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Global patterns of phylogenetic beta diversity components in bats

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ABSTRACT

Aim To investigate global patterns of phylogenetic beta diversity (phylobeta-diversity, PBD) components in bats (Chiroptera), testing whether the strong dispersal barriers among realms led to lineage differentiation between them and whether the flight capability of the study group created distance-decay patterns in PBD, with lower turnover rates between the closest biogeographical regions.

Location Global, delimited by biogeographical regions.

Methods Using the global distribution of bats and a supertree available for most species, we calculated PBD using the complement of the PhyloSor index. In addition, to distinguish the relative roles of local (e.g. lineage filtering) and regional processes (e.g. speciation) in shaping broad-scale patterns of PBD, we partitioned PBD into two components: the turnover component (PBD_{Turn}) and the phylogenetic diversity (PD) component (PBD_{PD}). We used a null model to test whether assemblages were more or less phylogenetically dissimilar than expected by chance. We also performed a Mantel analysis to analyse the distance-decay patterns of PBD and its two components.

Results The most striking difference in PBD was found between the Old World and the New World. In general, the PBD pattern was determined by PBD_{Turn}. For some adjacent regions we noticed the PBD_{PD} component was more important, indicating that the dissimilarity was mostly due to differences in phylogenetic diversity. On the other hand, for other adjacent regions, the observed PBD_{Turn} was higher than expected by chance and the PBD_{PD} was lower. This demonstrates that, although these regions are relatively close in space, there are other factors driving phylogenetic differences between them (i.e. ecological factors).

Main conclusions Our results suggest that at broad scales, the PBD of bats is determined by PBD_{Turn}. We postulate that the flight ability of bats led to low turnover rates between adjacent regions in the absence of other factors that can drive differences between them (e.g. strong environmental barriers).

Keywords

Biogeographical regions, Chiroptera, dispersal, distance-decay patterns, nestedness, phylobetadiversity, phylogenetic diversity, PhyloSor index, turnover component.

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INTRODUCTION

The limits of biogeographical regions are based on overall differences between species compositions (Cox *et al.*, 2001; Kreft & Jetz, 2010; Rueda *et al.*, 2010). This means that each of these regions tends to present, for a particular group of

organisms, a typical regional species pool. Thus, patterns of species replacement, known as species turnover, reveal the connections between different regions and allow evaluation of the importance of dispersion and local radiations on biodiversity patterns (e.g. Lomolino & Perault, 2001; Graham & Fine, 2008; Nakamura *et al.*, 2009). However, while species

turnover provides valid information about ecological and evolutionary processes, species composition is a component of biodiversity that takes no account of shared ancestry between species (Purvis & Hector, 2000). For example, two regions may have completely different species compositions (i.e. maximum species turnover), but may share much of their evolutionary histories (i.e. when many lineages are common in both regions) (Graham & Fine, 2008; Swenson, 2011a), which will be reflected by evolutionary relationships among species unique to each one. Thus, species turnover alone gives insights only into the processes that produce taxonomic diversity (Swenson, 2011b) when what is needed is metrics of turnover that incorporate information on the evolutionary history of species (Kubota *et al.*, 2011; Kissling *et al.*, 2012).

To this end, phylogenetic beta diversity (phylobetadiversity, PBD) measures were recently proposed to quantify the extant phylogenetic relationships between communities and provide information about when they were separated in evolutionary time (Graham & Fine, 2008). Additionally, following a framework recently proposed for partitioning beta diversity into distinct components (see Baselga, 2010, 2012), we highlight that community phylogenetic dissimilarity could be driven by the replacement of lineages between sites [the turnover component of PBD (PBD_{Turn})], and by the increase in differences in phylogenetic diversity (PD) between phylogenetically nested regions [the PD component of PBD (PBD_{PD})] (Leprieur *et al.*, 2012). Thus, discriminating between these two components allows us to infer the influence of spatial scale and some of the different processes that are related to spatial turnover and to the phylogenetic nestedness of assemblages. For example, time to speciation can increase turnover (vicariance between two regions) and lineage filtering can increase nestedness, because some lineages are filtered out from the regional pool in a given region, but not in the other (Leprieur *et al.*, 2012).

PBD metrics may also yield information about the degree of connectivity between regions and allow evaluation of the influence of environmental gradients, biogeography and geographical distance in the dispersion patterns of species (Graham & Fine, 2008). This influence can be understood by analysing deviations from the expected relationship between phylogenetic dissimilarity (both components of PBD) and geographical distance (e.g. Bryant *et al.*, 2008; Kooyman *et al.*, 2011; Morlon *et al.*, 2011). A negative relationship is expected between PBD_{PD} and geographical distance, because the more distant two communities are, the lower the probability that they are subsets of each other. On the other hand, a positive relationship is expected between geographical distance and PBD_{Turn} , because the probability of replacement between two communities increases (e.g. Svenning *et al.*, 2011). Thus, PBD and its components capture the geographically structured influence of the evolutionary history of each taxonomic group in current diversity patterns.

