

Amphibian Speciation Rates Support a General Role of Mountains as Biodiversity Pumps

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ABSTRACT: Continental mountain areas cover <15% of global land surface, yet these regions concentrate >80% of global terrestrial diversity. One prominent hypothesis to explain this pattern proposes that high mountain diversities could be explained by higher diversification rates in regions of high topographic complexity (HTC). While high speciation in mountains has been detected for particular clades and regions, the global extent to which lineages experience faster speciation in mountains remains unknown. Here we addressed this issue using amphibians as a model system (>7,000 species), and we found that families showing high speciation rates contain a high proportion of species distributed in mountains. Moreover, we found that lineages inhabiting areas of HTC speciate faster than lineages occupying areas that are topographically less complex. When comparing across regions, we identified the same pattern in five biogeographical realms where higher speciation rates are associated with higher levels of complex topography. Low-magnitude differences in speciation rates between some low and high complex topographies suggest that high mountain diversity is also affected by low extinction and/or high colonization rates. Nevertheless, our results bolster the importance of mountains as engines of speciation at different geographical scales and highlight their importance for the conservation of global biodiversity.

Keywords: amphibians, macroecology, macroevolution, FiSSE, HiSSE, topographic complexity.

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Introduction

More than 80% of the world's terrestrial diversity is concentrated in mountain regions and their adjacent lowland foothills (Rahbek et al. 2019). The relief complexity, climatic conditions, and environmental heterogeneity that predominate in those regions has been correlated with well-documented high levels of diversity for numerous taxa around the globe (Antonelli et al. 2018). For example, in Central and North America, mammal diversity is greater in regions dominated by mountains and complex reliefs (Simpson 1964); likewise, peaks of species richness and endemism of Afrotropical avifauna occur within mountains and mountain-lowland complexes (De Klerk et al. 2002). Globally, most centers of vascular plant richness (>5,000 species per 10,000 km²) occur in regions dominated by mountainous areas such as Costa Rica–Panama, Tropical Eastern Andes, Atlantic Brazil, Northern Borneo, and New Guinea (Barthlott et al. 2005). Although mountains around the globe cover less than 15% of the world's land surface (Antonelli 2015), they concentrate approximately 90% of the global hot spots of species diversity and 40% of the hot spots of endemism (Myers et al. 2000). Still, we lack a comprehensive understanding of the mechanisms that drive such extraordinarily high diversity in mountains (Graham et al. 2014; Rahbek et al. 2019).

Many hypotheses have been proposed to explain high biodiversity in mountains. From an evolutionary perspective, mountain systems have been hypothesized as engines of diversification, because of their potential to drive speciation both in allopatry and parapatry (Funk et al. 2016).

Evidence of allopatric speciation (Mayr 1963) promoted by the vicariant settings implicit in complex topographies has been widely documented in a variety of taxa (Rull 2005; Guarnizo et al. 2009). For many organisms, the irregular configuration of alternate mountaintops and valleys represents mosaics of favorable and unfavorable habitats (Kozak and Wiens 2006) that increases isolation among populations, thereby increasing opportunities for allopatric speciation (Moritz et al. 2000). Moreover, the distribution of such suitable regions has varied in response to historical climatic oscillations, increasing the chances of allopatric diversification in mountains (Wiens and Graham 2005). Mountains also cover wide environmental spectrums over short distances along their elevational gradients (Graham et al. 2014; Merckx et al. 2015). These transitions offer ideal conditions where ecological speciation in parapatry can take place (Rundle and Nosil 2005). Under these circumstances, some studies suggest that local pressures can drive adaptive divergence between populations, leading to the formation of new species, even in the absence of hard geographic barriers (Graham et al. 2004; Chapman et al. 2013).

Recently, some specific hypotheses based on this evolutionary framework have been proposed to explain the rich biotas in mountain regions (Graham et al. 2014). One of them is the Montane species pump hypothesis, which predicts that clades occurring in mountains have higher rates of net diversification (Smith et al. 2007). Such conditions would be likely associated with higher rates of speciation resulting from a combined effect of opportunity for allopatry and the presence of steep ecological gradients that may also promote species origination in parapatry (Perrigo et al. 2020). This combination of ecological, evolutionary, and geological events has often linked biological radiations in many groups to mountain building and climatic processes taking place in these regions (Badgley et al. 2017).

Evidence specifically supporting the species pump model has been reported for Mesoamerican hyliid frogs and for tanagers and butterflies from the Andes (Hall 2005; Fjeldsa and Rahbek 2006; Smith et al. 2007). In these cases, speciation is faster in montane clades than in those restricted to lowlands. However, attempts to determine the generality of this pattern have been scarce. Most studies testing whether regions of complex topography function as speciation pumps are too restrictive in terms of their phylogenetic scope (i.e., few specific clades) and geographical extent (i.e., explored mostly local to regional scales).

Here, we implemented assemblage-level analyses to test whether speciation rates differ between areas of high topographic complexity (HTC) and low topographic complexity (LTC) across the globe and within zoogeographic realms. Moreover, we implemented species-level analyses to test whether topographic complexity (TC) was associated with speciation rates across the entire amphibian phylogeny. To

test these hypotheses, we used an integrated worldwide biogeographic data set with a nearly complete phylogeny of amphibians (Jetz and Pyron 2018), using this vertebrate group as a study system.

