

## Quantitative versus qualitative distribution patterns of birds in the western Palearctic taiga

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We studied biogeographic distribution patterns of birds breeding in coniferous forests of the western Palearctic in 24 areas ranging from the Ural Mountains to the Atlas Range. In particular, we compared patterns produced by qualitative presence/absence data with census data derived from published sources. The qualitative data showed a decreasing, albeit irregular, trend in species richness from north to south. Rarefaction analysis of the census data, in contrast, revealed no general trends in diversity. The proportion of birds typically breeding in coniferous forests (“conifer birds”) was greater in the continuous boreal taiga than in more isolated southern forest areas according to the qualitative data. In contrast, census data showed that there were two separate maxima in the proportion of conifer birds: one in northern Finland and the Ural Mountains in the north, and the other in the southern European mountains. We studied the faunal similarity of the 24 areas with the Czekanowski-Sørensen index of similarity (qualitative data) and detrended correspondence analysis (DCA, quantitative data). The patterns emerging resembled each other in broad outline, Central Europe and southern Fennoscandia forming a tight group with central Russia. Northern Ural had its closest affinities to the Fennoscandian taiga in the north. The border between northern and central taiga appeared more distinct in qualitative than in quantitative data. A DCA-ordination, with pine and spruce forests treated separately, showed a clear north-south gradient, but there was considerable variation in the relations between the bird assemblages of the two habitats at different localities. In general, qualitative data tended to show more regular geographic patterns than census data did. We discuss the explanatory power of theories of interspecific competition and insular biogeography in relation to the observed patterns. In several cases predictions upheld when using qualitative data but failed when using quantitative data.

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### 1. Introduction

In a number of earlier papers we have raised the point that biogeographic patterns look different when based on quantitative, as opposed to qualitative, data (e.g. Haila & Järvinen 1981, 1983, Haila et al. 1983, Järvinen & Haila 1984). However, the focus of these studies has been restricted to very small areas, mostly to islands of a few km<sup>2</sup> at most. The differences in bird assemblages among islands can often be traced to habitat differences among islands in the archipelagoes we have studied.

On broader biogeographical scales habitat differences are not necessarily the most important reason for differences among areas, since the basic species sets do differ among areas that are distant enough from each other. This difference in species sets is the basis of many of the biogeographic

zonations and other divisions that have been presented in the literature.

In order to be able to compare quantitative and qualitative distribution patterns when the species sets in different areas are different (although not distinct), we have examined an area that covers much of western Eurasia — namely, the western Palearctic taiga from the Ural Mountains in the east to the Atlas Range in the southwest. How similar are the patterns emerging from qualitative (presence-absence) versus quantitative (census) data bases? There are good reasons to suppose that the patterns are not identical; as an example, compare the zoogeographical zonation of Finland by Lehtonen (1951), based on the range boundaries of birds, to the zonation by Järvinen & Väisänen (1973, 1980), based on censuses of breeding land birds.

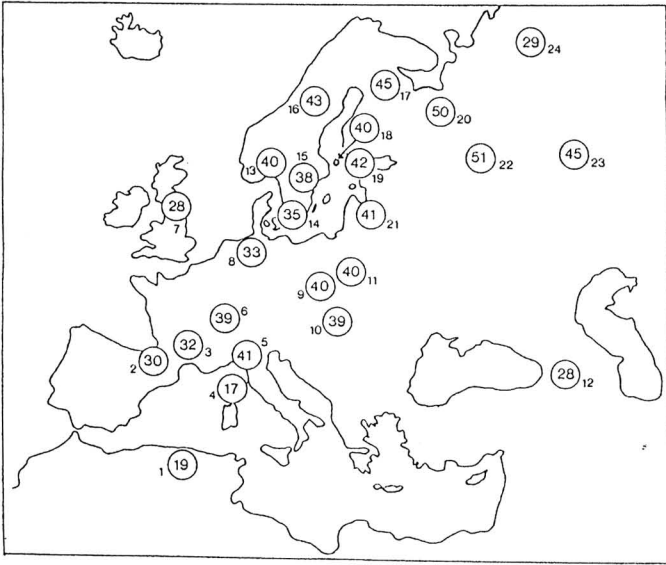


Fig. 1. Study areas. Numbers *outside* the circles refer to Appendix 1, where names of the areas are given. Numbers *within* the circles indicate the number of species present according to distribution maps (Appendix 2).

It is clear that the western Palearctic is much too vast for a simultaneous examination, in detail, of all habitat types. We have restricted our study to coniferous forests that cover much of Eurasia but also extend as outliers in mountains in South and Central Europe. This restriction to a single (albeit broad) habitat type also helps comparing the explanatory power of qualitative and quantitative data relative to specific hypotheses explaining patterns on a broad biogeographical scale.

Coniferous forests are typical of the boreal zone, but all boreal forests are not coniferous, and not all coniferous forests are boreal (e.g., Hämet-Ahti 1981). However, for birds the general appearance, "landscape" or "niche-gestalt", of the habitat is often decisively important as compared with the phytogeographical status of the area (Hildén 1965, James 1971, James et al. 1984; for a detailed example, see Götmark et al. 1978). We have thus defined our scope by habitat type rather than by phytogeographic regions.

We have included all bird species breeding in the western Palearctic that are characterized in handbooks as breeding particularly in coniferous forests. Two types of data sets were obtained: breeding distributions of individual species, and results of quantitative censuses conducted in coniferous forests in different parts of Europe and in the Atlas mountains. We examine problems of three major types in this paper:

1. Our study has a strong flavour of data-analytic exploration (see Birks 1987). At this stage we are

primarily interested in identifying and describing relevant patterns in the distribution of taiga birds in the European coniferous forests. Therefore, we map and compare patterns rather than test an array of well-argued hypotheses, but we think that much naive hypothesis-testing can be avoided by careful explorations of the main patterns. The study is not a "mere" description, however, for we use the results for evaluating problems inherent in traditional faunal analyses.

2. Our data also allow an appraisal of the adequacy of unified explanatory schemes in biogeography. Interspecific competition had such a status in the 1970s (MacArthur 1972, Diamond 1978; cf. Wiens 1977, 1983), and it gives rise to relatively straightforward predictions concerning distribution patterns.

Another candidate for a unifying explanatory framework in biogeographic studies is the theory of island biogeography (MacArthur & Wilson 1967; see also Brown & Gibson 1983), which has been used to predict the faunal composition of mainland habitat islands, comparable with the coniferous forests of southern European mountains.

