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 immidiately 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 breath, (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 × 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 × 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 (°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
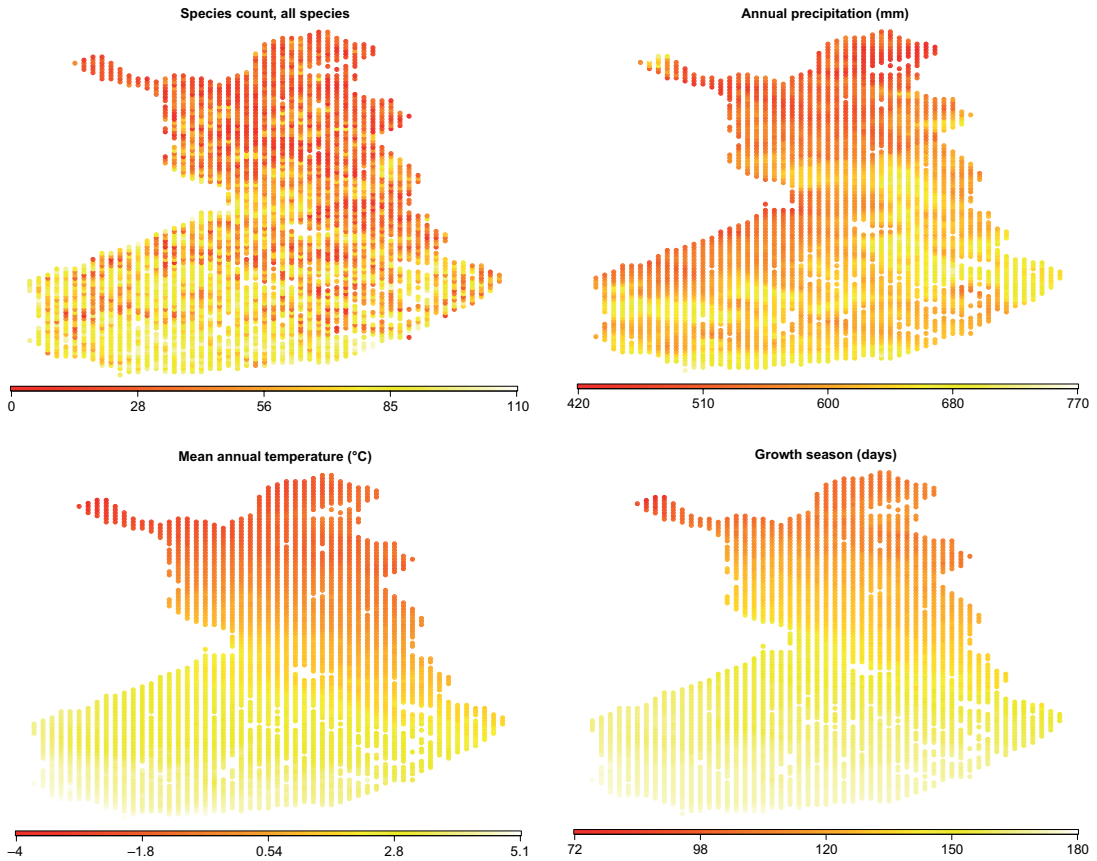
Fig. 1. The spatial patterns of the main variables used in this study.

