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Global mammal beta diversity shows parallel assemblage structure in similar but isolated environments

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The taxonomic, phylogenetic and trait dimensions of beta diversity each provide us unique insights into the importance of historical isolation and environmental conditions in shaping global diversity. These three dimensions should, in general, be positively correlated. However, if similar environmental conditions filter species with similar trait values, then assemblages located in similar environmental conditions, but separated by large dispersal barriers, may show high taxonomic, high phylogenetic, but low trait beta diversity. Conversely, we expect lower phylogenetic diversity, but higher trait biodiversity among assemblages that are connected but are in differing environmental conditions. We calculated all pairwise comparisons of approximately 110×110 km grid cells across the globe for more than 5000 mammal species (approx. 70 million comparisons). We considered realms as units representing geographical distance and historical isolation and biomes as units with similar environmental conditions. While beta diversity dimensions were generally correlated, we highlight geographical regions of decoupling among beta diversity dimensions. Our analysis shows that assemblages from tropical forests in different realms had low trait dissimilarity while phylogenetic beta diversity was significantly higher than expected, suggesting potential convergent evolution. Low trait beta diversity was surprisingly not found between isolated deserts, despite harsh environmental conditions. Overall, our results provide evidence for parallel assemblage structure of mammal assemblages driven by environmental conditions at a global scale.

1. Introduction

Global patterns of the diversity of life are driven by a multitude of forces, including past and present geographical isolation of assemblages, and the changes in environmental conditions across space [1–3]. By combining taxonomic, phylogenetic and trait dimensions of beta diversity, we can formulate spatially explicit hypotheses for the effects of geographical isolation and environmental dissimilarity on regional and global patterns of biodiversity [4–11]. While taxonomic beta diversity has been well studied, it ignores the shared evolutionary history and functional similarity of species. Phylogenetic beta diversity measures the relatedness of species between two assemblages (i.e. turnover of lineages [8]) and tends to increase with historical isolation [12–14]. Trait beta diversity measures morphological similarity between two assemblages and is related to similarity in environmental conditions [9,15,16].

Previous global beta diversity studies have mostly considered one dimension of diversity [5,11,17,18]. Alternatively, they have quantified distance decay from a focal cell, which limits the geographical and environmental extent of analysis [4,17]. Owing to their more limited scope, these approaches may not uncover mechanisms underlying patterns of different dimensions of biodiversity across global scales. Here, we provide the first global beta diversity study of a large clade to test specific hypotheses on how beta diversity dimensions might vary in relation to biogeographic and evolutionary mechanisms (figure 1). We use recent information on mammal distribution, evolutionary history and ecological traits, as well as high-performance computing, to perform a global beta diversity analysis for 4787 terrestrial mammal species.

In general, we expect the three dimensions of beta diversity to be highly correlated [10,19]. Changes in taxonomic beta diversity will likely be related to changes in phylogenetic and trait beta diversity, because species identities carry both trait and phylogenetic information. Regional analyses support low beta diversity in all dimensions when assemblages are geographically connected and located in similar environments [19,20]. Conversely, beta diversity is high when assemblages have been historically isolated and occur in different environments [12,19–21]. However, beta diversity dimensions could be decoupled (i.e. vary independently) because of limited historic isolation (low phylogenetic beta diversity) and differing morphological adaptations among related species living in dissimilar environments (high trait beta diversity). Alternatively, decoupling could result from convergent adaptation (low trait beta diversity) to similar local environmental conditions in which selection favours a common set of morphological and physiological adaptations in unrelated lineages (high phylogenetic beta diversity) [9,22]. Assemblage convergence in plant life-history traits has been previously highlighted at the global scale [23–25], but without consideration of phylogenetic beta diversity. While convergence patterns have received some support, their global generality across taxa and biomes remains unclear [26–28].

To evaluate the importance of the environment and isolation in shaping observed patterns of beta diversity, we delineated similar ecotypes into biomes and geographically connected regions into realms. Biomes, such as tropical forests or tundra, represent broad environmental conditions [29,30]. Realms represent evolutionary units through shared geographical connectivity and isolation [30–33]. Moreover, biomes and realms are discrete units that help connect findings to specific regions and to other studies on productivity, biome age and geological history of assemblages. For each of the four combinations of within and among realms and biomes, we generated an expected pattern of taxonomic, phylogenetic and trait beta diversity based on environmental conditions and historic isolation. For grid cells located in same realm and biome, we expected low taxonomic, phylogenetic and trait beta diversity, owing to adaptation to similar environments and no dispersal limitation (figure 1). For grid cells located in different realms and biomes, we expected high taxonomic, high phylogenetic and high trait beta diversity owing to historical isolation and local adaptation or environmental filtering (figure 1). For grid cells located in the same realm and different biomes, we expected low taxonomic, low phylogenetic beta diversity and high trait beta diversity owing to local adaptation or environmental filtering, but weak historical isolation

(figure 1). Finally, for grid cells located in different realms and in the same biome, we expected low trait beta diversity, high taxonomic and high phylogenetic beta diversity owing to similar environmental pressures shaping life-history strategies among unrelated lineages [9] (figure 1).