Good descriptive data are certainly useful for evaluating the realism of such unifying ideas.

3. Our work has a major methodological dimension. We compare distributional and quantitative data with each other: the potential they give for detecting biogeographic patterns and for testing alternative explanations given for these patterns.

## 2. Study area and material

### 2.1. Study area

Two main goals directed the decisions we made in defining the geographical design of the study. We wanted to cover the whole area of Europe to obtain an adequate scale for geographic comparisons and, on the other hand, we wanted to get data from as many regions covered by coniferous forests as possible.

Compromises were necessary, however. Local precision had to be sacrificed for geographic generalism. First, it is impossible to define unambiguous *a priori* criteria for what is and what is not a coniferous area of relevant extent for the continental scale of the study. We tried to cover the most interesting coniferous areas in western Europe and on South European mountains, but important regional variation was presumably lost. The second and much more important factor restricting the geographic representativeness of our study is the fact that we wanted to use quantitative data. Consequently, we had to exclude important coniferous areas where no habitat-specific breeding bird censuses have been made (according to publications accessible to us); this excludes several interesting areas, particularly in southeastern Europe. The resulting compromise is shown in Fig. 1.

The study areas are described in Appendix 1.

### 2.2. The species set

We defined the *conifer birds*, the set of bird species breeding particularly in coniferous forests, according to Harrison (1982) and Heinzel et al. (1974). Species had to be described in either source explicitly as breeding in coniferous forests; generalist forest species were not regarded as conifer birds but simply as forest birds. We also omitted species breeding in mountain coniferous forests if the evident reason for breeding in this habitat was the need of cliffs for nesting and not the coniferous forest habitat as such (e.g. the golden eagle *Aquila chrysaetos*). The sparrowhawk *Accipiter nisus* was the only species added to our list of conifer birds although it is not mentioned in either source as a conifer specialist (but is regarded as such in von Haartman et al. 1963–72).

### 2.3. Geographical distribution of the species

As the basis for defining the presence or absence of the species at our study areas we used the distribution maps of Harrison (1982). There are inaccuracies in details in the maps. Several species missing from the Pechora region according to Harrison (1982) were actually included in the census data available to us (Estaf'ev 1981). However, we preferred using an unambiguous and recent source and made only a few minor corrections, as regards the Åland Islands, according to an updated species list in Haila et al. (1979). A species was defined as being present at a study area if its range in the maps of Harrison (1982) overlapped with the study area as represented by a circle with a 50 km radius, with the coordinates of the study area as the mid-point. The resulting presence/absence ma-

trix is given in Appendix 2 where our corrections are also indicated. We also compiled similar lists of all forest birds present in the study areas in order to calculate the proportion of conifer birds among all forest birds.

### 2.4. Census data

We collected our census data by screening ornithological publications available at the University of Helsinki library. We tried to find censuses from all the 24 regions, but areas 4 (Corsica) and 21 (Baltic Republics) had to be excluded because of lack of suitable data. The sources and other details are given in Appendix 1. To accept a census study the following criteria had to be met: (1) the methods described accurately enough, (2) data given in such a form that original numbers of observations could be calculated, at least with the accuracy needed in our analyses, (3) adequate sample size and (4) habitat characteristics that indicated that the censuses were restricted to coniferous forests. We classified the habitats into six types according to their tree species composition. We had to rely on the descriptions given by the authors and assume that the forests were representative of their regions.

Because of the heterogeneity of the data it is important that single study areas are not given too much weight. Therefore, we have emphasized broad patterns in our exploration.

Analyses based on census data are in most cases based on all species included in the original data sets.

## 3. Species richness

Fig. 1 shows the numbers of species of conifer birds at the 24 study areas. The numbers range from 51 to 17, the maximum being in central Russia and the minimum on Corsica.

A decreasing trend from north to south is evident, but the gradient is not regular. In particular, the species numbers in the Alps are about the same as those in southern Fennoscandia. On the other hand, there is considerable variation in species numbers within the contiguous taiga in the north: Russia has clearly higher numbers than Fennoscandia. The very low number in the northern Ural Mountains (area 24) is an artefact, due to inaccuracies in the distribution maps in Harrison (1982). Including all species in Estaf'ev's (1981) data would raise the figure to 46, but this is presumably too high because Estaf'ev's (1981) censuses also covered areas to the south of our study area 24.

The regional species numbers are lowest where coniferous forests are isolated and cover a small area: Britain, the Atlas Mountains, Corsica and Caucasus. Area 24 belongs to the north-boreal phytogeographical zone (Hämet-Ahti 1981) as does point 17 in

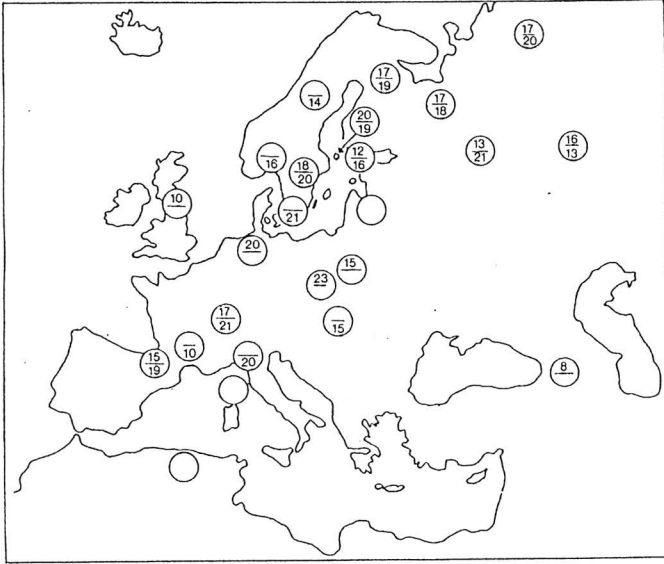


Fig. 2. Species richness in the quantitative samples from the study areas (data sources in Appendix 1). The numbers give the expected species numbers, estimated by rarefaction, in a sample of 50 pairs in pooled data sets from pine (upper figure) and spruce (lower figure) habitats in each area. The corresponding expectations in the data sets from mixed coniferous forests were: 17 species (area 1, Atlas), 15 species (area 11, northern Poland), and 21 species (area 22, central Russia). Blanks indicate missing data.

northern Finland. Realistic species numbers are quite similar in these two areas.

