



Towards the spatial coherence of biogeographical regionalizations at subcontinental and landscape scales

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ABSTRACT

Aim One of the fundamental tools in biogeography is the classification of the Earth surface into spatially coherent units based on assemblage distinctiveness. However, spatial coherence of biogeographical regions may be scale-dependent, that is, it may change with changing the size of spatial units used. We ask (1) how the clusters resulting from the classification of animal assemblages at different spatial scales differ in their spatial coherence, (2) whether there are geographical trends in the patterns of spatial coherence, and (3) what factors drive these patterns at different scales and in different areas of Europe.

Location Europe.

Methods We used data from distribution atlases at two spatial scales (50 × 50 km and c. 10 × 10 km) and, for each scale, we selected four different areas across Europe, each of them covered by 250 grid cells. We classified each area based on the distributions of mammals (coarser scale only) and birds (both scales). Subsequently, we calculated the spatial coherence of resulting clusters and correlated it with environmental factors and geographical distance.

Results Coarse-scale classifications provided more spatially coherent clusters than the classifications at the finer scale and this pattern was closely related to different strength of distance decay of similarity in the species composition at different scales. Spatial coherence revealed latitudinal trends, so that coarse-scale clusters were more spatially coherent in northern Europe. Geographical distance was the best predictor of spatial patterns at the coarser scale, although this effect was strong only in central and northern Europe. At the finer scale, topography and land cover composition were the most important.

Main conclusions Spatial coherence of biogeographical regionalizations depends on scale and varies geographically. It is closely related to different beta diversity patterns at different scales and in different areas. Heterogeneous areas with high beta diversity and endemism reveal more complex patterns than areas characterized by lower beta diversity but a stronger relationship between beta diversity and distance, and consequently coherent clusters. If the development of the species distribution databases provides fine-resolution data covering large areas in the future, the issue of the scale of biogeographical regionalizations will probably become even more crucial.

Keywords

beta diversity, biogeographical regions, birds, classification analysis, distance decay of similarity, endemism, mammals, spatial scale, species distribution

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INTRODUCTION

Classification of biota into meaningful geographical units, so-called biogeographical regions, is one of the main aims in the field of biogeography (Kreft & Jetz, 2010; Lomolino *et al.*, 2010; Holt *et al.*, 2013). These regionalizations are used for better understanding of biogeographical patterns or may serve as a spatial framework for further biogeographical and ecological studies as well as for effective application of conservation management practices. According to general definition, biogeographical delimitations should maximize the homogeneity in the taxonomic composition while maximizing differences between regions in the considered area (Stoddart, 1992; Kreft & Jetz, 2010). Traditionally, main attention has been paid to broad spatial scales, where criteria of taxonomical distinctiveness at the level of genera (or above) were originally emphasized for the division of Earth's surface into geographical units of approximately continental extent (Wallace, 1876, 1894). However, biogeographical regionalizations have become of special importance also at fine spatial scales, where assemblage distinctiveness at the level of species has been commonly used for the delineation of subregions, districts, zones etc. within global biogeographical regions (Crowe & Crowe, 1982; De Klerk *et al.*, 2002; Linder *et al.*, 2012), continents (Heikinheimo *et al.*, 2007; Rueda *et al.*, 2010) or even smaller areas (Pasinelli *et al.*, 2001; Moreno Saiz & Lobo, 2007; Filipe *et al.*, 2009). This inevitably consists of the decrease of both total spatial extent of the study and the grain (size of the basic sampling unit), because large grid cells may not be appropriate for the division of smaller areas. Recently, Kreft & Jetz (2010) pointed out that, in the use of assemblage distinctiveness for identifying distinct biogeographical regions, the question of the scale (i.e. grain and extent) of the classification analysis is critical. Despite this fact, issues concerning spatial properties of biogeographical regionalizations have been rarely discussed to date (e.g. Moreno Saiz *et al.*, 1998 or Morrone & Escalante, 2002).

Some findings about spatial properties of biogeographical regions in Europe were published by Heikinheimo *et al.* (2007) and Rueda *et al.* (2010) who classified the European continent based on the distribution of different animal taxa. Both studies used the same spatial framework represented by UTM grid cells spanning 50 × 50 km which are commonly used for mapping of the European biota (e.g. Hagemeyer & Blair, 1997; Mitchell-Jones *et al.*, 1999; Gasc *et al.*, 2004). Results of both studies showed that, at this spatial resolution, European biogeographical regions are highly coherent in space, that is, grid cells belonging to the same cluster are spatially connected and particular regions are thus geographically well distinguished from each other. Heikinheimo *et al.* (2007) thus argued that Europe can be divided into cohesive regions despite a long history of human presence and habitat modification. Generally, spatial coherence seems to be a common feature of biogeographical delimitations at broader scales of approximately continental extent (Heikinheimo

et al., 2007, 2012; Rueda *et al.*, 2010; Linder *et al.*, 2012). On the other hand, at finer spatial scales, biogeographical units resulting from the classification analysis often tend to disintegrate into spatially discontinuous patches (Pasinelli *et al.*, 2001; Bunce *et al.*, 2002; Eronen *et al.*, 2011; Divíšek *et al.*, 2014). The reason is that classification based on small grid size has a tendency to distinguish separate landscape types rather than regions with similar history, and these types, determined by particular and repeatable combination of environmental parameters, may occur in distinct places. Therefore, there is a good reason to assume that the spatial coherence of classified biogeographical regions changes with changing the scale of observation.

Several factors may largely influence the classification results and spatial properties of resulting biogeographical regions including their coherence in space. If we set aside the arbitrary choice of dissimilarity measure and clustering algorithm, which inevitably influence each classification (Murguía & Villaseñor, 2003), the classification results primarily depend on the spatial pattern in the dissimilarity of assemblages, that is, on the patterns in beta diversity (Legendre & Legendre, 2012). It has been recently shown that beta diversity decreases with coarsening the spatial resolution, so that grid cells become more similar and their similarity decreases with geographical distance slower than at finer scales (Lennon *et al.*, 2001; Keil *et al.*, 2012). We therefore expect that the spatial coherence of biogeographical delimitations at different scales is directly related to the scaling of beta diversity and that the spatial pattern of resulting biogeographical units could be consequently ascribed to the factors which also control beta diversity patterns at different scales. More explicitly, we predict that environmental factors are more important at fine scales, while geographical distance which reflects historical factors and species dispersal limitations plays a major role at broader scales.

