

Dimensions of Amphibian alpha diversity in the New World

Running title: Dimensions of Amphibian alpha diversity

Leticia Margarita Ochoa-Ochoa¹, Nancy R. Mejía-Domínguez², Julián A. Velasco³, Dimitar Dimitrov⁴ and Katharine A. Marske⁵

1. Facultad de Ciencias, Universidad Nacional Autónoma de México, México 04510, D.F., México. email: leticia.ochoa@ciencias.unam.mx
2. Red de Apoyo a la Investigación, Coordinación de la Investigación Científica, Universidad Nacional Autónoma de México, México 04510, D.F., México. email: nmejia@cic.unam.mx
3. Centro de Ciencias de la Atmósfera, Universidad Nacional Autónoma de México, México 04510, D.F., México. email: juvelas@gmail.com
4. Department of Natural History, University Museum of Bergen, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway. email: dimitard.gwu@gmail.com
5. Department of Biology, University of Oklahoma, 730 Van Vleet Oval Room 314, Norman, OK 73019, USA. email: kamarske@ou.edu

Corresponding author: Julian A. Velasco, juvelas@gmail.com

Handling editor: Lei, Fumin

Acknowledgements

We are grateful to D. Bickford for sharing his database and Ari Kleinberg for help in the design of figure 1. We thank the editor F. Lei and two anonymous reviewers for their constructive comments. We are also thankful to R. De Villa Magallón for the constructive comments that improved the manuscript.

Abstract

Aim: The links between taxonomic, functional and phylogenetic diversity and how these vary geographically are key to understanding how historical and contemporary processes have shaped communities at regional and local scales. Here, we evaluate the links between taxonomic, functional and phylogenetic diversity for the amphibians in the Continental Americas and how these vary geographically under an explicit hypothesis testing framework.

Location: Continental Americas

Taxon: Amphibia

Methods: We identify spatial disparities between biodiversity dimensions (taxonomic, functional and phylogenetic) using geographically weighted regressions. Based on these mismatches we examined whether different eco-evolutionary processes would fit (competitive exclusion, habitat filtering, available ecological space, strong biotic interactions, speciation rates and dispersion).

Results: We found extensive variation in spatial mismatches between the three dimensions of biodiversity examined here. In general, at higher latitudes, we detected relatively little phylogenetic diversity, suggesting rapid functional diversification from temperate clades. In contrast, at low latitudes, environmental filtering mechanisms appear to be restricting functional diversity.

Main conclusions: The geographical mismatches between dimensions of diversity suggest different eco-evolutionary causes. Patterns of diversification across amphibian lineages demonstrate how different environments can have contrasting effects on the different dimensions of diversity, potentially leading to decoupling. Neither dimension of alpha diversity of amphibians is a general predictor for another, and thus, general explanations for amphibian

diversity and evolution should be avoided. Nonetheless, these dimensions can provide critical insights about conservation measures that explicitly emphasize evolutionary history, functionality or classic species richness.

Keywords: Ecological opportunity, habitat filtering, competitive interactions, eco-evolutionary mechanisms, ecological functions, phylogenetic diversification.

Introduction

Departure from a general relationship across geography (e.g. a non-stationary process) provides insights into how evolutionary (e.g. speciation, extinction, and dispersal) and ecological processes (e.g. environmental filtering or competition) interplay to determine the specific set of ecological functions in a given site (Vellend, 2010; Chase & Myers, 2011; Safi et al., 2011). The links between taxonomic, functional and phylogenetic diversity (Jarzyna & Jetz, 2016, 2017) and their spatial variation are key to understanding how historical and contemporary processes have shaped communities at regional and local scales (Safi et al., 2011; D'Amen et al., 2015, 2017; Ordonez & Svenning, 2015, 2016). These three diversity dimensions, taxonomic (TD), functional (FD) and phylogenetic (PD), tend to covary linearly across sites (Safi et al., 2011; Swenson, 2011; Jarzyna & Jetz, 2017) but spatial mismatch among them remains unexplored.

Spatial patterns of diversity dimensions (TD, FD and PD) have been studied in some taxonomic groups (e.g. mammals, Safi et al., 2011; woody plants, Swenson et al., 2012; birds, Monnet et al., 2014; amphibians PD ~TD, Fritz & Rahbek, 2012; Vasconcelos et al., 2019; FD~PD Oliveira et al., 2019). Different dimensions of diversity have also been used or to make predictions about conservation outcomes (Rapacciuolo et al., 2019; Jetz & Pyron, 2018; Campos et al., 2017). However, integrative approaches that account for multiple dimensions of amphibian biodiversity jointly (TD, FD and PD) are still needed. This lack of understanding of how multiple dimensions of biodiversity vary across geography hampers any attempts to understand the mechanisms driving biodiversity patterns at global and regional scales. Although several ecological and evolutionary processes can explain the expected relationships between diversity dimensions and the spatial mismatches between these metrics, few studies have addressed these issues comprehensively. We suggest that ecological opportunity, habitat filtering, and

competitive interactions play a strong role in taxonomic, functional and phylogenetic diversity across geography (Fig. 1).

