

# The effect of scale, climate and environment on species richness and spatial distribution of Finnish birds

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We used 10-km grid data from the Finnish Bird Atlas data and high-resolution data on temperature and rainfall to estimate species richness from climate and environmental variables across spatial scales. We used an ordinary least-squares (OLS) linear-regression model with a quadratic error function to estimate the number of bird species that occur. As a baseline, we used a simple dummy model that estimated the number of species in each grid to be the average number of species over all grids. We found that the best estimator for avian species richness in Finland is the length of the growing season with  $R^2$  values from 0.5 to 0.8, depending on the scale. Our results support the energy-water hypothesis, and we suggest that the proximate control of species richness in the present case is productivity, which is in turn controlled by climate. Some of the effects conventionally attributed to scaling may have trivial causes associated with sampling, in particular the completion of missing data as primary units of observation are merged. For broad surveys of patterns, medium resolution may often be adequate and even superior to the highest nominal resolution available.

## Introduction

Species richness is the most commonly used metric of biodiversity, and is thought to capture taxonomic disparity as well as ecological and topographic diversity (Gaston 1996). The literature on species–area relationship is extensive and reaches back to classical island biogeography (MacArthur & Wilson 1967) and beyond (see Lomolino *et al.* 2004 for overview). In island

biogeography, richness is understood as a function of three variables: geographic area, distance of migration, and extinction/migration dynamics. Recent studies to estimate local species diversity have used habitat diversity or commonness and/or geographic range of the taxa present as variables (Lennon *et al.* 2004, Ruggiero & Kitzberger 2004, Kreft *et al.* 2006). Other studies have used range shifts in response to observed or predicted climate change to investigate species richness

(Thomas *et al.* 2004). Recently, Honkanen *et al.* (2010) studied the bird richness in Finnish boreal forests to investigate the role of area and energy in determining species richness. Jonsson *et al.* (2011) studied the role of island biogeography, niche theory and species–energy relationship in explaining the patterns of species richness in northern Sweden.

Here we use 10-km-grid data from the Finnish Bird Atlas, climate and environmental data to generate several models to estimate species richness of Finnish land birds. We test whether precipitation, temperature or growth season can be used to estimate species richness, and how well they perform. We also investigate if model performance is better at finer spatial scales, and whether all species give similar result to subgroups of the fauna based on migratory behavior. Finally, we explore — across scales and groups — the spatial coherence of taxon-based clusters, and compare how well the clustering pattern of birds corresponds to the vegetation-based biogeographic zonation of Ahti *et al.* (1968) and to the bird-based zonation of Järvinen and Väisänen (1980).

## Area and richness

The global pattern of species richness many times seems to covary with climatic variables (e.g. Hawkins *et al.* 2003, Currie *et al.* 2004, Rahbek *et al.* 2007), but the relationships between climatic variables and species richness are not clear (*see* Rosenzweig 1995).

In a recent study of the regional species richness of endemic South American birds using 1° latitude/longitude resolution, (Rahbek *et al.* 2007) found that only the occurrence of the widest-ranging species showed correlation with climate variables, with no significant climate effect observed for the rest of the species. They suggest that long history and strong topographic relief are the main reasons for the lack of correlation with local climate in their data (i.e., only widest ranging species had a correlation). Rahbek *et al.* (2007) identified as critical the question what patterns occur at finer spatial scales, predicting that local climate is a better predictor at finer

scales, at which only few distinctive habitats are sampled by each cell.

## Habitat diversity

It is not clear how specific habitats affect bird diversity, and how this is expressed at different scales. There is ongoing controversy about how the habitat heterogeneity affects richness. For example, Jeffries *et al.* (2006) found that insect richness in old forests is linked to heterogeneity, while others (e.g. Russell *et al.* 2006, Triantis *et al.* 2008) showed that habitat heterogeneity in itself is a poor predictor of species richness. For birds, micro-habitat variables, like vegetation structure, were many times linked to diversity (e.g., MacArthur *et al.* 1961, 1962, James & Wamer 1982). MacFaden and Capen (2002) concluded that while the microhabitat was very important, also “Two or more scales were significant for many species, suggesting that habitat selection can occur at multiple scales” (MacFaden & Capen 2002: 251). According to Virkkala (1991), both regional and local effects contribute to the population patterns of birds in northern Finland. In most settings it is difficult to disentangle the effects of specific habitats from the effects of global environmental variables. The Finnish terrestrial biota have only a 10 000-year post-glacial history at their present location, and the topographic relief is low for an area of this size.

There are only a few pieces of evidence about the pre-historic distribution of birds in Finland. Most of the available evidence comes from archaeological sites where bird remains are often found. The oldest finds are over 10 000 years old, and this suggests that birds moved in immediately after the ice had melted between 10 000–8000 years ago (*see* Mannermaa 2008 for a review). First, the open-habitat birds moved in, while the forest-dwelling species arrived together with the spread of trees 7000–4500 years ago (Mannermaa 2008). It is highly likely that the migration habits and routes are thousands of years old.

Thus, this area and these data are particularly suitable for exploring general relation-

ships between species richness and area because they largely exclude the two factors thought by (Rahbek *et al.* 2007) to account for the lack of correlation between climate and species richness: long history and topography.

## Energy

Models using climatic variables to predict species richness are known as energy-richness models. The first of these was the species-energy hypothesis, developed by Wright (1983) as a functional development of the species-area hypothesis: species richness is a function of the total number of individual entities within an area, and the number of individuals is limited by the productivity of the area. In recent years, the focus has shifted towards the mechanisms how energy might explain the richness. In their extensive review, Evans *et al.* (2005) summarized nine different mechanisms that may generate species–energy relationships at a macroecological scale. These are (1) sampling, (2) increased population size, (3) dynamic equilibrium, (4) niche position, (5) niche breadth, (6) more trophic levels, (7) consumer pressure, (8) range limitation, and (9) diversification rate. All of these can be understood in terms of two different categories of available energy: solar and productive. The former is the ambient available energy (temperature etc.), while the latter is a measure of available consumer resources. These are highly interrelated. Although they are not direct measures (*see* Rosenzweig 1995), climate data and net primary production can be used to estimate available and productive energy (*see* Evans *et al.* 2005, Honkanen *et al.* 2010 for reviews of species–energy relationships). One of the more influential energy-related species diversity hypotheses include the water–energy model (Hawkins *et al.* 2003, *see also* Whittaker *et al.* 2007) and the temperature–kinetics hypothesis (Allen *et al.* 2002). The dataset of Hawkins *et al.* (2003) included large variety of organisms (22 plants, 44 vertebrates, 19 invertebrates, *see* Hawkins *et al.* 2003: table 1). Hawkins *et al.* (2003) concluded that at the global scale water and evapotranspiration dominate the species

richness patterns, but at high latitudes available energy (temperature) and water are more important. Allen *et al.* (2002) developed a model in which only temperature was used as a predictor of species richness.

## Biogeography of Finland

The vegetation-based classifications (e.g. Ahti *et al.* 1968) have been used as a base for animal-based biogeographic zonations of Finland (e.g., Voipio 1956). Especially bird census data were used for investigating the large-scale distribution patterns of animals (e.g., Lehtonen 1951, Merikallio 1951, 1955). The first wholly objective quantitative zonation was that of Järvinen and Väisänen (1980), separating the Finnish bird fauna into six zones using “nuclear areas” of homogenous bird data as a starting point (for details *see* Järvinen & Väisänen 1980). They found that the zonation based on bird fauna largely follows the vegetation zonation of Ahti *et al.* (1968) in the northern part of Finland, but in the southern part it does not. According to Järvinen and Väisänen (1980), this is explained by resources used by birds: different forest types support similar bird communities, even if the actual plant community varies widely (Järvinen & Väisänen 1980: 16). They also suggested that extreme mobility of birds leads to an unusually fine-grained utilization of habitats.

## Material and methods

### Study area

The biogeography of Finland is essentially a temperature-driven zonation that has remained stable for over a century. The first biogeographic division of Finnish forests was made during the late 19th century (e.g., Nylander & Saelen 1859 in Merikallio 1955, *also see* Ahti *et al.* 1968 for review), and in the early 20th century many different classifications and biographic divisions were made (e.g., Linkola 1922, Cajander 1925, Kujala 1936, Kalela 1951). All these divisions share the same large-scale patterns. Northern

Finland is differentiated from south by the type of forest, and the area in-between is a transition zone. Also the elevated watershed areas in central (Suomenselkä) and eastern Finland (Maanselkä) are usually differentiated or highlighted. This pattern which was discovered very early (e.g., Cajander 1925, Kujala 1936) culminated in the influential vegetation zonation of Ahti *et al.* (1968), which is still widely used today. These biogeographic classifications used a combination of climatic, edaphic and vegetative patterns to define a number of vegetation zones in Finland, usually between three and eight (for reviews see Ahti *et al.* 1968, Hämet-Ahti 1981).