Besides the variation of the spatial coherence of regions with scale (grain), we expect some geographical variation. Beta diversity patterns in Europe vary considerably latitudinally, southern Europe being characterized by high beta diversity, small geographical ranges of species and high levels of endemism, related to enormous topographic heterogeneity (Baselga, 2008; Svenning *et al.*, 2011). Also, the peninsulas of southern Europe served as glacial refugia, leading to the persistence of fragmented populations of individual species (often genetically distinct; Hewitt, 2000; Sommer & Nadachowski, 2006). Due to all these factors, species distribution is often discontinuous and fragmented in southern Europe, possibly leading to low coherence of clusters based on assemblage similarity. We expect that this latitudinal trend diminishes when the regionalization is based on the smaller grain. The reason is that the smaller grain regionalization should reflect discontinuous landscape types rather than history and dispersal limitations regardless of the latitude.

Here, we focus on the evaluation of the spatial pattern of biogeographical units (regions, zones etc.) in Europe statistically delineated on the basis of assemblage distinctiveness

(beta diversity). Although the term 'biogeographical (zoogeographical) region' is often understood in relation to global biogeographical divisions, we use it also for divisions at finer scales throughout this study, as their primary purpose is to explore regional differences in the composition of species assemblages. We focus on the spatial coherence of regions assessed at two spatial scales (50×50 km and $c. 10 \times 10$ km) and in different areas of Europe. Based on the above-mentioned theoretical considerations, we test the following hypotheses: (1) The clusters based on fine-grained assemblage distinctiveness reflect rather different landscape types and thus are less spatially coherent than those based on large sampling units (grid cells). (2) Spatial coherence of the clusters decreases towards the south, due to higher fragmentation of species distributions in southern Europe. (3) This latitudinal trend diminishes for fine-grained regionalization, as the role of history and dispersal limitation decreases at these scales. (4) The factors which are responsible for spatial coherence of the clusters are the same as the factors responsible for beta diversity, and predictably vary with scale and geographical position.

MATERIALS AND METHODS

Spatial framework

To compare the spatial coherence of biogeographical regionalizations at different spatial scales across Europe, we considered two spatial resolutions (grains): 50×50 km and 10×10 km, which are most commonly used for mapping of the European biota. Coarser resolution (50×50 km) is used for mapping of entire European continent, whereas finer resolution (10×10 km) is often used in national or regional distribution atlases. However, central European countries (e.g. the Czech Republic or Germany) use slightly coarser grids based on the geographical coordinates; $10'$ of longitude and $6'$ of latitude which is $c. 12 \times 11.1$ km on the 50th parallel (Ehrendorfer & Hamann, 1965), but we supposed that this small difference should not influence our results. Therefore, we hereafter use the term 'fine scale' for both these resolutions.

At both spatial scales (resolutions), we applied following criteria to select model areas for biogeographical regionalizations: (1) availability of species distribution data; (2) selected areas should be as large as possible but each of them had to be covered by the same number of grid cells in order to make the spatial coherence of clusters comparable (the extent of each area was thus derived from the number of grid cells in the smallest available data set); (3) both the shape and the position should be chosen with respect to maximum connectivity of grid cells; (4) the selection of areas should follow latitudinal gradient; (5) areas selected at the same scale were not allowed to overlap each other. Using these criteria, we selected four areas at each spatial scale, each of them divided to 250 grid cells (Fig. 1). At the coarse scale, we selected the following areas from the north to the south: Scandinavia

(including Norway, Sweden and northern Finland), central Europe (including Germany, the Czech Republic and Poland), south-east Europe (including the Balkans, Slovenia and Hungary) and the Iberian Peninsula. According to Metzger *et al.* (2005), the Iberian Peninsula is situated predominantly in the Mediterranean environmental zone (also in the Atlantic zone in the north). South-east Europe is situated largely in the Pannonian and Continental zones, central Europe in the Continental zone (also in the Atlantic zone in the west), and Scandinavia is situated in the Boreal, Nemoral and North Alpine zones. At the fine scale, we selected the following areas: northern Finland, southern Finland, eastern Czech Republic and Provence-Alpes-Côte d'Azur in southern France. Provence-Alpes-Côte d'Azur is situated in the Mediterranean environmental zone, eastern Czech Republic is situated in the Continental and partly also in the Pannonian zone, southern Finland in the Boreal and partly also in the Nemoral zone, and northern Finland in the Boreal and North Alpine environmental zones (Metzger *et al.*, 2005).

Species distribution data

Coarse grain distribution data (presence/absence records) were extracted from European distribution atlases, which are based on the 50×50 km Universal Transverse Mercator (UTM) grid. We used both data on mammals (Mitchell-Jones *et al.*, 1999) and on birds (Hagemeyer & Blair, 1997). At the fine scale, we used data from national or local distribution atlases which were available for birds only. All used atlases are based on the 10×10 km grid except the Atlas of Breeding Birds in the Czech Republic, which uses a grid of $c. 12 \times 11.1$ km. In the case of Provence-Alpes-Côte d'Azur, breeding bird distributions were extracted from <http://www.faute-paca.org> (accessed in September 2014). For the eastern Czech Republic, the species data were extracted from Štátný *et al.* (2006) and for southern and northern Finland from Valkama *et al.* (2011). We excluded all records of species not native in the given area and all records of bats. For birds, we used records of probable and confirmed breeding only. Characteristics of species assemblages in each selected area can be found in Tables 1 and 2. For evaluation of the consistency between atlases in considered spatial resolutions, see Appendix S1 in Supporting Information.

Environmental data

To characterize environmental conditions within grid cells, we used the digital elevation model and the climatic data from the WorldClim database in resolution of $c. 1$ km (Hijmans *et al.*, 2005). For each grid cell, we calculated the maximum and minimum altitude as well as the maximum and minimum values of mean annual temperature and annual precipitation. We preferred maximum and minimum values instead of the arithmetic mean of these variables within each grid cell because, with increasing grain, the variability of maxima and minima may differ from the variability of the mean values.

