

RESEARCH PAPER

Amphibian functional diversity is related to high annual precipitation and low precipitation seasonality in the New World

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Abstract

Aim: We examined the geographical distribution of functional diversity for American amphibians and tested the relationship between functional diversity and environment. We also explored how the functional evenness of life-history traits varies across biogeographical regions.

Location: Continental Americas.

Methods: We performed a trait classification based on an Eltonian approach and calculated functional diversity using Hill numbers, Shannon and Gini-Simpson indices. We tested the relationship between functional diversity and different axes of environmental variation by using a series of spatial autoregressive (SAR) models.

Results: Based on 212 different functional attributes for 2,776 species, we found that functional diversity has a latitudinal gradient consistent with that of species richness, regardless of the diversity index used. Evenness of functional diversity of amphibian assemblages varies depending on the region, but in general they are close to the maximum possible value. Areas with more functional richness relative to species richness are associated with high annual precipitation and low precipitation seasonality regardless of temperature; in contrast, areas with fewer functions than expected are associated with high aridity.

Main conclusions: The highest functional diversity is located in mountainous regions. Overall, functional diversity is positively correlated with humid environments with low precipitation seasonality and low aridity regardless of temperature. This is especially relevant for amphibians facing contemporary climate change because it suggests that future variation in rainfall patterns, but not in annual mean temperature, might interact with functional diversity to pose an imminent threat to amphibian functional diversity.

KEYWORDS

amphibians, contemporary environment, Gini-Simpson index, Hill numbers, Shannon index, spatial autoregressive models, traits

1 | INTRODUCTION

Understanding the geographical distribution of functional diversity is crucial to comprehending how ecosystems function and maintain themselves and how communities cope with environmental stress or disturbance (Cadotte, Carscadden, & Mirotnick, 2011). Thus, documentation of the geographical patterns of functional diversity and their potential causes is an essential first step towards a more mechanistic understanding of how diversity is maintained across space (Toussaint et al., 2018). Although regional- (e.g., Monnet et al., 2014) and global-scale (e.g., Safi et al., 2011; Toussaint, Charpin, Brosse, & Villéger, 2016) estimates of functional diversity exist for other vertebrates, such as birds, mammals and even fishes, we lack estimates for functional diversity for amphibians at scales large enough to compare against species richness, phylogenetic diversity or environmental gradients at the continental scale. Given that amphibian species globally face extinction owing to disease, climate change, landscape alteration and a variety of other factors (Hof, Levinsky, Araújo, & Rahbek, 2011; Howard & Bickford, 2014), this represents a significant knowledge gap.

Trait-environment interactions have a direct impact on the fitness of populations (Roff, 2002). Therefore, functions, measured through traits, directly reflect how species use the environment where they occur and how the species survive in those places. For instance, in amphibians, such characteristics indicate requirements for reproduction (e.g., temporary ponds, rivers, aquatic vegetation), how often they reproduce, how many eggs they lay, how they disperse and upon what basis they might compete (Cadotte et al., 2011; Clark, Flynn, Butterfield, & Reich, 2012). Furthermore, functional diversity gives us information about how environments shape diversity at local and regional scales (Mason, Bello, Mouillot, Pavoine, & Dray, 2013). Thus, it is of great importance to explore these functional diversity patterns because they might help to elucidate not only the evolution of species and lineages but also the processes underpinning community assembly.

For amphibians, regional- to global-scale trait distributions are known only for body size (Olalla-Tárraga, Bini, Diniz-Filho, & Rodríguez, 2010; Whitton, Purvis, Orme, & Olalla-Tárraga, 2012). A few studies have adopted multi-trait values to evaluate correlates of amphibian extinction risk (Howard & Bickford, 2014; Sodhi et al., 2008), but there are no descriptions of functional diversity patterns based on multi-trait values, a combination of more than one trait (Walker, Kinzig, & Langridge, 1999). However, the way in which an organism interacts with its environment depends on several traits, not only one, and may vary across its range. Thus, functional diversity metrics, which capture information on multiple traits, will be able to give us information on aspects of the environment that might influence the persistence of a species (Morrison & Hero, 2003). Moreover, multi-trait estimates of functional diversity are likely to provide a more accurate approximation of how functional diversity is related to other emergent properties of amphibian communities, such as species distributions, climatic ranges and patterns of coexistence.

Here, we describe the geographical patterns of functional diversity for New World amphibians. First, we used multi-trait indices to estimate the richness and evenness of amphibian functional diversity at a resolution of 100 km/side equal-area grid and within different biogeographical regions within the Americas. Second, we compared functional and species richness for all amphibians, identifying regions with higher and lower functional diversity than expected based on species richness. Third, we tested for the prevalence of high versus low functional diversity along environmental gradients of primary productivity, temperature, precipitation and water availability. Our work is the first assessment of functional diversity spanning this hotspot of amphibian diversification, filling an important gap in our understanding of the macroecology of this diverse and at-risk group.

