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Altitude and temperature drive anuran community assembly in a Neotropical mountain region

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Abstract

Understanding the spatial variation in species richness and the mechanisms that limit species range sizes along geographical gradients belong to the central research issues in macroecology. Here, we aim to test the topographic and climatic effects on anuran species richness and community composition in mountainous regions in the Brazilian Atlantic Forest biome. We used Individual-Based Rarefaction Curve (interpolation and extrapolation), Generalized Additive Model (GAM), Midpoint method and Principal Coordinates Analysis (PCoA) to analyze the topographic and climatic effects on anuran community composition, richness, and range sizes in a global biodiversity hotspot. Our results showed that altitude and annual mean temperature and temperature seasonality were the main drivers of species altitudinal range sizes and community assembly in mountainous regions. In conclusion, Anuran community richness peaked at intermediate altitudes following thus a hump-shaped pattern and corroborated the Rapoport's altitudinal rule as range sizes increased with altitude in mountainous regions from the Atlantic Forest biome. This study revealed new insights into the patterns and drivers of Neotropical anuran communities.

Abstract in Portuguese is available with online material.

KEYWORDS
amphibians, atlantic forest, biodiversity hotspots, neotropical region, Poços de Caldas Plateau, range size, rapoport altitudinal rule

1 | INTRODUCTION

Understanding the spatial variability in species richness and the mechanisms that limit species range sizes along geographical gradients is an important issue in biogeography and macroecology (Gaston, 2003; Sexton et al., 2009). Such research questions have continued to fascinate biogeographers and macroecologists for several decades (McCain & Grytnes, 2010; Rahbek, 1995; Sanders & Rahbek, 2012), being still a current challenge (Gaston, 2000).

Several studies conducted with different taxa and geographic regions support the view that biodiversity (typically species richness) often shows a predictable variation along mountainous regions typically showing decreasing, increasing, or hump-shaped patterns (McCain & Grytnes, 2010; Rahbek, 1995; Sanders & Rahbek, 2012). Some mechanisms such as climatic, biological, evolutionary, and historical processes have been proposed to explain patterns of species richness in mountainous regions (McCain & Grytnes, 2010; Sanders et al., 2003; Sanders & Rahbek, 2012), but currently the

most important processes underlying species richness patterns are still poorly understood for many taxa and ecosystems (Brown, 2001; Gallou et al., 2017).

One of the biogeographical hypotheses proposed to explain species richness patterns focuses on species range size variation along geographical gradients, namely the Rapoport's rule (Stevens, 1989, 1992). Although Rapoport's rule has been initially proposed to explain species range size patterns along latitudinal gradients (Stevens, 1989), later it was extended to explain species range size along the altitudinal gradients too (Stevens, 1992; Teittinen et al., 2016). According to the Rapoport altitudinal rule, there is a positive correlation between altitude and species altitudinal range size (Stevens, 1992), with higher altitude species tending to have broader altitudinal ranges due to wider climatic tolerances than lower altitude species, and consequently, covering wider altitudinal ranges. On the other hand, lower altitude species have narrower climatic tolerances and hence narrower altitudinal ranges due to more stable environmental conditions in low altitude regions. It is worth noting that unlike the mid-domain effect based on a null model (Colwell & Lees, 2000), Rapoport altitudinal rule (Stevens, 1992) attempts to explain species spatial distribution patterns based on the climatic variation effects. Thus, for explaining Rapoport altitudinal rule, Stevens (1992) proposed the climatic variability hypothesis or simply Rapoport "rescue" hypothesis, which predicts that species that have broad physiological tolerance are able to become more widely distributed (Gaston & Chown, 1999; Stevens, 1992).

Anurans are considered an interesting animal group to test Rapoport altitudinal rule due to their complex life cycles (Duellman & Trueb, 1986), limited dispersal ability (Duellman & Trueb, 1986), and because they are ectothermic vertebrates highly sensitive to rainfall and temperature levels, which influence their development, metabolism, behavior, and reproductive rate (Buckley & Jetz, 2007; Duellman & Trueb, 1986; Vitt & Caldwell, 2009). Studies carried out specifically with anurans show that species richness peaks can be found in lower (Hofer et al., 1999 [Cameroon]; Goyannes-Araújo et al., 2015 [Brazil]), intermediate (Fauth et al., 1989 [Costa Rica]; Fu

et al., 2006 [China]; Kozak & Wiens, 2010 [North America]; Hutter et al., 2013[Andes]), and higher altitudes (Giaretta et al., 1999 [Brazil]; Naniwadekar & Vasudevan, 2007 [India]), depending on the region (McCain & Grytnes, 2010). However, we expected to find a peak of anuran species richness at intermediate altitudes showing thus "unimodal or hump-shaped pattern" because it is the most common trend for all vertebrate taxa (McCain & Grytnes, 2010; Rahbek, 1995).