Methods

Study System

Amphibians are a particularly suitable study system to test the montane pump hypothesis because they represent an ancient (>300 myr) radiation (~8,000 species; www.amphibia web.org), with widespread latitudinal and altitudinal distribution across the globe and growing availability of phylogenetic information (Jetz and Pyron 2018). Also, amphibians show high philopatry (Blaustein et al. 1994), restricted dispersal abilities (Beebee 2005), limited osmotic tolerance (Balinsky 1981), high sensitivity to temperature in early developmental stages (Berven and Grudzien 1990), and adaptations to particular elevations (Bonin et al. 2006). Such features, in most cases, bond their evolutionary fate strongly to their geographic settings, providing a valuable opportunity to investigate the forces shaping speciation patterns in mountain regions.

Amphibian Phylogeny

Considering the global character of our study, we attempted to improve the performance of our analysis by using a set of trees containing as many species as possible. We based our macroevolutionary analyses on recently published trees, which to date represent the most complete amphibian phylogenetic inference (Jetz and Pyron 2018). These trees were constructed using the phylogenetic assembly with soft taxonomic inferences (PASTIS) approach (Thomas et al. 2013) to update an existing molecular supermatrix (Pyron 2014) that contains sequence data (five mitochondrial and 10 nuclear genes) for ~56% of extant amphibian species. A maximum likelihood topology for these species then served as a backbone for a set of 10,000 trees containing 7,238 species, which represents ~90% of the known extant amphibian diversity and includes most families, subfamilies, and genera. For a detailed description of dating and tree construction, see Jetz and Pyron (2018).

Distribution of Amphibian Families with High Speciation Rates

To estimate speciation rates at the family level, we calculated tip-level rates with the diversification rate (DR) metric (Jetz et al. 2012) for 100 random trees from the posterior probability distribution and then averaged the rates for the species belonging to each family. The calculation of DR considers the number of splitting events and the internode distances

along the root-to-tip path of the phylogeny, while giving greater weight to branches closer to the present (Jetz et al. 2012). Although DR is a non-model-based approach to estimate macroevolutionary tip rates, it is a good metric to capture evolutionary dynamics, particularly speciation rates (Title and Rabosky 2019). Additionally, to support the DR results, we ran the Bayesian analyses of macroevolutionary mixtures (BAMM; Rabosky et al. 2014) across 10 random trees (details can be found in the supplemental PDF, available online). We found a significant correlation between both estimations (fig. S1; figs. S1–S4 are available online), which consistently returned the same five families with the higher speciation rates based on the 90th percentile of the mean rates at the family level.

To illustrate the distribution of fastest speciating lineages, we gathered range polygons from IUCN assessments for all species belonging to these five families ($N = 989$ species, >70% of the total species richness in these groups). For each of these species, we obtained a proxy of topographic complexity. To this end, we first generated a global topographic complexity index (TCI) by calculating the standard deviation of differences between elevations in 100×100 adjacent cells from a global layer of elevation at 30 arc-second resolution (~ 1 km at the equator; <http://www.worldclim.org/>) using the R package raster (Hijmans and van Etten 2010). This procedure has been demonstrated to more accurately represent topographic roughness than the elevation range, which only indicates the strength of a gradient within a cell (McCarroll and Nesje 1996). Next, using species range polygons, we extracted and averaged the TCI values for all the cells that overlap with the species distribution. With this information, we quantified the percentage of species of each fast diversification family distributed in heterogeneous topographies as those having mean TCI values above 300. This threshold classifies as heterogeneous areas having deviations of at least 300 m from the mean elevation of the species range. We consider this to be a conservative criteria given that previous work has defined as mountains areas with differences of 200 m between their lowest and highest altitudes (Körner et al. 2011). Additionally, we compiled elevation data from IUCN for a subset of 4,675 amphibian species ($\sim 60\%$ of the global amphibian diversity). Based on this, we categorized as lowland species those having maximum elevations below 1,000 m and as montane species all species reaching elevations above 1,000 m. Next, we estimated the percentage of lowland and montane species for each of these families.

Projecting Speciation in Geographical Space

To test the influence of topographic complexity on speciation dynamics, we projected tip-level DR values onto geography, using geographical range maps for 6,311 species

obtained from the IUCN (<http://www.iucnredlist.org>). These maps represent approximately 80% of the known extant amphibian species ($\sim 8,300$ species; <http://www.amphibiaweb.org>). Although we estimated macroevolutionary dynamics using $\sim 90\%$ of amphibian diversity represented in our phylogenetic tree, available range maps limited this analysis to a smaller number of species. We overlaid species range maps in a $1^\circ \times 1^\circ$ global grid to create a presence-absence matrix using the R package LetsR (Vilela and Villalobos 2015). To prevent the loss of species with very restricted distributions, we assumed presence of a given species in all the cells that intersect its range without defining a minimum percentage of cell coverage. With this approach, we estimated mean speciation rates based on species composition within each grid cell.

