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Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity

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ABSTRACT

Aim We tested whether the geographic variation in the proportion of beta diversity attributed to nestedness or turnover components was explained by the effect of past glaciation events. Specifically, we tested the hypothesis that most of the beta diversity in regions retaining ice until recent periods was due to nestedness. Additionally, we tested whether the variation was influenced by thermal tolerance and the dispersal ability of species.

Location This study analysed data from the New World.

Methods We used presence/absence data for amphibians, birds and mammals of the New World. We calculated beta diversity among each 1° × 1° cell and the adjacent cells using the Sorensen dissimilarity index that expresses the total beta diversity. Furthermore, we partitioned it into turnover and nestedness components. The relative importance of the two latter components was expressed as the proportion of total beta diversity explained by nestedness (β_{ratio}). We calculated the correlation between β_{ratio} and the time each cell was free of ice since the last glaciation (cell age). To control the effects of spatial autocorrelation, we calculated geographically effective degrees of freedom.

Results The proportion of beta diversity attributed to nestedness was negatively correlated with cell age. Moreover, this effect was stronger for amphibians than mammals, and stronger for mammals than birds.

Main conclusions Our results are in accordance with the hypothesis that the nestedness component of beta diversity is more important in areas affected by glaciations until recent time. The beta diversity in high latitudes is the result of past extinctions and recent recolonization, which result in higher levels of nestedness. This process is more evident for vertebrates with lower dispersal ability and lower temperature tolerance.

Keywords

Dispersal abilities, glaciation, latitudinal gradients, New World, past climate change, spatial autocorrelation, spatial turnover, temperature tolerance.

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INTRODUCTION

One of the main goals of macroecology is to understand the patterns of biological diversity at broad spatial scale (Gaston & Blackburn, 2000; Hawkins & Diniz-Filho, 2008). Biological diversity can be analysed by at least two components: the local component (alpha diversity) and the regional component, or

diversity among sites (beta diversity). Although there has been much success in understanding the patterns and processes that explain local species richness at broad scales (e.g. Hawkins, 2001; Hawkins *et al.*, 2003; Terribile *et al.*, 2009), there has been an increasing interest in the factors that drive changes in beta diversity at macroecological scales (e.g. Williams, 1996; Koleff *et al.*, 2003; Veech & Crist, 2007; Melo *et al.*, 2009). Beta diversity is a

well-established and widely used concept in ecology and has been measured in different ways and for various purposes (for a review see Tuomisto, 2010a,b).

Although beta diversity has been used synonymously with 'species turnover' (Wilson & Shmida, 1984; Gaston & Blackburn, 2000; Gaston *et al.*, 2007; Qian *et al.*, 2009), it has also been recognized (e.g. Harrison *et al.*, 1992) to be composed of distinct components that include both turnover (i.e. changes in species composition among local assemblages) and nestedness (i.e. the loss of species at certain sites results in a pattern in which the biota present there is a subset of species at richer sites). In a recent study, Baselga (2010) proposed a framework to evaluate beta diversity as an overall phenomenon evaluated by the Sorensen (β_{sor}) index. Baselga (2010) suggested that total beta diversity can be separated into two distinct parts: the species turnover, which is measured by the Simpson dissimilarity index (β_{sim}), and the nestedness component (β_{nes}) that was derived by Baselga (2010). Therefore, $\beta_{\text{sor}} = \beta_{\text{sim}} + \beta_{\text{nes}}$.

These components of beta diversity, however, should not be uniformly distributed in geographical space. It can be expected that in certain areas most of the beta diversity would be composed of species turnover, while in other areas the nestedness should be the principal component. In his original paper, Baselga (2010) proposed that the pattern of beta diversity partitioning found for beetles in Europe is explained by the effect of past glaciations. A specific mechanism was proposed to explain this pattern of beta-diversity partitioning: areas at low latitudes in the present climate suffered less variation in temperature during glaciation cycles, thereby maintaining a high number of species and representing centres of speciation, triggering high endemism (see Jansson, 2003) and allowing higher species turnover. In contrast, regions at high latitudes were severely affected by glaciations that caused extinctions in the past; therefore, beta diversity may be the result of past extinctions and recent recolonization, resulting in a higher relative importance of the nestedness component (Baselga, 2010).