The Atlantic Forest biome is one of the most biodiverse regions worldwide including rare, endemic, and threatened anuran species (Haddad et al., 2013; Rossa-Feres et al., 2017) and is considered one of the top-five global biodiversity hotspots in the world (Mittermeier et al., 2011; Myers et al., 2000). Despite the high species richness and endemism level, the Atlantic Forest has been under great human impact for about half a century due to habitat fragmentation, resulting in severe biodiversity loss (Ribeiro et al., 2009).

Climate change is also expected to force species distributions towards higher altitudes (Chen et al., 2011; Freeman & Freeman, 2014; Tingley et al., 2012), and species range shifts may accelerate in the future (Elsen et al., 2018). This would lead to the extinction of small-ranged species and weak dispersal (Davies et al., 2009; Janzen, 1967; Sandel et al., 2011) of small and isolated populations from their current geographical ranges (Midgley et al., 2002; Thomas et al., 2004), especially in tropical mountainous regions, where the risk of decline may be higher and more severe (Davidson et al., 2013; McCain & Colwell, 2011).

Here, we aim to analyze the topographic and climatic effects on anuran community composition, richness, and range sizes in a mountainous region in the Atlantic Forest biome. Specifically, we (1) determine the shape of the distribution pattern of anuran species richness along the altitudinal gradient; (2) test if the Rapoport rule explains anuran range size variation along the altitudinal gradient; and (3) investigate how anuran community composition varies along the altitudinal gradient. Our hypotheses are (1) Anuran species richness will exhibit either a decreasing or a unimodal hump-shaped pattern along the altitudinal gradient (Figure 1a,b); (2) Species recorded
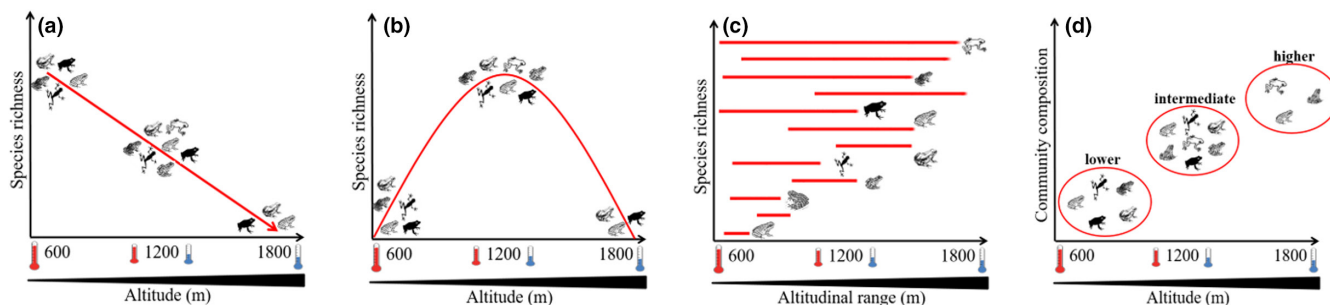

FIGURE 1 Hypothetical relationships of species richness and community composition in response to the topographic and climatic variables along an altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil. In panel (a) we hypothesize that species richness will decline with altitude as a consequence of temperature reduction; in (b) we hypothesize that in the intermediate altitudes, we will detect higher richness, because this range will share species from both lower and higher altitudes; in (c) we hypothesize that the species found in higher altitudes will have higher plasticity in their thermal tolerance, thus being also found across a range of altitudes; in (d) we present an alternative hypothesis, where community composition differs among lower, intermediate, and high altitudes with highest richness in intermediate altitudes, as presented in (b)

at higher altitudes will show wider range size than lower altitudes species along the altitudinal gradient (Figure 1c); and 3) Anuran community composition will show three distinct groups (lower, intermediate, and higher altitudes) along the altitudinal gradient mainly because of different environmental conditions at different elevations (Figure 1d).

2 | METHODS

2.1 | Study area

The study was carried out in Poços de Caldas Plateau region, considered one of the largest sets of alkaline rocks on Earth (Figure 2). The Plateau is located on the extreme western edge of the Serra da Mantiqueira, a mountain range in eastern South America, Southeastern Brazil (Christofoletti, 1973).

The Plateau region is characterized by a main volcanic caldera almost complete with 800 km^2 (Christofoletti, 1973), formed from the intrusion of alkaline rocks during the Upper Cretaceous (Ellert, 1959), about 80 million years ago (Thomaz-Filho & Rodrigues, 1999) on the border between Minas Gerais and São Paulo States (Figure 2).

