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Patterns of beta diversity in Europe: the role of climate, land cover and distance across scales

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ABSTRACT

Aim We test the prediction that beta diversity (species turnover) and the decay of community similarity with distance depend on spatial resolution (grain). We also study whether patterns of beta diversity are related to variability in climate, land cover or geographic distance and how the independent effects of these variables depend on the spatial grain of the data.

Location Europe, Great Britain, Finland and Catalonia.

Methods We used data on European birds, plants, butterflies, amphibians and reptiles, and data on British plants, Catalanian birds and Finnish butterflies. We fitted two or three nested grids of varying resolutions to each of these datasets. For each grid we calculated differences in climate, differences in land-cover composition (CORINE) and beta diversity (β_{sim} , $\beta_{jaccard}$) between all pairs of grid cells. In a separate analysis we looked specifically at pairs of adjacent grid cells (the first distance class). We then used variation partitioning to identify the magnitude of independent statistical associations (i.e. independent effects in the statistical sense) of climate, land cover and geographic distance with spatial patterns of beta diversity.

Results Beta diversity between grid cells at any given distance decreased with increasing grain. Geographic distance was always the most important predictor of beta diversity for all pairwise comparisons at the extent of Europe. Climate and land cover had weaker but distinct and grain-dependent effects. Climate was more important at relatively coarse grains, whereas land-cover effects were stronger at finer grains. In the country-wide analyses, climate and land cover were more important than geographic distance. Climatic and land-cover models performed poorly and showed no systematic grain dependence for beta diversity between adjacent grid cells.

Main conclusions We found that relationships between geographic distance and beta diversity, as well as the environmental correlates of beta diversity, are systematically grain dependent. The strong independent effect of distance indicates that, contrary to the current belief, a substantial fraction of species are missing from areas with a suitable environment. Moreover, the effects of geographic distance (at continental extents) and land cover (at fine grains) indicate that any species distribution modelling should take both environment and dispersal limitation into account.

Keywords

Beta diversity, biodiversity, dispersal limitation, dissimilarity, herptiles, Mantel test, spatial scale, species turnover, species–area relationship.

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INTRODUCTION

Numerous empirical studies have linked geographic patterns of species richness (alpha diversity) to climate (Mittelbach *et al.*, 2001; Hawkins *et al.*, 2003; Currie *et al.*, 2004; Field *et al.*, 2009) and described the dependence of species richness on a spatial scale (Preston, 1960; Rahbek, 2005). Efforts to relate broad geographic patterns of species turnover (beta diversity) to environmental conditions, however, have started only recently (e.g. Gaston *et al.*, 2007a; Qian & Ricklefs, 2007; Soininen *et al.*, 2007; Baselga, 2008; Svenning *et al.*, 2011). To our knowledge, none of these large-scale studies has simultaneously incorporated geographic distance, climate and land cover to explain patterns of beta diversity. Additionally, most of the published studies focused only on a single taxonomic group in a single region, and most have operated at only a single spatial scale.

If we are to make any progress in understanding the relationship between beta diversity and spatial scale, we must first come to grips with the meanings of the two terms themselves. There are various approaches to defining and measuring beta diversity (Koleff *et al.*, 2003; Anderson *et al.*, 2011). In this study, we define beta diversity as equivalent to 'species turnover' (but see Baselga, 2010) in order to describe *dissimilarity* (i.e. the mathematical complement of *similarity*) in species composition between any two sites. Thus, while there are various indices that can be used to measure beta diversity (reviewed by Koleff *et al.*, 2003), we will always focus on the dissimilarity aspects of these indices. Spatial scale is also a complex topic, incorporating at least two aspects: grain and extent (Nekola & White, 1999). This study focuses primarily on grain, which is the area for which a single observation is made (e.g. the size of a grid cell in a gridded distributional atlas), but we also examine the effects of spatial extent (the total area encompassed by the dataset as a whole).

Beta-diversity patterns can help shed light on the processes structuring ecological communities; depending on the relative importance of different processes, beta diversity should be expected to correlate with environmental dissimilarities and/or with geographic distance. Three recognized mechanisms generate and influence such patterns of beta diversity. The first mechanism is the limiting effect of environmental conditions, where a species' presence at a given site depends on its habitat requirements (niche) and the environment at the site (MacArthur, 1972; Tilman, 1988). Sites with different environments should host different sets of species, and the more different the environment, the greater the beta diversity should be (Nekola & White, 1999; O'Malley, 2008). The second mechanism comprises dispersal limitations, i.e. the interplay between landscape configuration, time and the dispersal abilities of species (Hanski, 1999; Nekola & White, 1999). If species composition varies in space due to spatio-temporal and physical limitations on dispersal, we should expect beta diversity to be more strongly correlated with geographic distance than with environmental dissimilarity *per se*. Finally, species interactions can also generate beta diversity regardless

of environmental conditions or dispersal barriers (MacArthur, 1972; Cornell & Lawton, 1992; Gotelli *et al.*, 2010), although this beta diversity would still tend to be expressed as shifts with distance and/or environment due to their effects on the interacting species themselves. Empirical evidence for the relative importance of these three drivers of beta diversity at different scales has been equivocal. Some studies have found beta diversity to depend mainly on environmental dissimilarity (Harrison *et al.*, 1992; Spencer *et al.*, 2002; Winter *et al.*, 2010), whereas others indicated geographic distance to be the main determinant (Tuomisto *et al.*, 2003; Qian *et al.*, 2005); a number of studies found that beta diversity was best explained by the interplay between the two (Baselga & Jiménez-Valverde, 2007; Qian & Ricklefs, 2007). Almost as a rule, studies that addressed environmental factors in this context have referred to either climatic variables only or to land cover only (Schweiger *et al.*, 2005; Dormann *et al.*, 2007; Hendrickx *et al.*, 2007; Ekroos *et al.*, 2010); exceptions to this being rare (e.g. Qian *et al.*, 2008; Pe'er *et al.*, 2011).

Beta diversity between adjacent grid cells should generally decrease with coarsening of the spatial resolution, at least over subcontinental extents. Between adjacent areas at a given grain, beta diversity is directly related to the local slope of the nested species–area relationship (SAR) at the area corresponding to that grain (Harte & Kinzig, 1997; Lennon *et al.*, 2001; Šizling *et al.*, 2011). Apart from extremely unrealistic cases, the SAR itself cannot be linear in the log–log space across all scales for geometrical reasons (Storch & Šizling, 2008; Rosindell & Cornell, 2009). The SAR is frequently found to be triphasic in nature (Preston, 1960; Rosindell & Cornell, 2009 and references therein); that is, the local slope of the SAR (which is directly related to beta diversity) generally decreases with increasing area from fine to moderately coarse scales, but then grows steeper again when biome boundaries are crossed at extremely coarse grains. Several mechanisms have been proposed to explain the decrease in beta diversity within areas smaller than biomes. First, as we increase the grain, we increase the probability of detecting rare species (i.e. those occupying a small area) in each grid cell, such that adjacent grid cells become more similar, whereas widespread species should be present in the grid cells regardless of the grain (Henle *et al.*, 2004). Also, the presence of different land-cover types in a grid cell is subject to the same sampling issue as the presence of rare species. Thus, coarse-grained grid cells are more likely to harbour both rare land-cover types and rare species specialized on these land-cover types (Qian *et al.*, 2005). Second, as sampling grain increases, the variability of the mean environmental conditions decreases as a result of spatial averaging (Levin, 1992; Mac Nally *et al.*, 2004; Gaston *et al.*, 2007b). Indeed, patterns of beta diversity decreasing with increasing grain have been shown in British birds (Lennon *et al.*, 2001; Gaston *et al.*, 2007b), Mexican mammals (Arita & Rodríguez, 2002) and bird assemblages in the Great Basin area of North America (Mac Nally *et al.*, 2004).

