Climate, history and neutrality as drivers of mammal beta diversity in Europe: insights from multiscale deconstruction

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Summary

1. Environmental sorting, historical factors and neutral dynamics may all drive beta diversity (change in species composition across space), but their relative importance remains unresolved. In the case of European mammals, key potential drivers of large-scale beta diversity include current climate, neutral dynamics and two historical factors: Pleistocene glaciations and peninsular dynamics (immigration from extra-regional eastern faunal source areas and inter-linked relictual survival and evolutionary differentiation in isolated areas).

2. We assessed the relative importance of these drivers using a novel analytical framework to deconstruct beta diversity of non-volant mammals in Europe (138 species) into its turnover (change in species composition because of species replacements) and nestedness components (change in species composition because of species richness differences) at continental and regional (250 000 km^2) scales.

3. We found continental-scale mammal beta diversity to be mainly caused by spatial turnover (99·9%), with only a small contribution (0·1%) from nestedness.

4. Current climate emerged as an important driver of beta diversity, given the strong continental-scale turnover, particularly in north–south direction, i.e., in line with the latitudinal climate gradient, and, more directly, the strong correlation of climate with spatial turnover at both continental and regional scales.

5. However, there was also evidence for the importance of non-climatic drivers. Notably, the compositional variation purely accounted for by space was greater than that purely accounted for by environment for both the turnover and the nestedness component of beta diversity. Furthermore, the strong longitudinal turnover within Southern Europe is in accordance with the region's long-term climatic stability having allowed multiple refugia and local evolutionary diversification. As expected from peninsular dynamics, there was increasing dissimilarity with geographic distance in an east–west direction because of nestedness, but only in Central and Northern Europe.

6. In conclusion, European mammal beta diversity mainly reflects spatial turnover and only to a limited extent nestedness and is driven by current climate in combination with historical – and perhaps, neutral – dynamics. These findings suggest that a key challenge for climate-change predictive studies will be taking the influence of non-climatic factors into account.

Key-words: biogeography, historical factors, ice-age refugia, macroecology, mammal community assembly, peninsular effect, Pleistocene ice ages, Post-glacial recolonization, species composition, vertebrate species distributions

Introduction

Geographic variation in species diversity fundamentally reflects the spatial distribution of individual species and their overlap. Hence, a primary feature of species diversity is the

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change in species composition of biological assemblages across space, i.e., beta diversity (Whittaker 1972). Understanding which factors drive beta diversity is therefore a crucial issue for ecology. The potential drivers can be grouped into three classes: (i) environmental sorting; (ii) neutral dynamics (Hubbell 2001); and (iii) historical factors, notably geographic patterns of speciation, extinction, and dispersal from areas of origin or recolonization from refugia. The latter two will both cause geographic distance decays in community similarity (Nekola & White 1999) beyond what can be explained by the environment. Focus has hitherto been on environmental drivers (Buckley & Jetz 2008; Melo, Rangel & Diniz-Filho 2009) or the relative importance of environmental drivers and either geographic distance overall irrespective of the underlying drivers (Nekola & White 1999; Bjorholm *et al.* 2008) or neutral dynamics specifically (Condit *et al.* 2002; Tuomisto, Ruokolainen & Yli-Halla 2003). In contrast, historical factors have received little attention (but cf. Normand *et al.* 2006; Baselga 2008, 2010).

A key obstacle for improving our understanding of the drivers of beta diversity is that the spatial patterns predicted by environmental turnover, neutral dynamics, or history can be quite similar and statistically difficult to tease apart (e.g., Baselga 2008; Qian, Badgley & Fox 2009). One novel avenue for progress is deconstructing beta diversity into two components, spatial turnover and nestedness-driven dissimilarity, which reflect different phenomena and must be generated by different mechanisms (Baselga 2010). Nestedness of species assemblages occurs when the species present in one site are a subset of the species occurring at another, more species-rich site (Wright & Reeves 1992; Ulrich & Gotelli 2007). Nested subsets of species constitute different assemblages because some species are present only in the richer sites; thus, nestedness generates beta diversity without species turnover (as there are no species replacements). Many processes may generate nested patterns (Ulrich, Almeida-Neto & Gotelli 2009). Notably, nestedness may result from ecological sorting (Greve *et al.* 2005), especially over short environmental gradients that range from environmental conditions suitable for numerous species to marginal environments with only broadly tolerant species present and no unique species pool (species with the geographic and ecological potential to be included in a given assemblage). Historical dynamics may also cause nestedness by dispersal-limited expansion (Svenning, Normand & Skov 2008) from regions of elevated speciation rates and/or reduced extinction rates (Fjeldså 1994; Svenning & Skov 2007a). An important point is that nestedness can only be a pronounced pattern for assemblages derived from the same overall species pool. As a consequence, nestedness is expected to be low at continental and global scales because the large majority of species have geographic ranges that are much smaller than a continent (Gaston 2003). In contrast, spatial turnover involves the replacement of species present at one site by different species at another site. Turnover can also reflect a number of mechanisms, notably ecological sorting over environmental gradients, neutral dynamics with spatially constrained dispersal or

historical dynamics involving more than one regional species pool. Nestedness and turnover therefore not only represent different patterns underlying beta diversity but are also in fact generated by fundamentally different processes (species richness differences vs. species replacements). Deconstructing beta diversity into its nestedness and spatial turnover components therefore will provide insight into the mechanisms that drive beta diversity.

