Scaling communities and biodiversity

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Introduction

One of the main targets of nature conservation is to protect biological diversity, or biodiversity. But what is biological diversity? In a simplest case, it is just a number of species living at given place, e.g. a habitat patch. Naturally, if this number is comparatively high, the place in question may deserve protection. However, there are two complications. First, the number of species depends on the area of the given habitat patch, so that it is not very suprising if we count many species on large habitat patches and lower number on smaller patches. We would need to assess whether the number of species is higher than would be typical for an area of that size. It does not make sense to quantify biological diversity without accounting for the area of the study plot.

Second, there are some landscapes that are not characterized by particularly high local species richness (so-called *alpha diversity*), but where the overall biological diversity across the landscape is high because very diverse sets of habitat patches are found within it, each of which hosts a uniquely different set of species. In such a case, the landscape has high *beta-diversity* (species turnover among individual sites or habitats) and consequently also high *gamma-diversity*, or regional diversity. Under such circumstances, protection of any particular habitat patch is of little value, and instead the whole landscape mosaic should be protected. The conclusion is clear: biological diversity is scale-dependent, and it is necessary to consider this scale-dependency whenever dealing with the number of species (Storch et al. 2007).

The classic way of examining this scale-dependency in species richness is based on a species-area relationship (or SAR): plotting the number of species found as a function of the area of a sample (e.g. a habitat patch, landscape or region). The fact that the number of species generally increases with area is actually tightly related to beta-diversity, i.e., to uniqueness of different places in terms in their species composition. Imagine a homogeneous landscape characterized by low beta-diversity, i.e., by very similar species composition on individual sites. In such a landscape, any increase of sampled area is followed by only a negligible increase of total number of species. In contrast, in landscapes characterized by high beta-diversity, where every spot is different in its species composition, species richness increases quickly with increasing area. Indeed, many indices of beta-diversity (Box 1) are mathematically related to the slope of the species-area relationship (Šizling et al. 2011). Understanding the SAR is thus crucial for understanding all patterns of biological diversity.

The species-area relationship (SAR)

The fact that the number of species increases with area is obvious, but the exact form of this increase deserves attention. It is only rarely linear, and if plotted in non-transformed, arithmetic axes, the rate of increase of species richness with area gradually slows down (Figure 1A). However, if we plot both axes on logarithmic scales, the relationship often becomes almost linear (Rosenzweig 1995) (Figure 1B), at least over a range of scales. A linear relationship in the log-log scale can be expressed as a power-law, so that the slope of the line becomes the exponent of the relationship, Z.

This form of the relationship has a useful property, i.e., that it is scale-invariant. This means that an increase of area by a given multiple leads to the increase of species number by a constant (different) multiple, regardless of the absolute values. This would also mean that if we know the slope Z and species richness for a particular area (scale) we should be able to predict species richness at both smaller and larger spatial scales. This has been used for the prediction of diversity loss due to area loss (e.g., May et al. 1995). For instance, it has been claimed as a rule of thumb (following Darlington 1957) that a 90% area loss should lead to the eventual extinction of about half of all species in that area, regardless of the size of the initial area. Such a claim is based on an assumption that the SAR is a power-law with the slope Z equal to 0.3 (a value sometimes observed on islands, see Rosenzweig 1995).

However, the situation is not that simple. The relationship between species richness and area is often not exactly linear in logarithmic space, and consequently several other forms of the SAR have been proposed (Tjørve 2003). Indeed, recent research suggests that if we plot the SAR across a sufficiently wide range of spatial scales (e.g., from square metres to continental scales), it tends to appear triphasic in logarithmic space: with species richness initially increasing steeply at fine scales, but with a decreasing slope (Harte et al. 2009), then becoming approximately linear (that is to say: power-law) over intermediate scales, and finally accelerating upwards to produce steep slopes at very coarse (continental) scales (Figure 2) (Storch et al. 2012). Different mathematical expressions of the SAR proposed in the literature may be actually related to the fact that

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different researchers have studied different parts of the whole triphasic curve. The non-linearity of the SAR implies that simple scale-invariant estimates of species richness changes with changing area are unlikely to give accurate predictions.

The curvilinearity of the SAR at fine scales is caused by the fact that species number is constrained by the limited number of individuals in a small sample area; to put it simply, you cannot sample more species than you have individuals, and you are unlikely to sample many individuals at scales that are close to the sizes of individual home ranges (Figure 3) (Šizling et al. 2011). At extremely fine scales, the slope of the SAR should approach 1 (as the first individual sampled will necessarily also sample 1 species). This has one nontrivial consequence: the local slope of the species-area relationship (its derivative) is related to the ratio between total number of individuals and number of species (Harte et al. 2009). If the number of species is relatively high in relation to total number of individuals, and mean population sizes of the species are thus small, the local slope of the SAR will be high, and vice versa. Moreover, since the increase of species richness with area is related to beta-diversity, beta-diversity is expected to be high whenever there is only a limited number of individuals per species, i.e., with low mean population sizes (species are relatively rare). In contrast, when the average population size is high (species are generally abundant), beta-diversity is expected to be relatively low at these scales.
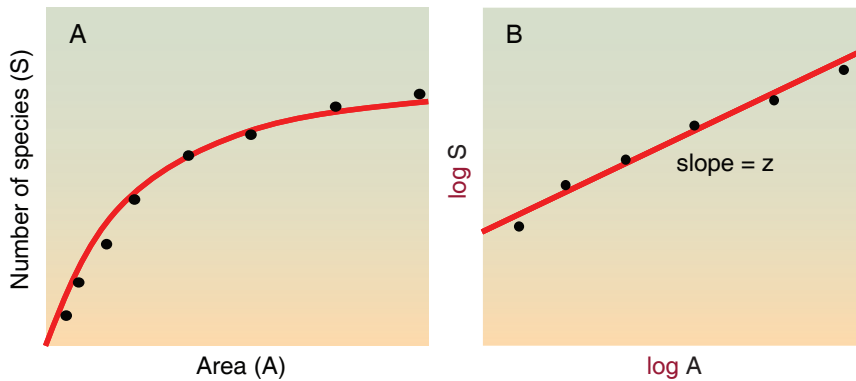

Figure 1. The typical form of the species-area relationship in arithmetic (A) and logarithmic (B) axes. The increase of the number of species is progressively decelerating in arithmetic space, but close to linear in logarithmic space, although particular measurements deviate from perfect linearity, and thus the straight line must always be taken as an approximation. Since the line can be expressed by the equation $y = ax + b$ where a is the slope of the line and b is the intercept, in this case it can be written as $\log(S) = Z\log(A) + \log(c)$, where S is the number of species, A is area, Z is the slope of the line, and c is a constant related to mean number of species per unit area. This equation in non-logarithmic form is expressed as $S = cA^Z$, i.e. the slope of the line in the logarithmically plotted SAR becomes the exponent of the power-law.