Although bats (Chiroptera) are the only mammals with real flight capability and represent more than 20% of current

mammal species (Simmons, 2006), their evolutionary history is relatively poorly understood (Simmons, 2005). Bat lineages shared a common ancestor about 60 to 70 million years ago (Ma), at the Cretaceous–Palaeogene boundary (Springer *et al.*, 2003; Jones *et al.*, 2005; Teeling *et al.*, 2005). At that time, Africa was isolated from South America, which, in turn, was indirectly connected to Australia by Antarctica, whereas North America was connected to Asia via the Bering Strait (Cox, 2000). An important characteristic of bats is their wide geographical distribution, covering all continents except the poles (Simmons, 2006). It is possible that their greater capacity for dispersion (Lim, 2008), due to their flight ability (Simmons, 2006; Lim, 2008), allied with the great variety of feeding strategies (Arita & Fenton, 1997), might have allowed the group to adapt to almost all terrestrial environments (Simmons & Conway, 2003).

The correspondence between biogeographical regions and species' assemblages was previously tested in Chiroptera for taxonomic diversity (Procheş, 2005), but the evolutionary history of bat lineages among these regions is still unverified. Moreover, as biogeographical regions have been defined based on patterns of biotic replacement, the dissimilarity caused by impoverished zones (differences in phylogenetic diversity between sites, captured by PBD_{PD}) must be distinguished from replacement zones (lineage turnover between regions, captured by PBD_{Turn}), because each case can be generated by different historical or environmental factors (Baselga, 2010). Therefore, we investigated the biogeographical patterns of PBD components to test whether: (H_1) the strong dispersal barriers between regions led to lineage differentiation between them; and (H_2) the flight capability of the study group allowed low turnover rates between the closest biogeographical regions (see Table 1). This framework allowed us to clarify the role of different mechanisms underlying current biodiversity patterns in bats at a global scale.

MATERIALS AND METHODS

Species distributions

We used maps of species distribution (IUCN, 2012) to produce a bat species list for each biogeographical region where this group is present (i.e. Neotropical, Nearctic, Palaearctic, Afrotropical, Indo-Malay, Australasian and Oceanic) (Udvardy, 1975). Each list included only species that were available in the phylogenetic tree used (Jones *et al.*, 2002, 2005). In this way, 253 species were not included in the analyses (about 22% of the species in the IUCN distribution database). Nevertheless, there was no bias in the location of these species according to biogeographical region. The percentages of missing species were 21% of species from the Neotropical, 13% from the Nearctic, 18% from the Palaearctic, 18% from the Afrotropical, 17% from the Indo-Malay, 21% from the Australasian, and 26% from the Oceanic regions.

Table 1 Two hypotheses and their predictions for the phylobetadiversity (PBD) patterns in Chiroptera among biogeographical regions. Phylobetadiversity (PBD) was partitioned into two components: the turnover-resultant component (PBD_{Turn}) and the phylogenetic diversity (PD) component (PBD_{PD}).

Hypotheses	Predictions	References
H ₁ : The geographical isolation among biogeographical realms caused dispersal limitations and <i>in situ</i> diversification	1.1. The patterns of PBD among biogeographical regions will be determined mainly by the PBD _{Turn} component 1.2. The PBD _{Turn} values among realms will be generally higher than expected by the null model and will have a positive relationship with geographical distances	Graham <i>et al.</i> (2009) Crisp <i>et al.</i> (2011) Kissling <i>et al.</i> (2012)
H ₂ : Flight ability, which gives bats good dispersal ability, allows regions that are historically less isolated to be more phylogenetically similar	2.1. For adjacent realms for which the boundaries do not represent strong barriers, the PBD _{Turn} values will be equal to or lower than expected by the null model 2.2. The PBD _{PD} component among closer realms will be more important than PBD _{Turn}	Ortega & Arita (1998) Lim (2008) Leprieur <i>et al.</i> (2012)

Phylogenetic information

We used a supertree that included branch lengths (i.e. divergence times) and the phylogenetic relationships of 916 bat species (Jones *et al.*, 2002, 2005). The number of species in the supertree was reduced to 887 due to 27 cases of taxonomic revision and two cases where geographical distribution was not available. These data thus represented almost all genera and 77% of the total species. The only genus not represented in our study was *Xeronycteris*, a Neotropical monotypic genus of the family Phyllostomidae, which is listed as Data Deficient (IUCN, 2012).

Phylobetadiversity and betadiversity

Beta diversity (BD) represents the composition dissimilarity of species found between two communities (i.e. variation of the species composition of assemblages), which can be the outcome of two different phenomena: spatial species turnover and the nestedness of assemblages (Baselga, 2010). On the other hand, phylobetadiversity (PBD) represents the variation in the phylogenetic composition of assemblages, being a measurement related to evolutionary time. PBD can also be partitioned into two components related to lineage turnover and the phylogenetic nestedness of assemblages (Leprieur *et al.*, 2012).

We calculated the BD between biogeographical regions using 1 minus the Sørensen index and partitioned BD into its components following Baselga (2010). We calculated the PBD between biogeographical regions using 1 minus the PhyloSor index. The PhyloSor index (Bryant *et al.*, 2008) is analogous to the Sørensen index and represents the proportion of shared branch lengths between pairs of assemblages. The PhyloSor index varies from 1 (when the species compo-

sition is identical) to nearly zero (when the communities share just a small proportion of basal branches). To capture differences in phylogenetic diversity between regions that may affect patterns in PBD, we used an additive partitioning framework (Leprieur *et al.*, 2012) built upon the original approach of Baselga (2010, 2012). This framework partitions the PhyloSor index (PBD) into one component that represents the turnover-resultant dissimilarity and another component that corresponds to a PD difference-resultant dissimilarity between regions. This metric controls the increase in dissimilarity between phylogenetically nested regions that is due to an increase in differences in phylogenetic diversity (PBD_{PD}), giving us the PBD turnover-resultant value (PBD_{Turn}) (Leprieur *et al.*, 2012).

