



Break the pattern: breakpoints in beta diversity of vertebrates are general across clades and suggest common historical causes

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ABSTRACT

The use of correlative analyses might be insufficient to understand the processes that control biodiversity, because the variables accounting for different hypotheses (e.g. current climate, past climate change, post-glacial dispersal limitation) are mutually correlated. We suggest here that, in order to gain insight, it could be useful to search for latitudinal thresholds that could provide information about qualitative changes in the way biodiversity varies in space. Such tipping points could inform about higher-level processes that are not reflected in correlative analyses. We test whether similar breakpoints in latitudinal beta-diversity patterns exist for different vertebrate groups with diverse life histories and dispersal abilities. In birds, bats and non-volant mammals we find breakpoints similar to those of amphibians. Differences in species composition are mainly due to species replacement from the equator to the breakpoint, but are dominated by nested species losses from the breakpoint to higher latitudes. Thus, marked thresholds discriminate two world regions where different processes appear to drive biodiversity.

Keywords

Beta diversity, breakpoints, endotherms, Last Glacial Maximum, latitudinal patterns, nestedness, replacement

Understanding the potential effect of abiotic factors on compositional variation (beta diversity; Whittaker, 1960) is crucial if we are to understand why regional diversity changes across latitudes. Beta diversity comprises two components (Baselga, 2010): turnover (compositional variation due to species replacement) and nestedness-resultant dissimilarity (variation due to species loss). Both components can be caused by different processes and might show contrasting latitudinal patterns (Leprieur *et al.*, 2011; Dobrovolski *et al.*, 2012). Baselga *et al.* (2012) hypothesized the existence of a latitudinal breakpoint defining two world regions where the variation in amphibian species composition is dominated by turnover or nestedness, respectively. If changes in the regime of latitudinal patterns of variation in species composition are general across other biological groups, it might be justified to adopt a general two-step analytical strategy in global analyses of beta diversity (and more generally in the analysis of global macroecological patterns). First, it would be necessary to search for the existence of breakpoints, and then for the potential predictors of beta-

diversity patterns. Here we assess if such a breakpoint can be found for New World mammals and birds. Considering that these groups are endotherms and have better dispersal capabilities than amphibians (in particular, flying animals could track suitable environments more quickly; Harrison *et al.*, 1992), it is possible that the effects of past climate on these groups are less clear than in amphibians (as the climatic constraints experienced by endothermic animals are different; Buckley & Jetz, 2007). If endotherms are more capable of tracking suitable climatic conditions in a scenario of climate change, the proportion of beta diversity due to species loss could be lower (Dobrovolski *et al.*, 2012); therefore, for these groups, different patterns of beta diversity could be expected. Specifically, we predict that, in endotherms, the latitudinal breakpoint at which the differences in species composition due to species losses start to be more important should be located at latitudes higher than those observed for ectotherms. In turn, species turnover should decrease less sharply at higher latitudes compared with ectotherms.

We calculated multiple-site dissimilarity due to spatial turnover (β_{SIM}) and due to nestedness (β_{SNE}) in regional cells of 500 km \times 500 km following a similar approach to that described by Baselga *et al.* (2012). The distribution ranges of 4265 species of New World birds and 1728 New World mammals were derived from expert-drawn range maps (Patterson *et al.*, 2007; Ridgely *et al.*, 2007). Bats (322 species) and non-volant mammals (1406 species) were split into independent datasets in order to assess the relevance of flight ability. We also independently analysed two avian and three non-volant mammalian orders that differ considerably in dispersal capabilities (see Appendix S6 in the Supporting Information): rodents (937 species), carnivores (80 species), even-toed ungulates (29 species), Passeriformes (2387 species) and Anseriformes (97 species). Body size is generally related to range size (Gaston & Blackburn, 1996), so we can assume that rodents tend to disperse less than carnivores or even-toed ungulates, or that Passeriformes generally disperse less than Anseriformes. Polygonal range maps were converted into presence–absence matrices of 1° \times 1° cells. Environmental variables for those cells were obtained from WorldClim (Hijmans *et al.*, 2005), both for present conditions and for the Last Glacial Maximum (about 21,000 years ago). The study area was divided in 500 km \times 500 km regional cells (Sastre *et al.*, 2009) superimposed over the aforementioned grid of 1° \times 1° cells, and, within these regional cells, multiple-site dissimilarity due to spatial turnover (β_{SIM}) and due to nestedness (β_{SNE}) was calculated among 1° \times 1° cells using the *betapart* package (Baselga & Orme, 2012) in R (R Core Team, 2016). Only regional cells with more than 15 terrestrial 1° \times 1° cells and more than five species of each one of the studied groups were used in the calculations (the number of regional cells used in the analyses was 115 for bats, 158 for non-volant mammals and 159 for birds). Due to the fact that each regional cell might contain a different number of 1° \times 1° cells, beta diversity was computed in 10 random samples of 15 1° \times 1° cells, calculating the arithmetic mean of β_{SNE} and β_{SIM} in each regional cell.