2 | METHODS

We compiled existing data on the following traits for American Amphibians from the scientific literature, including species descriptions, field guides, specialized assessments and specialized webpages: (a) body size; (b) primary habitat type; (c) fertilization type; (d) reproductive cycle; (e) reproductive type; (f) spawn site; (g) presence/absence of larvae; (h) site of development of larvae; and (i) presence/absence of parental care (e.g., Algar, Kerr, & Currie, 2011; De Lisle & Rowe, 2013; Han & Fu, 2013; Sodhi et al., 2008). This dataset contains 2,776 species occurring in Continental Americas (Frost, 2016). We classified body size (maximum lengths) in the five categories proposed by Sodhi et al. (2008), which vary depending on the Order: tiny, small, medium, large and giant (Supporting Information Appendix S1, Table S1). Where information on specific traits was lacking for some species, we coded this as missing data. Please see Supporting Information Appendix S1 for further details on the database construction and Supporting Information Appendix S2 for the full list of references consulted.

2.1 | Estimation of functional diversity

We measured functional diversity using a multi-trait index (Cadotte et al., 2011), in which each unique multi-trait was defined by a combination of the nine traits mentioned before.

Although most methods of quantifying functional diversity are based on the distance between traits, we implemented the functional attribute diversity (FAD), which is based on trait values (Walker et al., 1999). This is preferable for comparing functional profiles between localities because it calculates the different combinations of traits occurring in a community (Duarte, 2007; Walker et al., 1999). In this Eltonian approach, a multi-trait value is equivalent to a function, meaning that we can classify species according to a "functional taxonomy" of multi-trait values, which must be equal to or less than species richness (Ricotta, 2005; Walker et al., 1999). The main assumption of this index is that variation in one of the nine traits is enough for a species to be functionally distinct. We classified each

amphibian species by its unique combination of the nine traits. Using this index, we can calculate the abundance of traits within an assemblage, allowing us to use abundance-based diversity indices.

Geographical ranges for amphibians with trait information were acquired from the International Union for the Conservation of Nature (IUCN, 2014). We estimated functional diversity for the continental Americas using the Shannon index, the Gini-Simpson index and Hill numbers, using Bergmann's equal-area grid at a resolution of 100 km/side. The widely used Shannon index indicates the evenness of the distribution of the different functions in the assemblage, whereas the Gini-Simpson index gives the probability that two randomly chosen species have different functions.

We used Hill numbers to calculate functional diversity and evenness by means of the multi-trait as an attribute value (Chao, Chiu, & Jost, 2014; Chao & Jost, 2012). In this case, species are replaced by functional entities. The assumption here is that each ecological function is equally distinct, and therefore, we are measuring the effective number of functional entities using the following equation: ${}^qD = (\sum_{i=1}^s P_i^q)^{1/q}$, where q is the parameter that determines the sensitivity of the measure to species abundances. Abundances were estimated as the number of species that share the same function, P_i is the proportional/relative abundance of the i th function, and parameter q determines sensitivity to species relative frequencies or abundances. When $q < 1$, rare functions are given more weighting than abundant functions. Although this metric is undefined for $q = 1$, it tends to the exponential of the Shannon index, H , in its limits; 1D considers biological functions in proportion to their frequencies. In the cases of $q > 1$, the metric gives more weight to abundant (or dominant) functions, reducing the weight of the rare ones. When $q = 0$, abundances do not contribute to the metric; thus, 0D is equal to functional richness.

Given that metrics to quantify diversity are strongly influenced by the most abundant species in the assemblage (Chao & Jost, 2012), we used different values of q to test the sensitivity of the patterns to species abundance: 0 (equivalent to species richness), 0.25, 0.5, 0.75, 1 (equivalent to exponential of H), 2 and 3.

2.2 | Functional evenness

Hill numbers are used to explore the evenness of the functional assemblages (Chao et al., 2014). We plotted the Hill numbers (y axis) against the value of q (x axis) and fitted a curve to these data. The slope of the curve represents the unevenness of the relative abundance functions. The more steeply the curve declines, the more uneven the distribution of relative abundances. Conversely, for an even distribution of relative abundances, the curve would be constant at the level of species diversity. We plotted the values of the Hill numbers for the entire region and for each Wallacean biogeographical region as designated by Holt et al. (2013).

2.3 | Functional richness and species richness

To explore the relationship between functional richness and species richness, we ran an ordinary least squares (OLS) regression. The

p -value was corrected for spatial autocorrelation by performing a modified t test to assess the correlation between two spatial variables using Dutilleul's method (Dutilleul, Clifford, Richardson, & Hemon, 1993). We mapped the residuals to identify regions in which the correlation was positive or negative. Positive residuals indicate that these regions support more functions than expected by the relationship between functional richness and species richness. In contrast, negative residuals indicate that these regions have lower functional diversity than expected given the species richness in those regions.