The climate of the region is Cwb of Köppen class "subtropical of altitude" being mesothermic with a dry winter from April to September and with mild summers and a rainy season from October to March. Mean annual temperatures vary between 17.6 and 18.4°C, with the mean annual temperature of the coolest month around 16.5°C and of the warmest month not exceeding 22°C. Mean annual precipitation varies between 1300 and 1700 mm (Pell et al., 2007). The regional altitude from the Poços de Caldas Plateau varies from 600 to 1800 m a.s.l. (Fraenkel et al., 1985). The region belongs to the Atlantic Forest biome (Ab'Saber, 1989) considered one of top-five global biodiversity hotspots (Mittermeier et al., 2011; Myers et al., 2000). Sampling areas are located in a transition area between the

Atlantic semi-deciduous forest, Cerrado patches, and high-altitude fields enclaves (above 1200 m a.s.l) in the interior of the Poços de Caldas Plateau region (Veloso et al., 1991).

2.2 | Anuran sampling

We sampled the anuran communities in 25 landscapes distributed along an altitudinal gradient of 600 to 1800 m a.s.l. with a minimum distance of 3 km between each landscape (Figure 2). We defined our altitudinal boundaries as lower (600–900 m), intermediate (900 to 1200 m), and higher altitudes (above 1200 m a.s.l.). The sampled landscapes were delineated by a 1 km radius around the landscapes' centroid as this radius is considered a reasonable sized area comprising dispersion and migration movements for most anuran species (Collins & Fahrig, 2017). Moreover, we argue that the use of 1-km radius size ensures that landscapes can be regarded as independent sampling areas in data analyses.

Anuran sampling was performed monthly in the rainy season and bi-monthly in the dry season from December 2016 to December 2017. Visual (young and adults) and acoustic search (calling males) methods were used simultaneously to maximize the number of detected species (Heyer et al., 1994). Each landscape was investigated at night between 1800 and 2400h always by two researchers (RM and JMO). Different areas in the landscapes and all potential microhabitat present (rocks, fallen logs, leaf litter, branches of trees or forest vegetation, and lentic and lotic water bodies when presents) were sampled during the research. All the anurans encountered during the fieldwork were captured, identified in situ, and then most individuals were released (but see below). In order to standardize the sampling effort among the landscapes and to minimize the number of false absences, the landscapes were sampled 10 times in a randomized order and standardized by time (1 h/night), totalizing 10 h per each landscape (Heyer et al., 1994).
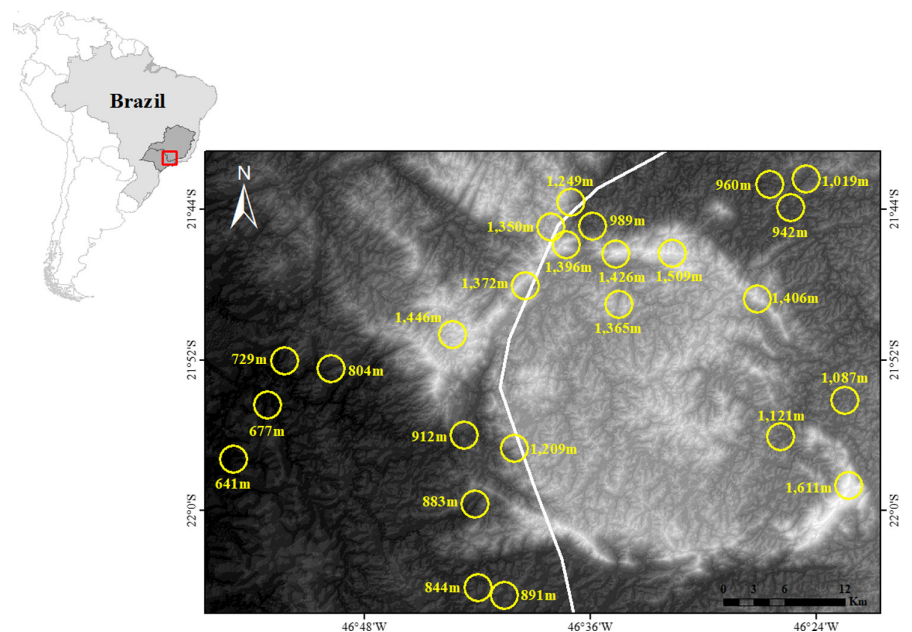

FIGURE 2 Study area covering 25 sampled landscapes distributed along an altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil. White line indicates the border between Minas Gerais (right) and São Paulo (left) States. Yellow circles (buffers 1 km) represent the sampled landscapes

Specimens that could not be identified in the field were collected (under SISBio license number #48526-1), anesthetized, and euthanized with xylocaine 20%, fixed in 10% formalin, and preserved in alcohol 70%. Vouchers were deposited in the Coleção Herpetológica do Laboratório de Zoologia de Vertebrados da ESALQ/USP (acronym VESALQ).

