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Elevational diversity gradients of amphibians in Mexican mountain ranges: patterns, environmental factors, and spatial scale effects

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SUMMARY

Mountains are estimated to harbor the highest diversity in many taxonomic groups. However, patterns of elevational distributions and their underlying explanatory environmental variables have not been well studied in amphibians. We explore elevational patterns of species richness in amphibians and evaluate seven environmental models that may explain such patterns. We also test how the spatial scale of elevational bands affects the perceived patterns and the power of the explanatory variables. We utilized records from the most comprehensive amphibian database of Mexico. Gradients were selected across five Mexican mountain ranges, for both coastal and continental slopes, according to four criteria that allowed for standardization. Species richness-elevation relationships were classified into five patterns as described in the literature. Generalized linear models / Generalized estimating equations were applied to test six models, which include temperature, precipitation, water-energy dynamics, topographic heterogeneity (TH), their interaction and area. Species richness and environmental factors for each model and each gradient were calculated at four spatial scales of elevational bands (100, 200, 300, and 500 m). A total of 20 gradients were evaluated, for which all five patterns of species richness reported in literature were observed at least once. The pattern of mid-peak richness was the most commonly observed, followed by a decreasing pattern of richness with elevation. The water-energy dynamic was the best model at smaller spatial scales, while temperature, TH and area, became increasingly important in explaining richness patterns as the spatial scale increased. The elevational distribution of species richness in amphibians showed similar tendencies as described in literature. This study demonstrated a larger variation in the power of explanatory variables between mountain ranges than between spatial scales. In general, the proportion of variance explained was high, showing that the chosen explanatory environmental variables are important in structuring the elevational patterns.

INTRODUCTION

Montane systems are viewed as natural experiments and, therefore, have received great attention in scientific research and hypothesis testing for at least the past two centuries (Grytnes and McCain 2013, Lomolino 2001). These systems occupy approximately 25% of earth's land cover and contain approximately 85% of the planet's amphibian, avian, and mammal species (Körner 2007, Rahbek et al. 2019), thus providing ample opportunity to evaluate natural experiments and test hypotheses at different spatial scales in its two components: extend or the geographical area under study and grain of the standardized unit of analysis (Schneider et al 2000).

Rahbek (2005) and McCain (2010) have classified the patterns of elevational variation in species richness into five categories (Fig. 1): (1) decreasing (D), in which species richness decreases as elevation increases (Fig. 1a); (2) low plateau (L), in which higher species richness is observed in the lowest part of the gradient, after which a steady decrease is seen as elevation increases (Fig. 1b); (3) low plateau with a mid-peak (LM), similar to L except that a peak of at least three additional species is observed above a certain elevation from the lowest elevational point in the gradient, followed by a steady decrease in species richness as elevation increases (Fig. 1c); (4) mid-peak (M), characterized by a unimodal curve with at least 25% more species at intermediate elevations than at lower and higher elevations, and whose maximum species richness is recorded at a certain elevation above from the lowest elevational point in the gradient (Fig. 1d); and (5) increasing (I), in which the sampling shows a pattern of increasing species richness as elevation increases (Fig. 1e).

Mexico is an ideal place to evaluate different hypotheses regarding these patterns, given the extensive mountain ranges that exist within the country (Quiñonez 1984). The spatial heterogeneity of Mexico is one of the many factors contributing to the country's high biodiversity. Due to its vast number of species, Mexico is recognized as a mega-diverse country (Sarukhán and Dirzo 2013). The mountain ranges and neighboring regions are thought to harbor the highest diversity of plant and vertebrate species within the country, given the large environmental variability associated with these systems (Espinosa and Ocegueda 2008). Among other vertebrate groups, amphibian diversity stands out in Mexico. While 5% of the planet's amphibian species are found in Mexico (over 420 recognized species, Frost 2019), approximately 70% of them represent endemic species.

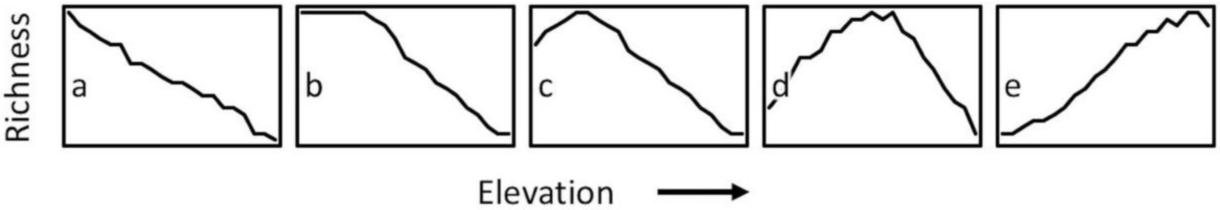

Figure 1. Patterns of distribution: a. Decreasing (D); b. Low plateau (L); c. Low plateau with Mid-peak (LM); d. Mid-peak (M); Increasing (I).

Amphibians are ectothermic terrestrial vertebrates with unique life cycles. The majority of species live conditionally on the availability of water for reproduction and the development of their larvae (Vitt and Caldwell 2014). Many large-scale studies have found evidence for a coupled relationship between species richness and climatic variables in amphibians. In particular, precipitation and temperature are considered the main environmental variables in explaining observed patterns of species richness (e.g. Buckley and Jetz 2007, Fu et al. 2006). It has been shown that in temperate zones the species richness patterns may be impacted by both past and present factors, while for tropical zones, topography also represents an important variable (Rahbek et al. 2019).

Additionally, the interaction between these two variables, precipitation, and temperature, has been suggested as a key factor in modeling the distribution of species richness. In most cases, both variables are correlated and thus present conflicts when being evaluated statistically in models (McCain 2007, 2010). One model that relates both variables, deemed water-energy dynamics (WED), was proposed by O'Brien (1993) to explain the distribution of woody plant species richness in South Africa. Recently, Vetaas et al. (2019) modified this model to test it in the Himalayas and found a model fit >90% for various taxonomic groups, including amphibians.

Until today, there is no general explanation for the altitudinal patterns of richness, since each altitudinal gradient presents unique environmental conditions as a combining result of its history, location and orientation (McCain 2005, 2007). In addition to this, the different biogeographic events (e.g. speciation and extinction) that have determined the distinct species regional pools have also caused differential assemblage responses to climatic conditions over time (Ricklefs 2006). For this reason, we believe that it is essential to test different environmental models when evaluating altitudinal gradients. Based on those models we would be able to recognize different trends exploring where and how certain environmental variables operate across geographic space for the different richness patterns that we observe.

Models

Seven models, all based on environmental hypotheses proposed in the literature, are examined herein: temperature (Model 1), precipitation (Model 2), water-energy dynamic (Model 3), topographic heterogeneity (Model 4), topographic heterogeneity-temperature interaction (Model 5), topographic heterogeneity-precipitation interaction (Model 6) and area (Model 7).