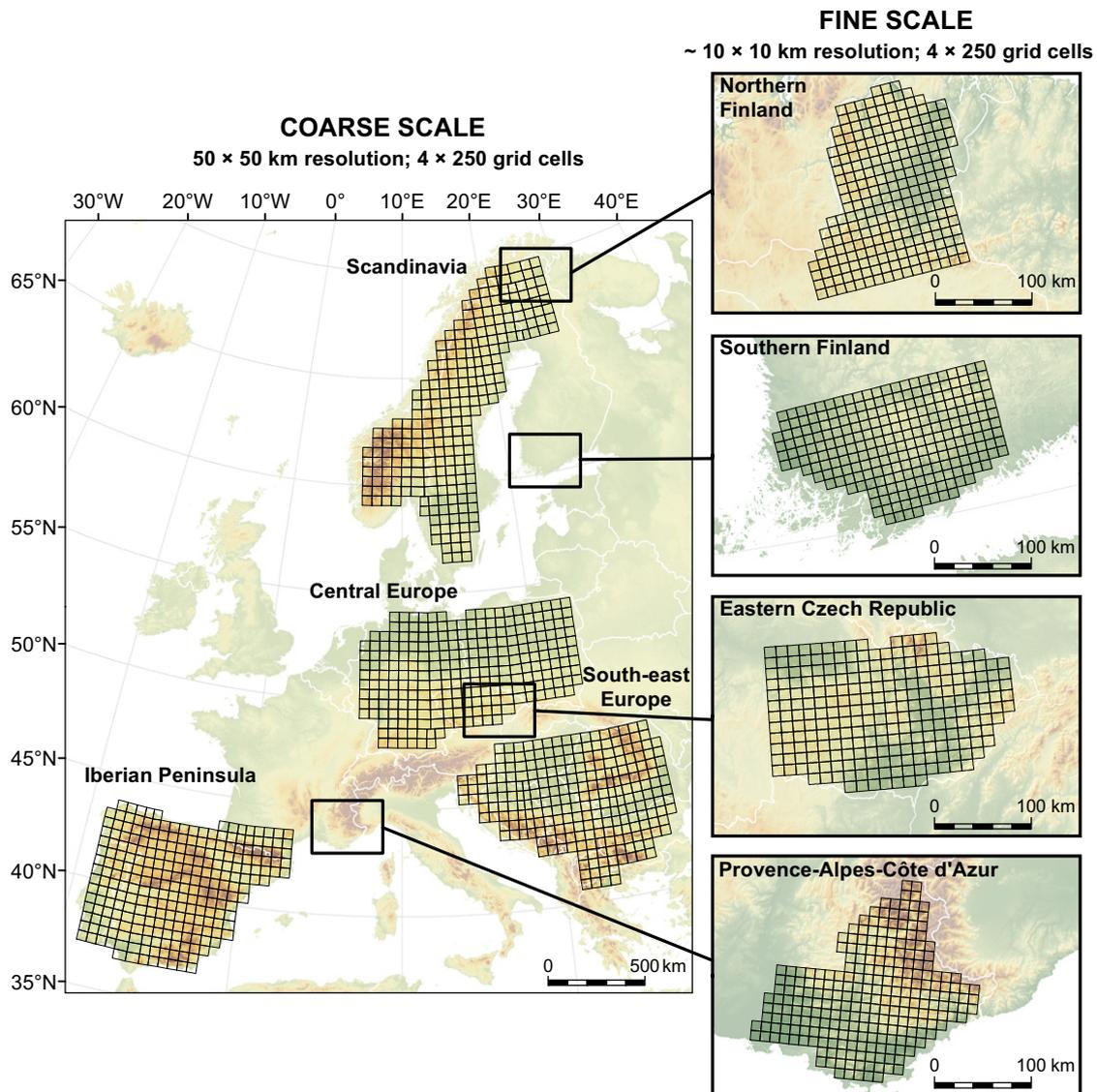


Figure 1 Maps of the selected areas in Europe at two spatial scales (resolutions). All maps are in Lambert Azimuthal Equal Area projection.

All grid cells were also characterized by the relative area of land cover types extracted from the CORINE 2000 Land Cover database (EEA, 2010). We adopted the classification by Keil *et al.* (2012) and reclassified the original 44 land cover types recognized in Europe into 18 broader classes which represent land cover types potentially relevant for the considered taxa. The data were processed using the ARCGIS 10.2 software (ESRI, 2014).

Classification analysis

In order to classify the selected areas into biogeographical regions, we first calculated the dissimilarity of species composition between each pair of grid cells in particular data sets. Note that we understand this dissimilarity as equivalent to beta diversity throughout this study. We used the beta-sim index (β_{sim}), which is independent of species richness gradient across the studied area (Koleff *et al.*, 2003a). The

β_{sim} index is used to calculate the compositional dissimilarity between two grid cells as:

$$\beta_{sim} = 1 - \frac{a}{\min(b, c) + a}$$

where a is the number of shared species, b is the number of species unique to the first grid cell and c is the number of species unique to the second grid cell. Values of β_{sim} vary between 0 for identical species composition in the compared grid cells and 1 for grid cells which do not share any species. This index is implemented in a 'betadiver' function of the 'vegan' package (Oksanen *et al.*, 2013) and its application to our data sets resulted in dissimilarity matrices, each of them containing 62,500 dissimilarity values (31,125 unique pairwise comparisons). These matrices were then used in the agglomerative hierarchical clustering procedure. We applied Ward's minimum variance method (Ward, 1963), that minimizes the sum of within-group sums of squares. Although other

Table 1 Characteristics of species assemblages in selected areas in Europe at a spatial scale of 50×50 km. See the Methods section for explanation. Note that mean endemism (*CWE* index) was multiplied by 100.

	Mean alpha diversity	Mean beta diversity	Beta-distance relationship	Gamma diversity	Mean endemism
Mammals					
Scandinavia	20.5	0.21	0.53	44	0.33
Central Europe	31.7	0.12	0.54	56	0.69
South-east Europe	24.8	0.32	0.03	76	9.44
Iberian Peninsula	20.9	0.26	0.16	54	0.99
Birds					
Scandinavia	109.9	0.22	0.62	231	0.55
Central Europe	142.0	0.09	0.40	243	0.46
South-east Europe	100.2	0.21	0.10	280	3.26
Iberian Peninsula	102.9	0.23	0.24	251	0.76

Table 2 Characteristics of bird species assemblages in selected areas in Europe at a spatial scale of $c. 10 \times 10$ km (12×11.1 km in the case of the Czech Republic). See the Methods section for explanation. Note that mean endemism (*CWE* index) was multiplied by 100.