Box 1. Beta-diversity measures and related problems

Differences in species composition of distinct spatial units may be – and have been – measured in many ways, which, however, are often not equivalent and measure different aspects of the pattern. The simplest index of beta-diversity is called Whittaker index (R.H. Whittaker introduced it in 1960 as the very first index of beta diversity), which is just the total (gamma) diversity of all samples together, divided by mean local (alpha) diversity. Clearly, if the individual local plots strongly differ in their species composition, the total species richness of all plots together (gamma diversity) must be much higher than mean diversity of one plot, resulting in high value of this index. Since the slope of the species-area relationship is also given by the ratio of species richness of a larger area (gamma) to richness of the smaller area (alpha), Whittaker beta-diversity index is mathematically linked to the slope Z of the SAR. However, this mathematical connection holds only for adjacent plots (in which the gamma diversity represents the species richness of the large area comprising all the adjacent smaller plots together). Beta-diversity may be calculated also for distant, non-adjacent plots, but the relationship to the species-area relationship is in this case more complex and not straightforward. Moreover, it is also affected by the *distance-decay of similarity*, i.e., on how the beta-diversity depends on the distance between plots.

There are indices of beta-diversity that are mathematically related to the Whittaker index; for instance the Jaccard index of similarity which simply calculates the ratio between the number of species shared by the plots and the total number of species. However, many other published indices are not directly linked to these indices or to each other, and thus they actually measure different things. For this reason, the literature concerning beta-diversity is quite messy. For some authors, beta-diversity is a synonym for spatial species turnover, whereas others try to distinguish these as two separate matters. There is no consensus about terminology and the exact purpose of different indices. The practical way to deal with this conceptual complexity is to use a selected index consistently throughout a given study, to report which index was used and why, and to be cautious when comparing results based on different beta-diversity indices.
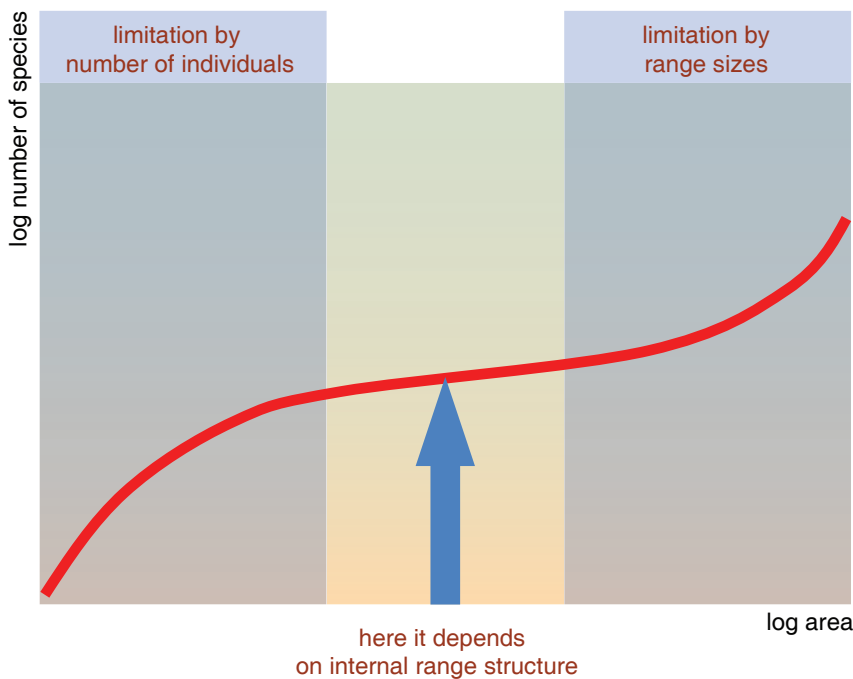
Figure 2. The species-area relationship across a wide range of spatial scales, with the finest scales corresponding to the size or home range of an individual, and the coarsest scales representing the size of whole continents. The curvilinearity at the finest scales is caused by the limited number of individuals sampled (see text and Figure 3), while the opposite curvilinearity at coarse spatial scales is due to limited range sizes (see text and Case Study 1).
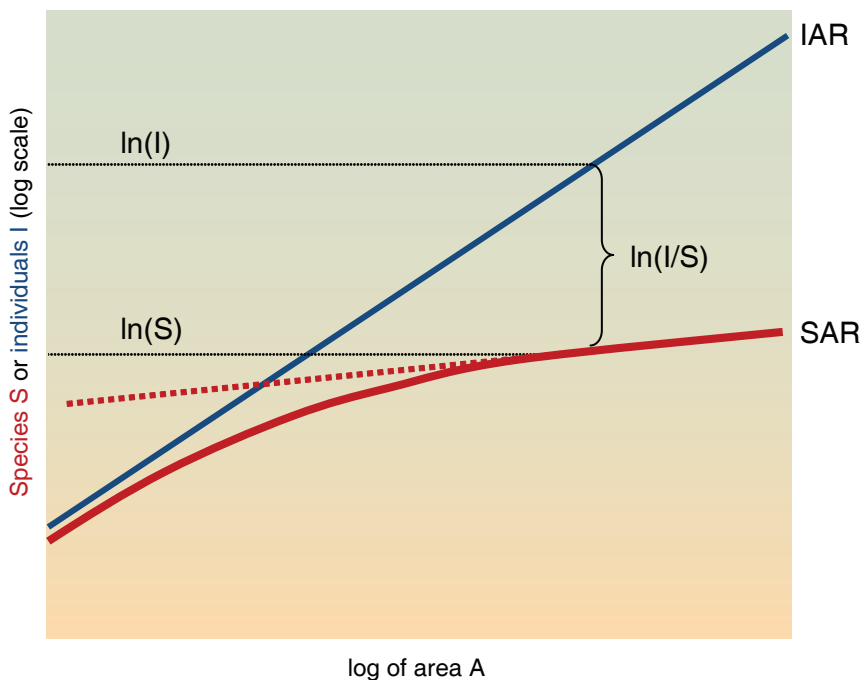
Figure 3. Species-area (SAR) and individuals-area (IAR) relationships at fine spatial scales. The average number of individuals in an area (summed across all taxa) has to increase linearly with area, i.e., in logarithmic space it is a line with a slope equal to 1. The number of species must be always lower than the number of individuals, and the increase in the number of species with area is less rapid than that of individuals, i.e. its slope must be less than one (unless every species is represented by just one individual; in such case both the curves coincide). This implies, however, that the species-area relationship cannot be linear across all spatial scales, since it cannot cross the individuals-area relationship (dashed line). This explains why the SAR is steeper when the number of species is closer to the number of individuals, i.e. when mean number of individuals per species is low. Mean population size is reflected by the distance between the two curves (since lnI-lnS=ln(I/S)), and thus related to the slope of the SAR, and consequently also to various measures of beta-diversity (Šizling et al. 2011).