Simple correlative analyses (Appendix S1) revealed that the variable that showed the strongest positive relationship with spatial turnover was mean elevation (albeit this relationship was somewhat weak: $r^2 = 0.14$ for bats, $r^2 = 0.20$ for non-volant mammals, $r^2 = 0.21$ for birds, all $P < 0.01$), suggesting that the presence of mountains creates barriers that promote speciation processes, or that the spatial heterogeneity allows the existence of diverse environments with different faunal composition (see also Melo *et al.*, 2009). For nestedness-resultant dissimilarity, the best predictors are current temperature variables (maximum temperature of warmest month $r^2 = 0.44$ for bats, $r^2 = 0.55$ for non-volant mammals, $r^2 = 0.37$ for birds, all $P < 0.01$). This could suggest that current temperatures determine species distributions, so that the species assemblages of colder regional cells tend to include nested patterns of species losses among their constituent 1° \times 1° cells.

When analysing the latitudinal variation of the components of beta diversity, we also assessed the existence of breakpoints by performing piecewise regressions (Crawley, 2007), testing all possible breakpoints at 1° intervals and selecting the breakpoint with the lowest residual standard error. In addition, we fitted cubic polynomial regressions and compared them with piecewise regressions using the Akaike information criterion (AIC) (Appendix S5). In general, the AIC of piecewise regressions was lower than that of cubic polynomial regressions, and in the only case where the AIC of the polynomial regression was lower (nestedness-resultant dissimilarity of non-volant mammals), the point of inflection of this model did not differ substantially from that of a piecewise regression and thus does not alter our interpretation of the results. The fit of piecewise regressions (Fig. 1) was significantly better than that of simple linear regressions in all cases (the reduction in residual standard error was compared by an ANOVA analysis; see Appendix S2).

Turnover increased from the equator to the breakpoint (the breakpoint was at 28° for bats and non-volant mammals and 29° for birds), and decreased towards higher latitudes (except in the case of birds, where the slope was not significantly different from zero above the breakpoint). Similar patterns of turnover were found in rodents and carnivores, with a peak at 29°, but not for even-toed ungulates, where piecewise regressions did not improve the fit of simple linear models ($\Delta\text{AIC} < 2$; Appendix S6). In Passeriformes, the patterns observed are similar to those of birds in general (Fig. S6.2), which is consistent with the fact that they comprise a large proportion of bird species. In Anseriformes, which disperse more, this peak in turnover does not appear (in agreement with our prediction that in very mobile organisms species turnover should decrease less sharply with latitude). Nestedness-resultant dissimilarity showed a flat relationship with latitude between the equator and the breakpoint, and increased steadily above the respective breakpoints. In mammals, the breakpoint was located at 29° for bats, 37° for non-volant mammals, and the same latitude for rodents and carnivores considered separately. In birds, the breakpoint was found at 58°, a latitude very similar to that of Anseriformes (56°) but higher than that of Passeriformes (42°), in agreement with the prediction that the greater the dispersal ability, the higher the latitude at which nestedness-resultant dissimilarity dominates beta-diversity patterns. The quantitative differences among groups in the breakpoints for the nestedness-resultant component might partially be an outcome of the extreme sensitivity of the method (i.e. minimizing standard error above and below the breakpoint). In fact, AIC values and the amount of variation explained are very similar when forcing the breakpoint at 29° in non-volant mammals (Appendices S2 & S3). This was not the case of birds, suggesting a more relevant difference in the nestedness component patterns of this group (likely related to their physiological traits rather than their dispersal ability, given the contrast with bats). Moreover, cubic polynomial regressions have inflection points that in most cases are located