Beta diversity should also be higher between pairs of areas that lie further apart than between pairs of neighbouring areas

(Nekola & White, 1999), and the exact form of the relationship between distance and beta diversity should be grain-specific (Harte & Kinzig, 1997; Harte *et al.*, 1999; Nekola & White, 1999). The simplest reason is that beta diversity between adjacent grid cells is the starting point of the distance–beta relationship. If this beta diversity decreases with increasing grain (for the reasons mentioned above) then we expect the whole relationship to change with grain, at least at the initial set of distances. Moreover, the rate of increase in dissimilarity with distance should be a function of the fraction of the regional species pool captured by an average sampling quadrat at the given grain, and this fraction indeed increases with grain. Harte & Kinzig (1997) provide another formalization of the relationship between distance and species turnover at different grains under the assumption of a power-law SAR.

Finally, we expect the environmental correlates of beta diversity (climatic and land-cover dissimilarities) to be grain dependent as well. This is based on the empirical observation that both the distributions of individual species (Mackey & Lindenmayer, 2001; Elith & Leathwick, 2009) and species richness (Willis & Whittaker, 2002) have different environmental correlates at different grains. However, there is no formal theory predicting exactly how grain size should affect the correlates of beta diversity.

Our study aims: (1) to test the prediction that beta diversity and its relationship with distance depend on spatial resolution (grain), (2) to identify whether patterns of beta diversity are driven by variability in climate, land cover or geographic distance, and (3) to explore how the relative effects of these drivers depend on spatial grain. We perform our analyses independently for four taxonomic groups: butterflies, birds, vascular plants and herptiles (i.e. amphibians and reptiles combined), and for different spatial extents and grain resolutions spanning from regions as small as Catalonia to the extent of Europe as a whole.

MATERIALS AND METHODS

We used two types of data. The first was distributional data arranged in a 50 km × 50 km Universal Transverse Mercator (UTM) grid over the whole of Europe. We used data for birds, butterflies, vascular plants and herptiles. The second type of data was characterized by smaller grain and extent, and involved national distributional atlases. These data were obtained for butterflies of Finland, birds of Catalonia (Spain) and vascular plants of Great Britain. Within each of these datasets, we generated a series of two to three nested grids with the same spatial extent but with varying grain. We included only data within the broadest-grain grid cells, of which no more than 10% covers the sea. For each grid cell in all grids, we characterized land-cover and climatic conditions as explained below. All of the land-cover and climatic data extractions, modifications of the grid systems and map creations were carried out in ArcGIS 9.2 (Esri Inc., Redlands, CA, USA). Data manipulations and statistical analyses were carried out in R (R Development Core Team, 2009).

Pan-European perspective

European birds

We used the *EBCC atlas of European breeding birds* (Hagemeijer & Blair, 1997). The bird atlas is based on the Common European Chorological Grid Reference System (CGRS) but there are some subtle differences in the shapes of some of the 50 km × 50 km grid cells. We used only 50 km × 50 km grid cells that were indicated as ‘good cells’ in the atlas (data received for at least 75% of expected breeding species in the grid cell). We did not apply this criterion on the subsequently aggregated 100 km × 100 km and 200 km × 200 km grids.

European butterflies

We used the data from the *Climatic risk atlas of European butterflies* (Settele *et al.*, 2008). We had no data on the sampling effort (completeness) within the 50 km × 50 km grid cells. As there are undoubtedly some under-sampled grid cells, we used only 50 km × 50 km cells with more than 10 reported species, which was an arbitrary criterion that should exclude the most severely under-sampled cells.

European vascular plants

Species distribution data for vascular plants were obtained from the *Atlas florae Europaeae* database (AFE; <http://www.luomus.fi/english/botany/afe/index.htm>; provided by the Secretariat of the Committee for Mapping the Flora of Europe and maintained by the Botanical Museum, University of Helsinki, Finland) at a resolution of 50 km × 50 km (Lahti & Lampinen, 1999). The plant data comprise only approximately 20% of the European flora. Note that these data have a bias towards well-represented groups in western and central Europe, while important families in the Mediterranean region are missing.

European amphibians and reptiles

We used the *Atlas of amphibians and reptiles in Europe* (Gasc *et al.*, 1997). We merged the data for amphibians and reptiles into one analysis because: (1) both groups have so few species that the low numbers could cause artefacts in the beta-diversity estimates, and (2) both taxa are ectothermic vertebrates with similar dispersal ability and hence are often merged in the literature into ‘herptiles’ (Hawkins *et al.*, 2008).

Land-use and climatic data

The land-cover data were extracted from the CORINE 2000 land-cover database (European Environmental Agency; <http://www.eea.europa.eu>). We used the Level 3 classification, which comprises 44 land-cover categories. These categories were merged into broader categories where necessary, according to the broad ecological requirements of each particular group. This resulted in 18 land-cover categories for birds and 25

categories for all other taxa (see Appendix S1 in Supporting Information for the exact classification used for each taxonomic group). The climatic data were derived from the 10' WorldClim dataset (Hijmans *et al.*, 2005). To characterize the climatic conditions within each grid cell we used the monthly averages of precipitation and temperature (from the period 1950–2000), resulting in 24 climatic variables in total. The values of precipitation and temperature were calculated from the 10' WorldClim grid by averaging values of all pixels lying within the grid cell of interest.

The grid we used for all pan-European analyses (Fig. 1) is based on the CGRS. The chorological data were inserted into a 50 km × 50 km grid map based on the UTM projection and

the Military Grid Reference System (Araújo, 2003; Whittaker *et al.*, 2007; Hawkins *et al.*, 2008). To vary the grain size, we merged the cells of the 50 km × 50 km grid to create a 100 km × 100 km and a 200 km × 200 km grid. Cells of the 200 km × 200 km grid that were overlapping with sea areas or not covered by the CORINE 2000 land-cover database were removed, and corresponding cells within the 50 km × 50 km and 100 km × 100 km grids were removed as well to ensure that all three analyses use an equal extent. We also excluded some areas from the Balkans that are undersampled in terms of biological data (the completeness of coverage criterion in the EBCC bird data was at least three). For the resulting grid system see Fig. 1.