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 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 agreement 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 10×10-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
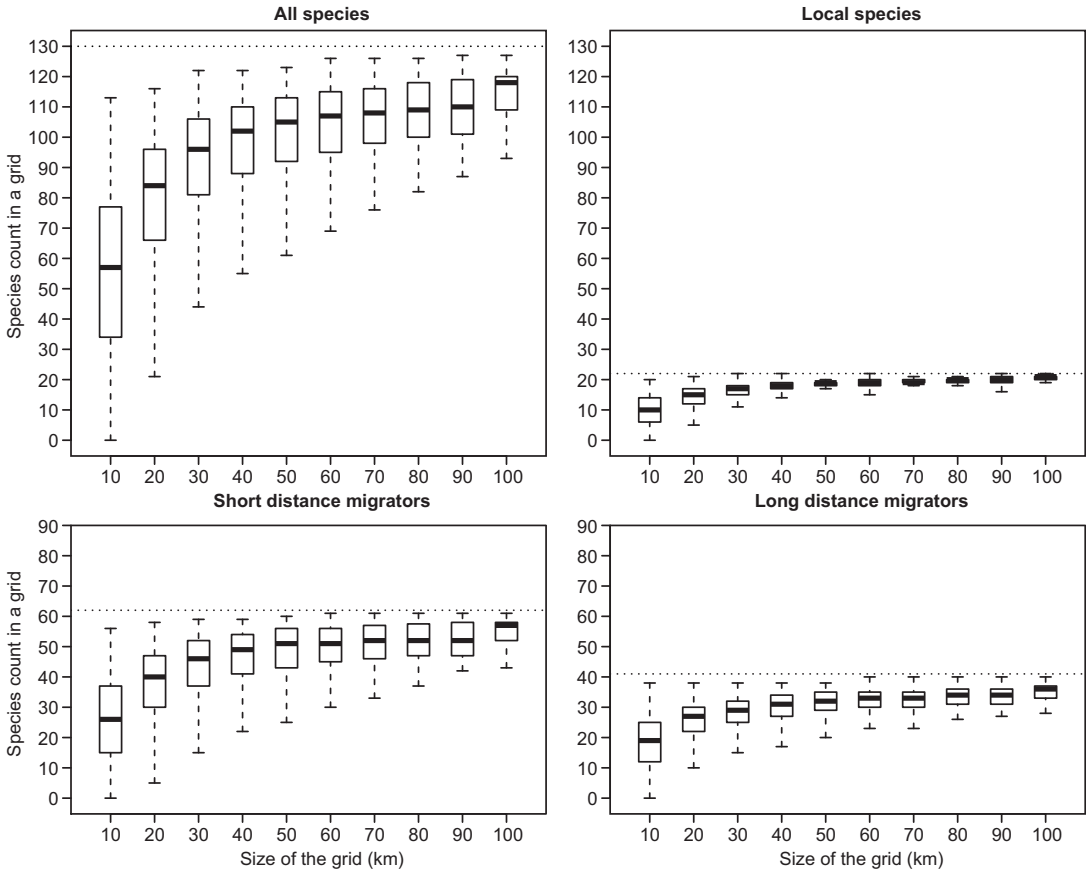
Fig. 2. Distributions of biodiversity, or species counts, across the map grids for varying grid sizes. The biodiversities are shown for all species, as well as for the various mover classifications. The number of species in each classification, and thus the upper limit