If this mechanism is true, then the effect of past glaciations should not have been the same for different species. The life history of species could have influenced the effects of this process on their current beta-diversity patterns. Two characteristics are expected to be very important in the response to climate change: the ability to regulate body temperature via metabolic heat (endothermy) and dispersal ability. Endothermy makes organisms more resistant to variations in environmental temperatures and, consequently, endotherms are able to survive in environments with lower temperatures (Angilletta, 2009). Ectotherms, in turn, are more sensitive to low energy in the environment (Buckley & Jetz, 2007). The capacity for dispersal may also influence the ability of organisms to track the optimal environmental conditions after climate change (Harrison *et al.*, 1992). Species with a lower dispersal ability recolonize areas affected by glaciations more slowly (Smith & Green, 2005). Volant animals are better dispersers than non-volant animals (Harrison *et al.*, 1992; Böhning-Gaese *et al.*, 1998). Consequently, the overall beta diversity, and

especially the beta diversity due to nestedness, should be higher in ectotherms and animals with poor dispersal abilities.

The aim of this study was to test the hypothesis that the relative portion of beta diversity due to nestedness is higher in areas where the effects of glaciation were stronger (i.e. the time for which the area remained covered by ice after the Last Glacial Maximum was longer). Additionally, we hypothesized that this effect would be most evident for ectotherms and species with poor dispersal capabilities. We used three different groups of organisms that, in general, differ in their abilities to control internal temperature and in their dispersal abilities: amphibians (ectotherms, non-volant), mammals (endotherms, mostly non-volant) and birds (volant and endotherms). We predicted that amphibians were extirpated earlier from areas that were subjected to coverage by ice and that their recolonization was slower, resulting in a higher proportion of beta diversity attributed to nestedness. In contrast, due to their better ability to control their own temperature, we expected that birds were able to resist climate change for longer, and because of their better dispersal capacity were able to recolonize earlier after ice melting, thereby generating a richer pool of species in these areas and enabling the existence of beta diversity not only due to nestedness but also due to the turnover of species.

METHODS

Data

We used digitized bird (Ridgely *et al.*, 2005), mammal (Patterson *et al.*, 2005) and amphibian (Stuart *et al.*, 2004) datasets for 3836 bird, 1641 mammals and 1303 amphibian species (available at <http://www.natureserve.org>). These databases were processed using ESRI ARCVIEW 3.1 to record a species' presence, as defined by its breeding range, in a 4200 1° by 1° cell grid covering the New World. Each species' presence was recorded when its range polygon covered > 50% of the cell area. Small islands and cells with < 50% of land area were excluded from the grid. The resulting presence/absence matrices for the New World were used to calculate beta diversity by different metrics.

To test the effect of ice ages on beta diversity partition, we used cell age data. This was estimated by changes in ice coverage at 1-kyr intervals since the Last Glacial Maximum (see Peltier, 1993; data available at ftp://ftp.ncdc.noaa.gov/pub/data/paleo/ice_topo). For those cells that remained non-glaciated during this period, we assigned an age of 22,000 years (see Hawkins & Porter, 2003).

Measuring beta diversity

Following Baselga (2010), we calculated three measures of beta diversity, the Sorensen dissimilarity index (β_{sor}), the Simpson dissimilarity index (β_{sim}) and the nestedness index (β_{nes}), by a routine that we wrote in R (R Development Core Team, 2009). The total beta diversity is represented by β_{sor} , where β_{sim} is the species turnover part of beta diversity and β_{nes} is the nestedness component of beta diversity. The formulae that we used are as follows:

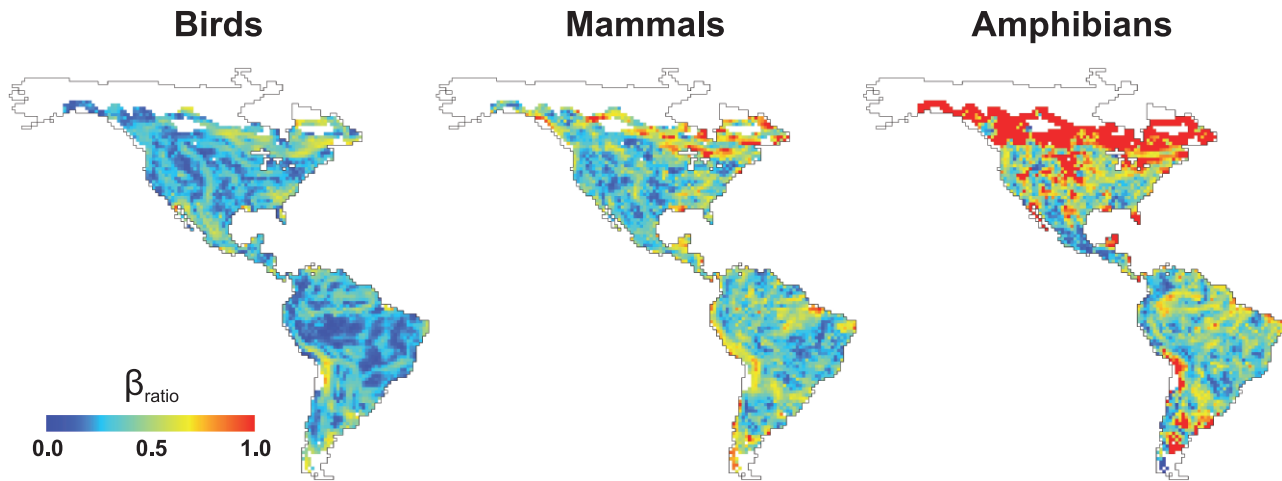


Figure 1 Beta diversity in the New World. The β_{ratio} index (i.e. the proportion of total beta diversity explained by nestedness) was calculated among each $1^\circ \times 1^\circ$ cell and all of its adjacent cells for birds, mammals and amphibians.

$$\beta_{\text{sor}} = b + c / (2a + b + c)$$

$$\beta_{\text{sim}} = \min(b, c) / [a + \min(b, c)]$$

$$\beta_{\text{nes}} = \{ [\max(b, c) - \min(b, c)] / [2a + \min(b, c) + \max(b, c)] \} \times \{ a / [a + \min(b, c)] \}$$

where a is the number of species in both cells, b is the number of species exclusive to the focal cell and c is the number of species exclusive to the adjacent cell. It is important to highlight that dissimilarity due to nestedness (β_{nes}) is related to, but different from, nestedness *per se* (Baselga, 2010). For example, nestedness has been measured by the nestedness metric based on overlap and decreasing fill (NODF) (Almeida-Neto *et al.*, 2008).

Beta-diversity components attributed to each cell represented the mean values between the focal cell and each of the eight adjacent cells. However, fewer values were used for coastal cells (see Melo *et al.*, 2009). Next, we obtained the ratio between β_{nes} and β_{sor} for each cell (hereafter ' β_{ratio} '). Thus, values smaller than 0.5 indicated that beta diversity was determined mainly by species turnover, whereas values greater than 0.5 indicated that nestedness was the most important component. Cells were eliminated from the analysis in the following cases: (1) discrepant values of β_{nes} in coastal cells that were most likely related to errors in the limits of the species distribution polygons; (2) cells with no species; and (3) cells where $\beta_{\text{sor}} = 0$. The final dataset included 3232 cells.

Statistical analyses

We evaluated the distribution and spatial structure of β_{ratio} for the three groups of organisms by comparing their respective correlograms, i.e. the plot of the Moran's I in different classes of distances (Legendre & Legendre, 1998; Diniz-Filho *et al.*, 2003). To calculate the correlograms, we used 22 classes of distance

determined by the criterion of an equal number of pairs to compute Moran's I .