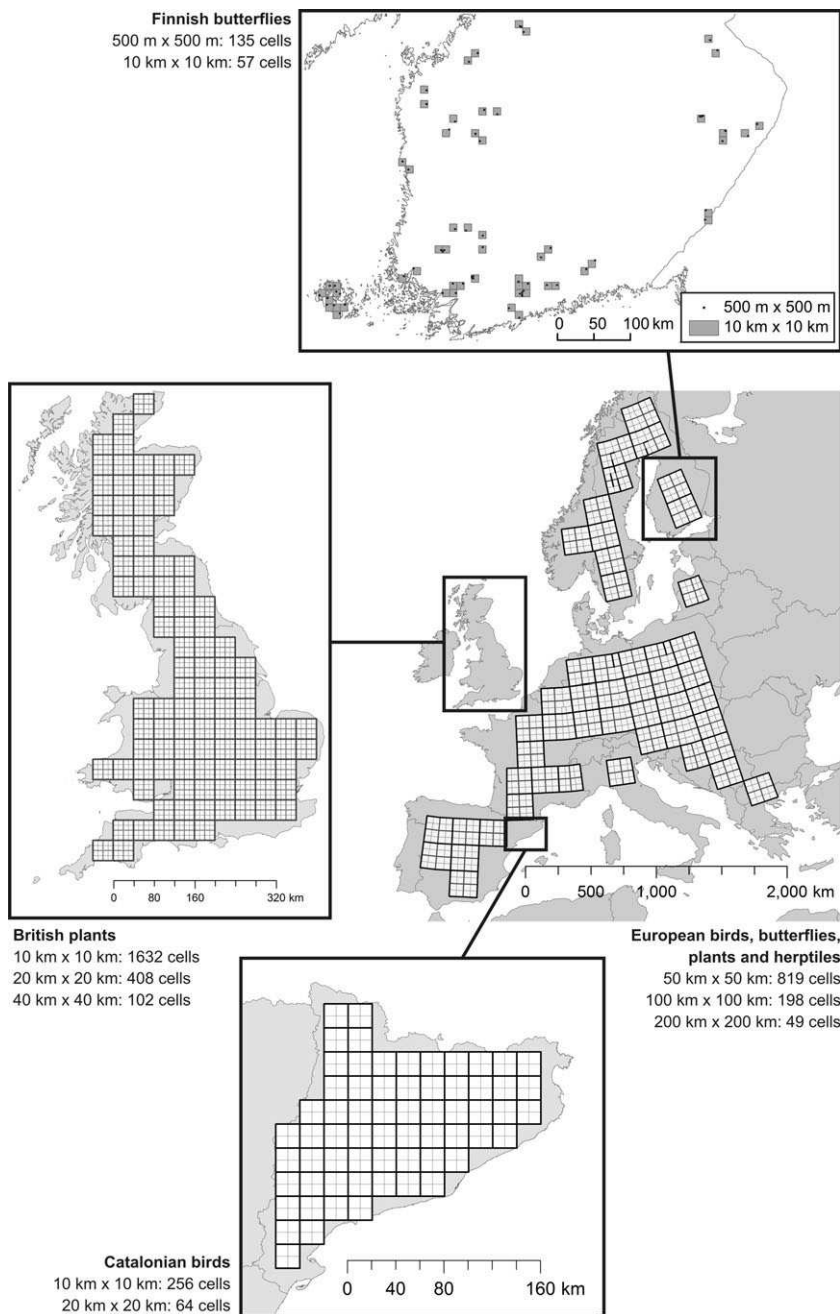


Figure 1 Nested grids used for the analysis of beta-diversity patterns across continental Europe (birds, vascular plants, butterflies and herptiles), Great Britain (vascular plants), Finland (butterflies) and Catalonia (birds). The different grains always cover the same area, except for Finland. We removed areas within the largest grid cells that overlapped a considerable area of sea, lacked land-cover data or were insufficiently surveyed. For each dataset we indicate the number of grid cells at each resolution.

Country-wide perspective

British plants

We used the 1987–1999 distributional data from the *New atlas of British and Irish flora* (Preston *et al.*, 2002). The atlas grid for Britain is based on the Ordnance Survey (OS) National Grid reference system, which is based on the OS Great Britain 1936 (OSGB36) datum; we used it to generate 10 km × 10 km, 20 km × 20 km and 40 km × 40 km grid resolutions covering exactly the same area (Fig. 1). We chose only data within 40 km × 40 km grid cells of which no more than 10% covers the sea. We derived the land-cover variables from the CORINE 2000 database as above (see Appendix S1 for land-cover classification). Average monthly values of temperature and precipitation for the same period (1987–1999) were extracted from British Met Office UK Climate Projections (UKCP09) dataset, with resolution of 5 km × 5 km which was then averaged for each cell of the relevant grain size.

Birds of Catalonia

We used the atlas of the breeding birds of Catalonia (Estrada *et al.*, 2004). It consists of 3078 1 km × 1 km sampling sites, which we then fitted into a 10 km × 10 km UTM grid and further coarsened into a 20 km × 20 km grid (Fig. 1). We derived the environmental variables from the same sources (CORINE 2000; WorldClim) as for the pan-European analyses (see above). Catalonia is of particular interest for our analysis because of its sharp climatic gradients, making it one of Europe's most diverse areas in terms of contrasting climates and habitats.

Butterflies of Finland

Unlike the aforementioned datasets this one does not comprise a continuous grid system. However, as the qualitative character of our results can be demonstrated as consistent for these data, we consider it worth reporting. We used two butterfly datasets that were collected using 0.5 km × 0.5 km and 10 km × 10 km grain sizes (Fig. 1). The first dataset consists of 67 pairs of 0.5 km × 0.5 km squares that were selected based on stratified random sampling from agricultural areas in different parts of southern Finland (Kuussaari *et al.*, 2007; Ekroos *et al.*, 2010). In each square, butterflies were counted seven times during summer 2001 in 10 independent 50-m long transects. The results of these counts were combined at the 0.5 km × 0.5 km resolution. The second dataset is based on the Finnish atlas monitoring scheme of butterflies in which observations are made in a 10 km × 10 km grid (Saarinen *et al.*, 2003). Within this dataset we focused only on 57 cells, 10 km × 10 km in size, which covered the more detailed sampling at the 0.5 km × 0.5 km resolution described above (Fig. 1), albeit using observations from the years 1997 to 2006. We derived the land-cover variables from the CORINE 2000 database using the Finnish version with 25-m resolution (Härmä *et al.*, 2004). Measures of mean monthly temperature and precipi-

tation for the period 1997–2006 were extracted from the Finnish Meteorological Institute.

Dissimilarity matrices

We performed analyses of beta diversity and its correlates for each taxonomic group at all spatial resolutions of the data. For each analysis we quantified dissimilarity in species composition (beta diversity, species turnover), climatic conditions, and land cover and calculated geographic distance between all pairs of grid cells. We arranged the dissimilarities into sites × sites triangular matrices ('dissimilarity' or 'distance' matrices).

Beta-diversity matrix

The majority of recent papers on beta diversity use similarity indices that reflect both the beta diversity and richness gradients. However, if beta diversity is to be understood at different grains, richness gradients must be removed from the analysed turnover patterns because species richness inevitably increases with increasing grain (because of the SAR). Therefore, we quantified dissimilarity in species composition (beta diversity) using the β_{sim} index (Koleff *et al.*, 2003), which is expressed as

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

where a is the number of species that are shared between two grid cells, b is the number of species that occur in the first cell but not in the second one and c is number of species that occur in the second cell but not in the first one. β_{sim} is a symmetric index, which has the advantage of being independent of species-richness gradients, reflecting relative rather than absolute differences between compared units (Lennon *et al.*, 2001; Koleff *et al.*, 2003). Additionally, we also used Jaccard's index (β_{jaccard} in this paper) due to its simplicity, its widespread use in distance-decay studies (Nekola & White, 1999) and its direct link to the SAR slope (Sizling *et al.*, 2011). The β_{jaccard} is expressed as

$$\beta_{\text{jaccard}} = 1 - \frac{a}{a + b + c}. \quad (2)$$

Note that we use β_{jaccard} as a dissimilarity measure, not as the more widely used similarity measure (Koleff *et al.*, 2003). We only use β_{jaccard} to explore the shape of the function of increase in dissimilarity with distance. The β_{sim} and β_{jaccard} matrices were calculated using the function 'betadiver' in the R package vegan (Oksanen *et al.*, 2009).

Climatic dissimilarity matrix

We rearranged the matrix of sites × monthly values of precipitation into a single vector. We standardized and centred values in this vector (to a mean of 0 and a variance of 1) and then rearranged it back to the sites × months matrix. The same was carried out for the temperature data. Based on these values we calculated a matrix of Euclidean distances between all pairs of grid cells. We also explored an alternative approach by using

minimum and maximum values instead of the arithmetic mean of climatic variables within each grid cell because, with increasing grain, the variability of minima and maxima may change differently from the variability of the mean values. However, the resulting dissimilarity matrices were strongly correlated with matrices based on the mean values, and also the results remained qualitatively similar irrespective of the method. We therefore report only results based on the mean climatic values.

Land-cover dissimilarity matrix

We log ($x + 1$)-transformed the values of area covered by each of the land-cover types within each grid cell (we summed the areas of CORINE pixels lying within the grid cell). Based on these values we calculated a matrix of Euclidean distances between all pairs of grid cells.

Geographic distance matrix

For the pan-European datasets, we used the Haversine formula to convert distances between the latitude and longitude coordinates of grid cells into distances based on kilometres. At the smaller scale of the country-wide datasets we used the Pythagorean theorem to find Euclidean distances between grid cells.

Statistical analyses

Grain dependence of beta diversity

In order to explore how beta diversity depends both on geographic distance and on spatial grain, we plotted β_{sim} and β_{jaccard} for each grain of resolution against the geographic distance between each pair of plots. To show the shape of the relationships, we fitted locally weighted polynomial regressions (LOWESS, smoothing span 2/3). We also plotted mean β_{sim} and β_{jaccard} at each grain for adjacent grid cells (the first distance class).

