



Environmental variation is a major predictor of global trait turnover in mammals

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Abstract

Aim: To evaluate how environment and evolutionary history interact to influence global patterns of mammal trait diversity (a combination of 14 morphological and life-history traits).

Location: The global terrestrial environment.

Taxon: Terrestrial mammals.

Methods: We calculated patterns of spatial turnover for mammalian traits and phylogenetic lineages using the mean nearest taxon distance. We then used a variance partitioning approach to establish the relative contribution of trait conservatism, ecological adaptation and clade specific ecological preferences on global trait turnover.

Results: We provide a global scale analysis of trait turnover across mammalian terrestrial assemblages, which demonstrates that phylogenetic turnover by itself does not predict trait turnover better than random expectations. Conversely, trait turnover is consistently more strongly associated with environmental variation than

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predicted by our null models. The influence of clade-specific ecological preferences, reflected by the shared component of phylogenetic turnover and environmental variation, was considerably higher than expectations. Although global patterns of trait turnover are dependent on the trait under consideration, there is a consistent association between trait turnover and environmental predictive variables, regardless of the trait considered.

Main conclusions: Our results suggest that changes in phylogenetic composition are not always coupled with changes in trait composition on a global scale and that environmental conditions are strongly associated with patterns of trait composition across species assemblages, both within and across phylogenetic clades.

KEYWORDS

beta diversity, convergence, distance matrices, mammals, mean nearest taxon distance, multiple regression, niche conservatism, phylogeny, traits

1 | INTRODUCTION

Phylogenetic and trait diversity (e.g. morphological and life-history traits), in conjunction with the distributional patterns of species, are important dimensions of biodiversity (Faith, 1992; Petchey & Gaston, 2002; Swenson, 2011a). Patterns of change in the composition of these biodiversity dimensions across assemblages of species (i.e. turnover) are particularly valuable when inferring the processes that shaped these assemblages (Graham & Fine, 2008; Swenson, 2011b; Whittaker, 1960). However, despite the widely recognized spatial scale dependence of community assembly mechanisms (Rahbek & Graves, 2001), information on turnover patterns is inconsistent across spatial extents and biodiversity dimensions. For example, the relationship between phylogenetic and taxonomic turnover has been evaluated globally (Holt et al., 2013), but few corresponding global analyses have been performed exploring variation in species trait composition at a global scale. Therefore, it is unclear whether the phylogenetic biogeographical patterns we see reflect patterns in trait variation.

Evolutionary mechanisms have the potential to decouple biodiversity dimensions, resulting in correlations between dimensions that are weaker than expected by chance. For example, two communities could have no shared species, but relatively little difference in trait composition. This might be expected where geographical barriers have driven allopatric speciation within similar environments, resulting in less difference in traits between communities than might be expected based on the levels of species turnover (Weinstein et al., 2014). Alternatively, such a pattern might also be driven by convergent evolution (Winemiller, Fitzgerald, Bower, & Pianka, 2015). Ultimately, three general factors are likely to influence the relationship between global phylogenetic and trait turnover. The first, phylogenetic trait conservatism, reflects the constrained evolution of traits on the phylogeny. If traits are very strongly conserved through

evolutionary time, then trait turnover would tend to be strongly associated with phylogenetic turnover (e.g. Swenson and Enquist, et al., 2012), independent of patterns of environmental variation. Such a tight link between these two biodiversity dimensions would allow researchers to use them interchangeably, that is, using phylogenetic turnover as a surrogate of trait turnover. The second factor, ecological adaptation, can occur when traits are highly evolutionarily labile and under selective pressure to adapt to environmental conditions (e.g. Ogburn & Edwards, 2015). In this case, traits will not be strongly associated with phylogenetic lineages and will be strongly correlated with environment conditions. Finally, a third possibility is that entire phylogenetic clades have adapted to specific environmental conditions. In such cases, covariation between phylogenetic turnover and environmental conditions will predict significant amounts of trait turnover. Other factors that can influence variation in phylogenetic or trait turnover, such as biotic interactions, tend to act at much finer scales and are likely less relevant at the global level (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012).

Mammals are a particularly well-suited group for the exploration of the drivers of global scale variation in biodiversity dimensions. They are a data-rich taxon with well-resolved phylogenies (e.g. Hedges, Marin, Suleski, Paymer, & Kumar, 2015), a large number of available ecological traits (Jones et al., 2009), and we have an in-depth knowledge of their geographical distributions (Rondinini et al., 2011; Schipper et al., 2008). Furthermore, they are a relatively stable taxonomic group and few additional species have been discovered in recent decades. Mammals show considerable variation in their morphology and life-history traits, which allows hypothesis testing based on a wide variety of trait characteristics.

A major challenge when comparing patterns of phylogenetic and trait turnover, across species assemblages, is that these two biodiversity dimensions tend to be measured in a fundamentally different manner. Most studies of trait diversity have focused on specific



traits, and patterns of trait diversity appear to be dependent on the trait being considered (Graham, Parra, Tinoco, Stiles, & McGuire, 2012; Swenson, Anglada-Cordero, & Barone, 2011). Phylogenetic diversity studies, in contrast, are typically based on phylogenetic hypotheses, which attempt to resolve general evolutionary relationships. This conceptual distinction between these two features of biodiversity has repercussions for studies that attempt to establish the shared and unique patterns of phylogenetic and trait compositional turnover. A potential way forward is to consider the consistency of patterns generated by multiple, independent traits. Evaluating traits both independently and in combination, therefore, provides a more holistic description of how assemblages vary in their trait composition. Within this study, we complement this holistic approach towards trait turnover analysis by using an analytical method that can be applied to phylogenetic and trait data, allowing comparisons of the two source of biological variation.

