Environmental factors explain the spatial mismatches between species
richness and phylogenetic diversity of terrestrial mammals

Running title: Environmental drivers of mammalian diversity

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Abstract

Aim Explore the spatial variation of the relationships between species richness (SR), phylogenetic diversity (PD) and environmental factors to infer the possible mechanisms underlying patterns of diversity in different regions of the globe.

Location Global

Time period Present day

Major taxa studied Terrestrial mammals

Methods We used a hexagonal grid to map SR and PD of mammals and four environmental factors (temperature, productivity, elevation and climate-change velocity since the Last Glacial Maximum). We related those variables through direct and indirect pathways using a novel combination of Path Analysis and Geographically Weighted Regression to account for spatial non-stationarity of path coefficients.

Results SR, PD and environmental factors relate differently across the geographic space, with most relationships varying in both, magnitude and direction. Species richness is associated with lower phylogenetic diversity in much of the tropics and in the Americas, which reflects the tropical origin and the recent diversification of some mammalian clades in these regions. Environmental effects on PD are predominantly mediated by their effects on SR. But once richness is controlled for, the relationships between environmental factors and PD (i.e. PD_{SR}) highlight environmentally driven changes in species composition. Environmental- PD_{SR} relationships suggest that the relative importance of different mechanisms driving biodiversity shifts spatially. Across most of the globe, temperature and productivity are the strongest predictors of richness, while PD_{SR} is best predicted by temperature.

Main conclusions Richness explains most spatial variation in PD, but both dimensions of biodiversity respond differently to environmental conditions across the globe, as

indicated by the spatial mismatches in the relationships between environmental factors and these two types of diversity. We show that accounting for spatial non-stationarity and environmental effects on PD while controlling for richness uncovers a more complex scenario of drivers of biodiversity than previously observed.

Key words: biodiversity measures, dimensions of biodiversity, geographically weighted regression, Last Glacial Maximum, latitudinal gradient, Mammalia, non-stationarity, path analysis, spatial patterns, structural equation modeling.

Introduction

Biodiversity encompasses multiple dimensions, such as phylogenetic and functional diversity, and species richness, which have varying degrees of spatial co-variation (Stevens & Tello, 2018). Environmental factors correlate differently with each dimension of biodiversity and this variation offers opportunities to explore the multiple mechanisms that underlie different biodiversity dimensions (Safi *et al.*, 2011; Oliveira *et al.*, 2016). However, most studies exploring environmental correlates of diversity have assumed that relationships are consistent across regions (e.g., a single regression is run), when they actually might vary considerable (Casseiro *et al.*, 2007; Gouveia *et al.*, 2013). The standard assumption of spatial stationarity may lead to erroneous conclusions about the magnitude of different relationships. For example, spatial stationary analyses may deem a variable of little or nil effect if its direction shifts regionally from positive to negative (Fotheringham *et al.*, 2002). Here we relaxed the stationarity assumption to explore the spatial variation of the relationships between environment, species richness and phylogenetic diversity of terrestrial mammals.

Mammals have a clear latitudinal gradient of higher species richness (SR) and phylogenetic diversity (PD) in the tropics, but the spatial patterns of each dimension are not always congruent, with some areas having more, or less, PD than expected based on richness alone (Davies & Buckley, 2011). Spatially structured differences between SR and PD reflects differences in species composition, which are likely influenced by environmentally-driven ecological and evolutionary processes (Davies *et al.*, 2007; Safi *et al.*, 2011; Penone *et al.*, 2016). Thus, comparing how SR and PD relate to each other and to environmental factors offers clues about the underlying mechanisms behind diversity patterns (Davies *et al.*, 2007). Path analysis (or Structural Equation Modeling in general) offers a way to explore the complex interactions between assemblage's

richness, phylogenetic diversity and environment, as it can disentangle the direct and indirect effects on a variable while controlling for covariates (Grace *et al.*, 2010). We designed a path model that is not only able to relate SR and PD (Fig. 1, path *i*) and to identify environmental factors responsible for promoting higher or lower PD and SR, but also to separate how much of the total environmental effect on phylogenetic diversity is due to (1) changes in species richness (Fig. 1, paths *a-d* mediated by path *i*) and (2) changes in species composition (i.e., PD controlled for richness; Fig. 1, paths *e-h*). The relationship between environmental factors and PD controlled for richness (hereafter, PD_{SR}) should offer insights on the relative influence of speciation and extinction in the generation of biodiversity patterns (Davies *et al.*, 2007).