Correlates of β_{sim} : all pairwise comparisons

At each grain, we measured the strength of the correlations between β_{sim} matrices and climatic, land-cover and geographic distance matrices by Spearman's correlation coefficient and we plotted all of the relationships. Because the distance matrices are built up of non-independent data points, we tested the statistical significance of these individual correlations by a Mantel test (Legendre & Legendre, 1998). To calculate the Mantel tests on our large matrices we used the fast *zr* software (Bonnet & Van de Peer, 2002).

To assess the independent effects of climate, land cover and distance on β_{sim} , we performed hierarchical variation partitioning (package *hier.part* in R; Chevan & Sutherland, 1991) based on ordinary least-squares multiple regression. Note that we use the term *effect* to indicate a statistical relationship rather

than a proven mechanistic causation (Hawkins, 2012). The plotted individual relationships indicated that linear terms are an acceptable approximation. We used bootstrapping (numbers of permutations are provided in Appendix S2) to calculate standard errors of the proportions of independent effects of each explanatory variable. We also tested the statistical significance of the multiple regression models. Potentially, to this end one could use a permutation test based on the *F*-statistic of each of the predictors of a multiple regression model, comparable to a pairwise Mantel test with multiple predictors (Legendre & Legendre, 1998; Winter *et al.*, 2010). However, this is a computationally demanding test, which was not possible to perform for such a number of large matrices. Hence, we used an *F*-test with reduced degrees of freedom: an alternative and conservative approach in which the degrees of freedom are reduced from the overall number of pairwise comparisons to the number of grid cells.

Correlates of β_{sim} : first distance class

From the dissimilarity matrices we extracted values for pairs of neighbouring grid cells whose centroids were less than *c.* 1.5 cell widths apart. In Finnish butterflies the grid cells were scattered across Finland and were rarely adjacent. Hence, we used all pairs of cells that lay less than 100 km apart in the 500 m \times 500 m dataset or less than 30 km apart in the 10 km \times 10 km dataset. Using these data we performed the same analyses as in the case of all pairwise comparisons: we measured the Spearman's correlations of β_{sim} values with climatic and land-cover distances (and tested their significance using permutation test) and we partitioned the variation of β_{sim} into the variation explained by independent effects of climate and land-cover dissimilarity (obviously, we did not use geographic distances as they were constant).

RESULTS

Grain dependency of beta diversity

As predicted, beta diversity decreased with coarsening grain both between adjacent grid cells (Fig. 2) and for pairs of grid cells at distances up to roughly 3000 km (Figs 3 & 4). At distances greater than 3000 km the effect of grain size was still strong for β_{sim} but diminished for β_{jaccard} in European plants, butterflies and herptiles (Fig. 4). In other words, coarsening of the grain shifted the distance- β_{sim} and distance- β_{jaccard} relationships downwards (Figs 3 & 4). Visual inspection revealed that the distance- β_{sim} relationships were approximately linear with the slope decreasing with increasing grain size (Fig. 3), while the distance- β_{jaccard} relationships were rather more curved in shape (Fig. 4).

Correlates of β_{sim} : all pairwise comparisons

All of the single-term correlations of β_{sim} with geographic distances and land cover, and climatic dissimilarities were

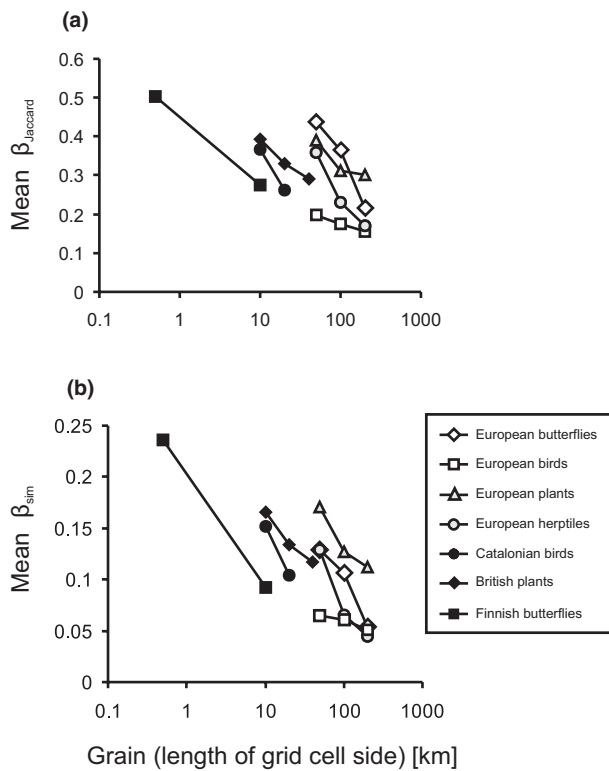


Figure 2 Here we show how mean beta diversity at first distance class depends on the grain of the data. Mean beta diversity always decreases with increasing grain size. Panel (a) shows the β_{Jaccard} index and panel (b) shows the β_{sim} index. Throughout the study we use both indices as measures of dissimilarity (not similarity) in species composition. The mean values in the plots were calculated using the following numbers of pairs of grid cells: British plants, 5989 (10 km \times 10 km), 1385 (20 km \times 20 km) and 299 (40 km \times 40 km); Catalanian birds, 898 (10 km \times 10 km) and 201 (20 km \times 20 km); European birds, butterflies, plants and herptiles, approximately 2500 (50 km \times 50 km; depending on the number of excluded grid cells in which no species was present), 507 (100 km \times 100 km) and 55 (200 km \times 200 km); Finnish butterflies; 1751 (0.5 km \times 0.5 km) and 64 (10 km \times 10 km).

positive for all datasets and grain resolutions (Mantel test, $P < 0.001$; 10,000 permutations), except for the Finnish butterflies and land-cover dissimilarities (See Appendix S3 for the significance values and the exact shapes of the relationships.).

All multiple regression models of β_{sim} versus climatic and land-cover dissimilarities were highly significant (F -test with reduced degrees of freedom, $P < 0.001$) with R^2 values ranging from 0.13 to 0.86 (Appendix S2). Results of the variation partitioning showed that geographic distance, climatic dissimilarities and land-cover dissimilarities all have distinct independent effects on β_{sim} (apart from the effect of land cover on beta diversity of Finnish butterflies) (Fig. 5, Appendix S2).

At the pan-European level, the independent effect of geographic distance was always the strongest, and it generally increased with increasing grain size (Fig. 5). In most of the pan-European datasets (except for birds) there was a striking

transition in the relative magnitude of independent effects of the two environmental factors; at the 50 km \times 50 km scale, land-cover dissimilarities had higher relative magnitudes of their independent effects than climatic dissimilarities, whereas at the grain resolution of 200 km \times 200 km the climatic dissimilarities had higher magnitudes (Fig. 5).

Over smaller spatial extents, at the country level, geographic distance no longer had the strongest independent effect on β_{sim} . At this level, the strongest independent effect was either due to climatic dissimilarities (Finnish butterflies, Catalanian birds) or a combination of both climate and land cover (British plants; Fig. 5). We additionally found that the magnitude of independent effects of climate mostly increased with increasing grain (Fig. 5). The butterflies of Finland showed a different and more variable pattern where land-cover dissimilarities were rather unimportant for predicting β_{sim} .

Correlates of β_{sim} : first distance class

The independent effects of land cover and climatic dissimilarity on β_{sim} were generally much weaker for the first distance class (Fig. 6) than for all pairwise comparisons (Fig. 5). The multiple regression models based on the first distance class all had R^2 values ≤ 0.24 (Appendix S2). At the pan-European scale the results were highly variable and showed highly variable scale dependence (Fig. 6, Appendix S2). The most consistent result across scales was for birds, where the effect of land cover increased with grain size. At the country-wide level, climatic dissimilarity was always more important as an independent predictor of β_{sim} than land-cover dissimilarities and the importance of climate increased with increasing grain (Fig. 6).

DISCUSSION

Beta diversity is grain dependent

Our results show strong evidence that beta diversity declines with coarsening grain. This was true at nearly any distance and for all taxonomic groups, indicating that the relationship between distance and beta diversity (Nekola & White, 1999) is consistently grain dependent. Similar observations have been reported in previous studies conducted on much smaller extents and grains of resolution than investigated here (Harte *et al.*, 1999; Lennon *et al.*, 2001; Arita & Rodríguez, 2002; Mac Nally *et al.*, 2004; Steinitz *et al.*, 2006). Our results and those of previous studies thus suggest that this seems to be a universal pattern up to extents of thousands of kilometres and grains of hundreds of kilometres. This is striking given the scarcity of classical patterns in ecology that can be considered universal in scope and behaviour (Lawton, 1999; Nekola & Brown, 2007).

