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

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2022-05

1 **Altitude and temperature drive anuran community assembly in a Neotropical**

2 **mountain region**

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4 Altitude and temperature drive anuran communities **(running title)**

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Abstract

 Aim: 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.

Location: Atlantic Forest, Southeastern Brazil.

Taxon: Amphibia: Anura.

Methods: 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.

Results: 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.

Main 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. Study revealed new insights into the patterns and drivers of Neotropical anuran

communities.

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 & Blackburn, 2000; Gaston, 2003; Sexton et al., 2009). Such research questions have continued to fascinate biogeographers and macroecologists for several decades (Rahbek, 1995; McCain & Grytnes, 2010; 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 (Rahbek, 1995; McCain & Grytnes, 2010; Sanders & Rahbek, 2012). Some mechanisms such as climatic, biological, evolutionary, and historical process have been proposed to explain patterns of species richness in mountainous regions (Sanders et al., 2003; McCain & Grytnes, 2010; Sanders & Rahbek, 2012), but currently the most important processes underlying species richness patterns are still poorly understood for many taxa and ecosystems (Brown, 2001; Grau et al., 2007; 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 (Steven, 1989), later it was extended to explain species ranges 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 (Stevens, 1992; Gaston & Chown, 1999).

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, behaviour, and reproductive rate (Duellman & Trueb, 1986; Buckley &

Jetz, 2007; 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 (Rahbek, 1995; McCain & Grytnes, 2010).

100   The Atlantic Forest biome is one of the most biodiverse regions worldwide

101   including rare, endemic and threatened anuran species (Haddad et al., 2013; Rossa-

102   Feres et al., 2017) and considered one of the top-five global biodiversity hotspots in the

103   world (Myers et al., 2000; Mittermeier et al., 2011). Despite the high species richness

104   and endemism level, the Atlantic Forest has been under great human impact for about

105   half a century due to habitat fragmentation resulting in severe biodiversity loss (Ribeiro

106   et al., 2009; Haddad et al., 2015).

107   Climate change is also expected to force species distributions towards higher

108   altitudes (Chen et al., 2011; Tingley et al., 2012; Freeman and Freeman, 2014) and

109   species range shifts may accelerate in the future (Elsen et al., 2018). This would lead to

110   the extinction of small-ranged species and weak dispersal (Janzen, 1967; Davies et al.,

111   2009; Sandel et al., 2011) of small and isolated populations from their current

112   geographical ranges (Midgley et al., 2002; Thomas et al., 2004), especially in tropical

113   mountainous regions, where the risk of decline may be higher and more severe (McCain

114   and Colwell, 2011; Davidson et al., 2013).

115   Here, we aim to analyze the topographic and climatic effects on anuran

116   community composition, richness, and range sizes in a mountainous region in the

117   Atlantic Forest biome. Specifically, we: (1) determine the shape of the distribution

118   pattern of anuran species richness along the altitudinal gradient; (2) test if the Rapoport

119   rule explains anuran range size variation along the altitudinal gradient; and (3)

120   investigate how anuran community composition varies along the altitudinal gradient.

121   Our hypotheses are: 1) Anuran species richness will exhibit either a decreasing or a

122   unimodal pattern along the altitudinal gradient (Figure 1A and 1B); 2) Species recorded

123   at higher altitudes will show wider range size than lower altitudes species along the

124   altitudinal gradient (Figure 1C), and 3) Anuran community composition will show three

125 distinct groups (lower, intermediate, and higher altitudes) along the altitudinal gradient

126 mainly because of different environmental conditions at different elevations (Figure