Model 1. The first model is based on the ambient-energy hypothesis, and proposes that the total number of co-existing species in a determined place is limited by the amount of available energy (Turner et al. 1987). Temperature is often considered a proxy for measuring available energy, as numerous biological processes are innately tied to it, particularly in ectotherms (e.g. metabolism and speciation rates, McCain and Sanders 2010). Given that temperature generally decreases with elevation, it can be expected that species richness follows suit. Accordingly, a positive relationship is expected between temperature and species richness (Fig. 1a).

$$\text{Model 1} = S \sim T, \tag{1}$$

where S is species richness and T is average temperature in degrees Celsius (ºC).

Model 2. The second model is based on the productivity hypothesis (Wright 1983), which argues that species richness is limited by primary productivity, therefore, in sites with higher productivity there will be a greater amount of biomass that will accumulate through trophic networks maintaining a greater diversity of species. Productivity is determined by the availability of water as a limiting factor, in tropical, subtropical, like Mexico, and high energy temperate places (Hawkins 2003). Furthermore, given their physiological characteristics, amphibians are dependent on the availability of water to complete their life cycles. This model predicts a positive relationship between species richness and elevational areas with higher precipitation; however, it does not predict a direct relationship with elevation, given that precipitation shows a more complex relationship with elevation compared to temperature (Grytnes and McCain 2013).

$$\text{Model 2} = S \sim P, \tag{2}$$

where S is species richness and P is precipitation measured in annual millimeters (mm).

Model 3. The third model, called WED (Water-Energy Dynamics), couples the effects of water (precipitation) and energy (measured by potential evapotranspiration, PET) and it is based on the same productivity hypothesis (Wright 1983). WED model predicts that both factors interact to limit the distribution of species, with precipitation in a linear fashion and PET as a parabolic function (O’Brien 1993). The prior is explained by the availability of water that is limited by the amount of rainfall, as well as water lost to evapotranspiration, while the latter is affected by amount of light, available liquid water, and heat—all things indispensable for essential biological processes such as photosynthesis and subsequently primary productivity (O’Brien 2006, Vetaas et al. 2019). According to this hypothesis, elevations with high energy will show low species richness due to the limited availability of water losses by evaporation. Also, areas with less energy input and therefore less PET, but where water availability is limited due to freezing, will show reduced biological activity and productivity leading to a pattern of decreased species richness. In areas with optimal PET and abundant precipitation, biological activity and productivity will be greatest, supporting high species richness (Vetaas et al. 2019). These hypotheses translate to a model predicting peak species richness at mid elevations (Fig. 1d).

$$\text{Model 3} = S \sim P + PET + (PET)^2, \tag{3}$$

where S is species richness and PET is the annual potential evapotranspiration measured in mm of liquid water evaporated by every 1° C per year.

Model 4. The fourth model is based on the habitat heterogeneity hypothesis (Pianka 1966, Simpson 1964), stating that species richness is determined by the amount of habitat generated from environmental topographic heterogeneity (sensu Stein and Kreft 2015), calculated as the standard deviation of the elevation. Sites with more environmental topographic heterogeneity (abbreviated herein as TH) are predicted to encompass greater climatic and habitat variation in relatively smaller areas (Rahbek et al. 2019, Stein et al. 2014). Elevation range is the most frequent metric used to determinate TH, however, elevation range does not reflect the variability inside the gradient or study unity and only reflects the length of the gradient (Stein and Kreft 2015). The standard deviation of elevation is the second most frequent metric used to determinate TH, and it is useful to quantifying the variability inside de gradient. Accordingly, this model predicts that elevational segments with greater TH will have higher species richness, and not necessarily a direct elevational pattern. In other words, elevational bands with greater TH would have higher species richness regardless of their location in the elevational gradient.

$$\text{Model 4} = S \sim TH, \tag{4}$$

where S is species richness and TH is topographic heterogeneity calculated as the standard deviation of the elevation, measured in meters (m).

Model 5. Topographic heterogeneity, together with climate, has been suggested to be an important predictor of amphibian species richness (Buckley and Jetz 2007, Rahbek et al. 2019). For example, topographic heterogeneity together with climatic variables such as precipitation was shown to have a positive relationship with species richness in amphibians (Hedges 1999). For this reason, the fifth model evaluates the relationship between TH and energy (temperature), predicting that species richness will not only be influenced by the number of habitats generated by a greater spatial heterogeneity, but also due to the combined effect with temperature. The resulting model predicts that elevations with greater spatial heterogeneity and higher temperatures will support greater species richness.

$$\text{Model 5} = S \sim (TH \times T), \quad (5)$$

where S is species richness, T is average temperature in degrees Celsius (ºC) and TH is topographic heterogeneity calculated as the standard deviation of the elevation, measured in meters (m).

Model 6. The sixth model assumes that species richness depends on the combined effect of available liquid water and available habitat given the TH. Under this model, species richness is predicted to have a positive relationship with TH and precipitation. For these two models, 5 and 6, a positive correlation of elevation with species richness is not expected.

$$\text{Model 6} = S \sim (TH \times P), \quad (6)$$

where S is species richness, P is precipitation measured in annual millimeters (mm) and TH is topographic heterogeneity calculated as the standard deviation of the elevation, measured in meters (m).

Model 7. This model is based on the hypothesis of the habitat diversity (Williams 1964), which maintains that the diversity of habitats is greater in sites of greater area that in turn maintains a greater species richness. This hypothesis predicts a positive species-area relationship, and in the case of the altitudinal gradient, altitudinal bands with greater area will register higher species richness due to the fact that they present a greater variation of habitats. In most cases, the area decreases as the elevation increases (Körner 2007), however, there are cases in which the greatest amount of area is concentrated at intermediate latitudes (~ 1500-2000 m a.s.l., McCain 2007). Therefore, a specific pattern related to this model is not expected.

$$\text{Model 7} = S \sim A, \quad (7)$$

where S is species richness and A is area measured in km^2.

Lastly, several studies have proven that an important factor influencing observed patterns of species richness is the spatial scale at which the study is carried out (Rahbek 2005). Both the extent of the study area and the grain utilized to evaluate gradients have been shown to influence observed patterns and explanatory variables of species richness (Nogués-Bravo et al. 2008). Because of this, we consider it necessary to evaluate how the spatial scale determines observed patterns and underlying explanatory variables.

In the present study, we (1) tested the effect of environmental variables on amphibian species richness along elevational gradients from the five largest mountain ranges in Mexico on the basis of the seven models described above, and (2) we evaluated whether the spatial scale, mediated by the amplitude of the altitudinal bands, has effects on the observed pattern and its explanatory variables.

MATERIALS AND METHODS

Study Sites and Data Acquisition

For the delimitation of mountain ranges in Mexico, the classification of Mexican physiographic provinces by Quiñonez (1984) was followed, which recognizes six montane systems: Sierra Madre Occidental (SMOc), Sierra Madre Oriental (SMO), Sierra Madre del Sur (SMS), Faja Volcánica Transmexicana (FVT), Cordillera Centroamericana, and the Sierras de Chiapas y Guatemala (Fig. 2). Given that these last two mountain ranges are considerably smaller in area than the others, the present study combines them into a single working unit (CCySCG), further justified by the fact that both are considered under the same region of herpetofaunistic regions of endemism (Flores-Villela and Martínez 2009).