## Data sources

We use the Finnish Bird Atlas Data from the first and second Finnish bird atlases (for details see Väisänen 1998, Väisänen *et al.* 1998, and for field methods see Väisänen 1989). The data cover the entire Finland in  $10 \times 10$ -km grids cells. The total bird atlas dataset has 3813 cells, 248 species and 246 535 species occurrences, where the evidence of probable or confirmed breeding has been interpreted as species occurrence, and the evidence of unlikely or possible breeding as non-occurrence (Väisänen 1998).

The species were further divided into three groups based on the migratory strategies provided in the Atlas (see Väisänen *et al.* 1998 for details): 43 local or wandering birds, 123 short-distance migrators and 69 long-distance migrators. Additionally, 13 species were not included in this classification. Local and wandering birds include partial movers. Short-distance migrators include species that migrate to Europe and Mediterranean. Long-distance migrators are those species that migrate south of Sahara (see Appendix).

As a climate data, we use a high resolution weather data provided by the Finnish Meteorological Institute (FMI), including annual average temperature, precipitation and length of the thermal growth season for each of the 10-km atlas cells (Venäläinen *et al.* 2005). We also run all our analysis with World Climate data with coarser resolution (Hijmans *et al.* 2005, used as in Heikinheimo *et al.* 2007) to control for local

*versus* regional effects that might have arisen from sampling. The main zonation of biogeographic regions, based on Ahti *et al.* (1968), has been combined for the 10-km map cells of the bird atlas (R. A. Väisänen unpubl. data).

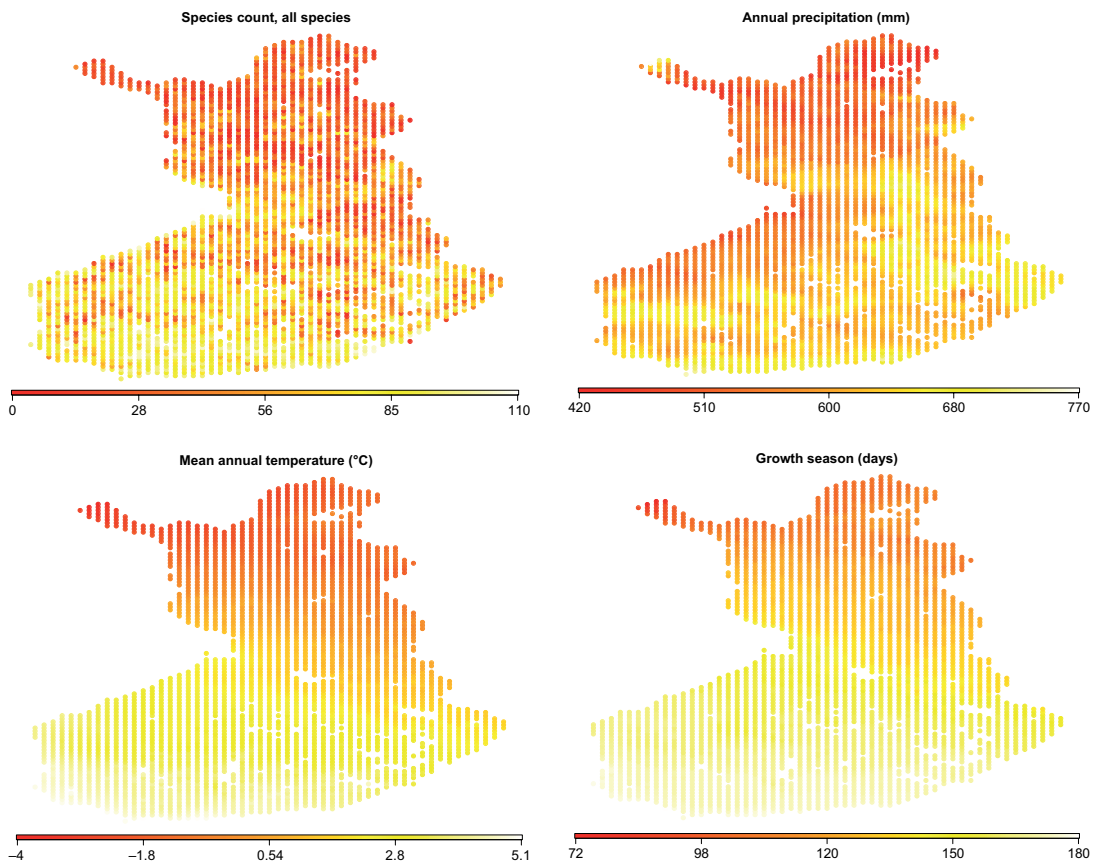
For the purpose of our analysis, we processed the data by removing the bird species that occur in fewer than 5% of the cells, as well as so-called project species that include species for which an extensive breeding study has been conducted. The distribution of the project species in the Atlas differs significantly from the other species. We were left with a total of 130 species (Appendix), including 22 local species, 62 short-distance migrators, 41 long-distance migrators, and 5 not classified.

We removed the map cells that were on the national borders and thus with limited access, as well as the coastal cells, which contain many species not found in non-coastal cells. We further removed cells in the hemiboreal region, because after removing the coastal cells the hemiboreal region was reduced to a very few cells. We used the remaining 3109 grid cells in the analysis. Figure 1 shows the distribution of the main variables used in this study as well as species count of the birds that were used on a 10-km grid.

## Data analysis

To test the effect of the map grid-size, we used the original 10-km grid to create new square grids having cell sizes from 20 km to 100 km by combining the original neighboring 10-km grid cells. A species was considered to be present in a larger cell if it was present in at least one  $10 \times 10$ -km cell within it.

We used an ordinary least-squares (OLS) linear regression model with a quadratic error function to estimate the number of bird species that occur, using the length of the growth season (days), annual precipitation (mm) and mean annual temperature ( $^{\circ}\text{C}$ ) as covariates. We fitted four models to the data: the full model that had all three covariates ("Full model"), a model that had only the growth period as a covariate ("Growth period"), a model that had only the annual precipitation as a covariate ("Precipitation"), and a model that had only the mean



**Fig. 1.** The spatial patterns of the main variables used in this study.

annual temperature as a covariate (“Temperature”). As a baseline, we used a simple dummy model that estimated the number of species in each grid to be the average number of species over all grids (“Baseline”).

To compare the spatial patterns of birds with vegetation zonation and earlier qualitative classifications, we performed clustering analysis. We associated a 0/1 presence/absence vector of each species with each cell in the map and used the k-means clustering algorithm of Hartigan and Wong (1979) to cluster the map cells. We used the initialization described in Arthur and Vassilvitskii (2007). The clustering algorithm was run 50 times and the solution with the smallest error was selected.

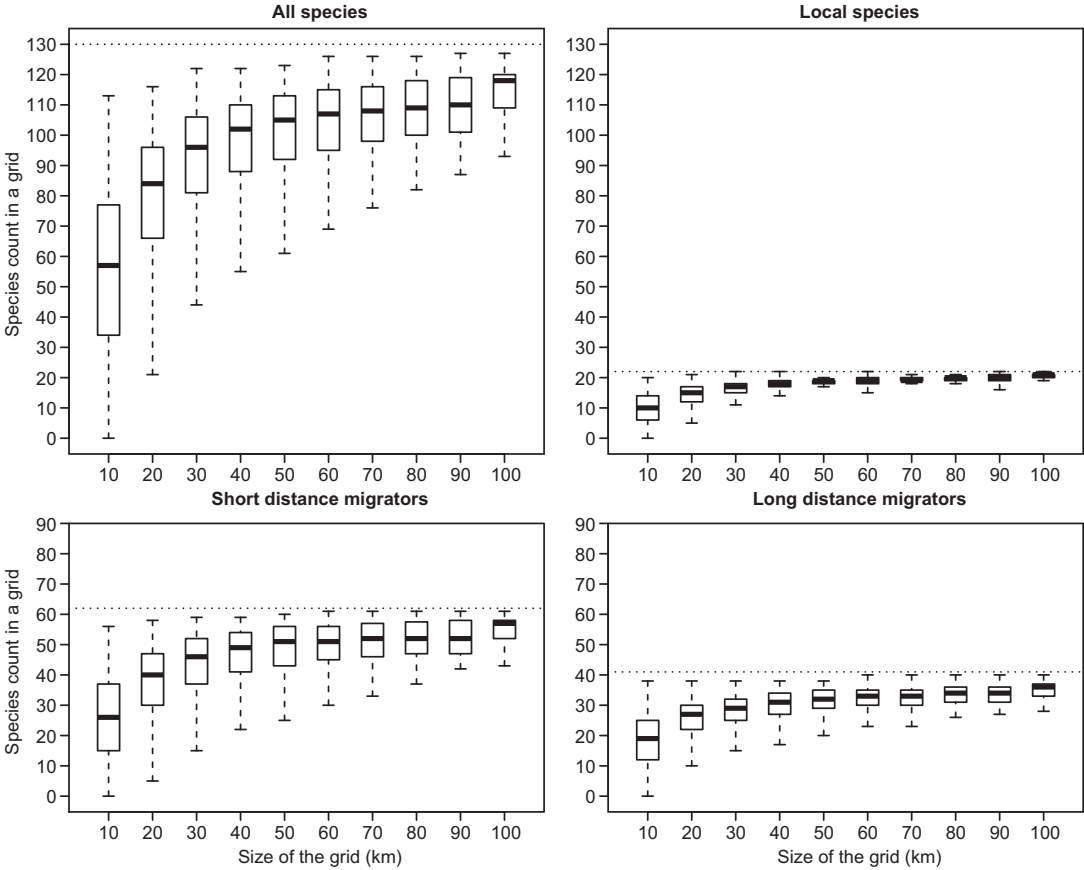
We use the kappa coefficient (Cohen 1960) to measure the agreement between the vegetation zonation and clusterings. The kappa coefficient is a statistic which measures the level of agree-

ment between two clusterings. Values smaller than 0.2 indicate poor agreement, between 0.2 and 0.4 indicate fair agreement, between 0.4 and 0.6 moderate agreement, between 0.6 and 0.8 good agreement, and greater than 0.8 very good agreement, and 1 indicates exact agreement.