127 1D).
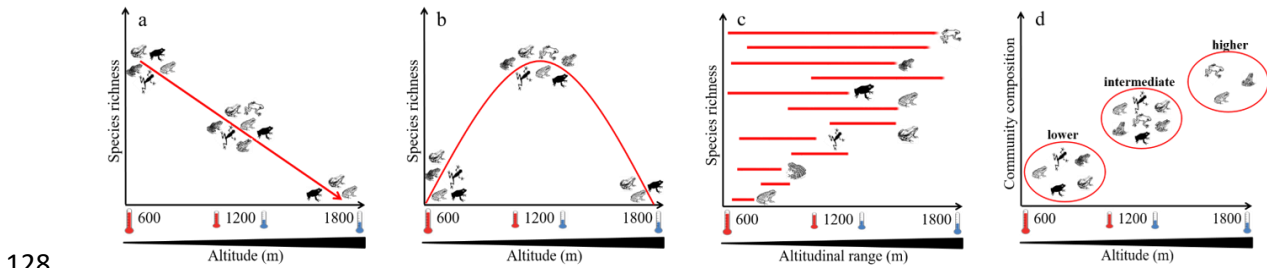
128

129 **Figure 1.** Hypothetical relationships of species richness and community

130 composition in response to the topographic and climatic variables along an

131 altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil. In

132 panel [a] we hypothesize that species richness will decline with altitude as a

133 consequence of temperature reduction; in [b] we hypothesize that in the

134 intermediate altitudes, we will detect higher richness, because this range will

135 share species from both lower and higher altitudes; in [c] we hypothesize that

136 species that are found in higher altitudes will also have higher plasticity in their

137 thermal tolerance, thus being also found in lower altitudes; in [d] we present an

138 alternative hypothesis, where community composition differs among lower,

139 intermediate, and high altitudes with highest richness in intermediate altitudes,

140 as presented in [b].

141

142 **2. METHODS**

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144 **2.1. Study area**

145   The study was carried out in Poços de Caldas Plateau region, considered one of

146 the largest set of alkaline rocks on Earth (Figure 2). The Plateau is located on the

6

147   extreme western edge of the Serra da Mantiqueira, a mountain range in eastern South

148   America, Southeastern Brazil (Christofoletti, 1973).

149   The Plateau region is characterized by a main volcanic caldera almost complete

150   with 800 km^2 (Christofoletti, 1973) formed from the intrusion of alkaline rocks during

151   the Upper Cretaceous (Ellert, 1959), about 80 million years ago (Thomaz-Filho &

152   Rodrigues, 1999) on the border between Minas Gerais and São Paulo States (Figure 2).

153
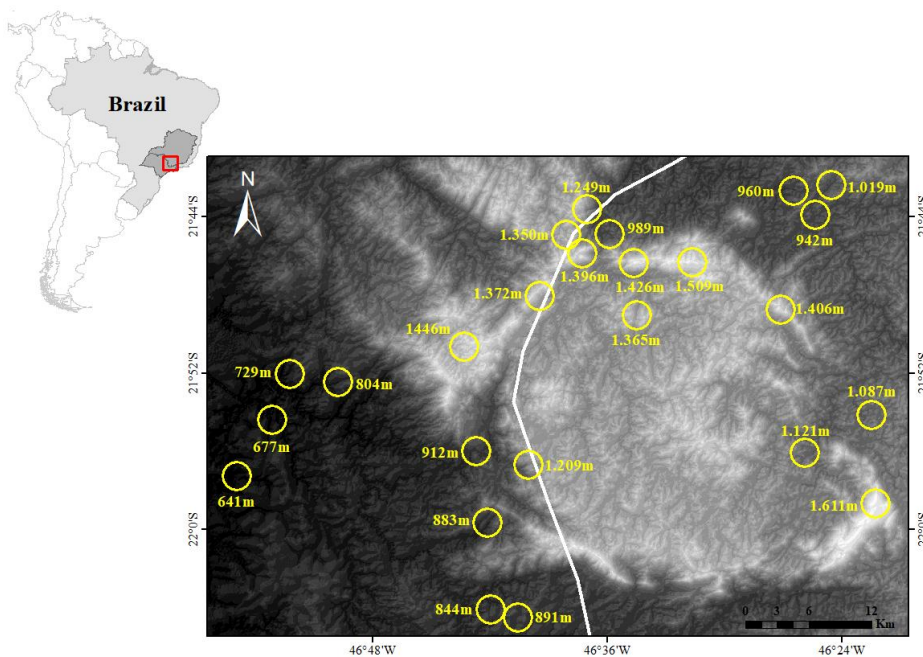
154

155   **Figure 2**. Study area covering 25 sampled landscapes distributed along an

156   altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil.