Figure 1 - Path model of hypothesized relationships among environmental factors, species richness (SR) and phylogenetic diversity (PD) of terrestrial mammals. Numbers indicate mean and standard deviation of standardized path coefficients across the entire globe.

In assemblages composed of closely related species, such as those resulting from rapid speciation, selective extinction of older lineages, or reduced lineages interchange, individual species contribute to a small fraction of the phylogenetic diversity (Cardillo, 2011; Tucker & Cadotte, 2013). In contrast, in assemblages composed of distantly related species, such as those with lower diversification rates and frequent interchange of distantly related species, each additional species yields a greater relative increase in phylogenetic diversity (Cardillo, 2011; Tucker & Cadotte, 2013). In the tropics, phylogenetic diversity (PD) should be lower than expected for the species richness (SR) because diversification rate seems to be higher (Rolland *et al.*, 2014) and mammals species tend to conserve tropical niches (Cooper *et al.*, 2011; Olalla-Tárraga *et al.*, 2011). Conversely, the relationship between PD-SR should be stronger (Fig.1, path *i*) in regions that harbor high diversity of early diverging mammalian lineages, such as in Africa when compared to the Neotropics (Davies & Buckley, 2012). Thus, mapping the strength of the PD-SR relationship highlights ecological and evolutionary processes that influence phylogenetic composition of assemblages.

Mammalian richness is strongly and positively related to productivity (Davies *et al.*, 2011; Oliveira *et al.*, 2016), and this relationship has been maintained for millions of years (Fritz *et al.*, 2016). Areas of higher productivity support larger population sizes, potentially reducing extinction and increasing speciation rates, which culminates in higher species richness (Coelho *et al.*, 2018; Storch *et al.*, 2018). Thus, productivity should relate positively to richness across the entire globe (Fig. 1, path *a*), but the magnitude of such relationship might vary across the globe (Gouveia *et al.*, 2013; Alves *et al.*, 2018). The relationship between AET and phylogenetic diversity when holding richness constant (i.e., PD_{SR}; Fig. 1, path *e*) will vary in direction depending on the relative importance of AET in reducing extinction and increasing speciation rates. A

humped relationship between PD_{SR} and AET observed in global parrots was interpreted as a result of decreasing extinction when AET is low and increasing speciation when AET is high (Davies *et al.*, 2007). Therefore, we expect the AET– PD_{SR} relationship to vary in both magnitude and direction across the globe, being positive where AET it is low and negative where it is high.

Mammalian richness also positively relates to temperature (Belmaker & Jetz, 2015), which is hypothesized to be the result of an acceleration in metabolic, mutation and speciation rates (Rohde, 1992; Brown *et al.*, 2004) or of most lineages having a tropical origin and conserved niches (Wiens & Donoghue, 2004). In both cases, the association between temperature and richness (Fig. 1, path *b*) should be consistently positive across the globe and any shifts in the magnitude of the relationship might follow a latitudinal gradient similar to that of temperature itself. However, the relationship between PD_{SR} and temperature (Fig. 1, path *f*) will vary depending on the mechanism at play, and there is no clear expectation of which mechanisms predominate in a particular region. If acceleration in speciation rates predominates, then PD_{SR} should relate negatively with temperature. On the contrary, a positive relationship between temperature and PD_{SR} is expected when the main effect of temperature on diversity is associated with constrained thermal tolerance to colder environments and traits are conserved, as has being noticed in mammals (Olalla-Tárraga *et al.*, 2011).