2.4 | Environmental gradients

We used different sets of environmental variables (all at 30 arc s or c. 1 km² resolution at the Equator) to explore their possible influence on functional diversity patterns. For net primary productivity (NPP), we used a global dataset (Imhoff & Bounoua, 2006; Imhoff et al., 2004); for climatic variables, we included annual mean temperature (AMT), annual precipitation (AP), temperature seasonality (TS) and precipitation seasonality (PS) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). For water availability, we used the annual mean global potential evapotranspiration (PET) and the aridity index of the same dataset (Trabucco & Zomer, 2009). We calculated the mean of each variable per grid cell.

We performed correlations to assess possible collinearity among the environmental variables. If two collinear variables were found, we discarded one of them to avoid overfitting of the models (Legendre & Legendre, 1998; see Supporting Information Appendix S1, Table S2). In all correlations, we also used the modified t test using Dutilleul's correction (Dutilleul et al., 1993). Final models were run with annual mean temperature, annual precipitation, temperature seasonality and aridity index.

2.5 | Spatial autoregressive models

To control for the effect of spatial autocorrelation, we used spatial autoregressive (SAR) models to test for a correlation between functional diversity and environmental conditions (Bivand, Pebesma, & Gómez-Rubio, 2008; Meynard et al., 2011). In these models, we assume that the response variable (i.e., functional diversity) is a linear function of a set of environmental variables, and random errors about the mean are not assumed to be independent. Also, explicit spatial dependence is allowed within a neighbourhood structure where the neighbouring cells that influence a given cell are identified. The parameter λ measures the impact of the spatial structure; where $\lambda = 0$ or non-significant, the error terms are in fact independent, thus no spatial structure is relevant (Bivand et al., 2008).

We generated an SAR model for each functional diversity metric. To assess whether the models accounted for any spatial autocorrelation given the neighbourhood structure, we performed a Monte Carlo test for Moran's I with 999 permutations. We also used null models for each of the SAR models by assuming a constant number of functions in all grid cells, which would be independent of any environmental variable or spatial structure. This can alleviate the

problem of spatial bias in geographical data (Hawkins et al., 2017). We calculated and compared competing models using Akaike information criteria (AIC). The model with the strongest empirical support has the lowest AIC score (Burnham & Anderson, 2002).

Finally, we ran two separate SAR models with the residuals of the OLS (functional richness as function of species richness) and the environmental variables: one for the grid cells with higher functional diversity than expected using the top quartile of the residuals (positive), and one with lower functional diversity than expected using the bottom quartile of the residuals (negative). These models were also run with annual mean temperature, annual precipitation, temperature seasonality and aridity index (see Supporting Information Appendix S3 for the data used in the analyses).

We plotted functional diversity against latitude to test for a latitudinal gradient in trait diversity. All analyses were performed in R v.3.4.2 (R Core Team, 2018), using the packages *vegan* (Oksanen et al., 2013; functional diversity indices) *SpatialPack* (Vallejos, Osorio, & Cuevas, 2018) and *spdep* (Bivand, Hauke, & Kossowski, 2013; for autoregressive models).

3 | RESULTS

3.1 | Geographical patterns of functional diversity

All metrics of diversity based on Hill numbers showed very similar geographical patterns of functional richness ($q = 0$) (Figure 1). Although the Shannon index showed several regions with higher functional richness than any of the Hill metrics, the relative distribution of higher- versus lower-diversity areas was broadly similar to the Hill estimates. The Gini-Simpson index yielded a strikingly different pattern of diversity from the Hill estimates, with regions of high diversity extending into the mid- to higher latitudes of North and South America (Figures 1 and 2).

We found a latitudinal gradient of increase in functional diversity, with the highest functional diversity around 0° latitude, and a second, lower peak c. 40° N. In North America, there was a reduction in the values of functional richness in latitudes corresponding to northern Mexico and from the Yucatan peninsula to Honduras. The highest variation at the same latitude occurred in the USA c. 40° N (Figure 2).

