Scaling the Heights: Understanding Frog Diversity Along the Altitudinal Gradient of Southern Bahia's Atlantic Forest

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Abstract

Background. Montane environments harbor a rich diversity of amphibians in Neotropical regions; however, it is still an ecology enigma to understand what drives this diversity along altitudinal ranges. In this sense, we described the anuran composition, richness, and distribution patterns along an altitudinal gradient in the Atlantic Forest of northeastern Brazil and how environmental variables can explain these patterns.

Methods. We characterized the richness, abundance, and composition of anuran species in 24 transects within the forest along an altitudinal range of 200–950 m in the Private Reserve of Natural Heritage (RPPN) Serra Bonita, southern Bahia state, northeastern Brazil. For each transect, we measured the following environmental variables: altitude, leaf litter depth and cover, canopy opening, number of tank-bromeliads, number of trees, and mean air temperature.

Results. We found 36 anuran species distributed in 10 families. Altitudinal strata play an important role in explaining the anuran composition, richness, and abundance, with direct-developing frogs being the most abundant species. Regarding environmental variables, the density of bromeliads was interpreted as having the most substantial support to explain the

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anuran abundance and richness in the Serra Bonita RPPN complex. The temperature and leaf litter depth also influenced the species composition. In addition, we found an inverse pattern for altitudinal Rapoport's rule, in which species with optimal altitudes in the highlands exhibit a lower range-size distribution, likely due to a habitat specialization or micro endemism at higher altitudes.

Conclusion. Understanding how species are distributed and identifying the most important filters of anuran diversity along altitudinal gradients in the Atlantic Forest is essential for developing management plans and conservation actions in this threatened region that harbors one of the world's most remarkable diversity of anurans.

Keywords Amphibians, Atlantic Rainforest, Highlands, Local heterogeneity, Rapoport's rule

Introduction

The distribution of organisms along geographic gradients has aroused interest in biologists since the middle of the 19th century (*Darwin, 1839; Von-Humboldt, 1849; Wallace, 1878*). Environmental conditions along altitudinal gradients might affect the local biota, resulting in fauna and flora zonation (*Ricklefs, 1993*). Hence, how mountains' environmental changes influence species richness, abundance, and composition is a reason for debates and studies in different parts of the world until the current day (*e.g. Rahbek et al., 2019; Villacampa et al., 2019; Carvalho-Rocha et al., 2021; Liu et al., 2022*).

Historically, altitudinal gradients were supposed to reflect latitudinal patterns as suggested by several authors (*MacArthur, 1972; Begon et al., 1990; Stevens, 1992*), and two main patterns are widely disseminated for different taxa: in the first, a monotonic decrease of species richness with altitude increases is expected (*Terborgh, 1977; Hunter & Yonzon, 1993*). This phenomenon might be associated with primary productivity, habitat heterogeneity, species-area relationship, and topography (*Lomolino, 2001; Siqueira & Rocha, 2013*). In contrast, other authors suggested a unimodal pattern with richness peaks at intermediate altitudinal bands (*Rahbek, 1995*), explained in most cases by the mid-domain effect (*Colwell & Hurt, 1994; Colwell & Lees, 2000*). Thus, understanding species richness and distribution in the mountains remains an unsolved enigma.

Because amphibians generally have a complex life cycle, with an aquatic larval stage followed by metamorphosis into an arboreal, semi-aquatic, or terrestrial adult, cutaneous respiration, and inhabiting different microhabitats, they are considered one of the most sensitive groups to environmental changes among vertebrates (*Duellman & Trueb, 1994; Wells, 2007*). Thus, they are interesting models for understanding how environmental variables influence the structure and distribution of the community. However, as in most other groups, these patterns are contentious in mountain frogs. For instance, some studies found richness peaks at intermediate altitudinal bands (*Hu et al., 2011; Carvalho-Rocha et al., 2021*), others a monotonic decrease of species richness with increasing altitude (*Khatiwada et al., 2019; Siqueira et al., 2021*), and the absence of a relationship between richness and altitude (*Goyannes-Araújo et al., 2015; Araújo, 2021*).

