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R-mode analysis of taiga bird distributions: comparison between qualitative and quantitative data

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The distribution patterns within qualitative presence/absence and quantitative census data were compared in an R-mode analysis of birds breeding in coniferous forests of the western Palearctic. R-mode analysis groups species with similar distributions into faunal types. Both data sets were collected from the literature and analysed by detrended correspondence analysis (DCA). The proportions of Siberian and European faunal types in single study areas were also calculated.

The DCA-ordination of the presence/absence data showed a clear gradient from north to south, species of Siberian and European faunal types forming their own groups in the ordination. The ordination of the census data did not group species belonging to the same faunal type as clearly as the analysis of qualitative data. Instead, there was considerable overlap between the distributions of Siberian and European faunal types. Palearctic and Holarctic species were distributed all over the study area in both analyses.

The presence/absence data tended to overestimate the proportions of Siberian faunal type and underestimate the proportions of European faunal type in regional bird communities compared with the quantitative data.

The concept of faunal type is discussed in relation to qualitative and quantitative data, as well as to different scales of investigation.

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1. Introduction

Biogeographic studies are traditionally based on qualitative presence/absence data (e.g. Lehtonen 1951, Hagmeier & Stults 1964, Proctor 1967, Fisher 1968, Holloway & Jardine 1968, Kikkawa & Pearse 1969, Baroni Urbani & Collingwood 1976, 1977, Birks 1976, Williams 1982, Smith 1983, Topham & Alphey 1985). Species lists have been collected from mainland areas or islands without paying any attention to the abundances of different species. In such lists thousands of individuals of an abundant species are thus considered equal to a few individuals of a rare bird. This is definitely a source of bias, especially if the results are used in influencing conservation policies. Because every species has its specific abundance, which, moreover, varies in space and time, quantitative data seem to describe faunas of different areas better than qualitative data (Järvinen & Väisänen 1973, 1980, Smith & Powell 1971, Bock et al. 1977, 1978, Haila & Järvinen 1981, 1983, Haila et al. 1983, Järvinen & Haila 1984, Haila et al. 1987a).

Two approaches have been used in analysing distribution patterns; so called Q- and R-mode analyses (e.g. Simberloff & Connor 1979). Q-mode analysis compares areas according to their faunas resulting in zoogeographic regions of different rank, while R-mode analysis groups species with similar distributions into faunal elements. Q- and R-mode analyses correspond to those used by Proctor (1967), i.e. "normal" and "inverse" analyses respectively. In this paper I present the results of an R-mode analysis based on qualitative and quantitative data sets of birds breeding in the western Palearctic taiga. This is the "next step" mentioned by Haila et al. (1987a) in our Q-mode analysis of the same data.

The term faunal element is used for different purposes by different authors, but traditionally it refers to groups of taxa that share not only a common distribution, but also a common origin and evolutionary history (Birks 1987). Here faunal elements are regarded as faunal types, which are defined according to Voous (1960; see also Stegmann 1938). Voous (1960, 1963) emphasizes the importance of present distributions when defining faunal types: "To say that a species is of a particular faunal type means that it is a characteristic element of the regional fauna indicated. The characters of a regional fauna result from the habitats afforded in the range covered."

This paper is primarily an analytic data exploration (sensu Birks 1987) comparable to its predecessor (Haila et al. 1987a). The aim of the study is to compare the patterns within the qualitative and quantitative data sets in the distribution patterns of bird populations.

2. Material and methods

The study area, the western Palearctic taiga, and the data used in the analyses are the same as in Haila et al. (1987a), where detailed descriptions are given. Coniferous forests range from the immense Eurasian taiga to isolated forest patches in southern Europe and the mountains of North Africa. In an area bounded by the Ural mountains in the east and the Atlas Range in the southwest, we compiled lists of conifer species breeding in the 24 study areas (Fig. 1) using the distribution maps of Harrison (1982). "Conifer birds" were defined according to two handbooks (Heinzel et al. 1974, Harrison 1982). Only those species described explicitly in either source as breeding in coniferous forests were included in our list. All other forest dwelling species were classified as "forest species".