The ecological opportunity hypothesis proposes that lineages will diversify after a colonization event driven by extensive ecological space availability (Ricklefs, 2010) and few existing competitor species (Wellborn & Langerhans, 2015; Stroud & Losos, 2019). When a given lineage colonizes a given site with an extensive ecological opportunity, we expect a rapid diversification both in functional traits and species numbers (Wellborn & Langerhans, 2015). As a result, these sites would exhibit high FD and low PD values (Fig. 1). For instance, functional traits of salamanders from the genus *Desmognathus* in the eastern United States diversified extensively during the early stages of their radiation and as the ecological space filled, trait diversity stopped increasing (Kozak et al., 2005). The replicated nature of trait evolution during independent *Anolis* lizard radiations in the Greater Antilles shows a similar pattern when the ecological opportunity is pervasive (Losos et al. 1998; Mahler et al., 2013; Stroud & Losos, 2020).

When ecological opportunity is limited or absent (e.g. sites with extreme environmental conditions as the case of desert or xeric habitats) there are strong constraints on lineages to diversify through trait functional space. For instance, Ochoa-Ochoa et al. (2019) found that amphibian species inhabiting arid habitats exhibited lower functional diversity than counterparts in habitats with higher humidity. We predict that in such areas FD values will be lower than expected based on PD or TD (Fig. 1a) as a response to habitat filtering mechanisms limiting the functional trait space under marginal environmental conditions when species do not meet the given environmental niche requirements (Götzenberger et al., 2012). In contrast, competitive

interactions between co-occurring species can lead to competitive exclusion but can also promote trait dissimilarity and therefore an increase in functional diversity (Schluter, 2000; Fig. 1a).

We also expect to observe high PD values as a consequence of many non-related lineages with similar functional traits colonizing successfully these regions. In some cases, it is possible that some groups diversify extensively in these extreme environmental conditions as it has been the case of phrynosomatid lizards in desert habitats. For instance, Wiens et al. (2013) found that these lizards have diversified extensively in arid habitats but exhibit larger niche breadth than their counterparts inhabiting more humid habitats. This suggests that habitat filtering mechanisms can facilitate species diversification but not functional diversification.

On the other hand, regions with high species richness and strong biotic interactions (e.g. tropical areas, Schemske et al., 2009) are expected to exhibit higher FD than expected based on their PD. In contrast, regions, where biotic interactions are more relaxed and contain fewer species (e.g. temperate areas), are expected to show lower FD than expected based on PD (Safi et al., 2011; Fig. 1b). Finally, PD is expected to be higher than predicted based on species diversity at sites with low rates of *in situ* speciation and high dispersal (immigration), and lower at sites with many recent speciation events and/or low dispersal rates (Davies & Buckley, 2011; Fig. 1c).

In this paper, we describe the geographical patterns of the multiple dimensions of alpha diversity for continental Amphibians from the New World. We previously found that the relationship between functional and taxonomic diversity is sensitive to precipitation, suggesting a key role for habitat filtering in shaping the geographic correlation and mismatches among the diversities (Ochoa-Ochoa et al. 2019). Here, we extend our analysis to phylogenetic diversity to gain further insight into how functional (FD), taxonomic (TD), and phylogenetic diversity (PD) are geographically correlated and where mismatches between these measures occur to gain better

insight into the underlying processes behind the fascinating amphibian richness that exists in the Continental Americas.