Regarding species distribution patterns, one of the most notorious hypotheses to explain the influence of the latitudinal gradient on their distribution is Rapoport's Rule (*Stevens, 1989*). It assumes species from higher latitudes occur in wider latitudinal ranges than species from lower latitudes (*Rapoport, 1975; Stevens, 1989*). This hypothesis was also extended (*Stevens, 1992*) and tested for altitudinal gradients for different taxonomic groups (*e.g. Almeida-Neto et al., 2006; Kim et al., 2019; Araújo, 2021; Kohlmann et al., 2021*). In amphibians, this assumption also remains an unsolved issue, with different patterns observed regarding their distribution in altitudinal gradients (*e.g. Goyannes-Araújo et al., 2015; Khatiwada et al., 2019; Chettri & Acharya, 2020; Araújo, 2021; Siqueira et al., 2021*).

Although studies dealing with anurans from mountains in northeastern Brazil have been increasing recently (*e.g. Xavier & Napoli, 2011; Roberto et al., 2017; Rojas-Padilla et al., 2020; Araújo, 2021; Bastos & Ramos, 2022*), the main drivers of species richness and distribution in most of these altitudinal gradients are still unknown. Among them, the Serra Bonita RPPN (Private Natural Heritage Reserve) complex, in Bahia state, is one of the amphibians' hotspots in the Atlantic Forest (*Dias et al., 2014*), but little is known about the influence of the altitudinal and environmental conditions on the anurans living there. In addition, describing these patterns might be useful for setting conservation proposals (*Pimm & Brown, 2004*).

Here, we investigate the anuran diversity and distribution patterns along an altitudinal gradient in the Serra Bonita RPPN complex, Bahia state, northeastern Brazil. First, we tested the altitudinal range influences on the anuran abundance, composition, and richness. We expect that these response variables will decrease with increasing elevation (*Lomolino, 2001; Siqueira & Rocha, 2013*). Second, we assess the role of local environmental structure on response variables, in which we expect the anuran abundance, composition, and richness will be affected because frogs are one of the most sensitive vertebrates to environmental characteristics (*Hopkins, 2007*). Finally, we tested if species distribution follows the predictions of Rapoport's rule for altitudinal ranges, expecting species with optimal altitudes at high elevations to have a wide distribution along the range because they were more adapted to extreme conditions at highlands (*Stevens, 1992*).

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Materials & Methods

Study area

Anuran sampling was conducted in the Serra Bonita RPPN complex in Camacan and Pau-Brasil municipalities, Bahia state, northeastern Brazil (-15.3836 S, -39.5502 W). It is a montane complex covering a total area of 7500 hectares in the Atlantic Forest with an altitudinal gradient range of 200 to 950 m (Fig. 1). The vegetation is composed of a mosaic with different succession stages of secondary forests interspersed with cocoa crops and pastures (see *Dias et al., 2014* for a detailed description of the study area).

Sampling methods

We conducted monthly field trips over six consecutive days from December 2009 to November 2010. Four altitudinal bands were defined: 200–300 (low), 400–500 (mid), 600–700 (mid-high), and 800–900 (high) m, and six 100 m long linear transects in the forest interior were marked in each band, giving a total of 24 transect sampling locations. A 700 m long main track was marked out within each altitudinal band, and 100 m transects were placed perpendicular to this track (Fig. 1). The installation site of the first transect was determined by a draw within 100 m from the start of the main trail. In addition, we randomly determined the side of the main trail (right or left) where each transect would be installed. Then, the other transects were installed systematically 100 m away from each other and on the opposite side of the previous transect. We did not set up transects near the forest edge or in water bodies to focus on species in the forest interior, with a minimum distance to the edge of 300 meters. Sampling was carried out by active visual and acoustic search (*Heyer et al., 1994; Rödel & Ernst, 2004*) conducted by two researchers for 40 min in each transect during the night. All transects were inspected once every sampling month.