We found that mean beta diversity at the first distance class always decreases with increasing grain size. This has a direct relationship with the scaling of species richness (the SAR), because beta diversity between adjoining grid cells is directly

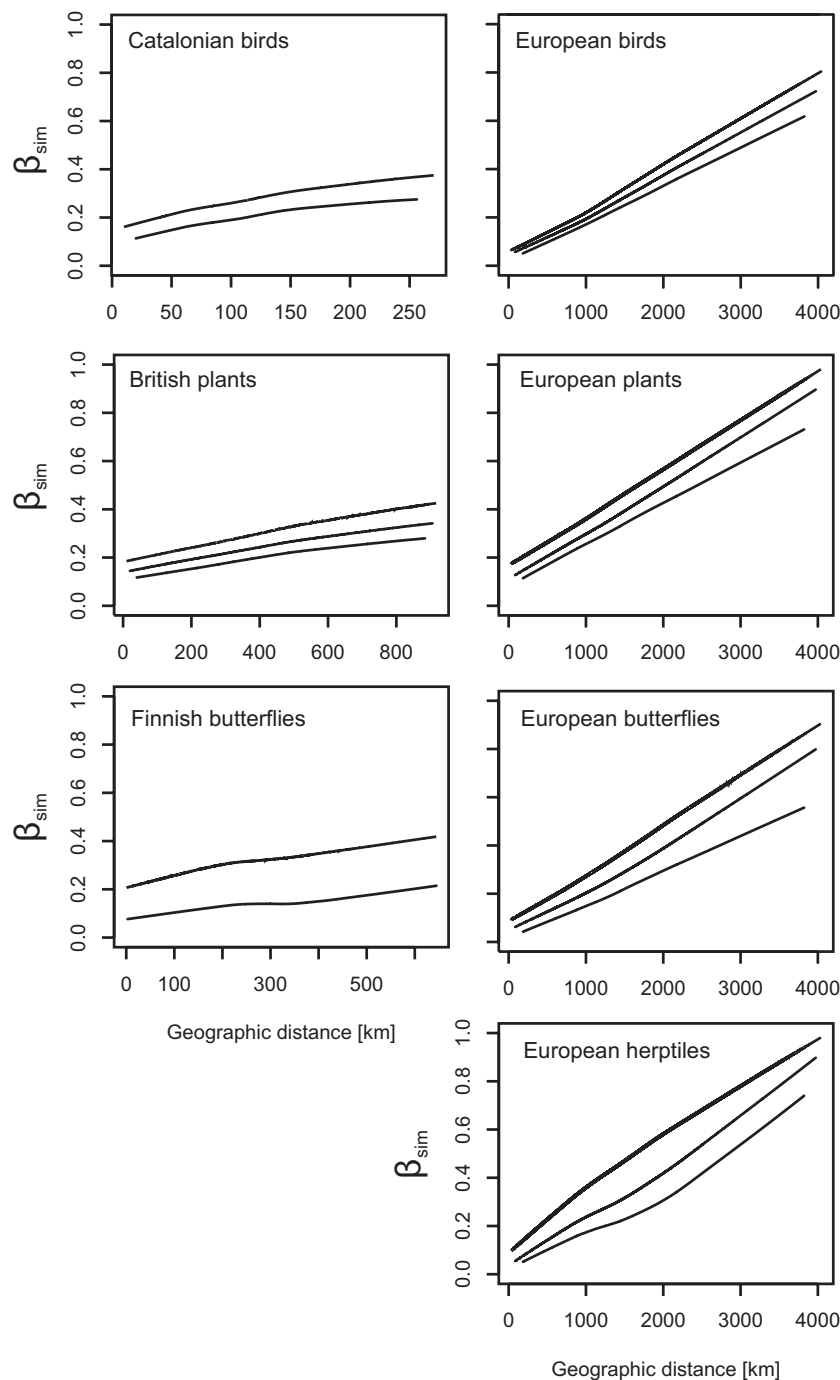


Figure 3 Distance rise of dissimilarity (or decay of similarity) expressed as the relationship between geographic distance and beta diversity (β_{sim}) at various grain sizes across continental Europe (birds, vascular plants, butterflies and herptiles), Great Britain (vascular plants), Finland (butterflies) and Catalonia (birds). The thickest lines indicate the largest grain, the thinnest lines the finest grain size (Fig. 1). Here we show that beta diversity decreases with increasing grain size at all geographic distances. In other words, the exact shape of the distance decay of similarity is grain-dependent. Lines were fitted by a locally weighted polynomial regressions (LOWESS) procedure with a smoothing span of 2/3.

related to the local slope of the SAR (Harte & Kinzig, 1997; Lennon *et al.*, 2001; Šizling *et al.*, 2011). It has recently been found that the slope of this relationship decreases with increasing scale (Harte *et al.*, 2009), although probably only within areas that are smaller than biomes (Preston, 1960). Our findings are in accordance with these theoretical expectations. Moreover, if we can link beta diversity with the slope of the SAR, we should be able to uncover mechanisms shaping the SAR directly, and to predict it from statistical models that link beta diversity at the first distance class with environmental dissimilarity.

Beta diversity at the first distance class

Our statistical models for the first distance class were less adequate than those for all possible pairs in explaining beta diversity. Beta diversity at the first distance class tended to be associated weakly with climatic dissimilarity and poorly with land-cover dissimilarities. We attribute the relatively poor predictive power of land-cover dissimilarities to the fact that CORINE land-cover categories are rather crude and do not successfully capture habitat heterogeneity at fine scales and across short distances. For example, Ekroos *et al.* (2010), using