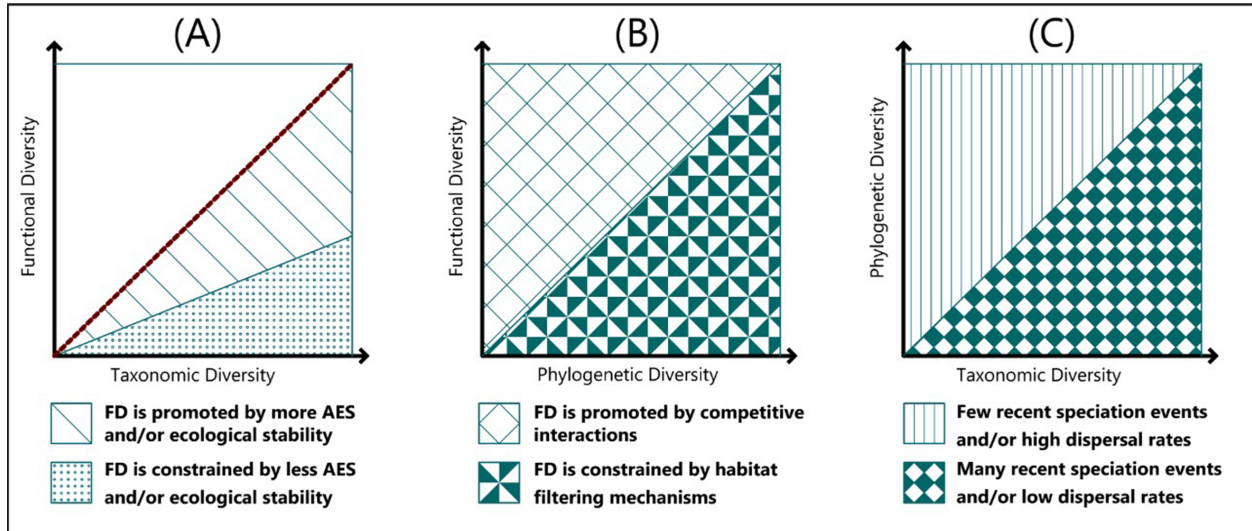


Figure 1. Expected general relationships between taxonomic, phylogenetic and functional diversity. *A* – Expected relationships between FD and TD. The red dotted line represents the maximum functional diversity allowed given the taxonomic diversity; in other words, there cannot be more functions than species and therefore the white space represents a forbidden space. Under this dotted red line, the thick dark blue line indicates an hypothetical model of linear relationship between FD and TD; above it FD is higher than predicted by TD. The proposed mechanism is that areas with higher FD have wide available ecological space (AES) and/or high ecological stability; thus, either mechanism can promote trait dissimilarity, increasing functional diversity. In contrast, below the thick blue line there is less AES and/or low ecological stability, limiting functional diversity. *B* – Expected pattern between FD and PD. Above the identity line (in dark blue) are sites with high habitat diversity and empty AES, both can promote an increment in FD leading to higher FD than expected by PD. In these areas, it is likely that rapid diversification occurred (i.e., low PD), with high phenotypic differentiation (i.e., high FD) driven by competitive interactions or adaptive radiation. By contrast, below the

identity line are sites with low habitat diversity (including sites with extreme environmental conditions), limiting FD relative to PD. Non-related lineages (i.e., high PD) with similar functional traits (i.e., low FD) can colonize such regions or converge via habitat filtering mechanism. C - represents the relationship between PD and TD. High PD is expected in sites characterized by few in situ speciation events and/or many dispersals from other sites, while low PD is expected in sites with many recent in situ speciation events and/or few dispersals from other sites. Based on this general model a 3D visualization of the empirical relationships between FD, PD and TD for Amphibians in the Continental Americas is available at this link (<https://plot.ly/~YcnanMej/21/#plot>). Colour in online version.

Material and Methods

Taxonomic diversity

Taxonomic diversity was calculated using the taxonomy of Frost (2019), the spatial distribution of global amphibians (IUCN 2019), and a grid cell system of 100*100 km (Bergmann's equal area) for the Continental Americas. We estimated TD as the count of species occurring in each grid cell (alpha diversity) by overlaying species distribution range maps. It is worth noting that we only used species for which we had trait information.

Functional diversity

Functional diversity was estimated using the data from Ochoa-Ochoa et al. (2019), which consists of nine traits for American Amphibians: 1) body size; 2) primary habitat type; 3) fertilization type; 4) reproductive cycle; 5) reproductive type; 6) spawn site; 7) presence/absence of larvae; 8) site of larvae development; and 9) presence/absence of parental care. This dataset

contains information for 2,776 amphibian species occurring in Continental Americas (Frost, 2016). To compile this information, we reviewed more than 1180 references (Ochoa-Ochoa et al., 2019).

We measured functional diversity using a multi-trait approach that calculates the different combinations of traits occurring in a community, assuming that variation in one of the nine traits is enough for a species to be considered functionally distinct (Walker et al., 1999; Duarte, 2007; Ochoa-Ochoa et al., 2019). Thus, the total number of species represents the maximum possible number of functional combinations. We calculated functional alpha diversity (FD) for each grid cell by counting the number of unique multi-trait combinations, or ‘functions’ (Fig. 1). In the extreme cases where all the species would have the same multi-trait combination, FD would be 1; whereas on the contrary if each species present a different multi-trait combination $FD = TD$.