2.3 | Topographic and bioclimatic variables

We extracted topographic variables (altitude and slope) from the Brazil Geomorphometric Database (TOPODATA) with spatial resolution 30 m – downloaded from (http://www.dsr.inpe.br/topodata) and 19 standardized climatic variables (Bio 1 to Bio 19) obtained from the Global Climate Data (WorldClim version^2) with spatial resolution of 30 seconds-arc "~1 km^2" (Fick & Hijmans, 2017) – downloaded from (http://www.worldclim.org). These variables were obtained from the interpolation of average climate measurements from weather stations (Fick & Hijmans, 2017). We included these variables into data analyses as topography and climate represent the most important factors that determine anuran distributions (Duellman, 1999; Vasconcelos et al., 2010).

2.4 | Data analyses

To test whether anuran species richness shows a unimodal hump-shaped pattern along the altitudinal gradient, we first used an individual-based rarefaction curve to control for confounding effects of species abundance on richness (Gotelli & Colwell, 2001). Such rarefaction is needed along the altitudinal gradients because abundance typically affects anuran population density and size, which in turn have a positive effect on species richness (Chao et al., 2014). Furthermore, we combined rarefaction (interpolation) and prediction (extrapolation) to make a meaningful comparison standardized by identical sampling effort (Chao et al., 2014). Whereas the interpolation was performed based on the landscape with the smallest number of individuals ($n = 105$), the extrapolation was based on a larger number of individuals ($n = 1145$). Chao et al. (2014) have extended the classical models of rarefaction for the most common diversity measures (species richness, Shannon index, and Simpson's index) throughout Hill numbers. We used the nearly unbiased Shannon estimation ($q = 1$, Jost, 2007), which represents the alpha diversity with proportional weight to rare and common species.

In addition, we also tested whether topographic (altitude and slope) and climatic variables (19 bioclimatic variables) affect species rarefied richness. Because we expected a non-linear relationship between altitude and species richness, we used a Generalized Additive Model (GAM) that is able to fit non-linear patterns using a smooth function (Zuur et al., 2009). To simplify the statistical model, we started with a global model including uncorrelated predictors (see below) and compared this model with nested, simpler models. In addition, this model simplification compares linear effects with

smoothed effects to obtain the best fit, as demonstrated in an example model:

> *gam.global <- gam (rarefied_richness ~bio1 + bio4 + bio15 + alt)*
> *summary (gam.global)*
> *gam.mod1 <- gam (rarefied_richness ~bio1 + bio4 + bio15 + s(alt))*
> *summary (gam.mod1)*

The function compares whether the smoothed (s) effects represent a best fit with the linear effects. Furthermore, to avoid the undesirable effects of multicollinearity on model parameters, we first compared with a multiple correlation all predictor variables and removed those highly correlated ($r > 0.6$). We also retained only variables with a recognized biological meaning for our hypothesis.

To test the Rapoport rule (that is, anuran range size variation) along the altitudinal gradient, we used the midpoint method (Rohde et al., 1993) and calculated the weighted occurrence mean (between lower and upper limits of distribution of each species) to understand the altitudinal trends of anuran range size. Species that were recorded only at one site were excluded from the analyses.

To visualize differences in anuran community composition along the altitudinal gradient, we performed a Principal Coordinates Analysis (PCoA) using the abundance-based distance method of Bray–Curtis (Legendre & Legendre, 2012). PCoA ordinates the samples so that the distance between points represents the dissimilarity between samples. Scores of PCoA represent a measure of species composition weighed by species abundance.

Finally, to test whether community composition varies significantly among altitudinal zones (i.e., among lower, intermediate, and higher altitudes), we performed a permutational multivariate analysis of variance (PERMANOVA – Anderson, 2001). PERMANOVA is a routine analysis for testing the simultaneous response of one or more variables to one or more factors, thus allowing the analysis of multivariate data in the context of more complex sampling structures. Probabilities were calculated with permutation method randomized 9,999 times. We also used the BETADISPER method to investigate if there is a variance heterogeneity affecting the results obtained from the PERMANOVA method (Anderson & Walsh, 2013). This is an essential step because PERMANOVA confounds location (a measure of composition) and group dispersion (a measure of within-group compositional variation). All analyses were conducted using the R software (R Development Core Team, 2017).