Species records for amphibians were taken from the Mexican herpetofauna database compiled by the Museum of Zoology, Faculty of

Sciences, at the Universidad Nacional Autónoma de México. This database contains information on Mexican records from more than 40 museums around the world. All records used in this study were manually inspected and compared with specialized literature, allowing for the removal of dubious and/or incorrectly geo-referenced records, as well as the actualization of taxonomy following Frost (2019).

Environmental data for temperature and precipitation were obtained from WorldClim version 1.4 (Hijmans et al. 2005), while data on potential evapotranspiration were obtained from the Global Aridity and PET Database version 1 (Trabucco and Zomer 2009), both with a 30 arc-second resolution grid. We decided to use those versions corresponding to the timeframe 1960–1990 in order to reduce temporal bias, given that the majority of species records in this study are from the previous century. Elevational data was obtained from the digital elevation model (DEM) of Mexico with a resolution of 60 m (INEGI 2013).

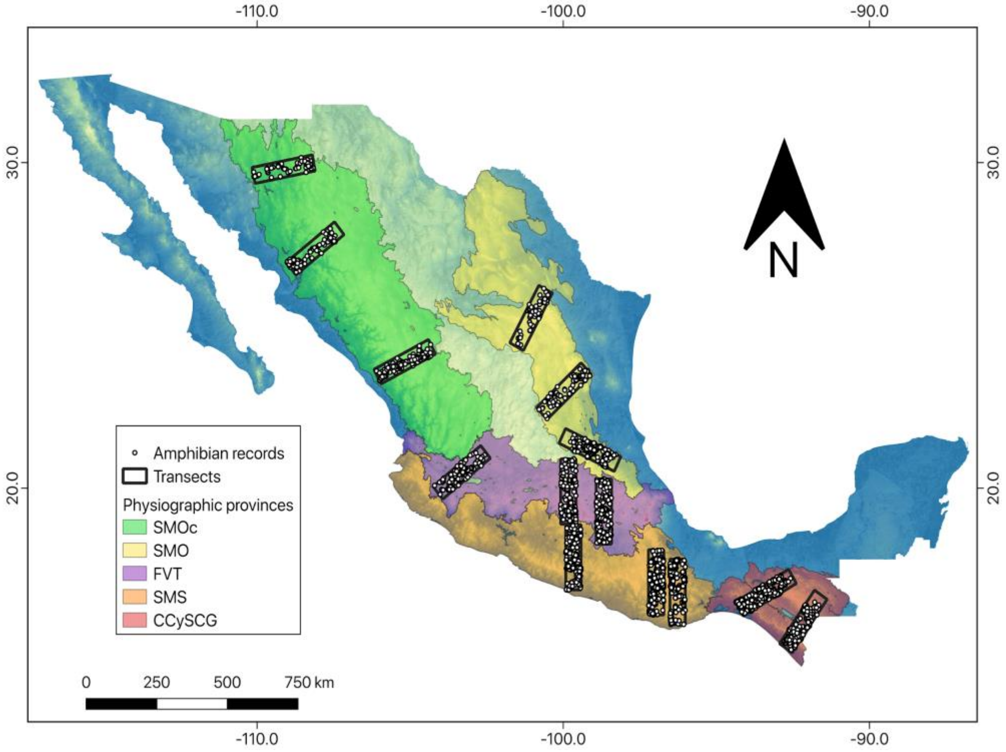

Figure 2. Location of the mountain ranges and transects for which species records and environmental variables were extracted for analysis. SMOc = Sierra Madre Occidental; SMO = Sierra Madre Oriental; FVT = Faja Volcánica Transmexicana; SMS = Sierra Madre del Sur; CCySCG = Cordillera Centroamericana and Sierras de Chiapas y Guatemala.

Gradient selection and quantifying variables

A total of 14 transects of 50 km × 200 km were placed— three for each mountain range, with the exception of CCySCG, for which only two transects were assigned given its smaller size (Fig. 2). Within each transect, elevational profiles were identified, analyzing each slope of the mountain range independently (i.e. coastal and continental slopes, Fig. 3). Once the gradients were defined, amphibian species records and environmental variables were extracted for the area of each transect. Each species record was assigned an elevational value using the MDE of Mexico (INEGI 2013). Next, the gradients were standardized for analysis using the following selection criteria outlined by McCain (2005, 2007, 2010), Rahbek (2005), and Nogués-Bravo et al. (2008): that the gradient (1) covered at least 1,000 m in elevation; (2) showed high sampling effort (described below); (3) included at least seven species of amphibians; (4) contained species records in at least 70% of the elevational bands conforming the gradient; and (5) due to climatic differences between coastal and continental environments we classified gradients in coastal slopes as those where water flows into the coasts, and continental slopes as those where water flows into the interior of the country (Fig. 3).

We used sampling coverage to estimate the completeness of samples from transects of different size. This method is based on the proportion of records pertaining to each species to the total number of records in the inventory (Chao and Jost 2012) and allowed us to ensure that transects were sufficiently well sampled, because each gradient has a different size and number of species records. Elevational ranges of species were delimited by the minimum and maximum elevation records for each species from the locality records, assuming their presence in the entire area between these two extremes (interpolation, Grytnes and McCain 2013). Each gradient was split in different spatial scales of elevational bands —100, 200, 300, and 500 m —, and species richness as well as each environmental variable was calculated for each spatial scale of elevational segment in each gradient. The environmental variables calculated were: average temperature, average precipitation, average PET, the standard deviations of elevation (SD), and area of each elevational band (A). To calculate the average of the environmental variables we generated a spatial point database based on the pixel centroids of the DEM. Afterwards we extracted all the environmental variables values for each elevational spatial point.

The SD was calculated as a proxy for topographic heterogeneity (Stein and Kreft 2015), extracting for each altitudinal band the altitude value of each pixel and calculating the standard deviation for the obtained data set. The area was calculated by transforming each altitudinal band into a polygon, based on contour lines of the DEM used previously. The planimetric area occupied by each altitudinal band was calculated. We used QGIS 3.4 (QGIS.org 2021) for all spatial analysis.