Spatially structured environmental relationships with SR and PD_{SR} are also expected in mountainous regions and in areas of past climatic instability. Mountains are cradles of biodiversity because they promote higher speciation rates by range fragmentation and lower extinction rates by acting as climatic refugia (Fjeldså *et al.*, 2011; Rangel *et al.*, 2018). Rapid speciation adds short terminal branches to the phylogenetic tree, and therefore, it is expected that spatial analysis will detect a clear

pattern of positive relationship between elevation and richness in mountainous regions (Fig. 1, path *d*). However, the relationship between elevation and PD_{SR} (Fig. 1, path *h*) should be negative if mountains are acting more as species cradles and positive if their main effect is on offering refugia and buffering extinction (Davies *et al.*, 2007; Voskamp *et al.*, 2017). Climatic instability since the Last Glacial Maximum (LGM) is also expected to have left imprints on SR and PD_{SR} given that it triggered extinction and range contractions, leading to reductions in species richness (Fig. 1, path *c*) (Sandel *et al.*, 2011; Svenning *et al.*, 2015). The effect of climate-change velocity on PD_{SR} depends on which lineages persisted and recolonized the region (Fig. 1, path *g*). Thus, climate-change velocity should relate positively with PD_{SR} where more distantly related species persisted and/or recolonized the region, but negatively where these species are more closely related (e.g. phylogenetic conservatism of traits that enable species to survive or recolonize) (Svenning *et al.*, 2015). A spatially explicit analysis may capture these different imprints of past climatic change on biodiversity, especially where changes were more extreme, such as in the formerly glaciated areas in North America and Europe (Hortal *et al.*, 2011; Gouveia *et al.*, 2013).

Materials and methods

Spatial grid

We built a geodesic dome from an icosahedron, triangulating its faces to compose a global hexagonal grid. Our grid is suitable for spatial analyses of global datasets because it minimizes geographic distortions in distances, shapes and areas caused by map projection (Sahr *et al.*, 2003). The 20,163 *quasi* equal-area cells in our hexagonal grid span on average 6,917.84 ($\pm$ 858.62 s.d.) km². Most importantly, variation in grid cell area does not correlate with latitude.

Diversity measures

We mapped the geographic distribution of terrestrial mammals by recording their presence in each grid cell. We used SAM (*Spatial Analysis in Macroecology*, Rangel *et al.*, 2006, 2010) to calculate the overlap between species range polygons (IUCN, 2017) and grid cells. Species richness map was estimated by the total count of species recorded in each grid cell. We removed 392 cells from analysis because they had less than 5 species.

We used mammal phylogenetic trees provided by Kuhn *et al.* (2011), which solved the polytomies that comprise approximately 50% of the most complete mammal super-tree (Bininda-Emonds *et al.*, 2007; Fritz *et al.*, 2009). We used public databases of taxonomic synonyms to match the 5,020 species on the phylogenetic trees to the species in the IUCN's geographic distribution database, resulting in a final dataset of 4,751 mammal species with phylogenetic and geographic data. We mapped phylogenetic diversity by summing the branch lengths connecting all species present in each cell (Faith, 1992).

Environmental predictors

To incorporate environmental productivity, temperature, elevation and climatic stability into our analyses we compiled, respectively, the following variables: (1) mean actual evapotranspiration (AET; Trabucco & Zomer, 2010), (2) mean annual temperature (Fick & Hijmans, 2017), (3) mean elevation (USGS, 1996), and (4) climate-change velocity since the Last Glacial Maximum, which is a proxy of the speed at which species must shift their ranges to track a given changing climate (Sandel *et al.*, 2011). Mean elevation was chosen instead of a measure of elevation heterogeneity to increase the chances of detecting the effect of mountains on biodiversity when using a spatial analysis based on circular kernels (see the *statistical analysis* subsection). We rescaled these four

environmental variables to our hexagonal grid using the “raster” package in R software (Hijmans, 2016), and excluded from the final dataset the cells missing environmental information, resulting in a final dataset of 17,151 cells.

Statistical analysis

We designed a path model according to a hypothesis of how the environmental factors likely influence richness and phylogenetic diversity, as well as how PD is influenced by SR (Fig. 1). The path model can assess (1) the direct effect of each variable on richness and PD, while controlling for the effect of the remaining variables (paths $a-i$), (2) the indirect effect of the environment on PD given its influence on richness (paths $a-d$ multiplied by path i), and (3) the total environmental effect on PD (i.e., sum of all direct and indirect path coefficients connecting environmental factors to PD). We Z-transformed all variables to allow direct comparison among estimated path coefficients, as in partial regression coefficients.