Some authors have argued that species ranges may be too dynamic and could mask any potential relationship between current distributions and the geography of speciation (Fitzpatrick and Turelli 2006). However, strong evidence supporting range stasis is available in the literature for a variety of organisms, from fossil mollusks to living insects and mammals (Ribera et al. 2011; Cardillo 2015). We considered that it is unlikely that all species have altered significantly their ranges enough to remove the geographical signal from their past distribution. Most amphibian species have low dispersal ability (Beebee 2005) and are highly sensitive to environmental conditions, resulting in a high proportion of species of small range sizes (Grenyer et al. 2006). Therefore, the effects of range dynamics on the geographical signal we are investigating should be a minor concern in this study, especially at the scales we are working.

Patterns of Speciation in Regions of Low and High Topographic Complexity

To evaluate whether there were differences in speciation rates between regions of varying topographic complexity, we adopted an assemblage-based analysis. First, we used mean values per cell to review the relations between topographic complexity and speciation rates in the global and regional scale. For this, we fitted spatial autoregressive (SAR) models with a spatial error term to consider spatial autocorrelation (Diniz-Filho et al. 2003). These models use weight matrixes that specify the strength of interaction between neighboring sites aiming to account for spatial autocorrelation (Dormann et al. 2007; Kissling and Carl 2008). We created a neighborhood matrix for each model using 1° as maximum connectivity distance, and an inverse square distance weighting function ($1/d^2$). To estimate the variance explained by each model, we calculated pseudo- R^2 based on the Nagelkerke formula (Nagelkerke 1991). Pseudo- R^2 represents the variance explained by both the predictor variable and space. To include the variance explained by the

predictor alone, we report the R^2 from least squares linear models (table 1; fig. S2).

TC is not evenly distributed around the world (Körner et al. 2017), and the number of cells with low values exceeds by multiple orders of magnitude the number of cells with high values across the globe. To account for this difference, we also applied a categorical approach. For this, we reclassified all grid cells according to two categories: LTC and HTC using the same 300 m in standard deviation of elevation cut-off value described above. Then, we compared whether assemblage speciation rates (i.e., tip-level speciation rates from all species occurring in a given grid cell) differed between LTC cells and HTC cells. Since HTC cells represent only a small fraction of the total number of cells across the globe (14.5% of all cells analyzed), we resampled 1,000 times the same number of cells categorized as HTC from the LTC pool to compare the distribution of values of speciation rate in LTC with the mean speciation in HTC (fig. S4).

To test how speciation rates vary between LTC and HTC regions at different latitudes, we conducted this same analysis within the updated zoogeographic realms (Holt et al. 2013). This classification defines robust biogeographic units based on global distributions and phylogenetic relations from >20,000 of the world's vertebrate species (Holt et al. 2013). Using this delimitation therefore also allows us to consider the unique evolutionary histories of the different zoological realms. To report significance, in each case we used t -tests to compare the mean speciation rate of HTC with the distribution of mean speciation rates of the LTC replicates (table S1; tables S1, S2 are available online).

Speciation Rates across the Gradient of Topographic Complexity

We used two diversification models of state-dependent speciation and extinction (SSE), where rates of speciation

and extinction are linked with exposure to topographic complexity exhibited by each amphibian species. In particular, we used the fast, intuitive state-dependent speciation and extinction (FiSSE) model (Rabosky and Goldberg 2017) and the hidden state speciation and extinction (HiSSE) model (Beaulieu and O'Meara 2016). We defined LTC and HTC as a binary character and categorize each species within these classes. We used a presence-absence matrix and estimated a mean topographic complexity value for each species based on the TC estimates of the cells where the species occur. Then, following the same procedure applied in the assemblage-based approach, we used as threshold a value of 300 m in standard deviation of elevation.

We first applied the HiSSE approach, which allows assessing the impact of hidden binary traits on diversification. We ran a set of 22 models including models under the binary state speciation and extinction (BiSSE) framework, null models under the HiSSE framework and 16 additional models under the HiSSE framework suggested in Beaulieu and O'Meara (2016; see table S2). We assessed models based on their corrected Akaike information criterion score (Akaike weights and delta Akaike). The best selected model was a BiSSE with all free parameters, and we ran this across 100 trees of the posterior probability distribution. We adopted this strategy due to the tree size (>7,000 terminals) and high computational cost to run all SSE models using 100 trees. These analyses were implemented using the R package *hisse* (Beaulieu and O'Meara 2016). Additionally, we applied the nonparametric method FiSSE, which explores the distribution of branch lengths in the different states instead of assuming an underlying model structure (Rabosky and Goldberg 2017). Accordingly, we used our categorization of species as LTC and HTC and performed a two-tailed test of FiSSE also on a set of 100 random trees of the posterior probability distribution.

Table 1: Regression coefficients, significance, and R^2 for the spatial autoregressive models implemented globally and at the realm level

Region	Slope	SE	P	Adjusted R^2	Pseudo- R^2
Global	6.47E-07	1.78E-07	.0003	.0057	.9689
Afrotropical	-5.13E-10	5.39E-07	.9992	0	.9495
Australian	5.91E-06	1.83E-06	.0012	.1783	.9215
Madagascan	-4.15E-07	3.13E-06	.8944	.0894	.6196
Nearctic	1.17E-06	5.77E-07	.0419	.0533	.9556
Neotropical	1.12E-06	3.12E-07	.0004	.0763	.7528
Oceania	2.01E-07	8.23E-07	.8071	0	.1191
Oriental	-7.26E-10	2.92E-07	.998	0	.8535
Palaearctic	1.03E-06	3.93E-07	.0086	.0114	.9721
Panamanian	3.37E-06	1.02E-06	.0009	.1798	.7017
Saharo-Arabian	8.07E-07	8.83E-07	.3611	.1878	.9353
Sino-Japanese	-1.16E-06	5.69E-07	.0419	.0619	.8867