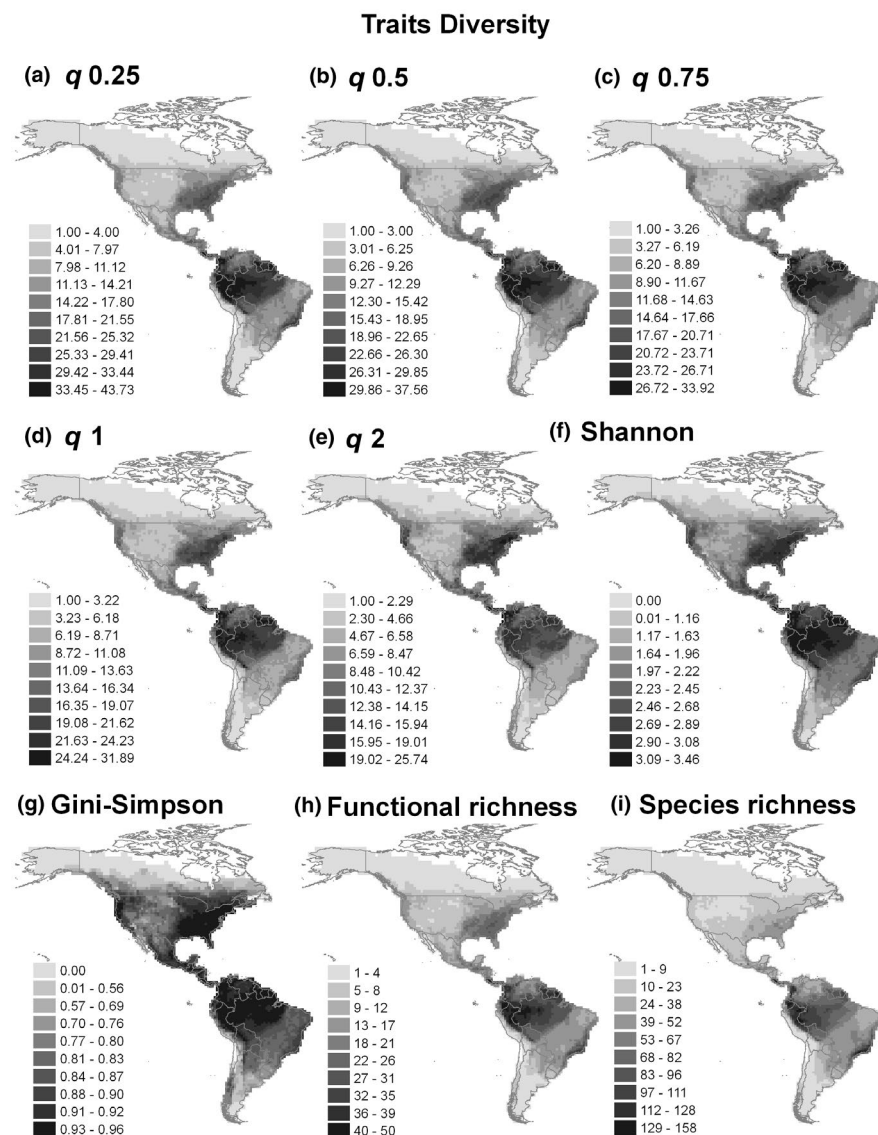


FIGURE 1 Distribution of functional diversity of amphibians in the Continental Americas, based on unique combinations of nine individual traits. Functional diversity is estimated using Hill numbers (a–e) when: $q = 0.25$ (a), $q = 0.5$ (b), $q = 0.75$ (c), $q = 1$ (d) and $q = 2$ (e); the Shannon (f) and Gini-Simpson (g) diversity indices, functional richness (h) and species richness (i)