## Results

### Diversity and scale

The Finnish Bird Atlas uses a  $10 \times 10$ -km grid as a base for census data. Figure 2 illustrates how the diversity of bird fauna increases with increasing grid-cell size, as expected from the species–area effect (*see e.g.*, Rosenzweig 1995). The increase is fast up to 30-km grid squares and thereafter the rate of species increase slows down as the area curve reaches saturation; thus



**Fig. 2.** Distributions of biodiversity, or species counts, across the map grids for varying grid sizes. The biodiversities are shown for all species, as well as for the various mover classifications. The number of species in each classification, and thus the upper limit for the biodiversity, is given by a horizontal dotted line. Species–area effect is obvious: as the grid size increases the biodiversities in the grids saturate to the upper bound.

the difference in diversity between 30-km and 100-km squares is almost the same as between 10-km and 20-km squares (Fig. 2 and Table 1). This effect is seen across all the groups, but is much less visible in the local birds, which are saturated faster than the more diverse groups of short- and long-distance migrators.

### Estimating cell richness directly from climate variables

We investigated how different regression models perform at different scales of spatial resolution and for subgroups of the fauna based on migratory behavior. We used three different models to

**Table 1.** Average number of species in different subgroups of fauna and respective grid sizes.

|               | Grid size (km) |      |      |      |       |       |       |       |       |       |
|---------------|----------------|------|------|------|-------|-------|-------|-------|-------|-------|
|               | 10             | 20   | 30   | 40   | 50    | 60    | 70    | 80    | 90    | 100   |
| All species   | 55.3           | 79.6 | 90.9 | 97.3 | 101.5 | 104.6 | 106.9 | 108.6 | 109.2 | 114.2 |
| Local species | 9.7            | 14.0 | 16.1 | 17.4 | 18.2  | 18.8  | 19.3  | 19.7  | 19.9  | 20.4  |
| Near movers   | 25.8           | 37.8 | 43.5 | 46.7 | 48.8  | 50.2  | 51.3  | 52.0  | 52.4  | 54.7  |
| Far movers    | 18.4           | 25.6 | 28.5 | 30.3 | 31.4  | 32.3  | 32.9  | 33.4  | 33.7  | 35.1  |

estimate the species count in individual cells, as well as a baseline model that simply assigned mean species richness to each cell.

Performance of the models based on the climate data from Finnish Meteorological Institute (FMI) indicates that the best single estimator for bird richness in individual cells is the length of the growing season, with temperature being almost as good (Fig. 3). The precipitation is a worse covariate than either of the above, but still distinctly better than the baseline. The combination of the three single covariates gives the best estimate, but the result is only marginally different from what is obtained using the length of the growing season alone. With an increasing cell size, the estimation error becomes smaller. Again, the largest change is between 10-km and 20-km squares, and enlarging the squares above 40-km does not improve the result much. This is especially true when using all species, while in the subgroups the errors are initially smaller and also decrease more slowly. For the local species, the estimation error remains essentially unchanged with increasing grid size. The full model overfits the data at the largest grid sizes in all sets, most clearly when using all species. Overall, full model estimates the species richness well, except that it grossly overestimates the biodiversity in restricted areas, at least in part where the local conditions are demanding for bird censuses and support a very rich bird fauna, like in the large peatland areas in northeastern Finland (not shown). The lower resolution World Climate data give similar results, which are not however reported here.

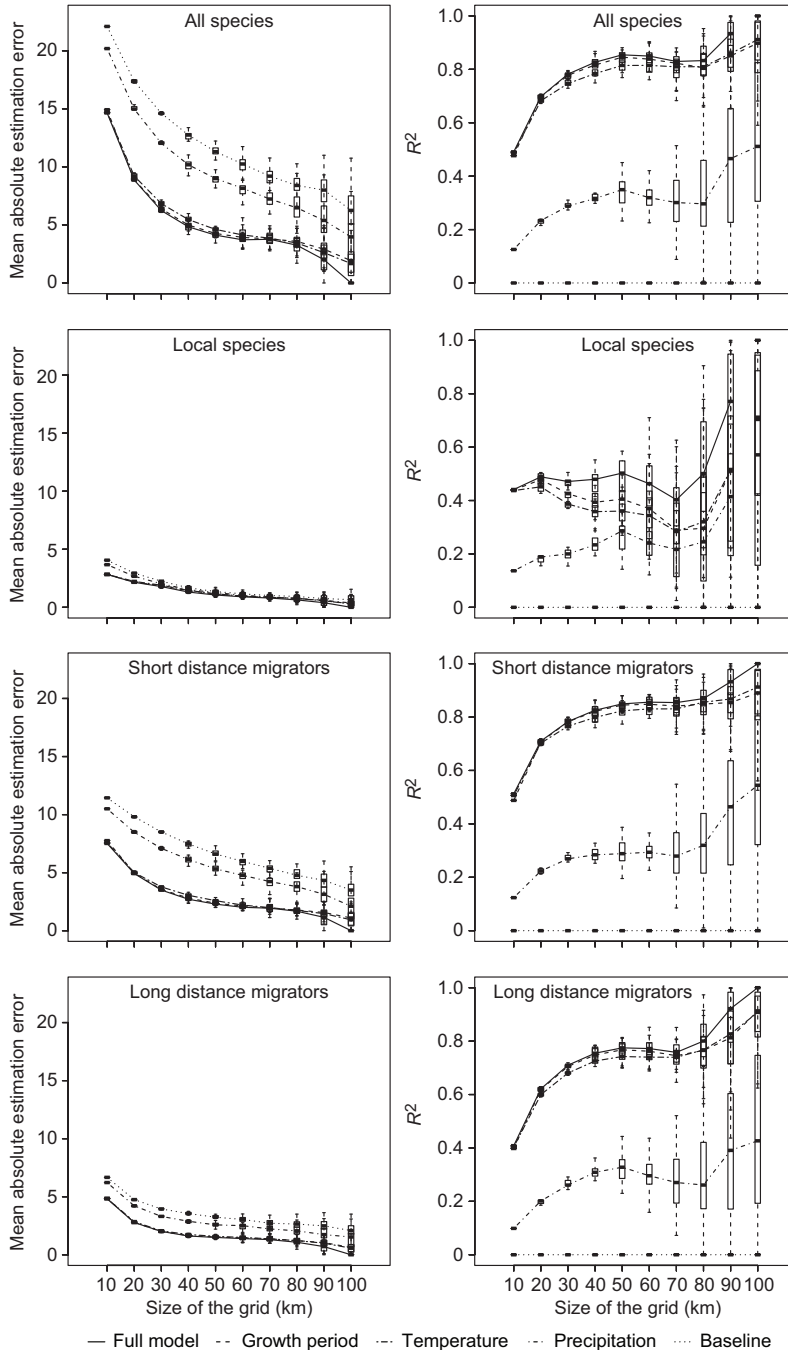
### Spatial distribution of taxonomic clusters across groups and scales

Clustering the cells to three and five clusters according to the species composition (Figs. 4–5) shows that the overall patterns largely follows the vegetation zonation of Ahti *et al.* (1968). With three clusters and 10-km squares, the northern part is distinguished clearly as the northern boreal zone, while the middle boreal and south boreal zones are not as clear. In accordance with the results of Järvinen and Väisänen (1980),