Here, we use recently updated range maps (Rondinini et al., 2011), an updated phylogenetic hypothesis (Hedges et al., 2015), and data on several morphometric and life-history traits (Davidson, Hamilton, Boyer, Brown, & Ceballos, 2009; Jones et al., 2009), to evaluate the spatial patterns and drivers of phylogenetic and trait turnover (i.e. replacement of phylogenetic lineages or traits among species assemblages), globally for mammals. We consider whether patterns of phylogenetic and trait turnover across assemblages are consistent with signals of specific ecological and evolutionary mechanisms, asking the following questions:

1. Are phylogenetic and trait turnover decoupled (i.e. less correlated than expected by chance)?

If not, this would be in accordance with the hypothesis that phylogenetic trait conservatism drives the global patterns of assemblage trait characteristics (e.g. Swenson and Enquist, et al., 2012).

2. Are trait turnover patterns more strongly associated with environmental variation than with phylogenetic turnover?

If so, this result would be in accordance with the hypothesis of ecological adaptation to specific environments across communities (e.g. Ogburn & Edwards, 2015).

3. Does the interaction between phylogenetic turnover and environmental variation predict patterns of trait turnover?

A positive interaction would be consistent with phylogenetic clades having traits associated with specific environmental conditions (e.g. Fine & Kembel, 2011).

4. Is the relationship of phylogenetic versus trait turnover statistically independent of the specific traits being considered?

If so, then this result would be consistent with the concept of a general influence on mammalian assemblage traits across the globe,

rather than results being specific to the particular trait under consideration (e.g. Corbelli et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Data

For our global mammalian distributional data, we used presence/absence data for 4,653 2° grid cells for 4,850 mammal species. This two-degree resolution was selected to focus on global scale patterns and reduce the influence of local-scale variation on results. Species distributions were originally in the form of 300-m pixels of suitable habitat inside known geographical ranges. Habitat suitability was determined based on land cover, elevation and presence of water, reclassified according to the habitat relationships identified in the IUCN Red List (IUCN, 2014). For details about these deductive species distribution models, please refer to Rondinini et al. (2011). For our phylogenetic measures, we used a newly compiled tree containing all mammal species (Hedges et al., 2015). Further details for this phylogeny, including consensus support values for nodes, are available from Center for Biodiversity (2017). This phylogeny was selected over less recent mammal phylogenies (e.g. Bininda-Emonds et al., 2007) as it is based on substantially more underlying data, with 70% of the taxa (3,738 species) placed within the phylogeny based on genetic data. The remaining species (1,626) have been interpolated by placing them into their genera and applying a birth–death polytomy resolution approach (Kuhn, Mooers, & Thomas, 2011). This process generates a distribution of possible phylogenies, the impact of which we evaluated by: (1) examining the consistency among one thousand randomly selected samples of the generated distribution of phylogenies via pairwise cophenetic correlation comparisons (Sokal & Rohlf, 1962) and (2) examining the consistency between pairwise global grid cell phylogenetic turnover matrices, produced using the same one thousand randomly selected phylogenies, via Pearson correlations of pairwise comparisons of these matrices. Phylogenetic data are handled using “picante” package (Kembel et al., 2010) in R version 3.2.3 (R Core Team, 2015).

For trait turnover, we used a compiled trait dataset on all mammals, based on Jones et al. (2009), Davidson et al. (2009) and completed with four additional sources (Appendix S1). This dataset originally contained a total of 26 continuous trait variables, with considerable variation in the extent of missing data per variable. Based on preliminary testing, we reduced this trait dataset to the 14 most complete trait variables, which included a mixture of morphometric and life-history traits (Table 1). After matching the phylogenetic data with the two other datasets, we retained 4,611 species. In total, 753 species were removed from the phylogeny (which included all marine species) and 239 from the distribution and trait data. Species that are endemic to small islands were retained within our analysis in order to maximize the taxonomic coverage of our study and to avoid arbitrary decisions such the maximum size of “small” islands, whether high altitude areas should be considered “islands,” etc.

We summarized the 19 bioclimatic global environmental data from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) via

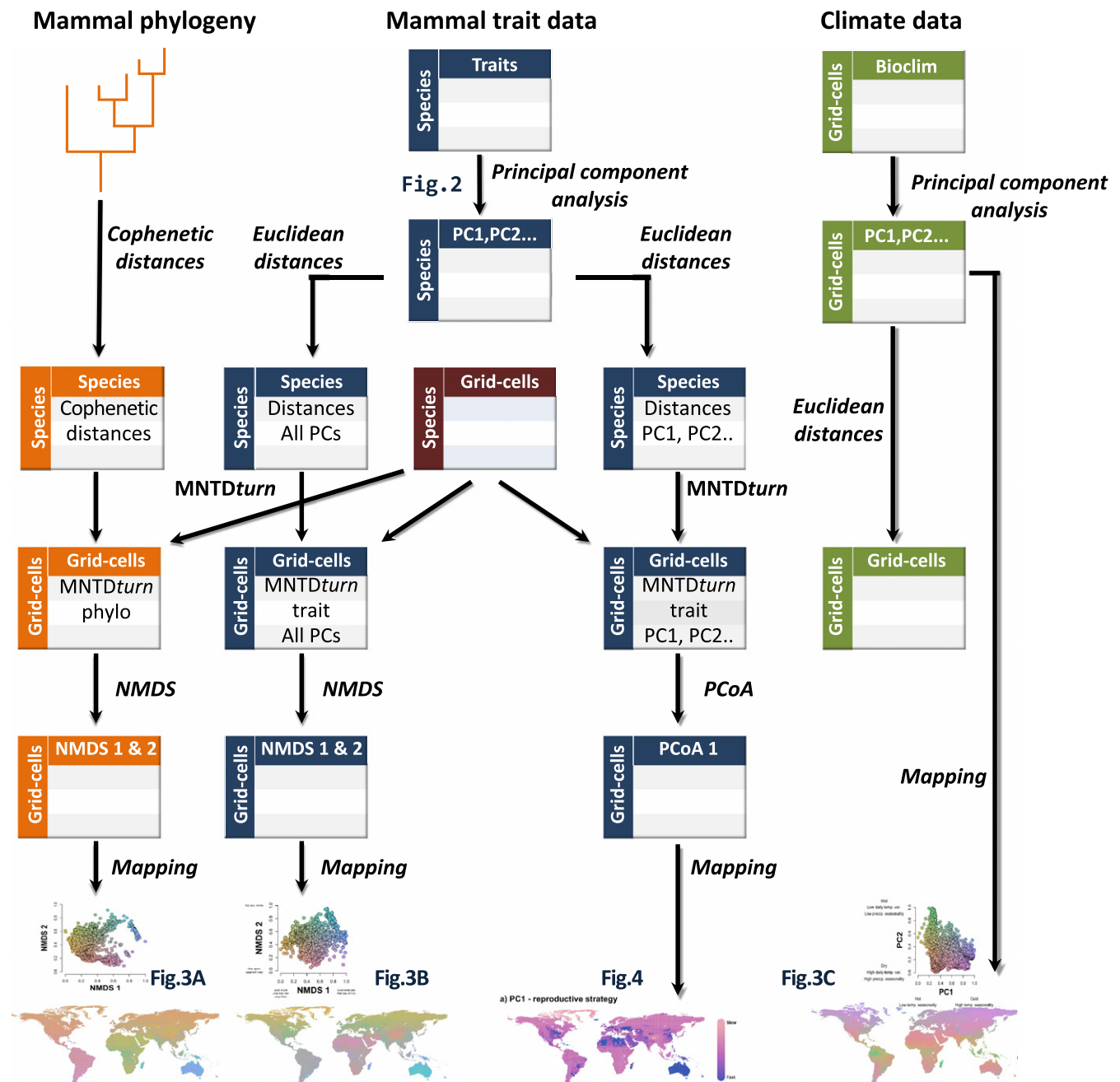
TABLE 1 Pearson correlation coefficients between grid cell NMDS values and mean grid cell trait values.