Phylogenetic diversity

We calculated Faith’s PD as the sum of branch lengths for all species occurring in a grid cell (Faith 1992) for the entire domain where amphibians occur in the Americas. We used Jetz & Pyron’s (2018) amphibian phylogeny, which includes 90% (i.e., 7238 species) of the currently known amphibian species (~8156 species; Frost, 2020). We pruned all species not occurring within the continental Americas. Data are available in

<https://figshare.com/s/090af8036b5060801eff>

Geographically weighted regression

To explore the relationship among the different dimensions of amphibian diversity, we performed geographically weighted regressions (GWR; Brunsdon et al., 1998). This method allows exploration of non-stationary relationships among variables (e.g. those that behave differentially through space). We used an adaptive kernel that takes into account different

neighbourhood sizes. The final neighbourhood for each grid cell was chosen using the cross-validation score by reducing the dominance of some observations in determining the neighbourhood size (Fotheringham et al., 2002; Páez et al., 2011). Thus, GWR is a useful tool for making spatial inferences of non-stationary processes. We performed three models to explore the relationships among dimensions of diversity and to assess the percentage of variation explained by each dimension: 1) FD ~ TD, 2) FD ~ PD, and 3) PD ~ TD. Local regressions were calculated for each model, allowing different coefficients (Brunsdon et al., 1998). Here we report only the local coefficients. All analyses were performed in R (R Core Team 2015) using the packages 'spgwr' (Bivand & Yu 2017) and 'spdep' (Bivand et al., 2013).

Residuals of the GWR were mapped to assess the magnitude and direction of mismatch between diversities, to test the hypotheses described above and in Figure 1. For FD ~ TD, positive residuals suggest adaptive divergence driven by competitive exclusion, and negative residuals indicate a strong role of habitat filtering mechanisms. For FD ~ PD, positive residuals indicate sites where ecological opportunity (i.e., large amount of available ecological space) and competitive interactions facilitate trait diversification, and negative residuals indicate where FD is limited by habitat filtering. For PD ~ TD, positive residuals indicate few recent speciation events and high dispersal rates (immigration), and negative residuals suggest many recent speciation events and/or low dispersal rates.

Results

Diversity patterns

The pattern of TD shows the highest richness in the region from Panama through the Amazonian basin, with another hotspot of richness along the southeast coast of Brazil (Fig. 2a). The regions with higher FD were in the eastern USA in the Appalachians, from Panama to Brazil

along the interior slope of the Andes facing the Amazonian lowlands, the Guiana Shield, and finally the southern part of the east coast of Brazil (Fig. 2b). The regions with lower FD included high latitude regions of both hemispheres, the Great Plains of the United States down to the Central plateau of Mexico, the Baja California Peninsula, the Pacific coast of South America up to Ecuador, the region of Los Llanos and La Gran Sabana of Colombia and Venezuela, respectively, and the lowlands of south-eastern Brazil. Notably, the regions with high FD have high altitudinal variation, specifically tropical mountain ranges and the Appalachians; conversely, the regions with low FD are either lowlands or have low topographic variation (e.g. the plains and plateaus). The PD pattern is very similar to those of the TD and FD (Fig. 2c). The highest FD in a single cell was 50, whereas TD reached a maximum of 158 and PD of 7628.

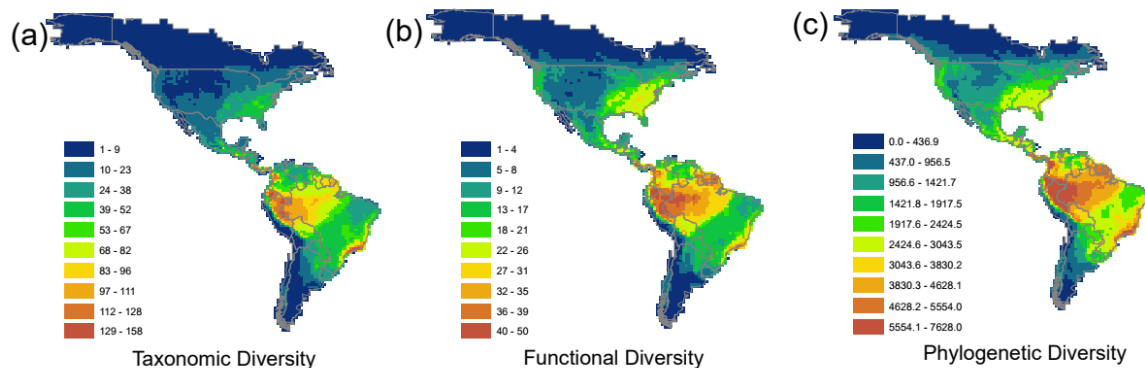


Figure 2. Geographical patterns of amphibian alpha diversities in the Continental Americas. (a) Taxonomic; (b) Functional; and (c) Phylogenetic. Scale of values was determined by Jenks natural breaks classification.

There is a positive latitudinal gradient of richness in all diversities (taxonomic, functional and phylogenetic), with two additional well-defined peaks, one in the northern hemisphere

around 30-35 degrees north and one in the south (Fig. 3). While all diversities exhibit a strong latitudinal trend, there is large variation in the range of values.