for the biodiversity, is given 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
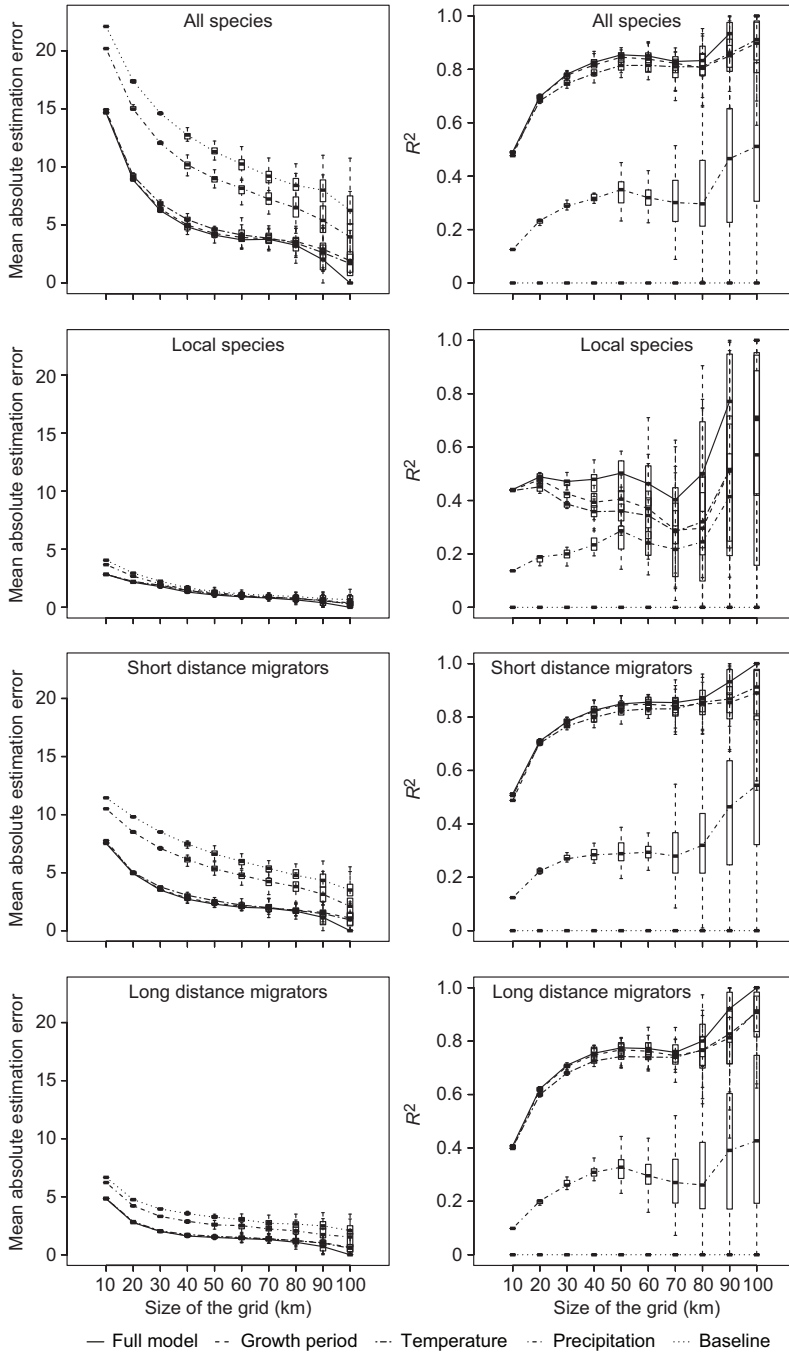
Fig. 3. Mean absolute estimation errors for the biodiversity, or species count, for all species, as well as for the various mover classifications. The box plots show the variance with respect to different alignments of the map grid. The "Full model" is a linear model of the biodiversity based on three 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.
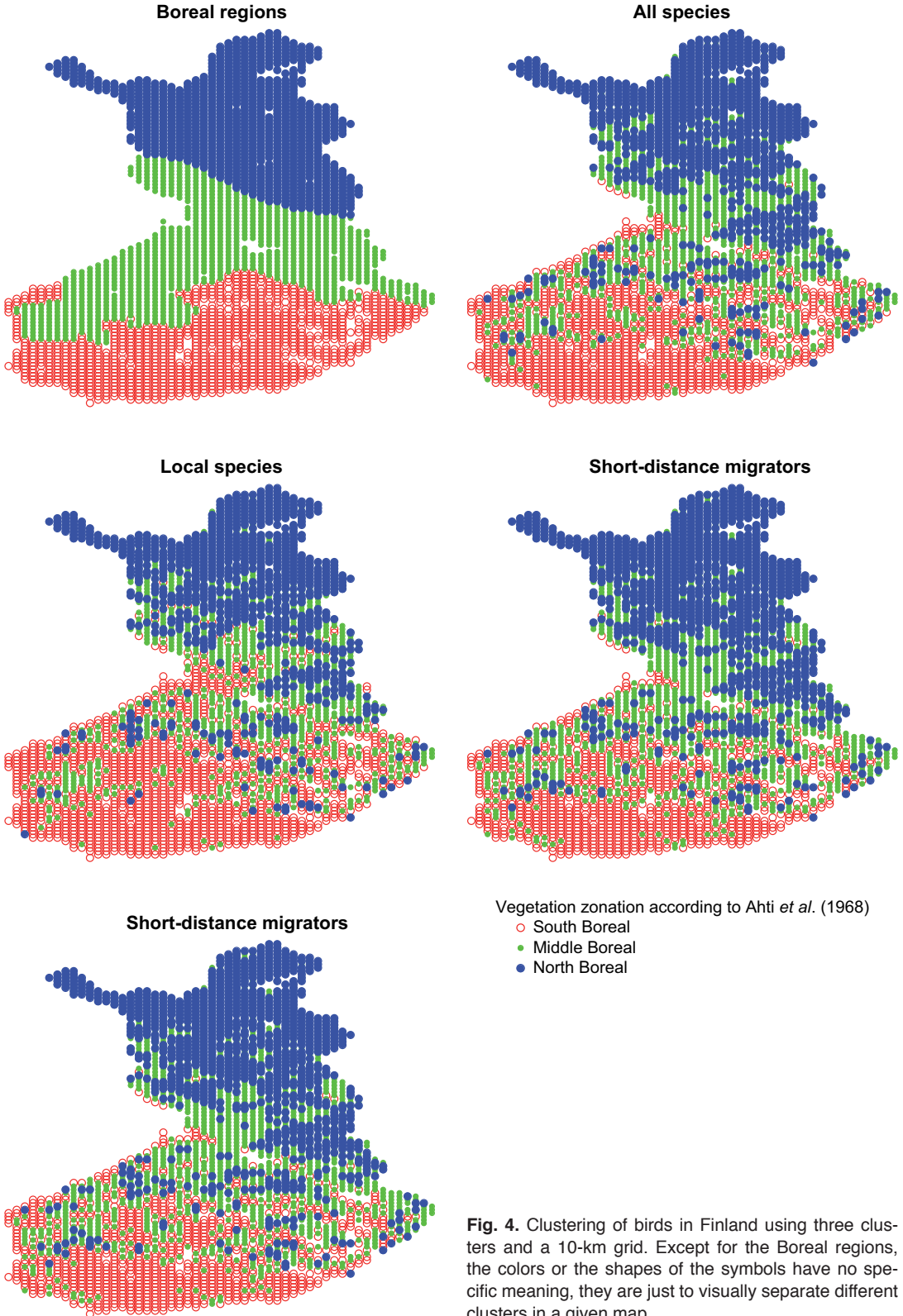
Boreal regions

