be represented by at least 16 km of line transect counts; if only main belt (50 m wide) data are employed, the corresponding minimum is 28 km.

An index related to H' was used to find where changes in bird species composition are maximal. Five zones are distinguished: (1) a hemiboreal, (2) a southern boreal, (3) a midboreal, (4) a northern boreal and (5) a hemiarctic zone. This zonation corresponds closely to certain vegetational zonations, fundamentally related to the macroclimatic pattern. Species diversity decreases towards the north. In most areas avifaunal changes are very gradual, but relatively abrupt changes do also occur. Several possible causal relationships are discussed.

1. Introduction

Indices of species diversity quantify the amount of specific variation in a community or area. Generally, the values of these indices increase either as the number of species increases, or as the distribution of individuals among species becomes more even (Lloyd & Ghelardi 1964, Pielou 1966 b, 1969). The concept of species diversity is often used in other senses, e.g. synonymously with the number of species. As a consequence, some workers have argued in favour of its abandonment (Hurlbert 1971 even calls species diversity a ”non-concept”), or that the word, though not the concept, should perhaps be eliminated (MACARTHUR 1972:197). We have used diversity to combine aspects of both the number of species and the evenness of their abundances, that is, to describe as accurately as possible the *composition* of the avifauna of a region.

Species diversity is often connected with such synthetic community properties as productivity, stability, and ecological succession (MACARTHUR 1955, MARGALEF 1963, 1968, LEIGH 1965, ODUM 1969), though many controversies exist (see WOODWELL & SMITH 1969, MAY 1971). In biogeography, species diversity, often not distinguished from the number of species, raises the problem of species diversity gradients (FISCHER 1960, PIANKA 1966, MACARTHUR 1972). In terrestrial ecology these gradients usually take the form of a decrease in the number of species from the equator towards the poles, and from topographically more varied areas toward more uniform ones (for North American land birds, see MACARTHUR & WILSON 1967:116).

Zoogeographical zonations based on analyses of species diversity have not been attempted for any group of animals (UDVARDY 1969:293). There are several obvious reasons for this: Firstly, adequate quantitative data on groups that are taxonomically well known and ecologically not too specialized have not been collected for any large areas. Secondly, analytical methods have only been available for a short time.

In this paper we analyse the species diversity of land birds breeding in Finland (for a list, see Appendix). Our focus of interest is one of the fundamental problems of zoogeography, the analysis of integrated faunas and of the causes producing these (see UDVARDY 1969, MACARTHUR 1972). Our aim has been to work out a natural (objective) zoogeographical zonation of Finland by comparing the composition of the avifaunas of different regions. Boundaries between zones are drawn where the differences in species composition are maximal. All our arguments are based on quantitative considerations, and only the importance of the different values is evaluated subjectively (see Section 3).

At this point, a brief description of our study area is appropriate. Finland is a relatively large country (337,000 km^2), about 1 100 km from south to north, and 250 to 550 km from west to east. The climatic differences are particularly pronounced between the northern and southern parts of the country (see ATLAS OF FINLAND 1960: 5—6). The whole country was covered by the ice sheet during the most recent (Würm) glaciation, and has been recolonized during the past ten thousand years. There are no endemic elements in the avifauna. On the other hand, birds are rapid colonizers (see MAYR 1965, MACARTHUR & WILSON 1967), and we have every reason to suppose that the situation is in equilibrium, apart from some effects by man (e.g. VON HAARTMAN 1973) and the recent climatic fluctuations (e.g. O. KALELA 1949, 1952). From the ornithological viewpoint, Finland is vividly described by PALMGREN (1960).

2. Methodology

2.1. Line transect method; primary data

In bird census methodology, the line transect method is associated with the work of MERIKALLIO (1946, 1958). His line transects were usually about 4 km long (if the densities were low, MERIKALLIO sometimes employed somewhat longer transects), often forming a closed square. The census was, as a rule, made during the first 5 to 6 hours after sunrise. Censuses were not made if cold weather, rain, or strong wind noticeably reduced bird song or its audibility. Every pair observed was recorded from (1) the *main belt*, a tract

50 m wide, 25 m on either side of the census-taker, and (2) the *supplementary belt*, including all pairs outside the main belt. Together, these belts formed (3) the *survey belt* (the "auditory" belt of MERIKALLIO; cf. MERIKALLIO 1946: 8).

The basic unit in the census was a pair. In the case of early breeders (e.g. *Loxia curvirostra,* partly *Sturnus vulgaris*), all flocks were transformed to pairs by dividing the size of the flock by the average size of a group consisting of two adults and their young. A nest was counted as a pair, and a singing male, as well as a single male or female, was also counted as a pair. Of course, only one of these criteria was applied at a time.

Distance from the transect was measured from the place where the bird was when it was first observed. This is especially important with respect to species which, like *Motacilla flava,* are attracted by man, or those with a wide-ranging song flight, such as *Carduelis flammea.*

MERIKALLIO and his co-workers chose their transects to represent the actual habitat distribution of the census area in general, and so practically all transect counts were made in mixed habitats. Therefore, it is not possible to analyse the data at the level of habitat types.

From the methodological work of ENEMAR (1959) on the mapping method, it is now clear that the line transect method suffers from several weaknesses. As pointed out by ENEMAR (1959:81), it is doubtful whether efficiency in line transect censuses is near 100 per cent. Rather, it would be of the order of 60 per cent (cf. also PALMGREN 1930). Further, MERIKALLIO "worked to a great extent in unknown terrain", and "apart from the registrations of the birds, he also had an orientation, determination of distance, habitat registration, etc., to think about, all of which can very well have a reducing influence on the survey effectivity" (ENEMAR 1959:81). ENEMAR's (1959:82) penetrating criticism of some of MERIKALLIO's density estimation procedures is not relevant here, because we have been able to use his primary data, deposited in Merikallio Archives, at the University of Oulu.

The line transect method has not, in fact, been totally abandoned. It provides a valuable supplement to the mapping method (ENEMAR & SJÖSTRAND 1967, 1970). In addition, EMLEN (1971) has improved transect count methodology by introducing certain correction procedures based on estimates of detectability.

Our data stem from line transects made during a 33-year period, 1941 to 1973 (Table 1.a). The total length of these 307 transects is 1278.2 km; their geographical distribution is shown in Fig. 1 (cf. also Fig. B in MERIKALLIO 1958). From the period 1941—1949 we have 548.3 km of line transects (42.9 per cent), and from 1952—1956 about the same length, 556.7 km (43.6 per cent). The rest, 173.2 km (13.6 per cent), comes from a later period, 1966 to 1973.

Altogether 21 persons have been involved in the census work (Table 1.b). The bulk (about 60 per cent) of our data was collected in the years 1941 to 1956 by MERIKALLIO himself. His five co-workers collected 27 per cent of the data in 1946—1956. With few exceptions, the transects made by these six persons cover the whole country. Supplementary censuses were made in 1966, 1967, and 1973 by 15 persons in those parts of the country from which the data were too scanty for our purposes.

Some transect areas are situated in the Soviet Union (see MERIKALLIO 1946) or in northern Norway (1973), all of them, however, within the squares shown in Fig. 1.

TABLE 1. Distribution of line transects among (a) years and (b) census-takers. The geographical distribution is shown in Fig. 1.

a.

Year	Transects (km)	Year	Transects (km)
1941	38.0	1952	134.0
1942	96.7	1953	100.0
1943	105.5	1955	275.4
1945	36.0	1956	47.3
1946	128.0	1966	50.0
1947	103.0	1967	8.8
1948	37.1	1973	114.4
1949	4.0		

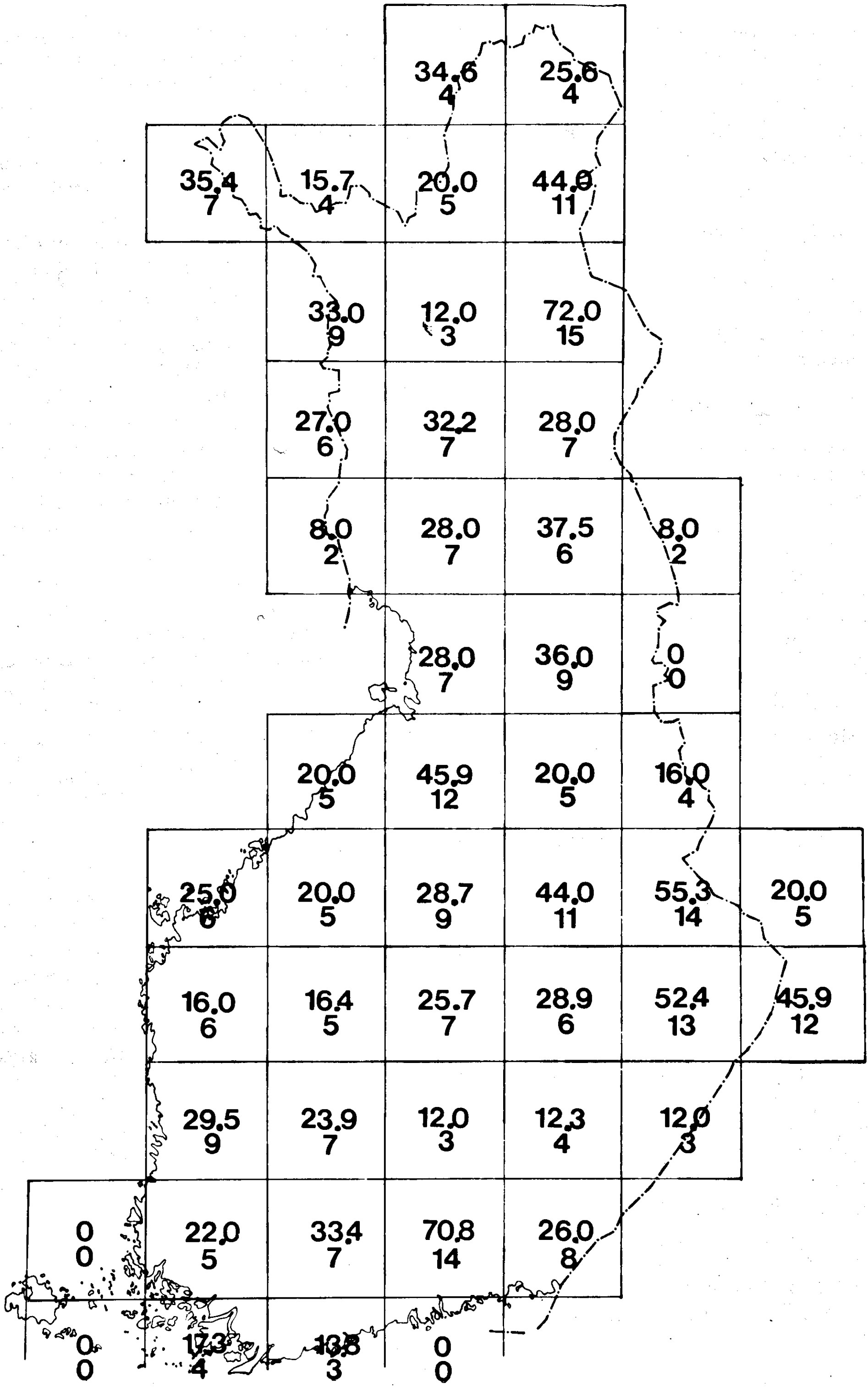
b.

Census-taker	Line transects (number)	Line transects (km)	Per cent of total	Period
Einari Merikallio	187	760.9	59.5	1941—56
Matti Nurminen	25	105.2	8.2	1953—55
Pertti Mikkola	22	93.2	7.3	1955
Väinö Heikkinen	18	70.0	5.5	1952
Olli Suhonen	11	43.7	3.4	1953
Åke Aaltonen	8	32.0	2.5	1946
Eero Hietanen	4	30.3	2.4	1966—67
Kalevi Hyytiä	7	28.5	2.2	1966
Yrjö Sihvo	4	25.6	2.0	1973
Risto A. Väisänen	5	18.7	1.5	1973
Esa Pitkänen	3	12.4	1.0	1973
Kari Vepsäläinen	2	8.4	0.7	1973
Ari Lyytikäinen	2	8.2	0.6	1973
Olli Järvinen	2	8.0	0.6	1973
Unto Laine	1	6.0	0.5	1973
Olavi Hildén	1	5.0	0.4	1973
Aimo Komonen	1	5.0	0.4	1973
Tapani Ormio	1	4.9	0.4	1973
Ahti Pasanen	1	4.2	0.3	1973
Karno Mikkola	1	4.0	0.3	1973
Torsten Stjernberg	1	4.0	0.3	1973
Totals	307	1278.2	100.0	

Most counts were made in June. Five counts were made in May (24—30.5.) in southern Finland, and 54 in July (35 counts 1—6.7., and 19 counts 7—11.7) mainly in northern Finland. Twelve counts made in mid-July (12—20.7.), and included in MERIKALLIO's (1958) survey, were discarded.

This report is based mainly on the survey belt data (exceptions are indicated). There are observations on 146 species and on 40 066 pairs of birds. The data for the main belt comprise 18.5 per cent of the total (7 422 pairs). The following eight species were not included in the data of MERIKALLIO

FIG. 1. Total lengths (km; above) and numbers (below) of line transects in the 100×100 km² squares of the Finnish uniform grid system.