The quantitative bird census data were collected from published sources available to us at the University of Helsinki library. We tried to find quantitative census data from all the 24 areas, but because of a lack of suitable data, areas 4 (Corsica) and 21 (Baltic Republics) had to be excluded. In cases where it was not possible to obtain census data from the same areas as the qualitative data, data from nearby areas were used. This means, that e.g. the quantitative data set not available in Hungary (study area 10) was obtained beyond the border from Czechoslovakia, and the data from eastern Fennoscandia (area 20) include censuses performed in eastern Finland and Russian Karelia.

The scale of any ecogeographical study is of immense importance (Wiens 1981, 1986, Wiens et al. 1986, Birks 1987). The results obtained from one scale, whether spatial or temporal, do not necessarily hold for other scales. By analysing data from large geographical areas one can detect only rough patterns, which neglect the variation in smaller areas. If there are many samples from a small area and only a couple from surrounding areas, the importance of those clumped samples will be overestimated (Kikkawa & Pearse 1969, Birks 1987). In this paper the distribution of study areas was dictated by the availability of quantitative data. The western Palearctic taiga is too vast an area to be sampled thoroughly, but I think that the area is well enough represented in these data to reveal the major patterns.

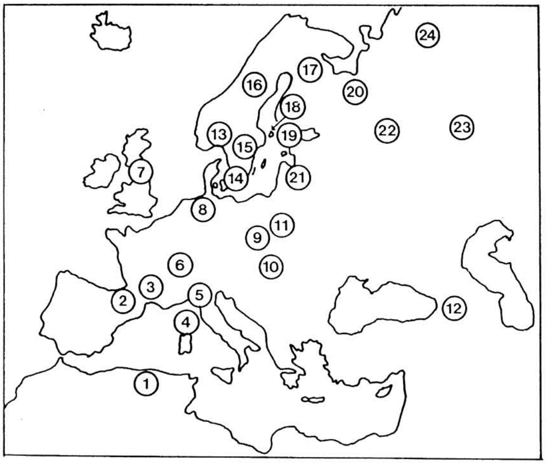

Fig. 1. Study areas: 1 = Atlas, 2 = Pyrenees, 3 = Southern France, 4 = Corsica, 5 = Alps, 6 = French Alps, 7 = Britain, 8 = Northern Germany, 9 = Southern Poland, 10 = Hungary, 11 = Northern Poland, 12 = Caucasus, 13 = Southern Norway, 14 = Southern Sweden, 15 = Central Sweden, 16 = Northern Sweden, 17 = Northern Finland, 18 = Åland Islands, 19 = Southern Finland, 20 = Eastern Fennoscandia, 21 = Baltic Republics, 22 = Central Russia, 23 = Southern Ural, 24 = Northern Ural.

The traditional way of performing an R-mode analysis is to collect distributional data from a study area after which species distributions resembling each other are grouped together by qualitative (Lehtonen 1951) or numerical methods (Holloway & Jardine 1968, Kikkawa & Pearse 1969, Birks 1976, Williams 1982, among others). Resulting faunal elements of various hierarchial ranks are then characterized usually on the basis of their common ecology and/or history (e.g. Holloway & Jardine 1968, Kikkawa & Pearse 1969, Holloway 1973, Birks 1976).

My approach is a methodological one. In order to compare the different distribution patterns within the qualitative and quantitative data sets, I performed a detrended correspondence analysis (DCA, Hill 1979, Hill & Gauch 1980, Gauch 1982) on both data sets. Computing was done using the Cornell Ecology Program DECORANA (Hill 1979).