157   White line indicates the border between Minas Gerais (*right*) and São Paulo

158   (*left*) States. Yellow circles (*buffers 1 km*) represent the sampled landscapes.

159   Altitudes represent the mean elevations within each landscape sampled (buffers

160   1 km).

161

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 17.6ºC

and 18.4ºC, with the mean annual temperature of the coolest month around 16.5ºC and

of the warmest month not exceeding 22ºC. Mean annual precipitation varies between

1,300 and 1,700 mm (Pell et al., 2007). The regional altitude from the Poços de Caldas

Plateau varies from 600 to 1,800 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 hotspot (Myers et al., 2000; Mittermeier et al., 2011). Sampling areas are

located in a transition area between the Atlantic Semi-deciduous Forest, Cerrado

patches, and high-altitude fields enclaves (above 1,200 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 1,800 m a.s.l. with a minimum distance of 3 km between

each landscape (Figure 2). We defined our altitudinal boundaries as lower (600 to 900

m), intermediate (900 to 1,200 m), and higher altitudes (above 1,200 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 (Guerry & Hunter, 2002; 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

187   acoustic search (calling males) methods were used simultaneously to maximize the

188   number of detected species (Heyer et al., 1994). Each landscape was investigated at

189   night between 1800 and 2400h always by two researchers (RM and JMO). Different

190   areas in the landscapes and all potential microhabitat present (rocks, fallen logs, leaf

191   litter, branches of trees or forest vegetation, and lentic and lotic water bodies when

192   presents) were sampled during the research. All the anurans encountered during the

193   fieldwork were captured, identified in situ, and then most individuals were released (but

194   see below). In order to standardize the sampling effort among the landscapes and to

195   minimize the number of false absences, the landscapes were sampled 10 times in a

196   randomized order and standardized by time (1 h/night), totalizing 10 hours per each

197   landscape (Heyer et al., 1994).

198   Specimens that could not be identified in the field were collected (under SISBio

199   license number #48526-1), anesthetized and euthanized with xylocaine 20%, fixed in

200   10% formalin and preserved in alcohol 70%. Vouchers were deposited in the Coleção

201   Herpetológica do Laboratório de Zoologia de Vertebrados da ESALQ/USP (acronym

202   VESALQ).

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204   **2.3. Topographic and bioclimatic variables**

205   We extracted topographic variables (altitude and slope) from the Brazil

206   Geomorphometric Database (TOPODATA) with spatial resolution 30 m – downloaded

207   from (http://www.dsr.inpe.br/topodata) and 19 standardized climatic variables (Bio 1 to

208   Bio 19) obtained from the Global Climate Data (WorldClim version2) with spatial

209   resolution of 30 seconds-arc "~1 km^2" (Fick and Hijmans 2017) – downloaded from

210   (http://www.worldclim.org). These variables were obtained from the interpolation of

211   average climate measurements from weather stations (Fick and Hijmans 2017). We

9

212 included these variables into data analyses as topography and climate represent the most

213 important factors that determine anuran distributions (Duellman, 1999; Menin et al.,

214 2007; Vasconcelos et al., 2010).

215

216 **2.4. Data analyses**

217   To test whether anuran species richness shows a unimodal hump-shaped pattern

218 along the altitudinal gradient, we first used an individual-based rarefaction curve to

219 control for confounding effects of species abundance on richness (Gotelli & Colwell,

220 2001). Such rarefaction is needed along the altitudinal gradients because abundance

221 typically affects anuran population density and size, which in turn have a positive effect

222 on species richness (Chao et al., 2014). Furthermore, we combined rarefaction

223 (interpolation) and prediction (extrapolation) to make a meaningful comparison

224 standardized by identical sampling effort (Chao et al., 2014). Whereas the interpolation

225 was performed based on the landscape with the smallest number of individuals (n =

226 105), the extrapolation was based on a larger number of individuals (n = 1,145). Chao et

227 al. (2014) have extended the classical models of rarefaction for the most common

228 diversity measures (species richness, Shannon index, and Simpson's index) throughout

229 Hill numbers. We used the nearly unbiased Shannon estimation (q = 1, Jost, 2007),

230 which represents the alpha diversity with proportional weight to rare and common

231 species.