We have refrained from testing the above patterns statistically because the species sets are not samples from a larger universe (statistical population) but represent all the species in question. Hence, all differences between study areas are real, within the limits of the accuracy of the distribution maps.

Presence/absence data can only be used on the regional scale because presence and absence at individual sites depends on sample size (e.g. Palmgren 1930). Indeed, Fig. 1 does not tell us anything about species richness in actual species assemblages in the different study areas! Such information is nevertheless essential if we want to examine the possible species impoverishment in local assemblages, particularly because some of the ecological processes (e.g. competition) thought to affect distribution patterns operate on the local scale.

For a comparison of local species richness in coniferous habitats we used census data and rarefaction which facilitates comparisons of species numbers in samples of varying sizes (Simberloff 1978, James & Rathbun 1981). Fig. 2 shows the expected number of species in a sample of 50 pairs in the main types of forest in the study areas. The numbers show great variability. The species richness tends to be lower in pine than in spruce forests, but southern Ural and the Åland Islands show the opposite; only in a few cases, however, is the difference statistically significant.

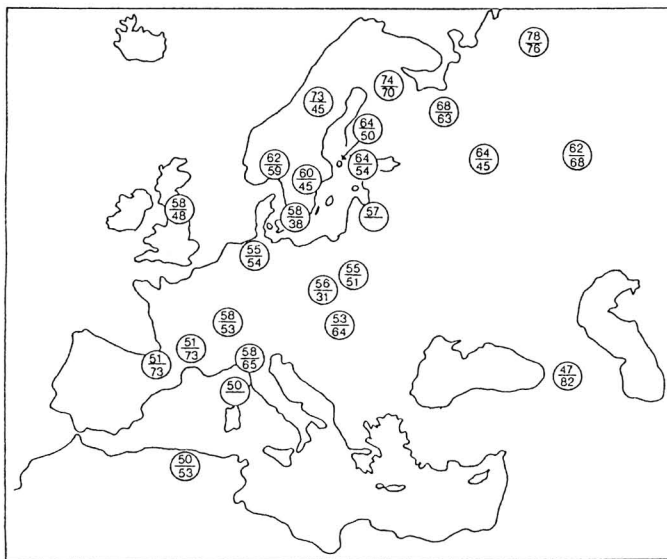
Clear geographic trends in local species richness in coniferous forests do not emerge in Fig. 2. We attribute the observed variation tentatively to local differences in habitat structure. This is supported by a comparison between the Åland Islands and the Hango Peninsula in SW Finland; the distance between the localities is about 200 km but the figures are close to the maximum and the minimum of the whole data set. The two areas are represented by large data sets that were collected using the same method (main belt observations in line transects), and the censuses embraced a wide range of variation in forest types (see Haila et al. 1980, Raivio 1986). The difference is explainable by the barren character of forests in the Hango Peninsula (see a detailed analysis in Raivio 1986).

#### 4. Frequency of conifer birds

The southern study areas are surrounded by entirely different habitats, and the distances to other coniferous sites are often long. In contrast, in the contiguous taiga the surrounding areas are coniferous forests. A natural expectation is, therefore, that conifer birds form a larger proportion of bird communities in the boreal taiga than in more southern coniferous forests.

We examined this expectation with both qualitative and quantitative data. Qualitative distribution data confirm the expectation. We calculated the proportion

Fig. 3. The proportion of conifer birds among all forest birds at each study area according to distribution maps (upper figure), and the proportion of conifer birds in the quantitative samples from each area with all forest types pooled (lower figure). Blanks indicate missing data.



of conifer birds out of all forest birds breeding in the study areas, and they show exactly the predicted trend (Fig. 3) from more than 70% in the northeast to about 50% in the southwest and in the southeast. The gradient is, moreover, quite regular.

Census data show an entirely different pattern (Fig. 3): extending the above conclusion to the level of local species assemblages is invalid. The proportion of conifer birds exceeds 70% in two regions: in the north-boreal zone in Kuusamo and northern Ural, and in the southern mountains in the Pyrenees, French Alps and Caucasus (the maximum!). The data set from Caucasus is relatively small, but the pattern is similar in southern France and in the Pyrenees. In addition, 60% is reached in the central taiga (eastern Fennoscandia and southern Ural) and in central European mountains (Czechoslovakia), but at other sites the proportions vary seemingly irregularly with the minimum (31%) in southern Poland.

In other words, the quantitative data refute the idea that conifer birds were a more important component of bird species assemblages in the continuous taiga than in isolated, more southern coniferous forests.

## 5. Faunal composition

The analysis of distribution patterns has traditionally led to two complementary approaches (see, e.g., Simberloff & Connor 1979): "Q-mode" analyses

trying to define *regions* according to the similarity of their fauna, and "R-mode" analyses constructing *faunal types* of species with similar distributions. Both types of analyses share two problems.

First, it is not obvious what kind of data are relevant, and how the analysis should be made. Simberloff & Connor (1979) argue for statistically rigorous approaches, which have the advantage of dispelling woolly subjectivity, but are difficult to apply to complex types of analyses. For example, it is fairly straightforward to compile presence/absence matrices representing the distribution of taxa in oceanic archipelagoes, but the selection of "representative" data points and decisions concerning presence and absence are problematic in continental areas. Quantitative data facilitate evaluating the ecological relevance of a species' "presence" in a region, but methods for analyzing geographical variation in quantitative data are still largely lacking (see, e.g., Pielou 1977, Pesenko 1982).

Second, the status of such descriptive concepts as faunal type or zoogeographic region is unclear, namely, what are the causative agents behind the patterns? Are there indeed simple, unifying explanations?