34.6
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52.4
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0
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33.4
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70.8
14
26.0
8
0
0
17.3
4
13.8
3
0
0

(1958), but were observed in later counts: *Porzana porzana, Streptopelia turtur, Acrocephalus scirpaceus, A. palustris, A. dumetorum, Sylvia nisoria, Ficedula parva,* and *Coccothraustes coccothraustes.*

2.2. Measurement of species diversity

The most common measure of species diversity seems to be the information-theoretical Shannon-Weaver index, defined as:

$$H' = -\sum_{i=1}^{S} p_i \log p_i,$$

where p_i = the estimate of the frequency of the *i*th species, and S = the number of species in the sample (consequently, $\sum_{i=1}^{S} p_i = 1$). The base of the logarithm can be chosen arbitrarily; the most common are 2 and e. In this paper natural logarithms (base e) are used.

Species frequencies are usually estimated by putting $p_i = \frac{N_i}{N}$, where N_i = the absolute observed frequency of the *i*th species in the sample, and N = the absolute number of observations in the sample (obviously, $\sum_{i=1}^{S} N_i = N$). This estimate is correct, if the sample values are estimates of frequencies in an indefinitely large population (PIELOU 1966b, 1969, LLOYD et al. 1968). In our case, there are no theoretical objections to using H'. In practical work no evident difficulties have arisen even when H' has been calculated from absolute, real frequencies (not estimates). In fact, extremely high correlations have been found between H' and theoretically correct indices (see DEBENEDICTIS 1973). In addition, H' has been shown to be relatively stable in incomplete bird censuses (JÄRVINEN & SAMMALISTO 1973). This improves the reliability of our results, because one of the major flaws in the line transect method is low census efficiency (Section 2.1).

Because the report is based on survey belt data, i.e. data coming from a very wide area on either side of the census-taker, it is important to clarify the effects of distance on diversity values. The only relevant data seem to be those published by MERIKALLIO (1946:14—19). He studied the effect of distance on the frequencies of 23 "Singvögel vom Typ *Phylloscopus trochilus* und *Fringilla coelebs*" (MERIKALLIO 1946:16). Compared with the main belt, 96.7 per cent of the expected number of pairs were observed at distances of 25 to 50 m; 88.5 per cent at distances of 50 to 100 m; not more than 18.9 per cent at distances of 100 to 200 m, and only 3.2 per cent at distances of 200 to 400 m. However, estimates of species diversity remain relatively stable up to 400 m (Fig. 2). More important still, the H' values for successively broader belts are as follows:

0—25 m	H' = 2.135
0—50 m	2.165
0—100 m	2.256
0—200 m	2.302
0—400 m	2.336

Species that are less easy to detect than the Willow Warbler or the Chaffinch are probably ignored if they are far from the census-taker. Inclusion of these species at least partially offsets the tendency of the H' values to increase. Thus, distance affects estimates of species diversity far less than estimates of density.

We provisionally compared the species diversities in the main belt and the whole survey belt. The sample sizes are not sufficiently large (Section 2.3) to permit an analysis of the main belt data on the basis of the 100 × 100 km² squares of the Finnish uniform grid system (HEIKINHEIMO & RAATIKAINEN 1971; see below). We have there-

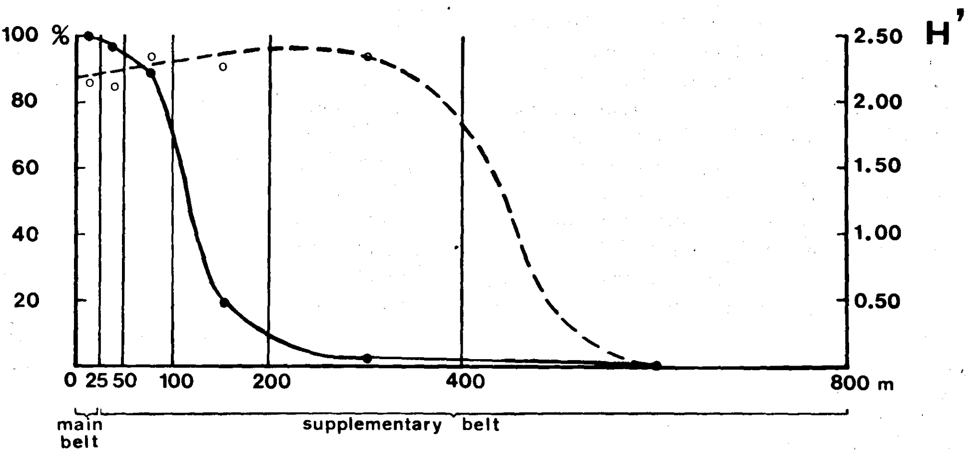

FIG. 2. Total pair density, given as percentage of the main belt density (———), and diversity (— — —) of 23 bird species in belts differing in distance from the census-taker (primary data from MERIKALLIO 1946, Table 3 and Fig. 1).

fore used the biological provinces of Finland as our basis. The correlation coefficient between the main belt and the survey belt diversities was highly significant ($r = 0.804$, d.f. $= 16$, $P < 0.001$). The survey belt, of course, includes data from the main belt (Section 2.1). To eliminate their effect we calculated the diversities on the supplementary belt. The correlation coefficient between the main belt and the supplementary belt diversities remained high ($r = 0.675$, $P < 0.01$). Most (95.5 per cent) of the diversity of the survey belt is explained by the diversity in the supplementary belt ($r = 0.977$, $P < 0.001$). In addition, the H' values for the main, supplementary, and survey belts are equally large, as is shown in the following tabulation (number of areas = 18):

	$\overline{H'} \pm$ S. D.
Main belt	3.059 ± 0.244
Supplementary belt	3.035 ± 0.262
Survey belt	3.095 ± 0.249

There is no statistically significant difference between the averages (t-test); also the standard deviations are equal (F-test).

Several factors may distort the estimates. We regard the following as the most important. (1) In some parts of the country habitat distribution may have been far from representative, because the choice of transect areas has been wholly arbitrary, and may have led to grave errors. However, a truly random choice seems hardly feasible. (2) Annual fluctuations in numbers (e.g. SIIVONEN 1952, ENEMAR & SJÖSTRAND 1970), unless synchronized, tend to increase species diversity values, if they occur in several of the abundant species and if the data stem from several years. (3) Annual fluctuations in range boundaries may well increase species diversity values in areas where records were gathered in several dissimilar years and where the range boundaries of several species fluctuate. (4) Species differ in their most active singing period. Accordingly, any bias in the geographical distribution of the transects with respect to season may influence the results. (5) The census hours may have varied in different parts of the country, so introducing a risk that those species which are active, for instance, during the darkest hours of the night are more likely to have been included in some parts of the country than in others. (6) Birds living in open areas are perhaps more easily observed than those inhabiting forests. Differences in actual habitat distribution may cause errors, because numbers of open-area species tend to be overestimated. (7) There may be differences between census-takers, though efforts were made to minimize this effect; only ornithologists with good field experience were asked to assist in the new supplementary censuses (Section 2.1). (8) Differences in climate may influence the results, too, although it is difficult even to guess at the kind of error possibly involved.

In spite of these mostly unavoidable sources of error, we are confident of the essential reliability of our results. Calculations of species diversity (H') are mostly influenced by the most abundant species. Accordingly, if some relatively rare species are included disproportionately, the results are likely to be practically unaffected. We believe that not very much precision is lost, after all, but that the results are sufficiently general and realistic to be of value. LEVINS (1966), in particular, has emphasized that "to sacrifice precision for generality and realism" is a valid strategy in population biology (cf. also MACARTHUR 1972:1).

2.3. Sample size

MARGALEF (1968, 1969) has stressed the necessity of studying the spectra of species diversity, by which he means a succession of diversity values obtained from a series of samples. The spectra differ in their appearance depending on the amount of spatial heterogeneity of the communities in question. If spatial heterogeneity is slight, the spectrum of species diversity soon levels off. But if local differences are pronounced, diversity values increase with area until all additional variation is incorporated. Calculation of species diversity spectra allows a distinction between "within-habitat" and "between-habitat" diversities (MACARTHUR 1965) or "species diversity" and "pattern diversity" (PIELOU 1966a). The mosaic pattern of the environment produces between-habitat, or pattern diversity, and the variation within the environmental patches gives rise to within-habitat, or species diversity. In any case, our data include much between-habitat diversity (Section 2.1), and so we are unable to distinguish between these two types of diversity.

To obtain a rough idea of the spectra of species diversity we selected 14 areas for further analysis. The areas were chosen from different parts of Finland. They had to be represented by the same number of counts of equal length (4 km). In this case, nine was the maximum allowing analysis of relatively numerous areas and transects. As far as possible, the areas were single squares of the Finnish uniform grid system (Fig. 1), and when this was not feasible, a group of line transects from nearby squares was used.

The analysis was made as follows. H' (Section 2.2) was calculated for all possible combinations of k line transects (k = 1, 2, . . . , 9); there are altogether $\binom{9}{k}$ possibilities[1] per square (or group of squares) for k transects. For k = 1, the average H' estimates the bird species diversity for an arbitrary (Section 2.2) line transect of 4 km in the square (or group of squares). For k = 2, the average H' estimates the diversity for an arbitrary line transect 8 km in length, and so on. The gain in additional diversity is clearly maximal in the beginning, and after 12 km the levelling off of the curve is relatively rapid

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[1] $\binom{n}{k} = \frac{n!}{k!(n—k)!}$, where $n! = 1 \cdot 2 \cdots n$; k! and (n—k)! are defined analogously.

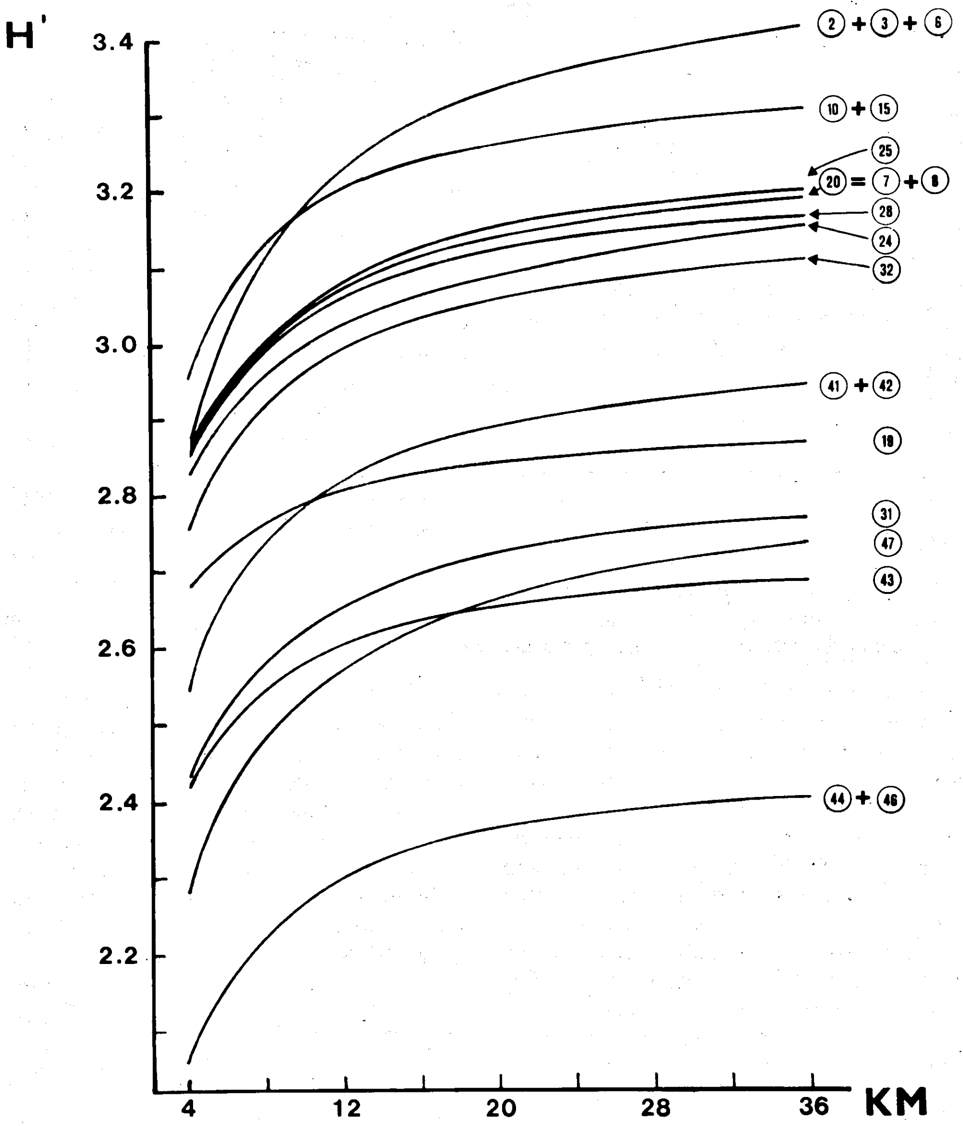


FIG. 3. Species diversity in the survey belt in 14 study areas plotted against the total length of the transects; for explanations, see Section 2.3. Figures in circles refer to Fig. 5.