232   In addition, we also tested whether topographic (altitude and slope) and climatic

233 variables (19 bioclimatic variables) affect species rarefied richness. Because we

234 expected a non-linear relationship between altitude and species richness, we used a

235 Generalized Additive Model (GAM) that is able to fit non-linear patterns using a

236 smooth function (Zuur et al., 2009). To simplify the statistical model, we started with a

237 global model including uncorrelated predictors (see below) and compared this model

238 with nested, simpler models. In addition, this model simplification compare linear

239 effects with smoothed effects to obtain the best fit, as demonstrated in an example

240 model:

241 *gam.global <- gam (rarefied_richness ~ bio1 + bio4 + bio15 + alt)*

242 *summary (gam.global)*

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

244 *summary (gam.mod1)*

245   The function compares whether the smoothed (s) effects represent a best fit with

246 the linear effects. Furthermore, to avoid the undesirable effects of multicollinearity on

247 model parameters, we first compared with a multiple correlation all predictor variables

248 and removed those highly correlated ($r > 0.6$). We also retained only variables with a

249 recognized biological meaning for our hypothesis.

250   To test the Rapoport rule (that is, anuran range size variation) along the

251 altitudinal gradient, we used the midpoint method (Rohde et al., 1993) and calculated

252 the weighted occurrence mean (between lower and upper limits of distribution of each

253 species) to understand the altitudinal trends of anuran ranges size. Species that were

254 recorded only at one site were excluded from the analyses.

255   To visualize differences in anuran community composition along the altitudinal

256 gradient, we performed a Principal Coordinates Analysis (PCoA) using the abundance-

257 based distance method of Bray-Curtis (Legendre & Legendre, 2012). PCoA ordinates

258 the samples so that the distance between points represents the dissimilarity between

259 samples. Scores of PCoA represent a measure of species composition weighed by

260 species abundance.

261   Finally, to test whether community composition varies significantly among

262   altitudinal zones (i.e., among lower, intermediate, and higher altitudes) we performed a

263   permutational multivariate analysis of variance (PERMANOVA – Anderson, 2001).

264   PERMANOVA is a routine analysis for testing the simultaneous response of one or

265   more variables to one or more factors, thus allowing the analysis of multivariate data in

266   the context of more complex sampling structures. Probabilities were calculated with

267   permutation method randomized 9,999 times. We also used the BETADISPER method

268   to investigate if there is a variance heterogeneity affecting the results obtained from the

269   PERMANOVA method (Anderson & Walsh, 2013). This is an essential step because

270   PERMANOVA confounds location (a measure of composition) and group dispersion (a

271   measure of within-group compositional variation). All analyses were conducted using

272   the R software (R Development Core Team, 2017).

273

274   **4. RESULTS**

275

276   **4.1. Patterns of species richness and abundance**

277   We recorded 10,935 specimens belonging to 10 families, 20 genera, and 70

278   species along the altitudinal gradient (Table S1), representing approximately 11% of

279   Atlantic Forest (Rossa-Feres et al., 2017) and 7% of the Brazilian anuran fauna (Segalla

280   et al., 2019). Hylidae was the richest family (37 species or 53%) followed by

281   Leptodactylidae (12 or 17,1%), Bufonidae (5 or 7,1%), Brachycephalidae (5 or 7,1%),

282   Hylodidae (4 or 6%), Odontophrynidae (3 or 4,2%), Craugastoridae (1 or 1,4%),

283   Phyllomedusidae (1 or 1,4%), Microhylidae (1 or 1,4%), and Ranidae (1 or 1,4%). The

284   most abundant species was *Dendropsophus minutus* (N=1,123 or 10% of sampled

285   individuals), followed by *Physalaemus cuvieri* (N=1,099 or 10%) and *Ischnocnema*

286 *juipoca* (N=894 or 8%). These three species represent approximately 28% of all

287 sampled individuals (Table S1). Anuran rarefied richness (interpolated and

288 extrapolated) showed a unimodal pattern along the altitudinal gradient, with the highest