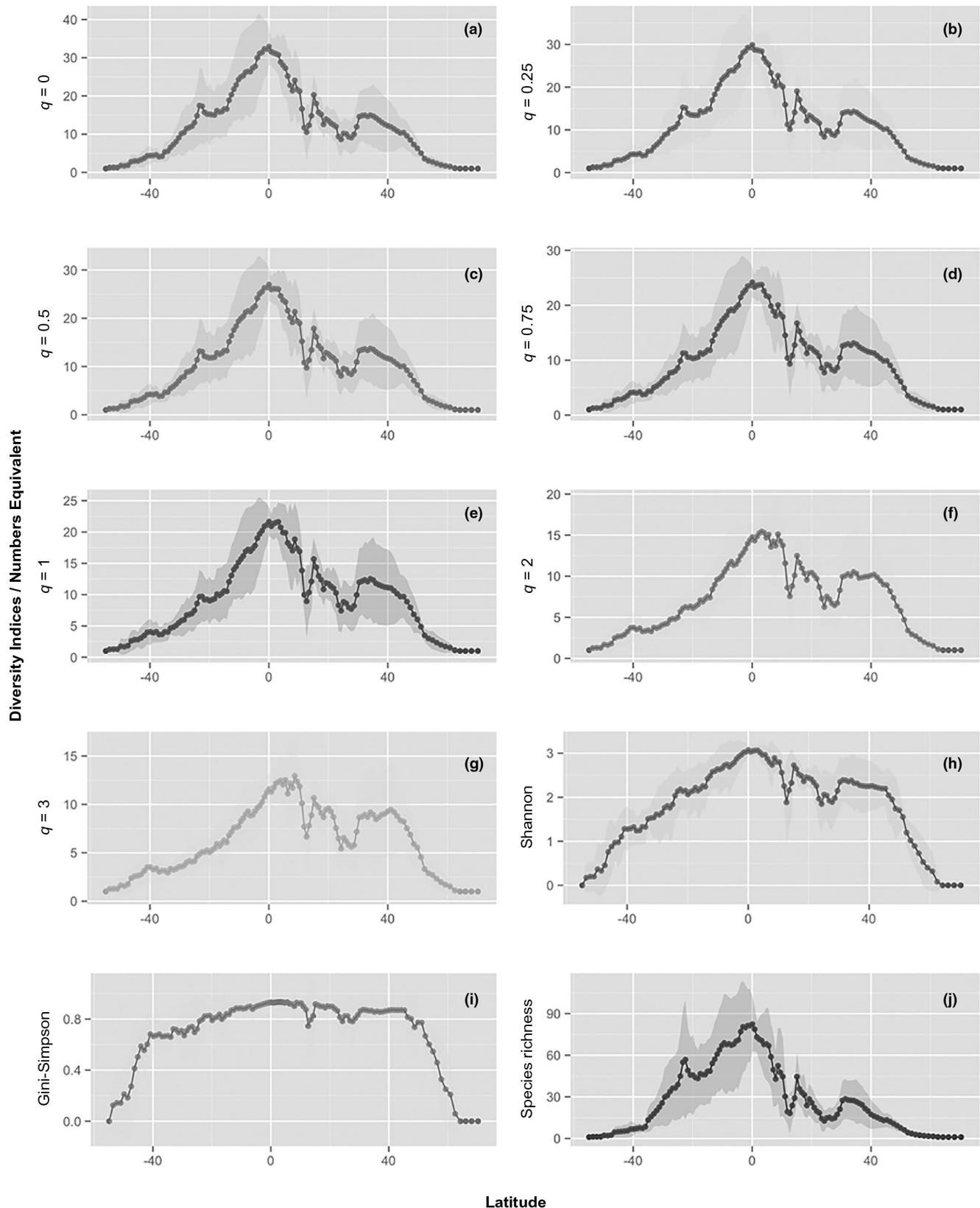


FIGURE 2 Latitudinal gradients of amphibian functional diversity in the Continental Americas. Hill numbers roughly follow the latitudinal gradient, whereas Shannon and Gini-Simpson indices show a different pattern. (a–g) Hill numbers when $q = 0$ (a), which represents functional richness, $q = 0.25$ (b), $q = 0.5$ (c), $q = 0.75$ (d), $q = 1$ (e), $q = 2$ (f) and $q = 3$ (g). (h–j) Diversity indices: Shannon (h), Gini-Simpson (i) and species richness (j)

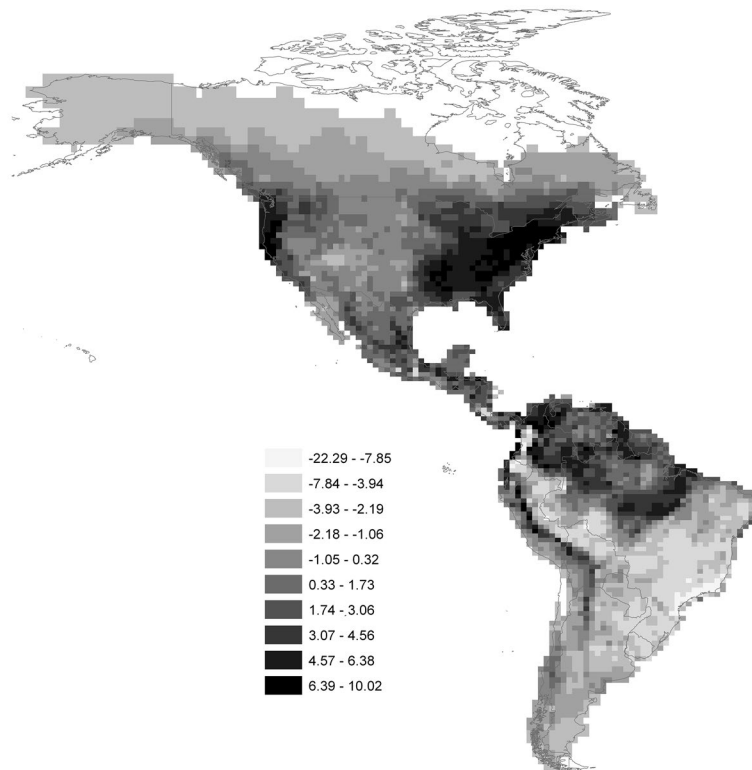


FIGURE 3 Residuals of the ordinary least squares (OLS) regression, functional richness as function of species richness ($r = 0.96$, $p < 0.001$), with the p -value corrected for spatial autocorrelation. Residuals broadly reflect regional patterns of species richness

The pattern of residuals of the OLS model of functional richness associated to species richness ($r = 0.96$, $p > 0.001$) showed that regions with higher functional diversity than expected include the Pacific Northwest, Appalachian Mountains and Interior Highlands in North America, the Sierra Madre Oriental in Mexico down to Guatemala and Honduras Highlands, the northern Andes and lowlands around Cartagena and Sierra de Santa Marta in Colombia, the interior slope of the Eastern Andes to Los Llanos, the Guyana Shield, the Sierra dos Cajadas region in Brazil, and the Andes in Ecuador, Peru and Chile. The regions with lower functional diversity than expected include the interior slope of the Andes down to the Amazon Basin and the southern part of the Brazilian Highlands along the Atlantic Coast (Figure 3).

Amphibian functional diversity, estimated using Hill numbers, was distributed in a relatively even manner across the Americas (Figure 4a). However, evenness varied extensively among regions, (Figure 4b–f), ranging from a nearly even distribution of functional diversity across North American assemblages (Figure 4b) to a highly uneven distribution across Amazonian assemblages (Figure 4e). Mexican, Panamanian and South American assemblages were moderately uneven (Figure 4c,d,f).