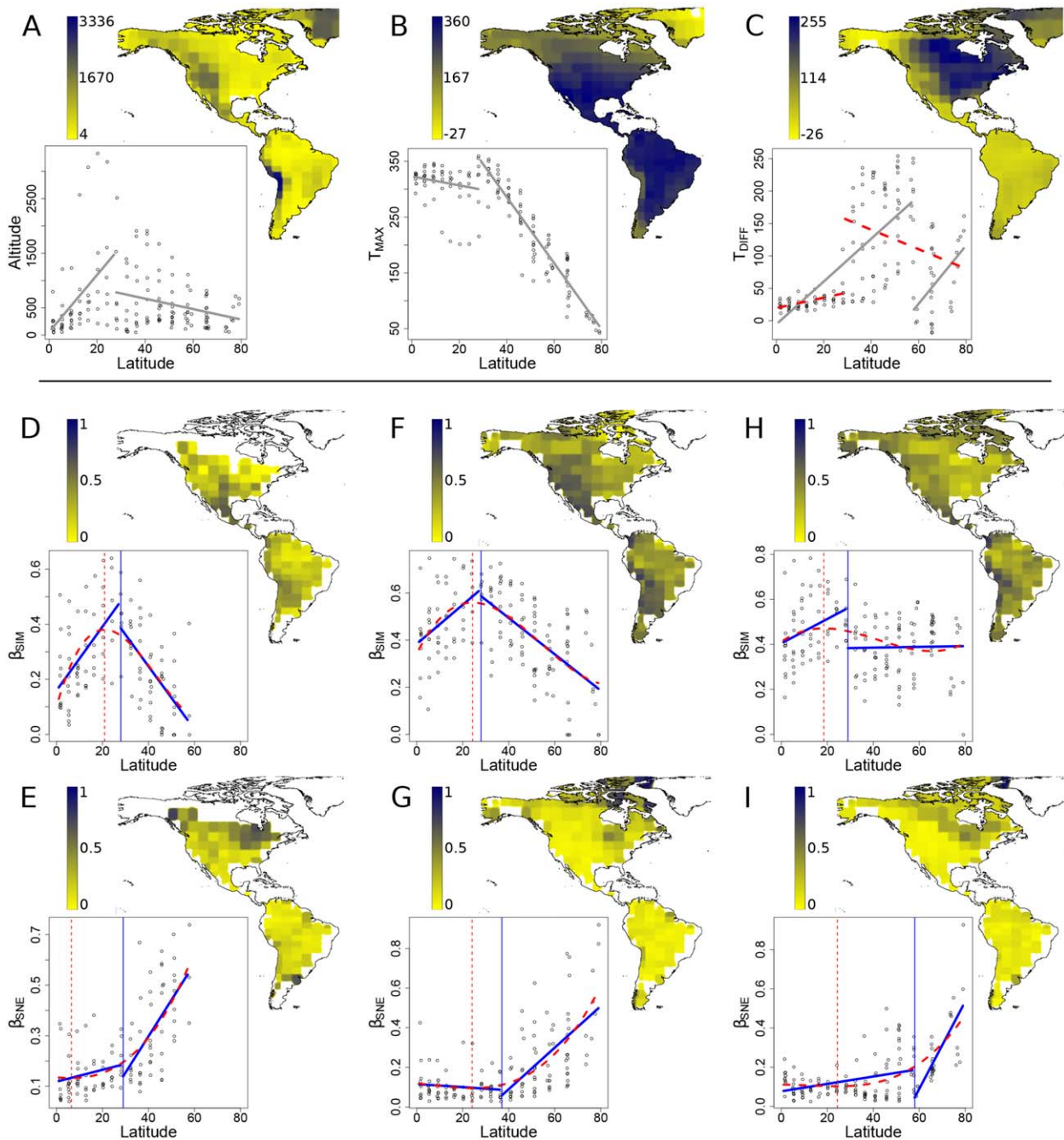


Figure 1 Latitudinal variation and breakpoints of (a) mean elevation (in metres), (b) maximum temperature of the warmest month, (c) annual mean temperature difference since the Last Glacial Maximum (*c.* 21,000 years ago, temperature in °C × 10), and, additionally, of the turnover (β_{SIM}) and nestedness (β_{SNE}) components of beta diversity for bats (d, e), non-volant mammals (f, g) and birds (h, i), with corresponding maps showing their spatial variation. In the case of climate change (c), the breakpoint which minimizes the residual standard error is at 58° (continuous line), but the scatter of this variable dramatically increases above 29° (dashed line). In the scatterplots that show the latitudinal variation of beta diversity (d–i), piecewise regressions are superimposed as a continuous line and cubic polynomial regressions as a dashed line. The vertical lines indicate the breakpoint in piecewise regressions and the inflection point in polynomial regressions.

around 20–25° (see Fig. 1), except for nestedness-resultant dissimilarity of bats (at 6°). We note that in this particular case the nestedness component of beta diversity increases constantly with latitude (the sign of the slope does not change), and the inflection point of a polynomial

relationship does not capture the abrupt increase in the slope of the relationship above *c.* 30° of latitude that is detected with piecewise regressions. A visual inspection of the scatterplots reveals that the nestedness components of all groups are very low below 30° and show a flat relationship with

latitude, while the scatter is very large above 30°. This was also observed for climate change since the Last Glacial Maximum (calculated as the difference in annual mean temperature between the present time and Last Glacial Maximum conditions; see Fig. 1c, Appendix S4) but not for elevation or current climate variables.