289 species richness found in midlands at ca. 900 m elevation (Figure 3).
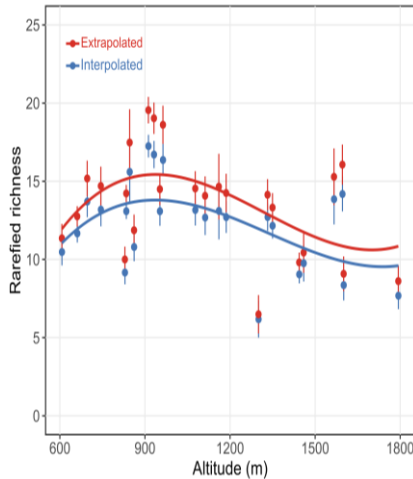
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291 **Figure 3.** Individual-based rarefaction curve on rarefied (interpolated and

292 extrapolated) richness along an altitudinal gradient in Poços de Caldas Plateau

293 region, Southeastern Brazil.

294

295   According to GAM model, altitude (p=0.004), annual mean temperature

296 (p=0.004) and temperature seasonality (p=0.005) were the main drivers influencing

297 anuran species richness along the altitudinal gradient (Table 1). The other variables did

298 not contribute significantly (P > 0.05) to variation in anuran richness.

299

300 **Table 1:** Influence of the topographic and climatic variables on species rarefied

301 (interpoled and extrapoled) richness through a Generalized Additive Model (GAM)

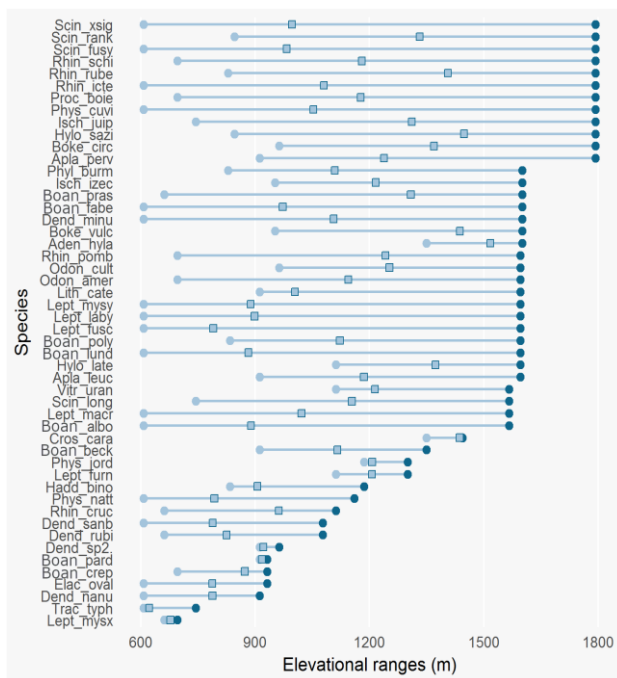302 along an altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil.

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INTERPOLATED RICHNESS				
Non linear models	**Edf**	**Ref.df**	**F**	**P-value**
sAltitude (Alt)	1.000.000	1.000.000	10.464.824	**0.004**
sTemperature Seasonality (Bio 04)	3.461.033	4.251.915	4.951.471	**0.005**
EXTRAPOLATED RICHNESS				
Linear models	**Estimate**	**Std. Error**	**t-value**	**P-value**
(Intercept)	-9.510.342	72.005.629	-1.320.778	0.201
Annual Mean Temperature (Bio 01)	1.235.705	0.3845988	3.212.972	**0.004**
Non linear models	**Edf**	**Ref.df**	**F**	**P-value**
sTemperature Seasonality (Bio 04)	3.450.829	4.246.575	4.978.777	**0.005**

305

4.2. Rapoport altitudinal rule

307   Anurans altitudinal range sizes increased with altitude, with higher-altitude

308 species showing wider ranges than lower-altitude species, thus corroborating the

309 Rapoport altitudinal rule (Figure 4).


310

Figure 4. Altitudinal range size distributions of anurans in Poços de Caldas

Plateau region, Southeastern Brazil. Bars show altitudinal range size along an

altitudinal gradient. Square: median abundance. The range profiles were based

on the lowest and highest elevation at which a species was observed.