3.2 | Functional diversity and environmental variables

The SAR models showed that functional diversity was positively associated with annual precipitation and negatively with aridity index (Table 1). The contribution of annual mean temperature and precipitation seasonality varied between the models. In many models, annual mean temperature was not a significant predictor, whereas

precipitation seasonality was a significant positive predictor. In every case, the models with environmental variables outperformed null models. Table 1 shows the results for all Hill number q values, Shannon and Gini–Simpson indices.

3.2.1 | Spatial autoregressive models for Hill numbers

In general, functional richness was positively correlated with annual precipitation and negatively correlated with aridity index. Nagelkerke's pseudo- R^2 was > 0.80 . Lambda was always high and significant, indicating that spatial structure is a significant predictor of the distribution of functional diversity even after accounting for climate. Moran's I of the residuals was very close to zero and non-significant.

3.2.2 | Spatial autoregressive models for Shannon and Gini–Simpson indices

In the SAR model for the Shannon index, the contribution of annual precipitation was significantly positive; annual mean temperature was negative and non-significant. Precipitation seasonality was significantly negative. The aridity index was always significantly negative. The value of λ was always significantly high. Moran's I of the residuals was very close to zero and non-significant.

In the SAR model for the Gini–Simpson index, the annual precipitation was positive and significant; aridity index was negative and significant. Finally, annual mean temperature and precipitation seasonality were positive and significant (Table 1). The value of λ was