In this study, we deconstructed European mammal beta diversity in this way to achieve a more thorough understanding of the processes driving beta diversity across a large geographical region. We achieved these goals by implementing a novel analytical framework for measuring and deconstructing beta diversity (Baselga 2010). This framework has thus far been applied only to one other case, a simple analysis of beta diversity in European longhorn beetles (Baselga 2010). In addition, while a number of studies have focused on mammal beta diversity patterns in the New World (Rodríguez & Arita 2004; Davis 2005; McKnight *et al.* 2007; Melo, Rangel & Diniz-Filho 2009; Qian, Badgley & Fox 2009; also see Riddle 1998; McGill, Hadly & Maurer 2005), beta diversity patterns in the European mammal fauna have not previously been studied. Studying beta diversity of European mammals is likely to be particularly instructive for understanding the influence of historical factors on beta diversity patterns, given the well-documented Quaternary climatic and faunal history of Europe (Kurtén 1968; Rodríguez 2006; Sommer & Nadachowski 2006; Markova 2007; Randi 2007; Fløjgaard *et al.* 2009; Markova, Simakova & Puzachenko 2009). Based on general beta diversity theory and the specific biogeographic history of the European mammal fauna, we formulated and evaluated the following competing but non-exclusive hypotheses regarding the drivers of mammal beta diversity in Europe at continental and regional (250 000 km^2) scales:

1. *Climate hypothesis*: beta diversity is driven by current climate. At the continental scale, this hypothesis predicts strong turnover and some nestedness, especially latitudinally because climate exhibits a particularly strong latitudinal gradient. Both turnover and nestedness would here reflect ecological sorting, with nestedness resulting from more species tolerating a warm climate because of niche conservatism (Wiens & Donoghue 2004) or general physiological requirements (all organisms need energy and fluid water). At smaller regional scales, this hypothesis also predicts strong turnover, with turnover correlating with topography-driven climatic heterogeneity, being highest in mountainous regions. There should be a strong nestedness component only in regions with strong environmental gradients that reach into marginal environments that few species tolerate, e.g., very cold climates.

2. *Glaciations hypothesis*: beta diversity patterns are a result of Quaternary climate change (Jansson & Dynesius 2002). At the continental scale, this hypothesis predicts particularly strong turnover in Southern Europe, where the glacial impacts were mild enough to allow numerous refugia as well as local evolutionary

differentiation and diversification (Rodríguez 2006; Randi 2007; Medail & Diadema 2009). Strong latitudinal nestedness is predicted because of incomplete postglacial recolonization from southern refuge areas (Svenning & Skov 2007a). As a result, turnover and nestedness should exhibit broad-scale spatial patterns beyond what climate can explain (Svenning & Skov 2005). For similar reasons, there should also be high turnover and nestedness at smaller regional scales in Southern Europe, but not elsewhere.

3. *Peninsular hypothesis*: At the continental scale, Europe can be considered a peninsula, and peninsular dynamics *sensu* Simpson (1964) may drive mammal beta diversity. Notably, spatially constrained dispersal from eastern faunal source areas (Kurtén 1968; Randi 2007) may cause nestedness in a longitudinal direction, reflected as a westward decline in the representation of widespread Palaearctic taxa (Baquero & Tellería 2001). Because these dynamics may involve competitive exclusion and, conversely, relictual survival and evolutionary differentiation in more isolated areas, we also expect turnover in the longitudinal direction. As a result, turnover and nestedness should exhibit broad-scale spatial patterns beyond what climate can explain (Svenning & Skov 2005). At regional scales, there should generally be low turnover and nestedness, because these peninsular dynamics are large-scale in nature, although with some repetition on smaller peninsulas (cf. Simpson 1964).

4. *Neutral hypothesis*: Neutral dynamics (species-neutral stochastic population dynamics and spatially constrained dispersal; Hubbell 2001) will generate spatially uniform turnover (Condit *et al.* 2002; Tuomisto, Ruokolainen & Yli-Halla 2003) and, hence, beta diversity at all scales, but will not generate nestedness. Again, turnover should exhibit spatial patterns beyond what climate can explain.

Materials and methods

STUDY AREA AND SPECIES

The study area was Europe eastwards to *c.* 30°E (Fig. 1), following the source of the species distribution data (Atlas of European Mammals, AEM) (Mitchell-Jones *et al.* 1999). The AEM was produced by a thorough review of species registrations per country and contains presence/absence data of species occurrences in a $\sim$50 × 50-km grid (Mitchell-Jones *et al.* 1999), with a total of 2462 grid cells included in this study. This study included records of 'species presence' as well as 'presence assumed' (observed before 1970 and no evidence of later extinction) of all native terrestrial non-volant mammals ($n = 138$ spp.).