Standard path analysis (and Structural Equation Modeling - SEM) of spatially distributed samples assumes that the relationship among variables is the same across space, which is unrealistic for very complex historical phenomena at large spatial scales (Hortal *et al.*, 2011; Gouveia *et al.*, 2013). To relax this assumption, we developed a Geographically Weighed Path Analysis (GWPath), which allows path coefficients to vary regionally (code available in the supplementary material). Contrary to the traditional path analysis that uses ordinary least square regression, GWPath uses Geographically Weighted Regressions (GWR) to fit the regressions that compose the path model. Thus, the path analysis was repeated for each grid cell, around which a distance-based Gaussian weighting function (kernel) was set, to assign greater weight to nearby cells than distant ones (Fotheringham *et al.*, 2002; Fig. S1). We implemented

GWPath by using the “gwr” function of “spgwr” R package (Bivand & Yu, 2017) within the framework of a path analysis.

The challenge of Geographically Weighted methods is to parameterize the bandwidth (radius) of the spatial kernel function. On one hand, if the bandwidth is too large, the analysis converges back to the spatial stationarity assumption, preventing variation of estimated coefficients. On the other hand, if the bandwidth is too narrow, the model overfits residual variation and the coefficients shift drastically even among nearby cells (Fotheringham *et al.*, 2002), leading to the formation of islands of coefficients that are easily detectable by visual inspection. We evaluated bandwidths ranging from 500 to 3,000 km, at 100 km intervals, visually inspecting spatial patterns in estimated coefficients for signs of artifacts caused by overfitting. We found the bandwidth of 1,000 km to be ideal for capturing large-scale patterns in coefficient variation while avoiding overfitting, as found in other studies using GWR on environmental drivers of large-scale biodiversity data (Davies *et al.*, 2011; Ficetola *et al.*, 2017).

Phylogenetic uncertainty

To account for uncertainty in the evolutionary history of mammals we replicated the GWPath analyses 1,000 times, each time using the phylogenetic diversity calculated from a differently randomly sampled phylogeny from a posterior distribution of 10,000 fully resolved trees (Kuhn *et al.*, 2011). We calculated mean and standard deviation of each path coefficient among replicates, which capture, respectively, the average effect and uncertainty in coefficient estimates due to phylogenetic uncertainty (Rangel *et al.*, 2015). The ratio between the mean and standard error of estimated coefficients follows Student’s *t*-distribution, so that $t > |1.96|$ have statistically large effects relative to the magnitude of phylogenetic uncertainty.

Results

Phylogenetic diversity of mammal assemblages is largely determined by the number of species it contains (SR), but the magnitude of the relationship between these two dimensions of biodiversity shifts across the geographic space (standardized path coefficients averaged across space 0.95 ± 0.17 , path *i* in Fig. 1) because of how phylogenetically related the species are. As predicted, changes in SR are associated with smaller changes on phylogenetic diversity (PD) in the tropics, ranging from 0.69 in South America, Central Africa and eastern Asia to 1.59 in the Sahara Desert, Arabian Peninsula and northern Eurasia (Fig. 2). Central North America is an exception to the latitudinal pattern, as its SR explains less of its PD.

Figure 2 - Standardized path coefficients estimating the regional relationship between species richness (SR) and phylogenetic diversity (PD) of terrestrial mammals (path *i* in Figure 1).

Spatially varying relationships are observed for all tested paths relating environmental factors to richness and phylogenetic diversity (Figs. 1 and 3).

Unsurprisingly, much of how the environment relates to PD (i.e., total effects) is a consequence of how it relates to richness (Figs. S2-S4), because the PD of an assemblage is largely determined by the number of species it contains (Figs. 1 and 2). However, when richness is held constant, there are considerable differences in the way the environment relates to PD (i.e., PD_{SR} ; paths *e* to *h* in Fig. 1) and to SR (paths *a* to *d* in Fig. 1), highlighting environmentally driven changes in species composition. Our results are robust to phylogenetic uncertainty, as most of the uncertainty in estimated path coefficients (i.e., cells with high standard errors) are in regions of small effect sizes (grey regions in Fig. 3 and white regions in Fig. 4).