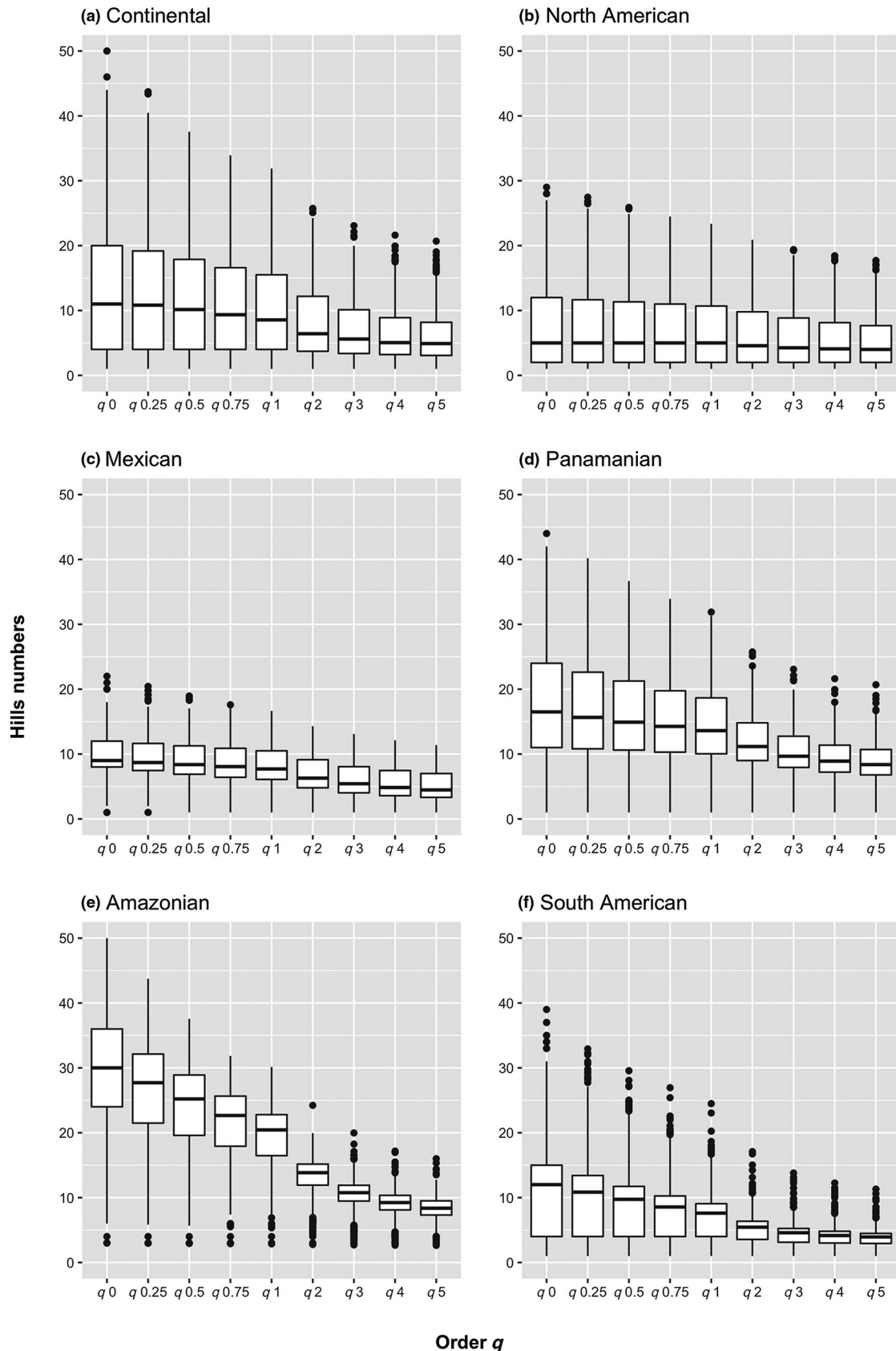


FIGURE 4 Functional evenness in assemblage structure of the New World Amphibians for the continental Americas (a) and the North American (b), Mexican (c), Panamanian (d), Amazonian (e) and South American (f) biogeographical regions (Holt et al., 2013). The slope of the curve indicates the level of unevenness in abundance of life-history traits within assemblages. A rapid decline of the curve indicates highly uneven abundance of functions, whereas a flat curve indicates an even distribution of the relative abundance of functions in the assemblage

TABLE 1 Summary of the spatial autoregressive models fitted to explain functional diversity of amphibians in the Continental Americas, including trait richness, Hill numbers when $q \cong 1$, and the Gini–Simpson index

Hill's number	Annual precipitation	Annual mean temperature	Precipitation seasonality	Aridity index	R ²	λ	Moran's I	AIC	AIC null model
$q = 0$ or traits richness	$2.08 \times 10^{-5***}$	5.94×10^{-7}	$4.47 \times 10^{-4***}$	$-2.37 \times 10^{-6***}$	0.82	0.94***	-0.07	-16,151	-16,010
$q = 0.25$	$2.08 \times 10^{-5***}$	2.42×10^{-7}	$4.47 \times 10^{-4***}$	$-2.37 \times 10^{-6***}$	0.82	0.94***	-0.07	-16,153	-16,016
$q = 0.5$	$2.08 \times 10^{-5***}$	-1.27×10^{-7}	$4.46 \times 10^{-4***}$	$-2.37 \times 10^{-6***}$	0.82	0.94***	-0.07	-16,155	-16,016
$q = 0.75$	$2.08 \times 10^{-5***}$	-5.05×10^{-7}	$4.46 \times 10^{-4***}$	$-2.37 \times 10^{-6***}$	0.82	0.94***	-0.07	-16,156	-16,014
$q = 1$ or exponential H	$2.08 \times 10^{-5***}$	-8.83×10^{-7}	$4.46 \times 10^{-4***}$	$-2.37 \times 10^{-6***}$	0.82	0.94***	-0.07	-16,157	-16,016
$q = 2$	$2.09 \times 10^{-5***}$	-2.27×10^{-6}	$4.45 \times 10^{-4***}$	$-2.37 \times 10^{-6***}$	0.82	0.94***	-0.07	-16,161	-16,020
$q = 3$	$2.09 \times 10^{-5***}$	-3.35×10^{-6}	$4.44 \times 10^{-4***}$	$-2.37 \times 10^{-6***}$	0.82	0.94***	-0.07	-16,163	-16,022
Shannon index	$3.18 \times 10^{-3***}$	-2.07×10^{-3}	$-1.48 \times 10^{-2***}$	$-1.75 \times 10^{-4***}$	0.95	0.97***	-0.03	16,262	16,522
Gini–Simpson index	$2.41 \times 10^{-4***}$	-3.87×10^{-4}	$4.69 \times 10^{-3***}$	$-2.52 \times 10^{-5***}$	0.85	0.95***	-0.08	2,379.7	2,561.4

Note: The regression coefficient presented is the Nagelkerke pseudo-R² for the autoregressive models (Liang & Zhou, 2010; Nagelkerke, 1991).

Abbreviation: AIC, Akaike information criterion.

Levels of significance signaled as follows: * < 0.05, ** < 0.01, *** < 0.001

always high and significant. Moran's I of the residuals was very close to zero and non-significant.

3.2.3 | Spatial autoregressive models for areas with residuals of species functional richness

The SAR model for the top quartile of positive residuals (higher functional diversity than expected) showed a negative and significant relationship with precipitation seasonality and a positive and significant (but less strong) relationship with annual precipitation (pseudo-R² = 0.35, AIC = -1,595). The SAR model for the bottom quartile of negative residuals (lower functional diversity than expected) behaved very differently, showing a significant and positive relationship with aridity index (pseudo-R² = 0.43, AIC = -635.22). In both cases, λ was moderately high and significant, and Moran's I of the residuals was very close to zero and non-significant.

4 | DISCUSSION

We show that the distribution of functional diversity in American amphibians follows a striking geographical gradient from Neotropical to extra-tropical regions (Figures 1 and 2), roughly mirroring the distribution of species diversity across this region and the latitudinal gradient of genetic diversity detected for Amphibians globally (Miraldo et al., 2016). This pattern of functional diversity is strongly associated with precipitation, temperature and aridity, suggesting that climate is a potentially important factor behind the functional diversity in amphibians.