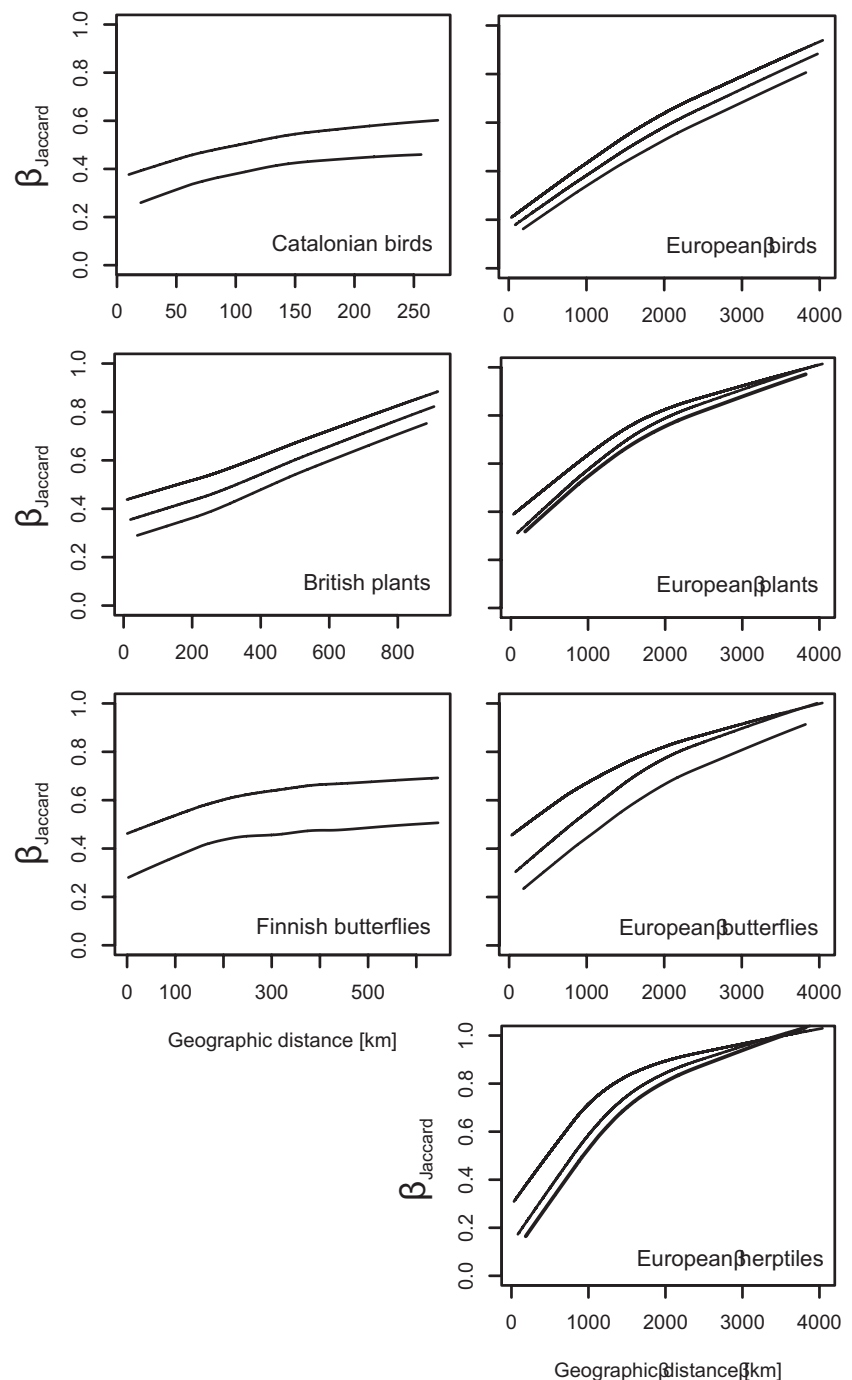


Figure 4 Distance rise of dissimilarity (or decay of similarity) expressed as the relationship between geographic distance and β_{Jaccard} at various grain sizes across continental Europe (birds, vascular plants, butterflies and herptiles), Great Britain (vascular plants), Finland (butterflies) and Catalonia (birds). The thickest lines indicate the largest grain, the thinnest lines the finest grain size. β_{Jaccard} decreases with increasing grain size at all geographic distances similarly to β_{sim} (Fig. 3), although the distance–decay relationships are somewhat more curved. Lines were fitted by a LOWESS procedure with a smoothing span of 2/3.

more detailed land-cover information based on aerial photographs, found a strong negative relationship between the cover of cultivated fields and butterfly beta diversity within 0.5 km \times 0.5 km landscapes in Finland, whereas this relationship was not significant in our analysis based on CORINE land-cover classes. Another possible explanation for the poor performance of environmental factors is competition and interaction among species. Although the effects of such interactions are difficult to assess, some macroecological signals of species interactions have been recently detected in birds (Heikkinen *et al.*, 2007; Gotelli *et al.*, 2010) and butter-

flies (Araújo & Luoto, 2007; Schweiger *et al.*, 2008, 2012). Second, species turnover at the first distance class may be structured not by the environmental variables considered here, but by the value of some other environmental factor, such as mean productivity (Gaston *et al.*, 2007a; but see Levanoni *et al.*, 2011).

Correlates of beta diversity at a European scale

One of the most important findings of our study at the European level is that geographic distance was the major

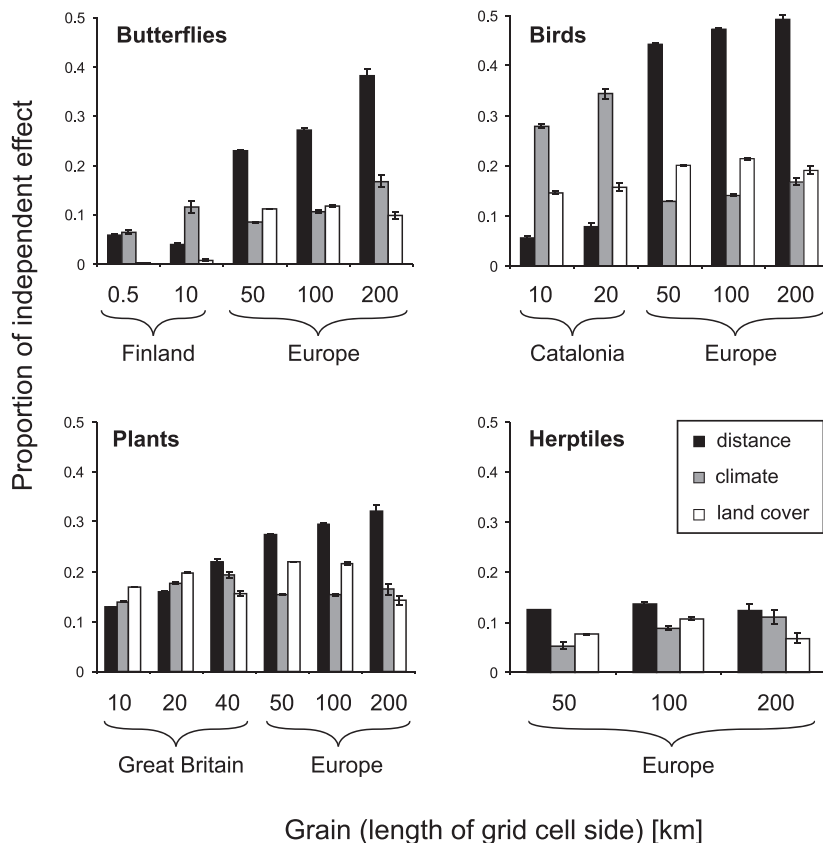


Figure 5 Independent effects of climate, land cover and geographic distance on beta diversity (β_{sim}) at various resolutions in continental Europe (birds, vascular plants, butterflies and herptiles), Great Britain (vascular plants), Finland (butterflies) and Catalonia (birds). The independent effects were obtained from hierarchical variation partitioning. Error bars are bootstrapped standard error (100 permutations). We can see that the independent effect of distance is the most important at the European scale with climate and land cover having weaker, but still important (and grain-dependent), effects. Within smaller regions beta diversity seems to be driven by a more complex interplay of distance, climate and land cover.

independent correlate of species turnover, and that its effect was considerably stronger than those of climate and land cover. This result is consistent across several taxonomic groups, despite major differences in their dispersal capacities and ecological traits. This finding implies that an important fraction of European biodiversity is not located where one would expect it based on environmental conditions alone. This discrepancy may be partly explained by considering that the CORINE land-cover categories are too coarse to adequately capture habitat heterogeneity (see above). Moreover, we did not account for environmental heterogeneity in other factors such as soil, geology and topography, some of which are relevant in modelling plant species distributions at European and regional scales (e.g. Pompe *et al.*, 2008). This limitation could be related to the weak correlations between land-cover dissimilarity and beta diversity reported here. The high explanatory power of geographic distance could arise because distance may work as a composite variable (surrogate) for other variables that went unaccounted for. However, given that the environmental data are the best to date and that the effect of distance was so pronounced (especially in birds and butterflies), we believe that distance per se has direct importance in explaining patterns in beta diversity.

We showed that European beta diversity increases with distance independently of environmental dissimilarity. This provides at least some support for the increasingly popular notion that dispersal limitations and historical processes are

still shaping large-scale patterns of species distributions in Europe and that species distributions are not in equilibrium with the current environmental conditions (Svenning & Skov, 2007; Svenning *et al.*, 2011). It has recently been shown that species distributions not only still lag behind the current climatic changes (Menéndez *et al.*, 2006), but that some have indeed not yet recovered from the last period of glaciation in Europe (Svenning & Skov, 2007). Our results are in accordance with these findings.

This study is not the first to highlight the importance of spatial distance rather than environment in explaining beta diversity. In a study of angiosperms in temperate eastern Asia and eastern North America, Qian *et al.* (2005) have found geographic distances to shape beta diversity at scales similar to our pan-European analysis. They suggested that their results might have been biased by low-quality climatic measures. Our measures of climate are certainly of high quality and yet our results are similar to those of Qian *et al.* (2005). Considering additional studies on the effect of dispersal limitation on species distributions (Qian & Ricklefs, 2007; Baselga, 2008; Svenning *et al.*, 2011), our results confirm that geographic distance is an important factor governing patterns of species turnover at continental scales.