Figure 3 - Map of standardized path coefficients of environmental determinants of terrestrial mammalian species richness (first column, *a* to *d*), and phylogenetic diversity controlled for richness (second column, *e* to *h*). Panels labels correspond paths labels in Figure 1. Gray areas indicate large phylogenetic uncertainty, where the direction of the coefficient could not be inferred accurately.

The way environment relates to richness and to PD_{SR} vary greatly over space, not only in magnitude but also in direction (Figs. 1 and 3). Less variation in the direction of the relationships is found for how richness relates to AET (+) and climate-change velocity (-), and for PD_{SR} and temperature (+) (Fig. 3). In general, PD_{SR} has more spatially varying relationships with environmental factors than does richness (Fig. 3), suggesting that environmental influences on diversification might have a more complex spatial pattern than previously anticipated based solely on richness patterns.

Temperature and AET are mostly positively associated with richness, but unlike our prediction, there are regions where both measures of energy relate negatively with richness (Fig. 3a and b). A notable exception to the positive relationships between temperature and richness is in the Rift Valley region (Fig. 3b), just where mammalian richness peaks. As expected, the relationships between AET and temperature with PD_{SR} shifts in direction (Fig. 3e and f). But contrary to our prediction, there is no clear pattern of how AET relates to PD_{SR} given the amount of AET, as there are positive and negative relationships in highly productive areas, such as the tropical region of Africa and South America, respectively (Fig. 3e). The strongest effects of AET are concentrated in the energy-limited Sahara Desert, where it is associated with an increase in richness and decrease in PD_{SR}, whereas the strongest effects of temperature are

concentrated in South America for richness (Fig. 3b) and on sub-Saharan regions for PD_{SR} (Fig. 3f).

Mountainous areas do not present a marked difference in coefficients of the relationship between elevation, richness and PD_{SR} as we predicted. The closest to our expectations are the negative coefficients between elevation and PD_{SR} in the Himalayan region (Fig. 3h), consistent with the hypothesis that mountains trigger rapid speciation events. However, contrary to our expectations, elevation relates negatively with richness in this area (Fig. 3d). Climate-change velocity is associated with decreases in mammalian richness across most of the globe, except in Madagascar and parts of North America and Europe where climate-change velocity was greatest (Fig. 3c). In these areas, climate-change velocity correlates positively with PD_{SR} (Fig. 3g). However, in general, the PD_{SR}-climate change velocity relationships vary considerably in direction across the globe without a clear pattern (Fig. 3g).

Among the environmental factors being considered, mammalian richness is most strongly influenced by AET and temperature across most of the globe, with temperature playing a more important role in most of the New World and AET being more important in the Old World (Fig. 4a). Temperature is the environmental factor that explains most spatial variation of PD_{SR} over the globe (Fig. 4b). Small differences on total environmental effects on phylogenetic diversity and on richness arise where SR is a weaker predictor of PD – much of the tropics and North America (Fig. 2) - and where environmental effects on PD_{SR} are strong (Fig. 3). Thus, when considering total environmental effects on PD, temperature becomes more important in South America and in central Africa, while climate-change velocity is more important in parts of Asia, Madagascar and central Africa (Fig. 4c).

Figure 4 - Categorical maps showing the strongest environmental correlates of terrestrial mammal (a) species richness (SR) and (b) phylogenetic diversity (PD), controlling for indirect effects via SR. (c) Depicts the total effects on PD when controlling and accounting for SR. Phylogenetic uncertainty prevents inference over white regions.

Discussion

Our spatial path analysis confirmed that while much of the relationship between environmental factors and phylogenetic diversity (PD) can be explained by species richness (SR), once SR is held constant, the environmental-PD_{SR} relationships offer insights on the relative importance of speciation and extinction on the phylogenetic composition of the assemblages. All the relationships tested in our path model shift across the geographic space in a more complex pattern that has been revealed by regional analyses (Safi *et al.*, 2011), and suggests that there are spatial changes in the relative importance of the different mechanisms driving mammalian diversity. Models may fail to identify relevant environmental effects on biodiversity if they have a strong effect in only a specific region or only via indirect paths (Hortal *et al.*, 2011; Calatayud

et al., 2016) and if the direction of the relationship (and potentially, the mechanism) changes across the globe (Fotheringham *et al.*, 2002; Gouveia *et al.*, 2013). Our analytical framework, which combines the path analysis and GWR, provides a new approach for exploring spatially complex phenomena. And because path analysis is a special case of Structured Equation Modeling, the framework can be further expanded to include geographically structured latent variables.