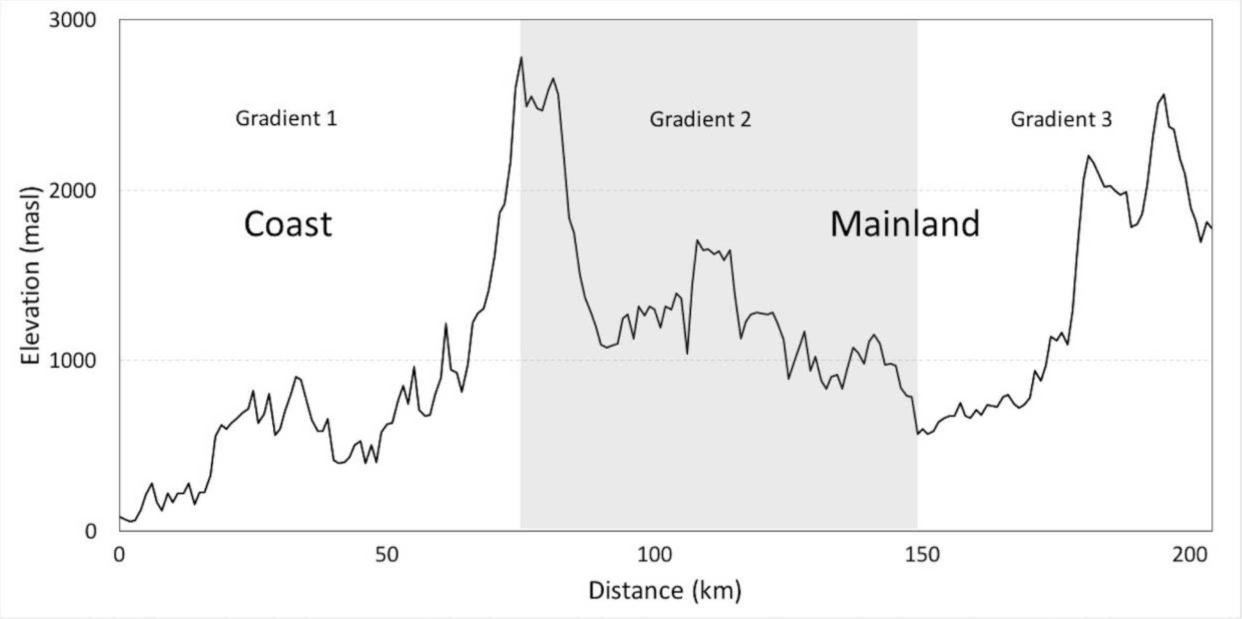

Figure 3. Example of gradients identification in the transects, considering each slope of the mountain range as an independent gradient.

Data Analysis

For each band size across all elevation gradients, the relationship between species richness and elevation was visually determined and classified according to one of the five categories following McCain's (2010) criteria described above. The proportion of each model observed across all gradients was calculated for each elevational band size.

To evaluate the relation between species richness and environmental variables, Generalized Linear Models (GLM) were utilized for each gradient with a Poisson error distribution. The use of GLMs with a Poisson error distribution for this kind of data (count data of species along elevational bands; McCullagh and Nelder 1989; Dobson and Barnett 2018) has been demonstrated to be an effective method when the distribution of the data does not conform normally, as is the case to species richness data (see Guisan and Hofer 2003, Fu et al. 2007, Vetaas et al. 2019). However, data that showed over-dispersion were modelled with a negative binomial error distribution. Each model was tested by evaluating the explanatory power for the observed species richness. Model selection was determined based on the corrected Akaike's Information Criterion value (AICc), which accounts for smaller sample sizes. When the difference between the best model and the other models was under two AICc units, model selection was determined by choosing the model with the highest fit value. Explained variance was reported for each of the GLM selected models.

To assess whether our models presented spatial autocorrelation, we used Moran's I test on the residuals of our models (Bivand et al. 2013, Dormann et al. 2007). When spatial autocorrelation was observed, we used generalized estimating equations (GEEs). These models are an extension of GLMs that allowed us to take account spatial autocorrelation in our model (Dormann et al. 2007). We use a first-order regressive process correlation structure (AR1), in our GEE approximation. The AR1 correlation structure is commonly used in time series analysis (Krispin 2019). In our data, AR1 correlation structure implies that the values in each elevational band are correlated with the previous elevational band. Because it is not possible to use the AIC in the GEE models a as a selection criterion, we used the generalized version that is the Quasi-likelihood Information Criterion (QICu, Hardin and Hilbe 2013, Liu 2015). When the difference between models with respect to the QICu value was less than 2 units, we used Pearson's correlation coefficient r between the richness values predicted by the model and the observed values (Hardin and Hilbe 2013), consequently selecting the model with a higher correlation value, thus r was reported in each of the cases that GEE models were used.

The Effects of Scale Size on the Selection and Fit of Models

To evaluate if the spatial scale of elevation bands influences the model selection, Fisher's exact test was conducted. This analysis was conducted on both the total dataset, as well as on the separate coastal and continental groupings. Furthermore, we used Fisher's exact test to test whether any model was associated with a specific pattern on each scale. For Fisher's tests, contingency tables were established for each model and its selection frequency for (1) Model-total gradients and for each gradient subgroup (coastal or continental), and (2) Model-pattern of richness reported for each scale analyzed. For both cases, it was evaluated on the different analysis scales through the length of the elevation bands.

Statistical analyses were performed in the R 3.6.3 (R Core Team 2020) platform. Sample coverage was calculated with the iNEXT package version 2.0.19 (Hsieh et al. 2016), GEE models were performed with geepack package version 1.3 (Højsgaard et al. 2016), overdispersion was evaluated with the function dispersiontest from package AER (Kleiber and Zeileis 2008). Moran's I test was calculated with spdep package version 1.1-7 (Bivand et al. 2013), while the graphics were created using the ggplot2 package version 3.2.1 (Wickham 2016).

RESULTS

Patterns of Distribution of Species Richness

A total of 29 gradients (between coastal and interior) spanning five mountain ranges were originally selected, encompassing 53,452 species records. Of these gradients, only 20 fulfilled the selection criteria comprising 43,912 records of 230 amphibian species, of which 168 are anurans, 60 are salamanders, and 2 are caecilians. 40% of the gradients were classified as coastal (8/20), while 60% were classified as continental (12/20). On average, each gradient contained 35 species, with a minimum and maximum of 13 and 71 species, respectively. The completeness of the species inventory in each gradient was very high, with an average sampling coverage of 0.9937 across all gradients, approaching the maximum sampling coverage of 1.0. The smallest gradient was 2,042 m long, while the largest extended slightly over 3,700 m; the average gradient length was 2,800 m. The mountain range with the least number of gradients selected was SMO (1), while the SMS had the most (8; Table 1, see Figure S1 in the Supplementary File S1).

Table 1. Elevational gradients evaluated in the mountain ranges of Mexico. The table includes the number of species records (R), species richness (S), and sampling coverage (S.C.) for each gradient.

GRADIENT	**GRADIENT LENGTH**			**SPECIES RICHNESS/RECORDS**				**S.C.**
	Total (M)	**Evaluated (M)**	**Evaluated %**	**Amphibia (S/R)**	**Anura (S/R)**	**Caudata (S/R)**	**Gymnophiona (S/R)**	
SMOC1	2359	2200	93.26%	21/642	19/436	2/206	0/0	0.9953
SMOC2	2887	2500	86.60%	13/488	11/398	2/90	0/0	1.0000
SMOC3	2845	2800	98.42%	38/1985	36/1705	2/280	0/0	0.9990
SMO1	3061	2600	84.94%	53/3980	41/2598	12/1382	0/0	0.9982
FVT1	2217	2000	90.21%	19/286	17/262	2724	0/0	0.9896
FVT2	3308	3000	90.69%	30/3069	19/1035	11/34	0/0	0.9997
FVT3	2345	2000	85.29%	23/9058	11/1243	12/15	0/0	0.9997
FVT4	3096	2896	93.54%	22/1505	17/397	5/1108	0/0	0.9980
SMS1	2968	2896	97.57%	55/2448	50/2288	4/157	1/3	0.9971
SMS2	2528	2356	93.20%	36/772	32/699	4/73	0/0	0.9974
SMS3	2261	2249	99.47%	28/1101	25/1062	3/39	0/0	0.9982
SMS4	2766	2354	85.10%	45/3238	35/1389	10/1849	0/0	0.9991
SMS5	3202	2500	78.08%	37/1262	25/569	12/693	0/0	0.9968
SMS6	3707	2700	72.84%	38/965	32/926	4/31	2/8	0.9990
SMS7	3103	2300	74.12%	15/103	13/97	2/6	0/0	0.9615
SMS8	3360	3199	95.21%	71/8993	52/5395	19/3598	0/0	0.9999
CCYSCG1	2042	1993	97.60%	39/1315	36/1241	2/65	1/9	0.9970
CCYSCG2	2346	1918	81.75%	39/689	34/655	4/31	1/3	0.9913
CCYSCG3	3080	3050	99.03%	43/1778	34/1292	7/473	2/13	0.9972
CCYSCG4	2873	2400	83.54%	35/235	31/189	4/46	0/0	0.9576