ENVIRONMENTAL DATA

The potential climatic drivers of beta diversity were represented by the following five variables that represent key aspects of macroclimate and the main driver of smaller-scale climate variation (topography): Annual mean temperature (AMT) and annual precipitation (PANN) are 1950–2000 means, interpolated to a 30″ resolution (Hijmans *et al.* 2005). Actual and potential evapotranspiration (AET and PET) represent *c.* 1920–1980 annual means at 30′ resolution (United Nations Environment Programme GNV183 data set; http://www.grid.unep.ch). All climatic variables were averaged for each 50 × 50-km grid cell. Topographic heterogeneity (TOPO), the main control of small-scale climatic heterogeneity, was represented by topographic range within each grid cell, calculated based on the 30″ resolution Shuttle Radar Topography Mission elevation data available from Hijmans *et al.* (2005).

STATISTICAL ANALYSES

Beta diversity was partitioned into its spatial turnover and nestedness components following Baselga (2010). In short, this method relies on the fact that Sørensen and Simpson dissimilarities are equal in the absence of nestedness, so their difference is a measure of
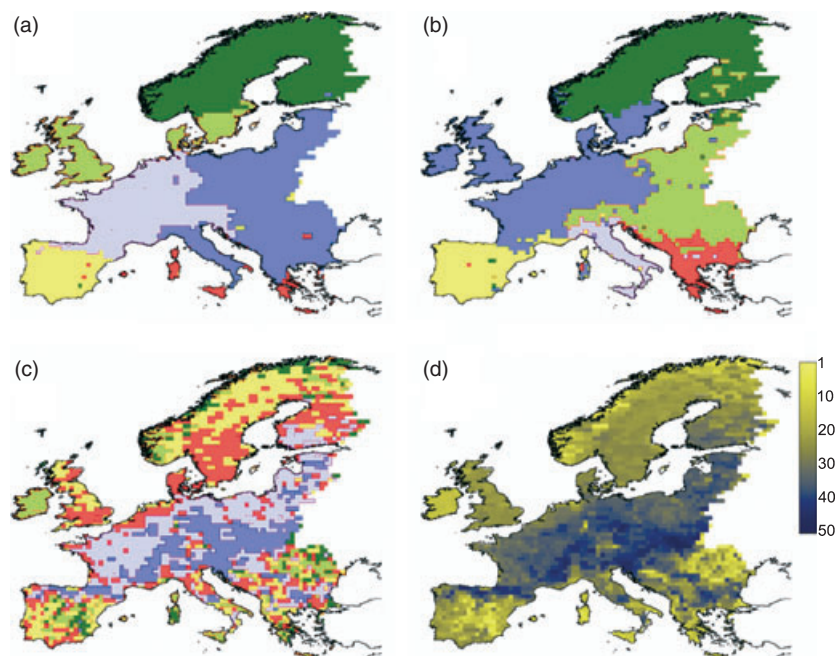

Fig. 1. Geographical distribution of six clusters derived from cluster analyses (Ward's agglomerative method) of species composition for mammals across Europe using dissimilarity matrices accounting for (a) total beta diversity (Sørensen dissimilarity, β_{sor}, i.e., both spatial turnover and dissimilarity resulting from nestedness summed together), (b) spatial turnover (Simpson dissimilarity, β_{sim}) and (c) dissimilarity resulting from nestedness (β_{nes}). Geographical distribution of mammal species richness (d) is also shown for comparison.

the nestedness component of beta diversity. Thus, using the equation $\beta_{sor} = \beta_{sim} + \beta_{nes}$, overall beta diversity (Sørensen dissimilarity) can be additively partitioned into two fractions representing spatial turnover in species composition (Simpson dissimilarity) and variation in species composition because of nestedness (nestedness-driven dissimilarity). We implemented this approach using multiple-site dissimilarity measures (Sørensen [β_{SOR}], Simpson [β_{SIM}], and nestedness-driven [β_{NES}]) dissimilarity) for Europe and large regions within Europe and pairwise dissimilarity matrices (Sørensen [β_{sor}], Simpson [β_{sim}], and nestedness-driven [β_{nes}]) dissimilarity for the grid cells. Computations were carried out in ʀ (version 2.10.1; R Development Core Team 2009) using the functions provided by Baselga (2010).