All species

Local species

Short-distance migrators

Short-distance migrators

Vegetation zonation according to Ahti *et al.* (1968)
- ○ South Boreal
- ● Middle Boreal
- ● North Boreal

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.
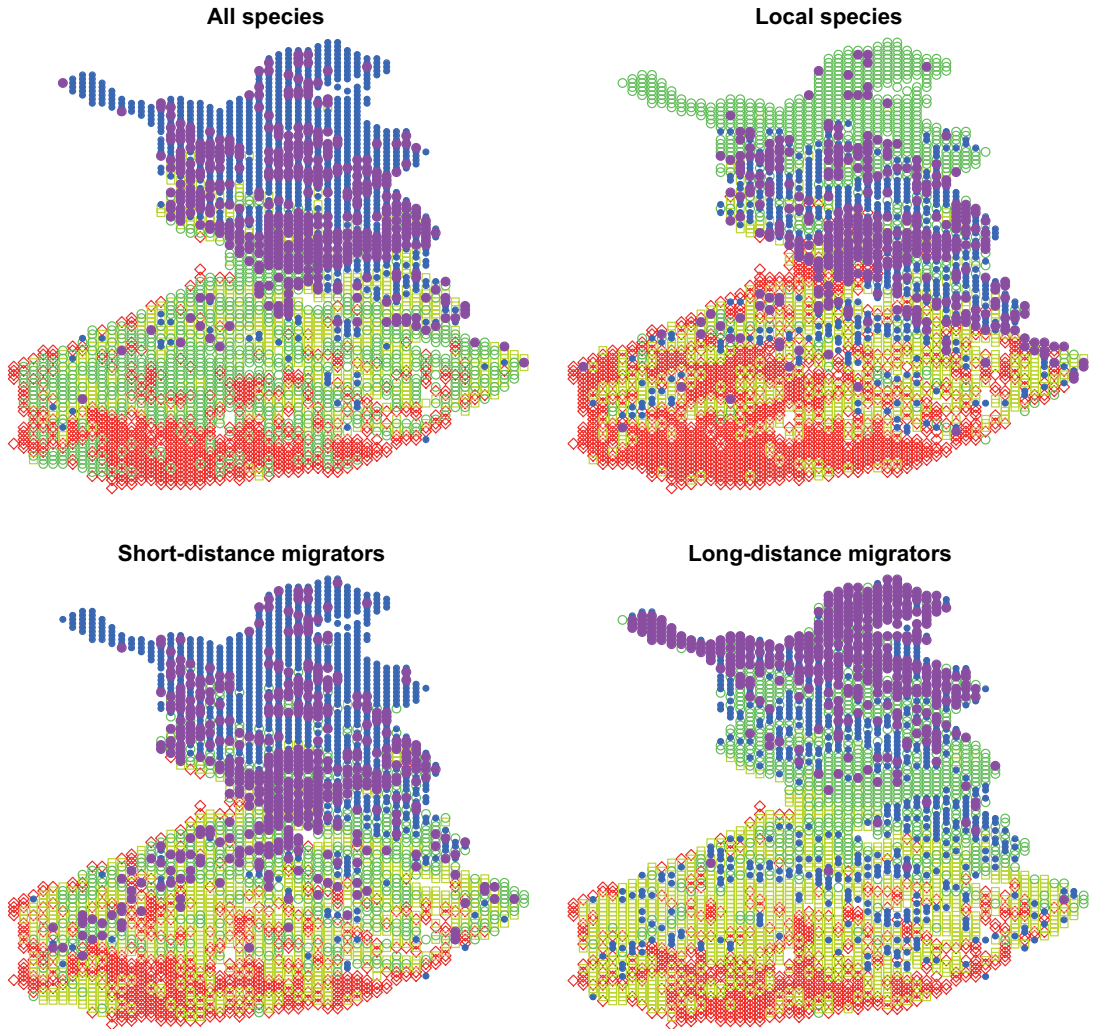
All species