	Mean alpha diversity	Mean beta diversity	Beta-distance relationship	Gamma diversity	Mean endemism
Birds					
Northern Finland	31.9	0.35	0.18	152	3.94
Southern Finland	103.2	0.11	0.11	196	0.93
Eastern Czech Republic	94.5	0.13	0.09	192	0.41
Provence-Alpes-Côte d'Azur	73.2	0.27	0.58	213	0.52

clustering algorithms such as Unweighted Pair Group Method using Arithmetic Averages (UPGMA) are usually recommended in biogeographical literature (e.g. Kreft & Jetz, 2010), we favoured Ward's algorithm, because UPGMA produced clusters of extremely different sizes (high proportion of one-cell clusters) in our analyses. As Ward's method works in Euclidean space, it should not be directly applied on the dissimilarity matrix calculated using the β_{sim} index (Legendre & Legendre, 2012). To make the dissimilarity matrix Euclidean, we used the correction developed by Cailliez (1983), computing and adding the smallest positive number (constant) to each dissimilarity value. This method is implemented in the 'ade4' package (Dray & Dufour, 2007).

Measuring of spatial coherence

For each dendrogram cut up to 20 clusters, that is, for each partition from 2 up to 20 clusters, we measured the spatial coherence of each cluster using modified connectivity measure (Turner *et al.*, 2001):

$$SC = \frac{LC_i}{p_i},$$

where LC_i is the number of grid cells in the largest patch of cluster i and p_i is the total number of grid cells in cluster i . SC value close to zero indicates low spatial coherence, whereas the SC value equal to 1 indicates a completely coherent cluster. The spatial connectivity of grid cells was assessed here using the rook connectivity scheme (Fortin & Dale, 2005). In this scheme, each grid cell is considered to be

connected with four neighbouring grid cells in four cardinal directions (N, S, E, W).

Analysis of spatial patterns

First, we calculated mean alpha and beta diversity, relationship between beta diversity and geographical distance (beta-distance relationship), gamma diversity and mean endemism in each considered area to explore relationships between these characteristics and mean spatial coherence of clusters resulting from the classification analysis. Mean alpha diversity was calculated as a mean number of species per grid cell. Mean beta diversity was calculated as a mean of all pairwise dissimilarities in species composition between grid cells measured using β_{sim} coefficient. Beta-distance relationship was calculated as a value of Mantel correlation (Pearson's correlation coefficient) between the original β_{sim} matrix and the matrix of pairwise geographical distances between the grid cells. Gamma diversity is the total number of species in given area. Endemism was calculated, for each grid cell, using the corrected weighted endemism measure (*CWE*; Crisp *et al.*, 2001):

$$CWE_j = \frac{\sum_{i=1}^k \frac{1}{c_i}}{k_j},$$

where c_i is the number of grid cells occupied by species i , and k_j is the total number of species in grid cell j . The higher the *CWE* value, the higher the endemism. To express mean endemism for each considered area, we calculated the arithmetic mean of *CWE* values and multiplied the result by 100 (Tables 1 and 2).

In order to assess the independent effects of topography, climate, land cover and spatial proximity on the spatial pattern of particular regionalization, we used hierarchical partitioning (Chevan & Sutherland, 1991). In this analysis, each regionalization was represented by a square binary matrix describing group allocations. This matrix contained 1 for grid cells which belong to the same cluster and 0 for grid cells which do not belong to the same cluster. Explanatory variables, that is matrices representing pairwise dissimilarities in topography, climatic conditions, land cover composition and geographical distance between grid cells, were calculated using Euclidean distance. All matrices were subsequently rearranged into vectors. In this case, the hierarchical partitioning performs logistic regressions to assess the independent effects of several continuous predictors (i.e. rearranged environmental and geographical dissimilarity/distance matrices) on the binary response variable representing a classification result. Within each considered area, we repeated this analysis for each partition from 2 up to 20 clusters. We also tested the independent effects of explanatory variables by 1000 randomizations using the 'rand.hp' function in the 'hier.part' package

(Walsh & MacNally, 2008). Note that we use the term 'effect' to indicate a statistical relationship, not a proven mechanistic causation (Hawkins, 2012). All the above-mentioned statistical analyses were done in the R software (R Core Team, 2013).

RESULTS

At the coarser spatial scale (resolution 50×50 km), clusters resulting from the classification analysis were generally more spatially coherent than those at the finer resolution of $c. 10 \times 10$ km (Figs 2 & 3) and the spatial coherence pattern was very similar for both mammals (Fig. 2a) and birds (Fig. 2b). At the broader scale, we also found that spatial coherence increased with increasing latitude. In southern Europe, clusters were generally less spatially coherent than in central Europe or in Scandinavia, respectively. On the other hand, at the finer scale, spatial coherence decreased with the increasing latitude (Fig. 2c), although this pattern was mainly caused by relatively coherent clusters in Provence-Alpes-Côte d'Azur. Schematic maps of all regionalizations from 2 up to 19 clusters can be found in Appendix S1.