To test whether pairs of assemblages were more or less phylogenetically dissimilar than expected by chance, we calculated the expected values of PBD and its components using a null model similar to that used by Graham *et al.* (2009). Species richness and the BD between regions were fixed and only the identity of the species in the phylogeny was randomized. A standardized effect size (SES) was calculated for PBD and its components, following Leprieur *et al.* (2012). SES values greater than 1.96 indicate a higher PBD than expected by BD while SES values below -1.96 indicate a lower PBD than expected by BD.

To verify the correlation between PBD and BD, we performed a Mantel test between the two matrices, testing its statistical significance using randomizations. To evaluate and represent the similarity between biogeographical regions, we performed a cluster analysis that was based on the phylogenetic dissimilarity matrix (1 minus the PhyloSor index) and the matrices of the PBD components. To perform these analyses, we used the VEGAN package (Oksanen *et al.*, 2011) implemented in R version 2.0-1 and the PICANTE package

(Kembel *et al.*, 2010) implemented in R version 2.13.2. We used the 2-norm measure (Mérigot *et al.*, 2010) to select the best cluster algorithm, which was the UPGMA method (unweighted pair-group method using arithmetic averages) (see Legendre & Legendre, 2012). To perform this analysis, we used the CLUE package (Hornik, 2005) implemented in R version 0.3-43. Moreover, we calculated the cophenetic correlation to describe the consistency of the clustering (i.e. the capability of the dendrogram to represent the multidimensional dissimilarity matrix).

Relationship between geographical distance and phylogenetic dissimilarity

We obtained the geodesic distances between the biogeographical regions. We gave a value of zero to adjacent regions (i.e. Neotropical and Nearctic, Afrotropical and Palearctic, Indo-Malay and Palearctic, Australasian and Indo-Malay, Australasian and Oceanic), while for the other combinations we measured and used the shortest coast-to-coast distance between regions. All maps were projected in World Geodetic System of 1984 (WGS84) datum. For the Oceanic region, we used the mean of the distances of the nearest five islands to the other regions. We then carried out a Mantel test (Legendre & Legendre, 2012) to verify the relationship of values of PBD and its components to geographical distances between regions. We also performed the same analyses but with the SES values (standardized effect size) of PBD and its components.

RESULTS

We found that 72% of the PBD_{Turn} variation was explained just by the turnover of species between biogeographical regions (Fig. 1a). However, even when the turnover of species was complete (turnover component of $BD = 1$), PBD_{Turn} still discriminated between regions with different degrees of phylogenetic dissimilarity (see also Appendix S1 in Supporting Information). This is evident from the column of dots for $BD = 1$ (Fig. 1a). The same is seen for PBD_{PD} , the PD component of PBD (Fig. 1b). Even when there was no nestedness in the species composition between regions (nestedness component of $BD = 0$), they could be phylogenetically nested. This is shown by the column of dots for $BD = 0$ (Fig. 1b).

Although the PBD pattern may be broadly explained by species dissimilarities between regions, just two of the observed values failed to differ from chance expectation (Neotropical and Nearctic, Indo-Malay and Palearctic) and the other values were higher than expected by the null model (Table 2). For PBD_{Turn} , three of the observed values did not differ from the null expectation (Neotropical and Nearctic, Indo-Malay and Palearctic, and Australasian–Oceanic). Similarly to PBD, we detected values of SES for PBD_{Turn} (Table 2, Fig. 2) that were higher between more distant regions (Fig. 2). As for PBD values, we noticed that most of