4.3. 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). These results were supported by the PERMANOVA (F = 12.867, R^2 = 0.35874, P < 0.001).
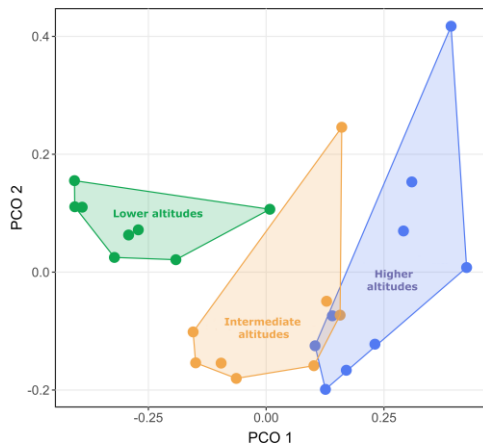
Figure 5. Principal Coordinates Analysis (PCoA) ordination of anurans communities' composition along an altitudinal gradient in Poços de Caldas Plateau region, Southeastern Brazil. Ordination was based on dissimilarity matrix calculated with the Bray-Curtis index accounting for species abundances.

5. DISCUSSION

5.1. Patterns of species richness and abundance

Mountains are topographically and geologically highly heterogeneous maintaining high biological diversity (Körner 2004; Spehn & Körner, 2005). Moreover,

334   the high anuran species richness and abundance found here may partly stem from the

335   high number of landscapes sampled along the altitudinal gradient.

336   Several empirical studies on anuran species richness in different tropical and

337   subtropical mountainous regions worldwide have documented from 16 to 60 species

338   (Giaretta et al., 1999; Siqueira et al., 2011; Malonza & Veith, 2012; Zancolli et al.,

339   2014; Goyannes-Araújo et al., 2015; Villacampa et al., 2019; Carvalho-Rocha et al.,

340   2021; Siqueira et al., 2021). In our study, we found 70 anuran species at Poços de

341   Caldas Plateau region. This species pool is an important subset of the anuran fauna from

342   the Brazilian Atlantic Forest (625 species in total - Rossa-Feres et al., 2017), considered

343   one of the 34 biodiversity hotspots in the world (Myers et al., 2000; Mittermeier et al.,

344   2011) with high anuran species richness and endemism (Haddad et al., 2013; Rossa-

345   Feres et al., 2017). However, direct comparisons with other studies carried out in

346   mountainous regions in Brazil or in other regions around the worldwide are not

347   straightforward because of different survey methods, protocols, and scales (Rahbek

348   2005; Haider et al., 2018).

349   Our finding of a hump-shaped richness pattern along the altitudinal

350   gradient agrees with several empirical studies and recent meta-analysis conducted with

351   different taxonomic groups and regions and indicates that hump-shaped pattern is

352   perhaps the most common richness pattern along mountainsides (Rahbek, 1995;

353   McCain & Grytnes, 2010; Sanders & Rahbek, 2012). On the other hand, despite these

354   similar hump-shaped richness patterns recorded in different mountainous regions with

355   equivalent altitudes worldwide, these mountainsides may vary substantially in their

356   climatic and vegetation features (Safford, 1999a, 1999b), and consequently, can

357   influence altitudinal anuran range size, the peaks of species richness, and community

358   segregation patterns in mountainous regions worldwide.

5.2. 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 (Hawkins & Diniz-Filho, 2006; McCain & Knight, 2013), with many studies disagreeing with the rule (Ribas & Schoereder 2006; McCain & Knight, 2013; 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 (Gaston et al., 1998; 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 (Stevens, 1992; Gaston & Chown, 1999). 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 anurans are highly dependent on the

384 environment temperatures to maintain their body temperature (Bakken & Angilletta,

385 2014). Temperature has a profound influence on behaviour, physiology, and ecological

386 performance of anurans, as well as on growth rates, metabolism, species diversity, and

387 geographic ranges (Navas, 2006; Navas et al., 2008; Angilletta, 2009). These factors

388 impose selective pressures on the geographical ranges of terrestrial vertebrate (McCain,

389 2009b; Sheldon et al., 2015; Chan et al., 2016), having a direct impact on the extinction

390 probability. According to Whitton et al. (2012) and Pintor et al. (2015), the current

391 climate patterns are consistently the best predictors for amphibian range sizes on a

392 regional scale. Overall, Rapoport altitudinal rule may help to understand the species

393 richness peak at the middle of the altitudinal gradient rather than promoting a monotonic

394 decrease in richness with altitude.