(Figs. 3 and 4). All the areas give rather similar results, as regards the *form* of the curve, though the absolute values differ. This is especially true if combinations of two or three squares are ignored. Combining squares evidently increases between-habitat variation considerably, causing some artificial steepness in the curves. We conclude that, to be acceptable, an area should be represented by at least 16 km of line transects. This principle has been

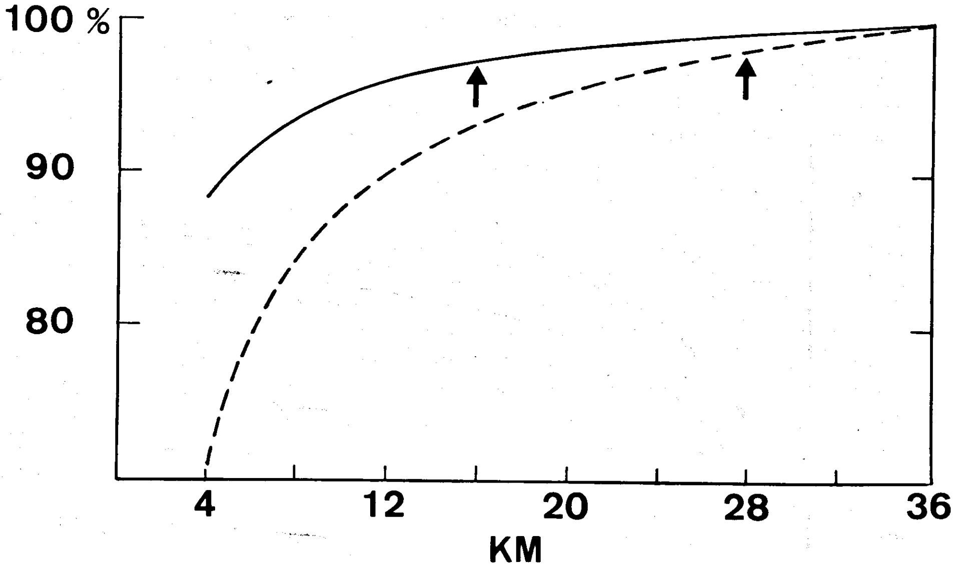


FIG. 4. The average species diversity in the survey belt (———) and the main belt (— — —) in 14 study areas, as a function of transect length (36 km = 100 per cent). Arrows indicate levelling of the curves (increase less than 1 per cent during the next 4 km).

followed in this paper; a value of 15.7 km has been rounded upwards (one case), and the respective square thus accepted. When all 14 areas are averaged, 97.5 per cent of the diversity present after 36 km is already present by 16 km. It should be observed that the line transect areas were chosen as representative of the habitat distribution of the region (Section 2.1). Some effective estimates of species diversity seem, accordingly, to be obtainable at a relatively low expenditure of effort compared with reliable estimation of densities (see EMLEN 1971).

We examined our main belt data in the same manner (Fig. 4). The limit corresponding to 16 km in the survey belt data proved to be about 28 km in the main belt. Thus, no valid analyses can be made from our present main belt data, using the 100 × 100 km² grid system. Where other zonations, acceptable in the sense that each area is represented by at least 28 km of transect data are used, the main belt values are presented in parentheses.

There is still one important consideration. The data used in the calculations were not independent of each other, but were derived from the same line transect data. This may have caused the curves to level off sooner than if the data had been independent.

2.4. Comparison of two areas

The species composition in any two areas can be compared as follows. The diversity values for the areas are first calculated. Then the amount of diversity due to the differences between the areas is calculated from the formula (HORN 1966, MACARTHUR et al. 1966, CODY 1970):

$$DIV_{diff} = DIV_{A+B} - \tfrac{1}{2}(DIV_A + DIV_B),$$

where DIV_{A+B} = diversity (in this paper, H') in area A + B, DIV_A = diversity in area A, and DIV_B = diversity in area B. Frequencies of species in area A + B can be obtained in three ways: either the observed numbers of pairs (N_i) or the observed densities (pairs/km) or the observed relative frequencies (p_i) may be averaged. The first method is applicable, when census efforts in the two areas have been equal, because the method takes into account possible density differences. The second method has been used exclusively here: the method is applicable, when census efforts have differed. Also this method takes into account possible density differences. The third method is based on relative frequencies, and densities have no effect on the results. It should be stressed that though all methods are basically different, they give rather similar results when applied to the present data (our unpublished data). Only in comparisons between two areas with very differing lengths of transects the results differ considerably.

DIV_{A+B} is best regarded as a measure of total specific variation (total diversity) in area A + B, and the term $\frac{1}{2}(DIV_A + DIV_B)$ represents the average diversity within the two areas. Consequently, DIV_{diff} is that part of the total diversity which is due to pooling the two areas, that is, due to differences between the areas. (It is possible to proceed in a manner analogous to the analysis of variance, and compare the average diversity of each area to the total diversity (LEWONTIN 1972); however, the interpretation of the ratio thus formed is not obvious.)

The significance of the formula for DIV_{diff} is readily grasped. It provides a measure of the difference in species composition (Section 1) between two areas, or, if necessary, between many areas, for the formula is easy to generalize. Thus, for example, the values of DIV_{diff} can be used effectively in a search for natural biogeographical boundaries (Section 3).

2.5. Computer programs

Two data forms have been used for storing the data of one line transect count. One of the forms is for the survey belt, and the other for the main belt. Data for the supplementary belt can be calculated from these. The following data are entered on both forms: serial number of the transect count (the same number for both the survey and the main belt); length of transect (0.1 km accuracy); code number of the census-taker; date (day, month, year); longitude and latitude (degrees, minutes); S-N and W-E cordinates in the Finnish uniform grid system (HEIKINHEIMO & RAATIKAINEN 1971) of the census area (to the nearest quarter of a 100 × 100 km^2 grid); code number for the position of the census area in the zonation of MERIKALLIO (1958); code number for biological province (zonation as in HEIKINHEIMO & RAATIKAINEN 1971, in the appended map), for botanical zone (AHTI et al. 1968), and mire vegetational zone (EUROLA 1968); numbers of observed pairs of each species in the respective belt.

The analysis was made by three computer programs, written in FORTRAN IV for the BURROUGHS 6700 computer of the Computer Centre of the University of Helsinki. Requests for the programs should be sent to R. A. Väisänen.

SURV1. This program employs two input files, including (1) the serial number indicating the systematic position of the species, several codes for faunal types, and the alphabetical scientific name and (2) data forms. Transect-specific vectors are formed; these consist of the number of pairs of each species in correct systematic order and the transect-specific codes listed above. Besides, serial numbers for four distinct grid systems (100 × 100 km^2 squares; Section 3) are calculated. Three disk files are written in the output: (1) survey belt, (2) main belt, and (3) supplementary belt. Complete data on transect variables, in addition to the numbers of pairs, are included in each file. (Minima and maxima of the variables were checked by HYLPS-library routine programs of the University of Helsinki.)

SURV2. This program computes the analyses of Section 2.3 by combining transect counts (max. 9), and calculates diversities for the combinations, writing parameters for these groupings in the output.

SURV3. This program groups transects on the basis of a chosen grouping variable, and calculates the number of transects, total length of transects, numbers of species and pairs, two ratios between the former variables, and diversities (H') in each group. Two matrices of DIV_{diff} values between the groups are calculated. In (1) the observed densities (pairs per km) and in (2) the observed numbers of pairs (N_i) are averaged (see Section 2.4). Not all species need be analysed simultaneously. Species selection may be restricted to a particular group, e.g. waders or passerines; other criteria can also be used for classification of the species, for instance the faunal types.

3. Zoogeographical zonation of Finland

As stated in Section 1, we have attempted to find boundaries which coincide with maximal differences in species composition between the areas separated by the boundary. The method for quantifying degrees of difference is described in Section 2.4, and the zonations are in Section 2.5.

We calculated (Section 2.5) the value of DIV_{diff} between all adjacent squares of the Finnish uniform grid system; accordingly, up to eight comparisons were made per square. All pairwise comparisons involving at least one square with an insufficient amount of data (less than 16 km; Section 2.3) were ignored. In several cases comparisons of this kind caused relatively large values of DIV_{diff}, probably explained by chance effects in small samples. The results of the comparisons are shown in Fig. 5. All DIV_{diff} values have been multiplied by 1000.

The same procedure was repeated for three new grid systems. These were formed as follows:

(1) The original grid system was transferred 50 km southwards (the original N-S lines unchanged).

(2) The original grid system was transferred 50 km westwards (W-E lines unchanged).

(3) The original grid system was transferred 50 km southwards and 50 km westwards (the mid-points of the new squares identical with the transect points of the W-E and N-S lines of the original grid system).

The following classification was adopted for the DIV_{diff} values:

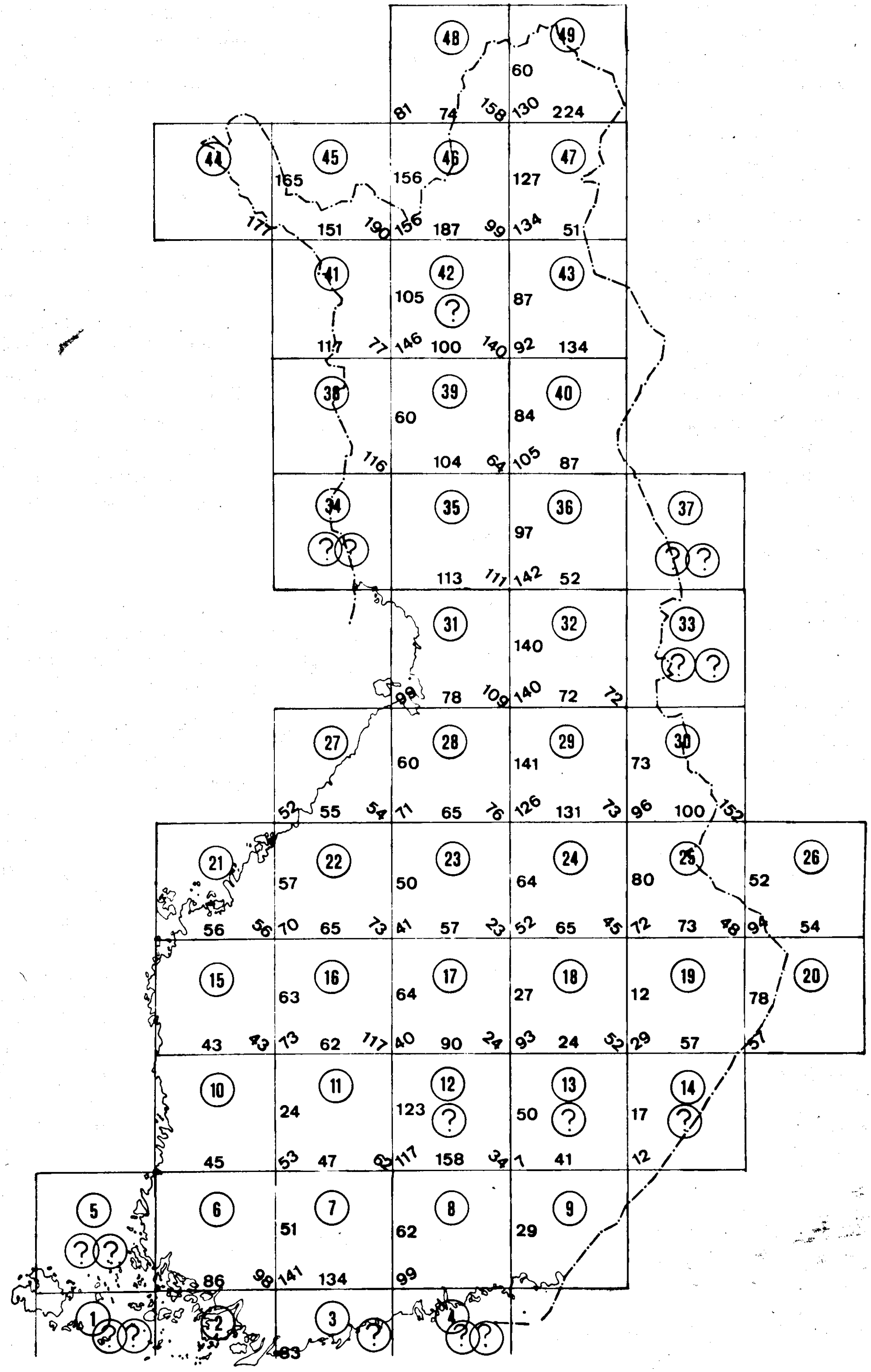
<60 = small difference
60—89 = moderate difference
90—119 = fairly great difference
120—149 = great difference
$\geqslant 150$ = very great difference

The result of all four analyses based on grid systems are summarized in Fig. 6 (moderate differences have not been indicated). The main results of the analyses are as follows.

1. Southern Finland seems to be a relatively homogeneous area, only one transition zone can perhaps be discerned in the south-westernmost parts of the country (see below for some confirmation). The method does not bring to light gradual changes, and as a result areas on the opposite sides within a zone are not necessarily very similar.