	NMDS1	NMDS2
Trait PC1—"Life-history speed"	-0.34	-0.45
Trait PC2—"Social group size versus litter size"	0.84	0.14
Trait PC3—"Species range size versus life-history speed"	0.06	-0.1
Trait PC4—"Species range size"	0.86	-0.3
Trait PC—"Placental/non-placental"	-0.68	-0.21

a principal components analysis (PCA), and we retained only the most important components for further analysis (i.e. sufficient principal components required to explain >90% of the total variation). Pairwise environmental distances between grid cells were calculated as the Euclidean distances within the resulting PCA space.

2.2 | Spatial turnover calculations

A visual summary of our analytic procedure is shown in Figure 1, see also detailed description in Supplementary Information and example R code available from (<http://dx.doi.org/10.5061/dryad.pc>

**FIGURE 1** A graphical representation of the analytical process performed within this study



1rs). We focused on compositional turnover, which is the component of turnover that measures only those aspects of diversity that change in a given pairwise combination (Baselga, 2010). This focus is related to the study goals, which are concerned with change in assemblage composition, rather than differences due to differing levels of biodiversity richness among assemblages. A wide variety of turnover metrics are available to incorporate either phylogenetic or trait information. We used an approach based on pairwise distances among species, since it can be applied to both trait and phylogenetic turnover, without artificially converting the trait data into a tree-like structure. We adapted the mean nearest taxon distance (MNTD) metric (Webb, Ackerly, & Kembel, 2008) in order to focus solely on turnover patterns (i.e. replacement of phylogenetic lineages or species traits across species assemblages). We chose the MNTD metric over the similar mean pairwise distance metric because it focuses on absolute distances between unique species. The formula for MNTD is as follows:

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

where *NNab* represents all the nearest taxon distances between assemblage *a* and assemblage *b* and *NNba* vice versa. It is simply the mean of all the nearest taxon distances. The turnover specific metric (MNTD_{turn}) is given by

$$\text{MNTD}_{\text{turn}} = \min(\text{mean}(\text{NNab}), \text{mean}(\text{NNba}))$$

Therefore, similar to other turnover metrics, only the assemblage with lower richness in each pairwise comparison will influence the result. If the least diverse assemblage has no unique species, then MNTD_{turn} will be zero. If both communities have completely different species and the within-assemblage diversity is equal, then MNTD_{turn} will be equal to MNTD.

To calculate trait-MNTD_{turn} pairwise trait distances between assemblages, between species pairwise distances were required. For the trait data, we performed preliminary tests to identify the most appropriate method to account for the missing data in our trait dataset (Appendix S1). Based on the results of these tests, we imputed missing data using the missForest function (Penone et al., 2014; Stekhoven & Bühlmann, 2012), without use of the phylogeny. In order to account for correlations between our trait variables, we performed PCA on the trait data. To aid interpretation of the resulting principal components (PCs), we calculated the variation of each principal component across major taxonomic clades (orders), along with the loadings of each trait variable. We then measured trait distances between species as the Euclidean distances derived from the major principal components (the minimum principal components required to account for >90% of the observed variation). These principal component distances were used to calculate the trait MNTD turnover (trait-MNTD_{turn}) between all possible pairwise combinations of global grid cells. We also recalculated specific trait-MNTD_{turn} patterns for each trait principal component globally. Associations between MNTD_{turn} calculated on all traits and MNTD_{turn} calculated using each single trait principal component were quantified using Pearson correlations, and the significance of these correlations was tested against null model results produced by randomizations described in the “Testing for the relative influence of

evolutionary history and environment on trait turnover” section below.

For phylogenetic turnover calculations, we calculated the pairwise distances between all species from the phylogeny as a cophenetic distance matrix (i.e. the phylogenetic branch length distance between species). This distance matrix was used to calculate the phylogenetic MNTD turnover (phylo-MNTD_{turn}) between all possible pairwise combinations of global grid cells using the same equation as for trait-MNTD_{turn}. In all cases, turnover calculations performed in this study represent spatial turnover, that is, turnover from an assemblage within one grid cell to an assemblage within another global grid cell.

2.3 | Visualization of results

In order to visualize our results, we first summarized the pairwise grid cell turnover matrices using two-dimensional non-metric multidimensional scaling (NMDS) for each of our global biodiversity matrices (i.e. phylogenetic turnover and trait turnover), as well as our environmental distance matrix. These ordinations were used as a basis to map turnover patterns by colouring grid cells according to their location in NMDS space (i.e. grid cells that were in close proximity in the ordination were also similar in colour) based on the hue, colour, luminance (HCL) colour scheme (Figure S1 in Appendix S1). We chose this colour scheme because it maximizes the accuracy of human perception of colour differences better than the red, green and blue colour scheme (Zeileis, Hornik, & Murrell, 2009). Lastly, we calculated the correlation of the trait-MNTD_{turn} between each of the NMDS axes and the original trait variables to gain insight into how the traits were associated with each axis.