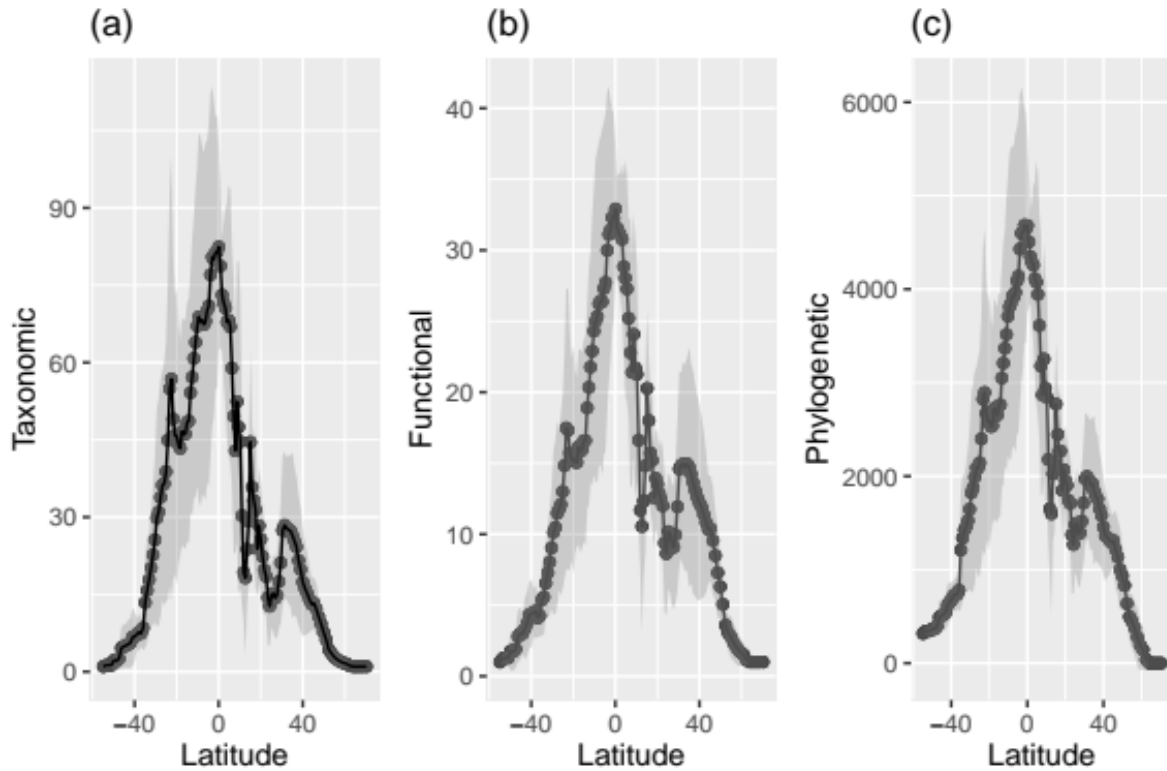


Figure 3. Latitudinal gradient of the amphibian alpha diversities in the Continental Americas.

(a) Taxonomic; (b) Functional; and (c) Phylogenetic.

Relationships among the different dimensions of alpha diversity

There is a wide variation of GWR, both spatially and numerically, in the relationships between the dimensions of amphibian alpha diversity for the Continental Americas (Fig. 4). Interestingly, in general, paired weighted geographic relationships are similar to each other (Fig. 4a-c). Nevertheless, there is extensive variation in the proportion of variance explained (local r^2) with a similar spatial pattern between FD~TD and FD~PD (Fig. 4a-b), but not with PD~TD, where there is a very different spatial pattern in the southern hemisphere (Fig. 4c).

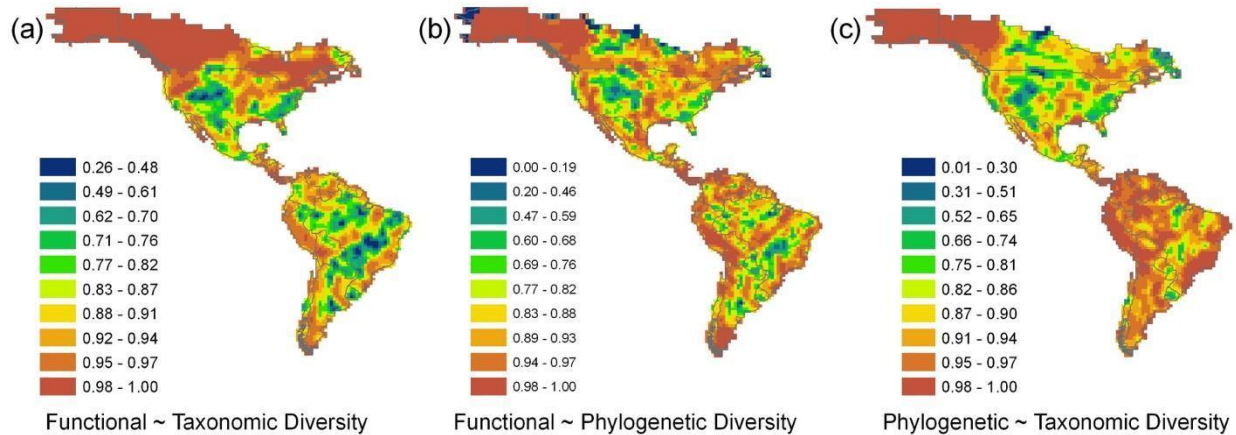


Figure 4. Geographically weighted regression of amphibian alpha diversities in the Continental Americas. The colour schemes represent the value of the local r -squared, scale of values was determined by Jenks natural breaks classification. (a) Functional ~ Taxonomic; (b) Functional ~ Phylogenetic; and (c) Phylogenetic ~ Taxonomic.