Areas where functional diversity is greater than expected from the taxonomic diversity are characterized by high amounts of rainfall with low precipitation seasonality throughout the year (see Supporting Information Appendix S1, Figure S1). This finding is consistent with studies showing that rainfall is key for amphibian reproduction (e.g., Alexander & Eiseheid, 2001). For instance, the Brazilian Atlantic has consistently high precipitation and contains a large number of reproductive modes compared with sites that have high precipitation seasonality, such as ephemeral habitats, where the amphibian community has a relatively low diversity of reproductive modes (da Silva, Almeida-Neto, do Prado, Haddad, & de Cerqueira Rossa-Feres, 2012). On the contrary, areas showing lower functional diversity than expected have high aridity levels. The species that occur in those arid regions are strongly limited by water availability (see Chan & Zamudio, 2009), and this is reflected in the limited number of functional traits found.

We were surprised to find that mean annual temperature was not a significant predictor of diversity in areas with higher than expected functional diversity. Amphibians have critical thermal minima lower than other ectothermic vertebrates, such as reptiles (Buckley, Hurlbert, & Jetz, 2012; Sunday, Bates, & Dulvy, 2011; Sunday et al., 2015), and this is reflected in their distributional limits and the resulting geographical species richness patterns. These thermal ranges seem to be associated with specific adaptations to live in

cold environments and that might result in large-scale convergence patterns across the entire radiation of amphibians (Navas & Chauí-Berlinck, 2007; Sunday et al., 2011), probably in the same way that arid or highly seasonally environments do.

Functional evenness, which is the degree to which the functions of a community are distributed in the available ecological space to allow effective utilization of the entire range of resources (Mason, Mouillot, Lee, & Wilson, 2005), varied across regions. Interpretation of this pattern thus relies on how resources are distributed. If we assume that resources are evenly accessible across space, sites with low functional evenness might indicate that some ecological space is underutilized (Mason et al., 2005). In contrast, the uneven distribution of functions might reflect that accessibility of resources is highly uneven through space. Communities with high functional evenness are also considered more stable (because of the redundancy in all functions) and less prone to be invaded (Gerisch, Agostinelli, Henle, & Dziok, 2012; Mouchet, Villéger, Mason, & Mouillot, 2010). If that is the case, our results suggest that communities within the North American region are potentially more stable, and those in the Amazonian and Panamanian regions could be more prone to changes. It would also make the latter more vulnerable to invasive species (Gerisch et al., 2012).

It could be argued that sites that are rich in both species and functions should become urgent priorities for conservation, particularly compared with sites where there is less functional diversity than expected given the number of species (e.g., the interior slope of Los Andes to the Amazon). However, unique or rare functions should also be prioritized, because they represent a very particular evolutionary history, which is reflected in the exceptional characteristics that the species have developed to deal with a particular environment (Morrison & Hero, 2003).

To date, several studies have explored the extent to which long-term persistence of amphibians and the success of conservation efforts depend on the functional diversity and trait structure of communities (Becker, Loyola, Haddad, & Zamudio, 2010; Estrada et al., 2015; Loyola et al., 2008; Sodhi et al., 2008), especially considering that amphibians are among the most exceptional species in terms of evolutionary uniqueness; they (as a group) have a higher average evolutionary distinctiveness score than mammals or birds (Morelli & Møller, 2018). For a group as functionally diverse as amphibians, effective conservation planning must necessarily incorporate information on functional traits and natural history observations (Becker et al., 2010). Although species richness has long been observed as key to preserving and restoring disturbed communities (e.g., Brook, Sodhi, & Ng, 2003), functional diversity is crucial to maintaining the structure of the communities and, therefore, the functionality of the ecosystems with which they are associated (Becker et al., 2010). However, this does not contradict the long-standing argument for preservation of species richness in the hope that it confers functional redundancy.

Understanding the relationship between functional diversity and the underlying environmental conditions is key to being able to predict the responses of amphibian communities to changes in

these conditions. There is extensive evidence that past climate variations have had different effects on different groups of amphibians, from shaping their geographical ranges (Olalla-Tárraga et al., 2011) to promoting niche conservatism or diversification (Vieites, Min, & Wake, 2007); thus, it is very likely that future climate change will also significantly affect the diversity and structure of communities (e.g., Loyola, Lemes, Brum, Provete, & Duarte, 2014). We demonstrate that the functional structure of amphibian assemblages varies among regions, and it is very likely that different climatic and other evolutionary processes have shaped these patterns (Mouchet et al., 2010). Further analyses with long-term environmental stability might be ideal to explore the evolution of functional assemblages in amphibians. Finally, understanding how functional diversity relates to other types of diversity (phylogenetic and genetic) and other factors (besides climate) can pave the way for a more mechanistic understanding of the relationship between amphibian diversity and present and past environments.


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AUTHOR CONTRIBUTIONS

L.M.O.-O., K.A.M. and C.R. conceived the ideas; L.M.O.-O. and K.A.M. collected the data; L.M.O.-O., N.R.M.-D. and J.A.V. analysed the data; L.M.O.-O., K.A.M., N.R.M.-D. and J.V. led the writing.

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BIOSKETCH

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SUPPORTING INFORMATION

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