Results

Distribution of Amphibian Families with the Highest Speciation Rates

Speciation estimates using the DR and BAMM approaches were significantly correlated (fig. S1). With both metrics, we consistently found that Alsodidae, Plethodontidae, Centrolenidae, Bufonidae, and Phyllomedusidae are those with the fastest speciation rates of all 75 families evaluated (fig. 1A). With the exception of Phyllomedusidae (23%), these families have 50% or more of their representatives predominantly occurring in highly complex topographies (fig. 1B). Moreover, most of the species belonging to these families occur in mountainous settings above 1,000 m elevation (fig. 1C).

Patterns of Speciation in Regions of Low and High Topographic Complexity

Speciation rates seem to be spatially decoupled from the geographic patterns of richness (fig. 2) but are positively as-

sociated with TC at the global scale (fig. 3; table 1). At the realm level, we found this same trend for the Australian, Neotropical, Nearctic, Palearctic, and Panamanian realms (fig. 3; table 1). We found an inverse relationship for the Sino-Japanese realm (table 1). For the remaining realms (Afrotropical, Madagascan, Oceania, Oriental, Saharo-Arabian), we did not find a significant effect of topography on speciation rates.

According to our classification, TC is highly unevenly distributed across the globe, with only ~14% of the global cells corresponding to HTC regions. Oceania and Panamanian realms show particularly rough terrains, with ~49% and ~47% of their total area corresponding to HTC, respectively. Contrarily, in the Australian and Afrotropical realms, <7.5% of their respective areas are classified as topographically complex (fig. S3). Using these categories, we also found faster rates of speciation in HTC regions than in LTC regions globally ($HTC_{\text{mean}} = 0.0635$, $LTC_{\text{mean}} = 0.0607$; $P < .05$). We found this same trend of faster speciation in HTC for five realms: Australian, Madagascan, Neotropical, Panamanian, and Palearctic (table 2). While we found some exceptions of higher speciation in LTC for the Nearctic,

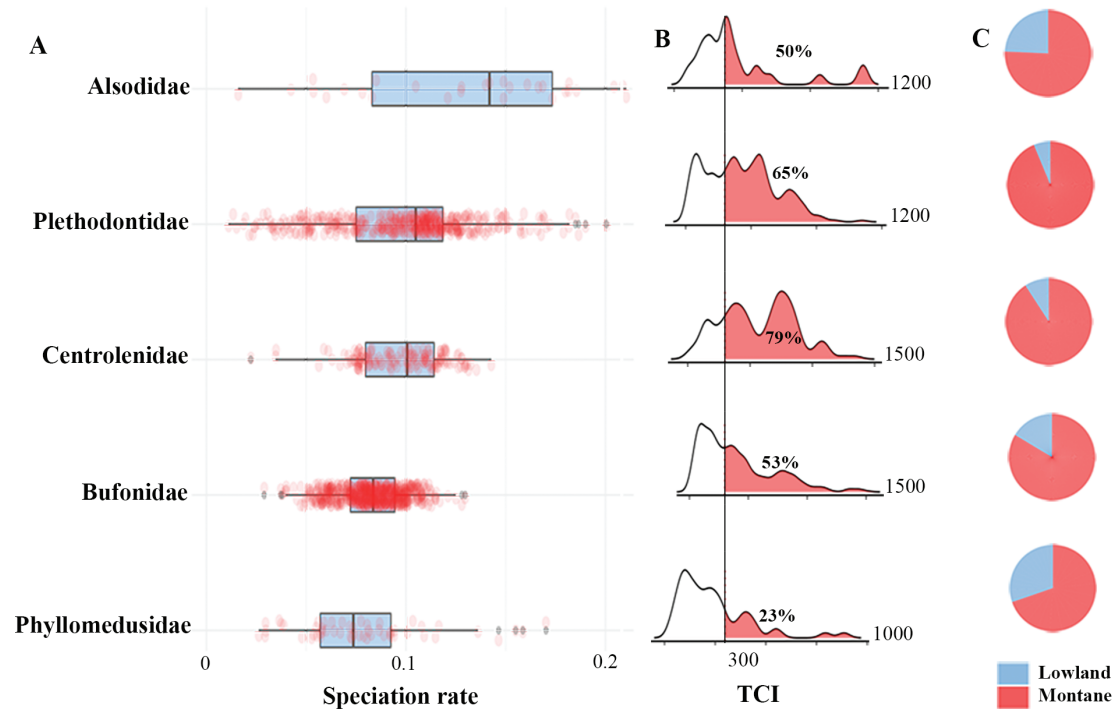


Figure 1: Diversification rates (DRs), topographic complexity, and altitudinal distribution in families of fast diversification. *A*, Mean speciation rates estimated across 100 random trees from the posterior distribution with the DR metric. *B*, Family's distribution in terms of topographic complexity. The red portion of the density plot represents species distributed in regions of complex topography, based on a 300 threshold of the topographic complexity index (TCI). *C*, Relative proportion of species within the family restricted to elevations below 1,000 m (blue) and those occurring in higher elevations (red).