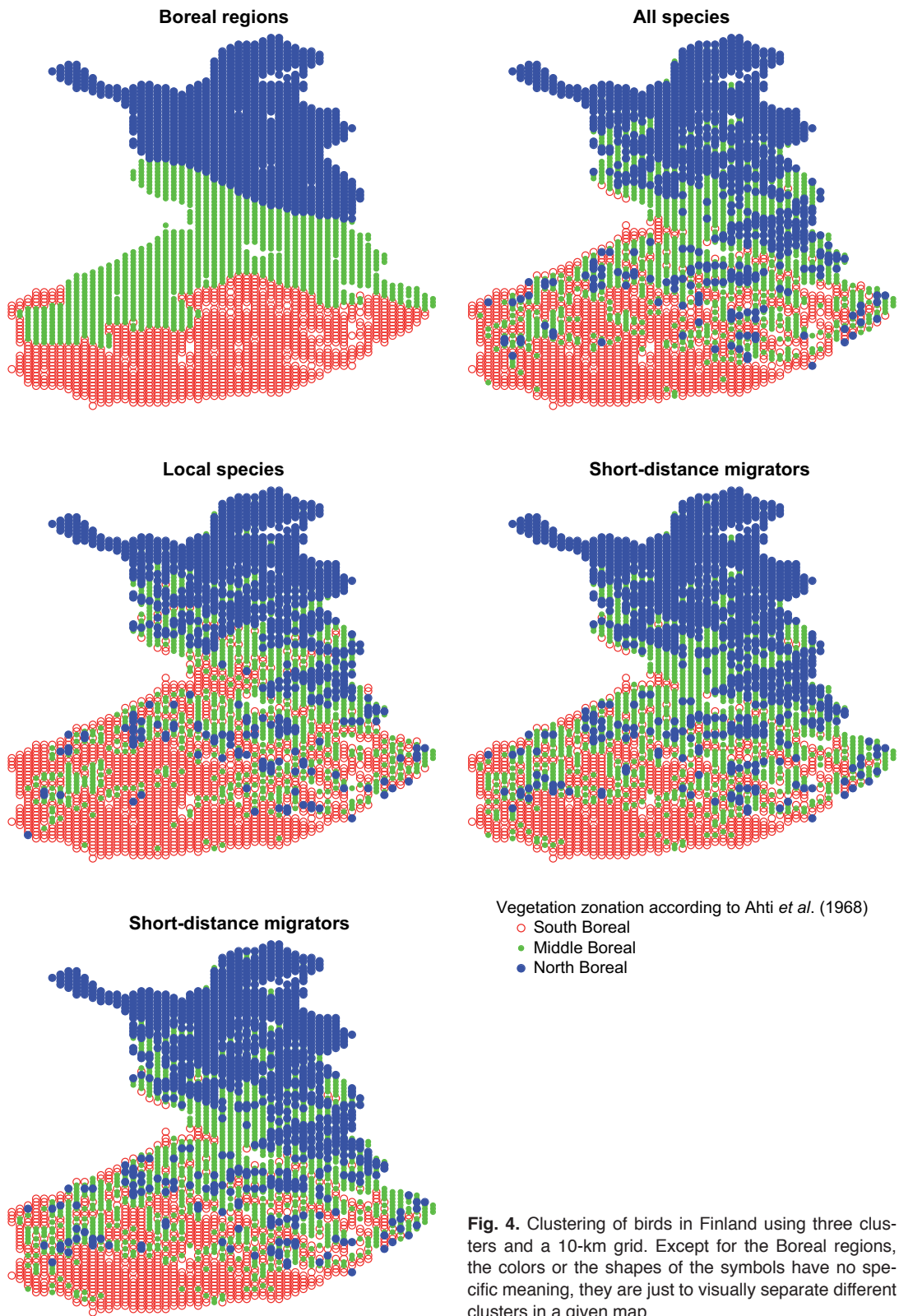
the southern part is more mixed and does not follow the vegetation zonation. Still, there is a clear southern cluster while the central part is more diffuse, with no clear-cut cluster borders. Subsets local species and short-distance migrator show similar picture as all species, while long-distance migrator have less coherent clusters. Increasing the grid size to 20 km improves the coherence considerably (Fig. 6). The northern boreal area is now very similar to the vegetation zone of Ahti *et al.* (1968), and also the middle and southern boreal zones are visible and quite similar to the Ahti *et al.* (1968) zones. The differences are mainly in the Suomenselkä and Maanselkä regions, where the vegetation is more northern-like than is presumed by its latitudinal location. This does not show clearly in the bird data. Instead, these regions belong to the southern cluster, or are mixed between middle and southern clusters boundary. In groups local species and short-distance migrators the northern boreal cluster is smaller, and the middle cluster spreads northwards, without a clear boundary between the northern and middle clusters. In contrast to the 10-km grid, the 20-km grid shows that long-distance migrators have a clear northern cluster that extends quite far to the south. The middle and southern clusters largely follow the vegetation zones, with Maanselkä and Suomenselkä together with Ostrobothnia belonging to the middle cluster.

The match between the boreal zonation and the three bird clusters is the best when the size of the map grid is 20 or 30 km, the kappa coefficients being 0.64 or 0.66, respectively. For 10- and 40-km grid sizes the kappa coefficients are lower, 0.53 and 0.62, respectively.

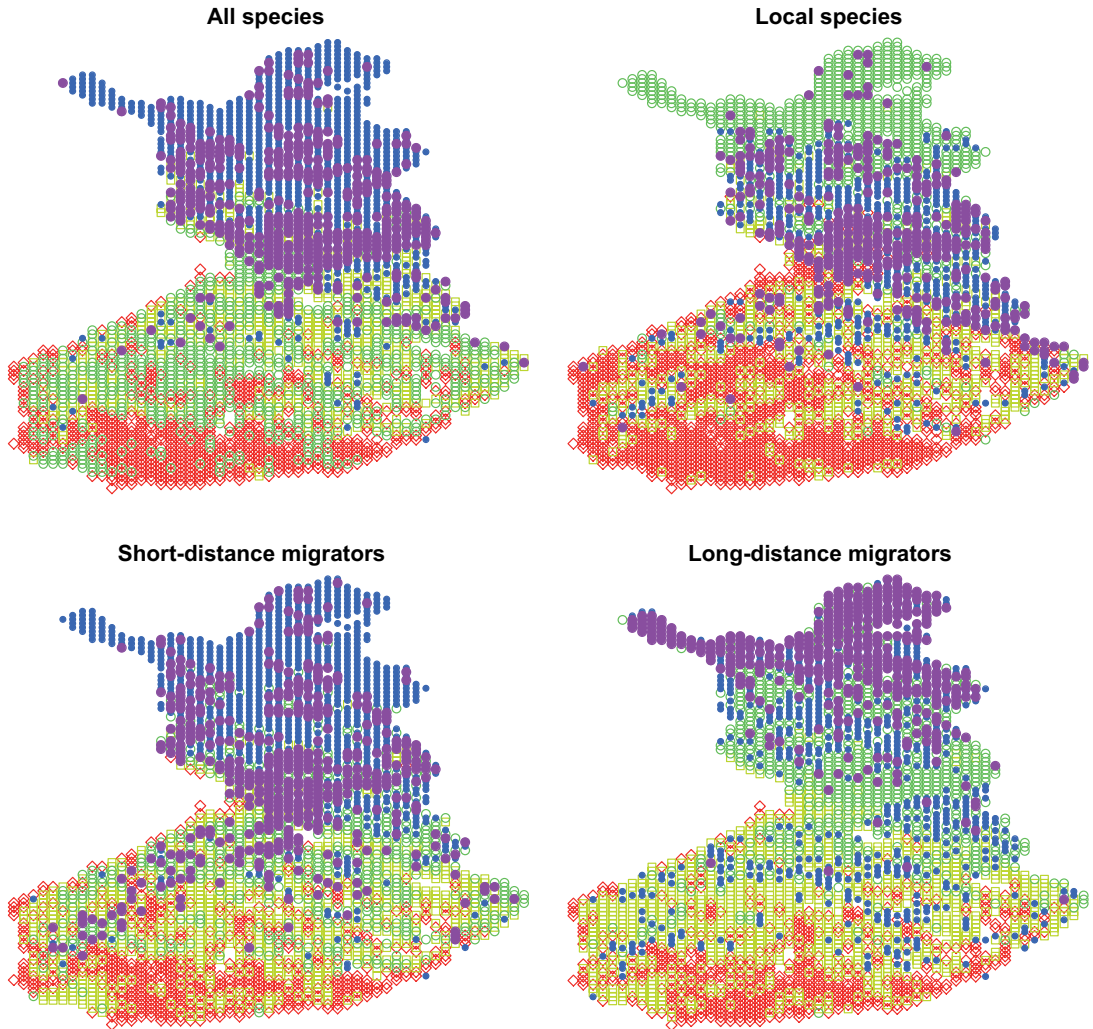
Increasing the number of clusters to five at the 10-km grid results in very incoherent clusters without clear-cut boundaries (Fig. 5). The clusters form a north–south oriented succession, with the main axis of each cluster trending approximately east–west. The “nuclear areas” of Järvinen and Väisänen (1980) cannot be clearly identified, but the orientation of the clusters is similar. For the 20-km grid, the large scale pattern and orientation of cluster is more similar to the three clusters (Figs. 6 and 7) and to the zonation of Järvinen and Väisänen (1980), but



**Fig. 3.** Mean absolute estimation errors for the biodiversity, or species count, for all species, as well as for the various mover classifications. The box plots show the variance with respect to different alignments of the map grid. The “Full model” is a linear model of the biodiversity based on three covariates: length of the growth period, average yearly temperature and yearly precipitation provided by the FMI. The “Growth period”, “Temperature” and “Precipitation” models have only one covariant, specified by the model name. The baseline model predicts the biodiversity to be the average biodiversity in all map grids. The  $R^2$  statistic gives the fraction of the variance of the species count explained by the model: a model with a  $R^2 = 1$  fits the to the data without error, while the baseline model has  $R^2 = 0$ . Either growth period or temperature alone give almost as good fit as the full model, while precipitation performs poorly. Small estimation error is better.