Our results have considerable implications for applied biodiversity research. First, our study shows that any large-scale, i.e. continent-wide, modelling of species distributions that relies on environmental niches (Thuiller *et al.*, 2005; Jetz *et al.*, 2007; Pompe *et al.*, 2008) should consider dispersal

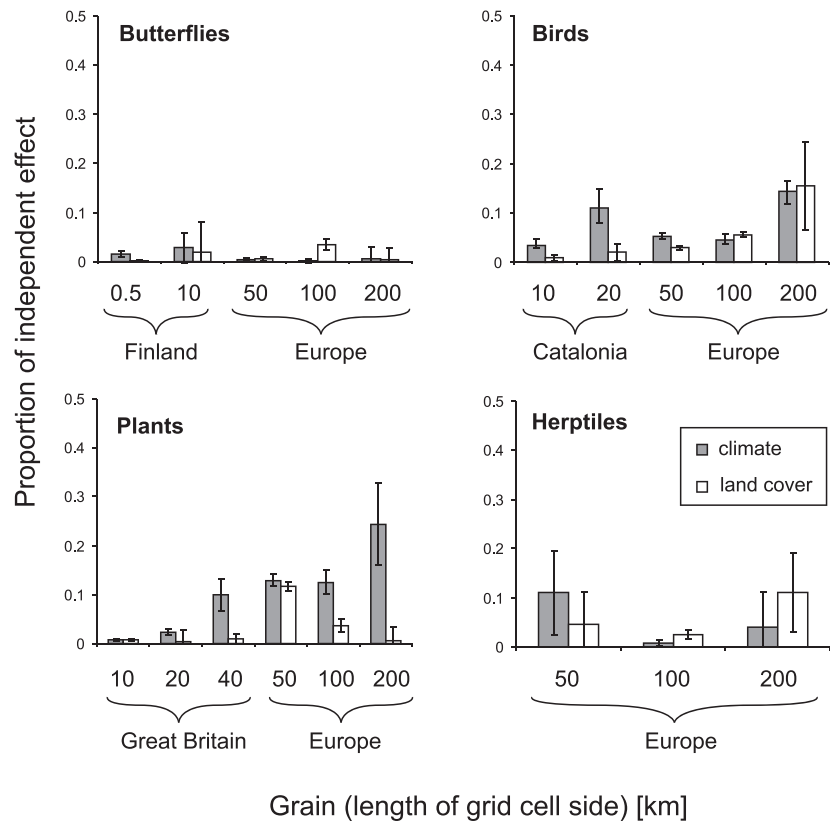


Figure 6 Independent effects of climate, land cover and geographic distance on beta diversity (β_{sim}) at the shortest distance class at various resolutions in continental Europe (birds, vascular plants, butterflies and herptiles), Great Britain (vascular plants), Finland (butterflies) and Catalonia (birds). The independent effects were obtained from hierarchical variation partitioning. Error bars are bootstrapped standard error (500 permutations). The effects plotted here are much weaker than in the case of pairwise comparisons (Fig. 5) and we were unable to demonstrate any systematic grain dependence of the effects, apart from somewhat increasing magnitude of the effect of climate in birds (in Catalonia and Europe) and British plants.

limitations. This is relevant not only for scenario-based projections of distribution shifts in response to climate change and land-use changes (Thuiller *et al.*, 2005; Jetz *et al.*, 2007; Settele *et al.*, 2008), but also for attempts to predict current distributions of species in poorly surveyed areas (Rocchini *et al.*, 2011). On the other hand, our results indicate that environmental factors, and especially climatic dissimilarities, largely determine species distributions at smaller spatial scales (country level and below) and, therefore, a predictive envelope modelling approach may be applied with a lower level of uncertainty at these scales.

Although we stress the important influence of geographic distance on patterns of European biodiversity, climatic and land-cover dissimilarity still had considerable effects. Moreover, the relative importance of climate and land cover mostly reversed when grain size increased above 100 km \times 100 km, with land cover being more important at finer grains and climate at coarse grains. These results suggest that species turnover cannot be explained by any single variable alone, but rather that they reflect a complex interplay between dispersal limitations and the climatic and habitat requirements of species. Correspondingly, studies of species distributions over continental extents (such as Europe) must consider all of these three drivers by addressing climate, connectivity (dispersal limitations) and land use (management) across different spatial scales. Our study provides some tools and evidence for factors relevant at particular scales, which are vital for securing the conservation of biodiversity across all spatial scales (Henle *et al.*, 2010).

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SUPPORTING INFORMATION

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

- Appendix S1** Land-cover classification used in our study.
Appendix S2 Tables summarizing the variation partitioning.
Appendix S3 Figures showing how β_{sim} correlates with environmental dissimilarity and geographic distance.

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BIOSKETCH

Petr Keil has just finished his PhD in insect macroecology and now works as a post-doctoral researcher at the Department of Ecology and Evolutionary Biology at Yale University. His main interest is in exploring geographic patterns of life by laying squares of different sizes on maps.

SCALES (Securing the conservation of biodiversity across administrative levels and spatial, temporal, and ecological scales; <http://www.scales-project.net>) is an international research consortium funded by the European Union. The project seeks ways to build the issue of scale into policy and decision making and biodiversity management. SCALES aims to provide the most appropriate assessment tools and policy instruments to foster our capacity for biodiversity conservation across spatial and temporal scales, and to disseminate them to a wide range of users.

Author contributions: P.K., D.S., O.S., I.K. and W.E.K. designed the main ideas; O.S., I.K., W.E.K., M.K., J.S., K.H., L.B. and H.S. provided the data; P.K., O.S., I.K., W.E.K., M.K., J.S., K.H., L.B., G.P., S.L., A.M. and D.S. contributed to the writing; P.K. analysed the data and led the writing.

Editor: Joseph A. Veech

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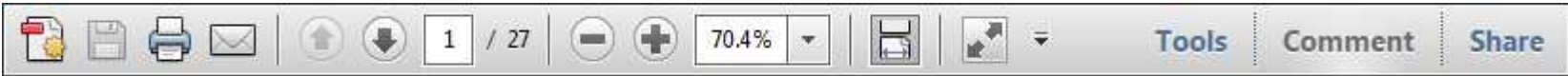
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Once you have Acrobat Reader open on your computer, click on the [Comment](#) tab at the right of the toolbar:



This will open up a panel down the right side of the document. The majority of tools you will use for annotating your proof will be in the [Annotations](#) section, pictured opposite. We've picked out some of these tools below:



1. **Replace (Ins)** Tool – for replacing text.




Strikes a line through text and opens up a text box where replacement text can be entered.


How to use it

- Highlight a word or sentence.
- Click on the [Replace \(Ins\)](#) icon in the Annotations section.
- Type the replacement text into the blue box that appears.

standard framework for the analysis of monetary policy. Nevertheless, it also led to exogenous shocks and a number of strategic decisions. The number of competitors in the market is that the structure of the main components of the level, are exogenous and important works on energy by Shiraz (M henceforth) we open the 'black b



2. **Strikethrough (Del)** Tool – for deleting text.

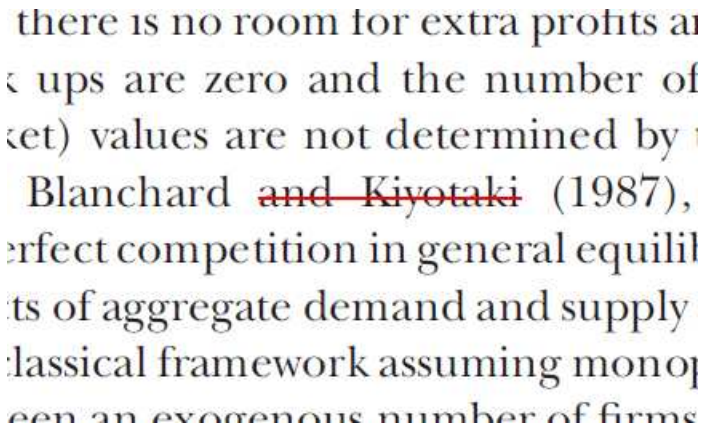


Strikes a red line through text that is to be deleted.