3 | RESULTS

3.1 | Patterns of species richness and abundance

We recorded 10,935 specimens belonging to 10 families, 20 genera, and 70 species along the altitudinal gradient (Table S1), representing approximately 11% of Atlantic Forest (Rossa-Feres et al., 2017) and 7% of the Brazilian anuran fauna (Segalla et al., 2019). Hylidae was the richest family (37 species or 53%) followed by Leptodactylidae (12 or 17.1%), Bufonidae (5 or 7.1%), Brachycephalidae (5 or 7.1%),

Hylodidae (4 or 6%), Odontophrynidae (3 or 4.2%), Craugastoridae (1 or 1.4%), Phyllomedusidae (1 or 1.4%), Microhylidae (1 or 1.4%), and Ranidae (1 or 1.4%). The most abundant species was *Dendropsophus minutus* (*N* = 1123 or 10% of sampled individuals), followed by *Physalaemus cuvieri* (*N* = 1099 or 10%) and *Ischnocnema juipoca* (*N* = 894 or 8%). These three species represent approximately 28% of all sampled individuals (Table S1). Anuran rarefied richness (interpolated and extrapolated) showed a unimodal pattern along the altitudinal gradient, with the highest species richness found in midlands at ca. 900 m elevation (Figure 3).

According to GAM model, altitude (*p* = .004), annual mean temperature (*p* = .004) and temperature seasonality (*p* = .005) were the main drivers influencing anuran species richness along the altitudinal gradient (Table 1). The other variables did not contribute significantly (*p* > .05) to variation in anuran richness.

3.2 | Rapoport altitudinal rule

Anurans altitudinal range sizes increased with altitude, with higher-altitude species showing wider ranges than lower-altitude species, thus corroborating the Rapoport altitudinal rule (Figure 4).

3.3 | Altitudinal variation in anuran composition

The Principal Coordinates Analysis (PCoA) revealed that anuran community composition clustered into three distinct groups along the altitudinal gradient (axis 1 = 41.43% and axis 2 = 14.84%): (i) first, group comprised "lower altitude species," (ii) second, "intermediate altitude species," and (iii) third, "higher altitude species" (Figure 5).
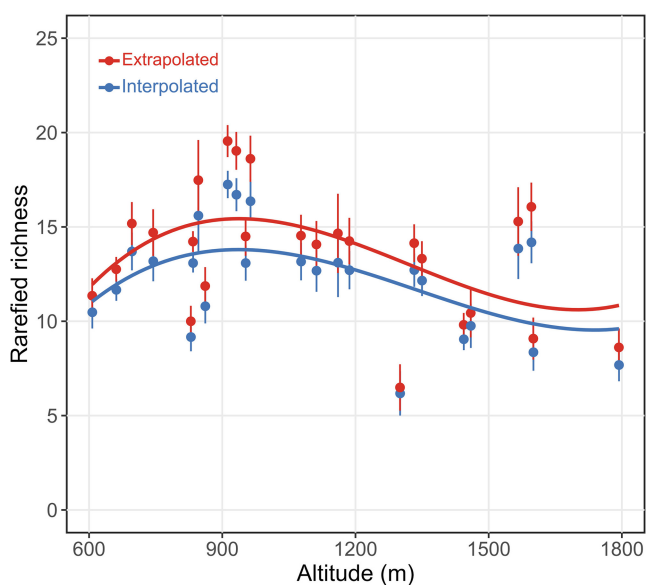

FIGURE 3 Individual-based rarefaction curve on rarefied (interpolated and extrapolated) richness along an altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil

These results were supported by the PERMANOVA (F = 12.867, R^2 = 0.35874, *p* < .001).

4 | DISCUSSION

4.1 | Patterns of species richness and abundance

Mountains are topographically and geologically highly heterogeneous maintaining high biological diversity (Körner, 2004). Moreover, the high anuran species richness and abundance found here may partly stem from the high number of landscapes sampled along the altitudinal gradient.

Several empirical studies on anuran species richness in different tropical and subtropical mountainous regions worldwide have documented from 16 to 60 species (Carvalho-Rocha et al., 2021; Giaretta et al., 1999; Goyannes-Araújo et al., 2015; Malonza & Veith, 2012; Siqueira et al., 2011, 2021; Villacampa et al., 2019; Zancolli et al., 2014). In our study, we found 70 anuran species at Poços de Caldas Plateau region. This species pool is an important subset of the anuran fauna from the Brazilian Atlantic Forest (625 species in total - Rossa-Feres et al., 2017), considered one of the top-five global biodiversity hotspots in the world (Mittermeier et al., 2011; Myers et al., 2000) with high anuran species richness and endemism (Haddad et al., 2013; Rossa-Feres et al., 2017). However, direct comparisons with other studies carried out in mountainous regions in Brazil or in other regions around the world are not straightforward because of different survey methods, protocols, and scales (Haider et al., 2018; Rahbek, 2005).