**Fig. 4.** Clustering of birds in Finland using three clusters and a 10-km grid. Except for the Boreal regions, the colors or the shapes of the symbols have no specific meaning, they are just to visually separate different clusters in a given map.



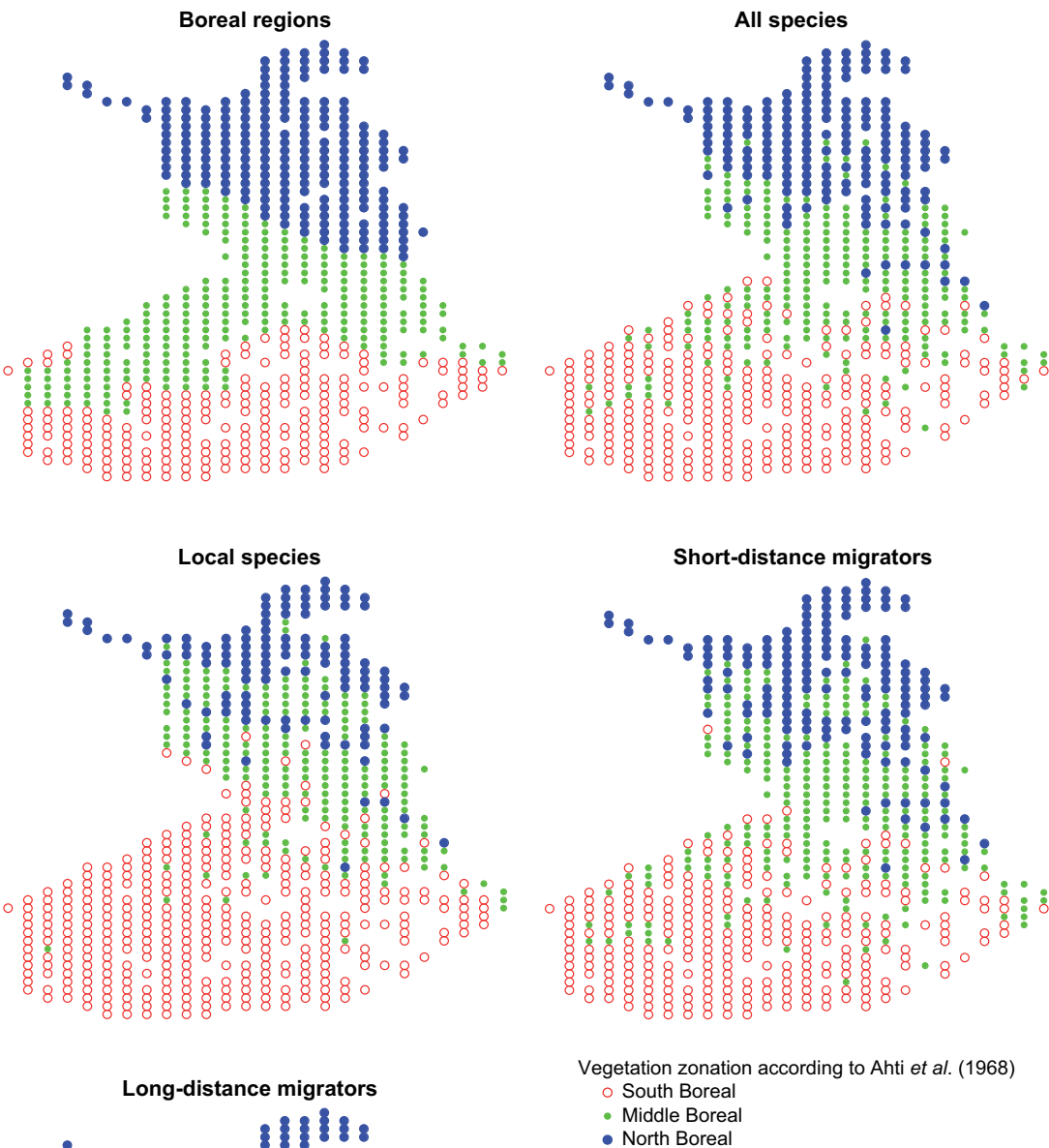
**Fig. 5.** Clustering of birds in Finland using five clusters and a 10-km grid. The colors or the shapes of the symbols have no specific meaning, they are just to visually separate different clusters in a given map.

the boundaries are still more diffuse. In contrast to the 10-km grid, four of the five nuclear areas (B–E of Järvinen and Väisänen (1980)) can now be identified, and the five clusters (Fig. 7) are reminiscent of zoogeographic zones 3 to 6B in Järvinen and Väisänen (1980).

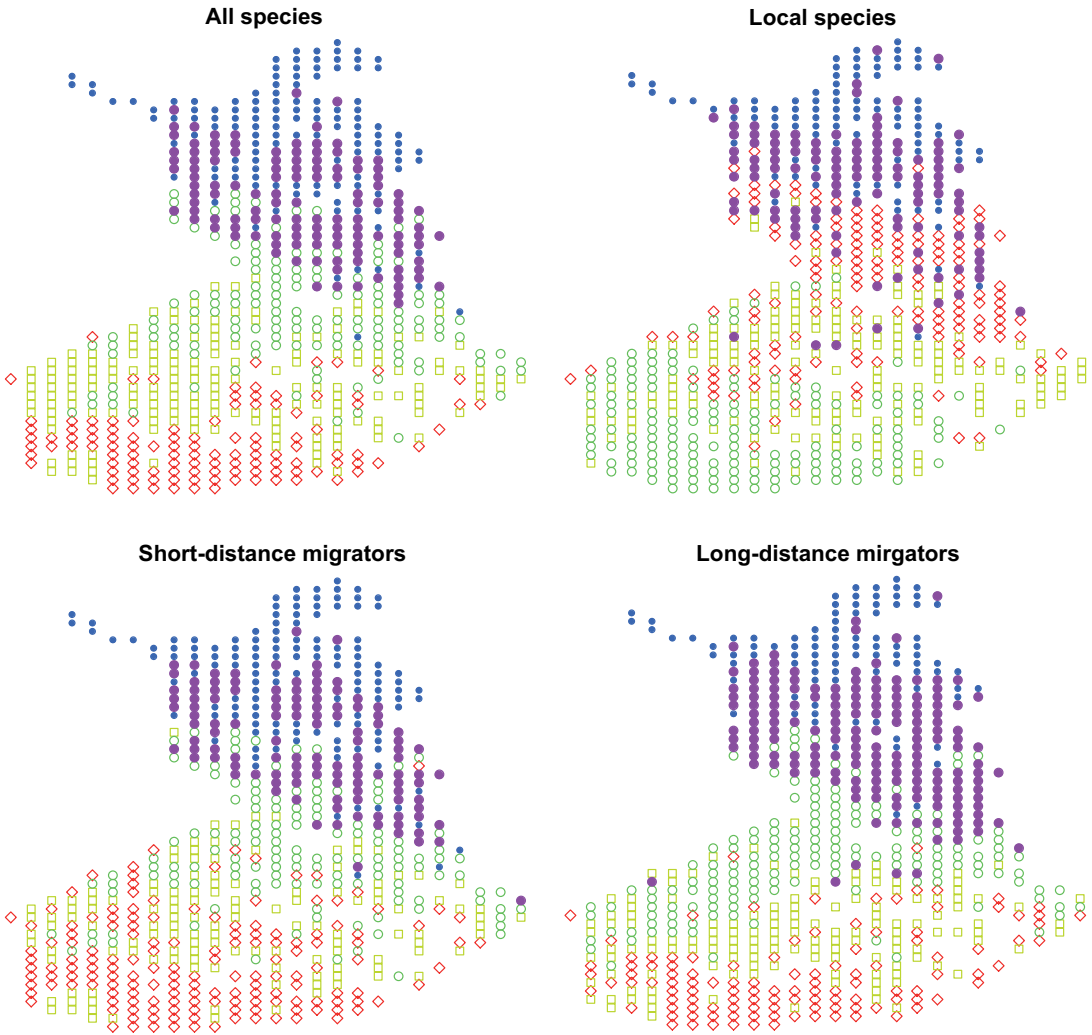
Successive increase of the grid size (Figs. 6–8) shows that the basic pattern remains the same, but the clusters become more coherent, and transition zones disappear. At the medium scale (30 and 40 km, Fig. 8) the topographic features like the Maanselkä and Suomenselkä regions are surprisingly more distinguishable than at finer or coarser scales.