Species richness, phylogenetic diversity and their relationship

Phylogenetic diversity (PD) of an assemblage is strongly determined by species richness (SR), but the relative change in PD between two regions is not always consistent with the relative change in richness between the same two regions (Tucker & Cadotte, 2013). Here we found that, at the regional scale, after controlling for environmental factors, tropical regions harbor relatively less mammalian PD than expected for SR. This “deficit” of tropical PD indicates that tropical regions host more closely related species than temperate regions. A notable exception is North America, which also has less PD than expected. The relatively smaller coefficient values of the PD-SR relationship in the tropics is consistent with the proposition that a substantial proportion of tropical mammalian biota has originated *in situ* (Rolland *et al.*, 2014; Marin & Hedges, 2016). Our results also support the hypothesis that diversification is faster in the tropics, which might be a consequence of multiple non-mutually exclusive mechanisms, such as area effects, time for speciation, stronger biotic interactions or increased mutation rates (reviewed in Mittelbach *et al.*, 2007). However, there is still much controversy about latitudinal variation in the rates of diversification. Studies of mammals have found all possible results: greater diversification in the tropics (Purvis *et al.*, 2011; Rolland *et al.*,

2014; Machac & Graham, 2017), absence of latitudinal differences (Soria-Carrasco & Castresana, 2012) and lower diversification in the tropics (Weir & Schluter, 2007).

The smaller PD-SR coefficients we observe in the tropics may also be related to species richness because adding a random species to a species-rich assemblage should promote a smaller increment to the assemblage's PD than adding the same species to a species-poor assemblage. In essence, there is a higher probability that the new species is more closely related to one of the species in the rich assemblage than to one of the species in the poor assemblage often resulting in a non-linear and asymptotic relationship between PD and SR at large spatial scales. However, the non-linearity problem is reduced in our spatial analysis because the regressions are performed at the regional scale, where there is limited variation in species richness (Fig. S1). Nonetheless, some non-linearity could persist, and the PD-SR coefficients should be interpreted with caution.

Richness accounts for less PD in the New World than in the Old World, in line with our expectations, which reflects the fact that the American mammalian fauna was strongly impacted by more recent events, such as the megafaunal extinction during the Quaternary and the Great American Biotic Interchange that followed the formation of the Isthmus of Panama 2.7 Ma ago (Webb, 2006; Barnosky & Lindsey, 2010). The faunal interchange between North and South America triggered the explosive radiation of Canidae, Cervidae, Mustelidae and Muridae families (Webb, 2006) that may explain why richness is associated with lower phylogenetic diversity in the Americas than in the Old World, where many lineages, especially those in the African continent, are the result of early and gradual diversification (Davies & Buckley, 2012; Marin & Hedges, 2016). The highest coefficients of the PD-SR relationship were found in the Sahara and Arabian deserts and in high-latitude Eurasia, suggesting the occurrence of species with

more dissimilar evolutionary histories, consistent with the observation that mammalian species tend to co-occur with phylogenetically distantly related species in these areas (Villalobos *et al.*, 2017).

Environmental correlates of species richness and phylogenetic diversity

Environmental conditions relate differently to assemblages' richness and phylogenetic diversity controlled by richness (PD_{SR}) across the space, varying in direction and magnitude, and supporting the idea that spatial mismatches between SR and PD are at least partially governed by environmentally-driven ecological and evolutionary processes (Davies *et al.*, 2007; Voskamp *et al.*, 2017). We found that AET and temperature relate positively with mammalian richness in most places, consistent with the hypotheses that energy contributes to the generation and maintenance of species (Evans *et al.*, 2005). The species-energy relationship is one of the strongest associations known in ecology and there are many possible mechanisms proposed to explain it, such as tolerance limits, available niches, metabolic rates and amount of energy flowing through food webs (Evans *et al.*, 2005); disentangling the importance of these mechanisms remains a challenge.