The increase in the local slope of the SAR at very coarse spatial scales is related to the fact that individual species' geographic ranges are limited, and they may be small in comparison to sample areas when we measure diversity at continental scales. If we increase the sampling window to be larger than the size of ecoregions or biomes, most species' ranges are included within the sampling areas, and further increases in area bring in completely new sets of species restricted to other areas, elevating the slope of the SAR. The precise spatial scale at which this upward bend in the SAR begins depend on mean geographic range of the taxon in question; e.g., if amphibians have on average smaller ranges than mammals, then this upward-increase will begin at finer scales for them and is more rapid. Indeed, if we rescale the values of area using mean range size for a given taxon and region, all the SARs collapse into one universal relationship at these large scales (Storch et al. 2012, Case Study 1).

The curvilinearity of the SAR at both very coarse and very fine spatial scales is therefore understandable from purely geometrical reasoning. The rapid increase of the number of species with area at fine scales is due to the limited number of individuals, while the increase at coarse scales is due to the geographic limits of species' ranges. However, most planning decisions relevant to conservation deal with intermediate scales: much larger than an individual's home range but much smaller than most species' geographic ranges. For such purposes, we can focus on the more linear (approximately power-law) middle section of the SAR, which is closely related to beta-diversity at these scales, as mentioned above. This then brings us to a vital issue: What are the factors responsible for determining beta diversity patterns?

Drivers of beta-diversity patterns and the SAR slope

Beta-diversity, and thus also the rate of increase in the number of species with area, is determined by the fact that species do not occur everywhere, and individuals of a given species are

typically aggregated into certain parts of the landscape. This may happen because of two sorts of reasons (Keil et al. 2012). Firstly, different habitats or climatic conditions are found in different places, and consequently any species that requires specific conditions will be restricted in where it can live. Secondly, species have only finite powers of dispersal, so that even if good habitat is available for them in a distant area, they may not be able to colonise it due to dispersal barriers and/or limited time to spread from the centres of origin. High beta-diversity (and a steep slope of the SAR) is thus expected whenever there is pronounced habitat heterogeneity or important dispersal barriers.

The effect of these contrasting factors may also be scale-dependent.

Analysis of patterns of beta-diversity in European plants and animals indicated that the effect of dispersal limitation prevails at coarse spatial scales when we compare species composition of large areas across large distances. Climatic differences are important for determining beta diversity at somewhat finer scales, but these still involve larger areas than land-use differences, which drive fine-scale patterns of beta-diversity. Additionally, beta-diversity is lower between large than between small areas, which is in accord with the observation above that the SAR is steeper at small spatial scales (Keil et al. 2012, Case Study 2).

Beta-diversity of European plants and animals is particularly high in southern Europe (Figure CS2.3). This may be related to quite complex topography (mountains, peninsulas) creating dispersal barriers or notable variation in environmental conditions. However, this pattern may also represent a historical legacy of ice ages, when most of European fauna and flora persisted in small refuges in southern Europe, and many species are still confined to these areas. In any case, the proximate driver of high beta-diversity lies in the fact that many species in southern Europe have small geographic ranges. As we have discussed above, patterns of species distribution are tightly related to patterns in species diversity revealed in the SAR and beta-diversity. *The more restricted distribution of species, the higher is beta-diversity, and the steeper is the increase of the number of species with area.*

This has non-trivial consequences for diversity changes due to human

Box 2. Scale-dependence of biodiversity changes

The way temporal changes of the number of species vary with spatial scale can be illustrated with the changes of the species-area relationship (SAR; here referring just to two spatial scales, local and regional) before (black line) and after (red line) a disturbance. When the disturbance leads to extinction of some species without any bias towards more common or rare species, we should expect a parallel decrease of species richness in both scales, and thus no change in beta-diversity (A). However, if the disturbance just decreases the sizes of species ranges without leading to regional extinction of any species, only local species richness decreases, with consequently steeper SAR and thus higher beta-diversity (B). Alternatively, regional extinction of species may be compensated by the spreading of remaining species, so that local species richness remains the same (C). In such a case, the SAR slope and beta-diversity decreases. This pattern can be strengthtened by further spread of common species, increasing local diversity above the levels before the disturbance and further depressing beta-diversity (D). Such a situation is predicted to follow from biological invasion. Situations (C) and (D) refer to the process of biotic homogenization.
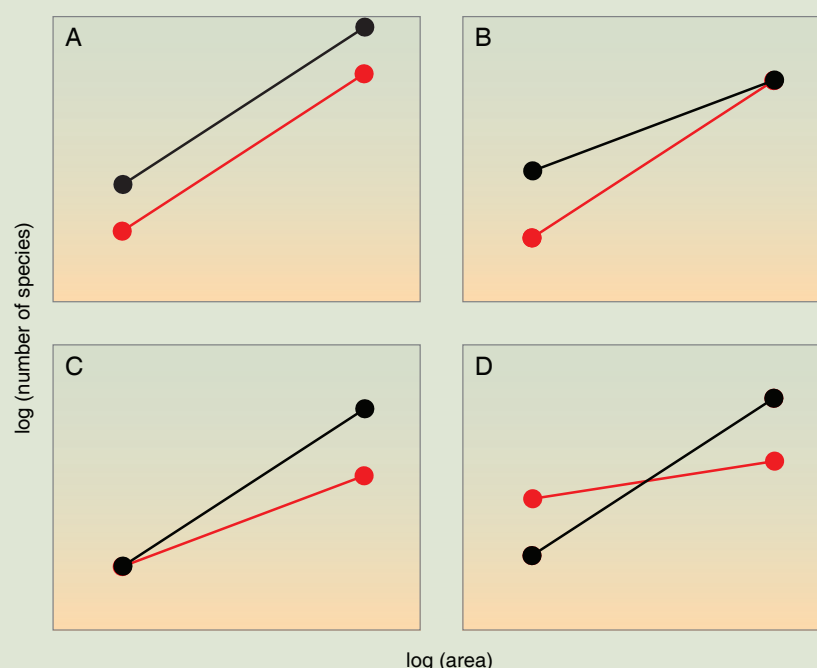
impact (Keil et al. 2011, Case Study 3). If human disturbance leads to the shrinkage of species' ranges, the average alpha-diversity (the number of species found on individual localities) should decrease, but beta-diversity is likely to increase. In contrast, the extinction of rare species leads to decreases in both alpha- and beta-diversity (and also regional diversity, i.e. gamma diversity). The spreading of invasive species, on the other hand, leads initially to increases in local (alpha) diversity (at least until the invasion begins to have adverse effects on native fauna and flora), and also beta-diversity, but when the invasive species becomes widespread, beta diversity characterized by the uniqueness of individual sites decreases (Box 2). This phenomenon is called biotic homogenization and is considered to be major process in the contemporary biosphere.

Case Study 1: Biodiversity scaling across continents

Traditionally, species-area relationship (SAR) has been approximated by a simple power function (i.e., a straight line if both the area axis and species richness axis are expressed in a logarithmic scale). It has been used for extrapolations of diversity across spatial scales or to estimate numbers of species that will go extinct after a given area is destroyed. It used to be assumed that if we know, e.g., the size of an area of a tropical rainforest which has been destroyed, we can use the species-area relationship to estimate the proportion of species which went extinct there. In reality, the relationship is more complex than a simple power law and it also differs across taxa and regions, which cast doubts on its usefulness.