For each transect, we measured the following environmental variables: altitude, leaf litter depth (LLD) and cover (LLC), canopy opening (OCA), number of tank-bromeliads (BRO), including both epiphytic and terrestrial bromeliads, number of trees (NTR), and air temperature (T). On each transect, five points were marked for collecting the variables (LLC, LLD, and OCA) at 10, 30, 50, 70, and 90 m from the beginning of the transect. At each of these points, a 1 x 1 m plot was established on each side of the trail and assigned values from 0 to 4 (0 = 0–20%; 1 = 20–40%; 2 = 40–60%; 3 = 60–80%; and 4 = 80–100%) to represent the percentage of leaf litter cover. In the center of these plots, we measured the leaf litter depth. A hemispherical photo of the canopy was taken at 1.20 m above ground level at each of the five points marked on the transects to assess the canopy opening. These photos were later analyzed with the Gap Light Analyzer 2.0 program. We counted all bromeliads (up to 5 m in height) and trees (> 5 cm in circumference at breast height) that were within 1.5 m on either side of the transect. The air temperature was measured at the beginning and end of each transect sampling with a digital thermometer with an accuracy of 0.5 °C. The air temperature was the average between the temperatures at the beginning and end of each collection.

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This research was approved by the Ethical Committee on Animal Use at the Universidade Estadual de Santa Cruz (CEUA-UESC 006/09). The specimens were collected under authorization (ICMBio #13708) conceived by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio/SISBIO) from the Ministério do Meio Ambiente (MMA) of Brazil. Voucher specimens were deposited in the herpetological collection of the Museu de Zoologia da Universidade Estadual de Santa Cruz (MZUESC), Ilhéus, Bahia state, Brazil, and are listed in Appendix I of *Dias et al. (2014)*. Anuran nomenclature and distribution follow *Frost (2024)*, whereas the species conservation status is according to *IUCN (2024)*.

Data analyses

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The species abundance in each transect was determined by the highest recorded abundance from the twelve field surveys conducted for that specific sampling unit. To evaluate our sampling efforts, we built individual-based accumulation curves with 999 randomizations (*Gotelli & Colwell, 2001*). Additionally, we used the Jackknife 1 and Chao 1 estimators to investigate the expected pool richness (*Magurran & McGill, 2011*).

We performed the Nonmetric Multidimensional Scaling method – NMS (*McCune & Grace, 2002*) to find and display the most robust anuran community structure based on the anuran species dataset (species abundance matrices A and B, Appendix 1). We elected the 1-dimensional solution of the NMDS analysis as a proxy to represent the community structure. A detailed explanation of methodological procedures and results regarding the NMS analysis is in Appendix 2.

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We used the Variance Inflation Factors (VIF) to detect collinearity problems among the studied variables (Altitude, LLD, LLC, OCA, BRO, NTR, and Temperature), in which we excluded the variable altitude from the GLM models (VIF ≥ 10; *James et al., 2013*). Our general model was response variable (composition [NMS-1], richness, or abundance) ~ leaf litter depth + leaf litter cover + canopy opening + number of bromeliads + number of trees + air temperature, family = Gaussian (link = identity). Additionally, we used the ANOVA test to show how the full model (with all predictors) is performing against the null model (with intercept only) and the Shapiro-Wilk's test to investigate the residuals normality distribution [H0, no association between the anuran community structure (NMS-1 axis), species richness, or species abundance and the environmental variables). After that, we used Akaike's Information Criterion with second-order bias correction for small samples (AICc) to compare models for each response variable alone or in combination (*Burnham & Anderson, 2002*). We considered ΔAICc and Akaike's weight (w) of each model. Models with ΔAICc lower than two were interpreted as having the most substantial support (*Burnham & Anderson, 2002*).