Local species

Short-distance migrators

Long-distance migrators

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
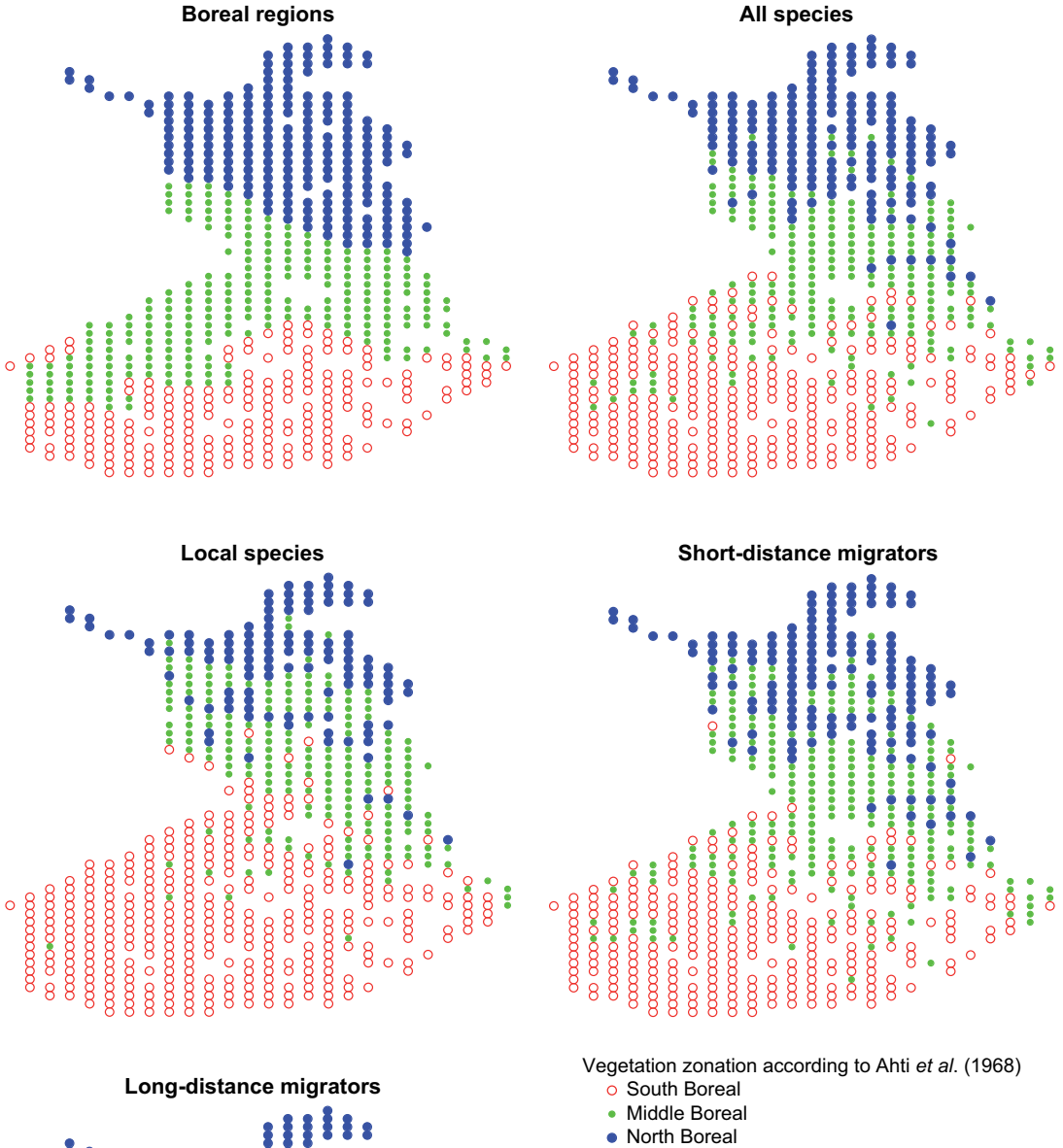
Boreal regions