A wide range of functions have been fit to species-area relationships, which might lead to an impression that different taxa and regions follow different scaling rules. However, the situation is not as complicated. Storch et al. (2012) have examined the distribution of all species of amphibians,

birds, and mammals across all continental landmasses. Surprisingly, the species-area relationship at these large scales follows simple and yet non-trivial rules. Instead of being linear in the logarithmic scale (that is power-law), it is upward-accelerating for all taxa and continents (Figure CS1.1). Moreover, its curvature depends on mean species geographic range, so that taxa with smaller ranges – for example amphibians – reveal more prominent curvature and consequently higher slope of the relationship at large areas. When we express the area in units corresponding to mean species range of a given taxon within a given continent, all of the curves collapse onto one universal relationship (Figure CS1.2). The number of species for given area can thus be estimated using the knowledge of mean species richness for some given area, with only one additional piece of information – mean range size of given taxon within the region.

Additionally, an interesting pattern emerges when we look at the relationship between area and the number of species which are restricted exclusively to this area, i.e. which are endemic to it (the so called endemics-area relationship). These species are particularly relevant for extinction estimates as they will become globally extinct if the area they occupy is destroyed. At continental scales, it is the endemic-area relationship that follows a simple power law, so that the number of endemic (and thus potentially extinct) species is roughly proportional to the potentially destroyed area, indicating high risk of extinction from area loss (Storch et al. 2012).

Case Study 2: Beta-diversity patterns in European plants and animals

Keil et al. (2012) examined the scaling properties of beta diversity on the basis of high-quality distributional data for birds, butterflies, vascular plants, amphibians, and reptiles that were all arranged into a 50 × 50 km UTM grid across Europe (Figure CS2.1). For the investigation of small-

er-scale patterns, national distributional atlases of butterflies (Finland), birds (Czech Republic and Catalonia), and vascular plants (United Kingdom) were used. Within each of these datasets, a series of 2-3 nested grids with the same spatial extent but with varying grain (resolution) was generated. Each cell within these grids was characterized by land cover and climatic conditions. Keil et al. (2012) then analyzed relationships between beta diversity, geographic distances, and environmental dissimilarities, and identified areas of rapid species turnover by mapping and analyzing patterns of beta diversity only in a set of adjacent grid cells (first distance class).

For birds, butterflies, vascular plants, amphibians, and reptiles beta diversity is higher and more variable at small spatial resolution. Hence, conservation efforts should be focused on preserving beta diversity at these smaller grains. In other words, the priority should be to preserve local uniqueness.

On the scale of Europe, dispersal limitation plays a major role in generating species turnover (Figure CS2.2). Hence, any efforts to conserve beta diversity (or local uniqueness) must carefully take into account not only the presence of natural migration corridors, but also natural migration barriers that can preserve beta diversity. It also means that European-wide modelling of shifts in species distributions must explicitly consider dispersal limitations.

Climatic and land-cover (habitat) differences have additional influence on beta diversity, and the relative importance of these variables differs at different spatial resolutions (Figure CS2.2). This shows that species turnover is a phenomenon driven by a complex interplay between dispersal limitations and climatic and habitat requirements of species. Correspondingly, conservation efforts on the continental scale (Europe) must consider all of the three phenomena by addressing climate change, connectivity (dispersal limitations), and land-use (management) on equal levels of importance.