We found higher temperatures to be associated with less phylogenetically diverse assemblages in some tropical areas, as would be expected if the main effect of temperature was an acceleration in metabolic and mutation rates that culminates in faster rates of speciation (Rohde, 1992; Brown *et al.*, 2004). However, in most of the globe we found that higher temperatures are mainly associated with assemblages that are phylogenetically more diverse. Recent studies have found a conflicting effect of temperature on the diversification rates of mammals (Belmaker & Jetz, 2015; Marin *et al.*, 2018), suggesting that either temperature is not the best measure of ambient energy

and other measures - such as solar radiation - should be considered (Clarke & Gaston, 2006), or that other mechanism may connect temperature to high richness. One possible alternative is that most clades originated in the tropics and only a few groups were able to adapt to colder environments (Wiens & Donoghue, 2004), thus explaining why lower temperatures are associated with less phylogenetic diverse assemblages. These results are supported by the evidence of tropical niche conservatism in mammals (Cooper *et al.*, 2011; Olalla-Tárraga *et al.*, 2011) and the positive association between temperature and clade age (Marin *et al.*, 2018).

Productive energy, here measured as AET, is considered to drive mammalian richness by supporting more resources and individuals (Wright, 1983), instead of by offering greater diversity of ecological niches (Oliveira *et al.*, 2016). The greater number of individuals potentially reduces extinction and accelerates speciation rates, leading to higher diversification rates and ultimately, higher species richness (Brown, 1981; Coelho *et al.*, 2018), as we found to be the case across most of the globe. The relative importance of productivity on speciation and extinction rates seems to change across the geographic space, given that the relationship between AET and PD_{SR} shift in direction across the geographic space, as found for parrots (Davies *et al.*, 2007). In much of North America and Eurasia, higher AET is associated with more phylogenetically diverse assemblages, suggesting that the main role of productivity in these regions is associated with the reduction in extinction rates. On the contrary, negative AET-PD_{SR} relationships were found in regions with limited productivity, such as the Sahara Desert and Saudi Arabia, and in highly productive areas, such as tropical South America, suggesting a higher relative importance of productivity in driving faster speciation rates. Thus, the relative importance of AET in driving rates of speciation and extinction does not seem to be linked to the amount of AET on the region, as previously

hypothesized (Davies *et al.*, 2007). Instead, spatially structured relationships between AET and diversity may reflect historical differences associated with pool-specific or clade-specific adaptations to environmental gradients, given that the effect of AET on mammalian diversification rates varies depending on the taxa and on age of the lineages (Oliveira *et al.*, 2016; Machac *et al.*, 2017), both of which are spatially structured (Davies & Buckley, 2011; Hawkins *et al.*, 2012).

Climate-change velocity has left considerable imprints on mammalian richness and PD_{SR}, as expected giving that past climatic instability is associated with local extinctions and range shifts (Davies *et al.*, 2009; Hortal *et al.*, 2011). Species richness decreases with climate-change velocity across most of the globe, consistent with what has been observed for multiple taxonomic groups (Svenning *et al.*, 2015). In northern North America and Europe, where change since the LGM has been strongest, higher velocity of climate-change is associated with increases in both, species richness and PD_{SR}, suggesting that phylogenetically distant lineages are recolonizing areas that were covered with ice during the last glaciation. This finding contrasts with the pattern observed with Scarabaeinae dung beetles (Hortal *et al.*, 2011) and to what would be expected given that cold tolerance is phylogenetically conserved in mammals (Olalla-Tárraga *et al.*, 2011). Increases in phylogenetically distant mammal species where climate-change velocity was greatest might be associated with the colonization by highly vagile species belonging to different clades (Torres-Romero *et al.*, 2017). Unexpectedly, climate-change velocity left strong imprints in the geographical patterns of SR and PD_{SR} in areas that have not experienced strong climatic changes since the LGM, as previously found to be the case for amphibian richness (Gouveia *et al.*, 2013). For instance, our spatial analysis shows that climate-change velocity is the strongest environmental variable explaining PD_{SR} in Madagascar, consistent with a previous

study that noticed that climate-change velocity is a strong predictor of the richness of some mammalian groups on the island (Descombes *et al.*, 2018).