Concentrating on one habitat type (coniferous forests) is profitable for both Q-mode and R-mode analyses. When all habitats are included in defining faunal zonation, the resulting patterns are largely, although not exclusively influenced by the variable proportions of different habitats in different zones

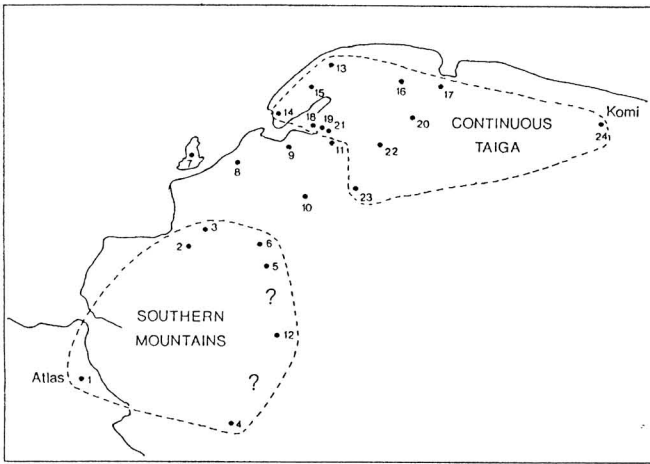


Fig. 4. The faunal similarity of the study areas according to the presence/absence data. The Czekanowski-Sørensen index of similarity was used for pairwise comparisons, and the result projected as a map of the western Palearctic. The numbers represent the study areas (Appendix 1 and Fig. 1). The coasts are drawn tentatively in order to help interpretation. The location of study area 12 is uncertain, as the projecting in two dimensions of its similarity relationships to other areas was not unequivocal.

(Järvinen & Väisänen 1980). While such zonation are real and interesting, another important but poorly known aspect is the pattern of variation in species assemblages within the same habitat type in different geographic regions. On the other hand, the definition of faunal types has to be habitat-specific in order to be reasonable at all. It would hardly make sense to let the definition of the taiga avifauna be affected by the distribution of the skylark or the snow bunting, denizens of entirely different environments!

In this paper we restrict ourselves to a Q-mode analysis and only compare areas with each other. An R-mode analysis comparing the distribution patterns of species is under progress.

### 5.1. Qualitative data

We first compared the localities based on the distribution matrix in Appendix 2. The analysis reveals compositional similarities of conifer bird faunas among the different study areas. For the comparison we used the Czekanowski-Sørensen index of similarity (recommended, for example, by Wolda 1981 and Pesenko 1982):

$$I = 2a / [(a+b) + (a+c)],$$

where  $a$  = the number of species common to both study areas, and  $b$  and  $c$  = the number of species found exclusively in one or the other of the areas. We calculated the index value for all pairwise comparisons, and compiled a map of the relative distances

among the localities by measuring the distance of each locality to the two closest geographical neighbours (starting from the pair Åland – southern Finland).

The resulting map is shown in Fig. 4. We expected considerable difficulties, but the compilation of the map was remarkably unambiguous and required little subjectivity, i.e., the relations among the localities can be summarized on a plane without major distortions. We preferred a map to an objective ordination because of the ease of comparison: differences between the maps in Fig. 1 and Fig. 4 show the most interesting patterns.

1. The conifer bird assemblages in the northern study areas are clearly more similar to each other in Fig. 4 than would be expected on the basis of geographical distances. In other words, the conifer bird fauna of the northern half of the taiga has a relatively similar species composition from northern Ural to northern Scandinavia. Southern Norway has close affinities with this zone, but it has close (hidden) connections to more southern localities as well.

2. The northernmost study areas form a continuum to southern Fennoscandia and Central Europe, where distances in Fig. 4 appear similar to those expected on the basis of Fig. 1, with the exception that central Russia and southern Ural bend very close to the localities near the Baltic and in Poland.

3. A relatively wide gap separates central Europe from the Alps and the Pyrenees, which form a coherent group on the map. Note that species number in



these study areas was quite similar to that in Central European areas, so the pattern is not a simple consequence of decreasing species numbers from north to south (cf. also Britain in Fig. 1 and Fig. 4).

4. The three localities in the far south, Corsica, Atlas and Caucasus, are relatively close to each other, but very distant from the other localities. The location of Corsica is particularly interesting: it has closer affinities with the southern mountains than with the Alps.

This grouping of the areas reflects the distribution patterns of the species: (1) a set of species ranges widely over the northern and central taiga (the Siberian faunal type of Stegman 1938), (2) another set of species is mainly restricted to the southwestern Palearctic (the European faunal type of Stegman 1938), whereas (3–4) the southernmost localities host a smaller subset of the total species pool but include some species peculiar to coniferous mountain forests (e.g. the citril finch *Serinus citrinella* and Corsican nuthatch *Sitta whiteheadi*). By and large the pattern agrees with Stegman's (1931, 1938, 1966) conclusion that spatial species turnover increases in the taiga avifauna from Siberia to southwestern Europe.

In principle the presence/absence matrix in Appendix 2 could be used for an R-mode analysis as well as for the Q-mode analysis presented in Fig. 4. There is a problem involved, however, concerning the representativeness of the study areas. A comparison among the localities is reasonable because our study areas represent, reasonably well, different distributional types of individual bird species. A comparison of the species, in contrast, would be problematic because similar *a priori* knowledge does not exist relative to the "geographic elements" over which the species are distributed. The row sums in Appendix 2 (and, consequently, the number of localities that any two species share) are naturally greatly influenced by the total number of localities as well as by their geographic locations.

## 5.2 Quantitative data

We made another comparison of the localities on the basis of the quantitative data sets (references in Appendix 1). It was far more complicated to map the relationships between the study areas on the basis of quantitative as opposed to qualitative data, because the pairwise comparison matrix could not so readily be represented on a plane. We used detrended corre-

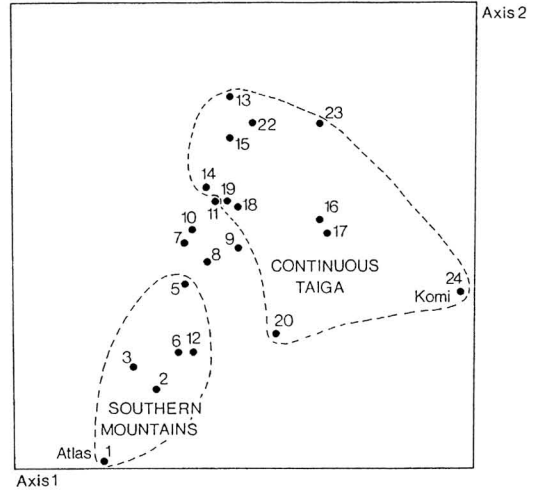


Fig. 5. Faunal relationships of the study areas according to the quantitative data. The pooled samples from each area were ordinated by the detrended correspondence analysis. The numbers represent the study areas (Appendix 1 and Fig. 1).

spondence analysis (DCA) (Gauch 1982) to make an ordination of the localities that shows their relative distances on a two-dimensional plot (only conifer birds included).