Our finding of a hump-shaped richness pattern along the altitudinal gradient agrees with several empirical studies and recent meta-analysis conducted with different taxonomic groups and regions and indicates that hump-shaped pattern is perhaps the most common richness pattern along mountainsides (McCain & Grytnes, 2010; Rahbek, 1995; Sanders & Rahbek, 2012). On the other hand, despite these similar hump-shaped richness patterns recorded in different mountainous regions with equivalent altitudes worldwide, these mountainsides may vary substantially in their climatic and vegetation features (Safford, 1999a, 1999b), and consequently, can influence altitudinal anuran range size, the peaks of species richness, and community segregation patterns in mountainous regions worldwide.

4.2 | Rapoport altitudinal rule

Our results also revealed that anuran altitudinal range sizes increased with altitude corroborating Rapoport altitudinal rule (Stevens, 1992). Our finding is consistent with other empirical studies encompassing different taxa such as butterflies (Fleishman et al., 1998), ants (Sanders, 2002), spiders (Chatzaki et al., 2005), harvestmen (Almeida-Neto et al., 2006), and dung beetles (Herzog et al., 2013), which also documented Rapoport altitudinal rule to occur in different regions. We note, however, that this rule is highly controversial

TABLE 1 Influence of the topographic and climatic variables on species rarefied (interpolated and extrapolated) richness through a Generalized Additive Model (GAM) along an altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil

| Interpolated richness				
Non linear models	Edf	Ref.df	*F*	*p*-value
sAltitude (Alt)	1.000.000	1.000.000	10.464.824	**.004**
sTemperature Seasonality (Bio 04)	3.461.033	4.251.915	4.951.471	**.005**
Extrapolated richness				
Linear models	Estimate	SE	*t*-value	*p*-value
(Intercept)	−9.510.342	72.005.629	−1.320.778	.201
Annual Mean Temperature (Bio 01)	1.235.705	0.384.598	3.212.972	**.004**
Non linear models	Edf	Ref.df	*F*	*p*-value
sTemperature Seasonality (Bio 04)	3.450.829	4.246.575	4.978.777	**.005**
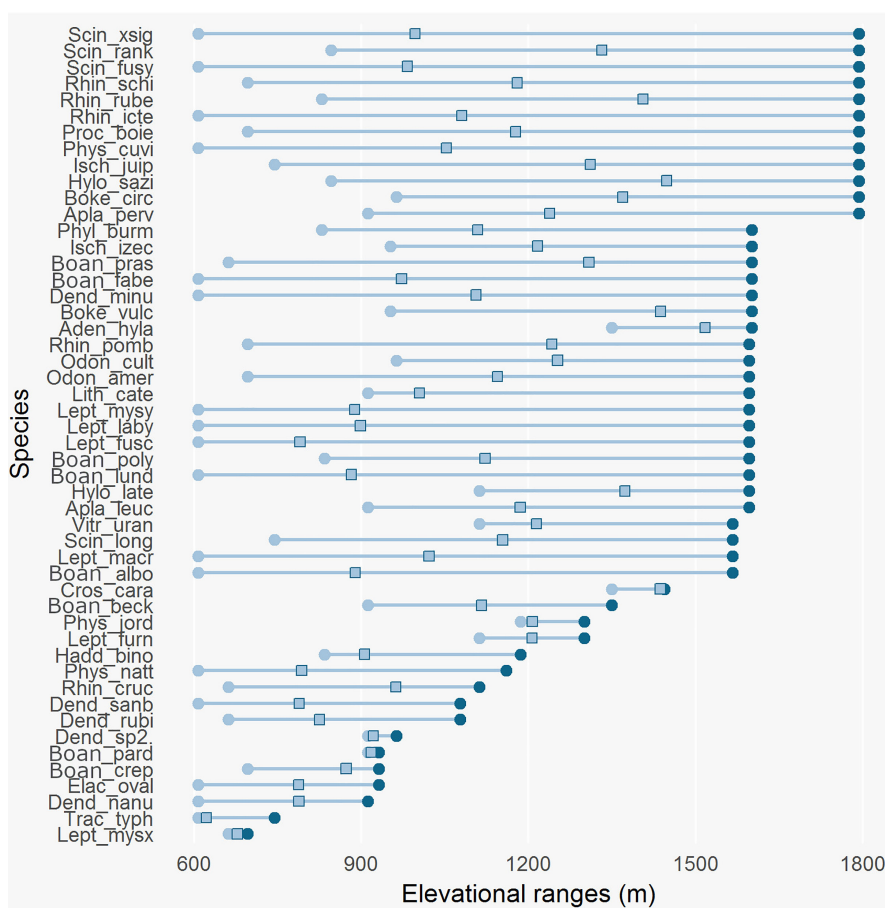
FIGURE 4 Altitudinal range size distributions of anurans in Poços de Caldas Plateau region, Southeastern Brazil. Bars show altitudinal range size along the altitudinal gradient. Square: median abundance. The range profiles were based on the lowest and highest elevation at which a species was observed