CCySCG = Cordillera Centroamericana and Sierras de Chiapas y Guatemala; FVT = Faja Volcánica Transmexicana; SMOC = Sierra Madre Occidental; SMO = Sierra Madre Oriental; SMS = Sierra Madre del Sur.

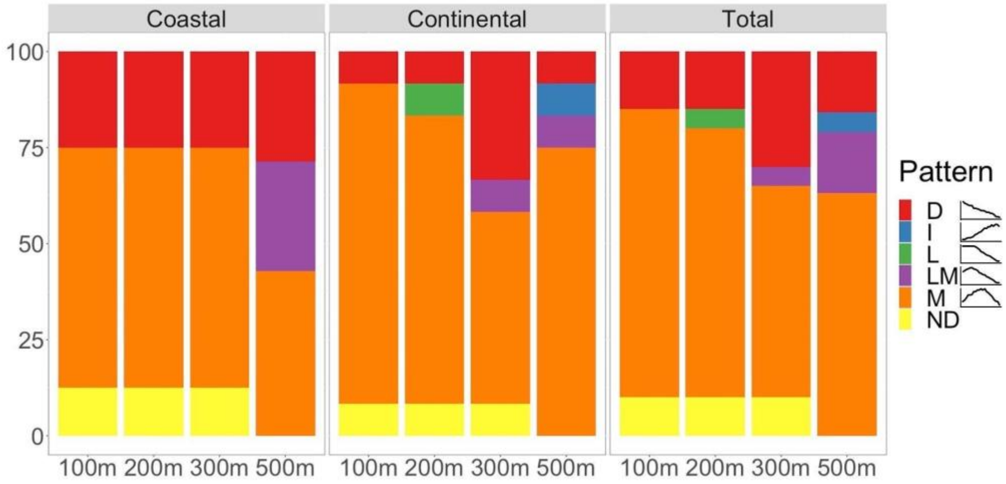

Figure 4. Proportion of elevational patterns observed in amphibians across all gradients, separated by coastal, continental, and combined gradients within the mountain ranges of Mexico.

Patterns of Diversity

Five patterns of elevational species richness were recovered across all scales of elevational bands analyzed — the first four described by McCaine (2010) and a fifth that shows increased species richness with elevation (Rahbek 2005). In general, the most-observed pattern was the mid-peak pattern (M). At the scale of 100 m elevational bands, this pattern was observed in 75% of the cases, the decreasing pattern (D) was observed in 15% of the gradients, and the patterns of 10% of the gradients could not be placed into any of the five patterns (ND). When analyzed separately, coastal and continental gradients showed the same patterns, albeit in different proportions (e.g. the decreasing pattern (D) was observed in 25% of coastal gradients compared to 8% of continental gradients) (Table 2, Fig. 4). At the scale of 200 m elevational bands, the mid-peak pattern (M) was seen in 70% of the gradients, and the low plateau pattern (L) was observed in one gradient. This latter instance was registered in a continental gradient, causing the proportion of mid-peak patterns (M) to be slightly lower in this group.

In elevational bands of 300 m, the mid-peak pattern was once again the most common, recovered in 55% of the gradients; however, the low plateau with mid-peak pattern (LM) was recovered in 5% of the gradients. The decreasing pattern (D) showed a higher frequency among gradients (35%) than in the previous analyses, and 10% of the gradients could not be determined (ND). Continental gradients showed a higher frequency of decreasing pattern than 100 m and 200 m scale with 33% of the gradients, and the only one gradient with low plateau with mid-peak pattern (LM) was recovered in these gradients. Costal gradients showed the same results as in the 100 m and 200 m scale.

At the scale of 500 m elevational bands, a total of four types of elevational patterns were observed: 12 (60%) of the gradients showed a mid-peak (M), 4 (20%) showed a decreasing pattern (D) and 3 (15%) displayed a low plateau with mid-peak pattern (LM), and only one gradient displayed the increasing pattern (I). Looking at the distinct slope types, coastal gradients displayed three types of elevational patterns: mid-peak (M), decreasing (D), and low plateau with mid-peak (LM), while continental gradients showed these same three patterns plus one gradient with the increasing pattern (I). Finally, it is important to highlight that the gradients for which none of the five described patterns could be assigned, SMOc2 and SM7, contained the least number of species, although not necessarily the least number of records.

Table 2. Model selection and observed patterns for each gradient at each scale of elevational band analyzed in the mountain ranges of Mexico. The type of gradient is also indicated (coastal or continental). In bold are highlighted the cases where Generalized Estimating Equations (GEE) were used due to the presence of spatial autocorrelation within the gradient, otherwise Generalized Linear Models (GLM) were utilized.