Overall beta diversity for the whole continent was measured using multiple-site dissimilarity measures (β_{SOR}, β_{SIM}, β_{NES}) for all cells to estimate the relative contribution of turnover and nestedness to the total amount of faunal heterogeneity in Europe. Hundred random samples of 50 cells were taken across the continent and used to compute the mean and SD for β_{SOR}, β_{SIM} and β_{NES} across samples to assess the significance of their differences. Subsequently, continental patterns of pairwise dissimilarity (β_{sor}, β_{sim}, β_{nes}) for the 50 × 50-km grid cells were described by means of cluster analyses. The three dissimilarity matrices were submitted to cluster analysis using the R cluster package (Maechler *et al.* 2005); with clusters built using the Ward linkage method because it minimizes the total error sum of squares in the dendrogram (Legendre & Legendre 1998). The significance of cutting the β_{sim}-based tree into n clusters (2 ≤ n ≤ 20) was assessed by means of ANOSIM tests (Analysis of Similarities; Clarke 1993) using the vegan package (Oksanen *et al.* 2007). A cut-off of $n = 6$ was selected as the minimum n for which n + 1 did not cause a significant increment in ANOSIM R. For comparability, the same cut-off was also used with the β_{sor}- and β_{nes}-based dendrograms. Therefore, for each dendrogram (β_{sor}, β_{sim}, and β_{nes}), six major clusters were extracted using the maptree package (White 2007), and the geographic distribution of these clusters was mapped using IDRISI 32.02 (Clark Labs 2000).

The spatial and environmental correlates of assemblage composition were assessed using the constrained ordination technique, Constrained Analyses of Principal Coordinates (CAP; Oksanen *et al.* 2007). This analysis allows testing and quantifying the relationship between variability in the table of species occurrences and the two sets of predictor variables (the five environmental factors and the second-order polynomial terms of longitude and latitude: X, Y, X^2, Y^2, XY) to be examined. CAP was used because it can be computed with any dissimilarity index and, therefore, β_{sim} and β_{nes} could both be represented in the constrained ordinations. Because of the large size of the matrices and computational limitations of R, variable significance could not be computed with the permutation tests (vegan command permutest; Oksanen *et al.* 2007). Finally, variation in species composition was partitioned among environmental and spatial predictors by subtracting the variation explained by each set from the variation explained by a complete model (Legendre & Legendre 1998), yielding estimates of its purely environmental (R_{PE}), mixed environmental–spatial (R_{MX}) and purely spatial (R_{PS}) fractions (Borcard, Legendre & Drapeau 1992).

To quantify beta diversity in longitudinal and latitudinal directions, Europe was divided into three longitudinal and three latitudinal bands. Within these bands, we assessed the increase in species dissimilarity with geographic distance (equivalent to the distance decay of similarity) derived from species turnover (β_{sim}) and nestedness (β_{nes}) measures. To account for the inherent dependence of the dissimilarity values, significance of the Pearson correlations was computed by means of Mantel permutation tests using the vegan package (Oksanen *et al.* 2007) in R. To test for differences in intercepts and slopes for this relationship among latitudinal and longitudinal bands, the frequency distributions of the parameters were estimated by bootstrapping ($n = 1000$ bootstraps) using the boot package (Canty & Ripley 2008). When assessing the significance of one parameter being larger in one region than in another, the probability of obtaining the opposite result by chance was empirically computed by comparing the bootstrap parameter distributions.

Regional-scale beta diversity was measured within 27 regional squares of 250 000 km^2, each containing 45–100 50 × 50 km^2 cells. The 'latitudinal squares' provided by the EDIT Geoplatform (Sastre, Roca & Lobo 2009) were used because this grid maintains the latitudinal range of all squares constant, while adjusting the longitudinal range in accordance with the latitudinal variation in the size of longitudinal degrees. These large squares ('regional squares') were superimposed on the original 50 × 50 km^2 AEM cells, and only regional squares that included >45 AEM cells were considered in subsequent analyses ($n = 27$). β_{SIM} and β_{NES} were used to compute values of multiple-site dissimilarity for each of the regional squares. Differences in the number of cases among squares were controlled for by re-sampling 45 cells from each square 100 times and computing the average β_{SIM} and β_{NES}. The environmental and spatial correlates of β_{SIM} and β_{NES} across Europe (and thus of the regional values of species turnover and nestedness-driven dissimilarity) were assessed by simple linear regressions of β_{SIM} and β_{NES} values against X and Y, as well as mean AMT, PANN, PET, and AET and the TOPO sum for the 50 × 50-km cells in a region for each regional square. Finally, simple and multiple linear regressions were used to partition the variation in β_{SIM} and β_{NES} among the significant predictors by subtracting the variation explained by the various subsets of predictors from the variation explained by a complete model with all predictors (Legendre & Legendre 1998).

Results

BETA DIVERSITY PATTERNS ACROSS EUROPE

Overall beta diversity of mammals in Europe ($\beta_{SOR} = 0.998$, $n = 2462$ cells) is mainly caused by spatial turnover ($\beta_{SIM} = 0.997$), with only a small contribution from nestedness ($\beta_{NES} = 0.0013$). The corresponding beta diversity values for random samples of 50 cells were $\beta_{SOR} = 0.933 \pm 0.004$ (SD), $\beta_{SIM} = 0.882 \pm 0.009$ and $\beta_{NES} = 0.051 \pm 0.008$. The overall beta diversity pattern for Europe, according to the β_{sor}-based cluster analyses, reflects six large clusters with strong geographic associations (Fig. 1): northern Scandinavia, Northwestern Europe, western Central Europe, Eastern Europe including the Balkans and Italy, the Iberian Peninsula and Mediterranean islands and small peninsulas.