To visualize trait turnover for specific traits (i.e. individual principal components), we show only the primary axis of variation (based on principal coordinate analysis, i.e. PCoA 1) since patterns based on single traits should typically only vary in one dimension.

2.4 | Testing for the relative influence of evolutionary history and environment on trait turnover

To test the relative contribution of different mechanisms that might explain large-scale patterns of trait turnover, we built a model of trait turnover based on phylogenetic turnover and environmental conditions and established the shared and unique contributions of these two predictive variables. We used a multiple regression on distance matrices (MRM) approach coupled with variance partitioning (Lichstein, 2007; Swenson, 2014) to test the relative contribution of trait conservatism (influence of phylogenetic turnover in the model) versus ecological adaptation (influence of environmental turnover in the model) on trait turnover. This variance partitioning approach provides both the unique and shared contributions of predictive variables to the overall R^2 value. Given the highly non-random nature of both mammal species distributions and environmental conditions across the world (coupled with the influence of species turnover on both phylogenetic and trait turnover), we expected that both

phylogenetic turnover and environmental distance might be statistically significant predictors of trait diversity. However, we were primarily interested in how this predictive power compared to expectations based on patterns of species richness and species turnover. The significance of the observed unique and shared R^2 components of our empirical MRM model were, therefore, compared to corresponding values for MRM models based on 1,000 null model randomizations, which randomized the species names in our species occurrence matrix. Species names within the phylogenetic and trait data were also randomized. Patterns of species richness and species turnover were left unaltered, allowing us to control for the spatial bias introduced by these patterns when considering our results. This approach is preferable to permutation-based approaches, such as partial Mantel tests, which are prone to type I errors (Harmon & Glor, 2010). The unique components of the explained MRM variance attributed to environmental turnover and phylogenetic turnover, and the shared component of the explained MRM variance, were all tested against null results in a two-tailed manner. These null model tests, therefore, allowed us to quantify the relative contributions of the unique components of the variation in trait turnover associated with either phylogenetic turnover or environmental turnover. Each relative effect of each model component was quantified as the standardized effect size (SES), which was calculated as the empirical R^2 minus the mean null R^2 values divided by the standard deviation of the null R^2 values.

3 | RESULTS

3.1 | Trait variation among species

Tests of consistency across the multiple phylogenies generated by our interpolation process demonstrated that the impact of this interpolation was minimal, with a mean cophenetic score of 0.9997 (C.I. \pm 0.0002) for pairwise comparisons of these phylogenies and a mean correlation coefficient of 0.9999 (C.I. \pm 0.0002) across pairwise comparisons of phylogenetic turnover matrices produced using different versions of the phylogeny.

Our PCA analyses reduced our 14 trait variables to five principal components that explained 91.5% of the total variation (Table S1 in Appendix S1). The first two principal components explained over two-thirds of the total trait variation (Figure 2), but there was some variation in all five principal component scores across major mammalian taxonomic groups (see Figures S2–S6 in Appendix S1). The primary principal component (trait PC1) appeared to reflect the fast–slow continuum in mammalian life-history patterns (e.g. Bielby et al., 2007; Oli, 2004; Purvis & Harvey, 1995) with high trait PC1 species representing those characterized by slow life history, high reproduction effort per individual, and long periods to sexual maturity (e.g. elephants, rhinos, gorillas). The low trait PC1 species represented fast life-history species, producing many offspring with low parental investment, and a short time until sexual maturity (e.g. shrews, opossums, many rodents). The secondary principal component (trait PC2) primarily distinguished bats from other mammal species (Figure 2, Figure S4 in Appendix S1), not directly through their aerial mode (which was not a

trait variable within our analysis) but through morphological, reproductive and demographical traits, that is, small species with high population densities (despite low litter sizes) had the highest trait PC2 scores. Most non-bat mammals had average to low values for trait PC2, with notable exceptions being some rodents, shrews and shrew opossums. The third principal component (trait PC3) was the most difficult component to interpret biologically and seemed to reflect a negative interaction between species range size (and social group size) versus reproductive speed. The most distinct taxonomic clade for trait PC3 was the carnivorous marsupials *Dasyuromorphia*, who tended to show negative scores, having solitary lifestyles, small to average range sizes, and slow reproductive strategies. The fourth principal component (trait PC4) was strongly positively associated with species range size. Finally, the fifth principal component (trait PC5) clearly separated placental and non-placental mammals, with placental mammals scoring highly, one exception being the placental order of gliders *Dermodontidae*, which group with the non-placental mammals and show “marsupial-like” reproduction (Macdonald & Norris, 2006).

3.2 | Dimensions of biodiversity

Both phylogenetic and trait diversity dimensions showed strong spatial patterns in their turnover across the globe (Figure 3a and b). Phylogenetic turnover patterns were generally consistent with previous studies (Holt et al., 2013) (Figure 3a). Overall trait turnover patterns were considerably different to their phylogenetic equivalents (given that both are based on the same distributional data), with higher levels intra-continental variation and lower levels of inter-continental variation, in specific regions (Figure 3b). Ordination axes of trait turnover results were most strongly correlated with body size, litter size, population density and range size (NMDS 1, Figure 3b, Table 1), and neonatal body mass and gestation length (NMDS 2, Figure 3b, Table 1). Phylogenetic NMDS axis 1 was positively correlated with marsupial orders, as well as bats and primates, and particularly negatively correlated with *Lagomorpha*: “rabbits, hares and pikas” (Figure S7 in Appendix S1). Phylogenetic NMDS axis 2 was particularly positively correlated with Australasian marsupial orders and particularly negatively correlated with ungulates, hydraxes and the *aardvark* (Figure S7 in Appendix S1).