2. Southern Finland is bounded in the north by a rather sharp transition zone in Tornio—Kainuu (region 6 in

FIG. 5. $1000 \times DIV_{diff}$ values between adjacent squares of the Finnish uniform grid system. Horizontal figures belong to horizontal and vertical comparisons, diagonal ones to diagonal comparisons. ? indicates a square with an insufficient length of transects (less than 16 km); these squares are not included in the analyses. ?? indicates that the total length of transects does not amount to 8 km; in these cases DIV_{diff} values are not given at all.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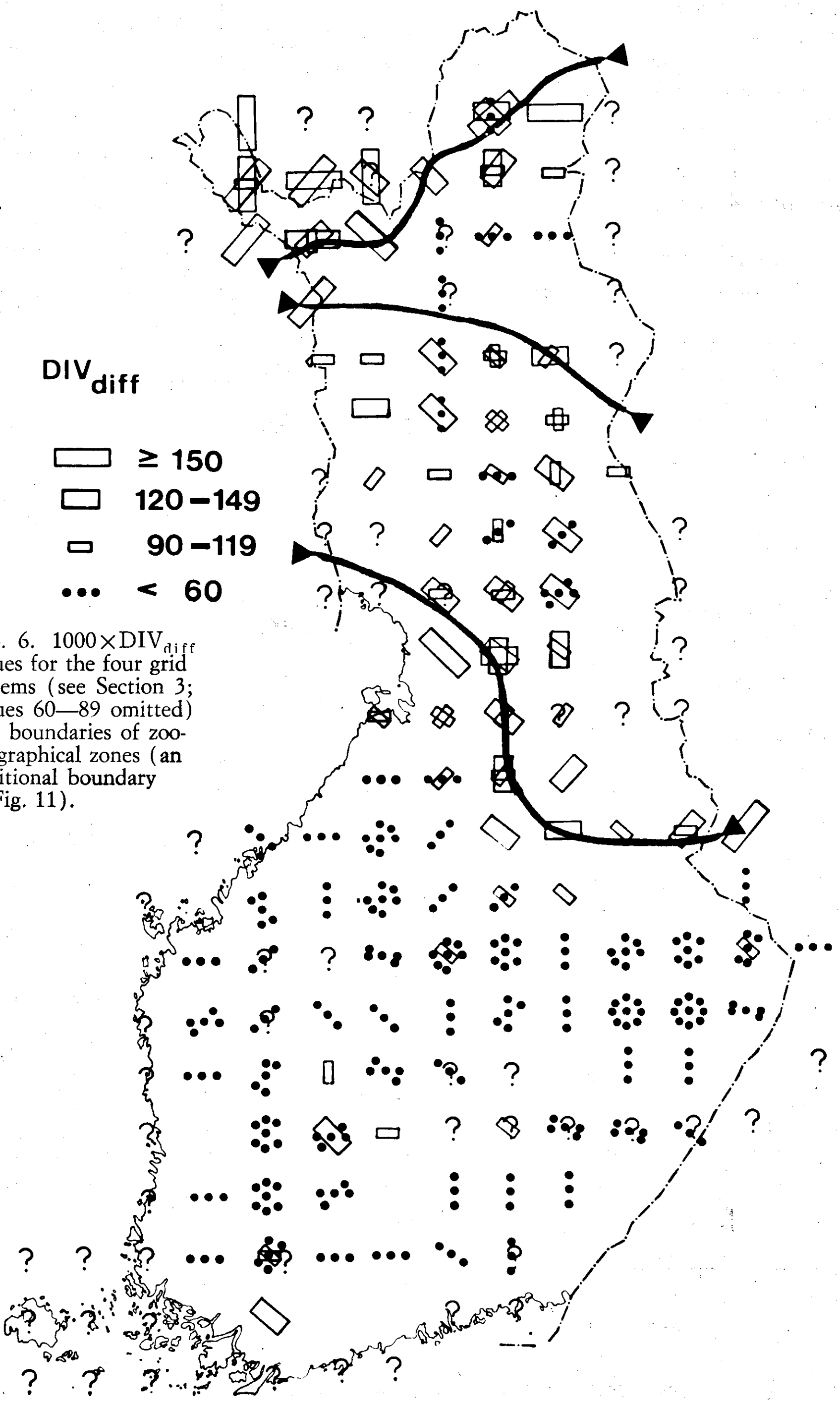


FIG. 6. 1000×DIV$_{diff}$ values for the four grid systems (see Section 3; values 60—89 omitted) and boundaries of zoogeographical zones (an additional boundary in Fig. 11).

Fig. 8). This transition zone appears in Fig. 6 as a zone of more or less large $\mathrm{DIV_{diff}}$ values. We have drawn our boundary to follow the southernmost great differences; the position of the boundary around the northern parts of the Gulf of Bothnia is rather uncertain, owing to the scant data from the surroundings of the towns of Kemi and Tornio.

3. There are strong indications of a broader transition zone in Peräpohjola (region 7 in Fig. 8). However, no distinct patterns emerge. The results suggest that once the avifaunal changes begin (at the Tornio—Kainuu transition zone), they continue northwards almost uninterruptedly to the borders of Forest Lapland (region 8).

4. Forest Lapland appears homogeneous.

5. There is an abrupt transition zone between Forest and Fjeld Lapland (regions 8 and 9), visible in Fig. 6 as a cluster of very large difference values.

The analyses suggest four zoogeographic zones. From the north, they are: (1) Fjeld Lapland, (2) Forest Lapland, (3) Peräpohjola, and about one half of the Tornio—Kainuu region (this third zone is characterized by relatively large intrazonal difference values, being possibly a "moderate transition zone" as a whole), and (4) southern Finland.

The next analysis was based on the biological provinces. This system of zonation dates back to MELA (1882), and is largely dependent on administrative boundaries (between communes); nevertheless, the biological provinces have been, to some extent, useful in faunistic work (cf. MERIKALLIO 1955, PALMGREN 1972).

Our line transects are distributed fairly evenly among the biological provinces (Fig. 7). Too few are available from provinces 1 (Ahvenanmaa, no transect counts), 2 (Varsinais-Suomi, 26.9 km), 4 (South Karelia, no counts), 5 (Satakunta, 33.5 km), and 8 (Ladoga Karelia, 8.0 km; this last province is mostly situated in the Soviet Union). In the other provinces the combined length of the transects ranged from 41 to 156 km.

In southern Finland $\mathrm{DIV_{diff}}$ values for the survey belts proved to be small. In fact, some values were even negative, a finding attributable to impoverishment of the avifauna of one of the areas compared with the other (cf. LEWONTIN 1972). Here impoverishment means changes without any (noteworthy) alterations in species composition. Accordingly, an area that has a less diversified avifauna (measured by H') than another is not necesarily impoverished. Only if the composition of the avifauna is essentially similar in the two areas, the $\mathrm{DIV_{diff}}$ value may be negative. Negative values were found in comparisons between South Savo (province 7) and adjacent areas. This fact probably reflects the relative barrenness of South Savo (for example, several animal species expanding their ranges northwards colonized South Savo comparatively late; see e.g. O. KALELA 1955:15, VON HAARTMAN 1973: 464).

The $\mathrm{DIV_{diff}}$ values of the main belt are larger, indicating that this belt may provide a better basis for the search for transition zones than the survey belt. Naturally, more data must be accumulated to allow analyses on the basis of 100×100 km^2 squares. Even now, the main belt values, as a rule, accord with the $\mathrm{DIV_{diff}}$ values of the survey belt in Fig. 5 ($r = 0.894$; $p < 0.001$, d.f. $= 34$). The same tendency is observed in Figs. 8 to 11.

The boundaries of Fig. 6 were drawn in Fig. 7 to show whether more transition zones should be distinguished. This was not the case. Moderate or large differences in comparisons involving the provinces 14—16 are clearly connected with the Tornio—Kainuu transition zone. The fairly great differences between the province 16, on the one hand,

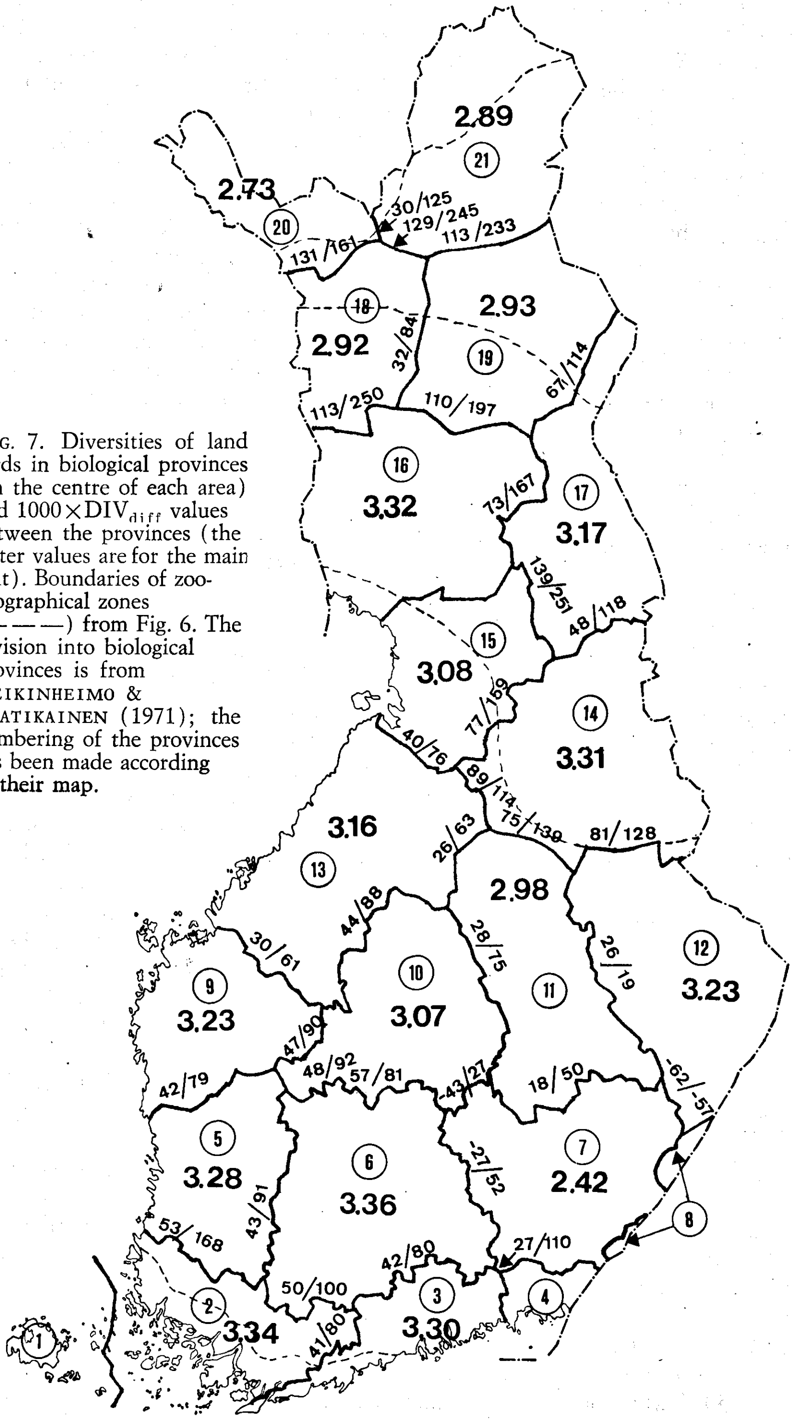


FIG. 7. Diversities of land birds in biological provinces (in the centre of each area) and $1000 \times \mathrm{DIV}_{\mathrm{diff}}$ values between the provinces (the latter values are for the main belt). Boundaries of zoogeographical zones (— — —) from Fig. 6. The division into biological provinces is from HEIKINHEIMO & RAATIKAINEN (1971); the numbering of the provinces has been made according to their map.

and provinces 18 and 19, on the other, suggest that the southern boundary of Forest Lapland should perhaps be shifted somewhat southwards, when additional material is accumulated. Large or fairly great differences between provinces 20 and 21, on the one hand, and provinces 18 and 19 on the other, correspond closely to the boundary between Fjeld and Forest Lapland. In the northern parts of the country, as compared with southern Finland, the avifaunal changes in N-S direction are much more pronounced.

The next analysis was based on the provinces used by MERIKALLIO (1955, 1958). The distribution of transects among regions is fairly even (range 74 to 186 km). Again, southern Finland is seen to be more or less homogeneous, and our boundaries seem appropriate (Fig. 8), though the zonation by MERIKALLIO is rather rough. In most cases the boundaries of the areas by MERIKALLIO do not coincide with changes in the composition of the avifauna, though density differences exist between the areas (MERIKALLIO 1955).

The vegetational zones of AHTI et al. (1968) differ markedly in size, and the distribution of the line transects in them is far from even, ranging from 41.1 to 329 km (Fig. 9). Although the transect coverage was poorest for area 1 (hemiboreal), we propose that the boundary between areas 1 and 2 should be regarded as a real transition zone. (In Fig. 5 several comparatively large values are shown in SW Finland, but for some of these the data are insufficient.) No other changes appear necessary; on the contrary, the boundaries coincide remarkably well, considering the wide differences between the zonations.

The zonation based on mire vegetation (EUROLA 1968) affords no additional information (Fig. 10). Of course, the zones are extremely useful for analysing peatland bird distributions (HÄYRINEN 1970), and possibly also their patterns of species diversity.

Our results are summarized in Table 2 and Fig. 11. The nomenclature closely corresponds to botanical usage; these terms fundamentally relate to the macroclimatic zonation (see AHTI et al. 1968). Our choice stresses similarities between the ornithological, vegetational, and macroclimatic patterns (cf. Section 4). A somewhat similar practice has been adopted by SALOMONSEN (1963; see Section 4.2). Other nomenclatural systems are reviewed by UDVARDY (1969).

In addition to statistics characterizing our zones, a matrix presenting the 1000×DIV_{diff} values between all pairs of our zones is given in Table 2. Most importantly, the values for adjacent zones are of about the same order (survey belt: 101—127, main belt: 142—178), indicating that the zones are more or less equally comparable as units, as regards the specific characteristics of the avifaunas.

When more data have accumulated, our zonation may have to be changed. One of the problems still to be solved is the exact characterization of the continuous, gradual changes in the zone 3. Future work may show that the faunal elements here are too diverse for inclusion in a single zone.