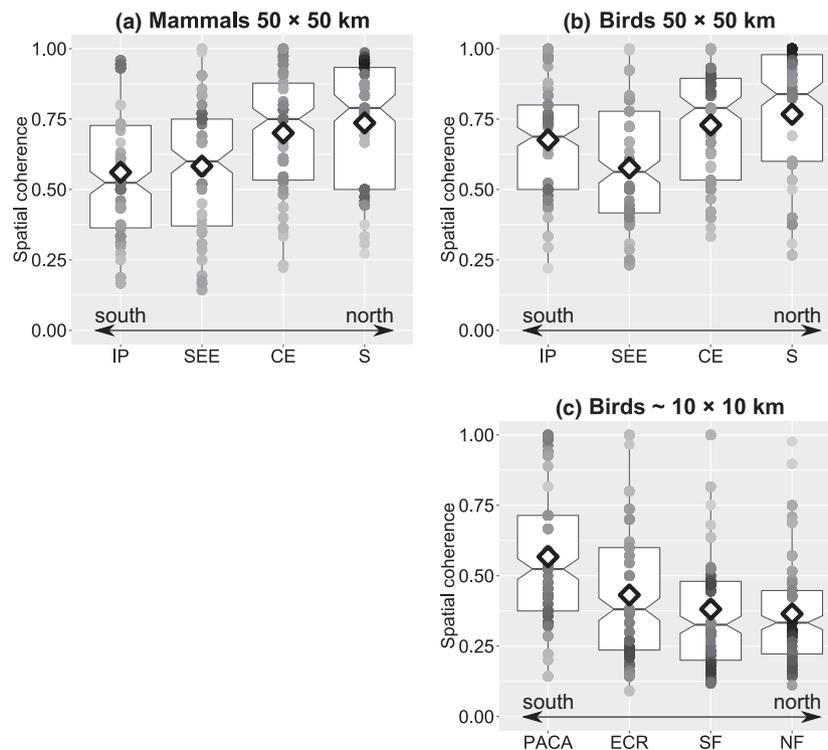


Figure 2 Spatial coherence of clusters resulting from classification analysis based on β_{sim} dissimilarity measure and Ward's clustering algorithm. Spatial coherence was measured for each cluster in each dendrogram cut up to 20 clusters, that is, in each partition from 2 up to 20 clusters. Each point in the diagram represents one region (cluster) from particular regionalization. Shades of grey indicate the density of points. (a) Mammal distributions in resolution 50×50 km. (b) Bird distributions in resolution 50×50 km. (c) Bird distributions in resolution $c. 10 \times 10$ km. IP – Iberian Peninsula, SEE – south-east Europe, CE – central Europe, S – Scandinavia. PACA – Provence-Alpes-Côte d'Azur, ECR – eastern Czech Republic, SF – southern Finland, NF – northern Finland. Thick horizontal lines in box-plots indicate the median and the diamonds indicate the mean. The bottom and top of each box indicates the 25th and 75th percentiles respectively. Non-overlapping box notches indicate strong evidence that the individual medians differ. The vertical lines (whiskers) represent either the maximum value or $1.5 \times$ interquartile range depending on which is closer to the mean. Values outside the range of whiskers are defined as outliers. When there are no outliers, the whiskers show the maximum and minimum values.

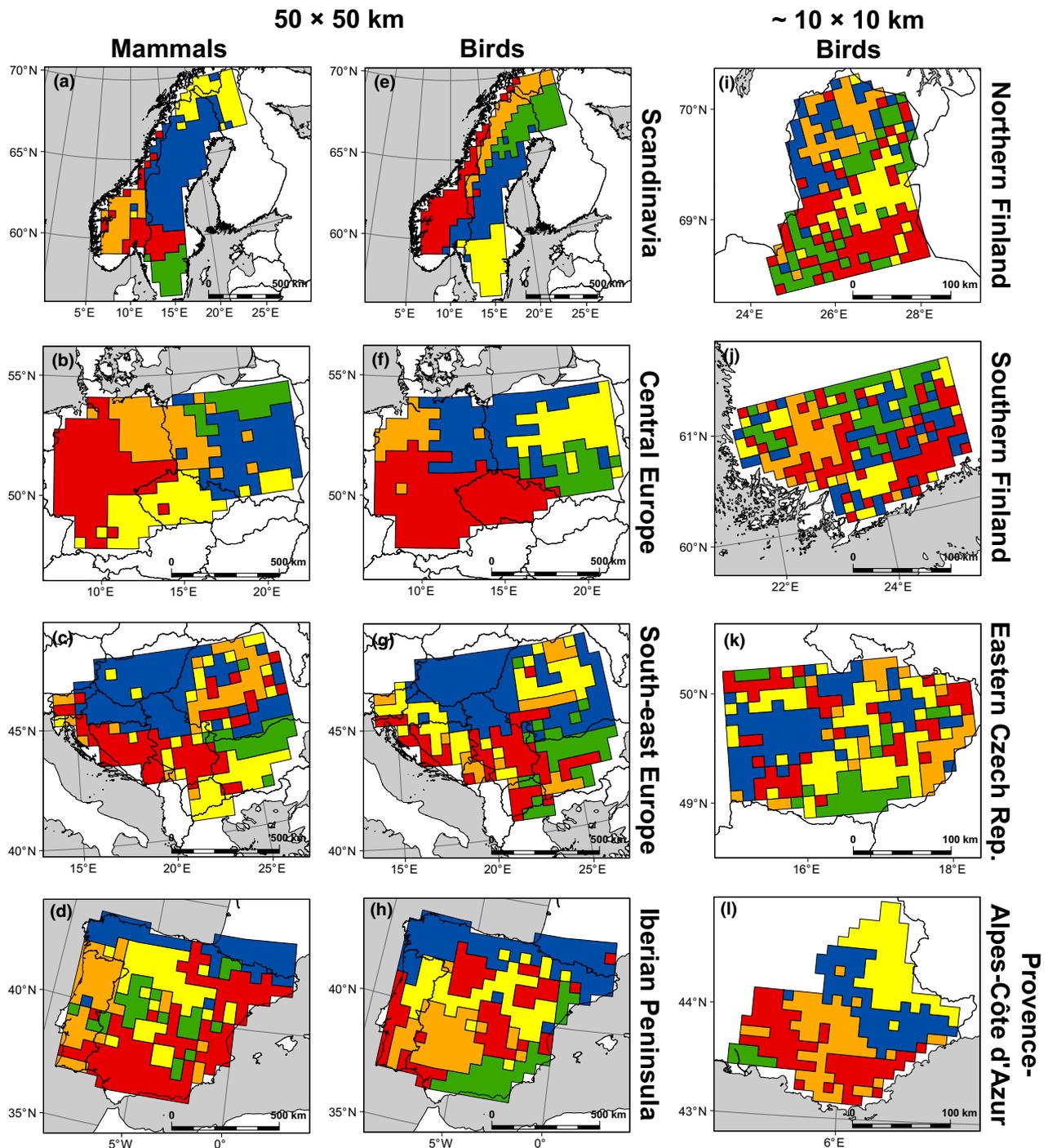


Figure 3 Examples of regionalizations resulting from classification analysis based on dissimilarity in bird and mammal assemblages (β_{sim}) in Europe. For each area, partition into five clusters is shown. Maps are in Lambert Azimuthal Equal Area projection.