## Discussion

When Rahbek *et al.* (2007) demonstrated that in South America, only the ranges of the most widespread species could be explained by water-energy model, they also noted that none of their models based on climate could predict the local richness of species with more restricted ranges. Instead, they showed that the topographic relief and ecosystem diversity were better predictors for local avian species richness in South America (Rahbek *et al.* 2007). In a similar vein, Rahbek (2005) argued that the scale has large effect on the explanatory power of topography; at larger



**Fig. 6.** Clustering of birds in Finland using three clusters and a 20-km grid. Except for the Boreal regions, the colors or the shapes of the symbols have no specific meaning, they are just to visually separate different clusters in a given map.

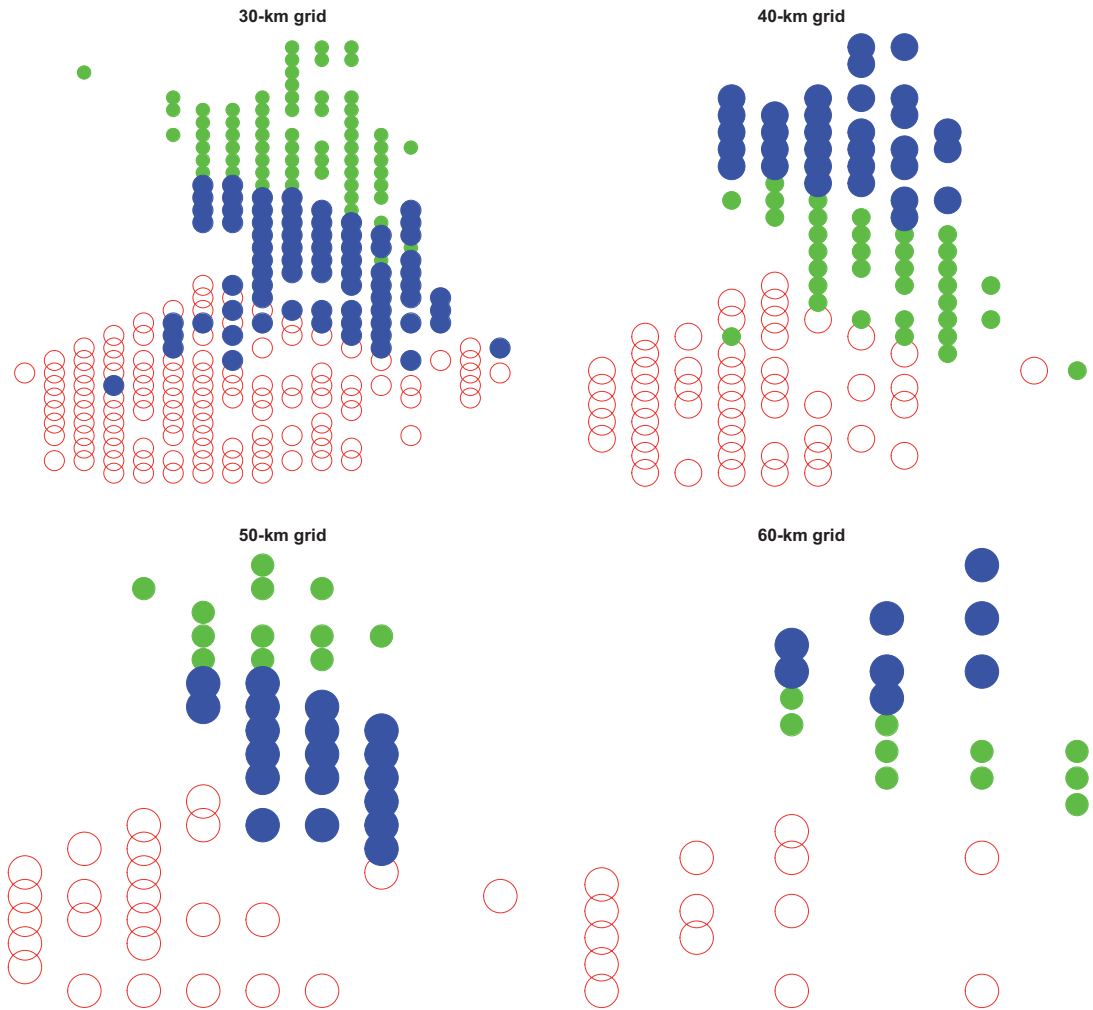


**Fig. 7.** Clustering of birds in Finland using five clusters and a 20-km grid. The colors or the shapes of the symbols have no specific meaning, they are just to visually separate different clusters in a given map.

scales the effect of topography is more prominent. Our results show that climate is very good predictor of species richness at various scales when topography has been excluded from the analysis. The estimates are best when the scale is from 20 to 30 km. It is likely that the major increase from 10-km to 20-km grid size contains a major effect of “patching” incompletely sampled by 10-km grid cells. Comparing the results from high- and medium-resolution climate data confirms this; the estimates are almost the same regardless if we used the high- or medium-resolution data. This has important practical implications: in the absence of other major factors,

medium resolution data are enough for precise estimates of species richness and studies with similar aims, and using the highest resolution available may not be the optimal solution.

Rahbek and Graves (2001) noted that the lack of high-quality data hinders the analysis of species richness at regional and continental scales. Our results indicate that resolution of the data may not matter as much as has previously been suggested (e.g., Rahbek and Graves 2001, Rahbek 2005, Rahbek *et al.* 2007), at least when geography of the area under investigation is simple. Our findings do agree with previous work showing that (climatic control of) produc-



**Fig. 8.** Clustering of birds in Finland using three clusters. The colors or the shapes of the symbols have no specific meaning, they are just to visually separate different clusters in a given map.

tivity is the best predictor of species richness at high latitudes at high to medium resolution (Hawkins *et al.* 2003, 2007).

Concerning the biogeographic expression of summed avian species ranges we showed here that the bird clusters and vegetation zones largely coincide when three clusters are used. The most important differences with regard to the vegetation zonation are the Suomenselkä and Maanselkä regions, which are not shown in the bird data for the 10-km grid. These regions belong to the southern cluster, or are scattered around the boundary between the middle and southern clusters. The results shown by five clusters are similar but considerably more fuzzy,

with a poorer match to the vegetation zonation. This indicates that at biogeographic scales the distribution of birds is governed either directly by vegetation, or by the same climatic variables that influence vegetation patterns. One possible explanation for this is that the plants and birds respond in a similar way to climate and bird clusters do not reflect real vegetation patterns but climatic patterns.

Increasing the size of the grid underlying the clusters stepwise from 20 to 60 km reveals another result of practical significance: the large-scale pattern remains the same, and is distinguishable even at the 60-km scale. It is interesting that the Maanselkä and Suomenselkä regions

are more visible at the medium scales of 30 and 40 km. The cluster boundaries also become more distinct as small-scale details progressively disappear. These results are in good agreement with Virkkala's (1991) multi-scale study of birds in northern Finland. He concluded that all scales from local to regional and biogeographic affect the distribution and abundance of birds. The biogeographic scale affects the overall trends, and large-scale patterns reflect this. Especially at the regional scale, environmental constraints affect the composition of bird communities, and local effects are incorporated to regional trends (Virkkala 1991).

It has been long known that the length of the growing season is also closely related to, and the best approximation of, net primary production (NPP) and vegetation patterns in Finland (e.g., Kalliola 1973, Solantie 1990). Jonsson *et al.* (2011) studied the relationship of bird richness and NPP in Sweden, and concluded that NPP is one of the major drivers of species richness. They could not rule out the effect of other more direct measures of energy availability. Global satellite-derived estimates of NPP (e.g., Nemani *et al.* 2003, Running *et al.* 2004) also show that temperature together with radiation is the most important controller of NPP at high latitudes (*see also* Churkina and Running 1998).

In conclusion, our results show that the best predictor for avian species richness in Finland is the length of the growing season. Our results support the energy-water hypothesis of Hawkins *et al.* (2003), but we further hypothesize that the proximate controlling factor of species richness in the present case is productivity, which is in turn controlled by climate.

Interestingly, and in accordance with the results from richness prediction discussed above, the 20-km grid clustering of birds is closer to the vegetation zonation than the original 10-km grid clustering, especially for the long distance migrator category.

On the practical side, the results presented here suggest that computational studies of biodiversity and biogeography need to pay more attention to data quality than has been customary, or indeed possible, in many cases. Some of the effects conventionally attributed to scaling may have trivial causes associated with sam-

pling. In particular, the completion of missing data as units of observation are merged to larger areas. For broad surveys of patterns, medium resolution may often be adequate and even superior to the highest nominal resolution available.