2. Methods

(a) Datasets

We extracted presence/absence data of terrestrial mammals from habitat suitability models that were created based on species ranges and habitat preferences [34]. We aggregated this information into 12 298 grid cells in a Mollweide equal-area projection equivalent to 1 degree at the equator (corresponding to approx. 110×110 km). We used cells only with two or more species ($n = 11\,995$). For trait data, we used a dataset compiled from different sources listed in electronic supplementary material, S1, and selected 12 continuous traits, which were the most complete and represented different aspects of mammal life history such as morphology, reproduction or social organization. These traits had between 18% and 80% of missing values (mean 69%). We thus imputed these trait values using the missForest function without phylogenetic information [35]. This method uses the relationships between traits to estimate the missing values and was shown to outperform other methods for imputation of trait datasets [36]. Phylogenetic data were extracted from the recently published time tree of mammals [37]. Climatic variables were extracted from the Worldclim database [38]. After combining these datasets, our analyses included 4787 terrestrial species for which we had geographical, phylogenetic and trait data.

(b) Beta diversity calculations

We calculated beta diversity among all pairwise combinations of cells. Beta diversity can be partitioned into nestedness and turnover components [39]. We considered only turnover (hereafter referred as 'beta diversity') in order to have a measure independent from species richness [39,40]. Taxonomic turnover was thus calculated, using the Simpson dissimilarity index (betasim) [39]. We calculated phylogenetic and trait beta diversity using the turnover component of the mean nearest taxon distance metric (MNTDturn; adapted from [41]). We chose this measure based on pairwise distances among species because it is independent from richness and can be applied to both traits and phylogenies. Furthermore, as with betasim, if the assemblage that has lower diversity has no unique species, then the turnover between the two communities will be zero. MNTDturn is defined as

$$\text{MNTDturn} = \min(\text{mean}(NNab), \text{mean}(NNba)),$$

where $NNab$ are all the nearest taxon distances between communities a and b and $NNba$ are all the nearest taxon distances between communities b and a. Therefore, MNTDturn is the minimum mean of the distances (phylogenetic or trait pairwise distances) between the species present in two assemblages. We calculated pairwise phylogenetic distances among species using patristic distances (i.e. distances between pairs of species using branch lengths of the phylogenetic tree) [42]. We reduced the trait variables using principal component analysis (PCA), and measured the Euclidean distance between species along the first three PCA axes. Owing to the extremely large number of combinations ($n = 71\,934\,015$), we parallelized our analysis using the Stampede supercomputing cluster at the Texas Advanced Computing Center.

We also calculated geographical distances between all pairs of terrestrial cells using great-circle distances (i.e. considering
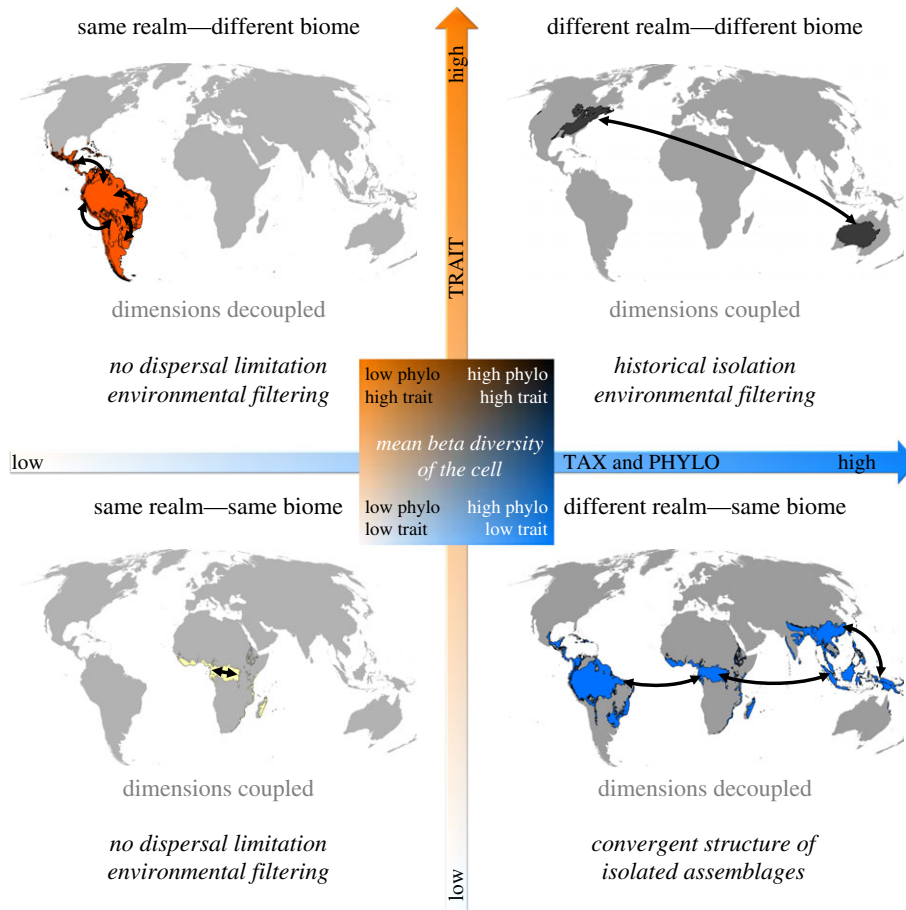
Figure 1. Hypothesis framework and expected mapped results. We expect trait and phylogenetic beta diversity to be coupled in most cases (bottom left and top right). Dimensions of beta diversity can be decoupled when assemblages are located in contrasting environments within a realm because of limited historic isolation and environmental filtering (top left) or in similar environments of different realms because of convergent structure of assemblages in similar environmental conditions (bottom right). Mechanisms corresponding to each combination of high and low beta diversity dimensions are in italics. Colours in maps highlight expected median beta diversity for specific examples (see Methods and electronic supplementary material, S3).