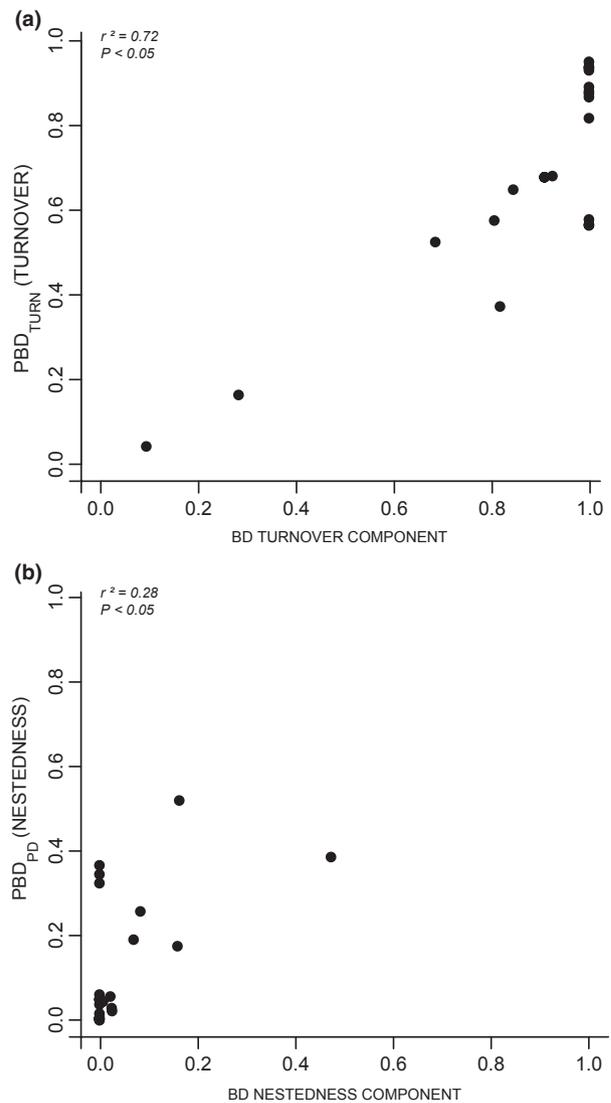


Figure 1 Relationship among the components of taxonomic beta diversity (BD) and phylobetadiversity (PBD) determined by Mantel analysis: (a) turnover-resultant component of PBD (PBD_{Turn}) and turnover-resultant component of BD; (b) phylogenetic diversity (PD) component of PBD [nestedness (PBD_{PD})] and nestedness component of BD.

the pairwise comparisons resulted in PBD_{Turn} values higher than 0.50. The PBD_{PD} had low values, in general lower than expected by the null model. The mean pairwise dissimilarity between regions was 0.82, with the turnover-resultant component (PBD_{Turn}) expressing $80 \pm 24\%$ of the dissimilarity and the PD component of PBD (PBD_{PD}) representing about $20 \pm 24\%$ of the total dissimilarity (Table 2).

There were some cases in which the PD component of PBD was high and then a notable discrepancy occurred between the PBD and PBD_{Turn} values. For example, in Table 2 the lowest values of PBD showed high levels of PBD_{PD} , demonstrating that if we had analysed only the PBD value, the replacement of lineages (PBD_{Turn}) would be overestimated. The most evident cases were between the Neotropical/Nearctic

Table 2 Pairwise phylobetadiversity (PBD) values among biogeographical regions are shown, along with values of the turnover-resultant component of PBD (PBD_{Turn}) and the PD (phylogenetic diversity) component of PBD (PBD_{PD}), together with their respective standardized effect size (SES) values ($SES < |1.96|$, in bold, indicates no difference with respect to null expectation).

Pairwise comparisons	PBD	PBD_{Turn}	PBD_{PD}	SES.PBD	SES. PBD_{Turn}	SES. PBD_{PD}
Afrotropical–Australasian	0.84	0.82	0.02	9.07	8.18	1.63
Afrotropical–Indo-Malay	0.73	0.68	0.05	5.64	4.08	1.52
Afrotropical–Nearctic	0.92	0.87	0.05	9.99	9.19	−4.77
Afrotropical–Neotropical	0.93	0.93	0.00	14.89	14.46	−4.02
Afrotropical–Palaeartic	0.61	0.58	0.03	2.01	2.25	−1.25
Afrotropical–Oceanic	0.91	0.57	0.35	2.93	3.10	−2.90
Australasian–Indo-Malay	0.55	0.53	0.02	3.60	3.41	−0.88
Australasian–Nearctic	0.94	0.89	0.05	11.00	10.28	−5.23
Australasian–Neotropical	0.96	0.95	0.00	16.13	14.93	−3.30
Australasian–Palaeartic	0.71	0.65	0.06	5.89	4.55	0.66
Australasian–Oceanic	0.90	0.37	0.52	2.55	1.48	−0.95
Indo-Malay–Nearctic	0.94	0.88	0.06	11.31	10.60	−6.00
Indo-Malay–Neotropical	0.95	0.94	0.01	16.53	15.15	−0.70
Indo-Malay–Palaeartic	0.34	0.17	0.18	1.44	−0.82	2.45
Indo-Malay–Oceanic	0.93	0.57	0.37	3.77	3.50	−3.13
Nearctic–Neotropical	0.43	0.04	0.39	−0.34	−0.50	0.04
Nearctic–Palaeartic	0.92	0.88	0.04	9.84	9.13	−3.45
Nearctic–Oceanic	0.87	0.68	0.19	3.31	4.09	−3.77
Neotropical–Palaeartic	0.95	0.94	0.01	14.55	14.11	−6.23
Neotropical–Oceanic	0.94	0.68	0.26	4.22	5.76	−5.65
Oceanic–Palaeartic	0.91	0.58	0.33	3.01	2.98	−2.67

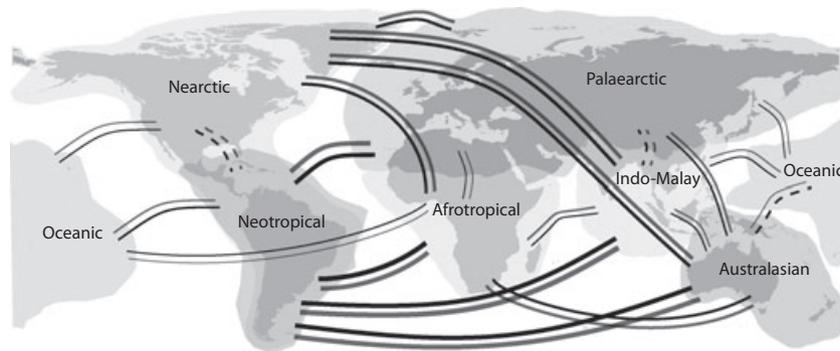


Figure 2 Map showing the standardized effect size (SES) values of phylobetadiversity (PBD) (grey lines) and the PBD turnover-resultant component (PBD_{Turn}) (black lines) among biogeographical regions. The dashed lines represent non-significant SES values. The full lines represent positive and significant values of SES, which indicate a higher PBD than expected by chance. The line width is proportional to the SES, that is, the wider the lines are, the more dissimilar the compared regions are.