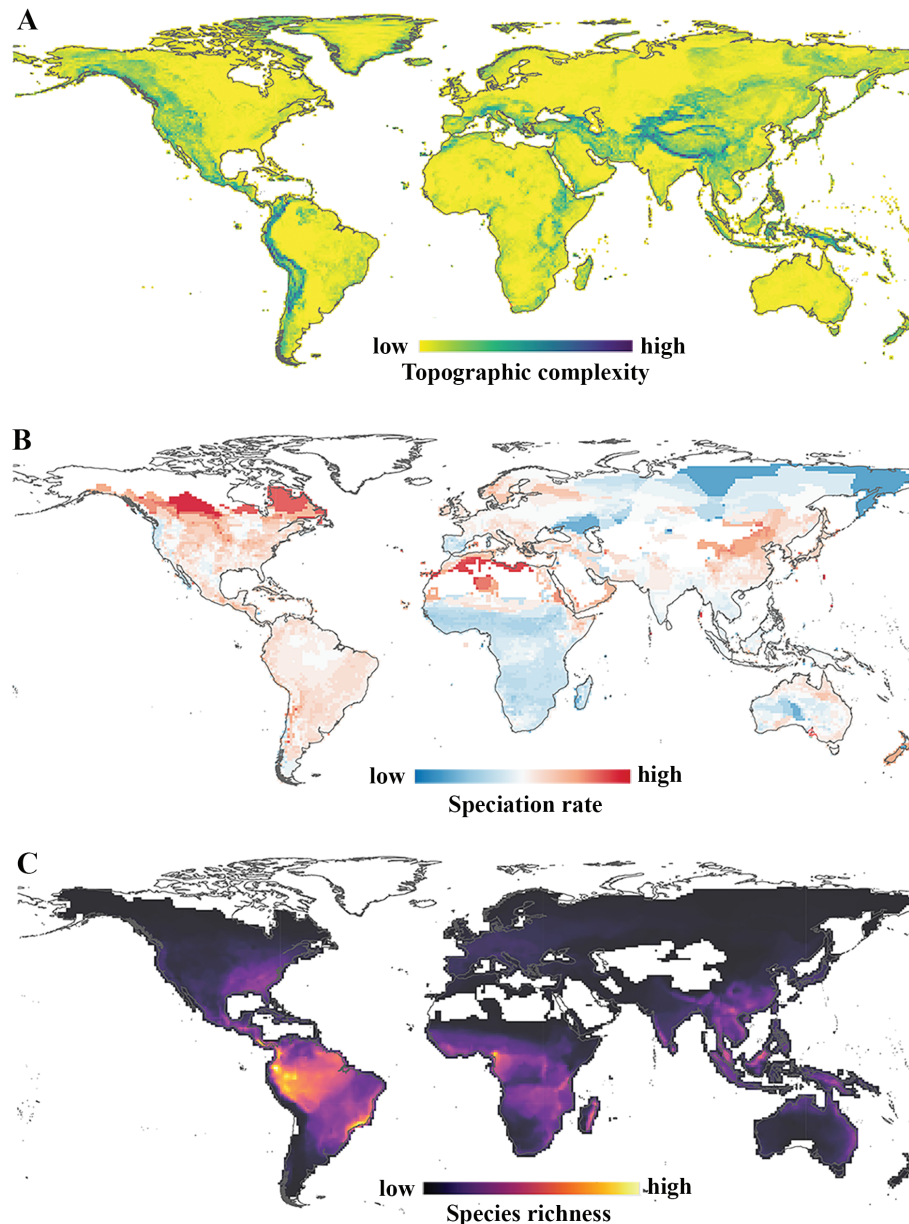


Figure 2: Global geographic patterns of topographic complexity (A), mean speciation rate (B), and species richness (C) in amphibians per 1° grid cell.

Saharo-Arabian, and Sino-Japanese realms (fig. 3), we did not find significant differences between LTC and HTC for the Afrotropical, Oceania, and Oriental realms.

Speciation Rates across the Gradient of Topographic Complexity

The SSE analyses were consistent with the differences we found among HTC and LTC in the assemblage-based ap-

proach. Regarding the HiSSE approach, the classic BiSSE model with parameters free outperformed all other models (table S1). With this model, mean speciation rates estimated across 100 replicates were 0.058 and 0.039 for HTC and LTC, respectively ($t(144) = -19.2, P < .05$; fig. 4). With the FiSSE approach, we confirmed this result showing differences among speciation rates in HTC and LTC areas in most comparisons ($t(188) = -17.1, P < .05$; fig. 4). Average tip-rate speciation in species occurring in highly