the spherical shape of the earth). We calculated environmental distances using Euclidean distances of the axes of variation of a PCA performed on all Worldclim variables [38].

(c) Analyses: global patterns of mammalian beta diversity

We first assessed the relationships among the three dimensions of beta diversity to determine whether they were globally coupled. Then, we explored the global relationship between the dimensions of beta diversity and changes in distance and environment using linear models. Finally, we took the residuals of beta diversity against distance, and fit them to changes in environment. In this way, we could account for differences in geographical distances and partition the effect of environment on changes in taxonomic, phylogenetic and trait composition of mammalian assemblages.

(d) Testing the hypothesis framework: biomes and realms

Our analytical framework is based on categories of high versus low isolation and environment. We used realms as proxies for current and past isolation and biomes as proxies for environment and climate. We extracted realm and biome data from Olson *et al.* [30]. In this established classification, most of the realms are separated by oceans or by important geographical barriers [43], therefore, they represent evolutionary units and long-term

isolation [14,44]. Biomes mostly represent environmental conditions and vegetation types [30].

We assigned each grid cell to one of the 13 biomes and six realms of the world defined by Olson *et al.* [30] (electronic supplementary material, figure S2.1). We separated our grid cells into categories based on four combinations of biome (same or different) and realm (same or different). Then, we tested if cell pairs classified in biomes and realms matched our hypothesis framework, i.e. if realms represented distances and biomes represented environment. For this evaluation, we compared the observed environmental and geographical distance of a given combination (e.g. same realm and biome) to the whole dataset using non-parametric bootstrapping. We randomly drew 1000 subsets from our whole dataset corresponding to the size of each combination (1000 subsets × 4 combinations), and calculated the median beta diversity of each subset. We then compared the medians of each of the four combinations to the distribution of medians of the random draws (see figure 3a and electronic supplementary material, figure S2.2a for a visual description of the method). We used medians because of the large number of extreme values leading to skewed distributions. In cases such as this, medians represent better the central tendencies of the distributions than means.