DCA has lately been criticized. Wartenberg et al. (1987) attacked the detrending and rescaling procedures (Hill 1979, Hill & Gauch 1980, Gauch 1982), which eliminate the arch effect (e.g. Gauch et al. 1977, Williamson 1978) artificially. These procedures can also be the reason for marked distortions in DCA-ordinations observed by Minchin (1987), when more complex data response models and non-regular sampling schemes were used in a simulation study. However, all multivariate methods are more or less affected by distortions. Because this study is not strictly hypothesis-testing but is more concerned with a description of patterns, I consider the method adequate for this purpose.

I did not try to find any faunal elements of my own, but labeled each species with its faunal type according to Voous (1960). Then I checked whether species in these data were distributed in discrete faunal types. The faunal types used were the European, Siberian, Holarctic and Palearctic faunal types of Voous (1960). The two last mentioned were pooled, because their wide distributions do not make any difference in this context. The only representative of Old World faunal type (golden oriole *Oriolus oriolus*) is included in this group. The European faunal type contains the group European-Turkestanian and the Siberian faunal type the group Siberian-Canadian. There are also some species not defined in Voous (1960). They were pooled with the few representatives of minor groups, e.g. Paleomontane (citril finch *Serinus citrinella*) and Chinese-Manchurian (oriental cuckoo *Cuculus saturatus*).

3. Results

3.1. Qualitative data

In the detrended correspondence analysis of the presence/absence data (Fig. 2) only conifer birds were included. The eigenvalue of the first axis was 0.245, and of the second axis only 0.099. Among others, the olive-backed pipit (*Anthus hodgsoni*), yellow-browed warbler (*Phylloscopus inornatus*), spotted redshank (*Tringa erythropus*), pine grosbeak (*Pinicola enucleator*) and arctic warbler (*Phylloscopus borealis*) form the other end of the first axis. All these species are clearly of Siberian distribution, although the two first mentioned cannot be found in Voous (1960). At the opposite end of the axis species distributed in the southern mountains, Levaillant's woodpecker (*Picus vaillanti*), Kabylie nuthatch (*Sitta ledanti*), Corsican nuthatch (*Sitta whiteheadi*), Krüper's nuthatch (*Sitta krüperi*), greenish warbler (*Phylloscopus nitidus*) and citril finch (*Serinus citrinella*), are typical. The first axis thus corresponds to a gradient from southern to northeastern distributions.

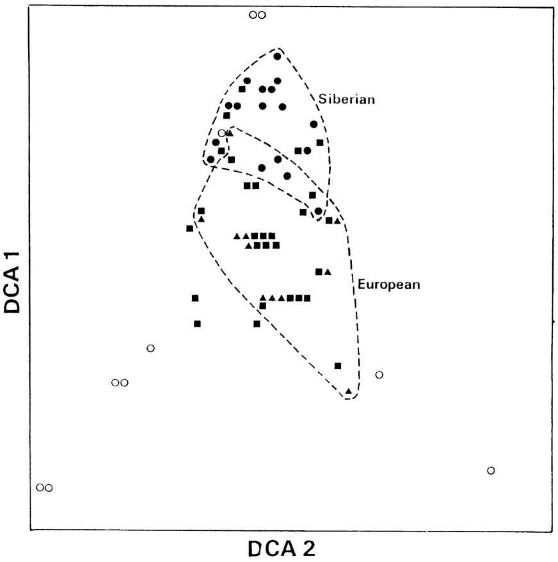

Fig. 2. DCA-ordination of the qualitative presence/absence data. Symbols represent the following faunal types: ● = Siberian, ▲ = European, ■ = Palearctic/Holarctic, ○ = minor groups/unknown.

In the ordination the species of Siberian and European faunal types form their own groups. The Siberian species are concentrated in the taiga proper (Ural, Central Russia and northern Fennoscandia), while in southern Scandinavia and Central Europe, most of the species are of European faunal type. The difference between these two groups is evident, as only one European species, the parrot crossbill (*Loxia pytyopsittacus*), intrudes among the species of Siberian faunal type.

Palearctic and Holarctic species (e.g. willow tit *Parus montanus*, goshawk *Accipiter gentilis*, treecreeper *Certhia familiaris*, common crossbill *Loxia curvirostra*, tawny owl *Strix aluco*) are distributed all over the study area, being a slightly more dominant group in the southern parts of the study area.