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**Appendix.** Bird species included in the study. Migratory classification is based on the information in Väisänen *et al.* 1998. ‘Used’ indicates whether or not species were included in the final analysis (see text for more details).

| Species                    | Migratory behaviour     | Used | Species                    | Migratory behaviour     | Used |
|----------------------------|-------------------------|------|----------------------------|-------------------------|------|
| <i>Accipiter gentilis</i>  | short distance migrator | no   | <i>Botaurus stellaris</i>  | short distance migrator | no   |
| <i>A. nisus</i>            | short distance migrator | no   | <i>Branta canadensis</i>   | short distance migrator | no   |
| <i>Acrocephalus</i>        |                         |      | <i>B. leucopsis</i>        | short distance migrator | no   |
| <i>arundinaceus</i>        | long distance migrator  | no   | <i>Bubo bubo</i>           | local or wandering bird | no   |
| <i>A. dumetorum</i>        | different               | yes  | <i>Bucephala clangula</i>  | short distance migrator | yes  |
| <i>A. palustris</i>        | long distance migrator  | yes  | <i>Buteo buteo</i>         | short distance migrator | no   |
| <i>A. schoenobaenus</i>    | long distance migrator  | yes  | <i>B. lagopus</i>          | short distance migrator | no   |
| <i>A. scirpaceus</i>       | long distance migrator  | yes  | <i>Calcarius</i>           |                         |      |
| <i>Actitis hypoleucos</i>  | long distance migrator  | yes  | <i>lapponicus</i>          | short distance migrator | yes  |
| <i>Aegithalos caudatus</i> | local or wandering bird | yes  | <i>Calidris alpina</i>     | short distance migrator | no   |
| <i>Aegolius funereus</i>   | local or wandering bird | no   | <i>C. maritima</i>         | short distance migrator | no   |
| <i>Alauda arvensis</i>     | short distance migrator | yes  | <i>C. minuta</i>           | long distance migrator  | no   |
| <i>Alca torda</i>          | short distance migrator | no   | <i>C. temminckii</i>       | long distance migrator  | no   |
| <i>Alcedo atthis</i>       | short distance migrator | no   | <i>Caprimulgus</i>         |                         |      |
| <i>Anas acuta</i>          | short distance migrator | yes  | <i>europaeus</i>           | long distance migrator  | no   |
| <i>A. clypeata</i>         | short distance migrator | yes  | <i>Carduelis cannabina</i> | short distance migrator | yes  |
| <i>A. crecca</i>           | short distance migrator | yes  | <i>C. carduelis</i>        | short distance migrator | no   |
| <i>A. penelope</i>         | short distance migrator | yes  | <i>C. chloris</i>          | short distance migrator | yes  |
| <i>A. platyrhynchos</i>    | short distance migrator | yes  | <i>C. flammea</i>          | short distance migrator | yes  |
| <i>A. querquedula</i>      | long distance migrator  | yes  | <i>C. flavirostris</i>     | short distance migrator | no   |
| <i>A. strepera</i>         | short distance migrator | no   | <i>C. hornemanni</i>       | short distance migrator | no   |
| <i>Anser anser</i>         | short distance migrator | no   | <i>C. spinus</i>           | short distance migrator | yes  |
| <i>A. caerulescens</i>     | short distance migrator | no   | <i>Carpodacus</i>          |                         |      |
| <i>A. erythropus</i>       | short distance migrator | no   | <i>erythrinus</i>          | different               | yes  |
| <i>A. fabalis</i>          | short distance migrator | yes  | <i>Cephus grylle</i>       | short distance migrator | yes  |
| <i>Anthus campestris</i>   | long distance migrator  | no   | <i>Certhia familiaris</i>  | short distance migrator | yes  |
| <i>A. cervinus</i>         | long distance migrator  | no   | <i>Charadrius dubius</i>   | short distance migrator | yes  |
| <i>A. petrosus</i>         | short distance migrator | no   | <i>C. hiaticula</i>        | short distance migrator | no   |
| <i>A. pratensis</i>        | short distance migrator | yes  | <i>C. morinellus</i>       | short distance migrator | no   |
| <i>A. trivialis</i>        | long distance migrator  | yes  | <i>Chlidonias niger</i>    | long distance migrator  | no   |
| <i>Apus apus</i>           | long distance migrator  | yes  | <i>Cinclus cinclus</i>     | local or wandering bird | no   |
| <i>Aquila chrysaetos</i>   | short distance migrator | no   | <i>Circus aeruginosus</i>  | long distance migrator  | no   |
| <i>A. clanga</i>           | long distance migrator  | no   | <i>C. cyaneus</i>          | short distance migrator | no   |
| <i>Ardea cinerea</i>       | short distance migrator | no   | <i>C. pygargus</i>         | long distance migrator  | no   |
| <i>Arenaria interpres</i>  | long distance migrator  | yes  | <i>Clangula hyemalis</i>   | short distance migrator | no   |
| <i>Asio flammeus</i>       | short distance migrator | no   | <i>Coccothraustes</i>      |                         |      |
| <i>A. otus</i>             | short distance migrator | no   | <i>coccothraustes</i>      | short distance migrator | no   |
| <i>Aythya ferina</i>       | short distance migrator | yes  | <i>Columba livia</i>       | local or wandering bird | yes  |
| <i>A. fuligula</i>         | short distance migrator | yes  | <i>C. oenas</i>            | short distance migrator | no   |
| <i>A. marila</i>           | short distance migrator | no   | <i>C. palumbus</i>         | short distance migrator | yes  |
| <i>Bombycilla garrulus</i> | local or wandering bird | yes  | <i>Corvus corax</i>        | local or wandering bird | yes  |
| <i>Bonasa bonasia</i>      | local or wandering bird | yes  |                            |                         |      |