(Hawkins & Diniz-Filho, 2006; McCain & Knight, 2013), with many studies disagreeing with the rule (McCain & Knight, 2013; Ribas & Schoereder, 2006; Wang & Soininen, 2017). Nevertheless, Stevens (1992) did not claim Rapoport's rule (latitudinal or altitudinal) to be valid for all taxa, and the lack of this consensus as a universal rule is a common basis for criticism (Ruggiero & Werenkraut, 2007).

One of the most common mechanisms proposed by Stevens (1992) to explain Rapoport altitudinal rule is the climatic variability hypothesis or simply Rapoport "rescue" hypothesis. It predicts that species that can withstand broad climatic variability (i.e., have

broad climatic niche) can become more widely distributed (Gaston & Chown, 1999; Stevens, 1992). Our results indeed confirmed that annual mean temperature and temperature seasonality were the main drivers on anuran altitudinal range sizes. This is consistent with previous studies that also supported the climatic variability hypothesis with different taxa, such as dung beetles (Gaston & Chown, 1999), ants (Sanders et al., 2003), birds (McCain, 2009a), and moths (Beck et al., 2016).

Tropical biodiversity is strongly influenced by climatic stability (Barron, 1995), especially because ectothermic organisms such as
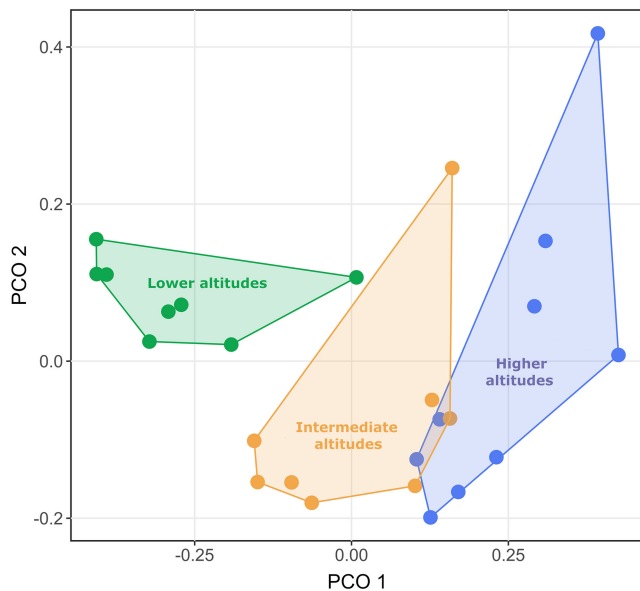
FIGURE 5 Principal Coordinates Analysis (PCoA) ordination of anurans communities' composition along an altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil. Ordination was based on dissimilarity matrix calculated with the Bray–Curtis index accounting for species abundances

anurans are highly dependent on the environment temperatures to maintain their body temperature (Bakken & Angilletta, 2014). Temperature has a profound influence on behavior, physiology, and ecological performance of anurans, as well as on growth rates, metabolism, species diversity, and geographic ranges (Angilletta, 2009; Navas, 2006; Navas et al., 2008). These factors impose selective pressures on the geographical ranges of terrestrial vertebrate (Chan et al., 2016; McCain, 2009b), having a direct impact on the extinction probability. According to Whitton et al. (2012) and Pintor et al. (2015), the current climate patterns are consistently the best predictors for amphibian range sizes on a regional scale. Overall, Rapoport altitudinal rule may help to understand the species richness peak at the middle of the altitudinal gradient rather than promoting a monotonic decrease in richness with altitude.

4.3 | Altitudinal variation in anuran composition

Anuran community composition exhibited a high species turnover revealing a clear segregation pattern along the altitudinal gradient forming three distinct communities. Some species were recorded only in lower (*Boana pardalis*, *Leptodactylus mystaceus*, *Trachycephalus typhonius*), intermediate (*Boana beckeri*, *Crossodactylus* aff. *caramaschii*, *Haddadus binotatus*, *Leptodactylus furnarius*, *Physalaemus jordanensis*), and higher altitudes (*Adenomera hylaedactyla*, *Bokermannohyla vulcaniae*, *Trachycephalus imitatrix*, *Ischnocnema* gr. *lactea*). This emphasizes the contribution of altitude and temperature on explaining species distribution in mountainous regions. Such community segregation has been documented in birds (Rahbek, 1997), dung beetles (Davis et al., 1999), gastropods (Presley et al., 2011), small mammals

(Andrade & Monjeau, 2014), and anurans (Malonza & Veith, 2012) in some tropical montane ecosystems.