We decided to distinguish zones on the basis of a DIV_{diff} value of about 100 (survey belt data). A different zonation would certainly have been obtained, if a different value had been taken as the limit. It should be obvious why exact limits of DIV_{diff} have not been used for zonal distinction: Our work is based on many earlier (non-ornithological) areal divisions. An iterative process is involved, because DIV_{diff} values can be calculated only on the basis of an existing areal division. However, because we have attempted a synthesis of the best features of earlier zonations, we have had to adopt a some-

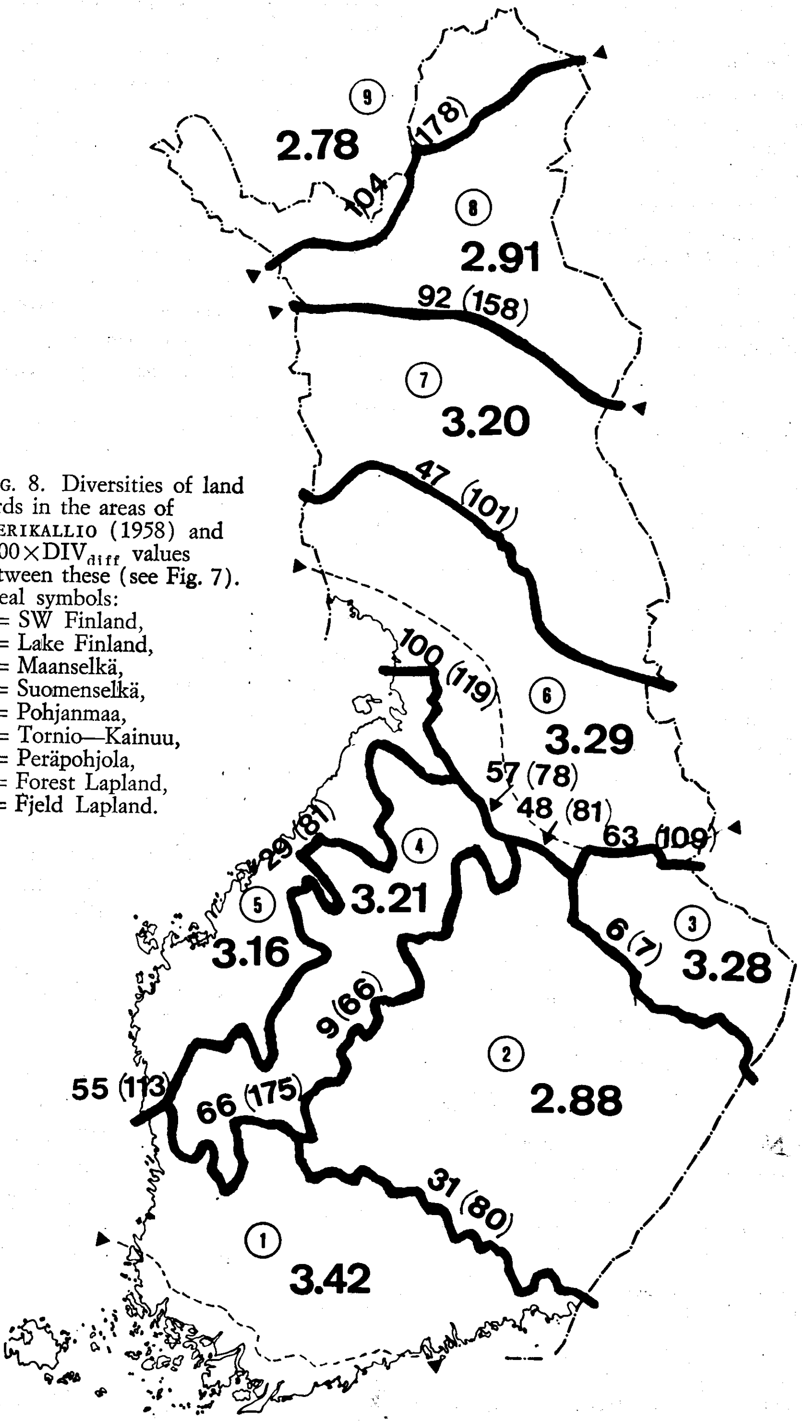


FIG. 8. Diversities of land birds in the areas of MERIKALLIO (1958) and $1000 \times \mathrm{DIV}_{\mathrm{diff}}$ values between these (see Fig. 7). Areal symbols:
1 = SW Finland,
2 = Lake Finland,
3 = Maanselkä,
4 = Suomenselkä,
5 = Pohjanmaa,
6 = Tornio—Kainuu,
7 = Peräpohjola,
8 = Forest Lapland,
9 = Fjeld Lapland.

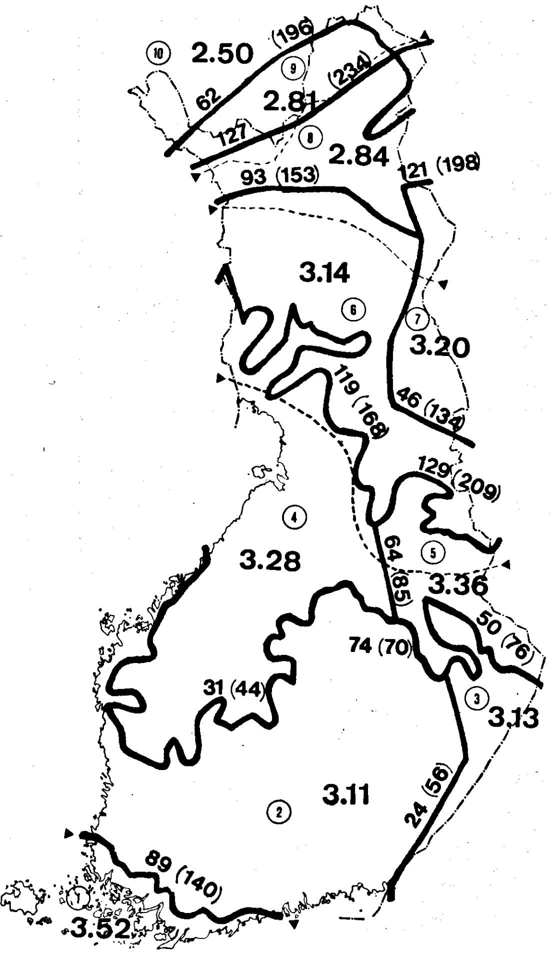


FIG. 9. Diversities of land birds in vegetation zones and their sections (AHTI et al. 1968, Fig. 9) and $1000 \times \text{DIV}_{\text{diff}}$ values between these (see Fig. 7). Areal symbols: 1 = Hemiboreal, 2—3 = S. BOREAL, 2 = OC, 3 = OC —Cl, 4—5 = M. BOREAL, 4 = OC, 5 = OC —Cl, 6—10 = N. BOREAL, 6 = OC, 7 = Ol, 8 = Cl, 9 = OC, 10 = Ol; here Ol = slightly oceanic, OC = indifferent, Cl = slightly continental. This analysis gives an additional zoogeographical boundary separating the hemiboreal zone.

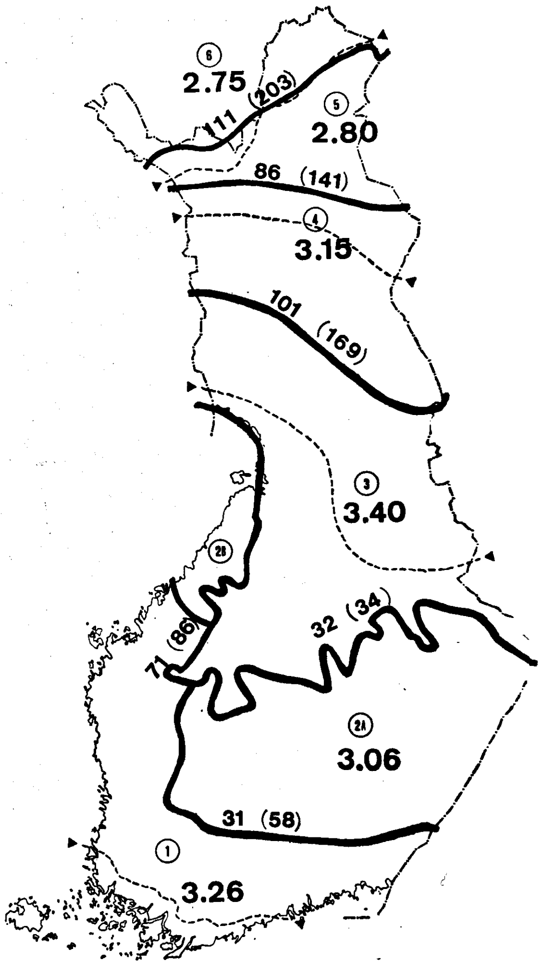
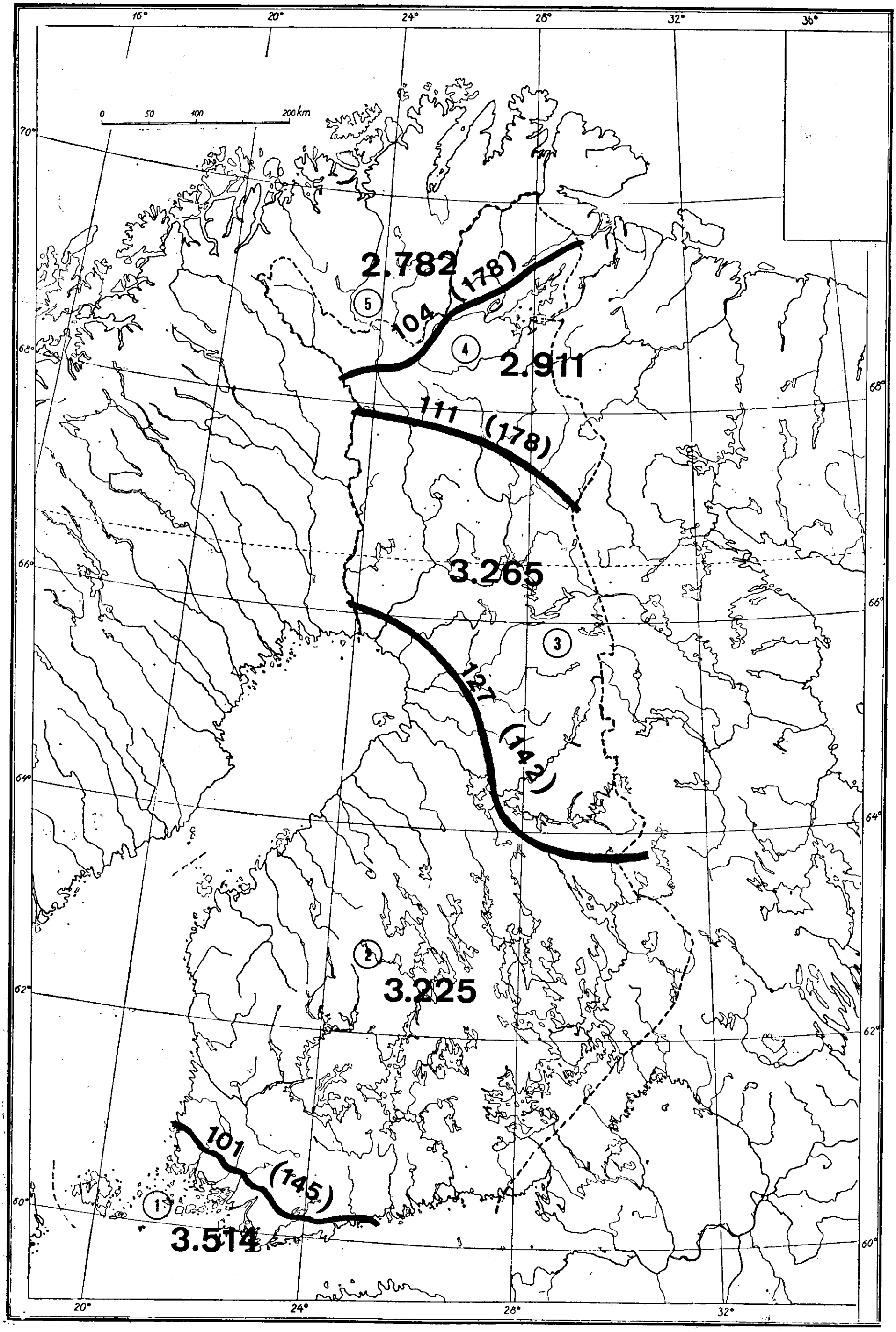


FIG. 10. Diversities of land birds in mire vegetation zones (EUROLA 1968, Fig. 3) and $1000 \times \text{DIV}_{\text{diff}}$ values between these (see Fig. 7). Areal symbols: 1 = HEMIBOREAL, 2—5 = BOREAL, 2 = S. Boreal, 3 = M. Boreal, 4 = N. Boreal (continental), 5 = N. Boreal (oceanic), 6 = OROARCTIC-OROHEMIARCTIC. Boundaries from Fig. 9.

what subjective approach. It would, of course, be possible to experiment with an immense number of arbitrary zonations. But the work would be regrettably tedious, expensive (measured by computer time), and very likely fruitless, at least at this stage. The results in the matrix of Table 2 serve as a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28°
32°
36°
0 50 100 200 km
70°
68°
66°
64°
62°
60°
2.782
(178)
104
5
4
2.911
111
(178)
3.265
3
127
(142)
2
3.225
101
(145)
1
3.514
20°
24°
28°
32°

TABLE 2. Zoogeographical zonation of Finland: (a). Statistics characterizing the zones. The number of species in zone 1 is given in parentheses because the data are meagre. (b). The matrix shows $1000 \times \mathrm{DIV}_{\mathrm{diff}}$ values for pairwise comparisons between the ornithological zones. Survey belt data are used in both *a* and *b*.

a.

Zone	Line transects number	Line transects km	Diversity (H′)	Species	Pairs/km
1. Hemiboreal	9	41.1	3.514	(90)	53.6
2. South boreal	184	716.1	3.225	119	36.2
3. Middle boreal	51	224.7	3.265	88	26.7
4. North boreal	37	157.0	2.911	70	20.7
5. Hemiarctic	26	139.3	2.782	56	19.0

b.

Zone	1	2	3	4
2	101			
3	268	127		
4	480	319	111	
5	586	451	272	104

kind of an objective check for our conclusions. As far as we can see, the result is satisfactory.

Species lists with absolute and relative abundances are presented in the Appendix. The absolute values are expressed as pairs per km of transect count; the relative abundances are percentages of the total in the respective zone.