We evaluated the effects of ice age on β_{ratio} (and on the other components of beta diversity, β_{sor} , β_{sim} and β_{nes}) separately by simple linear correlation analyses. To avoid the overestimation of degrees of freedom due to spatial autocorrelation, we used the method from Clifford *et al.* (1989) to calculate geographically effective degrees of freedom. Thus, we obtained unbiased estimates of Type I errors for the correlations. All spatial analyses were performed using Spatial Analysis in Macroecology software (SAM, v.4.0; Rangel *et al.*, 2006, 2010; freely available at <http://www.ecoevol.ufg.br/sam>).

RESULTS

The proportion of the nestedness component in the overall beta diversity (β_{ratio}) was higher for amphibians (mean \pm SD = 0.527 ± 0.278) than mammals (0.426 ± 0.187) and birds (0.302 ± 0.135) (Figs 1 & 2). The distribution of β_{ratio} also varies among taxonomic groups. Skewness was highest for mammals (0.787), and was followed by birds (0.681). The distribution of values of β_{ratio} tended to be closer to normal for amphibians (0.329) (Fig. 2). Geographically, the peaks of β_{ratio} for amphibians and mammals were found at high latitudes (Fig. 1).

Although we focused on β_{ratio} in this study, we also mapped the separate components of beta diversity for birds, mammals and amphibians (see Appendix S1 in Supporting Information). Total beta diversity (β_{sor}) was higher for amphibians and similar for birds and mammals. Higher values were concentrated in mountainous areas. The nestedness component (β_{nes}) for amphibians was greater both in mountainous areas and at higher latitudes. The absolute values of β_{sim} were higher than β_{nes} , but the magnitude of this difference was higher for birds than mammals and amphibians.

We found negative relationships between cell age and β_{ratio} that were stronger for amphibians ($r = -0.413$, $P = 0.005$) than mammals ($r = -0.342$, $P = 0.001$) and birds ($r = -0.179$,

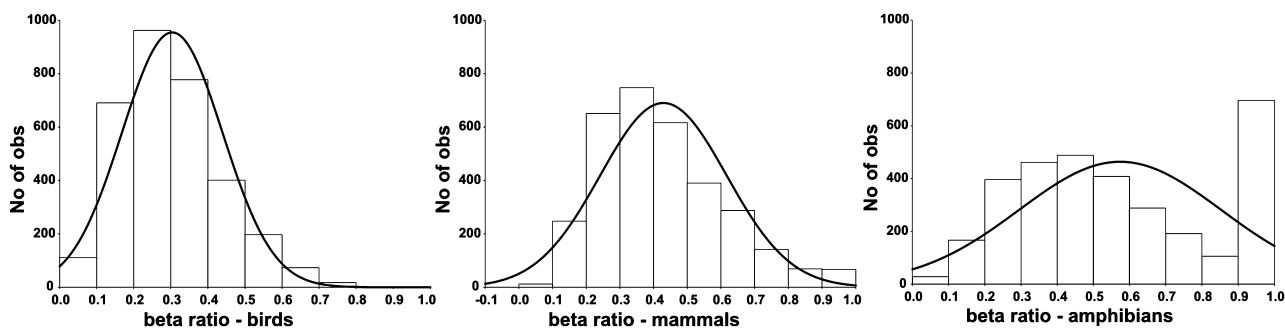


Figure 2 Histograms of β_{ratio} for birds, mammals and amphibians of the New World. β_{ratio} is the proportion of total beta diversity explained by nestedness.

Table 1 Correlation of β_{ratio} for birds, mammals and amphibians of the New World with cell age (the time each cell was free of ice since last glaciation).

Cell age			
Group	<i>r</i>	d.f.	<i>P</i>
Birds	-0.179	127.0	0.043
Mammals	-0.342	99.9	0.001
Amphibians	-0.413	17.4	0.005

The degrees of freedom were corrected using the method proposed by Clifford *et al.* (1989). Pearson's *r* (*r*); degrees of freedom (d.f.) and probability value (*P*).