The small group of species distributed in the southern mountains form their own group in the ordi-

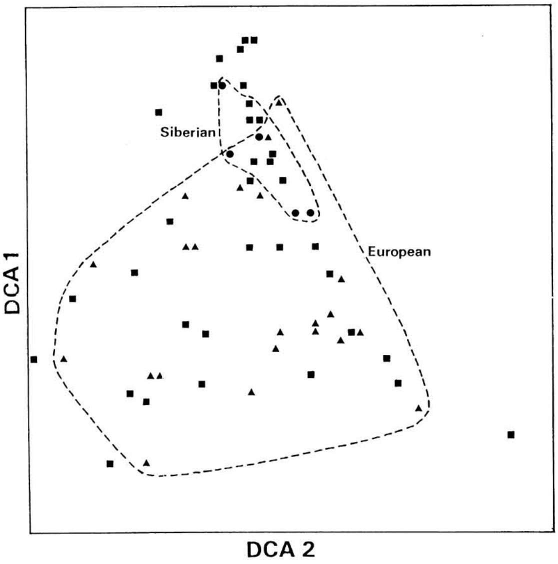

Fig. 3. DCA-ordination of the quantitative census data. Symbols as in Fig. 2.

nation. All these species have very restricted distributions and cannot be attributed to clear faunal types (except the citril finch) according to Voous (1960).

The main pattern did not change when rare species (present in fewer than three and five areas respectively) were omitted: The Siberian and European species still form distinct groups of their own. The species distributed in the southern mountains and those of unknown faunal type are thus lacking because of their scarcity.

However, the analyses of the qualitative data have an air of circularity, because faunal types as such are defined on the basis of distributions. The problem will be discussed further later on.

3.2. Quantitative data

In the DCA-ordination of the census data (Fig. 3) I included all species that were met in at least five areas to avoid distortions in the ordination by extreme outliers. No other transformations were made. To use all the observed species, instead of only conifer ones in the analysis, gives a more realistic picture of the composition of actual bird communities in the taiga.

The eigenvalue of the first axis was 0.461. The extreme ends of the axis were dominated by species like the redpoll (*Carduelis flammea*), swift (*Apus apus*), white wagtail (*Motacilla alba*), common crossbill (*Loxia curvirostra*), capercaillie (*Tetrao urogallus*) and brambling (*Fringilla montifringilla*) on the one hand, and the short-toed treecreeper (*Certhia brachydactyla*), firecrest (*Regulus ignicapillus*), marsh tit (*Parus palustris*), blue tit (*Parus caeruleus*) and blackbird (*Turdus merula*) on the other. The distributions of these species form a gradient from north to south, corresponding to study areas from the Urals and northern Scandinavia to southern mountains in France, Spain, Caucasus and North Africa. At the northern end of the gradient only the brambling is of Siberian faunal type, all the others representing Holarctic or Palearctic distributions. The swift and white wagtail are not typical species of northern forests, but in these data they abound in the northeasternmost study areas. At the other extreme of the gradient, species are of European or Holarctic/Palearctic faunal types. The eigenvalue of the second axis was only 0.069, and it mainly reflects the faunal differences between the Caucasus and other southernmost study areas.

The ordination of the census data does not group species belonging to the same faunal type as clearly as the previous analysis; instead, there is more overlap between the distributions of Siberian and European faunal types. Still, the former are concentrated in the northern taiga and the latter in Central and southern Europe. Species of Holarctic and Palearctic faunal types are distributed all over the study area resembling the ordination of the qualitative data. The small group of species distributed in the southern mountains is lacking from the ordination, because the species were not encountered in any of the censuses or their numbers were too low to be included in the analysis.