4. Discussion

”Are the boundaries of (the) communities sharp, with many species dropping out synchronously, or do the species drop out independently?” is one of the problems discussed by the late ROBERT H. MACARTHUR in his recent book (1972) — a question left more or less unanswered, in absence of sufficient evidence. However, as MACARTHUR (1972:250) notes, the existence of the classic biogeographic ”realms” is beyond dispute. The integrity of the alternate ”realms” provides an excellent example of diffuse competition, defined as competition with several species (a constellation of species). If species interactions (competition and predation in the widest sense) are important in producing such patterns, we are more justified in invoking a concept like ”community structure” or ”organization” (see CONNELL 1971, MACARTHUR 1972; cf. PIELOU 1971).

Our present data are insufficient to answer MACARTHUR's question. However, one of our major results, evidence for the existence of several relatively sharp transition zones, is obviously relevant in this context. In the following, we attempt to relate our results to some other fields of investigation, and present hypotheses concerning possible causal relations.

FIG. 11. Zoogeographical zonation of Finland. Diversities in the centre of each zone, $1000 \times \mathrm{DIV}_{\mathrm{diff}}$ values along the boundaries (main belt values in parentheses). Areal symbols: 1 = Hemiboreal, 2 = Southern Boreal, 3 = Midboreal, 4 = Northern Boreal, 5 = Hemiarctic.

4.1. Botanical zonations

The zonation of the vegetation in the north-western parts of Europe is basically caused by macroclimatic patterns. Various criteria — climatic, edaphic, ecological, and phytosociological — have been used for the delimitation of vegetation zones (summarized by AHTI et al. 1968). The resulting synthetic zonation depends largely on the weights given by each researcher to these criteria. Certainly, the resemblance of our zonation to that by AHTI et al. (1968) is not necessarily evidence of a causal connection (see Fig. 9). Another zonation closely resembling ours is that proposed by A. KALELA (1961), based on forest vegetation. Most of KALELA's zones are remarkably close to ours; the only notable exception is that our south boreal zone corresponds to two zones in KALELA's zonation.[1]

In an early work, PALMGREN (1928) brought forward arguments to show the importance of forest type classifications for animal (avian) ecology. Later work (e.g. PALMGREN 1930, SOVERI 1940, HAAPANEN 1965) has confirmed his views. Our results bring out another, and perhaps even more fundamental, correspondence between vegetational and zoological classifications, namely the rough identity of the respective zonations. The causal relationships nevertheless remain unexplained. We can suggest at least four explanations, not mutually exclusive. First, the climate may be directly responsible for the coinciding patterns. This would mean that the ornithological zones are primarily climatic phenomena. Climate is certainly one factor, as is evidenced by the occurrence of climatically conditioned phenomena in the determination of the ranges, e.g. annual fluctuations in the marginal areas due to temperature conditions during the spring migration (see VÄISÄNEN 1965, HILDÉN 1966). More data from the transition zones are badly needed to clarify how profoundly climatic fluctuations exert their influence on the community as a whole. (Vegetation is much more constant, and the effects of climate and vegetation are thus separable.)

Second, the ornithological zones may be products of adaptation to vegetational zones. The correspondence between the ornithological and vegetational zones would obviously result from the characteristic distribution of resources in each vegetational zone. That this explanation is undoubtedly correct to some extent is shown by the fruitfulness of forest and related classifications in avian ecology (see above). The validity of this explanation is shown by the fact that a competent field ornithologist can, from the appearance of a certain area, make a rather accurate guess at the species which inhabit it.

The third possible cause is related to the second. Bird species diversity (i.e. a measure of community structure) within a habitat is related to structural characteristics — the diversity of the foliage layers — of the habitat. This has been shown to be true in very different environments (MACARTHUR & MACARTHUR 1961, MACARTHUR 1964, 1965, KARR 1968, RECHER 1969, CODY 1970, KARR & ROTH 1971).

The diversity values of the ornithological zones (or smaller mixed-habitat areas) might be correlated with the structural properties of the vegetational zones. This problem is, unfortunately, complicated. We should first require a general measure of habitat diversity. Perhaps this can be obtained by computing an H' value from estimates of the proportions of the different habitat types in each area. The main problems

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[1] KALLIOLA's (1973) extensive phytogeographical work was, unfortunately, published after our manuscript was completed. His zonation (KALLIOLA 1973:181) corresponds closely to those of A. KALELA (1961) and AHTI et al. (1968).

are involved in the next stage. We should take into account that different types of habitat vary considerably in the number of foliage layers (in the sense of MACARTHUR & MACARTHUR 1961; see also MACARTHUR & HORN 1969). In addition, to predict species diversity we should need accurate information on the similarity of different habitat types with respect to the composition of the avifauna. Last but not least, there are geographical gradients, such as the thinning of forests and the decreasing height of the trees towards the north — factors not to be ignored.

A fourth possibility is discussed in Section 4.2.

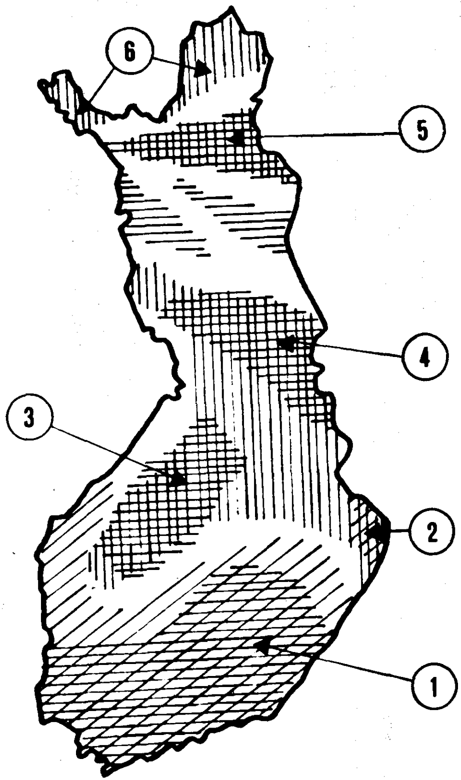
4.2. Zoogeographical zonations

LEHTONEN (1951) attempted an ornithological zonation of Finland on the basis of range boundaries (Fig. 12). The method regards clusters of distributional boundaries as decisive in determining boundary zones. This is unsatisfactory in two respects. First, quantitative data on the frequencies are disregarded (though LEHTONEN considered the abundances of the total avifauna); additionally, limits or boundary zones are determined on the basis of species occurring at the margins of their ranges. This implies that ecologically dominant species make no direct contribution to zonation. (They may, at least theoretically, make an indirect contribution. If the abundance of a dominant species increases or decreases considerably within a relatively short distance, the species associated with it by competition, commensalism, etc. may reach the boundaries of their ranges in this area.) Second (cf. also LEHTONEN 1951), the determination of the range boundaries of a species is an arbitrary process. In fact, there are few species with clear-cut range boundaries. Another observation that needs further study from this point of view is that marginal populations often occupy only optimal habitas (e.g. HILDÉN 1965).

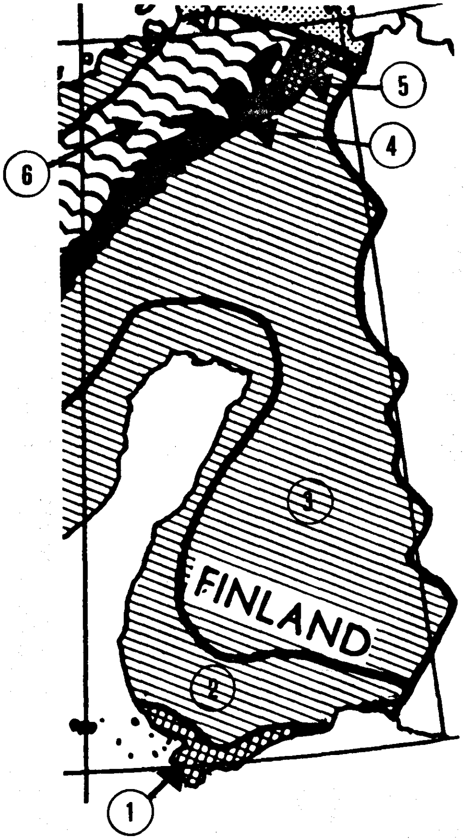
For these reasons we consider our present approach an essentially more effective biogeographic procedure than the mapping of range boundaries, regarded as the only possible method by LEHTONEN (1951:47). LEHTONEN's zonation roughly corresponds to ours in northern Finland, but he divides southern Finland very differently. Detailed comparisons with our zonation are hampered by the broadness of LEHTONEN's transition zones.

A similar method, with the same flaws, was employed by SALOMONSEN (1963), although his zones were separated by narrow boundaries, not by broad borders (Fig. 12). Regrettably, the lack of precision of SALOMONSEN's (1963) map renders comparisons difficult. Our hemiarctic zone corresponds to 3 or 4 zones in SALOMONSEN's system (high alpine, low alpine, subarctic, subalpine). Another obvious discrepancy is caused by the genuine high boreal — Bothnian transition of SALOMONSEN. We suggest that this transition is partially caused by the inclusion of marine birds in SALOMONSEN's study. Thus the transition zone should probably follow the coasts of the Baltic as closely as possible. Our hemiboreal zone, for which we have the least evidence, is identical with SALOMONSEN's Baltic transition, as regards south-western Finland.

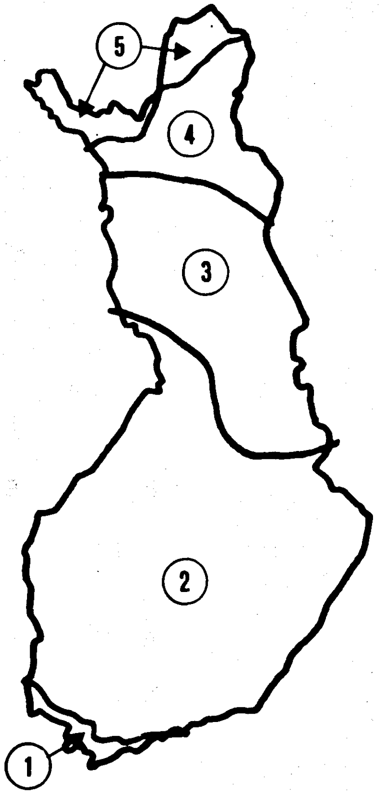
Some zoogeographers have argued that certain botanical zonations should be taken as a definite basis for zoological work. The system most commonly recommended is that by KUJALA (1936), based on differences in soil fertility. It has been fully discussed from the zoogeographical point of view by O. KALELA (1944). The most notable example of KUJALA's zonation, as employed in ornithology, is provided by MERIKALLIO (1955, 1958); its demerits are shown in Section 3.



LEHTONEN 1951



SALOMONSEN 1963



JÄRVINEN & VÄISÄNEN 1973

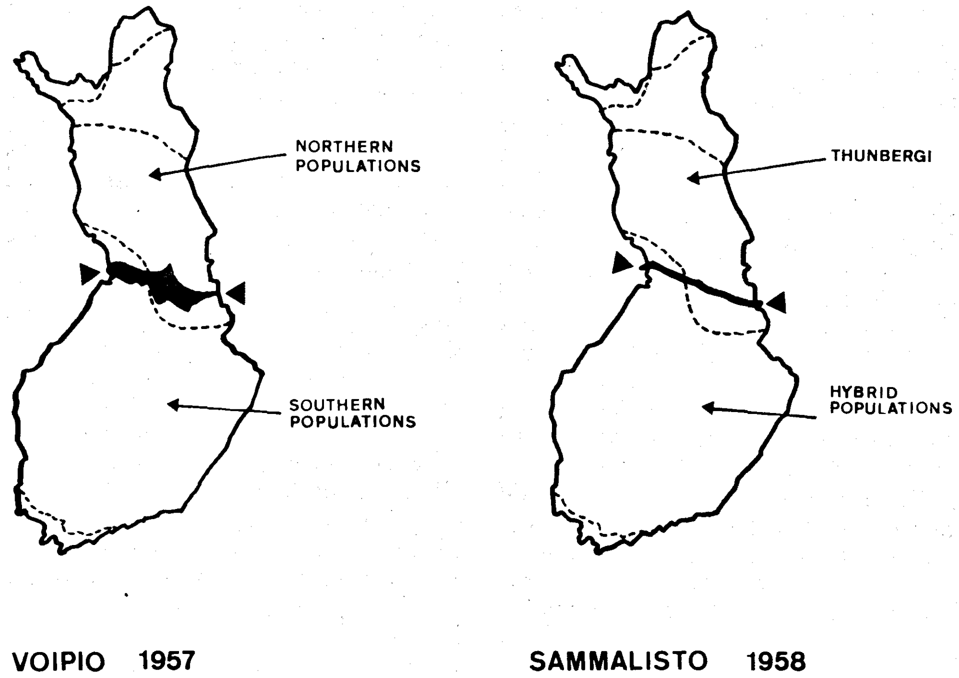


FIG. 13. Transition zones in the variation pattern in the Red Squirrel *Sciurus vulgaris,* from VOIPIO (1957), and in the Grey-Headed Wagtail *Motacilla flava,* from SAMMALISTO (1958). Our zonation is indicated in both maps (— — — —).

Two conspicuously varying, carefully studied vertebrate species, the Red Squirrel, *Sciurus vulgaris,* and the Grey-Headed Wagtail, *Motacilla flava,* provide interesting comparisons. We certainly do not wish to identify faunal and intraspecific transition zones in the following discussion, but use comparisons, at most, to suggest relevant hypotheses.