Deconstructing the overall pattern into its turnover (β_{sim}) and nestedness (β_{nes}) components made it clear that these two components exhibit divergent spatial patterns. Spatial turnover strongly drives the overall beta diversity pattern, as can be seen from the similarity of the β_{sim} and β_{sor} groups, while the β_{nes} pattern differs markedly, instead coinciding with the species richness pattern (Fig. 1).

SPATIAL AND ENVIRONMENTAL CORRELATES AT THE CONTINENTAL SCALE

Using CAP to analyse and partition the continental-scale variation in species composition resulting from turnover and nestedness, we found that for β_{sim}, the purely spatial component is larger ($R_{PS} = 6.9\%$) than the purely environmental component ($R_{PE} = 2.6\%$), although the mixed environmental–spatial component is the largest ($R_{MX} = 15.1\%$). The main environmental correlates in the CAP model are AMT and PET, bivariately accounting for 12·2% and 11·1% of the variation in species composition, respectively. The other three environmental variables each accounts for 0·9–7·3% of the variation. In the case of β_{nes}, R_{PE} (2·9%), R_{MX} (4·2%) and R_{PS} (4·5%) account for similar amounts of variation, although R_{PE} again is the smallest. The strongest environmental correlate of compositional variation resulting from nestedness is AET, but it accounts for only 2·0% of the variation.

LATITUDINAL AND LONGITUDINAL PATTERNS

Comparison of the β_{sim}-geographic distance relationship (as represented by the Mantel correlations) within the three latitudinal bands and three longitudinal bands showed that turnover is strongest in north–south direction, although also strong in east–west direction (Fig. 2a–f). Pairwise comparisons between bootstrapped slopes and intercepts of different bands showed that all pairs of parameters were significantly different ($P < 0.01$). Therefore, comparing latitudinal bands, although the slope is higher in the northern (2.25×10^{-7}) than in the middle (1.40×10^{-7}) and southern (1.24×10^{-7}) bands, a markedly larger intercept in the southern band (0·28) than in the middle (0·07) and northern (0·09) bands implies that spatial turnover is higher in the south. For longitudinal bands, no marked differences were found among the western, middle and eastern slopes (1.9×10^{-7}, 2.2×10^{-7} and 1.8×10^{-7}, respectively), but considering intercepts (0·12, 0·10 and 0·18, respectively), spatial turnover is slightly higher in Eastern Europe. The β_{nes}-geographic distance relationship is much weaker (Fig. 2g–l). While β_{nes} increases with geographic distance in east–west direction in Central and Northern Europe, the slope is negative in Southern Europe (Fig. 2i), reflecting that turnover there is so high that distant cells do not constitute nested subsets at all. The south–north β_{nes}-geographic distance relationship is of negligible strength in the western and central bands and slightly negative in Eastern Europe, again reflecting that distant cells here do not constitute nested subsets (Fig. 2l).

BETA DIVERSITY PATTERNS WITHIN SMALLER REGIONS

As for Europe overall, beta diversity within the 250 000-km^2 regions generally reflects turnover (β_{SIM}) much more than nestedness (β_{NES}). Turnover is highly variable among the regions; it is high in much of Southern Europe, south–central and eastern parts of Central Europe, and parts of Scandinavia, and especially low in Northwestern Europe (Fig. 3a). In contrast, β_{NES} is weak everywhere but highest in Northwestern Europe (Fig. 3b). In simple regression analyses of environmental and spatial correlates of regional β_{SIM} and β_{NES}, TOPO and PET emerged as the only two significant predictors for β_{SIM}, and TOPO, AET and PET for β_{NES}. Turnover increases with TOPO and PET, with the pure TOPO, pure PET and mixed TOPO-PET variation components accounting for 21·6%, 6·9% and 20·7%, respectively. In contrast, β_{NES} decreases with TOPO, AET and PET. When the variation in β_{NES} was partitioned, the pure TOPO and mixed TOPO-AET-PET variation components account for most of the explained variation (12·0% and 12·8%, respectively), whereas the pure AET and pure PET fractions are negligible ($< 1.5\%$), and the mixed TOPO-AET, TOPO-PET and AET-PET are small ($< 3.5\%$).

Discussion

The present study provides the first comprehensive analysis of beta diversity patterns in the European mammal fauna and the first multiscale deconstruction of beta diversity into its turnover and nestedness components. Mammal beta diversity across the whole of Europe mainly reflects species turnover, with only a small contribution from nestedness. The turnover component geographically reflects that Europe can be subdivided into six regions, each with a suite of characteristic species, namely Northern Europe, Western and Central Europe, and Eastern Europe plus the three Mediterranean regions, the Iberian, Italian, and Balkan peninsulas. While there are minor differences, these clusters are broadly consistent with those identified by Heikinheimo *et al*. 2007 despite the different clustering approaches used in that study. Our results provide some support for all four hypothesized drivers, suggesting that beta diversity of mammals in Europe may be a product of their joint effects.