On the scale of individual countries, the most important factor influencing beta diversity is climate, which means that climatic envelope modelling of species distributions may be relevant and
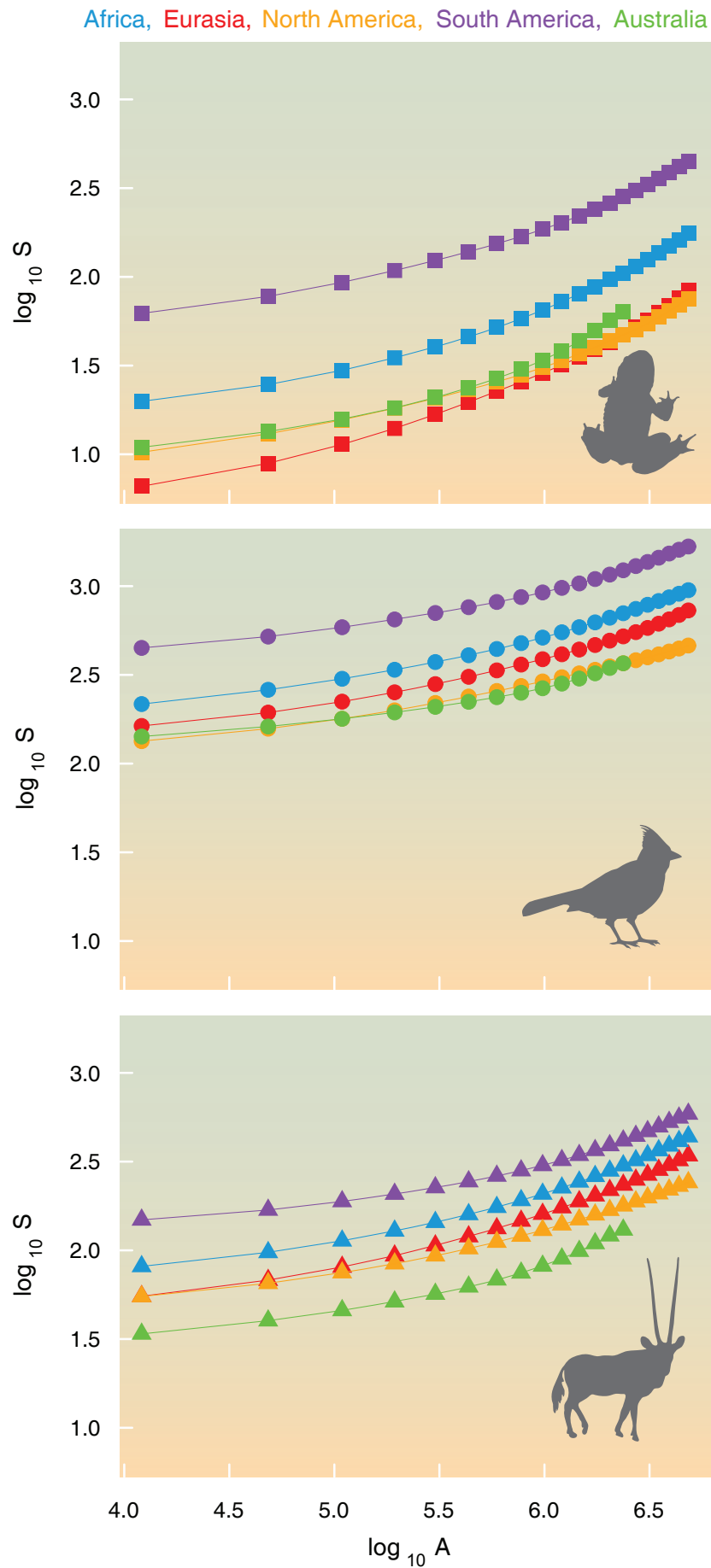
Figure CS1.1. SARs across five continents and three vertebrate classes. The SARs for amphibians, birds and mammals reveal an upward-accelerating shape for logarithmic axes.
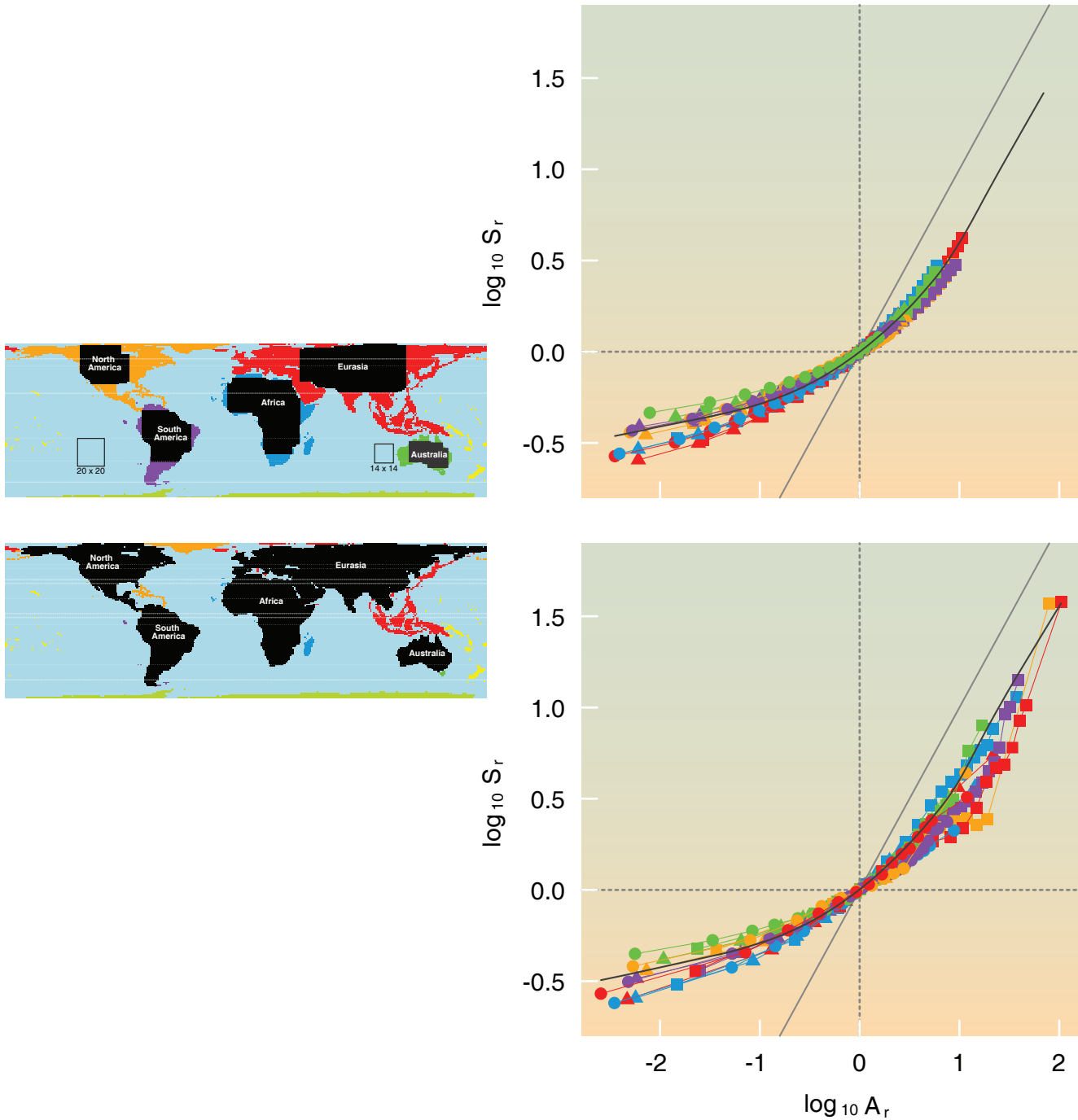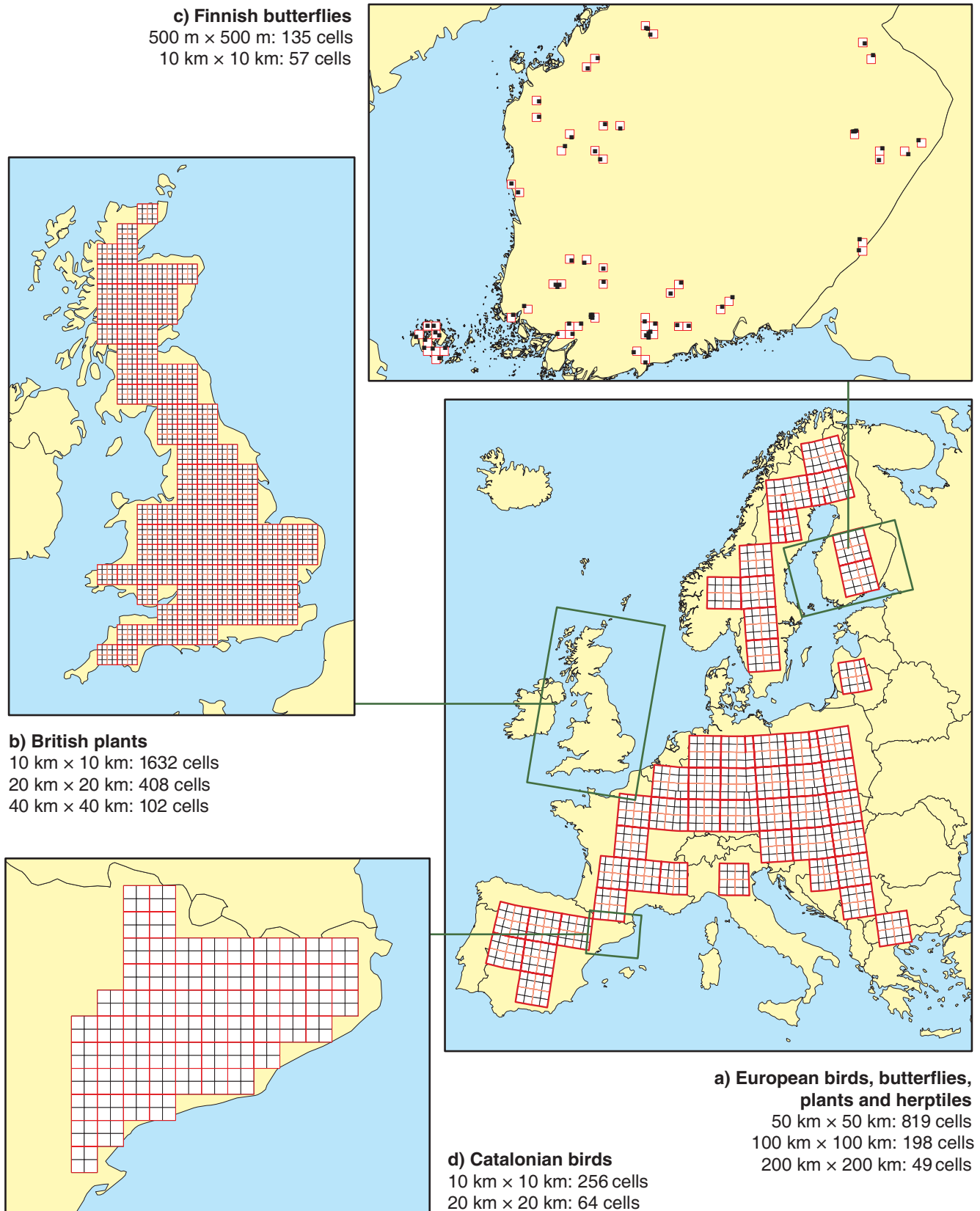
Figure CS1.2. SARs after rescaling for the sampling design based on square sample plots (above) and based on an alternative, continental shape design, in which sample areas are not quadrats but keep the shape of the given continent (below). After expressing the area in units corresponding to mean range size and standardizing the vertical axis so that it represents species richness relative to mean richness for a given unit area, all the SARs collapse into one universal relationship, although some deviations exist, particularly in small areas. Solid black lines refer to rescaled SARs predicted by simulations based on a random placement of simplified ranges. Solid grey lines all have slope of 1. The horizontal axis has been rescaled so that $A_r = A/\bar{R}_{t,c}$ where A_r is the rescaled area, A is the area of the study plot and $\bar{R}_{t,c}$ is the mean range size for taxon t and continent c. Vertical axis represents species richness proportional to the richness of an area equal to $\bar{R}_{t,c}$, i.e. $S_r = S_A/S_{\overline{R(t,c)}}$, where S_r is the rescaled number of species, S_A is mean number of species for a given area, and $S_{\overline{R(t,c)}}$ and $E_{\overline{R(t,c)}}$ are mean richness values for the area that equals the mean geographic range size of a given taxon and continent.