(e) Testing the hypothesis framework: beta diversity dimensions

In order to test the validity of the hypothesis framework, we also separated our pairwise beta diversity values into categories based on biomes (same or different) and realms (same or
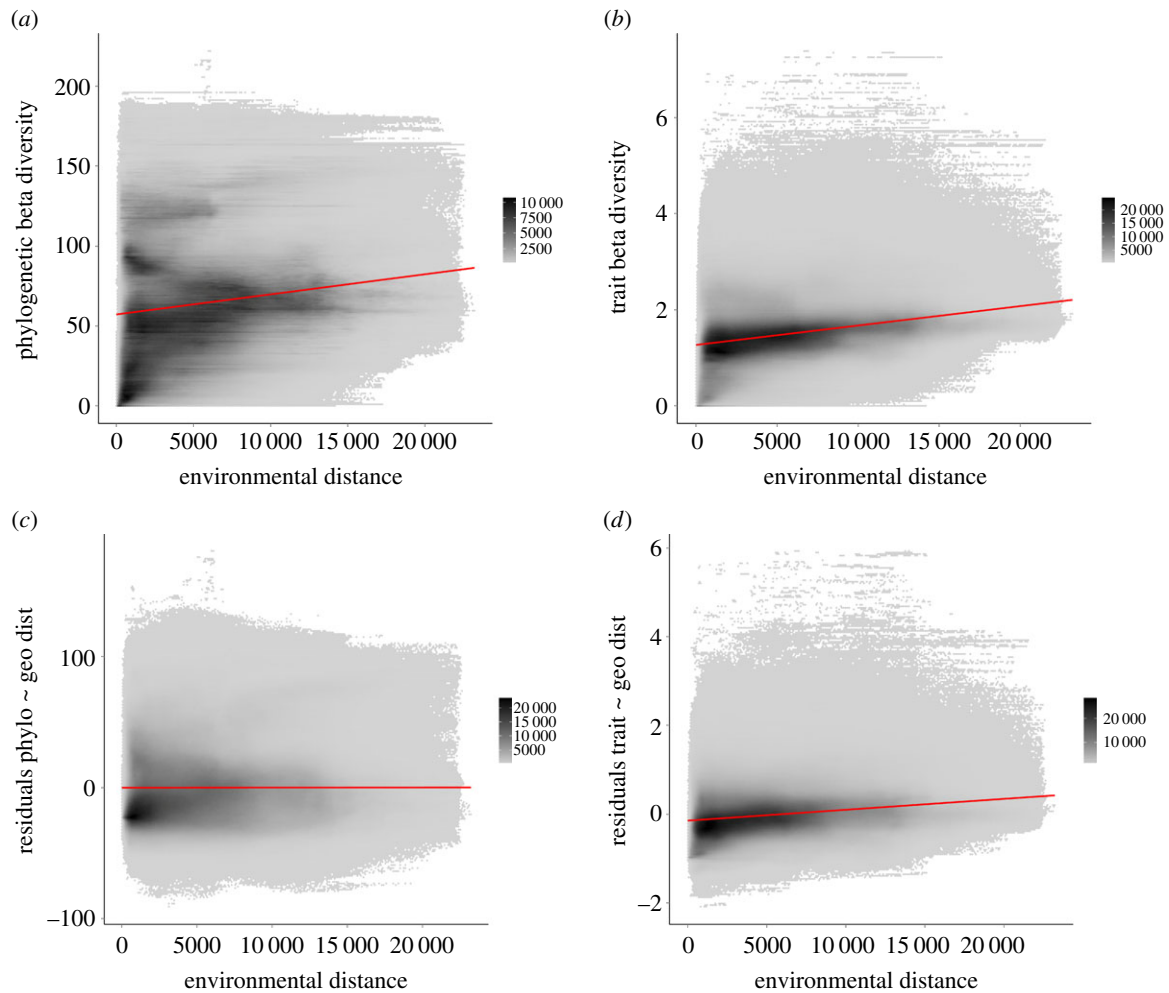
Figure 2. Relationships between phylogenetic (*a*), trait beta diversity (*b*) and environmental distances. Panels (*c*) and (*d*) show the residuals of the relationship between phylogenetic (*c*), trait beta diversity (*d*) and geographical distance plotted against environmental distances. Bins represent point densities. Figures show relationships with geographical distance and figures for the four combinations of biomes and realms reported in electronic supplementary material, S4. (Online version in colour.)

different). To determine whether the beta diversity of assemblages in each of the combinations of biomes and realms was different from expected given the entire dataset, we compared the observed beta diversity of a given combination with the whole dataset using the same non-parametric bootstrapping method described above for biomes and realms (figure 3*a*). To determine whether all biomes followed the same pattern, we repeated this analysis separately per biome. We evaluated if the beta diversity among cells within a biome was greater than expected given the global beta diversity pool. For example, to determine whether beta diversity values between tropical forests in different realms were lower than expected, we separately compared beta diversity values between tropical forest grid cells in different realms to beta diversity values between all combinations of cells. For each hypothesis (figure 1), we compared the true value with the null distribution to determine whether we could accept or reject our hypothesis for the global patterns of biodiversity, isolation and environment.

(f) Mapping beta diversity
For each grid cell, we calculated the median beta diversity value compared with all the other cells for each beta diversity dimension ($n = 11\,995$). We then mapped this median beta diversity to visualize global patterns of beta diversity in each dimension. To highlight the geographical areas associated with each combination of biome and realms, we mapped the median beta diversity for each cell to all other cells in that combination. For example, for the combination same realm/same biome, we calculated the median beta diversity between each cell in, e.g. Amazonia (realm, neotropic; biome,

tropical moist broadleaf forest) and to all other cells in Amazonia. We then repeated this for all biome comparisons and overlaid the results in a single map (see electronic supplementary material, S3 for more details on mapping methods).