All species

Local species

Short-distance migrators

Vegetation zonation according to Ahti *et al*. (1968)
- ○ South Boreal
- ● Middle Boreal
- ● North Boreal

Long-distance migrators

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.
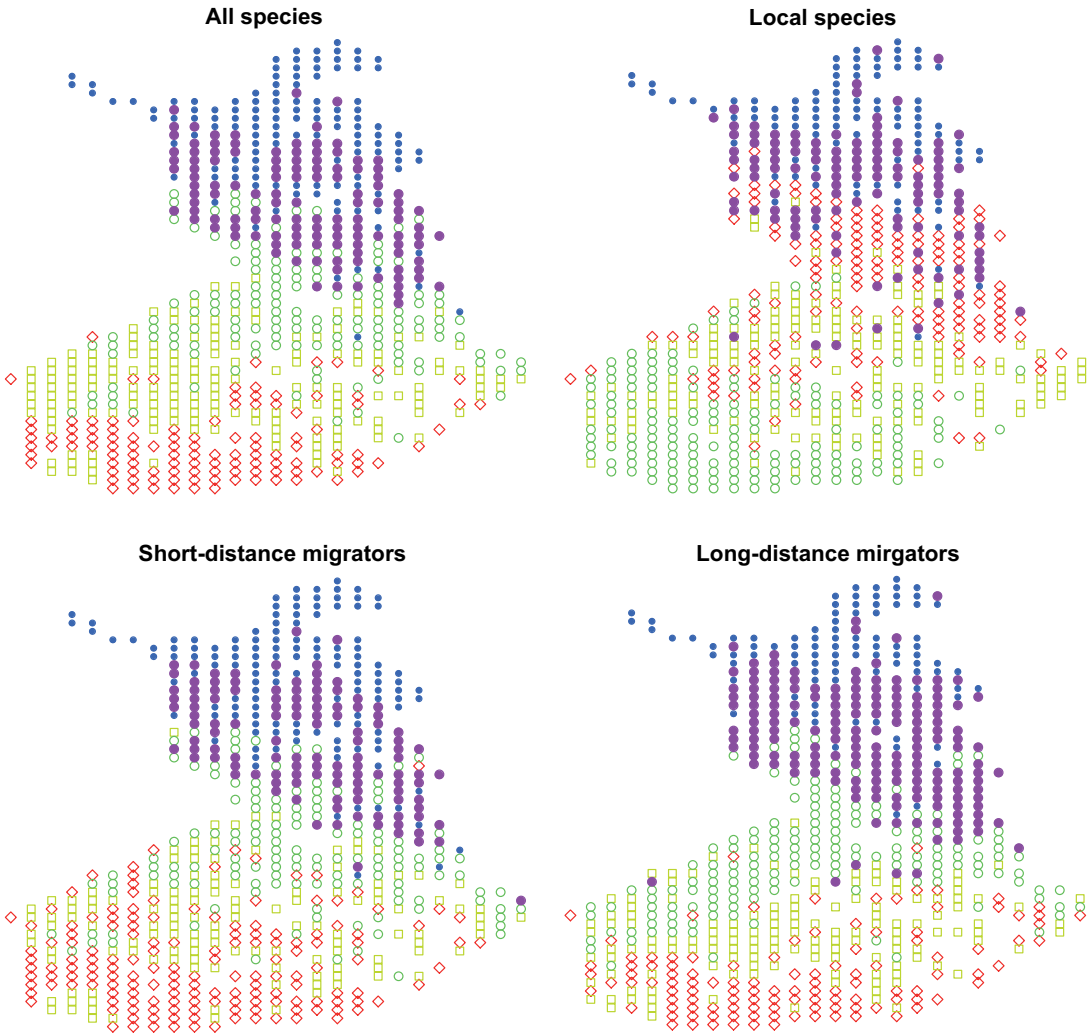
All species