and Indo-Malay/Palaeartic regions, showing very low levels of PBD_{Turn} (0.04 and 0.17, respectively) when compared with their PBD values (0.43 and 0.34, respectively). This demonstrates that the dissimilarity was mostly explained by differences in phylogenetic diversity (PD), as shown by their comparably high PBD_{PD} values (0.39 and 0.18, respectively). The other cases for which we had high values of PBD_{PD} were always related to the Oceanic region (Afrotropical–Oceanic: 0.35; Australasian–Oceanic: 0.52; Indo-Malay–Oceanic: 0.37; Nearctic–Oceanic: 0.19; Oceanic–Palaeartic: 0.33; Table 2).

The cluster analysis revealed the same pattern of two well-defined groups based on PBD and PBD_{Turn} values separating

the Old World from the New World (Fig. 3). However, the cluster of PBD_{Turn} (Fig. 3b) shows how the relationship between regions can change when we control for the differences related to PD (PBD_{PD}), as happened for the Oceanic region. We also observed a modification in the pairwise comparison similarity, in which the Neotropical and Nearctic regions are the most similar (the lowest value of $PBD_{Turn} = 0.04$), rather than the Indo-Malay and Palaeartic regions (compare Fig. 3a with Fig. 3b).

We found a positive relationship between the PBD and PBD_{Turn} and the geographical distances between regions (Fig. 4a,b). Despite the positive relationship, we can see that for long distances the values were often high, but there is