Similarly, we mapped environment dissimilarity using the median environment dissimilarity of each cell. In order to visualize the cells for which our hypotheses were confirmed, we compared the median trait and phylogenetic beta diversity of a cell in a given combination (e.g. same realm/same biome) to the median beta diversity of all the combinations. All the cells matching the hypotheses were then coloured (electronic supplementary material, S3).

3. Results

(a) Global patterns of mammalian beta diversity
We calculated the taxonomic, phylogenetic and trait dimensions of beta diversity for all global terrestrial cells resulting in ≈71 million pairwise calculations per dimension. Overall, the beta diversity dimensions were strongly coupled ($\beta_{\text{tax-phylo}} = 0.74$, $\beta_{\text{tax-trait}} = 0.63$, $\beta_{\text{trait-phylo}} = 0.65$, electronic supplementary material, figure S4.1). Environmental dissimilarity was more strongly correlated to trait and taxonomic beta diversity ($\beta_{\text{trait-env}} = 0.30$, $\beta_{\text{phylo-env}} = 0.16$, $\beta_{\text{tax-env}} = 0.32$), whereas geographical distance was more related to phylogenetic and taxonomic beta diversity ($\beta_{\text{trait-geo}} = 0.48$, $\beta_{\text{phylo-geo}} = 0.63$, $\beta_{\text{tax-geo}} = 0.61$), see figure 2*a,b* and S4.2 and
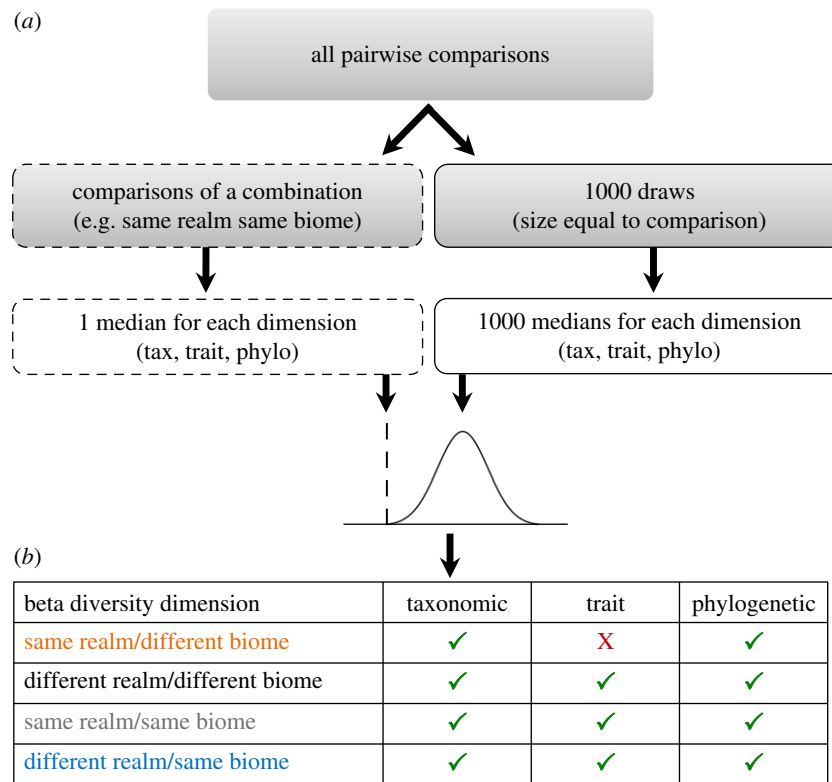
(a)

(b)

beta diversity dimension	taxonomic	trait	phylogenetic
same realm/different biome	✓	X	✓
different realm/different biome	✓	✓	✓
same realm/same biome	✓	✓	✓
different realm/same biome	✓	✓	✓

Figure 3. Methods (a) and summarized results table (b) of the randomization test to compare beta diversity of each combination of realm/biome and the whole dataset (see Methods for details). Check marks denote that predictions derived from theoretical framework are corroborated. X denote that predictions were not supported. All the figures comparing medians are reported in electronic supplementary material, S5. (Online version in colour.)

S4.3 in electronic supplementary material. Trait and taxonomic beta diversity were still related to environment (figure 2d), after taking into account geographical distance ($\beta_{\text{residTrait-env}} = 0.19$, $\beta_{\text{residTax-env}} = 0.18$), whereas the relationship between phylogenetic beta diversity and environment (figure 2c) became weak after accounting for geographical distance ($\beta_{\text{residPhylo-env}} = 0.002$).

(b) Hypothesis framework: biomes and realms

Our framework using realms and biomes as proxies for isolation and environmental distances, respectively, was mostly verified. The results of the analyses using randomizations showed that cell pairs located in the same realm and biome had lower environmental and geographical distance than the overall dataset. The same happened in cell pairs located in the same realm and different biomes (contrary to our expectations; figures S2.2 and S2.3 in electronic supplementary material). In contrast, cell pairs located in different realms and different biomes showed higher environmental and geographical distances. Cell pairs located in different realms but in the same biome showed higher geographical distance and lower environmental distance compared with the global dataset.