Mapped patterns of turnover for specific trait principal components (Figure 4, Figure S8 in Appendix S1) were not significantly correlated with overall trait turnover patterns, in all cases (Table S2 in Appendix S1). In addition, turnover patterns of specific trait principal components were frequently significantly less correlated with each other than would be expected at random (Table S2 in Appendix S1), suggesting that global patterns of trait turnover vary considerably depending on the specific trait(s) under consideration.

3.3 | Relative influence of evolutionary history and environment on trait turnover

Principal component analysis of the global environmental data reduced these data to four principal components, which accounted

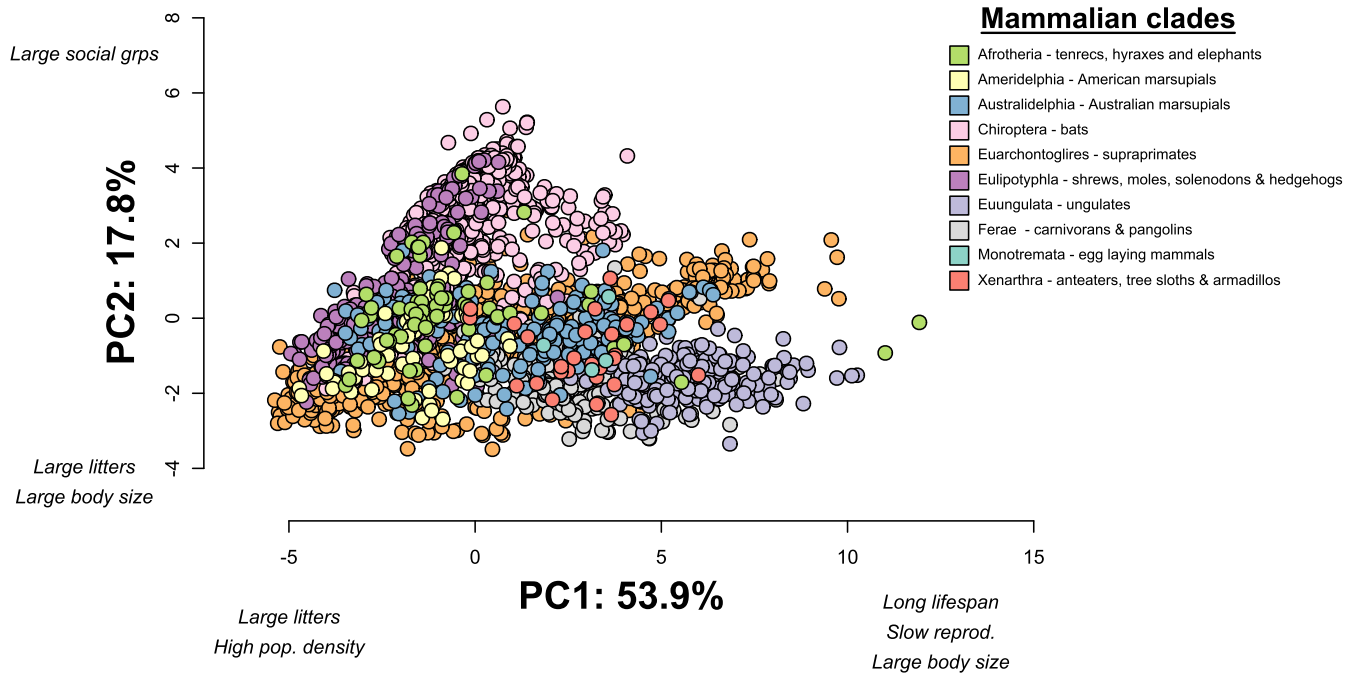


FIGURE 2 First two principal components resulting from principal component analysis for 14 continuous trait variables across 4,611 terrestrial mammal species. Percentage values represent proportion of the total variation explained by each component. Different colours represent selected higher mammalian taxonomic clades

for 91.1% of the total variation. Environmental conditions, as defined by the first two principal components (environmental PCs 1 and 2, which accounted for 55.2% and 23.8% of the total environmental variation, respectively) showed strong geographical patterns globally (Figure 3c).

A multiple regression on distance matrices (MRM) model, which predicted trait turnover based on phylogenetic turnover and environmental conditions, had an overall adjusted R^2 of 0.61, which was not significantly above null expectations ($p = .680$). However, the unique and shared contributions of the predictors all differed significantly from null expectations (Figure 5). The relatively large proportion of the variance explained by phylogenetic turnover (partial $R^2 = 0.35$) was lower than null expectations but not significantly so (Standardized Effect Score (SES) = -1.13 , $p = .260$, Figure 5, see Methods for details of SES score calculations). The unique component of the variance explained by environmental conditions and the *shared* component of the explained variance (i.e. shared between environmental distances and phylogenetic turnover) were both significantly higher than expectations (environmental turnover: partial $R^2 = 0.06$, SES = 5.01 , $p < .001$; shared component: partial $R^2 = 0.20$, SES = 10.04 , $p < .001$, Figure 5).

Equivalent results for specific trait principal components were fairly consistent with the overall patterns. For all five principal components, trait turnover was consistently more strongly associated with environmental turnover than null expectations (Figure 5, Figure S9 in Appendix S1), whereas the strength of associations with phylogenetic turnover was always close to null expectations. Some specific trait principal components (trait PC1 and trait PC4) did show

a significant positive association between phylogenetic turnover and trait turnover, but the strength of the deviation from null expectations was always considerably weaker than the corresponding association between trait turnover and environmental turnover (phylogenetic SES ranging from 1.0 to 2.0, p from .02 to .22 with environmental SES ranging from 5.4 to 58.7, p from .01 to $<.001$, Figure 5, Figure S9 in Appendix S1). The shared component of the explained variance was significantly higher than expectations for each of the specific trait principal components (SES ranging from 23.4 to 32.0, all $p < .001$, Figure 5, Figure S9 in Appendix S1).