Maps of residuals from GWR show clearly the mismatches among the different dimensions of alpha diversity (Fig. 5). For FD ~ TD, positive residuals (Fig. 5a) indicate higher FD than expected given the TD, in the Appalachian region, the northern west coast of the USA, scattered regions in Middle America (north of Mexico to Central America), the Orinoco basin and the Amazon basin. In contrast, areas where there is lower FD than expected given the TD (negative residuals) are in the interior slope of the Andes, the arid diagonal of South America, and the Brazilian Atlantic Forest. The spatial pattern for FD ~ PD is roughly similar to that of FD ~ TD (Fig. 5a-b). For PD ~ TD, high positive values indicate more PD than expected given TD (Fig. 5c) along the west coast of the United States in North America, the Gulf of Mexico, Central America highlands, the higher altitudes of the Andes and in the Amazonian delta basin.

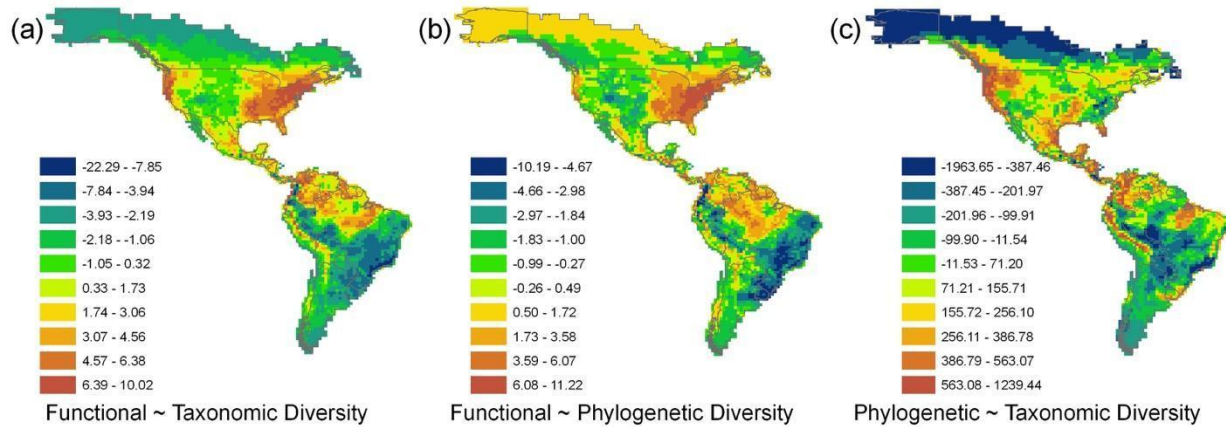


Figure 5. Residuals of the geographically weighted regression of amphibian alpha diversities in the Continental Americas. (a) Functional ~ Taxonomic; (b) Functional ~ Phylogenetic; and (c) Phylogenetic ~ Taxonomic. Scale of values was determined by Jenks natural breaks classification.

Discussion

At continental scales, amphibian FD mirrors patterns of species richness and PD. This is not surprising as it has been proposed that species richness, FD and PD must be related (but see De Bello et al., 2006; de Bello, 2012). Our results showed that although the general trend is a positive and significant relationship between the three dimensions of diversity (functional, taxonomic and phylogenetic), there is a wide range of geographical variation in the local relationships among these metrics, suggesting different underlying drivers (ecological or historical) of the observed spatial patterns. These results raise the question as to whether the high number of functions allow many species to coexist by means of niche partitioning or the high number of species promotes diversification of functions irrespective of the tempo and mode of species diversification. The answer may vary depending on the focal group or the mechanism proposed to structure the assemblages (Mason et al., 2013). For example, Blankers et al., (2012) tested whether morphology and microhabitat use were related in plethodontid salamanders (189

species analysed), with just one group –the supergenus *Bolitoglossa* (44 species analysed) showing a decoupling in ecological and evolutionary radiation. In contrast, for *Desmognathus* (18 species analysed), a strong correlation between morphology and microhabitat ecology has been found; however, rates of diversification seem to be linked with the persistence of the community over evolutionary time (Kozak et al., 2005). Thus, different constraints might be shaping the correlation between diversities at different geographical, temporal and phylogenetic scales.