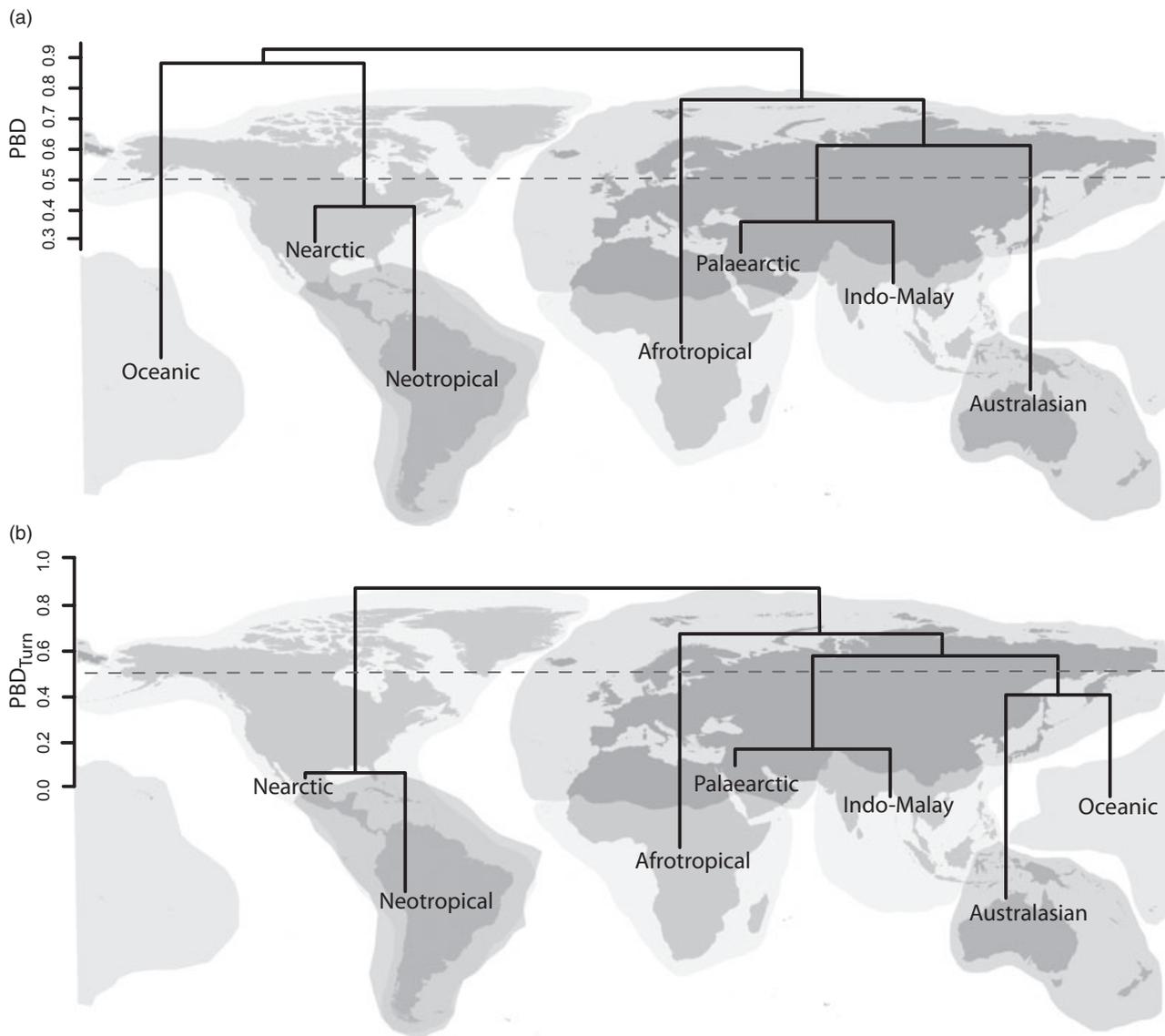


Figure 3 UPGMA (unweighted pair-group method using arithmetic averages) cluster analysis for (a) phylobetadiversity (PBD) values (cophenetic correlation coefficient = 0.96), and (b) PBD turnover-resultant component values (PBD_{Turn}) (cophenetic correlation coefficient = 0.94) among global biogeographical regions. The nodes that are below the dashed line have values under 50%.

wide variation in the values of PBD between closer regions. The Mantel correlation between components of PBD (PBD_{Turn} and PBD_{PD}) and geographical distances demonstrated that these spatial patterns in PBD were consistently determined by its turnover component (PBD_{Turn}) and not by PD difference-resultant dissimilarity (Fig. 4). Although a negative relationship was expected between PBD_{PD} and geographical distances, we did not observe such a pattern. Moreover, there were high values of PBD_{PD} even between distant regions (Fig. 4c). We observed almost the same pattern for SES values, which showed that higher values of SES were generally associated with long distances. However, these analyses also showed that even the higher values of PBD_{PD} were actually smaller than expected by chance (see Appendix S2). The only value of PBD_{PD} higher than expected by

chance was between the Indo-Malay and Palaeartic regions (i.e. adjacent regions).

DISCUSSION

Bat biogeographical patterns of PBD

In broad terms the PBD values between global biogeographical regions corroborate the global species composition pattern previously established for bats (Procheş, 2005, 2006) (Fig. 3). This indicates that the strongest barrier to the dispersal of bats during their period of diversification in the Eocene (Simmons, 2005) was the Atlantic Ocean (Procheş, 2006). Moreover, despite the good dispersal ability of bats, the actual disposition of the continents may have prevented dispersion

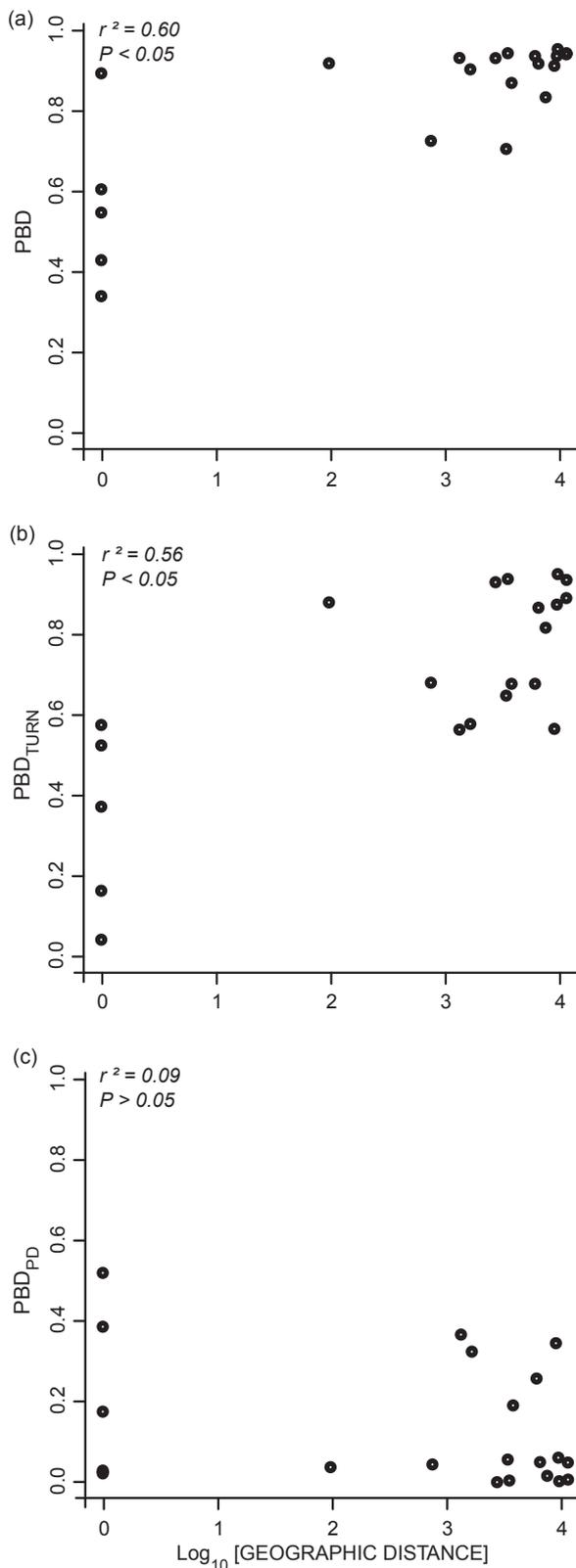


Figure 4 Distance relationship among biogeographical regions determined by Mantel analysis in relation to (a) phylobetadiversity (PBD), (b) the turnover-resultant component of PBD (PBD_{TURN}), and (c) the phylogenetic diversity (PD) component of PBD (PBD_{PD}).

between the Old World and the New World. This is observed for some groups of animals that are temperature-sensitive (Sanmartín *et al.*, 2001), which were not able to cross the Bering Strait until 1 Ma (Cox, 2000). The only bat families that occur in both the Eastern and Western Hemispheres are Emballonuridae, Molossidae and Vespertilionidae. The Emballonuridae are confined to the Southern Hemisphere and it is believed that a single dispersal event across the Atlantic Ocean might have occurred about 30 Ma (Teeling *et al.*, 2005). Vespertilionidae and Molossidae, which are mostly distributed in the Northern Hemisphere, might have crossed the Bering Strait (e.g. Stadelmann *et al.*, 2004).