Overall trait turnover was most closely associated with the main component of environmental turnover (environmental PC1), which distinguished tropical versus temperate climates. The primary trait principal component (fast versus slow life-history continuum) was also particularly well correlated with this environmental axis and communities with a high proportion of species that showed high values for this trait (i.e. slow reproduction/high parental care) occurred in areas with high seasonality and low temperatures. The trait PC4 (species range size) was also strongly correlated with this environmental axis, with assemblages at extreme northern latitudes tending to contain species with large geographical ranges. The trait PC2 (social group size versus litter size; which predominantly splits bats from other mammals) appeared to be negatively associated with certain environmental extremes, such that species assemblages with low values (i.e. few bats and bat-like species) occurred in areas with either extreme high seasonality or extremely dry climates/high daily temperature variation. Conversely, areas associated with communities characterized by higher values for trait PC2 seem to cover a wide range of more moderate environments.

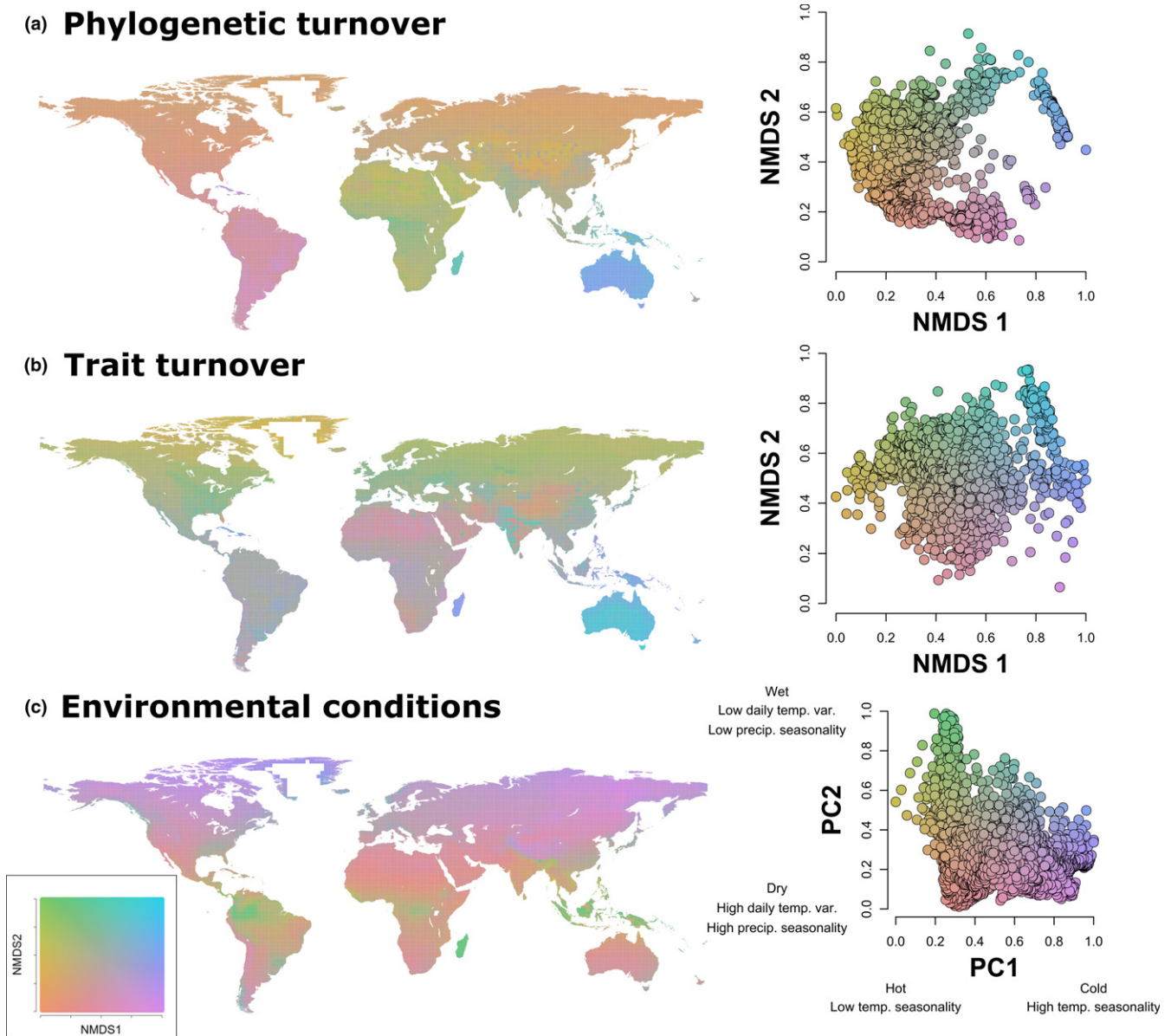


FIGURE 3 Global patterns of (a) phylogenetic turnover and (b) trait turnover across mammalian assemblages within 2° grid cells, as well as (c) environmental conditions across the same grid cells. “Turnover” refers to differences in species assemblages due to changes in composition (i.e. composition of phylogenetic lineages or phenotypic traits). Plots on the right of turnover maps show the results of NMDS ordinations on matrices of pairwise turnover comparisons between global grid cell assemblages for each of the two biodiversity dimensions, which attempt to show variation within these matrices as accurately as possible within two-dimensional space. Stress values for the NMDS ordinations are 0.20 and 0.24 for phylogenetic turnover and trait turnover, respectively; which reflect the amount of error in the correlation between pairwise distances in the original distance matrix and those calculated from the NMDS plot. The environmental data ordination is based on the first two principal components (associated with 55.2% and 23.8% of the total environmental variation, respectively) produced by a principal component analysis. All ordination points are plotted within the HCL colour space shown in the bottom left inset, and these colours are then transposed onto the maps. Therefore, locations on the maps with similar colours are similar with regard to the focal variable (i.e. phylogenetic turnover, trait turnover or environmental conditions) and the locations with more distinct colours are more distinct in respect of this variable