395

396 **5.3. Altitudinal variation in anuran composition**

397 Anuran community composition exhibited a high species turnover revealing a

398 clear segregation pattern along the altitudinal gradient forming three distinct

399 communities. Some species were recorded only in lower (*Boana pardalis*,

400 *Leptodactylus mystaceus, Trachycephalus typhonius*), intermediate (*Boana Beckeri*,

401 *Crossodactylus caramaschii, Haddadus binotatus, Leptodactylus furnarius*,

402 *Physalaemus jordanensis*), and higher altitudes (*Adenomera hylaedactyla*,

403 *Bokermannohyla vulcaniae, Trachycephalus imitatrix, Ischnocnema* gr. *lactea*). This

404 emphasize the contribution of altitude and temperature on explaining species

405 distribution in mountainous regions. Such community segregation has been documented

406 in birds (Rahbek, 1997), dung beetles (Davis et al., 1999), gastropods (Presley et al.,

407 2011), small mammals (Andrade & Monjeau, 2014), and anurans (Malonza & Veith,

408 2012) in some tropical montane ecosystems.

409   Some previous empirical studies have revealed that dispersal limitation

410   dominates at regional and large scales (Condit et al., 2002; Tuomisto et al., 2003) while

411   environmental filtering dominates at smaller scales (Davidar et al., 2007; Hardy et al.,

412   2011). Dispersal limitation occurs mainly with organisms less vagile such as anurans

413   studied here (Smith & Green, 2005; Buckley & Jetz, 2007; Qian & Ricklefs, 2012),

414   which corroborates our results. However, the dispersal limitation and environmental

415   filtering can vary with study region and spatial scales (Soininen et al., 2007; Wang et

416   al., 2015). On the other hand, it is worth noting that other factors can also influence

417   anuran community assembly in our study region, such as isolation, complex topography

418   (physical barriers), climatic history and historical, and evolutionary processes (Currie,

419   1991; Brown, 2001; Hawkins et al., 2003; Steinbauer et al., 2016; Laiolo et al., 2018).

420   Finally, anuran community composition from the Poços de Caldas Plateau region

421   revealed a high species turnover and a clear community segregation pattern corroborates

422   the idea that the altitude (dispersal limitation) and temperature (environmental filtering)

423   are important drivers to shape community assembly from the Brazilian Atlantic Forest

424   mountainous regions.

425

426   6. Implications for conservation

427   Montane ecosystems are expected to experience high biodiversity losses in the

428   next decades (McCain & Colwell, 2011; Davidson et al., 2013; Peters et al., 2019). This

429   has been occurring mainly because of the intensification of hard anthropogenic

430   activities (Barnosky et al., 2011; Dirzo et al., 2014) as well as an accelerated climate

431   change (Chen et al., 2011; Bellard et al., 2012; Catenazzi, 2015). These negative effects

432   are jointly imposing unprecedented pressures on the world's biodiversity (Díaz et al.,

433   2019) and some taxa are currently experiencing range shifts (Chen et al., 2009; Elsen &

434 Tingler, 2015; Badgley et al., 2017). This may accelerate in the future (Elsen et al.,

435 2018) resulting higher extinction probability. It may be most severe especially in

436 tropical montane ecosystems (McCain & Colwell, 2011; Davidson et al., 2013), and

437 particularly affecting montane species (Elsen and Tingley 2015).

438   Preserving biodiversity in an era considered the sixth mass extinction (Barnosky

439 et al., 2011) will be the greatest challenge of this century (Sala et al., 2000; Cardinale et

440 al., 2012; Ruffell et al., 2017). Our research revealed a high species turnover because

441 several species presented narrow altitudinal range size, resulting in a clear anuran

442 community segregation pattern along the mountainsides from the Poços de Caldas

443 Plateau region. These results demonstrated that, in order to maintain high biodiversity

444 levels, different conservation strategy would be needed in tropical mountainous regions.