By regressing the mean spatial coherence of regionalizations on each of the five characteristics of species assemblages in considered areas (Fig. 4), we found that spatial coherence was strongly positively related to the strength of beta-distance relationship and this relationship was consistent across both scales (Fig. 4c,h,m). At the coarse scale, negative relationships were found with mean beta diversity, gamma diversity and mean

endemism. At the fine scale, relationships were weaker and sometimes even opposite to those found at the coarse scale (Fig. 4l,n).

Results of the hierarchical partitioning showed that at the broader spatial scale, the geographical distance fundamentally influenced the spatial coherence of the clusters (Fig. 5a,b). However, this effect was geographically very specific and it was pronounced only in higher latitudes, that is, in central Europe

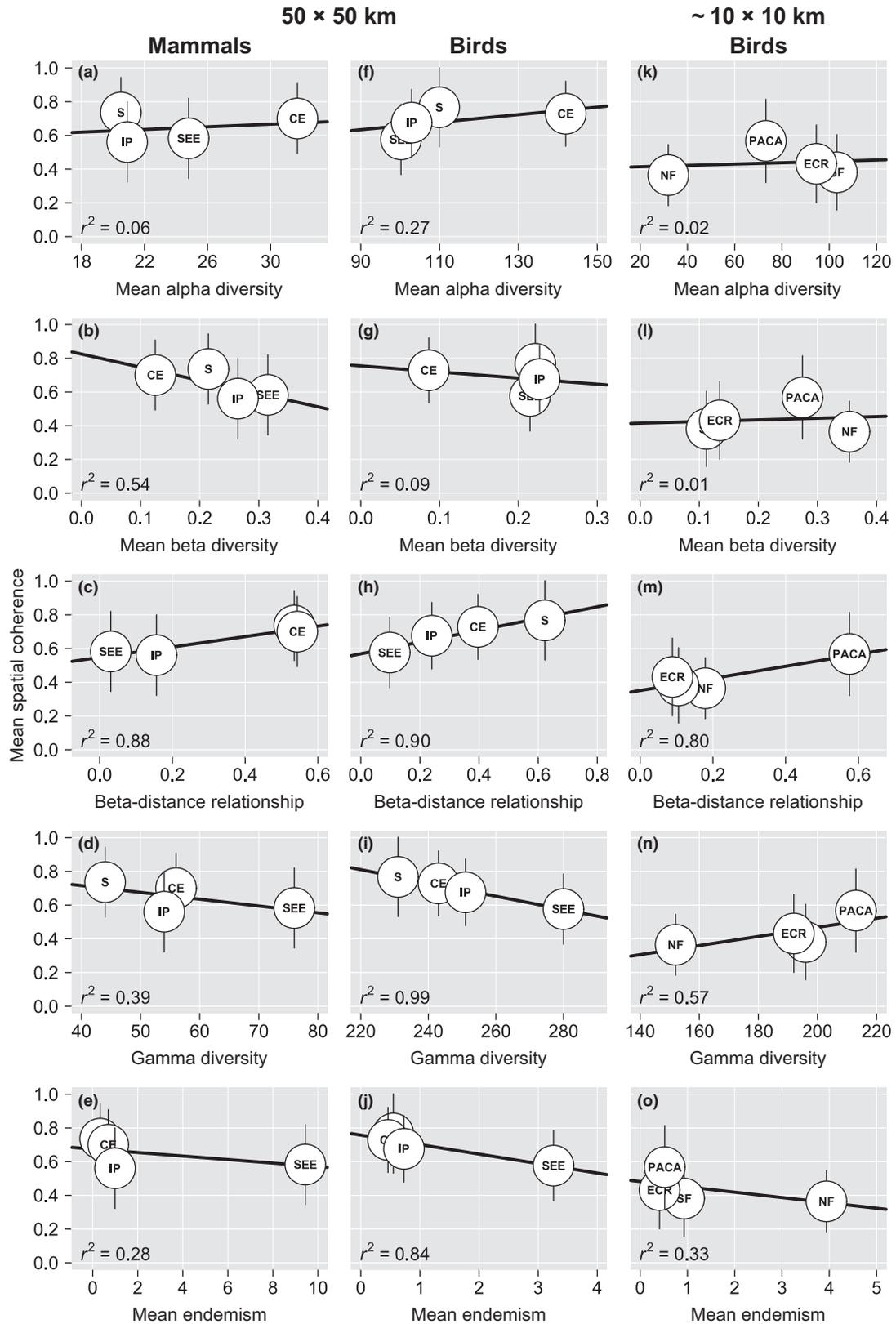


Figure 4 Relationships between mean spatial coherence of clusters (each cluster in each partition up to 20 clusters was considered) and five characteristics of bird and mammal assemblages in selected areas in Europe (see also Tables 1 and 2). IP – Iberian Peninsula, SEE – south-east Europe, CE – central Europe, S – Scandinavia. PACA – Provence-Alpes-Côte d’Azur, ECR – eastern Czech Republic, SF – southern Finland, NF – northern Finland. Error bars indicate standard deviations of spatial coherence values.