Gradient	**Slope**	**100 m**						**200 m**					
		Pattern	**Model**	**Model type**	**Exp var/r**	**AICc/ QICu**	**Delta**	**Pattern**	**Model**	**Model type**	**Exp var/r**	**AICc/ QICu**	**Delta**
SMOC1	Continental	M	5	GLM	93.9	100.1	0	L	5	**GEE**	**97**	**-302.2**	**0**
SMOC2	Coastal	ND	5	GLM	58.7	92.1	0.78	ND	4	GLM	32.6	52.5	0
SMOC3	Coastal	M	4	GLM	58.9	139.1	0	M	4	GLM	76.5	76.6	0
SMO1	Coastal	M	3	GLM	92.7	139.8	0	M	3	**GEE**	**95.5**	**-1190.2**	**0**
FVT1	Continental	M	3	GLM	83.1	87.9	0	M	3	GLM	80	59.7	0
FVT2	Continental	M	3	GLM	79	115.9	0	M	3	**GEE**	**93.7**	**-369.7**	**0**
FVT3	Continental	M	3	**GEE**	**82.6**	**-430.5**	**0.3**	M	7	GLM	61.9	65.2	0
FVT4	Continental	M	7	**GEE**	**80.1**	**-332.3**	**0**	M	7	**GEE**	**82.6**	**-199.3**	**0**
SMS1	Coastal	M	3	**GEE**	**90.6**	**-1725.4**	**0**	M	3	**GEE**	**92**	**-1020**	**0**
SMS2	Continental	M	3	**GEE**	**86.4**	**-959.8**	**0**	M	3	**GEE**	**88.9**	**-545.3**	0
SMS3	Continental	M	3	GLM	79.3	118.9	0	M	3	GLM	84	70.3	0
SMS4	Coastal	M	3	**GEE**	**96.6**	**-1240**	**0**	M	3	**GEE**	**97.7**	**-750**	**0**
SMS5	Continental	M	3	**GEE**	**94.8**	**-729.3**	**0**	M	3	**GEE**	**97.6**	**-451**	**0**
SMS6	Coastal	M	5	GLM	76.9	139.2	0	M	5	**GEE**	**93.1**	**-444.8**	**0**
SMS7	Continental	ND	2	GLM	13	82.3	0	ND	2	GLM	43	47	0
SMS8	Continental	M	7	**GEE**	**75.8**	**-3640.6**	**0**	M	5	**GEE**	**88.9**	**-1958.2**	**0**
CCYSCG1	Coastal	D	1	**GEE**	**93.4**	**-1398.9**	**0**	D	1	**GEE**	**93.6**	**-640.4**	**0**
CCYSCG2	Continental	M	3	**GEE**	**84.3**	**-877.1**	**0**	M	3	**GEE**	**87.6**	**-550.3**	**0**
CCYSCG3	Coastal	D	3	GLM	97.9	148.5	0.89	D	3	**GEE**	**99.2**	**-1026.7**	**0.9**
CCYSCG4	Continental	D	1	GLM	78.2	106.5	0	D	1	GLM	63	61.6	0
SMOc1	Continental	D	5	**GEE**	**99**	**-228.5**	**0.9**	M	4	GLM	81.7	34.5	0
SMOc2	Coastal	ND	1	GLM	27.5	39.4	0	D	1	GLM	55.1	30.4	0
SMOc3	Coastal	M	4	GLM	24.2	52.6	0	LM	1	GLM	33.2	37	0
SMO1	Coastal	M	3	GLM	92.1	65.4	0	M	7	GLM	73.1	50.4	0
FVT1	Continental	M	7	GLM	60.7	40.5	0	M	4	GLM	84.7	30.9	0
FVT2	Continental	M	7	GLM	45.1	53.2	0	M	7	GLM	89.8	33.7	0
FVT3	Continental	D	2	GLM	71.4	47.2	0	M	7	**GEE**	**94.5**	**-156.9**	**0**
FVT4	Continental	D	7	GLM	67.9	51.9	0	M	7	GLM	64.5	38	0
SMS1	Coastal	M	3	GLM	91	66.7	0	M	7	GLM	62.6	47.8	0
SMS2	Continental	M	3	GLM	80.3	64.1	0	M	3	**GEE**	**97.3**	**-314.5**	**0**
SMS3	Continental	LM	7	GLM	61.1	46.4	0	M	7	GLM	65.9	38.4	0
SMS4	Coastal	M	3	GLM	87.5	66	0	M	4	GLM	79.2	45.6	0
SMS5	Continental	M	3	**GEE**	**96.8**	**-363.9**	**0**	M	3	**GEE**	**99.9**	**-286.5**	**0.4**
SMS6	Coastal	M	5	GLM	89.6	60.5	1.14	LM	5	**GEE**	**93.5**	**-272**	**0**
SMS7	Continental	ND	7	GLM	41.9	34.8	0	I	1	GLM	49.1	28.5	0
SMS8	Continental	M	7	GLM	75	70.5	0	LM	4	**GEE**	**97.5**	**-1013.8**	**0**
CCySCG1	Coastal	D	1	GLM	80.4	43.5	0	D	NA	NA	NA	NA	NA
CCySCG2	Continental	M	3	GLM	74.8	69.2	1.05	M	7	GLM	52.6	52.2	0
CCySCG3	Coastal	D	1	GLM	89.4	63.1	0	D	3	**GEE**	**99.6**	**-508.4**	**0**
CCySCG4	Continental	D	7	GLM	66.2	49.9	0	D	1	GLM	82.4	33.9	0

Acronyms: Mountain Ranges: SMOc = Sierra Madre Occidental; SMO = Sierra Madre Oriental; FVT = Faja Volcánica Transmexicana; SMS = Sierra Madre del Sur; CCySCG = Cordillera Centroamericana and Sierras de Chiapas y Guatemala. Elevational patterns: D = Decreasing; L = Low-plateau; LM = Low plateau with mid-peak; M = Mid-peak; I = Increasing; ND = undetermined; NA= Not applicable, given than the number of elevational bands was less than 5; * models that showed over-dispersion were selected under a negative binomial error distribution.

Explanatory Variables

Model selection, based on Fisher's exact test, was only significant when comparing between the 100 m and 500 m scales (P = 0.02); for the total of the gradients the test showed no significant differences for the subgroups of coastal and continental gradients (P > 0.05). Spatial autocorrelation, according with Moran's I test, was also variable at different spatial scales, with a higher incidence at 200 m scales with 65% of the gradients affected, while at 300 m only 10% of the gradients presented spatial autocorrelation. 45% and 32% of the gradients at 100 m and 500 m scales, respectively, also showed spatial autocorrelation. A similar trend was observed for the subgroups of coastal and continental gradients (Fig. 5).

Six of the seven models were selected through all the scales, only the model that related topographic heterogeneity with precipitation (Model 6) was not selected at all (Fig. 5). Model 1 (temperature) was selected through all scales and showed an increase in its selection through the scale of 10% selection at 100 m and 200 m scale to more than 21% selection at scale of 500 m, its selection was higher for coastal gradients, where Model 1 achieved a selection of up to about 35% of the gradients at the 300 m scale. Its explanatory power was moderate to high at scales of 100 m and 200 m with ~ 63-94% of explained variance in GLMs and ~ 93-94 of Pearson correlation in GEEs, based on AICc or QICu respectively, and related mainly to decreasing patterns. While for the 300 m and 500 m scales its explanatory power was from low to high with ~ 37-89% of explained variance in GLMs, and related to different types of patterns. There were no GEEs at these last scales with Model 1.