Patterns of diversification across amphibian lineages demonstrate how different environments can have contrasting effects on the different dimensions of diversity, potentially leading to decoupling. For example, in species with large geographic distributions, a deeper intraspecific genetic structure (phylogeographic structure) has been found in specialists associated with forests and topographically complex regions than in those inhabiting open habitats, potentially leading to higher probabilities of speciation in the anurans that inhabit forested and topographically complex regions (see Fig. 2c; Rodríguez et al., 2015). In contrast, amphibians in arid environments with highly seasonal precipitation reproduce in ephemeral pools and in some cases must travel considerable distances to find these breeding opportunities (obs. pers. LMOO). This diminishes the potential for population isolation and species diversification, reducing phylogenetic structure (e.g. Chan & Zamudio, 2009), which might explain the low PD observed in the central US towards the Mexican plateau (Fig. 2c; Pyron et al., 2015). In more temperate and humid places with higher climatic stability (or low seasonality), the requirement for dispersal is significantly lower, promoting genetic isolation, speciation and a preponderance of small-ranged species (e.g. Fitzpatrick et al., 2009). For example, the diminutive salamanders of the genus *Thorius* have undergone extensive species

diversification as a result of repeated geographical isolation (Rovito et al., 2013). This suggests that in regions with different ecological regimes but stable conditions (e.g. humid forests, either tropical or temperate), a single clade can achieve high species richness rapidly, leading to a regional decoupling of taxonomic and phylogenetic diversity (more species than expected given its phylogenetic diversity). In contrast, in places with harsh or variable ecological conditions (e.g. arid or highly seasonal areas), lineages must adapt to the conditions or perish, with environmental filtering limiting the number of functions that may persist in an area (Ruhí et al., 2014) and leading to a decoupling between functional and phylogenetic diversity (less ecological functions than expected given its phylogenetic diversity; Fig. 2b).

The geographical mismatches between dimensions of diversity suggest different eco-evolutionary causes (Safi et al., 2011), like historical processes such as *in situ* speciation or dispersal and colonization dynamics, or ecological processes such as variation in available ecological space, precipitation and climate seasonality, where the measures of diversity are decoupled (Pyron et al., 2015). We predicted that positive $FD \sim TD$ and $FD \sim PD$ residuals should occur in regions that have both significant available ecological space and strong competitive interactions that together promote functional diversification through niche partitioning (Fig. 1). Our results show that in the Amazon basin towards the Venezuelan Tepuis (Fig. 5a,b) fulfil this hypothesis, there are more functions than expected given the taxonomic and phylogenetic diversity. That is, we suggest that sites exhibiting higher FD than expected given their species richness would have experienced extensive *in situ* speciation and exhibit unique functional traits that have evolved repeatedly across space. Some studies support this contention, showing that amphibian lineage diversification is decoupled from trait diversification (Blankers et al., 2012). Our results corroborate previous findings from Santos et al. (2009), showing that

multiple dispersal events from adjacent Andean regions have shaped the Amazonian poison frog species pool. Our results also suggest extensive functional diversification (decoupled from either taxonomic or phylogenetic diversity) in the Appalachians, the west coast of the US, the highlands of Mexico and Central America. While the exact mechanisms underlying these relationships require further study, evidence from the most diverse amphibian families (e.g. Plethodontidae, Hylidae, Craugastoridae) generally supports adaptive radiation with functional divergence (e.g. ecomorphological divergence; Rovito et al., 2013), similar to patterns found in other taxa like *Anolis* lizards (Losos & Ricklefs, 2009).

Under a strong role of habitat filtering mechanisms, we predicted negative residuals of $FD \sim PD$ and we found it in the southern hemisphere, at lower latitudes where there is less FD given the TD because there can be no further functional diversification due to a low capacity to diversify by environmental constraints or filtering. In the Mesoamerican lowlands, which have limited ecological space coupled with high seasonality there are fewer functions than expected given the high phylogenetic diversity, consistent with environmental filtering driving the mismatch between FD and PD (Fig. 5b).

According to our hypotheses we predicted high positive residuals of $PD \sim TD$ where few recent speciation events and/or high dispersal rates (immigration) occurred. We found that pattern, from North to South, west coast of the USA, Gulf Coast, Mesoamerica, and in Andean highlands. At low northern latitudes, around the Mexican Gulf Coast and the Yucatan Peninsula, high number of dispersal events within the Mesoamerican Transition Zone have likely promoted higher PD than expected given the TD (Fig. 5c). In contrast, sites with a high diversity of habitats (e.g. northern latitudes of North America around the Appalachian) show that fewer clades have successfully dispersed. We suggest that competitive interactions promoted the

dissimilarity of functions by niche partitioning (as species diversify), with low PD and negative residuals (Fig. 5b).