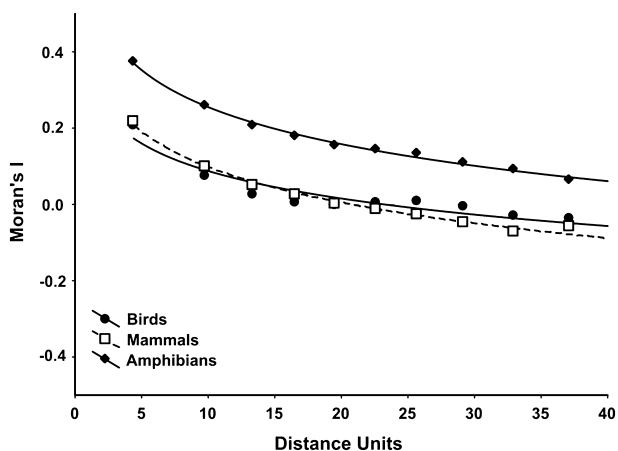


Figure 3 Spatial correlograms based on Moran's *I* autocorrelation coefficients for β_{ratio} for birds, mammals and amphibians of the New World. Distance units are degrees. β_{ratio} is the proportion of total beta diversity explained by nestedness.

$P = 0.043$) (Table 1). The spatial structure was more evident for amphibians than mammals and birds, as shown by their spatial correlograms (Fig. 3) and by the reduction in degrees of freedom (Clifford *et al.*, 1989). The turnover component had a positive relationship with cell age for mammals ($r = 0.390$, $P = 0.022$) and amphibians ($r = 0.0331$, $P = 0.031$) (see Appendix S2).

DISCUSSION

Previous studies have shown beta-diversity patterns for amphibians, mammals and birds (McKnight *et al.*, 2007; Buckley & Jetz, 2008; Melo *et al.*, 2009; Qian, 2009b) and have attempted to correlate those patterns with current environmental predictors (e.g. Gaston *et al.*, 2007; Buckley & Jetz, 2008; Melo *et al.*, 2009; Qian *et al.*, 2009). Here, we show the geographic distribution of the different components of beta diversity for these groups in New World. Although we did not perform a formal evaluation, the concentration of higher values of the separate components of beta diversity (β_{sor} , β_{sim} and β_{nes}) in mountainous areas probably reflects the importance of altitude range (e.g. Melo *et al.*, 2009) and geographic distribution of mean range sizes (Graves & Rahbek, 2005; Hawkins & Diniz-Filho, 2006).

The focus of our work was to show the spatial pattern of the relative importance of nestedness and turnover components of beta diversity in the New World. This variation was highly dependent on the group of organisms analysed and can be explained by the time that the regions were free of ice cover since the last glaciation, in accordance with the hypothesis of Baselga (2010). In relation to his original paper on beta-diversity partitioning, we were able to advance the following aspects. Baselga (2010) evaluated the beta diversity of beetles based on national inventories and compared southern and northern European countries. Additionally, Baselga (2010) evaluated the two components of beta diversity (turnover and nestedness) separately. Here, we combined both components in an index (β_{ratio}) that expressed the relative importance of each component. We evaluated this partition for three groups of vertebrates (amphibians, mammals and birds) of the New World, which generally have different dispersal abilities. This allowed us to test the proposed mechanisms underlying the geographic patterns in beta diversity. Additionally, Baselga's (2010) *ad hoc* explanation of the partition of beta diversity among northern and southern European countries was based on the effect of past glaciations. Therefore, we used an explicit variable that reflected the time that each cell was free of ice since the last glaciation (cell age). This variable enabled us to formally test the hypothesis of Baselga (2010).

As our results suggest, the higher prevalence of the nestedness component of beta diversity is the result of the extinction and

slow recolonization of species in areas covered by ice in the last glaciations. In areas not covered by ice, the extinction events should have been milder, maintaining a greater number of species and allowing the emergence of endemism (Jansson, 2003) and the eventual turnover of species. Our predictor variable of cell age reflected an extreme climate change caused by glaciations. Glaciations probably caused great rates of extinction where they occurred. However, after the ice melted, some species were able to recolonize the cells that were free of ice. The higher cell ages allowed more time for recolonization. This mechanism explains why we found higher levels of the nestedness component in areas where the effect of glaciation was higher (i.e. lower cell age). The species present in areas that were covered by ice during the last glaciations were subsets of species that remained in the areas free of ice.