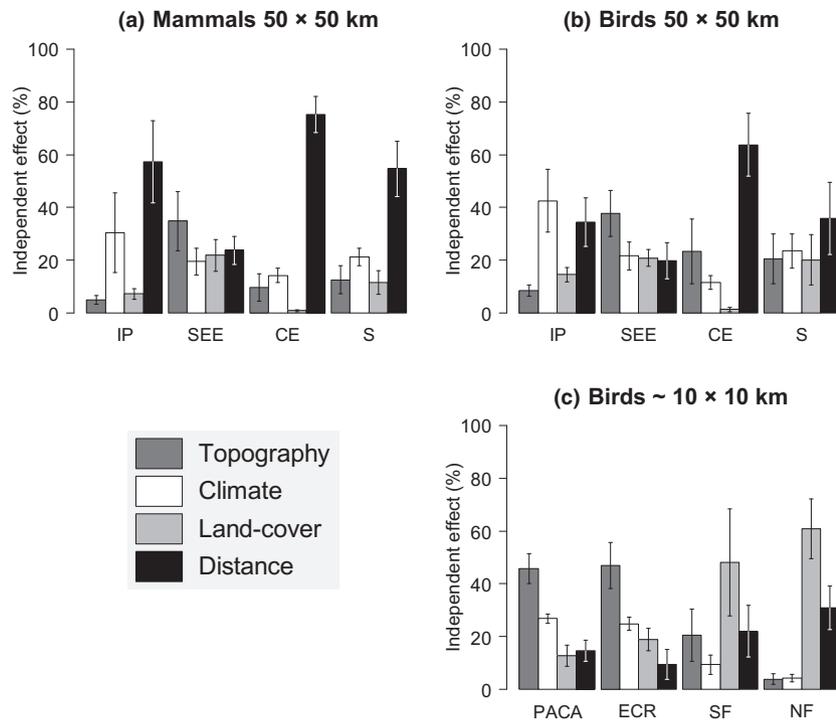


Figure 5 Independent effects of topography, climate, land cover and geographical distance on the assignment of grid cells into clusters resulting from classification analyses of birds and mammals in Europe. The independent effects were obtained from hierarchical partitioning. Bars show mean independent effect of each predictor across all partitions up to 20 clusters. Error bars show standard deviations. (a) Mammal distributions in resolution 50×50 km. (b) Bird distributions in resolution 50×50 km. (c) Bird distributions in resolution $c. 10 \times 10$ km. IP – Iberian Peninsula, SEE – south-east Europe, CE – central Europe, S – Scandinavia. PACA – Provence-Alpes-Côte d’Azur, ECR – eastern Czech Republic, SF – southern Finland, NF – northern Finland. All independent effects were statistically significant ($P < 0.05$).

and Scandinavia. In southern Europe, spatial coherence was influenced rather by environmental factors, that is, by climate or topography. At the finer scale, the independent effect of geographical distance on the spatial pattern of clusters was rather weak, outperformed by the independent effects of topography in Provence-Alpes-Côte d’Azur and eastern Czech Republic or by the land cover in Finland (Fig. 5c). All the independent effects were statistically significant ($P < 0.05$). Numerical results of the hierarchical partitioning as well as Mantel correlations among β_{sim} , environmental and distance matrices can be found in Appendix S2.

DISCUSSION

The role of spatial scale

We attempted to show that the question of scale in biogeographical regionalizations based on assemblage distinctiveness is crucial. Spatial scale is a very complex issue that includes at least resolution (grain) and spatial extent of the study (Nekola & White, 1999). In our study, the two components of spatial scaling are integrated. We kept the same number of grid cells in both resolutions in order to make the spatial coherence of regionalizations comparable across the two considered scales. Thus, the increase of spatial grain was coupled

with the enlargement of total spatial extent of the area under study. Due to this approach as well as due to the lack of fine-resolution data covering large areas, we were not able to distinguish between the effects of the two main spatial scale components, that is, between the pure effect of the spatial resolution and the total spatial extent of the study on the spatial coherence of biogeographical regionalizations. Nevertheless, our results confirmed our expectation that clusters resulting from the classification analysis at the fine spatial scale often disintegrate into spatially discontinuous patches, whereas at the broad spatial scale, clusters are rather spatially coherent. Considering that biogeographical regionalizations are based on dissimilarity of assemblages (Legendre & Legendre, 2012), the different patterns of spatial coherence at different scales can be directly related to the scaling of beta diversity. The scale dependence of beta diversity was documented by a number of studies which showed that beta diversity between grid cells decreases with coarsening the spatial resolution (Lennon *et al.*, 2001; Arita & Rodríguez, 2002; Gaston *et al.*, 2007; Keil *et al.*, 2012). This is a consequence of scaling the species richness with area (species area relationship, SAR), as beta diversity between neighbouring grid cells is directly related to the local slope of SAR (Harte & Kinzig, 1997; Lennon *et al.*, 2001; Šizling *et al.*, 2011). This slope decreases with the increasing grain, albeit only in

areas smaller than biomes (Harte *et al.*, 2009), then it increases again (Storch *et al.*, 2012).

The increase of similarity between the neighbouring grid cells with coarsening the spatial resolution may explain to a certain degree the differences in spatial coherence of clusters resulting from biogeographical regionalizations at different scales. However, these differences may be rather attributed to the strength (goodness-of-fit) of the positive relationship between beta diversity and distance (Fig. 4 c,h,m), which increases with the coarsening the spatial scale; this pattern is supported also by Keil *et al.* (2012; see Appendix S2 and S3). If the beta-distance relationship is weak, a hypothetical cluster may contain also some distant grid cells, because they may be more similar than the neighbouring cells. In other words, if the similarity of adjacent grid cells is higher than the similarity of distant grid cells, clusters resulting from the classification analysis will be spatially coherent. It might be argued that the strength of distance decay may increase towards the coarser resolution and wider extent just due to the difference of sampling designs (Steinbauer *et al.*, 2012), but it seems that the different patterns of spatial coherence at different scales are at least partially driven by ecologically relevant factors. In Finland, the spatial pattern of regionalizations based on fine-scale grid was explained by differences in the land cover composition, whereas in the eastern Czech Republic and Provence-Alpes-Côte d'Azur, the pattern was attributable to differences in topography. It is thus probable that regionalization based on fine-scale grid reflects environmental variation (which may not be strongly autocorrelated and thus resulting clusters may not be contiguous), but this variation is averaged-out when using coarse-scale grid, so that coarse-scale regionalization reflects rather dispersal limitation which naturally leads to strong spatial autocorrelation.