Contrary to our expectations, we did not find marked shifts in the slopes of the relationship between elevation and diversity in mountainous regions. The higher elevation in the Himalayas is directly linked to less PD_{SR}, consistent with the higher diversification rates of mammals in the region (Oliveira *et al.*, 2016) and the fact that mountains are important centres of speciation (Rangel *et al.*, 2018). However, as elevation is associated with a decrease in richness in the area, its association with less phylogenetic diversified communities may result from environmental filtering as the main mechanism driving diversity in mountains. In addition, we also note that the relative importance of mountains may be underestimated in our analysis, because (1) the poor spatial resolution of species ranges causes inaccurate description of global biodiversity patterns along slopes of mountains, (2) the size of grid cells used in the analysis is unable to capture fine-scale biodiversity patterns and their environmental correlates (Hortal *et al.*, 2008), and (3) the isotropic assumption of our model (i.e., circular kernel function) precludes accurate analysis of spatial patterns that are long and narrow, such as those generated by the Andes and Himalayas.

Among the advantages of using a spatially explicit approach is the identification of which predictor has the greatest effect on a response variable in each region. From the set of predictors used here, we noticed an east-west geographical change in the primary factor determining mammalian richness, being temperature most important in much of the New World and AET in the Old World. The limiting factor to species richness is expected to shift latitudinally in response to limitations in water and energy from the tropics to northern latitudes (Hawkins *et al.*, 2003), but as AET is a measure of the balance between water and energy, we cannot directly test this hypothesis. In

contrast to the effects on species richness, in much of the globe, temperature is the most important environmental factor for phylogenetic diversity once richness is controlled for (PD_{SR}). This is similar to Davies' *et al.* (2007) findings for parrots that while SR is strongly linked to productive energy, PD_{SR} is mostly associated with ambient energy. This suggests that mammal diversification seems to be more associated with temperature than productivity, supporting the claim that it is linked to warmer, but not necessarily more productive areas (Davies & Buckley, 2011; Safi *et al.*, 2011). Non-stationary spatial patterns, such as the ones we found, may arise because particular clades in each region might relate differently to the environment as a consequence of their ecology and biogeographical and diversification histories (Buckley *et al.*, 2010; Machac *et al.*, 2017). Indeed, different diversity-environmental relationships are known to occur among mammalian groups (Buckley *et al.*, 2010; Oliveira *et al.*, 2016).

Concluding remarks

Previous studies have shown that even though species richness (SR) and phylogenetic diversity (PD) are strongly correlated, the spatial patterns in mammalian SR does not account for the variation in PD and such mismatches provide insights into ecological and evolutionary processes (Davies & Buckley, 2011; Safi *et al.*, 2011; Penone *et al.*, 2016). Here we demonstrate that regionally structured mismatches between richness and phylogenetic diversity of terrestrial mammals are associated with the group biogeographical history and with the different ways that both dimensions of biodiversity relate to current and past environmental factors. We found more complex spatial patterns than previously anticipated based on per-realm analysis (Davies *et al.*, 2007; Gouveia *et al.*, 2014; Voskamp *et al.*, 2017), supporting our claim that Geographically Weighted Path Analysis and other GWR-based methods are promising tools to explore

complex systems with varying relationships over the space, overcoming the need to arbitrarily split the data into geographical sub-regions. We argue that spatial variation in environmental-diversity relationships might emerge from either different mechanisms being at play or from different species pools having specific adaptations to environmental gradients (Ricklefs, 2006; Hawkins *et al.*, 2012; Fergnani & Ruggiero, 2017). Such spatial variation in the relative importance of different environmental factors may explain why results differ among studies and why a theory might receive more, or less support, depending on where the study was conducted (Casseiro *et al.*, 2007).

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Data accessibility statement: The R code to perform Geographically Weighed Path Analysis and a spatial file containing the global hexagonal grid cell with all variables and results of this study is available online in the Dryad repository, doi:10.5061/dryad.nq8hg19

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Biosketch

Elisa Barreto is a PhD student in Ecology and Evolution interested in understanding what drives the spatial patterns of multiple dimensions of biodiversity.

Catherine H. Graham is interested in macroecology and community ecology, particularly integrating theories and tools from different disciplines to evaluate the mechanisms that generate and maintain diversity.

Thiago F. Rangel is a geographical ecologist interested in the drivers of organic and cultural evolution at large spatial and temporal scales.