Isolation and *in situ* diversification

In general, the pattern of dissimilarity of PBD between biogeographical regions was largely determined by lineage turnover (PBD_{TURN}) between regions, not by differences in phylogenetic diversity (PBD_{PD}) (Table 2), consistent with hypothesis H₁. This is indeed expected at this broad scale, e.g. when considering that biogeographical regions differ both in ecological and historical events (e.g. Kissling *et al.*, 2012). In other words, the PBD values (phylogenetic dissimilarity) are not simply the result of spatial gradients of phylogenetic diversity (Leprieur *et al.*, 2012). We also observed a positive relationship of PBD with geographical distance, following the spatial pattern of the turnover component (PBD_{TURN}), which reflects the importance of isolation by distance in determining phylogenetic dissimilarities (Fig. 4a,b). Empirically supported PBD analysis has shown that communities are primarily structured by geographical distances and by dispersal limits (Kooyman *et al.*, 2011).

As predicted, the PBD and PBD_{TURN} values between biogeographical regions were mostly higher than expected by chance (Table 2). Thus, the species that belong to the biogeographical regions are from lineages that present different evolutionary histories (Graham & Fine, 2008). This can be caused by past speciation and extinction events, dispersal limitation of lineages, niche-based processes, or a combination of these factors (Leprieur *et al.*, 2012). The same result has been documented between communities delimited by environmental gradients (Bryant *et al.*, 2008; Graham *et al.*, 2009), or by barriers such as oceans or large geographical distances (Chaves *et al.*, 2007; Forest *et al.*, 2007; Fine & Kembel, 2011; Morlon *et al.*, 2011). We also noticed that PBD and PBD_{TURN} values of SES (standardized effect size) were, in general, high and did not differ much between each other. This emphasizes the great significance of the phylogenetic dissimilarity between regions, especially when comparing more distant regions (Table 2, Fig. 2, Appendix S2).

Although the majority of cases between distant regions had high values for the turnover component and low values of PD difference-resultant dissimilarity, there were five comparisons for which the values of PBD_{PD} were high (Table 2, Fig. 4c). All were related to oceanic regions. In these cases, we found that PBD was overestimated as a result of the

differences between the regions' phylogenetic diversity (PD) (Leprieur *et al.*, 2012), because the Oceanic region presents low PD in relation to all other regions. Although the Oceanic region is geographically distant from five realms, it has a degree of phylogenetic nestedness with all of them. This may indicate that the Oceanic pool is the result of different events of colonization of multiple origins, of which the main one is the Australasia region (lowest PBD_{Turn} and higher PBD_{PD} related to the Oceanic region), the only one adjacent to the Oceanic region. This can be visualized by means of the cluster analysis, where the relationships with the Oceanic region changed when just the PBD_{Turn} was considered. The Oceanic region was initially shown to have high levels of dissimilarity with all other regions, but after decomposing PBD it clustered with the Australasian region (Fig. 3a,b, Appendix S1).

Flight capability implicates low lineage turnover between the closest regions

Three comparisons between adjacent regions showed PBD_{Turn} values that did not differ from expectations due to chance (Australasian and Oceanic, Neotropical and Nearctic, Indo-Malay and Palaeartic), consistent with predictions from hypothesis H_2 (Table 2, Fig. 2). This reveals a random pattern in the phylogeny with respect to the geographical structure (Graham & Fine, 2008) and indicates that the turnover component of PBD observed between these regions is attributable only to the differences in the species composition (i.e. beta diversity, BD). Furthermore, these cases were the only ones in which the PD component of PBD was more important than the lineage turnover, showing that the dissimilarities between these realms are mostly due to differences in phylogenetic diversity rather than to real lineage turnover (PBD_{Turn}) between them (Leprieur *et al.*, 2012). Despite the fact that these results were found between the Australasian and Oceanic regions, they are separated by a considerable maritime barrier (even considering them as adjacent regions), which is contrary to our first prediction. However, their turnover component of PBD was much higher than for the other comparisons (Neotropical and Nearctic, Indo-Malay and Palaeartic) (Table 2).