(c) Hypothesis framework: beta diversity dimensions

We assigned each pair of cells to a geographical realm and environmental biome such that each comparison of assemblage was either within or between a biome and realm. Results are shown in electronic supplementary material, S5 and summarized in figure 3b. Cell pairs located in the same realm and biome showed lower beta diversity in all dimensions than the overall dataset, as did the cell pairs located in the same realm and different biomes. In contrast, cell

pairs located in different realms and different biomes showed higher beta diversity for all three dimensions. Cell pairs located in different realms but in the same biome showed higher phylogenetic and lower trait beta diversity compared with the global dataset.

For the cell pairs in different realms and the same biome, we also ran the same analysis separately for each biome to determine which biomes matched the hypotheses (table 1 and electronic supplementary material, S5.2). For example, tropical moist broadleaf forests in different realms have high phylogenetic beta diversity and low trait beta diversity compared with the global distribution of beta diversity values. In contrast, tundra have low phylogenetic beta diversity and low trait beta diversity (table 1). Deserts and xeric shrublands have both high trait and phylogenetic beta diversity (table 1).

(d) Maps of mammalian beta diversity

Using a median global beta diversity measure per grid cell, we mapped information on the most unique taxonomic, phylogenetic and trait mammal assemblages (electronic supplementary material, figure S6.1). Australia and Madagascar have high taxonomic and phylogenetic mammal beta diversity. Australian mammalian assemblages also show high trait beta diversity, as do deserts and polar regions (electronic supplementary material, figure S6.1). Mountain regions generally show high beta diversity in the three dimensions, as previously found in regional [6,17] and global taxonomic beta diversity analyses [11]. The phylogenetic and taxonomic maps of median beta diversity also show some interesting similarities to maps of mammal endemism [45]. This similarity suggests a link between global scale endemism and

Table 1. Results of randomization tests comparing beta diversity of the whole dataset to beta diversity of cell pairs located in different realms and in the same biome using the median beta diversity value. Check marks denote that predictions derived from theoretical framework (i.e. high phylogenetic and low trait beta diversity) are corroborated. X denote that predictions were not supported. All the figures comparing medians are reported in electronic supplementary material, S5.2.

beta diversity dimension	phylogenetic	trait
tropical and subtropical moist broadleaf forest	✓	✓
tropical and subtropical dry broadleaf forest	✓	X
tropical and subtropical coniferous forest	X	✓
temperate broadleaf and mixed forests	X	✓
temperate conifer forests	X	✓
boreal forests/taiga	X	✓
tropical and subtropical grasslands, savannahs and shrublands	✓	X
temperate grasslands, savannahs and shrublands	✓	X
flooded grasslands and savannahs	✓	✓
montane grasslands and shrublands	✓	✓
tundra	X	✓
mediterranean forests, woodlands and scrub	✓	X
deserts and xeric shrublands	✓	X

turnover of species and lineages. It also indicates more broad applications and generalizations of our beta diversity mapping approach.

The maps of the combination of phylogenetic and trait beta diversity dimensions show contrasting patterns for different regions (figure 4 and electronic supplementary material, figure S6.3). Comparisons of cells within the same realm and within the same biome show low phylogenetic and low trait beta diversity (figure 4). Comparisons between cells in different realms and different biomes show high phylogenetic and trait beta diversity (figure 4). These results highlight coupling among beta diversity dimensions and represent the majority of global comparisons. However, comparisons among the same biome in different realms showed low trait beta diversity despite high phylogenetic beta diversity. This pattern is most pronounced in tropical forests in comparisons among South America, Africa and the Indotropics. The hypothesis for cells in the same realm and different biomes was poorly supported except for Palaearctic deserts, tundra and montane grasslands, some tundra zones in Nearctic, few zones in Patagonia and Papua New Guinea forests. Maps of environmental dissimilarities (electronic supplementary material figure S2.4) show that biomes represented environmental information but some biomes, such as deserts, were heterogeneous and showed high environment dissimilarity.

4. Discussion

By comparing global patterns across beta diversity measures, we begin to unravel the role of multiple mechanisms that act together shaping diversity and move macroecology towards using more predictive frameworks. This first global analysis of the three dimensions of beta diversity shows that historical isolation and environmental conditions act in concert to shape patterns of global mammal diversity. We found that phylogenetic beta diversity was more correlated to geographical distance, whereas trait beta diversity was more related to environmental dissimilarity, suggesting that these two dimensions are not tightly coupled. We also found that high taxonomic beta diversity was related to both increased distance and increased differences in environment, showing that this dimension might lead to incorrect inferences when considered alone. These results suggest that mammal beta diversity at a global scale is driven by different mechanisms balancing both evolutionary responses to long-term isolation and local adaptation to environments. More generally, these conclusions are consistent with previous studies performed in different taxonomic groups, geographical scales and applying different metrics and methodologies [6,11,12,15,16].