Interestingly, there are places where our predictions are not fulfilled. For example, the interior slope of the Andes has high absolute FD (Fig. 2) but it has remarkably lower relative FD given its high phylogenetic or taxonomic diversity (Fig. 5a,b). According to our proposed hypotheses, in those sites with negative residuals $FD \sim PD$, low functional diversity should reflect environmental filtering, promoting convergence of functional traits, or more relaxed biotic interactions, resulting in less functional diversification. The interior slope of the Andes would appear to contradict this hypothesis, but although there is high FD, there is even higher PD, suggesting that there is enough available niche breadth to allow for relaxed biotic interactions. The negative residuals for $FD \sim TD$ in the interior slope of the Andes seem unlikely to result from habitat filtering since the environment in this region is stable with high levels of humidity and precipitation, in contradiction to our hypothesis. Here we may be detecting either a community limited- membership or a “saturation” of the possible functions that can co-exist in an area given the physical limits of the amphibian group (Hubbell, 2001). From this perspective communities are assembled by rules that are based on the functional role of each constituent species. However, this hypothesis would be difficult to test and further work will be necessary here.

We predicted that negative $PD \sim TD$ residuals suggest many recent speciation events and/or low dispersal rates. We found that pattern in the north of North America (although this is likely an artefact due the low number of species), interior slope of both, the Appalachians and the Andes. It has been proposed that mountain ranges can act simultaneously as species pumps (cradles) and museums (refugia) for anurans and salamanders (Smith et al., 2007; Parra-Olea et

al., 2012). But at least the evidence with glass frogs for the tropical Andes points to the museum hypothesis (e.g. low rates of extinction) with strong climatic-niche conservatism (Hutter et al., 2013). On the other hand, it has also been found that in mountain ranges (including tropical mountains), constraining dispersal of lineages to environments at lower and higher elevations may promote speciation (Wiens et al., 2007; Rahbek et al., 2019a,b; but see Mendoza et al., 2015). The tropical Andes harbour a huge number of species of the *Pristimatis* genus which is an excellent example to illustrate this phenomenon and the resulting decoupling of taxonomic and phylogenetic diversity. Chejanovsky and Wiens (2014) found that in the case of hylids, the great diversity in tropical warm zones is due to species with narrow climatic niches that limit dispersal out of their ancestral stable environments. These two processes, limited dispersion and the museum hypothesis, combined allowed time for speciation generating areas of great diversity taxonomic diversity but low phylogenetic diversity, like the interior slope of the Appalachians and the Andes (Fig. 5c).

The extensive geographical variation in the relationship between taxonomic, functional and phylogenetic diversities required contrasting explanations. Our results show that residuals based on different diversity metrics do not necessarily follow the same spatial pattern. Due to their evolutionary histories as centres of diversification or refugia, regions with positive residuals potentially represent critical areas for conservation. Thus, setting conservation priorities is not trivial and may require analyses on which is the most important dimension of diversity to be conserved, as recent evidence indicates that these diversities are becoming decoupled in the Anthropocene (see Oliveira et al., 2019). Thus, there is a growing challenge either to give priority to history (e.g. antique lineages, evolutionary uniqueness), to high functional diversity (with rare or unique functions) or to taxonomic diversity (number of species). Multi-dimensional

analyses of diversity, as the one presented here for the New World amphibians, which identify variation in the spatial relationships among the dimensions of alpha diversity and the processes shaping this variation, can therefore yield critical new insights into whether conservation measures should emphasize evolutionary history, functionality or species richness. Thus, these analyses could also help for setting the basis of actions to be performed for preserving any of the dimensions. However, we must stress that conservation is not just about preserving species but preserving eco-evolutionary processes.

In an ideal world, if we want to preserve a wider range of the evolutionary spectre, the aim should be to conserve at least one of each different phylogenetic lines and life history traits (functions). It is generally accepted that the number of species that remain in a community is instrumental in the fight to preserve and restore perturbed communities (Brook et al., 2003). However, the number of functions that are preserved is crucial to maintain the structure of communities and thus the function of ecosystems in the long run (Harvery et al., 2017). We found that neither dimension of alpha diversity of amphibians is a general predictor of the others, despite their broad geographic correlation, and the resulting mosaic of spatial mismatches among diversity dimensions shown by our results suggests that conservation planning based on using one dimension as surrogate for another should be avoided (Devictor et a., 2010). Finally, general explanations for the patterns of amphibian diversity dimensions and their eco-evolutionary drivers should be evaded as well.

Data accessibility: Data are available in <https://figshare.com/s/090af8036b5060801eff>

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Biosketch

Leticia M. Ochoa-Ochoa is a full professor at the Faculty of Science, UNAM. She is interested in the processes that shape and maintain amphibian communities in a landscape; and how these aspects mold diversity patterns.

Author contributions: LMOO, NRMD and JV conceived the ideas; LMOO, KAM and DD collected data; LMOO, NRMD and JV analysed the data; LMOO wrote the first draft of the manuscript, and all authors contributed substantially to revisions. No new data were used.