There is evidence of mammalian lineage exchanges between the Nearctic and Neotropical regions in the early Cenozoic period. However, the connection between them could have taken place by island-hopping, even before the formation of the Panama Isthmus itself (Cox, 2000), in the Pliocene (Marshall, 1985; Webb, 1985). This possibility would be even more plausible for Chiroptera, because they have the ability to migrate through island chains (Presley & Willig, 2008; O'Brien *et al.*, 2009). The main barrier between the Palaeartic and the Indo-Malay regions is the Himalayan chain. Although the mountain chain ranges over 3000 km and its width reaches 80 km to 300 km (Mani, 1968; Wadia, 2001), its relief is greatly variable (Bharti, 2008). Moreover, the disappearance of the Tethys Sea (about 10 to 15 Ma) opened paths that allowed cross-Himalayan migration

through the Indo-Gangetic flood plains and the coastal strips (Khan, 1980; Leviton & Anderson, 1984). We believe that the limits between these regions (Neotropical and Nearctic, Indo-Malay and Palaeartic) can act as transition zones, instead of well-delimited boundaries (Ortega & Arita, 1998; Corona *et al.*, 2007; Procheş & Ramdhani, 2012). The fact that bats comprise a group of mammals with adaptations for flight (Norberg & Rayner, 1987; Arita & Fenton, 1997) may imply that their response to geographical barriers might be different to those of other mammals (Ortega & Arita, 1998). A zoogeographical map recently produced, using phylogenetic relationships among groups of tetrapods, showed these transitional areas cited above as independent regions (Holt *et al.*, 2013).

A large variation in turnover was observed at smaller geographical distances (Fig. 4b), and for some comparisons between adjacent regions (i.e. Afrotropical and Palaeartic, Australasian and Indo-Malay) the PD component of PBD was not important in the determination of the phylogenetic dissimilarity (Table 2). This result demonstrates that, although these regions are relatively close, there are other factors driving the phylogenetic turnover between them. Deviances from the expected distance-decay relationship usually happen if the distances are associated with marked geographical barriers to dispersal and with environmental distances. In these cases, the turnover of lineages will be faster than expected based only on the turnover of species (Graham & Fine, 2008). The Australasian and Indo-Malay regions were connected up to the end of the Mesozoic (c. 66 Ma) and today the shortest distance connecting these regions is 35 km (between Bali and Lombok). Currently, these regions are separated by deep water, specifically the Lombok Strait, Makassar Strait and Celebes Sea, which persisted even during the last glacial maxima, in the Pleistocene (Voris, 2000; Sathiamurthy & Voris, 2006).

Our findings corroborate expectations that differences between localities at different latitudes (i.e. Neotropical and Nearctic, Indo-Malay and Palaeartic) tend to be better explained by the PD component of PBD (Baselga, 2012). This is predictable because of the environmental components (e.g. glaciations) acting throughout evolutionary time, reducing richness at higher latitudes (e.g. Dobrovolski *et al.*, 2012). However, we showed that this is not true for the comparison between the Afrotropical and the Palaeartic regions. A clear environmental barrier between the Afrotropical and Palaeartic regions is the arid portion of northern Africa (the Sahara Desert). However, as most of the species that occur in this transition zone present older diversification dates than the completion of the formation of the desert (c. 6000 years ago; Schuster *et al.*, 2006), other factors (e.g. ecological factors) might have contributed to turning this region into a barrier to species dispersion. In previous analyses, the Afrotropical and Australian regions were the only ones with exclusive genera for each of the seven groups of studied tetrapods, which emphasizes the effective isolation of the Afrotropical region (Procheş & Ramdhani, 2012).

CONCLUSIONS

We demonstrate that PBD and BD are not appropriate measures for delineating biogeographical regions (e.g. as used in Kreft & Jetz, 2010; Holt *et al.*, 2013) (Figs 1 & 2, Appendix S2). By decoupling phylobetadiversity into turnover and PD components it was possible to disentangle the effects of local-scale and regional processes in shaping the phylogenetic structure of bats. This partitioning of dissimilarity into components has contributed to a better understanding of the historical and current determinants of beta diversity (e.g. Baselga, 2012; Leprieur *et al.*, 2012). We noticed that the interpretation of results can change greatly by analysing each component of dissimilarity (PBD) separately, and there are also contrasting spatial patterns among these components (PBD_{Turn} and PBD_{PD}) (Svenning *et al.*, 2011; Baselga *et al.*, 2012; Diniz-Filho *et al.*, 2012).

Overall, our results suggest that at coarse biogeographical scales the phylogenetic dissimilarities for bats are more determined by turnover, as a result of both ecological and historical events (e.g. Kissling *et al.*, 2012). However, beyond the effect of distance and geographical barriers, we also have to consider the importance of environmental gradients for bat assemblages. It has been demonstrated that for organisms with good dispersal ability, turnover may be better predicted by environmental characteristics than by historical effects (Graham *et al.*, 2006). We postulate that flight ability, which gives bats good dispersal possibilities (Presley & Willig, 2010), has led to low turnover rates between adjacent regions in the absence of strong environmental barriers.

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SUPPORTING INFORMATION

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

Appendix S1 Cluster analysis for turnover component of beta diversity (BD) and phylobetadiversity (PBD).

Appendix S2 Distance relationship among biogeographical regions with standardized effect size values of phylobetadiversity (PBD) and its components.

BIOSKETCHES

Franciele Parreira Peixoto is currently a PhD student in the Ecology and Evolution graduate program in the Universidade Federal de Goiás, Brazil. Franciele's main research interests lie in macroecology and biogeography.

Author contributions: F.P.P. led the writing and compiled the data; J.A.F.D.-F.; F.P.P. and M.V.C. conceived the ideas and interpreted results; P.H.P.B. and F.P.P. ran analyses, generated maps, figures and data matrices. D.B., P.H.P.B., J.A.F.D.-F. and M.V.C. contributed to the writing.

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