Our results thus reveal the existence of two distinct regions separated by a latitudinal breakpoint, showing that these patterns are universal across terrestrial vertebrates. When we looked for correlations with environmental variables, we only found a strong relationship between nestedness-resultant dissimilarity and current temperature conditions, which might be explained by mammals and birds being more at equilibrium with current temperature conditions than amphibians because of their endothermy and better dispersal capabilities (Araújo & Pearson, 2005; Dobrovolski *et al.*, 2012). However, elevation and the historical change in temperature conditions show interesting latitudinal breakpoints (which are not observed in current temperature conditions) parallel to those found in the components of beta diversity. This might suggest that historical processes have imprinted the beta-diversity patterns of all groups regardless of their life histories. First, mountains (acting as refuges and sources of diversification) are responsible for higher levels of species replacement at a regional scale (500-km squares). Second, glaciations would have wiped out the vertebrate assemblages independently of temperature regulation capabilities, and these regions had to be recolonized after the retreat of the ice (e.g. Dufresnes & Perrin, 2009; Sommer & Zachos, 2009; Alexandri *et al.*, 2012), driving ordered patterns of species losses to higher latitudes. The quantitative differences in latitudinal thresholds of the nestedness component could, in turn, reflect the different dispersal or, most likely, temperature requirements of different groups.

Some other macroecological studies have also found thresholds which define changes in the tendencies of biodiversity patterns, or zones where different factors might determine these patterns. For example, Kerr & Packer (1997) found that potential evapotranspiration (PET) below values of 1000 mm year⁻¹ was an important predictor of mammalian species richness in North America, but not in high-energy regions (PET ≥ 1000 mm year⁻¹), where habitat heterogeneity (variation in topography and local variation in energy availability) explains more variation in species richness, as energy does not seem to be a limiting factor in these high-energy areas at lower latitudes. Consistent with this idea that energy might be limiting species richness mainly at higher latitudes, Hawkins *et al.* (2003), in a review of studies on the relationship between climate and species richness, observed that water variables seem to be stronger predictors below a given latitudinal threshold with energy variables being more determinant at latitudes above that threshold. Whittaker *et al.* (2007) tested this hypothesis for several taxa in Europe, and found some evidence that water variables could be more important at lower latitudes and energy variables could be the limiting factor at higher latitudes (although

their results were not consistent across taxa). There are some other examples of breakpoints, such as the one Zagamajster *et al.* (2014) found for the range size of groundwater crustaceans in Europe, which starts to increase markedly with latitude only above 43° N. This pattern is mainly associated with long-term climatic variability. Taking into account that these sorts of breakpoints can be important for explaining or clarifying some patterns in ecology, we encourage macroecologists to consider threshold-based exploration of their data, as it can give additional insight compared with analyses that consider biodiversity to vary spatially in a smooth manner.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Linear relationships between environmental variables and beta-diversity components.

Appendix S2 Comparison of piecewise regressions and simple linear regressions.

Appendix S3 Comparison of different breakpoints for the nestedness-resultant dissimilarity of non-volant mammals and birds.

Appendix S4 Standard deviation of climatic change since the Last Glacial Maximum below different latitudinal breakpoints.

Appendix S5 Results of cubic polynomial models and comparison with piecewise regressions and simple linear regressions.

Appendix S6 Supplementary results for different orders of non-volant mammals and birds.

Table S6.1 Akaike information criterion of three different models to assess the relationship between latitude and beta diversity due to species turnover and to species losses: ordinary least squares, piecewise regressions, and cubic polynomial regressions.

Figure S6.1 Scatterplots showing the latitudinal variation in turnover and nestedness for rodents, carnivores and even-toed ungulates.

Figure S6.2 Scatterplots showing the latitudinal variation in turnover and nestedness for Passeriformes and Anseriformes.

BIOSKETCHES

Adrián Castro-Insua is a PhD student interested in macroecology and macroevolution of vertebrates.

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