In Fig. 5 we show an ordination of the pooled data sets of 22 data localities. The first axis identifies a clear north-south gradient (eigenvalue 0.69); the second axis lacks a clear ecological interpretation, but its eigenvalue is only 0.11. Fig. 5 has some interesting similarities with Fig. 4. First, Central Europe and southern Fennoscandia form a tight group in the middle of the ordination, and with central Russia in the same group close to southern Fennoscandia. Second, northern Ural has its closest affinities to the Fennoscandian northern taiga (Kuusamo, Northern Sweden), but eastern Fennoscandia and southern Ural are relatively close as well. The border between northern/central taiga and the "European" localities is more diffuse in Fig. 5 than in Fig. 4, however. This may partly be a function of the scarcity of data localities in the taiga proper. The southern mountains from the Alps to the Atlas mountains merge into one loose group in Fig. 5 (in distinction to Fig. 4).

There is an important difference between Figs. 4 and 5: Central Europe is relatively much more compact in Fig. 5 than in Fig. 4. In other words, the bird species assemblages in Central European coniferous forests are quite similar in terms of quantitative composition, but there are differences in the species sets of conifer birds. The actual species assemblages ap-

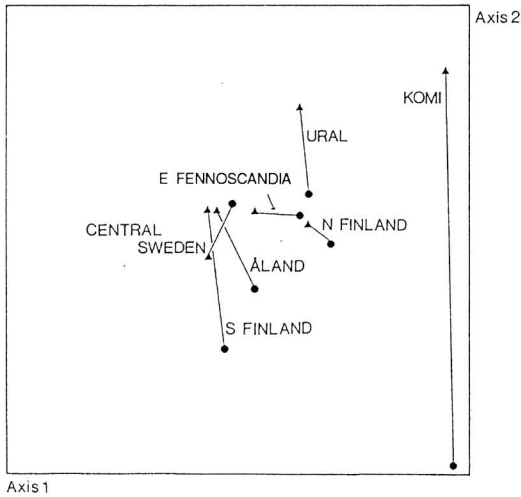


Fig. 6. The relative positions of the bird species assemblages in pine (circle) and spruce (triangle) habitats in the seven study areas where both habitat types were included in our data sets. The figure is based on a DCA ordination of all the study areas; the other areas are omitted from the figure for clarity, but the general structure is quite similar to the ordination in Fig. 5.

pear to differ less than the qualitative data based on distribution maps would suggest.

Next we made another DCA ordination of 29 data sets with the spruce and pine forests treated separately (Fig. 6). Again the first axis identifies a north-south gradient (eigenvalue 0.70), whereas the second axis (eigenvalue 0.24) is dominated by the pronounced difference between pine and spruce forests in the data from northern Ural.

There is important variation in the relations between pine and spruce forests at different localities. The difference is remarkably large in the data from northern Ural, caused mainly by the relatively high frequencies of such sedentary species of the taiga as the black grouse *Tetrao tetrix*, capercaillie *Tetrao urogallus*, three-toed woodpecker *Picoides tridactylus*, Siberian jay *Perisoreus infaustus* and rustic bunting *Emberiza rustica* in pine habitats, and of the nutcracker *Nucifraga caryocatactes*, waxwing *Bombycilla garrulus*, Siberian tit *Parus cinctus* and half a dozen scarce specialists in spruce habitats. A geographic trend may also be involved in this difference, as the northernmost and southernmost census localities of Estaf'ev (1981) were at a distance of about 400 km from each other.

In central taiga the communities in pine forests are very close to each other, whereas differences among spruce forest communities seem greater. The pine-

spruce gradient appears very similar in southern Finland and on the Åland Islands, while it is reversed in Uppland, although the geographical distances involved are very small.

The quantitative data are heterogeneous, and as we lack detailed habitat descriptions, an overinterpretation of the ordinations must be avoided. A comparison between Figs. 5 and 6 nevertheless suggests that the north-south zonation is similar, i.e., it seems to be relatively robust and not influenced by the heterogeneity in habitat structure or in census methods.

Note that in Fig. 6 the between-habitat difference is in many cases pronounced compared with the geographical differences. This is all the more striking as the comparisons between areas involve a between-observer comparison as well, whereas the pine and spruce forests at each locality were censused by the same person(s).

## 6. Guild patterns

It is evident from above that qualitative and quantitative data often give rise to different interpretations. Above all, presence/absence data tend to show more regular geographic patterns than the censuses.

The analysis has to be deepened to the level of individual species and their abundance variation over our study localities. Here the heterogeneity of the data becomes a problem; individual species are certainly influenced by such habitat variation that we cannot control in this data set. Using guilds, groups of species with similar resource requirements, we can resolve this difficulty to a certain extent.

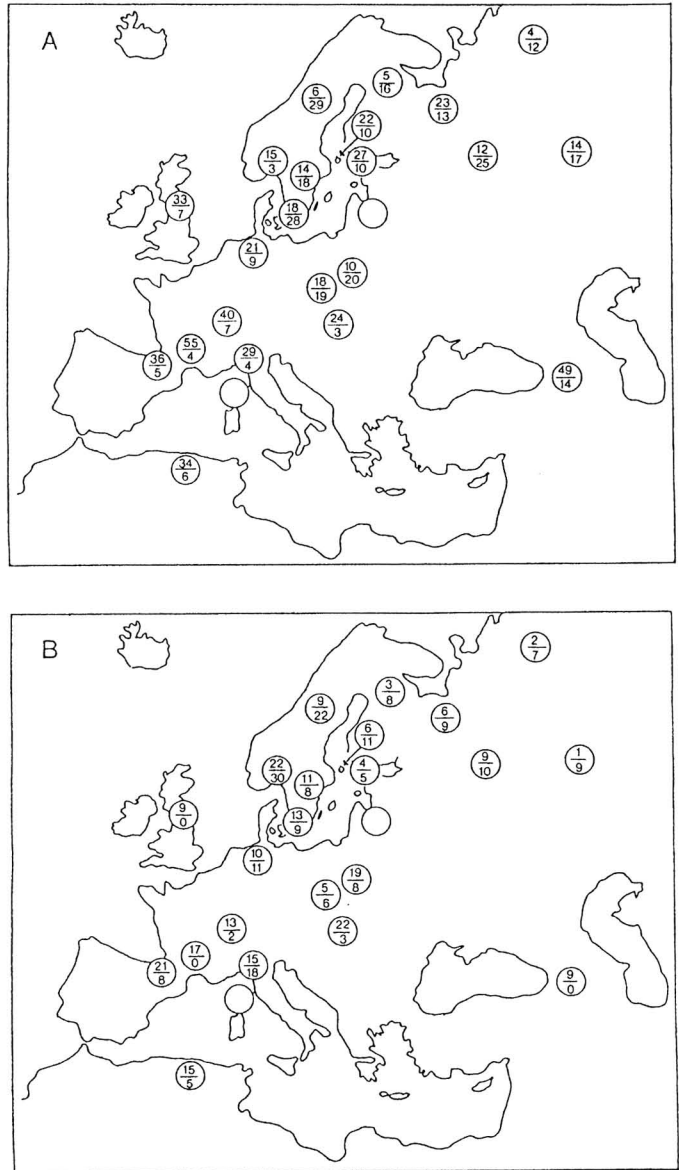
In Figs. 7A–B we show the proportion of some of the main feeding guilds over the localities: (1) *Parus* spp. and *Regulus* spp. (mainly sedentary foliage insectivores), (2) *Phylloscopus* spp. and *Sylvia* spp. (mainly migratory foliage insectivores), (3) small robin-like species (*Erithacus*, *Prunella* and *Troglodytes*), and (4) thrushes (*Turdus*). The following conclusions emerge.