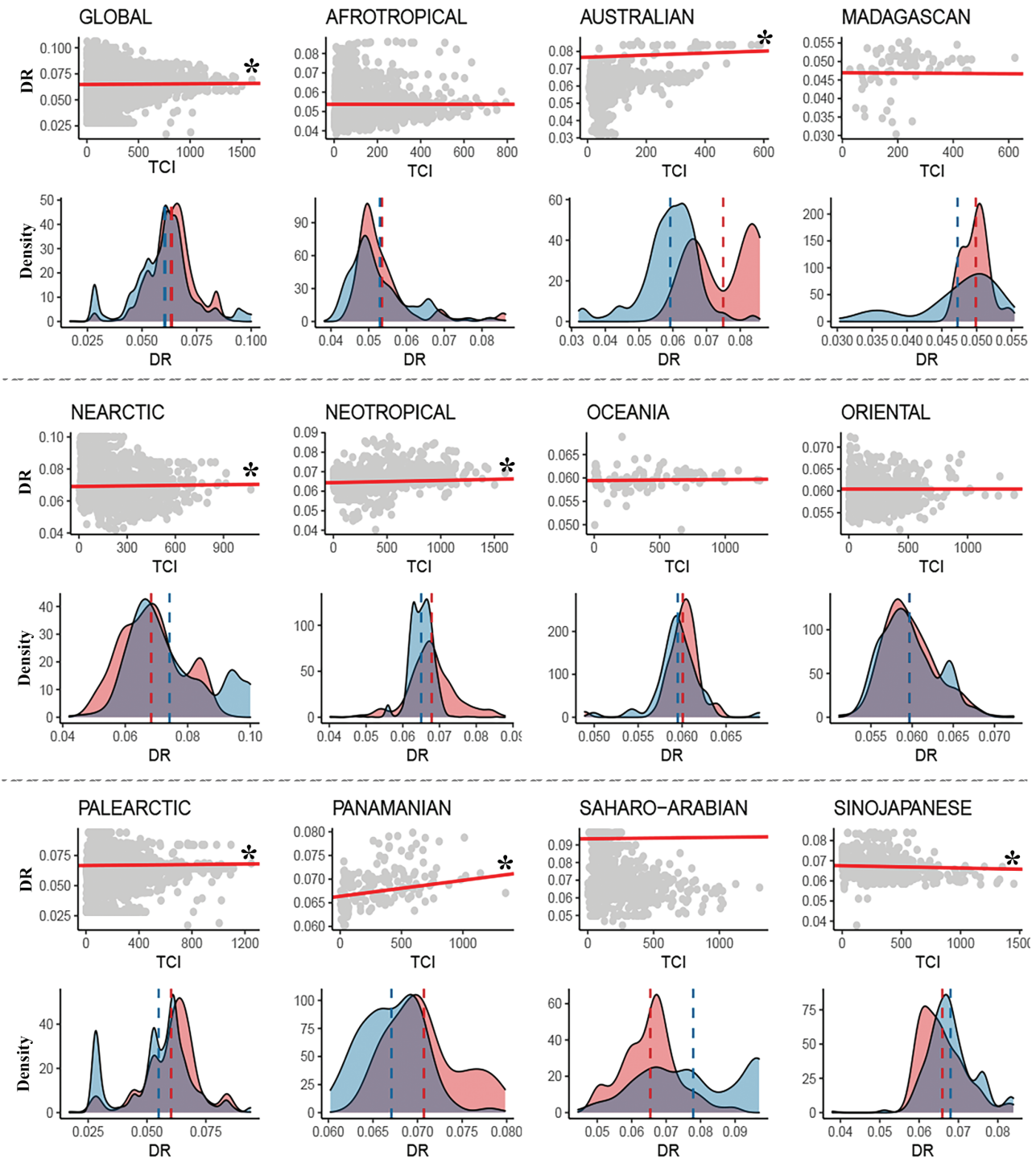


Figure 3: Relations between speciation rates and topographic complexity and comparisons of speciation estimates in low topographic complexity (LTC) and high topographic complexity (HTC) areas for the studied regions. In the scatterplots, the red lines correspond to the fitted spatial autoregressive (SAR) model. In the density, the distribution of speciation estimates in areas categorized as LTC are shown in blue, while those in HTC areas are shown in red. Dashed lines represent the mean speciation rate within each category, using the respective colors. Asterisks in the regressions represent significance in the respective SAR model. DR = diversification rate; TCI = topographic complexity index.

Table 2: Results of *t*-tests for the comparison between mean speciation rates in low topographic complexity (LTC) and high topographic complexity (HTC) areas at each of the studied regions

Region	% HTC	LTC mean speciation rate	HTC mean speciation rate	<i>t</i>	df	<i>P</i>
Global	14.219	.060	.064	13.44	4,626.60	<.05
Afrotropical	7.432	.054	.053	.95	232.72	.344
Australian	3.131	.059	.075	9.74	32.77	<.05
Madagascan	23.611	.047	.050	2.78	69.99	<.05
Nearctic	17.781	.074	.068	-10.74	792.54	<.05
Neotropical	16.834	.065	.068	7.95	401.87	<.05
Oceania	49.123	.060	.060	1.31	109.73	.194
Oriental	23.304	.060	.060	.03	417.17	.977
Palaearctic	12.011	.055	.060	10.58	1,029.00	<.05
Panamanian	47.799	.067	.071	6.01	143.68	<.05
Saharo-Arabian	26.165	.078	.065	-15.58	689.09	<.05
Sino-Japanese	42.504	.066	.068	-4.31	568.00	<.05

Note: Also shown in this table is the relative area covered by rough landscapes (HTC) within each region.

complex topographies was also higher than in those of more homogeneous regions: $\lambda_{\text{HTC}} = 0.087$, $\lambda_{\text{LTC}} = 0.074$ (fig. 4).