even useful within these smaller scales. It also shows that the expected climatic changes will most severely influence patterns of species turnover at the scale within individual European countries.

Interestingly, both *species rich* areas of southern Europe (Mediterranean peninsulas) and *species poor* areas of northernmost Europe (Fennoscandia) have high beta diversity (Figure CS2.3, CS2.4). Therefore, the value of the species-rich European areas lies not only in the species richness, but also in the rapid spatial species turnover. Moreover, it is also worth conserving the species poor areas in the north because they are unique – not only when compared with the rest of Europe, but also when compared with adjacent areas within Fennoscandia itself.

c) Finnish butterflies
500 m × 500 m: 135 cells
10 km × 10 km: 57 cells

b) British plants
10 km × 10 km: 1632 cells
20 km × 20 km: 408 cells
40 km × 40 km: 102 cells

a) European birds, butterflies,
plants and herptiles
50 km × 50 km: 819 cells
100 km × 100 km: 198 cells
200 km × 200 km: 49 cells

d) Catalonian birds
10 km × 10 km: 256 cells
20 km × 20 km: 64 cells

Figure SC2.1. Nested UTM grids used for the analyses of pan-European beta diversity patterns; a) across continental Europe, b) across the UK, c) Finland, and d) Catalonia. The different grains always cover the same area. Areas within the largest grid cells that overlapped sea, lack land-cover data, or those insufficiently surveyed were removed.
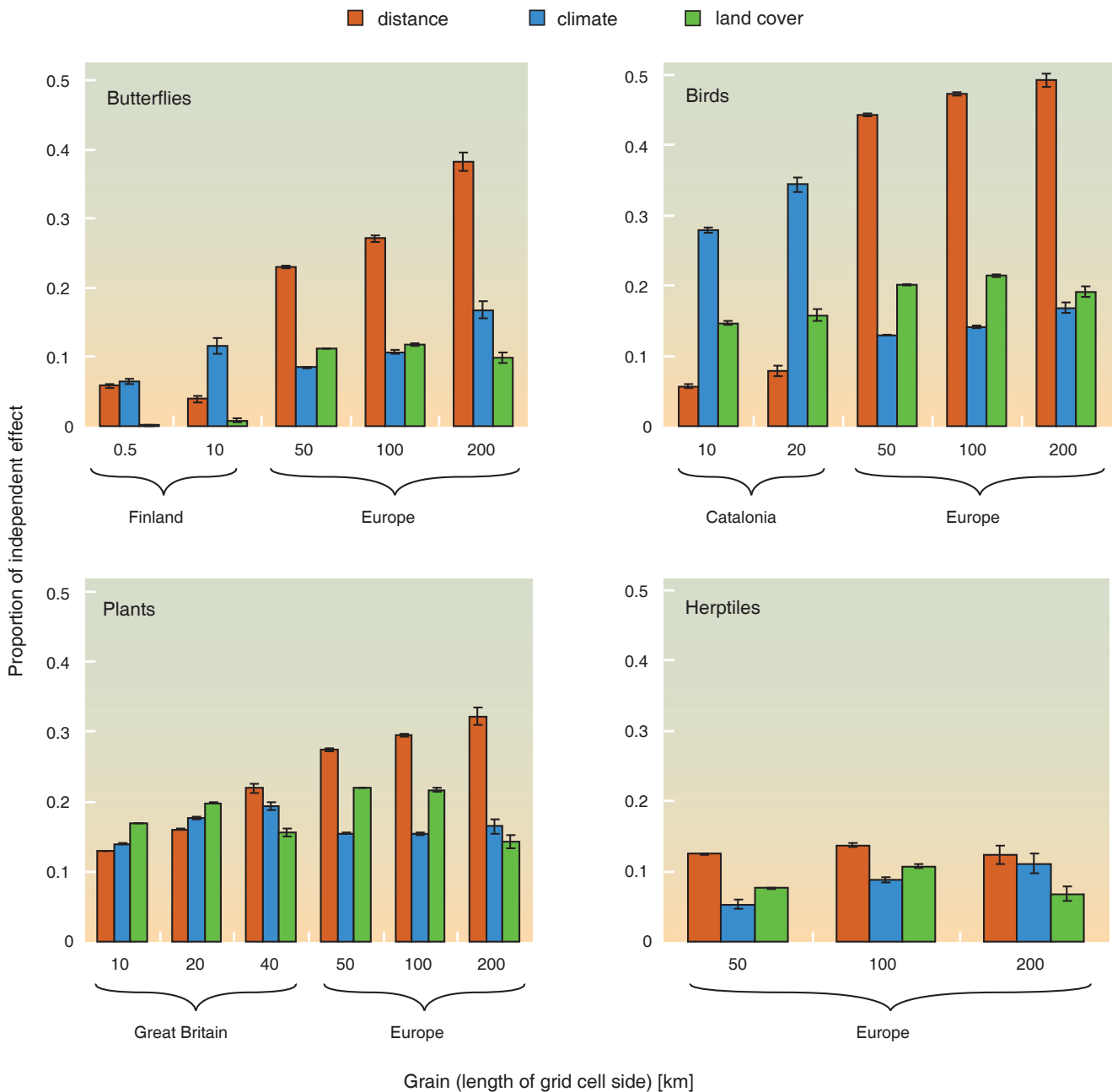
Figure CS2.2. Independent effects of climatic, land-cover, and geographic distances on beta diversity (measured as βsim index which estimates only pure species turnover controlled for the effect of different diversities in sampled areas) at various grain resolutions. At large scales geographic distance is the most important factor, while at the small scales climatic dissimilarity plays a major role in shaping patterns of beta diversity.