Local species

Short-distance migrators

Long-distance mirgators

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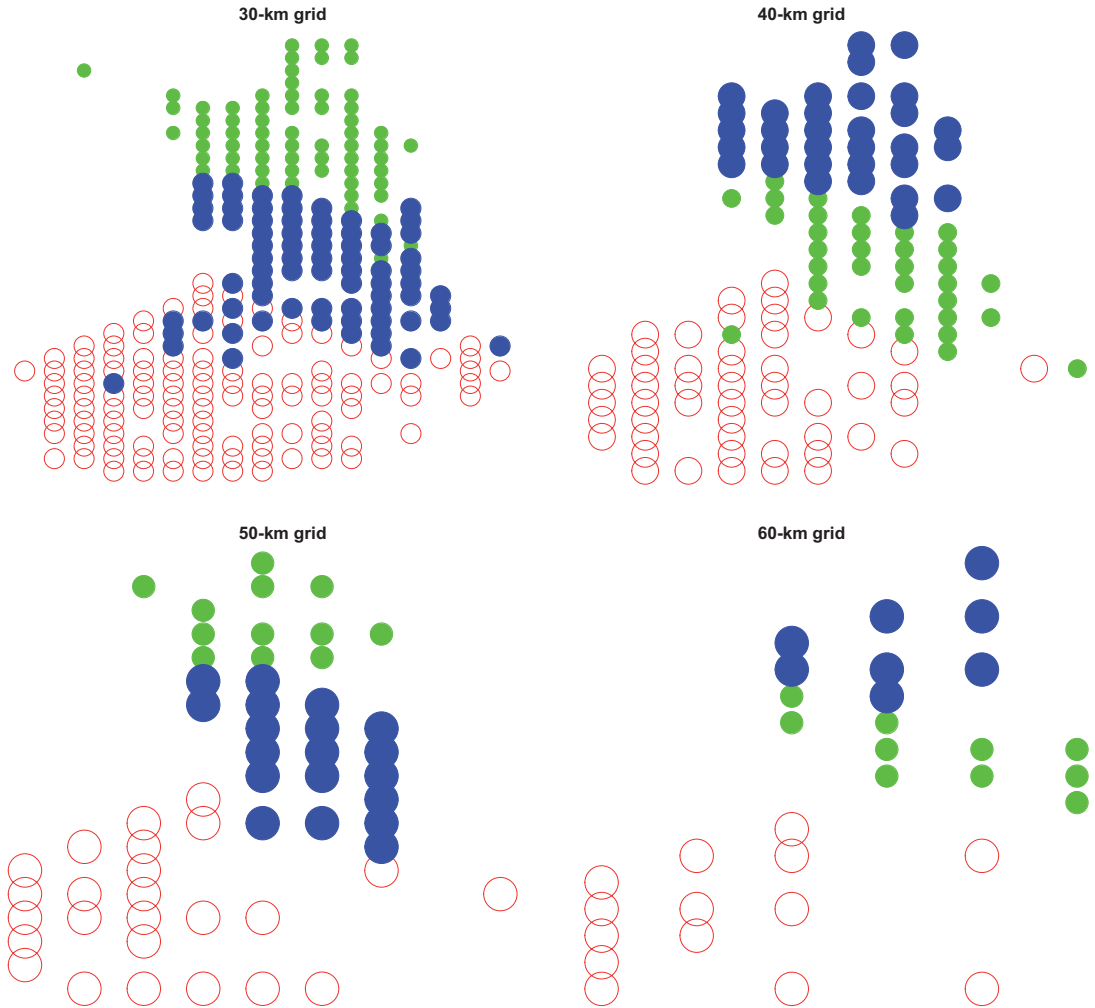
Fig. 8. Clustering of birds in Finland using three clusters. The colors or the shapes of the symbols have no specific meaning, they are just to visually separate different clusters in a given map.

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 constrains 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 sampling. 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.

Acknowledgements

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

Appendix. Continued.

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

Appendix. Continued.

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