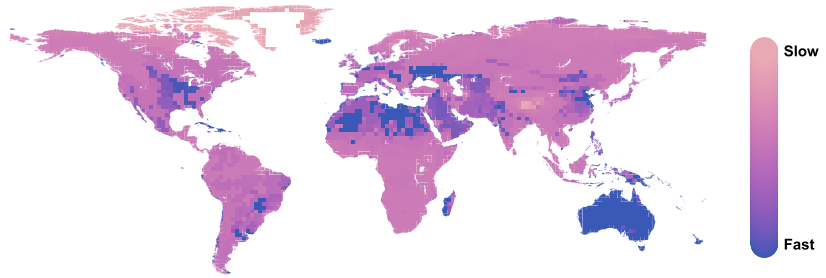
4 | DISCUSSION

A clear pattern from our results is that turnover in phylogenetic lineages between global mammalian assemblages cannot independently predict levels of trait turnover between the same assemblages. Our null model analysis revealed that the predictive power of phylogenetic turnover was no stronger than random expectations based on

observed species turnover among assemblages. Therefore, turnover in these two major biodiversity dimensions, as defined in our analyses, is decoupled within global mammal assemblages. Conversely, the predictive power of environmental conditions within these models of trait turnover was substantially, and significantly, higher than null expectations. The interaction between phylogenetic turnover and environmental variation did have considerably more predictive power



(a) PC1 - reproductive strategy



(b) PC2 - bat-like vs non bat-like

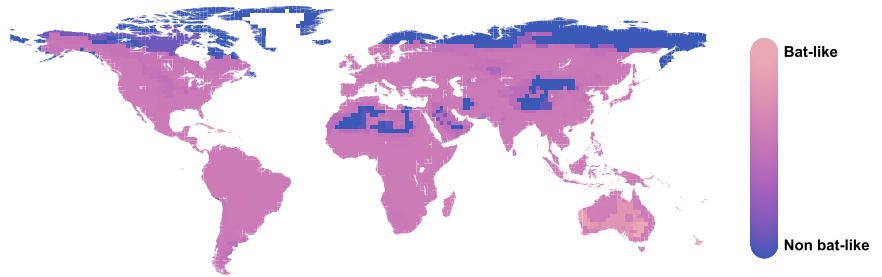


FIGURE 4 Dominant global patterns of trait turnover among mammalian assemblages, within 2° grid cells, for the first two principal components of variation of trait values among mammals. Dominant patterns produced by PCoA ordination of all possible pairwise comparisons of grid cells, with only the primary axis plotted. Headings give subjective descriptions of the variation trait PCs

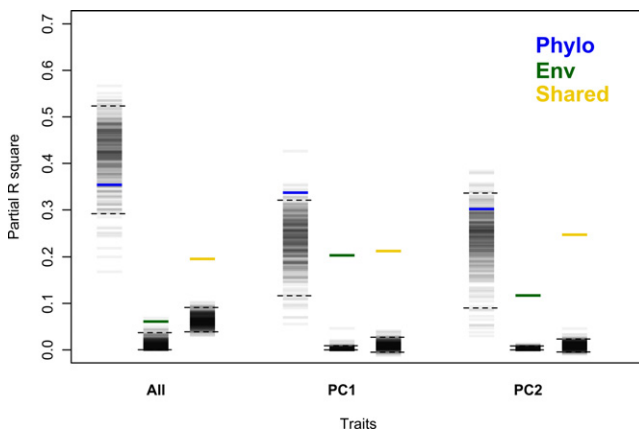


FIGURE 5 Observed and null results for variance partitioning of multiple regression on mammal assemblage trait turnover, based on overall trait turnover and on trait turnover for specific trait components. Full model contains environmental turnover and phylogenetic turnover as predictors of trait turnover (Adj. R^2 of 0.61). Coloured lines on plot show the observed unique and shared components of the total trait turnover variation explained by these predictive variables. Semi-transparent black lines reflect corresponding null values based on 1,000 null model randomizations. Dotted lines represent the 95% quantiles of null values

than expected, suggesting clade-specific environmental adaptation. Patterns of turnover for specific trait components were idiosyncratic, showing no sign of a general pattern across traits. Nevertheless, trait-specific associations with environmental turnover were consistently higher than random expectations, suggesting a pervasive influence of ecological adaptation on the trait characteristics of mammalian assemblages globally.

There is little evidence from our results of a significant association between phylogenetic turnover and trait turnover. This result is

consistent with a recent global analysis of phylogenetic trophic niche conservatism in mammals, which found limited general evidence of such phylogenetic conservatism (Olalla-Tárraga, González-Suárez, Bernardo-Madrid, Revilla, & Villalobos, 2017). Mammalian behavioural traits have long been shown to be evolutionarily labile (Gittleman, Anderson, Kot, & Luh, 1996); more recently, morphological traits such as body mass have been shown to evolve at rates that are fairly independent of the phylogeny (Venditti, Meade, & Pagel, 2011; Pant, Goswami, & Finarelli, 2014; but see Huang, Stephens, & Gittleman, 2012). There is no evidence that phylogenetic-based biogeographical divisions (Holt et al., 2013), which indicate isolation of even mobile mammal groups, such as bats (Peixoto, Braga, Cianciaruso, Diniz-Filho, & Brito, 2014), have had a major influence on patterns of trait turnover across mammal assemblages. Possibly rapid evolution of species-level traits (relative to the slow evolution of phylogenetic clades), in response to environmental conditions, has significantly influenced global trait diversity patterns. While the total variance in trait turnover explained by the environment was fairly weak, the fact that it was considerably higher than null expectations indicates a role for environmentally driven trait adaptation.