Current climate clearly constitutes an important driver of mammal beta diversity in Europe. There is strong continental-scale turnover, especially in north–south direction, as predicted from the strong latitudinal climate gradient; and, more directly, climate was a strong correlate of species composition. Similarly, European mammal species distributions have recently been found to be well explained by current climate (Dormann *et al*. 2010). Large-scale beta diversity patterns have also been linked to climate for other organism groups and areas (e.g., Buckley & Jetz 2008), including mammals in North America (Qian, Badgley & Fox 2009). Furthermore, our results indicate an important role for climate at smaller scales; the strongest correlate of species turnover within the 250 000-km^2 regions is topographic heterogeneity, itself strongly correlated with within-region climatic variation. Again, topographic heterogeneity has also been identified as the main driver of mammal beta diversity across the New World at a similar scale (neighbouring 1° grid cells; Melo, Rangel & Diniz-Filho 2009).

The results for nestedness were more equivocal. While there is a small purely environmental component, dissimilarity because of nestedness does not increase with distance in
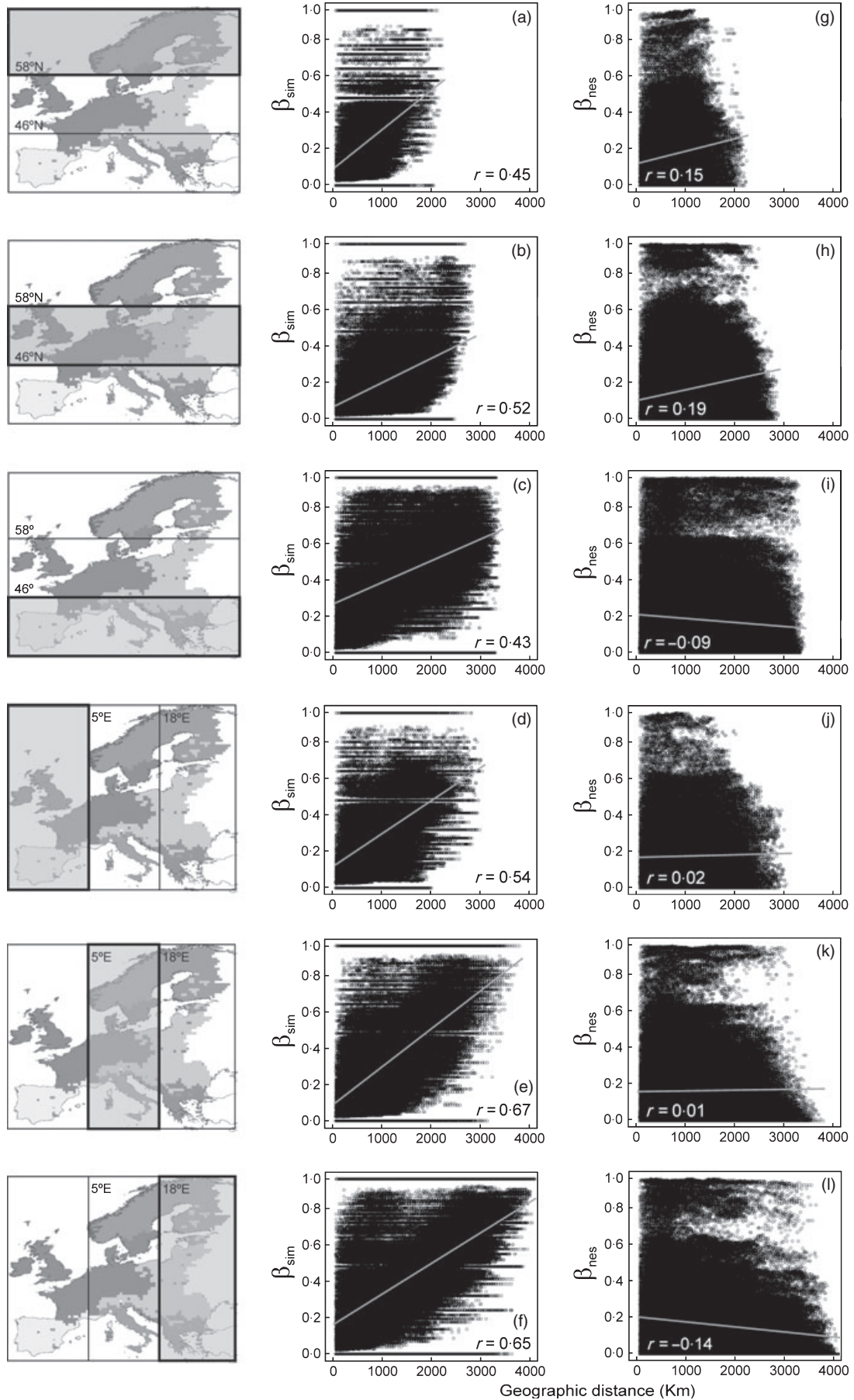
Fig. 2. Mammal species turnover (β_{sim}: a–f) and dissimilarity resulting from nestedness (β_{nes}: g–l) relationships (linear fits) with geographic distance within three latitudinal (a–c, g–i) and three longitudinal bands (d–f, j–l) in Europe. Significance of the corresponding correlations (Pearson r) was assessed with Mantel tests (all $P < 0.01$).
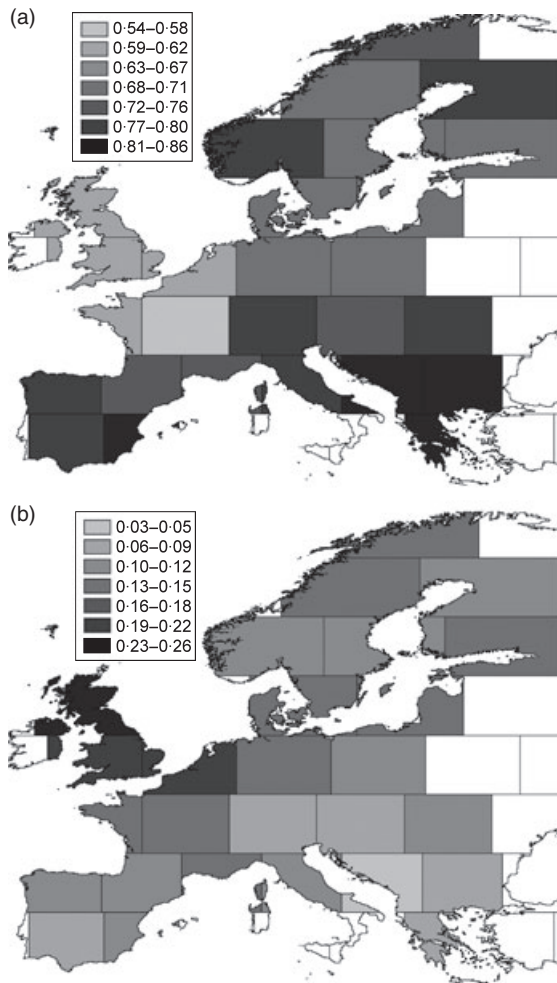