1. There is huge variation in the frequencies even between close localities, e.g., in southern Scandinavia.

2. Some regional patterns exist, however. The following groups are relatively quite abundant in some regions: *Parus* in the southern mountains, *Phylloscopus* and *Sylvia* in the north, the small robin-like species in the south, and *Turdus* in the north. These patterns account for some of the broad patterns noticed above. For example, we observed that the



Fig. 7. The proportion of species belonging to the main feeding guilds in the pooled quantitative samples of each area. A. *Parus* spp. and *Regulus* spp. (upper figure) and *Phylloscopus* spp. and *Sylvia* spp. (lower figure). B. Small robin-like species (upper figure) and *Turdus* spp. (lower figure). Blanks indicate missing data.



proportion of conifer birds was high in the censuses made in the southern mountains, which is clearly due to the high frequency of *Parus* and *Regulus* there.

## 7. Concluding remarks

Traditionally biogeographical analysis has been based on qualitative data, but this has a clear drawback in ecological biogeography. Presence/absence

data allow a distinction between local and regional scales only if the patterns are striking, although it may be crucial in real ecological situations (e.g., Wiens et al. 1986, 1987). It is simply impossible to attribute unambiguous ecological significance to a species' "presence" in an area!

The analyses in this paper show clearly that census data may give a picture about biogeographic patterns that is not identical with, nor even similar to the one based on qualitative data.

Whittaker (1975) coined the terms alpha, beta and gamma diversity to diversity in local species assemblages, species turnover between assemblages, and diversity in a large region, respectively. Diversity studies have mainly dealt with the alpha component, and ecologists have tended to assume that factors controlling diversity operate at the alpha scale as well (for a US-biased overview, see Ricklefs 1987). Such a tendency may lead to a temptation to use species lists for characterizing local species assemblages. Quantitative data are nevertheless required for making clear distinctions between the different types of diversity.

Our analyses allow us to draw some conclusions about the explanatory power of unifying hypotheses that have been suggested for interpreting biogeographical patterns. The theory of island biogeography (and the related peninsular biogeography) propose that, owing to a decreased immigration rate, isolated areas support less species than less isolated areas do. Fig. 1 supports this idea, but only partially so, as discussed in Section 3. The distribution patterns of Eurasian taiga birds have their historical origin in the Pleistocene glaciations, and the patterns have not necessarily "equilibrated" to correspond with the present configuration of taiga islands and peninsulas (that the plant world has been in a remarkable flux all the time since the last glaciation has been conclusively shown by palaeobotanists; see, e.g., Huntley & Birks 1983, Birks 1985, 1986).

The contiguous taiga invites an interpretation in terms of peninsular biogeography, which predicts fewer species near the tips of peninsulas than at the base (Simpson 1964, Taylor & Regal 1978; cf. Taylor 1987). In this case the "mainland" would be the immense Siberian taiga. It is true that species numbers of conifer birds in Russia are greater than in Fennoscandia. However, the species numbers are high in western Russia, and the westward decrease in the number of Siberian species seems to be more or less compensated by western species not extending particularly far to the east (cf. Appendix 2).

Habitat factors may also play a role in continental "peninsulas". Thus, Haila (1983) attributed the faunal impoverishment of forest bird communities in northern Scandinavia to the lack of spruce forests, which extend to the subarctic in northwestern Russia.

The problems with the predicted effects of (pen)insularity on the distribution patterns of conifer birds may be connected with the migration patterns of different species. This suggestion follows from Fig.

7 which shows that there are clear differences in the relative densities of different species groups that also tend to have different migration patterns (e.g. *Parus* and *Regulus* either sedentary or, in the north, short-distance migrants, but *Phylloscopus* and *Sylvia* are mostly long-distance migrants). As the migration patterns of different populations of the same species frequently vary in Europe, we have not followed this lead further, but the problem needs further study. Also, it has to be born in mind that many species live in the western part of the taiga "peninsula" or in the isolated taiga "islands" only during part of the year, which reduces the explanatory power and credibility of the immigration-extinction model of the theory of island biogeography.

Another explanation that has been offered widely in the context of ecological biogeography is the theory of interspecific competition. As shown in Section 4, and as is evident from a comparison of Figs. 1 and 3, other species do not seem to compensate for the conifer birds missing from many southern assemblages. To the contrary, conifer birds comprise quite high proportions of individuals in assemblages in coniferous habitats in the south, although their proportion in the regional species pool is lower than in the north (Fig. 3).