Geographical variation in spatial coherence

Using the fixed spatial resolution and extent, we found that the pattern of spatial coherence is not consistent across Europe and varies with latitude. In southern Europe, clusters resulting from the classification analysis were generally less spatially coherent than in central Europe and Scandinavia, respectively. This pattern, which was found also by previous studies (Heikinheimo *et al.*, 2007, 2012), is in accord with differences in the strength of distance decay which was stronger in northern areas for both mammals and birds but relatively weaker in southern Europe (see Table 1 and Fig. 4c,h). This result is partially supported by results of Svenning *et al.* (2011) who found the strongest beta-distance relationship in central Europe, weaker in northern Europe and the weakest in southern Europe. On the other hand, this finding is in contrast with the general pattern found in the North American continent. Although there are several exceptions, it has been documented that the relationship between beta diversity and distance as well as beta diversity itself generally increases with the decreasing latitude there. The pattern was documented for North American vascular plant assemblages

(Qian & Ricklefs, 2007), New World owls (Koleff *et al.*, 2003b), and North American mammals (Stevens & Willig, 2002; Rodríguez & Arita, 2004; Qian *et al.*, 2009).

At the coarse scale, the different effects of geographical distance and environmental dissimilarity on the spatial pattern of regionalizations across Europe can be partly related to the different history of northern and southern parts of the European continent. While the southern parts of Europe were influenced by orogenic processes during the Palaeogene and Neogene periods, forming high and rugged mountain ranges, the northern and central parts of Europe, including the Caledonian mountains of Scandinavia, were exposed to intensive denudation during the ice ages. Glacial processes thus created a relatively flat and homogeneous landscape in the northern half of Europe. In such a landscape without important topographical barriers, it may be expected that the dissimilarity of coarse-scale species assemblages and consequently the spatial coherence of biogeographical regions will depend primarily on geographical distance. On the other hand, the unglaciated southern Europe retained the rugged landscape with a high altitudinal and climatic variability, and nowadays also with a high diversity of land cover types (Kallimanis & Koutsias, 2013). Consequently, the Mediterranean fauna and flora is characteristic by exceptional species richness, high beta diversity and high level of endemism and population fragmentation (Svenning & Skov, 2005, 2007; Baselga, 2008; Svenning *et al.*, 2011). It seems that all these characteristics of species assemblages negatively influence spatial coherence of biogeographical regions at least at coarse scale (Fig. 4). As our results indicate, the heterogeneous landscape with numerous glacial refugia may be the main reason why the biogeographical regions in south-east Europe and on the Iberian Peninsula tend to disintegrate into spatially discontinuous patches even at this relatively coarse scale. The pronounced effect of spatial environmental variability on Iberian biogeographical regions is supported also by Moreno Saiz & Lobo (2007), but other studies stress rather the role of history (Filipe *et al.*, 2009). Nevertheless, beside the environmental effect, we have to acknowledge that the spatially disparate patterns on the Iberian Peninsula and especially in south-east Europe may also partly arise from uneven survey efforts.

At the fine spatial scale, where the spatial coherence of clusters was generally low, we found some latitudinal pattern too, but the pattern was opposite to that found at the broader scale and driven mainly by the Provence-Alpes-Côte d'Azur where the clusters were surprisingly very coherent, despite the fine grid resolution. This pattern was probably strongly influenced by our arbitrary selection of study areas – due to the limited availability of species data in this spatial resolution, we were not able to repeat the analyses in other areas at the same latitude. Therefore, the pattern of spatial coherence that we found at this scale could not be explicitly related to latitude. Fine-scale regionalization seems to be driven by environmental variables which may or may not be autocorrelated, leading to contiguous or discontinuous

landscape types. Provence-Alpes-Côte d'Azur provided an exceptional example of the territory with a strongly spatially autocorrelated environmental gradient that separates species assemblages. Consequently, this area could be divided into geographically distinct and contiguous regions or altitudinal zones, respectively.

Considerations for biogeographical regionalizations

Although our study has some limitations, primarily due to relatively small spatial extent of the considered areas, we believe that it provides some valuable implications for biogeographical regionalizations. We can expect that the development of species distribution databases will provide fine-resolution data covering large geographical areas in the future. Such a data can serve for both the delineation of new regions or critical revision of existing ones, for example, biogeographical regions used in nature conservation policy of the European Union. Therefore, the issue of the scale in biogeographical regionalizations will probably become even more crucial than it is now. Whatever the delineation of biogeographical regions, ecological zones or landscape types should respect primarily the purpose of the study or conservation management requirements. Therefore, it is probably not possible to decide which spatial resolution is more appropriate for the classification analysis. Dispersal limitation or historical events are expected to be more important at broader spatial scales (Verleyen *et al.*, 2009), creating a stronger distance decay of similarity in the composition of species assemblages and consequently spatially distinct 'true regions'. On the other hand, environmental conditions operating at relatively finer spatial scales often cause spatial separation of populations leading to spatially disparate clusters, which may identify isolated areas with unique assemblages deserving protection. If it is required to obtain spatially coherent regions using fine grid data at fine spatial scales (e.g. as a baseline or complementary material for conservation decisions), or to delineate 'true regions' in very heterogeneous areas with high species richness, beta diversity and endemism, it is possible to weigh the dissimilarity matrix by geographical distances (see Moreno Saiz & Lobo, 2007) or to use spatially constrained clustering (Legendre & Legendre, 2012). Although the regions resulting from the spatially constrained classification are more internally heterogeneous as compared with the clusters resulting from the spatially unconstrained classification, they may be more readily interpretable if we are interested in general regional pattern in species composition which may indicate different history of individual sites within studied area. At the landscape level, results of this clustering method are well comparable to regionalizations delineated on the basis of expert knowledge (Divíšek *et al.*, 2014).

ACKNOWLEDGEMENTS

We thank Martin Večeřa for fruitful discussions on the concept of this paper. We also thank Walter Jetz, Juan Carlos

Moreno Saiz and two anonymous referees for helpful comments on a previous version of the manuscript. J.D. was supported by a Specific Research project at Masaryk University (MUNI/A/1315/2015) and the long-term development support of the Institute of Geonics (RVO: 68145535). D.Z. was funded by the Czech Science Foundation (P505/12/1022).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Atlases and schematic maps.

Appendix S2 Complete results of hierarchical partitionings.

BIOSKETCH

Jan Divíšek finished PhD study at the Department of Geography, Masaryk University. He is interested in alpha and beta diversity patterns at various spatial scales, and their drivers.

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Author contributions: J.D., D.Z and D.S. conceived the ideas; J.D. processed and analysed the data; J.D. and D.S. wrote the manuscript; D.Z. and M.C. commented on the manuscript.

Editor: Walter Jetz