Discussion

Using a combination of macroecological and macroevolutionary approaches, we found differences in speciation rates between amphibian lineages inhabiting regions with different degrees of TC. Our results were consistent across multiple taxonomic groupings (i.e., across the entire amphibian radiation and across families) and geographical scales (i.e., globally and across biogeographical realms). We showed that lineages with faster speciation rates tend to inhabit regions with complex topographies using both assemblage-based and species-level approaches. Our study supports the findings of many previous studies that showed faster speciation rates in specific mountain regions (Hall 2005; Fjeldsa and Rahbek 2006; Smith et al. 2007) and is the first to reveal the generality of this pattern at global scale for amphibians.

Our results show that most families with fast speciation rates are predominantly distributed in mountainous settings, with many of them specifically in the Andes. Among them, we recovered Alsodidae as the amphibian family with the fastest speciation rates. This family has ~50% of its representatives distributed in complex topographies (fig. 1) from the Andean settings of Argentina and Chile (<http://www.iucnredlist.org>). Another predominantly Andean family showing fast speciation rates is Centrolenidae (Pyrton and Wiens 2011), with the 79% of the species evaluated occurring in regions of complex topography and most reaching montane elevations. Consistent with our results, several studies have reported accelerated diversification rates in Andean lineages (Santos et al. 2009; Sedano and Burns 2010). For example, rapid shifts of diversification

have been previously documented (Hutter et al. 2017) in several families with representatives in the Andes, including some here reported as families of fast diversification (e.g., Centrolenidae and Bufonidae). In general, these studies highlight the relevance of montane conditions and geomorphology as drivers of diversification but also recognize the complementary importance of evolutionary time in shaping the richness patterns in this biodiversity hot spot (Hutter et al. 2013, 2017).

We also found examples of fast diversification at the family level in other regions. For example, we detected high speciation rates in the Plethodontidae family of lungless salamanders. Plethodontids are widely distributed in the Nearctic realm, with several species occurring in North American Sky Islands (Kozak et al. 2006). However, the highest diversity is represented by the Bolitoglossines, the unique salamander lineage to have colonized the Neotropics and radiated in Mesoamerica (Rovito et al. 2015), where the rough topography had shaped micro-endemic distributions and many species are restricted to highland forests (Boza-Oviedo et al. 2012). Overall, this provides additional examples of the key role of mountainous areas as cradles of diversity for many amphibian lineages across the globe.

Using an assemblage-based approach, we confirmed that the trend of faster speciation in complex topographies is a general pattern at global scale. Moreover, we consistently found evidence of higher speciation rates in areas of HTC for five biogeographical realms, reinforcing the importance of mountainous regions for evolutionary processes. Rates of speciation can be influenced by both intrinsic biological attributes and extrinsic environmental factors (Funk et al. 2016). Some of the latter factors may be magnified in topographically complex landscapes. For example, characteristic rugged reliefs in mountainous regions are more likely to impose physical barriers, fragmenting