One example suggesting negative interactions between taxa is provided by Fig. 7A. The correlation between the proportions of *Parus* spp. and *Phylloscopus* spp. is statistically significant ( $r = -0.55$ ,  $P < 0.01$ ,  $df = 19$ ). Moreover, both Ulfstrand (1976) and Nilsson & Ebenman (1981), in studies of local assemblages in southern Sweden, have considered it possible that intergeneric competition occurs between at least some species in the two genera. Inferences of process from pattern fail to convince, however, for the simple reason that alternative explanations are difficult to exclude. For example, the two genera have quite different migrating patterns, as noted above. We regard it as highly plausible that the seasonal distribution of food resources available for foliage insectivores is quite different in the southern and northern parts of the western Palearctic. In particular, the availability of food is poor in the north during the long, dark, and cold winter. On the other hand, the resource peak there during the summer may be perfectly adequate for many long-distance migrants that stay only a few months in the north. The theme was elaborated by Herrera (1978).

One important point still requires attention. Human-caused changes in the forest environment are

known to affect the quantitative composition of the bird species assemblages very much (Helle & Järvinen 1986 and references there). But the qualitative composition of the faunas is also affected by human-caused environmental changes (see, for example, Järvinen & Ulfstrand 1980), so it is not clear whether human effects are greater in analyses based on qualitative or quantitative data.

Our exploration has only begun. The next step is evidently an R-mode analysis to examine the similarities of the distribution patterns of the species based

on qualitative and quantitative data. Due to limited space, this analysis will be postponed to a later paper.

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Appendix 1. Descriptions of the 24 study areas (geographical location, distance from continuous taiga, percentage (20 % accuracy) of area of coniferous forests within 200 km). The census data sets follow their respective areas. Mixed forest: P = mainly pine, S = mainly spruce, C = coniferous, D = deciduous. Mapping? = borderline case.

Study area Census data sets	Forest habitat	Method	Area (ha)	No. of species	Sample size	Reference
1. Atlas (36°00'N, 5°00'E, 2300 km, 0 %) Ifrane and Daïet-Hachlaf, Central Plateau, Morocco	MixedC	I.P.A.	15	24	114	Thevenot 1979
2. Pyrenees (43°00'N, 0°30'E, 1750 km, 20 %) Spanish Pyrenees	Pine Spruce	Line transect Line transect	106 82	19 38	357 950	Purroy 1974
3. Southern France (45°00'N, 4°00'E, 1450 km, 20 %) Massif du Pilat, Loire, France	Spruce	Mapping	12	10	80	Lebreton et al. 1971
4. Corsica (42°30'N, 9°00'E, 1500 km, 0 %) No census data found that would allow our analyses						
5. Alps (46°00'N, 10°30'E, 1100 km, 20 %) Lenk, Bernese Oberland, Switzerland	Spruce Spruce Spruce	Mapping Mapping Mapping	14 12 15	30 22 17	91 115 86	Luder 1981
Chalet à Roche, Vaud, France	Spruce	Mapping	68	20	167	Catzeflis 1979
Solothurn – Herzogenbuchsee – Büren, Switzerland	Spruce	Mapping	14	31	163	Christen 1983
6. French Alps (48°00'N, 7°00'E, 1050 km, 0 %) Regensburg, FRG	Pine Spruce Spruce	Mapping Mapping Mapping	10 10 5	16 22 11	51 58 20	Vidal 1975
Vosges du Nord, Philippsbourg, France	Pine	Mapping + I.P.A.	125	33	752	Muller 1981
7. Britain (55°30'N, 2°30'W, 600 km, 20 %) Central Highland, UK	Pine	Study plot	10	11	129	Watson 1969
8. Northern Germany (53°00'N, 9°00'E, 500 km, 0 %) Hermannsburg, Lüneburger Heide, FRG	Pine Pine MixedP	Mapping Mapping Mapping	194 93 113	29 32 34	326 232 476	Dierschke 1973
Uhyst, Kreis Hoyerswerda, GDR	Pine	Mapping	30	23	77	Socher 1983
Spandauer Forst, Berlin (West)	MixedP	Mapping	37	25	253	Witt 1974
9. Southern Poland (51°00'N, 18°30'E, 350 km, 40 %) Sobibor Landscape Park, Chelm, Poland	Pine	Mapping	25	21	96	Cieslak 1984
Niepolomice Forest, near Cracow, Poland	Pine	Mapping	8	23	50	Glowacinski & Weiner 1980
Legnica, Lower Silesia, Poland	MixedP MixedP	Mapping? Mapping?	10 15	31 28	92 78	Tomialojc 1974
10. Hungary (48°00'N, 20°00'E, 600 km, 0 %) Ore Mountains, Bohemia, Czechoslovakia	Spruce	Mapping	22	17	76	Stastny & Bejcek 1985
11. Northern Poland (52°30'N, 22°00'E, 100 km, 40 %) Bialowieza National Park, Poland	Pine MixedCD	Mapping Mapping	50 32	22 21	176 108	Tomialojc et al. 1984