3.3. Proportions of different faunal types in study areas

The proportions of Siberian and European faunal types in single study areas according to the qualitative and quantitative data sets are shown in Figs. 4 and 5. In both analyses only conifer birds were used. In the census data the figures represent proportions among all *pairs* of conifer birds, while in the presence/absence data the only possibility was to calculate the proportions of different faunal types among all conifer *species*. The proportions of conifer birds among all forest birds in the census data can be found in Fig. 3 of Haila et al. (1987a).

The proportions of species of Siberian faunal type (Fig. 4) in the quantitative data are generally much

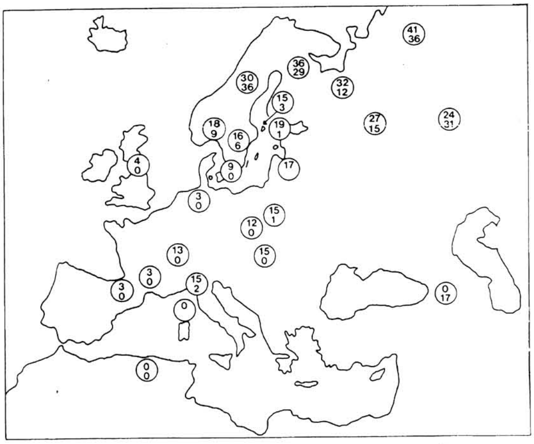

Fig. 4. Proportions of Siberian faunal type at each study area according to the distribution maps (upper figure) and the census data (lower figure). Blanks indicate missing data.

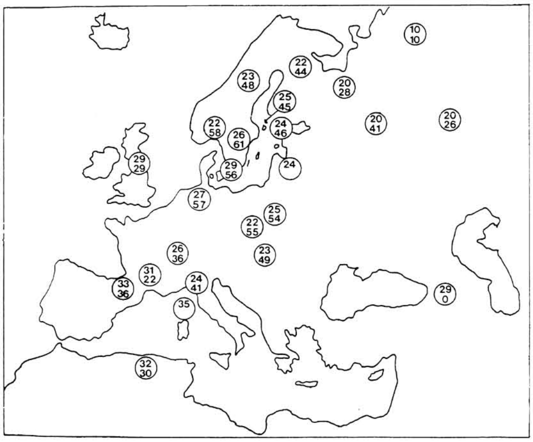

Fig. 5. Proportions of European faunal type in each study area according to the distribution maps (upper figure) and the census data (lower figure). Blanks indicate missing data.

smaller, with only a few exceptions (areas 12, 16, 23), than in the qualitative data. Only in the northernmost study areas in the contiguous taiga, where the species of Siberian faunal type form a rough third of the regional bird communities, are the proportions approximately of the same order of magnitude in both data sets.

The proportions of European species (Fig. 5) show an opposite trend as the proportions are mostly much higher in the quantitative than in the qualitative data. Study area 12 is an extreme case with the proportions of Siberian and European faunal types being quite opposite, depending on which of the data sets is analysed. This may be partly due to inaccuracies in distribution maps.

4. Discussion

4.1. Qualitative versus quantitative data

As ecological processes in nature are far more complex than mere presences and absences of species, one would expect that distribution patterns produced by quantitative data would also be more complex than those based on presence/absence data. The results of the DCA-ordinations confirm this expectation. The patterns produced by the qualitative versus quantitative data sets resemble each other in broad outline, but there are also important differences. The ordination of the quantitative data is not so simple as those of the presence/absence data. This means that the distribution patterns of species of different faunal types are not so clear in nature as expected on the basis of qualitative data. Instead, the faunal types overlap broadly even in the geographic extremes of the study area.

Biogeographic analyses with quantitative data are rare. Pitelka (1941) was among the first to discuss the distribution patterns of certain groups of birds on the basis of quantitative data. He underlined the importance of knowing relative abundances, and therefore, the relative importance of different species in communities.