Case Study 3: Scale-dependence of biodiversity changes

Since the Rio summit in 1992, the issue of biodiversity loss has been high on the global list of priorities. Yet it is surprisingly difficult to measure whether biodiversity has increased or decreased, in part because of issues of scale. If biodiversity is intrinsically tied to scale, it is logical to assume that biodiversity change is also scale-dependent (Box 2). In fact, it is perfectly possible to have net *increases* in the species richness for each site in a landscape, but still have a *decrease* in species in the landscale as a whole.

While many researchers and conservationists have examined biodiversity change in the past, the issue of scale-dependent change has only recently been considered. Keil et al. (2012) examined hoverfly records in two European countries, the Netherlands and United Kingdom, examining biodiversity database records from before and after 1980. Only subtle scale-dependence in species richness change were found in the Netherlands, but strikingly different patterns of diversity change were found at different scales in the UK, with substantial declines in species richness at local scales shifting to either no change or even diversity increases at national scales (Figure
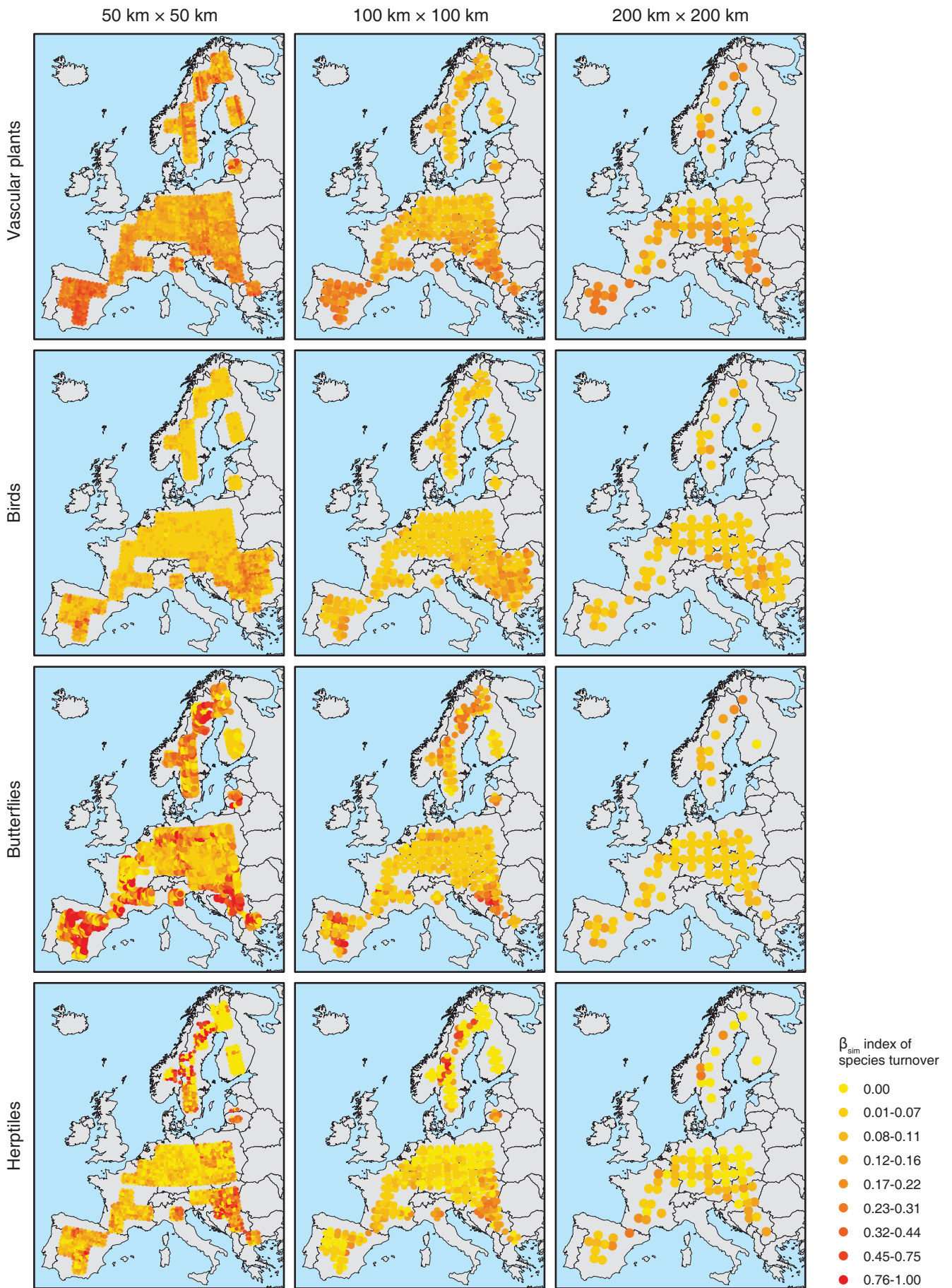
Figure CS2.3. Geographic patterns of beta diversity (measured as βsim) at first distance class (all pair-wise comparisons of all adjacent grid cells) for the four taxonomic groups at three grain resolutions. βsim value of 0 means identical species composition and value of 1 means completely different composition of species.

Column headers: 50 km × 50 km, 100 km × 100 km, 200 km × 200 km

Row labels: Vascular plants, Birds, Butterflies, Herptiles

β_{sim} index of species turnover

- 0.00
- 0.01-0.07
- 0.08-0.11
- 0.12-0.16
- 0.17-0.22
- 0.23-0.31
- 0.32-0.44
- 0.45-0.75
- 0.76-1.00