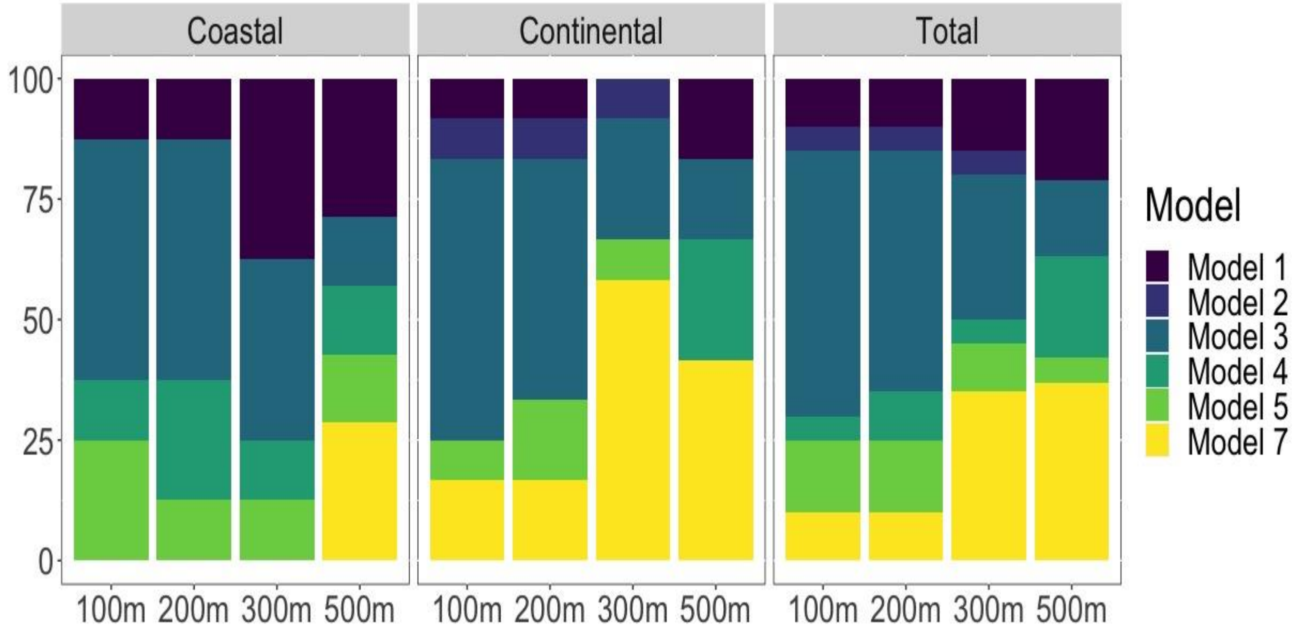

Figure 5. Proportion of selected models for amphibians separated by coastal, continental, and combined gradients within the mountain ranges of Mexico.

Model 2 (precipitation) was the least selected model, with only 5% of the gradients (3 gradients), selected for the 100 m to 300 m scales, and its selection was restricted to continental gradients. Its explanatory power increased across the scale from low to high (~13-71% explained variance in GLMs). It is interesting to note that one of the gradients that was explained by this model presented spatial autocorrelation at the scale of 500 m. Model 3

(WED) was the most selected at scales less than 300 m with about 50% of the total gradients as for the subgroups of coastal and continental gradients. At these same scales, a greater relationship was found between Model 3 and the peak pattern at mid-altitudes according with Fisher's test (P = 0.0185). At scales of 300 m and 500 m, their selection was from 30% to 16% of the gradients, and although it was more related to the peak pattern at medium altitudes, this relationship was not significant according with Fisher's test (P > 0.05), with similar trends between coastal and continental gradients. The explanatory power of Model 3 was high across all scales ~74-98% of explained variance in GLMs and ~ 82-99 of Pearson correlation in GEEs.

Model 4 (TH), showed a low and constant selection at scales equal to or less than 300 m, selected from 1 to 2 gradients and with an increase in its selection at scales of 500 m. This selection was kept constant in the coastal gradients, while for continental gradients only 500 m elevational bands were selected. The explanatory power ranged from low to high from ~ 24-85% of explained variance in GLMs and ~97 of Pearson correlation in only GEE. The explanatory power of this model was greater at the 500 m scale. The peak pattern at mid-altitudes was the one most associated with this model. Model 5 (HT-T ratio), like Model 4, maintained a low selection throughout the spatial scales with a greater selection at scales equal to and less than 200 m and a decrease for the scales of 300 m and 500 m. The explanatory power of this model was medium to high with a range of explained variance in GLMs (58-94%) and ~ 88-99 of Pearson correlation in GEEs. For this model the most associated pattern (five times out of nine) was mid-peak.

Finally, Model 7 (area) showed an increase in its selection by increasing the spatial scale, starting with a 10% selection at a 100 m scale to just over 36% selection at a 500 m scale. For coastal gradients this model was only selected at the 500 m scales, while for continental gradients it was selected at all scales. The explanatory power of this model was moderate to high from ~ 41% to 90% of explained variance in GLMs and ~ 75-94 of Pearson correlation in GEEs. Model 7 was more related to peak patterns at mid altitudes at a scale of 500 m according to Fisher's test (P = 0.026), while for the other spatial scales it did not show a significant relationship with any pattern. Full results of the models, patterns found and an example of the R script used are available in the Supplementary Files S1-S5.

DISCUSSION

With about ~7% of Mexico's land cover evaluated, the number of species included in the selected gradients of this study represent over 56% of the known amphibian diversity for Mexico (Frost 2019). This supports the claim that the mountains and neighboring zones harbor the highest species richness in Mexico (Espinosa and Ocegueda 2008). In the 29 gradients chosen for this study, 9 were excluded due to less than 70% of their area containing species records. In most gradients, the highest elevational zones were those with the least records, especially in the Sierra Madre Oriental, where only one gradient fit the selection criteria. The Sierra Madre Occidental showed the least number of species records (see Table 2). These regions represent high priority areas for documenting species composition and distribution.

Patterns of Distribution

The elevational distribution of amphibian species richness in Mexico showed a general pattern of mid-peak (M), as this was the most represented pattern across all gradients and at all scales. This result corroborates the works of Rahbek (2005) and Guo et al. (2013), who performed an extensive review of literature across different taxonomic groups and found that 50–60% of studies reported this same pattern. The second most common pattern observed in these studies across all scales was that of decreasing richness with elevation (D).

Similarly, McCain (2010) found that the elevational distributional patterns of species richness in salamanders showed a higher proportion of mid-peak patterns (~65% of the cases), while in anurans this pattern was approximately 30%. However, of the nine gradients evaluated in Mexico by McCain (2010), more than 55% of the cases showed peak richness at mid elevations. Throughout the different scales, 55% of gradients showed the same pattern: eight with a mid-peak and three showing a decreasing pattern. The selective inclusion or exclusion of certain parts of a gradient has been shown to affect the observed richness patterns, particularly when the high elevation regions are excluded (Nogués-Bravo et al. 2008). In this study, this extension bias was limited due to the selection criteria employed for the gradients, thus leaving the second scalar component, grain, to explain the changes observed in some patterns across gradients.

In terms of elevational gradients analyzed at different scales of segmenting, the mid-peak pattern is most frequently observed when bands are between 100–300 m wide in elevation; above this, other patterns are seen (Rahbek 2005). However, Hu et al. (2011) evaluated the distribution of Dicroglossid frogs' diversity at different scales of elevational bands and found no difference in the general patterns observed. This coincides with the results of the 11 gradients in this study for which the observed pattern remained constant across different scales analyzed.

For the other nine gradients for which the observed pattern changed with the scale of elevational band employed, it appears that the observed patterns are affected by the grid size utilized, as seen in other studies (e.g. Rahbek and Graves 2001). In latitudinal studies, the increase in grid size has been shown to affect the observed pattern in two ways — in the shape of the area of distribution, and in the relative area that a species occupies (Rahbek 2005). However, the increase in band size results in a modification of the elevational range of species distributions, especially for species with small distributions and in gradients with a high species turnover (beta diversity). This causes an inflation in the species richness recorded at certain elevations due to the sum of local species diversity of smaller elevational bands, effectively altering the observed pattern. In the present study, Mexican amphibians display a similar trend between coastal and continental gradients, only differing when the elevational band scale is increased, which causes two patterns to appear in the continental gradients that are not observed in coastal gradients (L and I).