Variation in the Red Squirrel has been investigated by VOIPIO in a series of publications (e.g. 1957, 1970). The populations of southern Finland are rather monomorphic up to a narrow transition zone (Fig. 13). From this zone northwards, variation increases steadily, with the exception of the northernmost populations. The dark and red "phases" of the species differ in morphological features connected with thermoregulation (VOIPIO & HISSA 1970). The pronounced variability in northern Finland seems to be due to adaptation to extreme temperature variations (VOIPIO 1972; see also LEVINS 1968).

FIG. 12. Zoogeographical zonations of LEHTONEN (1951, redrawn from his map 15), SALOMONSEN (1963:24—25) and this study (Fig. 11). Areal symbols: LEHTONEN: 1 = Southern Finland, 2 = Karelia, 3 = Suomenselkä, 4 = Transition zone of Kainuu, 5 = Maanselkä Lapland, 6 = Fjeld Lapland. LEHTONEN's marine zone is omitted. SALOMONSEN: 1 = MIDBOREAL (Baltic transition), 2—5 = HIGH BOREAL, 2 = Bothnian transition, 3 = Genuine, 4 = Subalpine, 5 = Subarctic, 6 = ALPINE (high and low alpine).

In the Grey-Headed Wagtail, studied by SAMMALISTO (e.g. 1958, 1968), there is a sharp and largely coinciding transition zone in a closely corresponding position (Fig. 13). In this case, the zone runs between the south-Finnish hybrid populations of *Motacilla flava* (historically, subspecies *flava* and *thunbergi* are involved), and the northern, more or less "pure" *thunbergi* populations. The transition zone is narrow, of the order of some tens of kilometres (VEPSÄLÄINEN 1968). Temperature minima during the breeding season seem to be of importance in determining the variation pattern (SAMMALISTO 1968).

These are surprising coincidences. (Of course, we should be cautious, because we are restricted to two comparisons only.) Our south boreal zone, i.e. the whole of southern Finland (excluding the tiny hemiboreal zone), with its fairly homogeneous avifauna (Section 3), shows no notable changes in the variation pattern of the Red Squirrel or the Grey-Headed Wagtail. The boundary between our south and middle boreal zones almost coincides with the narrow intergradation zones of these two species (Fig. 13). Northwards from this transition zone, there are gradual, progressive changes in the avifauna and in *Sciurus*, but apparently no abrupt transitions. (There is the very sharp transition in the avifauna in northernmost Finland (Fig. 6). We refer here to those parts of Finland which lie between this transition and the south boreal — middle boreal transition.)

The occurrence of sharp gradients within a species in a gradually changing environment presents an intricate problem. Most abrupt steps seem to be due to secondary intergradation, that is, contact between populations which have previously been geographically isolated for long enough to have undergone genetic differentiation (MAYR 1970:223). CLARKE (1966) has convincingly shown that this is not the only possibility. In a gradually changing environment, stepwise clines may be produced by relatively simple genetic systems, granting proper interactions between genes (modifying loci are involved in CLARKE's model). VOIPIO (1952) also stressed this point. He noted that balanced genecomplexes are an effective strategy for coping with gradual changes in the environment. As a consequence, wide areas may be inhabited by genetically similar populations (e.g. southern Finland in the cases of *Sciurus vulgaris* and *Motacilla flava*). However, when environmental conditions within the range of a subspecies or race "become too different, the limit of tolerance will be exceeded in a certain zone (stage), whereupon a new gene complex appears as a new substitute" (VOIPIO 1952:6). We do not regard VOIPIO's argument as a model for race formation (cf. MAYR 1970); however, it appears fully acceptable with respect to gene-complexes, which are by no means equivalent to subspecies or races.

We should like to present one more hypothesis concerning the transition zones observed. The hypothesis was suggested by analogy from the previous discussion, though its correctness does not depend on the correctness of the analogy. If we may suppose that species interactions (predation and competition) are important in zoogeography, as MACARTHUR (1972:21) argues, it seems that communities are in a way comparable to gene-complexes: in neither case is it permissible to ignore interactions between the components. Analogous patterns can perhaps be traced in both cases. Consequently, homogeneous regions, transition zones in the absence of abrupt environmental changes, and so on, might be expected in biogeographical contexts, too. For the solution of these problems there is at least one line of theoretical research which seems promising. If communities are described by community matrices (LEVINS 1968, VANDERMEER 1970), and due allowance is made for geographic patterns, are transition zones possible when interactions between species are weak, and, simultaneously, the changes in the environment are not abrupt? Or are at least moderately strong interactions necessary to produce sharp transitions in a gradually changing environment?

The hypothesis thus conceives zoogeographical transition zones as products of shifts from one balanced constellation to another. If this is true, we are returning to DARWIN (1859:81), who wrote: "We shall best understand the probable course of natural selection by taking the case of a country undergoing some physical change, for instance, of climate. The proportional numbers of its inhabitants would immediately undergo a change, and some species might become extinct. We may conclude, from what we have seen of the intimate and complex manner in which the inhabitants of each country are bound together, that any change in the numerical proportions of some of the inhabitants, independently of the change of climate itself, would most seriously affect many of the others."

We finally comment on the view that zoogeographical regions do not correspond to any objective realities in nature but are mere conventions of classification. It may, of course, be true that while there are distinct faunas composed of species with ranges of related shape (e.g. STEGMANN 1938, ref. UDVARDY 1969; VOOUS 1960), there are no distinct zoogeographical regions (VOOUS 1960, UDVARDY 1969). As UDVARDY (1969:285) states the argument, there are "no rigid boundaries or 'transitional zones' of biogeographic districts, for boundaries are artifacts and do not conform to the real situation of the mosaiclike blending of animals of different origins and ecologic affiliations." We wish to emphasize two points. Zonation should not, in our view, be thought of as if absolute boundaries were the only alternative to absolute continua. Transition zones, that is, zones where changes are more pronounced than elsewhere although not abrupt, do also exist. Secondly, we should question UDVARDY's suggestion (above) that communities are mosaics of animals. This view seems *a priori* to neglect species interactions, such as competition.

Acknowledgements

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Selostus: **Suomen pesimälinnuston lajidiversiteetti, I: Maalinnustoon perustuva eläinmaantieteellinen aluejako.**

Tutkimuksessa on käytetty hyväksi lajidiversiteettiin (H', Shannonin-Weaverin funktio) perustuvaa menetelmää muodostettaessa Suomen eläinmaantieteellinen aluejako. Lajidiversiteettiä voidaan pitää tarkkana lajiston monipuolisuuden mittana, ja se ottaa huomioon sekä lajien määrän että niiden suhteelliset runsaudet tarkasteltavalla alueella. Perusaineistona on 307 linja-arviointimenetelmällä vv. 1941—73 tehtyä maalinnustolaskentaa, joiden yhteispituus on 1278.2 km (taulukko 1). Laskennoissa on havaittu 40 066 lintuparia, kaikkiaan 146 lajia. Linja-arvioinnissa on kultakin reitiltä tilastoitu parimäärät 50 m leveältä pääsaralta ja sen ulkopuoliselta apusaralta; yhdessä nämä muodostavat **tutkimussaran** (= MERIKALLIOn kuulosarka).

Arviointisaran leveys vaikuttaa voimakkaasti linja-arviointimenetelmän antamiin paritiheyksiin. Diversiteetti riippuu sen sijaan paljon vähemmän saran leveydestä (kuva 2). Pääsaran, apusaran ja tutkimussaran diversiteetit korreloivat voimakkaasti ja ovat samansuuruisia.

Jotta pesimälinnuston diversiteetin arvio olisi luotettava, vaaditaan analyysimme perusteella alueelta vähintään 28 pääsarkakilometriä tai 16 tutkimussarkakilometriä. Jaettaessa aineisto yhtenäiskoordinaatiston 100×100 km² suuruisiin ruutuihin todettiin sen nykyisellään riittävän pääasiassa vain tutkimussarka-analyysiin, koska kovin moniin ruutuihin tuli alle 28 km aineistoa (kuva 1).

Kahden alueen linnuston koostumusta tehokkaasti vertaavaa menetelmäämme ehkä parhaiten havainnollistaa käytetyintä lintutieteellistä aluejakoa esittävä kuva 8. Kunkin alueen keskellä on lihavalla diversiteettiarvo. Vierekkäisten alueiden rajoilla olevat indeksit ilmaisevat alueiden diversiteettieron (DIV_{diff}-indeksi) tutkimussarka- ja (suluissa) pääsarka-aineistosta. Mitä suurempia arvot ovat, sitä enemmän verratut kaksi aluetta eroavat toisistaan.

Kuvaan 6 on yhdistetty neljää erilaista koordinaatistoruudukkoa analysoimalla saadut diversiteettieroarvot. Niiden ja kuvien 7—10 analyysien pohjalta Suomi (alustavasti) jaettiin eläinmaantieteellisiin vyöhykkeisiin. Tulos lienee ensimmäinen lajidiversiteetteihin perustuva eläinmaantieteellinen aluejako. Alueet (kuva 11) ovat etelästä pohjoiseen lukien: (1) hemiboreaalinen vyöhyke, (2) eteläboreaalinen vyöhyke, (3) keskiboreaalinen vyöhyke, (4) pohjoisboreaalinen vyöhyke ja (5) hemiarktinen vyöhyke. Taulukossa 2 on esitelty vyöhykkeiden linnustojen ominaisuuksia; liitteessä ovat lajiluettelot, joista selviävät sekä absoluuttiset että suhteelliset runsaudet tutkimussarka-aineistossamme. Verrattaessa aluejakoa aikaisempiin kasvi- ja eläintieteellisiin aluejakoihin tuodaan esille useita, toisiaan pois sulkemattomia mahdollisia syy-vaikutussuhteita.

Tärkeimpinä yleisinä havaintoina mainitsemme: (1) Linnuston diversiteetti pienenee etelästä pohjoiseen. (2) Linnustossa on havaittavissa toisaalta alueita, joilla muutoksia tapahtuu niukasti (Etelä-Suomi), toisaalta selviä vaihettumisvyöhykkeitä, joita luonnehtivat voimakkaat muutokset (vyöhykkeiden 2 ja 3 raja, vyöhykkeiden 4 ja 5 raja). (3) Vyöhykkeet vastaavat huomattavan tarkoin eräitä kasvitieteellisiä vyöhykkeitä, jotka viime kädessä liittyvät suurilmaston vyöhykkeisyyteen.

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Appendix:

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ABUNDANCES OF 146 LAND BIRD SPECIES OF THE SURVEY BELT IN THE FIVE ZONES OF FINLAND.

 1 = HEMIBOREAL                  ***** = NO OBSERVATIONS
 2 = SOUTH BOREAL
 3 = MIDDLE BOREAL               -------------------------  -------------------------
 4 = NORTH BOREAL                NUMBER OF PAIRS PER 1 KM   RELATIVE ABUNDANCE (%)
 5 = HEMIARCTIC                  -------------------------  -------------------------

                                     1    2    3    4    5      1    2    3    4    5


BOTAURUS STELLARIS                0.02 0.00***************    0.0  0.0***************
AQUILA CHRYSAETOS                ***** 0.00 0.00 0.01*****  *****  0.0  0.0  0.0*****
BUTEO BUTEO                       0.02 0.02 0.01**********    0.0  0.1  0.0**********
BUTEO LAGOPUS                    *************** 0.07 0.09  ***************  0.3  0.5
ACCIPITER NISUS                  ***** 0.01***************  *****  0.0***************
ACCIPITER GENTILIS                0.05 0.01***************    0.1  0.0***************
PERNIS APIVORUS                  ***** 0.01 0.01**********  *****  0.0  0.0**********
CIRCUS CYANEUS                   ***** 0.00 0.00***** 0.02  *****  0.0  0.0*****  0.1
PANDION HALIAETUS                 0.02 0.00 0.00 0.01*****    0.0  0.0  0.0  0.0*****
FALCO SUBBUTEO                   ***** 0.02***************  *****  0.1***************
FALCO PEREGRINUS                 ***** 0.00***************  *****  0.0***************
FALCO COLUMBARIUS                ***** 0.00 0.01 0.03 0.03  *****  0.0  0.0  0.1  0.2
FALCO TINNUNCULUS                 0.02 0.02 0.01 0.01 0.01    0.0  0.0  0.0  0.1  0.1
LAGOPUS LAGOPUS                  ***** 0.01 0.05 0.06 0.06  *****  0.0  0.2  0.3  0.3
LAGOPUS MUTUS                    *************** 0.01*****  ***************  0.0*****
LYRURUS TETRIX                    0.05 0.16 0.17 0.04*****    0.1  0.4  0.6  0.2*****
TETRAO UROGALLUS                  0.02 0.05 0.05 0.05 0.01    0.0  0.2  0.2  0.2  0.1
TETRASTES BONASIA                 0.07 0.09 0.04 0.01*****    0.1  0.2  0.2  0.0*****
PERDIX PERDIX                    ***** 0.00***************  *****  0.0***************
COTURNIX COTURNIX                ***** 0.00***************  *****  0.0***************
GRUS GRUS                        ***** 0.05 0.17 0.06 0.02  *****  0.1  0.6  0.3  0.1
PORZANA PORZANA                  ***** 0.00***************  *****  0.0***************
CREX CREX                        ***** 0.00***************  *****  0.0***************
VANELLUS VANELLUS                 0.22 0.09***************    0.4  0.3***************
CHARADRIUS HIATICULA             ***** 0.00***** 0.02 0.04  *****  0.0*****  0.1  0.2
CHARADRIUS DUBIUS                ***** 0.00***************  *****  0.0***************
CHARADRIUS APRICARIUS            *************** 0.06 0.57  ***************  0.3  3.0
CHARADRIUS MORINELLUS            *************** 0.05 0.03  ***************  0.2  0.2
CAPELLA GALLINAGO                 0.32 0.14 0.26 0.19 0.12    0.6  0.4  1.0  0.9  0.6
LYMNOCRYPTES MINIMUS             ***** 0.00 0.03 0.04 0.09  *****  0.0  0.1  0.2  0.5
SCOLOPAX RUSTICOLA                0.05 0.01***************    0.1  0.0***************
NUMENIUS ARQUATA                  0.17 0.28 0.09**********    0.3  0.8  0.3**********
NUMENIUS PHAEOPUS                ***** 0.03 0.26 0.31 0.29  *****  0.1  1.0  1.5  1.5
TRINGA OCHROPUS                   0.05 0.05 0.01**********    0.1  0.1  0.0**********
TRINGA GLAREOLA                   0.05 0.12 0.81 0.66 0.65    0.1  0.3  3.0  3.2  3.4
TRINGA HYPOLEUCOS                 0.10 0.03 0.03 0.01 0.01    0.2  0.1  0.1  0.0  0.0
TRINGA TOTANUS                    0.02 0.00 0.00**********    0.0  0.0  0.0**********
TRINGA ERYTHROPUS                ********** 0.08 0.17 0.14  **********  0.3  0.8  0.7
TRINGA NEBULARIA                 ***** 0.12 0.40 0.42 0.12  *****  0.3  1.5  2.0  0.6
CALIDRIS TEMMINCKII              ********** 0.00***** 0.04  **********  0.0*****  0.2
LIMICOLA FALCINELLUS             ***** 0.00***** 0.06 0.04  *****  0.0*****  0.3  0.2
PHILOMACHUS PUGNAX               ********** 0.03 0.03 0.11  **********  0.1  0.2  0.6
PHALAROPUS LOBATUS               ******************** 0.09  ********************  0.5
STERCORARIUS LONGICAUDUS         ******************** 0.15  ********************  0.8
COLUMBA OENAS                     0.07 0.01***************    0.1  0.0***************
COLUMBA PALUMBUS                  0.97 0.35 0.01**********    1.8  1.0  0.0**********
STREPTOPELIA TURTUR               0.02********************    0.0********************
COLUMBA LIVIA                     0.46 0.01***************    0.9  0.0***************
CUCULUS CANORUS                   0.90 0.78 0.70 0.52 0.27    1.7  2.1  2.6  2.5  1.4
SURNIA ULULA                     ***** 0.00 0.01 0.01*****  *****  0.0  0.0  0.0*****
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ABUNDANCES OF 146 LAND BIRD SPECIES OF THE SURVEY BELT IN THE FIVE ZONES OF FINLAND.