Figure CS2.4. Beta diversity does not depend on species number. One may find high values in species rich areas, e.g., in Mediterranean regions (left) (photo: Mathias Scholz/UFZ), as well as in species poor areas of Scandinavia (right) (photo: Reinhard Klenke).
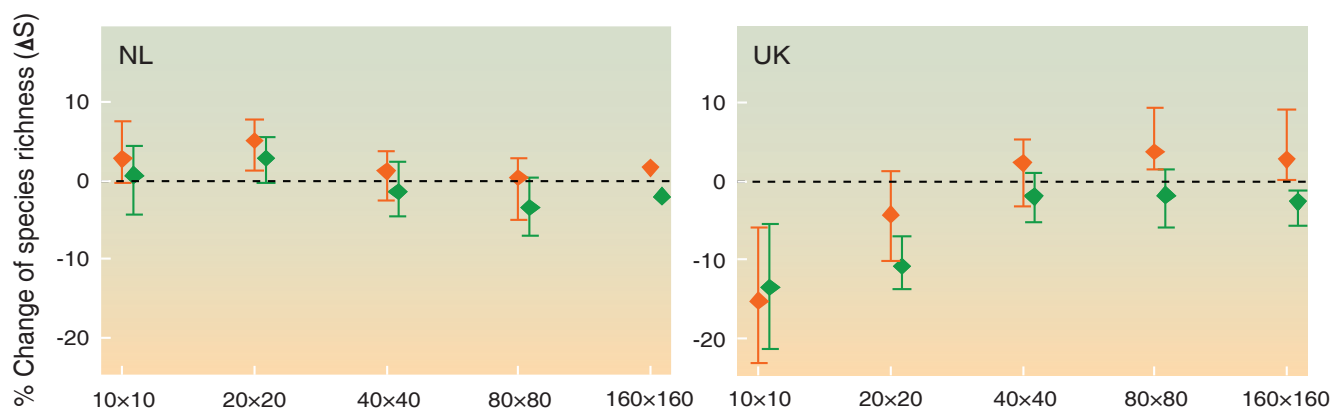

Figure CS3.1. Changes in species richness in hoverflies in the Netherlands (NL) and United Kingdom (UK) at different spatial scales. Orange symbols represent analyses comparing pre- and post 1980 records, while green symbols represent analyses comparing two equal time periods (1954–1979 and 1980–2005). Note that species richness showed signs of increasing in the NL at relatively fine spatial scales, but not at coarser scales, while in the UK substantial fine-scale declines coincide with either no change or even richness increases at coarser scales.

CS3.1). Carvalheiro et al. (2013) have additionally assessed shifts in beta diversity across scales, examining a range of plant and pollinator taxa (including bees and butterflies, as well as hoverflies), dividing biodiversity records into three 20-year periods, stretching from 1950 to 2009. The study showed evidence that biodiversity declines in most of these groups (at multiple scales) had slowed substantially in recent decades, but it also provided evidence of increasing biotic homogenisation in almost all of the taxa (Figure CS3.2). This suggests that the scaling of biodiversity in these groups is continuing to shift.

Taken together, these studies suggest that we need to take spatial (and temporal) scale into account when trying to assess how biodiversity has changed. It may well be that our biodiversity goals may themselves be scale-dependent. Thus for example, the role of pollinators or biocontrol agents in providing ecosystem services to agriculture may depend on diversity measured at a fine scale (that of a field or landscape). On the other hand, our conservation goals (such as those adopted at the Rio summit and in subsequent accords) may be more concerned with maintaining biodiversity at a national, continental or even global scale.

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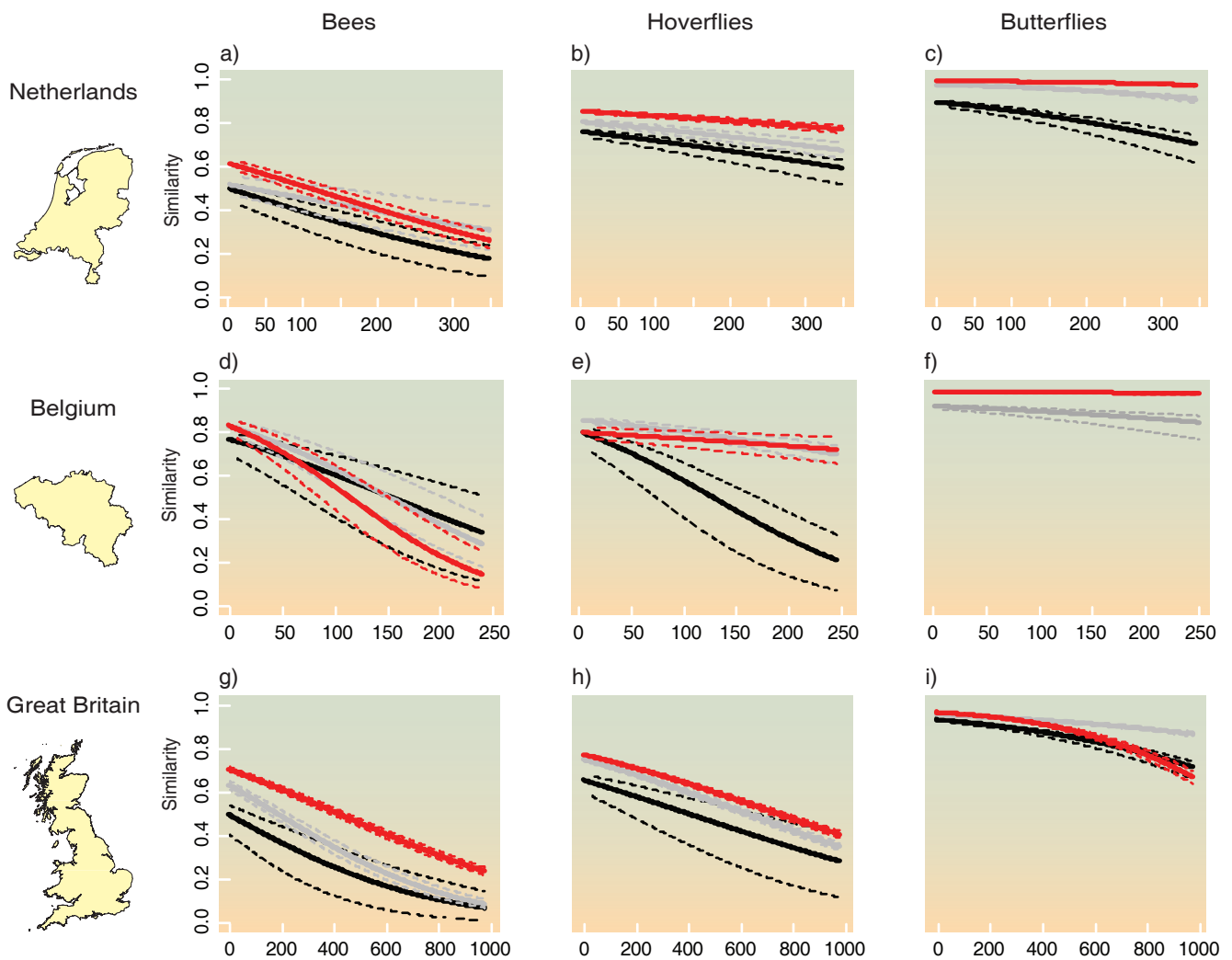
Figure CS3.2. Biotic homogenisation in NW European pollinators. These panels represent the similarity between species composition of samples taken different distances apart (measured using 1-βsim) for three groups of pollinating insects (bees, hoverflies and butterflies) over time. In most cases, recent decades (represented by the red lines) show higher similarity at a given distance than was found in the mid 20th century (black lines).

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