Bock et al. (1978) demonstrated in their study of fringillid distributions in North America that abundance data showed certain areas as larger and more distinctive compared with those obtained from presence/absence data, which emphasized the extent and patchiness of some regions. The data of Bock et al. (1978) derive from the results of Christmas bird counts, which include the numbers of each species observed and the number of party-hours as a measure of total census effort. In an earlier paper, also based on Christmas bird counts, Bock et al. (1977) analysed the distribution patterns of some bird species wintering on the Great Plains of the USA. There is also a clear difference between the qualitative (Lehtonen

1951) and quantitative (Järvinen & Väisänen 1973, 1980) ornithogeographic zonation of Finland.

Other animal groups are poorly represented in the literature, but the results of e.g. Smith & Powell (1971; see Echelle & Schnell 1976) seem similar. In their study of fish species distributions they concluded that presence/absence data were adequate for broad geographic analyses, but quantitative data were needed for more fine-grained studies.

4.2. Effects of habitat structure

The use of quantitative data is not the only reason for the observed differences in distribution patterns, but habitat structure can also influence the results. Conifer forest as a habitat type is a broad concept. The proportion and age structure of different tree species, foliage cover, density of shrub layer and other factors certainly vary among study areas, and consequently regional bird faunas are also different. The heterogeneity of habitats can explain the abundance of, e.g., the scarlet rosefinch (*Carpodacus erythrinus*), lesser whitethroat (*Sylvia curruca*) and whitethroat (*S. communis*) in censuses of coniferous forests in the easternmost study areas. All these species are usually elements of more open and bushy habitats than of closed climax forests. The abundance of the white wagtail and swift in the same study areas also suggests the effects of habitat structure.

The habitat composition of surrounding areas also has an effect on the bird community of a single study area (Haila et al. 1987b). Coniferous forests surrounded by large clear-cuts are more likely to have species preferring open habitats compared with study areas surrounded by large tracts of forest. This can influence the proportions of different faunal types, because their proportions usually differ between habitats (cf. Voous 1960, 1963, Järvinen 1985).

The heterogeneity of habitats is inevitable, not least because of the fact that we had to rely on habitat descriptions given by the authors when collecting the census data. Natural and also human-modified habitats are always patchy on one scale or another. However, there is no way to demonstrate whether the differences in habitat structure or in the regional composition of habitat types affect the patterns observed.

4.3. On the concept of faunal type

Faunal types are traditionally defined on the basis of global distributions of species. Thus, the exact testing of faunal types — whether they are real or not — leads to circularity of reasoning, if the same area is analysed with qualitative data. However, it is interesting, and legitimate, to analyse the relations of faunal types in more restricted areas, like the western half of the Palearctic or regional study areas.

Stegmann (1938; map also in Udvardy 1969) represents his faunal types in the whole Palearctic as a gradual transition from the southern to the northeasternmost faunal types. Darlington (1957) has the same idea on a larger scale, when describing the transition between e.g. Afrotropical and Palearctic regional faunas. When only the western half of the Palearctic is analysed on the basis of presence/absence data, the transition between European and Siberian faunal types is very abrupt (Fig. 2). The ordination of quantitative data are in better accordance with the original scheme of Stegmann (1938), as the different faunal types overlap broadly (Fig. 3). Stochasticity may play an important role in qualitative data, because range boundaries are difficult to draw when the marginal populations are sparse. Thus, qualitative data may greatly overestimate the importance of rare species.

On finer scales the qualitative data are even more likely to be affected by stochasticity. This is shown by the great differences in the proportions of European and Siberian faunal types in single study areas when the results of qualitative and quantitative data are compared (Figs. 4 and 5). The qualitative data overestimate the proportions of Siberian species, which are mostly rare in the western Palearctic, and underestimate those of European species (mostly common) in these regional bird communities.

The results correspond well with those obtained by Blondel et al. (1978) in France: European, Palearctic and Holarctic species were much more important in regional communities when analysed on the basis of quantitative census data as compared with qualitative species lists.

Allowing for the abundances of different species and thus for their importance in regional communities as well as on broader scales, quantitative data seem to be more useful in defining avian faunal types, as they are reasonable on all scales of inference and above all, produce more reliable results.

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