Taxonomic and phylogenetic beta diversity were highly correlated, and we therefore focus on differences between trait and phylogenetic beta diversity to tease apart the mechanisms shaping assemblages across space. We found that comparisons among assemblages in the same realm and same biome had low beta diversity in all dimensions. This is likely owing to geographical connectivity and dispersal of lineages adapted to similar environmental conditions. This conclusion is also supported by previous work that highlighted low phylogenetic turnover between adjacent biomes [13]. In contrast, comparisons of assemblages in different realms and different biomes had high beta diversity in all dimensions. This could be due to current and historic isolation, and environmental filtering or local adaptation to different environmental conditions. These results are in line with previous work that highlighted a general congruence between dimensions but also a decoupling in some regions for both alpha and beta diversity [19,46–49].

As expected, we found low phylogenetic beta diversity between assemblages in different biomes within a realm. However, contrary to our prediction, trait beta diversity also tended to be low across biomes. There are two plausible and non-mutually exclusive explanations for these results. First, contrary to our expectations, we found that environmental distances between biomes within the same realm are usually low. Our prediction of high trait turnover among biomes requires that the environment in these biomes represents major changes that allow for evolutionary and/or ecological pressures on traits. Many factors may rule biome transitions, and geographical proximity of biomes within realms seems to reflect low environmental turnover. Second, there may be particularly high levels of trait conservatism within realms. Lineages within realms show low trait turnover. Traits in these closely related species might be non-labile owing to lack of genetic variation, insufficient time for mutation or morphological trade-offs [50].

While coupling of beta diversity dimensions was generally consistent across biomes and realms, tropical forests in different realms had low trait beta diversity and high phylogenetic beta diversity, as predicted in our hypothesis
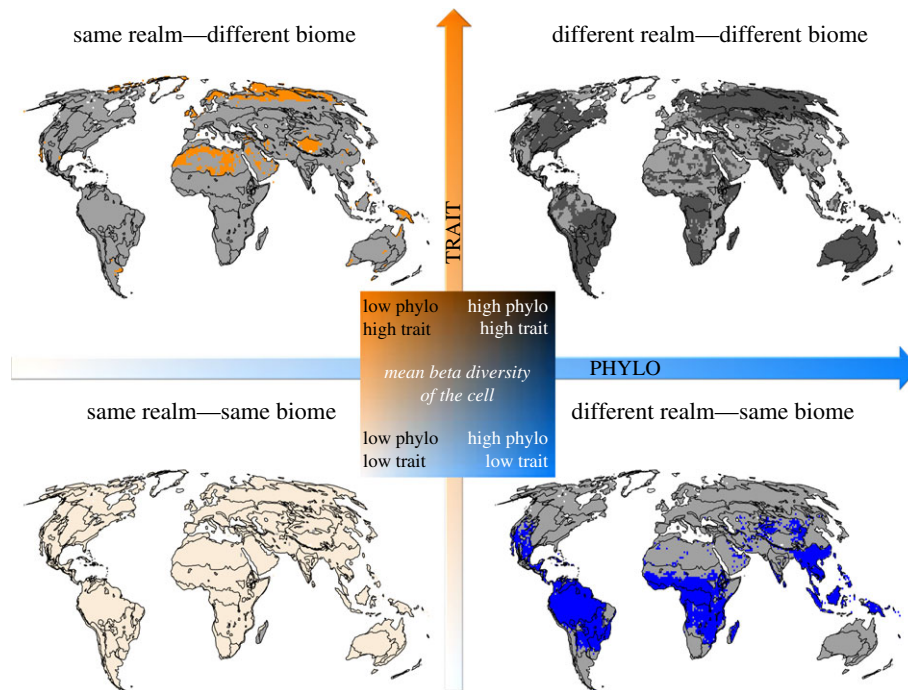
Figure 4. Maps of cells matching the hypotheses for both trait and phylogenetic beta diversity, for each of the four combinations of biome/realm. Cells matching the hypotheses (i.e. medians of the cells higher or lower than the median beta diversity of the dataset) are coloured. Light grey represents areas were the predictions were not corroborated. Top left: realms plotted independently. Bottom left: biomes within realms plotted independently. Bottom right: same biomes in different realms plotted independently. Note that the bottom left panel is almost completely beige because the hypothesis was verified in most cells. Please refer to electronic supplementary material, S6 for median values mapped with a continuous scale.