A large, and significant, proportion of variation in trait turnover was attributed to the shared environment/phylogenetic turnover component. This result suggests, as a possible mechanism, that mammalian evolutionary lineages have adapted to specific environments and environmental filtering influences the composition of species assemblages. An important caveat is that this shared component of the explained variation does not necessarily represent an interaction between these two explanatory variables; it is simply the proportion of explained variation that cannot be disentangled between them. The alternative explanation for this result is that the explained variance is primarily driven by environmental turnover and is only coincidentally associated with phylogenetic turnover. This explanation



seems plausible given the weak performance of the unique contribution of phylogenetic turnover; however, since the shared environmental/phylogenetic turnover component represents the strongest performing predictive variable according to our results, the potential signature of clade-specific adaptation should not be discounted. In addition, other potential factors, not explicitly explored in our analysis, could have contributed to explain variation in trait turnover. For instance, past climate variation (e.g. Sandel et al., 2011), past migratory events (e.g. Great American Biotic Interchange—Morales-Castilla, Olalla-Tárraga, Purvis, Hawkins, & Rodriguez, 2012) and biotic interactions, including human-driven extinctions, have contributed in shaping global mammal diversity patterns (Faurby & Svenning, 2015; Rapacciuolo et al., In Press). These factors could have influenced trait diversity in different ways. For example, human-driven extinctions could have disproportionately affected species with larger body sizes (Rapacciuolo et al., In Press). Migratory events and past climate change may have reshaped the trait space of assemblages erasing (or diluting) the signal of evolutionary relationships and inflating the effects of environmental variations (Morales-Castilla et al., 2012). Adding this information into future analyses could improve our understanding of extant mammalian trait turnover.

Phylogenetic and trait turnover global maps showed the Northern and Southern Hemispheres to be distinct from each other. The Australasian and Madagascan regions had particularly high distinctness for both dimensions, albeit slightly less so for trait turnover. Marsupials that show a very distinct reproductive strategy and bats that have a fast life history and live in large groups drive patterns in the Australasian region. Patterns in the Madagascan region are driven by groups with fast reproductive strategies and small range sizes, such as tenrecs and lemurs (Dewar & Richard, 2007). Assemblage trait composition showed somewhat higher within-region turnover than its phylogenetic counterpart, for example, within the Nearctic. The southeastern areas of the Nearctic had similar trait composition to the Western Palearctic, and the low diversity assemblages of the northern Nearctic had relatively unique trait characteristics. In the Southern Hemisphere, the Afro-tropical, Neotropical and Oriental regions had assemblages that were more similar in their trait composition than might be expected based on phylogenetic patterns. The Neotropics were not particularly distinct in terms of traits (and redundant with e.g. Afrotropics), but highly phylogenetically distinct (e.g. South American marsupials or xenarthans). Overall, the global trait map shown by this study is highly distinct in comparison to previous global biodiversity maps.

At local to regional scales, there has been equivocal evidence for a coupling of trait and phylogenetic biodiversity dimensions, with more recent studies pointing to a general lack of correspondence between trait and phylogenetic diversity, in particular for alpha diversity, i.e. total amount of diversity shown by a biodiversity dimension within a location (Carboni et al., 2014; Liu et al., 2014). A decoupling of phylogenetic and trait alpha diversity has also been shown on a global scale (Oliveira et al., 2016; Safi et al., 2011). Decoupling of these aspects of biological turnover would contradict the hypothesis that phylogenetic trait conservatism drives the global

patterns of assemblage trait characteristics (e.g. Swenson and Erickson, et al., 2012 for tropical and temperate tree communities). Such studies suggest that abiotic filtering influences beta diversity in traits, but not in phylogeny (Swenson and Erickson, et al., 2012), at local to regional scales. In contrast, trait and phylogenetic beta diversity corresponded more closely in French bird communities (Meynard et al., 2011), and many Andean hummingbird communities (Weinstein et al., 2014). However, in general, environmental factors tend to be the clearest predictor of trait beta-diversity patterns, and our results for global mammalian turnover are consistent with the general picture emerging from more localized beta-diversity studies.

Comparisons among studies are complicated by inconsistent focal traits across studies. Trait diversity is often quantified using a set of species traits that influence how an organism interacts with its environment (Petchey & Gaston, 2002). Although some studies emphasize traits that are relevant to ecosystem function (Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Suding et al., 2008), many other studies (including this one) focus on phenotypic diversity in general, irrespective of implications for ecosystems processes. We considered traits that represent different aspects of mammalian biology and life history, using the best available information on mammalian biology (Davidson et al., 2009; Jones et al., 2009). Most of these traits, perhaps all, are much more closely related to evolution via natural selection, rather than sexual selection, and it would be interesting to see how results for sexually selected traits might compare. Such work would likely have to be more narrowly taxonomically focused in order to identify homologous sexually selected traits across species. Given the high level of phenotypic variation among terrestrial mammals, it could be expected that global patterns might depend, in part, on the traits under consideration and indeed we found little, if any, consistency among the specific traits we examined.

The strongest trait/environment association we found was between life-history speed (fast versus slow life-history continuum) and tropical versus temperate climates. Our results show that mammal communities in regions with high seasonality and lower temperatures tend to have a higher proportion of species in the slow portion of the life-history spectrum. This pattern may also be driven by the large diversity of bats and rodents (fast life history) in tropical regions. We also found a strong correlation between range size and the environmental axis containing temperature. Associations between environmental factors and range size, which were independent of other species traits, have been identified in terrestrial vertebrates (Li et al., 2016) and range size relationships among higher mammal taxa have been shown to be consistent through geological time (DeSantis, Tracy, Koontz, Roseberry, & Velasco, 2012; Hadly, Spaeth, & Li, 2009). Our range size results show that assemblages at northern latitudes contain species with larger geographical ranges, a pattern that is consistent with Rapoport's rule (Rapoport, 1975; Stevens, 1989). Interestingly, this pattern was not evident within the Southern Hemisphere, which has much less land area at high latitudes. Hemispheric (North/South) asymmetries in biodiversity have been discussed and related to environmental factors (Chown, Sinclair, Leinaas, & Gaston, 2004; Gaston, 1996). Range size results will

have been influenced by the inclusion of “small island endemic” species and high values for our range size principal component were seen in the archipelagos of the Indo-Pacific. However, the consistency with Rapoport's rule in the Northern Hemisphere is clear within continental regions.

We found that patterns of global trait turnover are not a general trend across all traits. In fact, our results show that trait turnover is a summary of unique patterns shown by specific trait components. However, for all five of the trait principal components that we considered, trait turnover was significantly associated with environmental turnover and showed little significant association with phylogenetic turnover, except when covarying with environmental turnover. These results suggest an influence of abiotic environmental factors on the trait characteristics of species assemblages, and that ecological adaptation is an important factor for determining global trait turnover.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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