*continued*

## Appendix. Continued.

| Species                     | Migratory behaviour     | Used | Species                       | Migratory behaviour     | Used |
|-----------------------------|-------------------------|------|-------------------------------|-------------------------|------|
| <i>C. coronecornix</i>      | short distance migrator | yes  | <i>L. ridibundus</i>          | short distance migrator | yes  |
| <i>C. frugilegus</i>        | short distance migrator | no   | <i>Limicola falcinellus</i>   | long distance migrator  | yes  |
| <i>C. monedula</i>          | short distance migrator | yes  | <i>Limosa lapponica</i>       | short distance migrator | no   |
| <i>Coturnix coturnix</i>    | long distance migrator  | no   | <i>L. limosa</i>              | short distance migrator | no   |
| <i>Crex crex</i>            | long distance migrator  | no   | <i>Locustella fluviatilis</i> | long distance migrator  | no   |
| <i>Cuculus canorus</i>      | long distance migrator  | yes  | <i>L. luscinioides</i>        | long distance migrator  | no   |
| <i>Cygnus cygnus</i>        | short distance migrator | no   | <i>L. naevia</i>              | long distance migrator  | yes  |
| <i>C. olor</i>              | short distance migrator | no   | <i>Loxia curvirostra</i>      | local or wandering bird | yes  |
| <i>Delichon urbica</i>      | long distance migrator  | yes  | <i>L. leucoptera</i>          | local or wandering bird | no   |
| <i>Dendrocopos</i>          |                         |      | <i>L. pytyopsittacus</i>      | local or wandering bird | yes  |
| <i>leucotos</i>             | local or wandering bird | no   | <i>Lullula arborea</i>        | short distance migrator | no   |
| <i>D. major</i>             | local or wandering bird | yes  | <i>Luscinia luscinia</i>      | long distance migrator  | yes  |
| <i>D. minor</i>             | local or wandering bird | no   | <i>L. svecica</i>             | different               | yes  |
| <i>Dryocopus martius</i>    | local or wandering bird | yes  | <i>Lymnocyptes</i>            |                         |      |
| <i>Emberiza aureola</i>     | different               | no   | <i>minimus</i>                | short distance migrator | yes  |
| <i>E. citrinella</i>        | short distance migrator | yes  | <i>Melanitta fusca</i>        | short distance migrator | no   |
| <i>E. hortulana</i>         | long distance migrator  | yes  | <i>M. nigra</i>               | short distance migrator | no   |
| <i>E. pusilla</i>           | different               | no   | <i>Mergus albellus</i>        | short distance migrator | no   |
| <i>E. rustica</i>           | different               | yes  | <i>M. merganser</i>           | short distance migrator | yes  |
| <i>E. schoenichus</i>       | short distance migrator | yes  | <i>M. serrator</i>            | short distance migrator | yes  |
| <i>Eremophila alpestris</i> | short distance migrator | no   | <i>Milvus migrans</i>         | long distance migrator  | no   |
| <i>Erithacus rubecula</i>   | short distance migrator | yes  | <i>Motacilla alba</i>         | short distance migrator | yes  |
| <i>Falco columbarius</i>    | short distance migrator | no   | <i>M. cinerea</i>             | short distance migrator | no   |
| <i>F. peregrinus</i>        | short distance migrator | no   | <i>M. citreola</i>            | different               | no   |
| <i>F. rusticolus</i>        | short distance migrator | no   | <i>M. flava</i>               | long distance migrator  | yes  |
| <i>F. subbuteo</i>          | long distance migrator  | no   | <i>Muscicapa striata</i>      | long distance migrator  | yes  |
| <i>F. tinnunculus</i>       | short distance migrator | no   | <i>Nucifraga</i>              |                         |      |
| <i>Ficedula hypoleuca</i>   | long distance migrator  | yes  | <i>caryocatactes</i>          | local or wandering bird | no   |
| <i>F. parva</i>             | different               | no   | <i>Numenius arquata</i>       | short distance migrator | yes  |
| <i>Fringilla coelebs</i>    | short distance migrator | yes  | <i>N. phaeopus</i>            | long distance migrator  | yes  |
| <i>F. montifringilla</i>    | short distance migrator | yes  | <i>Nyctea scandiaca</i>       | local or wandering bird | no   |
| <i>Fulica atra</i>          | short distance migrator | yes  | <i>Oenanthe oenanthe</i>      | long distance migrator  | yes  |
| <i>Gallinago gallinago</i>  | short distance migrator | yes  | <i>Oriolus oriolus</i>        | long distance migrator  | yes  |
| <i>G. media</i>             | long distance migrator  | no   | <i>Pandion haliaetus</i>      | long distance migrator  | no   |
| <i>G. chloropus</i>         | short distance migrator | no   | <i>P. biarmicus</i>           | local or wandering bird | no   |
| <i>Garrulus glandarius</i>  | local or wandering bird | yes  | <i>Parus ater</i>             | short distance migrator | yes  |
| <i>Gavia arctica</i>        | short distance migrator | no   | <i>P. caeruleus</i>           | short distance migrator | yes  |
| <i>G. stellata</i>          | short distance migrator | no   | <i>P. cinctus</i>             | local or wandering bird | yes  |
| <i>Glaucidium</i>           |                         |      | <i>P. cristatus</i>           | local or wandering bird | yes  |
| <i>passerinum</i>           | local or wandering bird | no   | <i>P. cyanus</i>              | short distance migrator | no   |
| <i>Grus grus</i>            | short distance migrator | no   | <i>P. major</i>               | local or wandering bird | yes  |
| <i>Haematopus</i>           |                         |      | <i>P. montanus</i>            | local or wandering bird | yes  |
| <i>ostralegus</i>           | short distance migrator | yes  | <i>Passer domesticus</i>      | local or wandering bird | yes  |
| <i>Haliaeetus albicilla</i> | short distance migrator | no   | <i>P. montanus</i>            | local or wandering bird | no   |
| <i>Hippolais icterina</i>   | long distance migrator  | yes  | <i>Perdix perdix</i>          | local or wandering bird | no   |
| <i>Hirundo rustica</i>      | long distance migrator  | yes  | <i>Perisoreus infaustus</i>   | local or wandering bird | yes  |
| <i>Jynx torquilla</i>       | long distance migrator  | yes  | <i>Pernis apivorus</i>        | long distance migrator  | no   |
| <i>Lagopus lagopus</i>      | local or wandering bird | yes  | <i>Phalaropus lobatus</i>     | long distance migrator  | yes  |
| <i>L. mutus</i>             | local or wandering bird | no   | <i>Phasianus colchicus</i>    | local or wandering bird | yes  |
| <i>Lanius collurio</i>      | long distance migrator  | yes  | <i>Philomachus pugnax</i>     | long distance migrator  | yes  |
| <i>L. excubitor</i>         | short distance migrator | yes  | <i>Phoenicurus ochruros</i>   | short distance migrator | no   |
| <i>Larus argentatus</i>     | short distance migrator | yes  | <i>P. phoenicurus</i>         | long distance migrator  | yes  |
| <i>L. canus</i>             | short distance migrator | yes  | <i>Phylloscopus borealis</i>  | different               | no   |
| <i>L. fuscus</i>            | long distance migrator  | no   | <i>P. collybita</i>           | long distance migrator  | yes  |
| <i>L. marinus</i>           | short distance migrator | no   | <i>P. sibilatrix</i>          | long distance migrator  | yes  |
| <i>L. minutus</i>           | short distance migrator | yes  |                               |                         |      |

continued

## Appendix. Continued.

| Species                      | Migratory behaviour     | Used | Species                       | Migratory behaviour     | Used |
|------------------------------|-------------------------|------|-------------------------------|-------------------------|------|
| <i>P. trochiloides</i>       | different               | yes  | <i>S. turtur</i>              | long distance migrator  | no   |
| <i>P. trochilus</i>          | long distance migrator  | yes  | <i>Strix aluco</i>            | local or wandering bird | no   |
| <i>Pica pica</i>             | local or wandering bird | yes  | <i>S. nebulosa</i>            | local or wandering bird | no   |
| <i>Picoides tridactylus</i>  | local or wandering bird | yes  | <i>S. uralensis</i>           | local or wandering bird | no   |
| <i>Picus canus</i>           | local or wandering bird | no   | <i>Sturnus vulgaris</i>       | short distance migrator | yes  |
| <i>Pinicola enucleator</i>   | local or wandering bird | no   | <i>Surnia ulula</i>           | local or wandering bird | no   |
| <i>Plectrophenax nivalis</i> | short distance migrator | no   | <i>Sylvia atricapilla</i>     | short distance migrator | yes  |
| <i>Pluvialis apricaria</i>   | short distance migrator | yes  | <i>S. borin</i>               | long distance migrator  | yes  |
| <i>Podiceps auritus</i>      | short distance migrator | yes  | <i>S. communis</i>            | long distance migrator  | yes  |
| <i>P. cristatus</i>          | short distance migrator | yes  | <i>S. curruca</i>             | long distance migrator  | yes  |
| <i>P. grisegena</i>          | short distance migrator | yes  | <i>S. nisoria</i>             | long distance migrator  | no   |
| <i>Porzana parva</i>         | long distance migrator  | no   | <i>Tachybaptus ruficollis</i> | short distance migrator | no   |
| <i>P. porzana</i>            | long distance migrator  | yes  | <i>Tadorna tadorna</i>        | short distance migrator | no   |
| <i>Prunella modularis</i>    | short distance migrator | yes  | <i>Tarsiger cyanurus</i>      | different               | no   |
| <i>Pyrrhula pyrrhula</i>     | short distance migrator | yes  | <i>Tetrao tetrix</i>          | local or wandering bird | yes  |
| <i>Rallus aquaticus</i>      | short distance migrator | no   | <i>T. urogallus</i>           | local or wandering bird | yes  |
| <i>Regulus regulus</i>       | short distance migrator | yes  | <i>Tringa erythropus</i>      | long distance migrator  | yes  |
| <i>Remiz pendulinus</i>      | short distance migrator | no   | <i>T. glareola</i>            | long distance migrator  | yes  |
| <i>Riparia riparia</i>       | long distance migrator  | yes  | <i>T. nebularia</i>           | long distance migrator  | yes  |
| <i>Saxicola rubetra</i>      | long distance migrator  | yes  | <i>T. ochropus</i>            | short distance migrator | yes  |
| <i>S. torquata</i>           | different               | no   | <i>T. stagnatilis</i>         | long distance migrator  | no   |
| <i>Scolopax rusticola</i>    | short distance migrator | yes  | <i>T. totnus</i>              | short distance migrator | no   |
| <i>Serinus serinus</i>       | short distance migrator | no   | <i>Troglodytes</i>            |                         |      |
| <i>Sitta europaea</i>        | local or wandering bird | no   | <i>troglodytes</i>            | short distance migrator | yes  |
| <i>Somateria mollissima</i>  | short distance migrator | yes  | <i>Turdus iliacus</i>         | short distance migrator | yes  |
| <i>Stercorarius</i>          |                         |      | <i>T. merula</i>              | short distance migrator | yes  |
| <i>longicaudus</i>           | long distance migrator  | no   | <i>T. philomelos</i>          | short distance migrator | yes  |
| <i>S. parasiticus</i>        | long distance migrator  | no   | <i>T. pilaris</i>             | short distance migrator | yes  |
| <i>Sterna albifrons</i>      | long distance migrator  | no   | <i>T. torquatus</i>           | short distance migrator | no   |
| <i>S. caspia</i>             | long distance migrator  | no   | <i>T. viscivorus</i>          | short distance migrator | yes  |
| <i>S. hirundo</i>            | long distance migrator  | yes  | <i>Uria aalge</i>             | short distance migrator | no   |
| <i>S. paradisaea</i>         | long distance migrator  | yes  | <i>Vanellus vanellus</i>      | short distance migrator | yes  |
| <i>Streptopelia decaocto</i> | local or wandering bird | no   | <i>Xenus cinereus</i>         | different               | no   |