Study area Census data sets	Forest habitat	Method	Area (ha)	No. of species	Sample size	Reference
12. Caucasus (41°30'N, 44°30'E, 1450 km, 20 %) Lake Gek-gelji, Azerbaidzhan, USSR	Pine	Line transect	10	8	88	Drozдов 1965
13. Southern Norway (60°00'N, 10°00'E, 0 km, 60 %) Sörkedalen, near Oslo, Norway	Spruce	Mapping	15	12	114	Fremming & Slagsvold 1966, 1967
Baerum, near Oslo, Norway	Spruce	Mapping	28	27	119	Hogstad 1967/68
14. Southern Sweden (56°30'N, 14°00'E, 0 km, 40 %) Stensoffa Ecol. Station, Krankesjön, Sweden	Pine	Mapping	6	15	31	Svensson 1975a
Marsholm, Lake Möckeln, Sweden	Spruce	Mapping	3	12	25	
	Spruce	Mapping	16	34	232	Nilsson 1980
	Spruce	Mapping	7	24	64	
15. Central Sweden (59°00'N, 15°00'E, 0 km, 80 %) Grimsö, Sweden	Pine	Mapping	31	18	51	Svensson 1975b
	Pine	Mapping	33	8	16	
	Pine	Mapping	53	17	63	
	Spruce	Mapping	12	11	23	
	Spruce	Mapping	39	24	87	
Fyrholmen, Karlstad	Pine	Mapping	26	32	159	Svensson 1972
Dösjön, Gnarp + Järva sumpskog, Järvafältet, Sweden	Spruce	Mapping	39	29	137	
16. Northern Sweden (65°00'N, 16°30'E, 0 km, 80 %) Ammarnäs, Sweden	MixedS	Mapping	83	19	115	Svensson 1972
17. Northern Finland (66°00'N, 29°00'E, 0 km, 100 %) Oulanka, Kuusamo, Finland	Pine	Line transect	115	21	100	Helle 1985
	Spruce	Line transect	68	27	109	
18. Åland Islands (60°00'N, 20°00'E, 0 km, 40 %) Åland, Finland	Pine	Line transect	86	33	166	Haila et al. 1980
	Spruce	Line transect	98	39	382	
19. Southern Finland (60°00'N, 23°00'E, 0 km, 40 %) Hanko Peninsula, Finland	Pine	Line transect	272	25	432	Raivio 1986
	Spruce	Line transect	218	36	660	
20. Eastern Fennoscandia (63°00'N, 33°00'E, 0 km, 100 %) Kivach Natural Park, Karelian ASSR, USSR	Pine	Line transect	250	34	543	Ivanter 1962
	Spruce	Line transect	1000	40	2904	
Kuopio, Finland	Pine	Study plot	58	21	102	Mönkkönen 1984
	Spruce	Study plot	88	27	196	
21. Baltic Republics (56°30'N, 25°00'E, 0 km, 80 %) No census data found that would allow our analyses						
22. Central Russia (59°30'N, 42°00'E, 0 km, 100 %) Kostromskij and Moskovskij oblastj, near Moscow, USSR	MixedC	Line transect	600	41	1342	Butjev 1970
	MixedC	Line transect	725	49	1825	
River Uchi, near Moscow, USSR	Spruce	Line transect	450	53	1818	Babenko & Konstantinov 1983
Tambovskij oblastj, Morshanskij raion, USSR	Pine	Line transect	230	45	1037	Šegolev 1978
23. Southern Ural (56°00'N, 55°30'E, 0 km, 60 %) Sverdlovskij oblastj, Sysertsij raion, USSR	Pine	Study plot	178	29	326	Danilov 1966
	Spruce	Study plot	50	14	324	
Sverdlovskij oblastj, Polevskij raion and Visimskij raion, USSR	Pine	Line transect	300	30	647	Danilov 1958
	Pine	Line transect	100	19	326	
	Spruce	Line transect	100	18	165	
24. Northern Ural (65°00'N, 58°00'E, 0 km, 80 %) River Pechora, Komi ASSR, USSR	Pine	Line transect	100	27	448	Estaf'ev 1981
	Pine	Line transect	1000	33	1242	
	Pine	Line transect	1000	26	2790	
	Pine	Line transect	1000	30	2349	
	Spruce	Line transect	100	44	630	
	Spruce	Line transect	1000	41	2228	
	Spruce	Line transect	1000	54	3031	

Appendix 2. Presence (1)/absence (0) matrix of birds of coniferous forests in different study areas.

Species	Area																								Total areas
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Accipiter gentilis</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	23
<i>A. nisus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	24
<i>Tetrao urogallus</i>	0	0	0	0	1	1	0	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	16
<i>T. tetrix</i>	0	0	0	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	18
<i>Bonasa bonasia</i>	0	0	0	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	17
<i>Tringa erythropus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2
<i>T. ochropus</i>	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	16
<i>Scolopax rusticola</i>	0	1	1	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	20
<i>Columba palumbus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	23
<i>Cuculus saturatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2
<i>Asio otus</i>	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1*	1	1	1	1	1	0	21
<i>Glaucidium passerinum</i>	0	0	0	0	1	1	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	0	15
<i>Aegolius funereus</i>	0	1	1	0	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	18
<i>Surnia ulula</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	7
<i>Strix aluco</i>	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1*	1	0	1	1	1	0	19
<i>S. nebulosa</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	6
<i>S. uralensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	8
<i>Caprimulgus europaeus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	21
<i>Dryocopus martius</i>	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1*	1	1	1	1	1	1	21
<i>Picoides tridactylus</i>	0	0	0	0	1	1	0	0	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	15
<i>Dendrocopos major</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	24
<i>Picus canus</i>	0	0	1	0	1	1	0	0	1	1	0	1	0	1	0	1	0	0	1	1	0	1	1	0	13
<i>P. vaillanti</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Anthus trivialis</i>	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	21
<i>A. hodgsoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Bombycilla garrulus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	5
<i>Prunella modularis</i>	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1*	1	1	1	1	1	0	21
<i>Phylloscopus bonelli</i>	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>P. borealis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	4
<i>P. collybita</i>	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1*	1	1	1	1	1	1	21
<i>P. trochiloides</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1*	1	1	1	1	1	0	7
<i>P. nitidus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>P. inornatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Regulus ignicapillus</i>	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
<i>R. regulus</i>	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	21
<i>Ficedula parva</i>	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	1*	1	1	1	1	1	0	12
<i>Muscicapa striata</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	24
<i>Phoenicurus phoenicurus</i>	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	23
<i>Erithacus rubecula</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	23
<i>Tarsiger cyanurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	4
<i>Turdus viscivorus</i>	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1*	1	1	1	1	1	0	23
<i>T. pilaris</i>	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	19
<i>T. philomelos</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1*	1	1	1	1	1	0	22
<i>Parus cristatus</i>	0	1	1	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1*	1	1	1	1	1	0	19
<i>P. ater</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	23
<i>P. lugubris</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>P. cinctus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	3
<i>P. montanus</i>	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1*	1	1	1	1	1	0	19
<i>Sitta ledanti</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>S. whiteheadi</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>S. krüperi</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Certhia familiaris</i>	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	21
<i>Troglodytes troglodytes</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	22
<i>Emberiza rustica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	5	
<i>Fringilla montifringilla</i>	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	1	9
<i>Pyrrhula pyrrhula</i>	0	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	21
<i>Serinus citrinella</i>	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
<i>Carduelis spinus</i>	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	21
<i>C. flammea</i>	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	1	0	1	11
<i>Loxia curvirostra</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	23
<i>L. pytyopsittacus</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1*	1	1	1	1	0	1	11
<i>L. leucoptera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2
<i>Pinicola enucleator</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	4
<i>Nucifraga caryocatactes</i>	0	0	0	0	1	1	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1	1	0	13
<i>Garrulus glandarius</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	23
<i>Perisoreus infaustus</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1	0	1	1	1	7
Total species	19	30	32	17	41	39	28	33	40	39	40	28	40	35	38	43	45	40	42	50	41	51	45	29	

\* Breeds on Åland (Haila et al. 1979) even if missing from Harrison's (1982) map.

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