Fig. 3. Spatial variation of regional mammal beta diversity components: (a) turnover (β_{SIM}) and (b) dissimilarity resulting from nestedness (β_{NES}). Multiple-site dissimilarity within regions (250 000-km² squares) was estimated by re-sampling 45 cells of each square 100 times and computing the average β_{SIM} and β_{NES}.

the north–south direction: Furthermore, the only regions with rather high nestedness-driven dissimilarity are in oceanic Northwestern Europe, contrary to the prediction that nestedness should be strong only in regions with strong environmental gradients that reach into marginal environments (cold or drought extreme). Within regions, nestedness-driven dissimilarity increases with decreasing PET and TOPO, negative relationships that were not anticipated by any of the study hypotheses and may be a simple consequence of the negative correlation between β_{NES} and β_{SIM} ($r = -0.766$, $P < 0.001$). The predicted climate–nestedness relationship is based on the assumption that more species tolerate a warm climate because of phylogenetic niche conservatism and a warm-climate origin of many major taxa (Wiens & Donoghue 2004). However, recent findings show

that this assumption is only to a limited extent upheld in mammals: Many young mammal clades show negative species richness slopes on a global scale (Buckley *et al.* 2010), and there is evidence that realized climatic niches of European mammal species have been highly flexible on an evolutionary time-scale and thus exhibit negligible phylogenetic conservatism (Dormann *et al.* 2010).

While mammal species turnover in Europe clearly is linked to current climate, other aspects of our results provide support for the hypothesized alternative beta diversity drivers. Notably, the finding that the purely spatial components of spatial turnover and nestedness were markedly to slightly greater than the purely environmental components is in agreement with all three alternative hypotheses (cf. Svenning & Skov 2005). Other studies of large-scale beta diversity patterns have similarly found a strong purely spatial beta diversity component (Bjorholm *et al.* 2008; Qian, Badgley & Fox 2009; Baselga 2010).

Our results also provide more specific support for the glaciations and peninsular hypotheses. Several patterns suggest that persistent glacial legacies affect mammal beta diversity in Europe. Notably, the strong longitudinal turnover within Southern Europe is consistent with the relatively mild impact of glacials here, allowing multiple local refugia as well as local evolutionary differentiation and diversification. Supporting this interpretation much of this turnover can be ascribed to the occurrence of numerous localized endemics within Southern Europe (Mitchell-Jones *et al.* 1999), as high endemic species richness has been linked to areas least affected by the Pleistocene glaciations (Jansson 2003; Svenning & Skov 2007b; Araújo *et al.* 2008). In fact, palaeoecological evidence shows that the Pleistocene climatic cycles caused strong disruptions in mammal communities in Central and Northern Europe, but not in Southern Europe, where structural continuity was maintained (Rodríguez 2006). The decline in β_{nes} with geographic distance in Southern Europe indicates that at larger distances, southern faunas are increasingly not from the same overall species pool, i.e., also consistent with local evolutionary differentiation and diversification as expected under the glaciations hypothesis. However, the strong β_{sim} but negligible β_{nes}-distance relationship in north–south direction and negligible β_{NES} in most regions is contrary to predictions under this hypothesis; i.e., counter to the assumption that *in situ* last glacial maximum survival was largely restricted to Southern Europe, with the rest of Europe being recolonized from this source region during the late- and postglacial periods. In line herewith, there is increasing evidence from paleontological, phylogeographic and hind-casting studies that not only arctic species but also many boreal mammal species survived *in situ* in Central and Eastern Europe, with some temperate species surviving at least in southern parts of Central Europe (Sommer & Nadachowski 2006;

Markova 2007; Fløjgaard *et al.* 2009; Markova, Simakova & Puzachenko 2009). The surprising differentiation of Central and Northern European faunas may reflect the importance of such northern refugia.