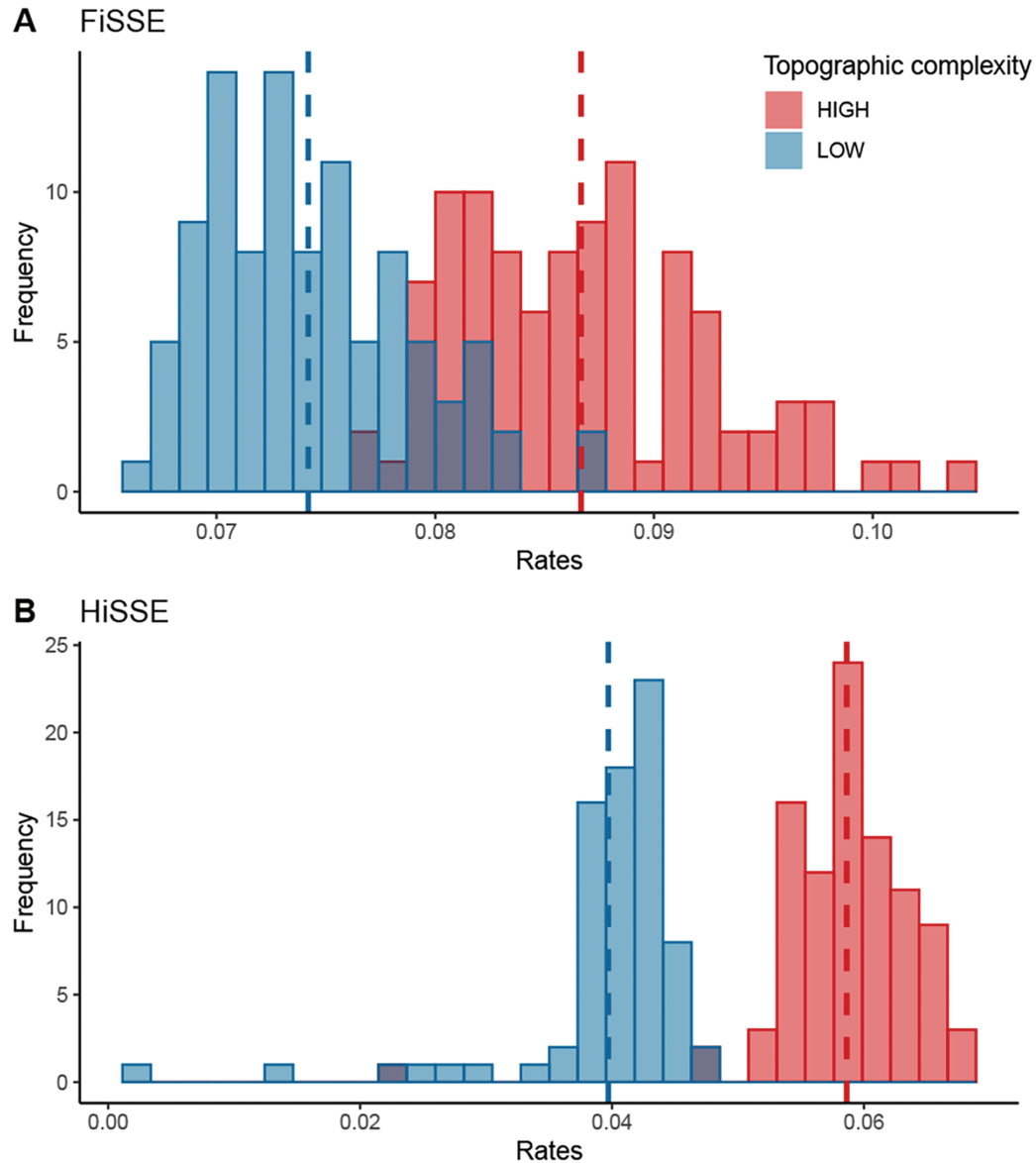


Figure 4: Comparison of average speciation rates corresponding to species occurring in homogeneous landscapes (blue; low topographic complexity) and topographically complex regions (red; high topographic complexity) based on two approaches. *A*, Results from the fast, intuitive state-dependent speciation and extinction (FISSSE) analysis. *B*, Results from the hidden state speciation and extinction (HiSSE) analysis. Bars represent the distribution of estimates from 100 random trees, and dashed lines represent the respective mean values for each group.

species ranges and promoting geographical isolation (Mayr 1963; Rundle and Nosil 2005). Furthermore, altitudinal gradients in these complex landscapes provide heterogeneous environmental conditions that could promote ecological specialization and niche divergence based on trait differences (Guarnizo and Cannatella 2013). Both scenarios restrict gene flow, driving speciation whether in allopatric or parapatric conditions. Although the pattern is consistent across many regions, we found a negative association between topography and speciation rates in the Sino-Japanese

realm. This is not a large geographical area and it also does not hold a particularly diverse amphibian biota. It is possible that this result is influenced by a few lineages that have high speciation rates and are also distributed in LTC areas.

Results from our species-level analyses that incorporate the evolutionary history of the group also support the relevant role of mountains as speciation pumps. Using two different approaches, we found that species distributed in regions characterized as topographically complex have higher speciation rates. Certainly for groups with low dispersal

rates, such as amphibians, intermittent conditions of suitability among peaks and valleys appear to have a major impact during incipient population differentiation, ultimately fueling the process of speciation (Guarnizo et al. 2009). In that same context, a growing body of literature provides evidence supporting the role of several mountains, for example, the Australasian Sky Islands (Atalay 2006), Henguan Mountains (Xing and Ree 2017), and Tropical Andes (Rangel et al. 2018), as species cradles not only for amphibians but also for numerous taxa. While most of those studies often focused on few clades and specific geographic regions that exhibit high diversity (Fjeldsa et al. 2012; McGuire et al. 2014; De-Silva et al. 2016), our study is one of the few (Quintero and Jetz 2018) that contrasts evolutionary rates in areas of complex and homogeneous topographies, using both species-level and assemblage-based approaches in regional and global scales. We provide strong evidence to support the notion of a general role of mountain ranges as speciation pumps across the globe and for different lineages.

Our findings bolster the general importance of mountains as engines of speciation at different geographical scales and independent of latitude. Unfortunately, many mountain ranges remain unexplored due to their remote conditions, while in many others, human pressures increase extinction risk (Elsen et al. 2020). In this scenario, mountains' unique diversity could disappear before we recognize its real contribution to the origin and maintenance of global biodiversity. The evidence presented here highlights the role of such areas in the evolutionary history of modern patterns of diversity. We suggest that mountains around the world must be considered as conservation priorities in local and regional agendas. Further efforts must be oriented to increase knowledge about mountain geodiversity and biodiversity to guide future decisions for the protection of their particular biotas.

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Statement of Authorship

A.G.R., P.A.M., B.F.O., and G.C.C. conceived and designed the study; A.G.R. and R.A.P. compiled the data; A.G.R., B.F.O., and J.A.V. conducted analyses; A.G.R. and J.A.V. were in charge of data visualization; and A.G.R., B.F.O., and G.C.C. wrote the manuscript, which all authors reviewed and edited.

Data and Code Availability

The phylogenies used come from a random set of trees extracted from the posterior distribution of probabilities made available by Jetz and Pyron (2018) at https://vertlife.org/files_20170703/#amphibians. The topographic complexity index was calculated using an elevation layer available at <http://www.worldclim.org> at 30-s resolution. Codes and data used in our analyses are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.547d7wm7q>; García-Rodríguez et al. 2021).

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