Some previous empirical studies have revealed that dispersal limitation dominates at regional and large scales (Condit et al., 2002; Tuomisto et al., 2003) while environmental filtering dominates at smaller scales (Davidar et al., 2007; Hardy et al., 2012). Dispersal limitation occurs mainly with organisms less vagile such as anurans studied here (Buckley & Jetz, 2007; Qian & Ricklefs, 2012; Smith & Green, 2005), which corroborates our results. However, dispersal limitation and environmental filtering can vary with study region and spatial scales (Soininen et al., 2007; Wang et al., 2015). On the other hand, it is worth noting that other factors can also influence anuran community assembly in our study region, such as isolation, complex topography (physical barriers), climatic history and historical, and evolutionary processes (Brown, 2001; Currie, 1991; Hawkins et al., 2003; Laiolo et al., 2018; Steinbauer et al., 2016). Finally, anuran community composition from the Poços de Caldas Plateau region revealed a high species turnover and a clear community segregation pattern corroborates the idea that the altitude (dispersal limitation) and temperature (environmental filtering) are important drivers to shape community assembly from the Brazilian Atlantic Forest mountainous regions.

4.4 | Implications for conservation

Montane ecosystems are expected to experience high biodiversity losses in the next decades (Davidson et al., 2013; McCain & Colwell, 2011; Peters et al., 2019). This has been occurring mainly because of the intensification of disruptive anthropogenic activities (Barnosky et al., 2011; Dirzo et al., 2014) as well as accelerated climate change (Bellard et al., 2012; Catenazzi, 2015; Chen et al., 2011). These negative effects are jointly imposing unprecedented pressures on the world's biodiversity (Díaz et al., 2019) and some taxa are currently experiencing range shifts (Badgley et al., 2017; Chen et al., 2009; Elsen & Tingler, 2015). This may accelerate in the future (Elsen et al., 2018) resulting in higher extinction probability. It may be most severe especially in tropical montane ecosystems (Davidson et al., 2013; McCain & Colwell, 2011), and particularly affecting montane species (Elsen & Tingler, 2015).

Preserving biodiversity in an era considered the sixth mass extinction (Barnosky et al., 2011) will be the greatest challenge of this century (Cardinale et al., 2012; Ruffell et al., 2017; Sala et al., 2000). Our research revealed a high species turnover because several species presented narrow altitudinal range size, resulting in a clear anuran community segregation pattern along the mountainsides from the Poços de Caldas Plateau region. These results demonstrated that, in order to maintain high biodiversity levels, different conservation strategy would be needed in tropical mountainous regions. Montane ecosystems with high species turnover among sites can support several and spatially separated species pools and, therefore, only large enough protected areas can maximize biodiversity conservation (Franklin, 1993). On the

other hand, montane ecosystems with high richness difference among sites (that is, high degree of nestedness) would suggest that it is better to protect biodiversity hotspots (Cutler, 1994). Our findings revealed that beta diversity patterns in mountainous regions also have important implications for species conservation. Furthermore, our rarefaction curves highlight that the distributions of common, rare, endemics, and threatened species all deserve attention, and conservation plans need to encompass the entire mountainous region and not just total diversity hotspots (Grenyer et al., 2006; Orme et al., 2005) or simply only one altitudinal zone.

Some studies have reported that the new protected areas also need to focus on species' range shifts in order to minimize the effects of climate change on species distribution (Hannah, 2010; Lemes & Loyola, 2013; Mawdsley, 2011). Small-ranged species constitute most to Earth's species diversity (Gaston, 2003) and maybe overall more vulnerable and threatened by climate change effects, thus presenting higher risk of extinction (Bellard et al., 2012; Chen et al., 2009; Davies et al., 2009; Elsen et al., 2018). Our findings revealed that protecting the whole montane ecosystem (lower, intermediate, and higher altitudes) is important to preserve the whole regional species pool, species with narrow range sizes, and diverse communities in tropical mountainous regions. Therefore, studies on Rapoport altitudinal rule may not only help us to understand the variability in species altitudinal range sizes, but also help to conserve the species that occupy different narrow altitudinal ranges. To understand the species richness spatial patterns and the potential climate change effects are crucial to target conservation actions properly in the long term (Zancolli et al., 2014; Zhang et al., 2016).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

RM conceived the idea and MCR helped in designing the research; RM and JMO conducted the fieldwork and collected the data, and RM led the writing with assistance from JS and JB.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.cjsxksn77 (Matavelli et al., 2022).

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