Model Selection and Explanatory Variables

Despite amphibians' dependency on available water to complete their life cycles, it is noteworthy that of the two models involving precipitation, one was never selected in any of the cases (Model 6), and the other was rarely selected with a weak explanatory power (Model 2). However, it is important to highlight that water tends to flow away from where it falls, especially in sloped habitats. Moreover, water loss from evapotranspiration is not constant, and may vary in space and time, effectively limiting the actual amount of available water (Stephenson 1998). Combined with this, humid air originating in the oceans generates fog upon reaching extensive mountain ranges, accounting for an important quantity of water that condenses on vegetation. This aspect is often not reflected in precipitation records (Rahbek 1997). For this reason, precipitation does not necessarily reflect an adequate representation of available water in mountain ranges, potentially causing Model 2 to only be chosen for continental slopes, where conditions are more arid than their coastal counterparts. Furthermore, precipitation is a more efficient explanatory variable at scales of elevational bands of 200 and 300 m (~ 40–70% of the variance explained), while at the smaller and larger spatial scales evaluated in this study, this factor showed a weak explanatory power (< 40%).

The interaction between water and energy as explanatory variables for the observed diversity has been proposed several times for different taxonomic groups (e.g. Fu et al. 2006, Hawkins et al. 2003, Vetaas et al. 2019). In the present study, Model 3 showed considerable predictive power (averaging over 80%), being the most important factor in gradients with mid-peak pattern. This is similar to the results of Vetaas et al. (2019), whose model predicted with good fit the distribution of over ten taxonomic groups of plants and animals in the central Himalayas, including amphibians. However, this relationship seems to be more prevalent in analyses conducted at a smaller scale (i.e. less than 500 m).

Model 3 stems from the idea that the availability of liquid water is vital for the development of organisms, and, furthermore, that this quantity can be measured by the amount of rainfall minus the amount of water lost through evapotranspiration (O'Brien 2006). Given that amphibians are closely associated with water availability, both for reproduction and for preventing desiccation, many of the species are restricted to habitats with sufficiently humid conditions (Vitt and Caldwell 2014). Despite this coupling, it seems that this effect is not widespread—while this model was selected for the majority of mountain ranges in this study, the gradients in the Sierra Madre Occidental did not conform to this model.

On the other hand, the model that included temperature (Model 1) was the model that best explained the decreasing patterns of species richness with elevation, as predicted. However, this model was not selected for every case across all scales. This caused the model's average explanatory power to decrease as the scale size increased. In contrast, the fit values of the same Model 1 for decreasing gradients stayed constant at high values, explaining between 55% and 95% of the variance. This partially supports the theory that temperature is one of the best explanatory variables in the distribution of species richness for different vertebrate and plant groups (Currie 1991, Hawkins et al. 2003).

The environmental energy hypothesis proposes that a high level of energy produces great diversity because organisms can use energy for their reproduction and food, helping to maintain larger populations and reducing the probability of extinction (Turner et al. 1987). For ectotherms such as amphibians, environmental temperature has been shown to be important in the different aspects of their life as a source of energy, such as the elevation of metabolic rates, foraging capacity, and embryonic development, especially in places where water is not limiting (Bennett 1990). The results of the present study support this idea, as the gradients for which temperature had a higher explanatory power are located in the Cordillera Centroamericana and the Sierras de Chiapas y Guatemala (CCySCG), all places that receive the highest precipitation (Vidal-Zepeda 1990).

Model 5 proved to be an interesting case, given that it was found to be a predictor with high fit for gradients showing a mid-peak pattern (fit values above 88%). Also, similar to Model 3, it was most commonly selected at elevational bands of less than 500 m, and it was present on both coastal and continental slopes. The interaction between topography and precipitation has previously been suggested as a determining factor for the distribution of amphibians (Hedges 1999). The present study suggests that the interaction between temperature and topographic heterogeneity is a good predictor for the distribution of species richness in amphibians, even at small scales.

Topography (Model 4) increased in importance and explanatory power as the scale size increased. The positive effect of the scale size on several variables including topography was observed in South American birds (Rahbek and Graves 2001). This effect makes sense, as topographic heterogeneity provides more potential habitats, an effect that is amplified in montane habitats. This results in a diverse variety of habitats and climates over relatively short distances (Rahbek et al. 2019, and references therein). However, Model 7 (area) was another of the models that was favored in its selection through the spatial scale of analysis, and mainly related to the mid elevation peak pattern. The habitat availability hypothesis tells us that in a larger area we can find a higher number of available habitats, favoring the coexistence of a greater quantity of species (Williams 1964). And precisely, in most mountainous areas, the greatest amount of available area is found at intermediate altitudes, rather than at the base of the gradient, as was originally thought (Lomolino 2001). For the case of the cordilleras of Mexico, something similar happens, since in most gradients, the area increases to the intermediate part of the gradient and decreases towards the extremes. Area has been suggested to be a good predictor of species richness at larger spatial scales (McCain 2005). And it is at higher spatial scales where it is possible to find a greater number of habitats due to topographic heterogeneity when the sampling area increases, mainly in mountainous areas. The reason why Model 7 was the most selected at larger spatial scales.

In this sense, across different scales of elevational bands, different parts of the same story are revealed. At small scales, classic environmental factors (temperature and precipitation, Models 1 and 2) and their interactions (Model 3) appear as the most common predictors of amphibian richness at the local level; but, on larger scales, the importance of topography increases as it generates gradients of the aforementioned factors, leading to a greater availability of diverse habitats for amphibians and other biological groups (O’Brien 2006). This observation emphasizes the caution and the necessary forethought when choosing the scale size for estimating the relationship of diversity and environmental variables across elevational gradients. Additionally, as seen in the results of this study and others (Nogués-Bravo et al. 2008), evaluating less than 70% of the total length of a gradient can have drastic effects on the observed patterns of diversity.

Without a doubt, the key factors in determining elevation patterns of species richness are the climatic variables in combination with other factors such as topography and geological history (Rahbek et al. 2019). Mountainous regions generate a much greater diversity of climates than lowlands, and experience much greater environmental variability over both short and long temporal scales (Chan et al. 2016), beyond the inherent variation of temperature and atmospheric pressure within the elevational gradient (Valencia et al. 2016). Additionally, the latitudinal location of the mountain and the orientation of its slopes generate unique climates that directly influence its biota. In this sense, every mountain is unique, and the observed pattern is the distinct sum of these characteristics—a singular blanket pattern and underlying explanatory variable for describing biological diversity in all mountains apparently does not exist.

DATA AVAILABILITY

Elevational data are available through the MZFC web page (https://www.fciencias.unam.mx/vida-en-ciencias/instalaciones/cu/instalaciones-academicas/museos/museo-zoologia-colecciones/herpetologica).

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SUPPLEMENTARY MATERIAL

Supplementary File S1: Additional results.

Supplementary File S2: Full results of the Generalized Linear Models (GLM).

Supplementary File S3: Moran's I test results.

Supplementary File S4: Full results of the Generalized Estimating Equations (GEE).

Supplementary File S5: Example of the script used in the calculations for each of the models at different elevational bands.

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