How to use it

- Highlight a word or sentence.
- Click on the [Strikethrough \(Del\)](#) icon in the Annotations section.

there is no room for extra profits and the number of firms are zero and the number of (net) values are not determined by Blanchard and Kiyotaki (1987), perfect competition in general equilibrium of aggregate demand and supply in the classical framework assuming monetary policy. An exogenous number of firms



3. **Add note to text** Tool – for highlighting a section to be changed to bold or italic.




Highlights text in yellow and opens up a text box where comments can be entered.


How to use it

- Highlight the relevant section of text.
- Click on the [Add note to text](#) icon in the Annotations section.
- Type instruction on what should be changed regarding the text into the yellow box that appears.

dynamic responses of mark ups consistent with the VAR evidence



4. **Add sticky note** Tool – for making notes at specific points in the text.




Marks a point in the proof where a comment needs to be highlighted.


How to use it

- Click on the [Add sticky note](#) icon in the Annotations section.
- Click at the point in the proof where the comment should be inserted.
- Type the comment into the yellow box that appears.

land and supply shocks. Most of the number of firms in the standard framework is consistent with the VAR evidence

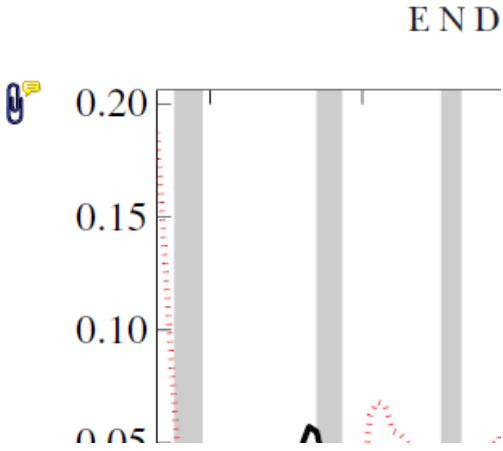


5. **Attach File** Tool – for inserting large amounts of text or replacement figures.


 Inserts an icon linking to the attached file in the appropriate place in the text.

How to use it

- Click on the **Attach File** icon in the Annotations section.
- Click on the proof to where you'd like the attached file to be linked.
- Select the file to be attached from your computer or network.
- Select the colour and type of icon that will appear in the proof. Click OK.

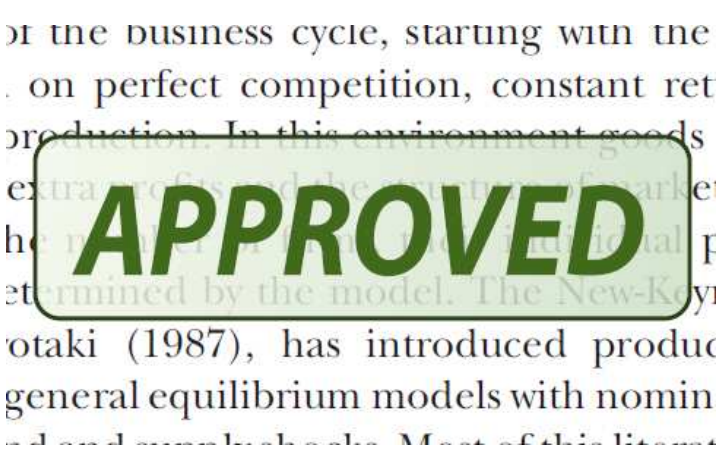


6. **Add stamp** Tool – for approving a proof if no corrections are required.


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How to use it

- Click on the **Add stamp** icon in the Annotations section.
- Select the stamp you want to use. (The **Approved** stamp is usually available directly in the menu that appears).
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▼ Drawing Markups

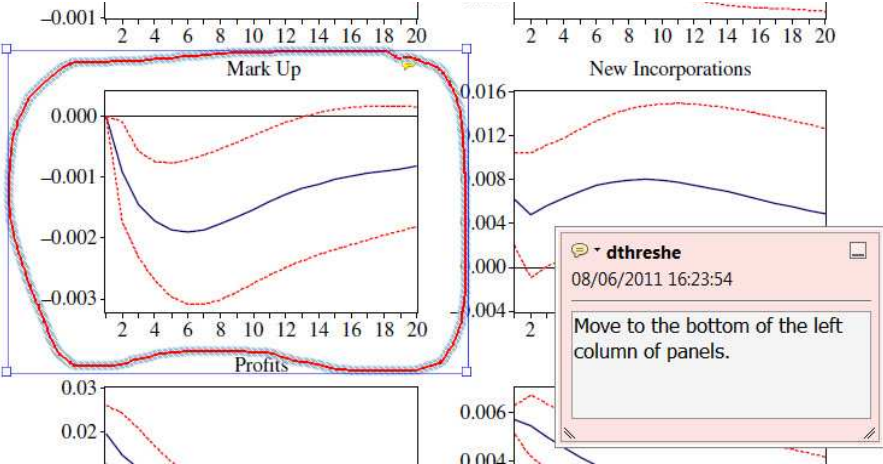


How to use it

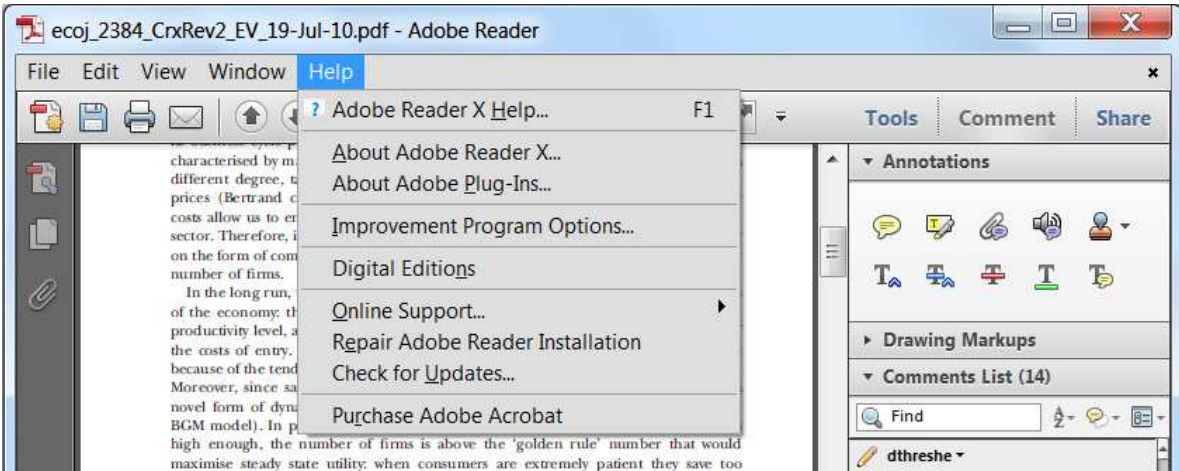
- Click on one of the shapes in the **Drawing Markups** section.
- Click on the proof at the relevant point and draw the selected shape with the cursor.
- To add a comment to the drawn shape, move the cursor over the shape until an arrowhead appears.
- Double click on the shape and type any text in the red box that appears.

7. **Drawing Markups** Tools – for drawing shapes, lines and freeform annotations on proofs and commenting on these marks.

Allows shapes, lines and freeform annotations to be drawn on proofs and for comment to be made on these marks..



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A screenshot of the Adobe Reader application window. The title bar shows 'ecoj_2384_CrxRev2_EV_19-Jul-10.pdf - Adobe Reader'. The 'Help' menu is open, displaying options like 'Adobe Reader X Help...', 'About Adobe Reader X...', 'About Adobe Plug-Ins...', 'Improvement Program Options...', 'Digital Editions', 'Online Support...', 'Repair Adobe Reader Installation', 'Check for Updates...', and 'Purchase Adobe Acrobat'. On the right side, the 'Annotations' panel is visible, showing icons for various annotation tools and a 'Comments List (14)'. The main document area shows a snippet of text from a paper.