  1 = HEMIBOREAL             ***** = NO OBSERVATIONS
  2 = SOUTH BOREAL
  3 = MIDDLE BOREAL          -------------------------  -------------------------
  4 = NORTH BOREAL           NUMBER OF PAIRS PER 1 KM   RELATIVE ABUNDANCE (%)
  5 = HEMIARCTIC             -------------------------  -------------------------

                                1    2    3    4    5      1    2    3    4    5

STRIX URALENSIS              *************** 0.01*****  ***************  0.0*****
ASIO OTUS                    ***** 0.00***************  *****  0.0***************
ASIO FLAMMEUS                ***** 0.00 0.03 0.01*****  *****  0.0  0.1  0.1*****
AEGOLIUS FUNEREUS            ***** 0.00***************  *****  0.0***************
CAPRIMULGUS EUROPAEUS         0.02 0.00***************    0.0  0.0***************
APUS APUS                     0.63 0.12 0.05 0.01*****    1.2  0.3  0.2  0.1*****
PICUS CANUS                   0.02********************    0.0********************
DENDROCOPOS MAJOR             0.12 0.13 0.14 0.02*****    0.2  0.4  0.5  0.1*****
DENDROCOPOS LEUCOTOS         ***** 0.00***************  *****  0.0***************
DENDROCOPOS MINOR             0.07 0.00 0.00**********    0.1  0.0  0.0**********
PICOIDES TRIDACTYLUS         ***** 0.01 0.06 0.03*****  *****  0.0  0.2  0.1*****
DRYOCOPUS MARTIUS             0.10 0.09 0.08 0.03*****    0.2  0.3  0.3  0.1*****
JYNX TORQUILLA                0.05 0.03 0.01 0.01*****    0.1  0.1  0.0  0.1*****
LULLULA ARBOREA               0.05********************    0.1********************
ALAUDA ARVENSIS               0.58 0.35 0.04**********    1.1  1.0  0.1**********
EREMOPHILA ALPESTRIS         *************** 0.09 0.11  ***************  0.4  0.6
HIRUNDO RUSTICA               0.46 0.39 0.12**********    0.9  1.1  0.4**********
DELICHON URBICA               0.78 0.17 0.04***** 0.01    1.5  0.5  0.1*****  0.0
RIPARIA RIPARIA              ***** 0.24 0.12 0.27*****  *****  0.7  0.4  1.3*****
ORIOLUS ORIOLUS               0.02 0.03***************    0.0  0.1***************
CORVUS CORAX                  0.05 0.03 0.04 0.05 0.14    0.1  0.1  0.2  0.2  0.8
CORVUS CORONE                 0.92 0.66 0.33 0.21 0.07    1.7  1.8  1.2  1.0  0.4
CORVUS MONEDULA               0.12 0.03***************    0.2  0.1***************
PICA PICA                     0.41 0.31 0.16 0.02 0.01    0.8  0.9  0.6  0.1  0.0
GARRULUS GLANDARIUS           0.29 0.15 0.01**********    0.5  0.4  0.0**********
PERISOREUS INFAUSTUS         ***** 0.02 0.18 0.23 0.04  *****  0.1  0.7  1.1  0.2
PARUS MAJOR                   1.65 0.29 0.08 0.01*****    3.5  0.8  0.3  0.0*****
PARUS CAERULEUS               0.32 0.00***************    0.6  0.0***************
PARUS ATER                    0.27 0.02 0.00**********    0.5  0.1  0.0**********
PARUS CRISTATUS               0.54 0.42 0.16**********    1.0  1.2  0.6**********
PARUS CINCTUS                ********** 0.20 0.36 0.06  **********  0.7  1.7  0.3
PARUS MONTANUS                1.17 0.92 0.58 0.13 0.02    2.2  2.6  2.2  0.6  0.1
AEGITHALOS CAUDATUS          ***** 0.01***************  *****  0.0***************
CERTHIA FAMILIARIS            0.10 0.02 0.00**********    0.2  0.1  0.0**********
CINCLUS CINCLUS              ******************** 0.01  ********************  0.0
TROGLODYTES TROGLODYTES       0.02 0.02***************    0.0  0.1***************
TURDUS VISCIVORUS            ***** 0.17 0.15 0.04*****  *****  0.5  0.6  0.2*****
TURDUS PILARIS                1.17 0.73 0.15 0.07 0.01    2.2  2.0  0.6  0.3  0.1
TURDUS PHILOMELOS             1.24 0.75 0.52 0.17*****    2.3  2.1  1.9  0.8*****
TURDUS ILIACUS                1.19 0.51 0.81 1.67 1.59    2.2  1.4  3.0  8.0  8.3
TURDUS MERULA                 1.05 0.03***************    2.0  0.1***************
OENANTHE OENANTHE             0.44 0.13 0.04 0.08 0.37    0.8  0.4  0.2  0.4  2.0
SAXICOLA RUBETRA              0.36 0.33 0.19 0.01*****    0.7  0.9  0.7  0.1*****
PHOENICURUS PHOENICURUS       0.36 0.69 1.66 1.31 0.37    0.7  1.9  6.2  6.3  1.9
LUSCINIA LUSCINIA             0.05********************    0.1********************
LUSCINIA SVECICA             ********** 0.00 0.04 0.45  **********  0.0  0.2  2.3
ERITHACUS RUBECULA            1.14 0.46 0.01**********    2.1  1.3  0.0**********
ACROCEPHALUS SCIRPACEUS       0.12********************    0.2********************
ACROCEPHALUS PALUSTRIS        0.02********************    0.0********************
ACROCEPHALUS DUMETORUM       ***** 0.00***************  *****  0.0***************
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ABUNDANCES OF 146 LAND BIRD SPECIES OF THE SURVEY BELT IN THE FIVE ZONES OF FINLAND.

  1 = HEMIBOREAL              ***** = NO OBSERVATIONS
  2 = SOUTH BOREAL
  3 = MIDDLE BOREAL           -------------------------    -------------------------
  4 = NORTH BOREAL            NUMBER OF PAIRS PER 1 KM     RELATIVE ABUNDANCE (%)
  5 = HEMIARCTIC              -------------------------    -------------------------

                                  1    2    3    4    5        1    2    3    4    5

ACROCEPHALUS SCHOENOBAENUS     0.05 0.02********** 0.01      0.1  0.0**********  0.1
HIPPOLAIS ICTERINA             0.22 0.01***************      0.4  0.0***************
SYLVIA ATRICAPILLA             0.34 0.02***************      0.6  0.0***************
SYLVIA NISORIA                 0.27********************      0.5********************
SYLVIA BORIN                   1.48 0.82 0.04***** 0.01      2.8  2.3  0.2*****  0.0
SYLVIA COMMUNIS                0.85 0.17 0.00**********      1.6  0.5  0.0**********
SYLVIA CURRUCA                 0.36 0.22 0.05**********      0.7  0.6  0.2**********
PHYLLOSCOPUS TROCHILUS         4.99 7.30 3.80 3.73 3.44      9.3 20.1 14.2 18.0 18.1
PHYLLOSCOPUS TROCHILOIDES      0.19 0.01***************      0.4  0.0***************
PHYLLOSCOPUS COLLYBITA         0.39 0.54 0.13**********      0.7  1.5  0.5**********
PHYLLOSCOPUS SIBILATRIX        0.34 0.09***************      0.6  0.2***************
PHYLLOSCOPUS BOREALIS         ***** 0.00********** 0.01    *****  0.0**********  0.0
REGULUS REGULUS                0.78 0.33 0.01**********      1.5  0.9  0.0**********
MUSCICAPA STRIATA              1.12 0.74 0.42 0.08 0.01      2.1  2.1  1.6  0.4  0.0
FICEDULA HYPOLEUCA             0.39 0.42 0.20 0.08*****      0.7  1.1  0.7  0.4*****
FICEDULA PARVA                ***** 0.00***************    *****  0.0***************
PRUNELLA MODULARIS             0.36 0.04***************      0.7  0.1***************
ANTHUS PRATENSIS              ***** 0.11 0.17 0.38 1.05    *****  0.3  0.6  1.8  5.5
ANTHUS TRIVIALIS               3.38 1.92 3.01 1.26 0.09      6.3  5.3 11.3  6.1  0.5
MUTACILLA ALBA                 0.51 0.26 0.11 0.08 0.06      1.0  0.7  0.4  0.4  0.3
MOTACILLA FLAVA                0.07 0.28 0.34 0.25 0.54      0.1  0.8  1.3  1.2  2.8
BOMBYCILLA GARRULUS           ***** 0.01 0.01 0.02*****    *****  0.0  0.0  0.1*****
LANIUS EXCUBITOR              ********** 0.00 0.01 0.01    **********  0.0  0.0  0.1
LANIUS COLLURIO                0.51 0.02***************      1.0  0.1***************
STURNUS VULGARIS               1.02 0.22 0.01**********      1.9  0.6  0.0**********
COCCOTHRAUSTES COCCOTHRAUSTES  0.02********************      0.0********************
CARDUELIS CHLORIS              0.29 0.02 0.01**********      0.5  0.1  0.0**********
CARDUELIS SPINUS               0.90 0.98 0.19 0.04*****      1.7  2.7  0.7  0.2*****
CARDUELIS CANNABINA            0.02 0.00********** 0.05      0.0  0.0**********  0.3
CARDUELIS FLAMMEA             ***** 0.19 1.49 3.26 3.50    *****  0.5  5.6 15.7 18.4
PYRRHULA PYRRHULA              0.12 0.21 0.22 0.02*****      0.2  0.6  0.8  0.1*****
CARPODACUS ERYTHRINUS          0.12 0.04***************      0.2  0.1***************
PINICOLA ENUCLEATOR           ********** 0.03 0.06 0.04    **********  0.1  0.3  0.2
LOXIA CURVIROSTRA              0.51 1.11 0.92 0.48 0.03      1.0  3.1  3.4  2.3  0.2
LOXIA PYTYOPSITTACUS           0.02 0.05 0.02 0.03*****      0.0  0.1  0.1  0.1*****
LOXIA LEUCOPTERA              ***** 0.00***************    *****  0.0***************
FRINGILLA COELEBS             10.58 7.47 2.19 0.08*****     19.8 20.6  8.2  0.4*****
FRINGILLA MONTIFRINGILLA       0.02 0.28 2.90 2.81 2.68      0.0  0.8 10.8 13.5 14.1
EMBERIZA CITRINELLA            2.00 0.92 0.29 0.01 0.01      3.7  2.5  1.1  0.1  0.0
EMBERIZA HORTULANA             0.19 0.20 0.10**********      0.4  0.5  0.4**********
EMBERIZA RUSTICA              ***** 0.19 0.61 0.13*****    *****  0.5  2.3  0.6*****
EMBERIZA PUSILLA              ********** 0.01**********    **********  0.0**********
EMBERIZA SCHOENICLUS           0.02 0.03 0.15 0.15 0.29      0.0  0.1  0.6  0.7  1.5
CALCARIUS LAPPONICUS          *************** 0.02 0.80    ***************  0.1  4.2
PLECTROPHENAX NIVALIS         ******************** 0.15    ********************  0.8
PASSER DOMESTICUS              1.24 0.21 0.04**********      2.3  0.6  0.2**********
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