framework (table 1 and figure 3). While the tropical broadleaf forests of South America, Africa and the Indopacific share very few species, they all occur on the equator in warm and humid climates with little variation in day length. Mammals in these forests may have evolved similar arboreal strategies for exploiting the trophic and physical environment owing to similar demands for shelter, resources, and predator escape space, regardless of their taxonomic identity. For example, the Indotropical tree kangaroos, South American kinkajous and African bushbabies are distantly related, but all omnivorous, mostly nocturnal, arboreal mammals with strong long limbs, large eyes and long tails. Alternatively, tighter niche packing, increased competition and functional redundancy in tropical systems may explain low trait beta diversity, despite high phylogenetic beta diversity [19]. In addition, tropical areas, especially in Southeast Asia, are the centre of mammalian endemism, and tropical forests are older and more stable environments in comparison with temperate biomes [51]. Therefore, the greater time since colonization or speciation may have resulted in a fuller filling of niche space in each of these isolated, but ecologically similar environments [52,53].

In contrast to tropical biomes, tundra, taiga and temperate conifer forests had low phylogenetic and low trait beta diversity despite occurring in different realms. Low taxonomic beta diversity in these regions has also been found for amphibians and birds [11,54]. The low level of phylogenetic beta diversity, despite current isolation, likely stems from historical biogeography. During the Pleistocene, Nearctic and Palaearctic realms were connected by the Bering land bridge, which served as a refugium and dispersal corridor [55]. Mammals of northern biomes also show large range sizes, likely shaped by glacial history and past climate changes [56,57], which can also explain low beta diversity in these regions.

Based on our hypothesized relationship between isolation and local adaptation or environmental filtering in promoting beta diversity, we expected deserts to show strong convergence in traits owing to the extreme temperature and xeric conditions. However, our analysis showed an unexpected pattern of high trait and phylogenetic beta diversity in deserts. While it is possible that the life-history traits used in this analysis do not capture the limiting factors that shape desert mammal lineages, such as physiological adaptations to xeric conditions or increased nocturnality, these complex traits are highly correlated with body size, or reproductive traits [58,59]. We believe that our result is owing to two factors. First, deserts are actually a rather heterogeneous environmental category, and the differences between warm African deserts (such as the Sahara and Kalahari) and cold Asian deserts (such as the Gobi) result in high environmental beta diversity (electronic supplementary material, figure S2.4). The diversity of environmental conditions in deserts over time could also explain the high values of trait beta diversity for this biome [59,60]. Second, one fundamental assumption in our analysis is that similar environmental conditions will apply selective pressures and filter species with similar morphological strategies for exploiting niches. This hypothesis is based on the repeatability of evolution, as well as the importance of trade-offs in limiting morphological adaptation [61]. For example, if there are strong trade-offs, then selection for a trait, such as nocturnal behaviour, may translate into morphological characters such as large eyes or ears to promote foraging in low light levels resulting in similar eye and ear traits for desert mammals. However, if trade-offs are weak, and selection for nocturnality does not require morphological adaptations, we may see a diversity of morphologies making up a desert community. While the presence of remarkably similar desert bipedal rodents with

reduced forelimbs and elongated ears in North America, South American, African and Asian deserts would suggest convergent selection pressures [62], these anecdotal examples were not borne out as general findings in our analysis. In contrast, our results are consistent with previous intercontinental comparisons of small mammal assemblages in desert regions, in which small mammal communities also showed a high heterogeneity of species and traits within and among continents [59,60].

The current patterns of beta diversity are undoubtedly impacted by humans since their emergence, through extinctions and range contractions [63]. Therefore, the historical patterns of convergence or radiation between and among realms and biomes might also have been obscured. While fossil comparisons across geological time will always be fraught with sampling uncertainty, they allow comparison of past and present beta diversity [64], and thus provide an unparalleled opportunity to test our assumptions on the drivers of beta diversity [65]. Differences in biome age may also help explain why tundra and taiga, two rather young biomes [51], have relatively low phylogenetic beta diversity, and tropical forests, one of the oldest biomes, have high phylogenetic beta diversity. Combining beta diversity with geological and palaeo records, as well as measures of environmental productivity through time, may be a promising way to further unravel historical mechanisms shaping current diversity [51,65].

This work constitutes the first global assessment of mechanisms based on a predictive framework underlying phylogenetic and trait beta diversity for a large clade. We show that considering different dimensions of beta diversity provides an opportunity to assess large-scale connectivity, isolation, adaptation or environmental filtering. By considering all possible comparisons, our beta diversity maps show assemblage uniqueness in terms of phylogenetic and trait diversity. These maps can be used to identify zones of overlap and incongruence of different dimensions of biodiversity and may be helpful in identifying priority zones for mammal conservation. The hypothesis framework used here may serve as a basis for studies of other taxonomic groups at different spatial and temporal scales.

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