Two additional mechanisms may also play a role in creating latitudinal turnover rather than nestedness: post-glacial (re)colonizations of Northern Europe from eastern refuge areas in Russia (Oshida *et al.* 2005; Fedorov *et al.* 2008), and regional extinctions of some boreal and arctic species in Southern and Central Europe during the late-glacial because of climatic warming (Dalén *et al.* 2007; Fløjgaard *et al.* 2009) or during the Holocene because of human activity (Mitchell-Jones *et al.* 1999). The decline in β_{nes} with geographic distance in the eastern longitudinal band, but not in the central and western bands is consistent with recolonization of northern parts from northerly Russian refuge areas, producing a non-nested latitudinal pattern in this part of Europe. Overall, it is clear that the view of Central and Northern Europe as long-term sink areas and Southern Europe as a long-term source area for European biota (Bennett, Tzedakis & Willis 1991) needs to be modified for mammals, although the greater turnover in the latter region does point to greater possibilities for refugial survival and evolutionary differentiation there. Interestingly, our findings for European mammals contrast with the results of the only previous study involving similar, albeit more limited analyses, namely for European cerambycid beetles (Baselga 2010): in that work, northern faunas were strongly nested within southern faunas as predicted by the glaciations hypothesis. We note that this discrepancy may involve a scale issue, as the cerambycid study used a much coarser country-level grain size. Just as for the cerambycids, most Central European mammal species are also present in northern parts of Southern Europe and would be recorded for many countries in this region.

While the peninsular hypothesis (Simpson 1964) has largely been ignored in previous studies of the European mammal fauna (except Baquero & Tellería 2001), our results suggest that peninsular dynamics play an important role in the assembly of mammal communities across Europe. Notably, spatially constrained dispersal from eastern faunal source areas (Kurtén 1968; Randi 2007) should cause nestedness in east–west direction, and in agreement herewith the only β_{nes}-geographic distance relationships of non-negligible strength were those within the Central and Northern European bands. The weak, negative relationship in Southern Europe reflects strong turnover in this region (discussed earlier). Peninsular dynamics also involve competitive exclusion and relictual survival and evolutionary differentiation in more isolated areas (cf. Randi 2007), so we would also expect species turnover in east–west direction, as we did indeed find within all three latitudinal bands. At the regional scale, dissimilarity attributable to nestedness is strongest in the northwest, i.e., the regions furthest removed from both eastern and southern source areas, perhaps indicating a combined effect of limited colonization from both the south and the east within this region (resulting from the various ocean barriers around the British Isles) and lacking possibilities for *in situ* speciation because of strong glacial impacts on this area.

Under the neutral hypothesis, there should be uniform spatial turnover and no nestedness, as species-neutral stochastic population dynamics and spatially constrained dispersal entirely drive spatial patterns (Hubbell 2001). In addition, there should not be any relationships between turnover and climate beyond coincidence arising from spatial autocorrelation. Our results clearly did not correspond solely to this hypothesis, showing clear links to climate, non-uniform turnover patterns and non-negligible nestedness-driven dissimilarity. However, the generally strong turnover in both the north–south and east–west directions as well as in most regions and the generally limited nestedness-driven dissimilarity suggest that neutral dynamics could potentially also be an important driver of European mammal beta diversity.

Deconstructing beta diversity into its spatial turnover and nestedness components across multiple scales provided novel insights. We found evidence for a strong impact of current climate, an impact of the Pleistocene glaciations, in particular evident from a stronger longitudinal turnover in the most stable region (Southern Europe), an impact of peninsular dynamics, and at least scope for an important effect of neutral dynamics. Our results question the classic view of Central and Northern Europe as long-term sink areas and Southern Europe as a long-term refuge and source area for European biota. Notably, the generally weak nestedness effect may reflect the importance of northern refugia, post-glacial (re)colonizations from eastern refuge areas, and regional extinction of some boreal and arctic species in the south, in combination with limited phylogenetic climatic niche conservatism. Importantly, the influence of non-climatic factors on mammal beta diversity patterns in Europe suggests that predicting faunal responses to future climate changes will be difficult (Levinsky *et al.* 2007; Dormann *et al.* 2010). A key challenge for predictive studies will be to integrate the effects of climate with the non-climatic factors that also constrain mammal community assembly.

Acknowledgements

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