445 Montane ecosystems with high species turnover among sites can support several and

446 spatially separated species pools and, therefore, only large enough protected areas can

447 maximize biodiversity conservation (Franklin, 1993). On the other hand, montane

448 ecosystems with high richness difference among sites (that is, high degree of

449 nestedness) would suggest that it is better to protect biodiversity hotspots (Cutler,

450 1994). Our findings revealed that beta diversity patterns in mountainous regions also

451 have important implications for species conservation. Furthermore, our rarefaction

452 curves highlight that the distributions of common, rare, endemics, and threatened

453 species all deserve attention, and conservation plans need to encompass the entire

454 mountainous region and not just total diversity hotspots (Orme et al., 2005; Grenyer et

455 al., 2006) or simply only one altitudinal zone.

456   Some studies have reported that the new protected areas also need to focus on

457 species' range shifts in order to minimize the effects of climate change on species

458 distribution (Hannah, 2010; Mawdsley, 2011; Lemes and Loyola, 2013). Small-ranged

459   species constitute most to Earth's species diversity (Gaston, 2003) and maybe overall

460   more vulnerable and threatened by climate change effects, thus presenting higher risk of

461   extinction (Chen et al., 2009; Davies et al., 2009; Bellard et al., 2012; Elsen et al.,

462   2018). Our findings revealed that protecting the whole montane ecosystem (lower,

463   intermediate, and higher altitudes) is important to preserve the whole regional species

464   pool, species with narrow range sizes, and diverse communities in Tropical

465   mountainous regions. Therefore, studies on Rapoport altitudinal rule may not only help

466   us to understand the variability in species altitudinal range sizes, but also help to

467   conserve the species that occupy different narrow altitudinal ranges. To understand the

468   species richness spatial patterns and the potential climate change effects are crucial to

469   target conservation actions properly in the long-term (Zhang et al., 2012; Zancolli et al.,

470   2014).

471

484 (SP). We thank also Instituto Chico Mendes de Conservação da Biodiversidade

485 (ICMBio/SISBio) for the collection license (Authorization # 48526-1).

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984

985   **SEPARATE FIGURE LEGEND:**

986   Figure 1. Hypothetical relationships of species richness and community composition in

987   response to the topographic and climatic variables along an altitudinal gradient in

988   Poços de Caldas Plateau region, Southeastern Brazil. In panel [a] we hypothesize

989   that species richness will decline with altitude as a consequence of temperature

990   reduction; in [b] we hypothesize that in the intermediate altitudes, we will detect

991   higher richness, because this range will share species from both lower and higher

992   altitudes; in [c] we hypothesize that species that are found in higher altitudes will

993   also have higher plasticity in their thermal tolerance, thus being also found in lower

994   altitudes; in [d] we present an alternative hypothesis, where community

995   composition differs among lower, intermediate, and high altitudes with highest

996   richness in intermediate altitudes, as presented in [b].

997   Figure 2. Study area covering 25 sampled landscapes distributed along an altitudinal

998   gradient in Poços de Caldas Plateau region, Southeastern Brazil. White line

999   indicates the border between Minas Gerais (right) and São Paulo (left) States.

1000   Yellow circles (buffers 1 km) represent the sampled landscapes.

1001   Figure 3. Individual-based rarefaction curve on rarefied (interpolated and extrapolated)

1002   richness along an altitudinal gradient in Poços de Caldas Plateau region,

1003   Southeastern Brazil.

1004   Figure 4. Altitudinal range size distributions of anurans in Poços de Caldas Plateau

1005   region, Southeastern Brazil. Bars show altitudinal range size along the altitudinal

1006   gradient. Square: median abundance. The range profiles were based on the lowest

1007   and highest elevation at which a species was observed.

1008   Figure 5. Principal Coordinates Analysis (PCoA) ordination of anurans communities'

1009   composition along an altitudinal gradient in Poços de Caldas Plateau region,

1010   Southeastern Brazil. Ordination was based on dissimilarity matrix calculated with

1011   the Bray-Curtis index accounting for species abundances.

1012

1013