The effect of this relatively recent environmental change (glaciations) was found to be important in the determination of the diversity (alpha and beta) patterns for several groups (Hawkins & Porter, 2003; Jansson, 2003; Araújo *et al.*, 2008; Baselga, 2008; Davies *et al.*, 2009). This environmental change also was responsible for driving geographical patterns in species traits, such as body size (Diniz-Filho *et al.*, 2009). However, the effect of glaciation cycles on the patterns of beta-diversity partitions that our work supports does not exclude the role that other processes could play in explaining the patterns of diversity. These other processes could have acted over evolutionary time, and could have included niche conservatism (Wiens & Donoghue, 2004), climate changes over a longer time-scale (Hawkins *et al.*, 2006), the effect of time and area or differences in the diversification rates (Mittelbach *et al.*, 2007). Nevertheless, the spatial patterns in β_{ratio} and the variation among birds, mammals and amphibians suggest that a simpler process, acting over a shorter time-scale (approximately 20,000 yr BP), may be responsible for most of the beta-diversity patterns that we currently see, despite these more complex processes acting over much broader time-scales.

Dispersal ability has an important effect on diversity patterns. Its effects have been shown for alpha diversity (Hillebrand, 2004) and also for beta diversity (Qian, 2009a,b; Jiménez-Valverde *et al.*, 2010). Here, we demonstrated the effect of dispersal ability on beta-diversity partitions and showed that this trait interacts with past climate dynamics to create current patterns of species turnover and nestedness. As expected, the resulting pattern was not the same for different groups of organisms. Birds can fly and are endotherms. Consequently, they were able to recolonize the ice-free areas quickly and with more species, thereby generating beta diversity by nestedness and turnover. In contrast, amphibians have poor dispersal abilities (Smith & Green, 2005; Buckley & Jetz, 2007) and are ectotherms. Therefore, they are more prone to extinction in the areas covered by ice and the recolonization process is more difficult for them. Consequently, the nestedness patterns for amphibians were stronger than for the other groups analysed. Mammals are endotherms and better dispersers than amphibians, but are worse dispersers than birds (Böhning-Gaese *et al.*, 1998). Consequently, their pattern of beta-diversity partition was, as expected, between that of birds and amphibians. The difference

among the three groups of vertebrates was also expressed by the difference in the spatial structure of the data. The higher spatial autocorrelation for amphibians is consistent with the more limited dispersal abilities of species in this group (making surrounding areas more similar).

Our work applied Baselga's (2010) beta-diversity partition in order to test the hypothesis of the effect of glaciations on the current patterns of beta diversity. Our analyses provide insights into how the beta-diversity partition method can contribute to a better understanding of the mechanisms underlying the community assemblage patterns of beta diversity at the macroecological scale in response to environmental change. Moreover, our results reveal that these changes may be different for various organisms in accordance with their traits, such as their dispersal abilities.

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SUPPORTING INFORMATION

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

Appendix S1 Beta diversity in the New World. Different components of beta diversity, including total (*Sorensen*), turnover (*Simpson*) and nestedness components, were calculated among each focal $1^\circ \times 1^\circ$ (latitude \times longitude) cell and all of its adjacent cells for birds, mammals and amphibians.

Appendix S2 Correlation of the different components of beta diversity, β_{sor} , β_{sim} , β_{nes} , and β_{ratio} for birds, mammals and amphibians of New World with cell age. The degrees of freedom were corrected by the method proposed by Clifford et al. (1989). Pearson's r (r); degrees of freedom (d.f.) and P value (P).

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BIOSKETCH

Ricardo Dobrovolski is interested in large-scale patterns in ecology, including global diversity gradients, and the mechanisms driving them. He is especially interested in the impact of human activities, such as agriculture, on these patterns.

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