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We tested whether the anuran community structure (NMS-1 axis), species richness, or species abundance could be explained by the altitudinal gradient (altitude in meters; independent or predictor variable) using the linear regression analysis (H0, no association between the anuran composition, richness, or abundance and the altitudinal gradient). The following assumptions were checked for the analysis: linear relationship, roughly verified by projecting the response variable on the predictor variable; normality, visually inspecting if residuals from the bivariate model were normally distributed using Q-Q plots and by the Shapiro-Wilk's test on the residuals; independence of residuals (absence of residuals' autocorrelation), by the Durbin-Watson test; and homoscedasticity, by the Breusch-Pagan test.

To understand the anuran species distribution patterns in the studied mountain, we measured the maximum and minimum altitude where each anuran species was recorded to estimate their range-size distribution (the highest altitude minus the lowest altitude where each species was recorded). We give a range of 100 m to species recorded at a single sampling point (*Kim et al., 2019*). The optimal altitude of each species might be understood as the local where it has a maximum abundance (*Whittaker, 1967*); thus, we used two methods to calculate it: the average of the altitudinal range of each species (see *Stevens, 1992*) and the "Specimen method" (to consult *Almeida-Neto et al., 2006* for more details about formulas and methods). Then, we first assessed the normality of the data distribution using the Shapiro-Wilk test and evaluated the homoscedasticity with the Fligner-Killeen test. As the residuals of our data did not meet the assumptions of normality and homoscedasticity required for simple linear regression, we opted for the non-parametric Kernel regression test (*Nadaraya, 1964; Watson, 1964*) to investigate if the anuran distribution along the mountain studied follows Rapoport's rule using the three methods cited above.

Statistical analyses were performed using the R packages bbmle (*Bolker & Team, 2016*), BiodiversityR (*Kindt & Coe, 2005*), ggplot2 (*Wickham, 2016*), usdm (*Naimi et al., 2014*), and vegan (*Oksanen et al., 2016*). Only the individual-based accumulation curves were generated using PAST 4.09 (*Hammer et al., 2001*).

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Results

We registered 612 individuals belonging to 36 anuran species nested in the following ten families (number of species in parentheses): Brachycephalidae (3), Bufonidae (2), Craugastoridae (1), Eleutherodactylidae (1), Hemiphractidae (1), Hylidae (21), Leptodactylidae (1), Microhylidae (1), Odontophrynidae (1), and Strabomantidae (4). Of these species, about 80% are restricted to the Atlantic Forest, and *Brachycephalus pulex* is listed as endangered (EN), while *Bokermannohyla lucianae* is considered vulnerable (VU) to extinction (*IUCN, 2024*). The dominant species were *Pristimantis vinhai* (135 specimens), *Pristimantis* sp. 2 (80 specimens), and *Haddadus binotatus* (70 specimens), all of which are direct-developing species. In contrast, other seven species (*Aplastodiscus ibirapitanga*, *Bahius bilineatus*, *Boana pombali*, *Chiasmocleis crucis*, *Dendropsophus novaisi*, *Ischnocnema verrucosa*, and *Physalaemus erikae*) had only one individual recorded each (Table 1).

The observed species richness represented about 83% of the richness estimated by the Jackknife 1 (43.3 ± 3.22) and Chao 1 (43.3 ± 6.90) estimators. In addition, the accumulation and rarefaction curves evidenced a slight tendency toward stabilization, which suggests our sampling effort was adequate (Fig. 2).

The NMS axis obtained from the 1-dimensional solution evidenced structuring in the anuran community. The solution resulted in a minimal stress value of 23.78 (minimal stress value of randomized data 30.80), and the NMS axis was stronger than expected by chance (Monte Carlo test, P < 0.0010). The variance explained by the NMS axis accounted for 77% of the variance present in the original multidimensional space. The NMS axis was able to express a gradual species substitution pattern of the anuran community (Figure S3, Appendix 2), but with some inconsistency between low (200–300 m) and middle (400–500 m) altitudinal strata.

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We found a significant influence of leaf litter depth (T = -2.372, P = 0.029) and temperature (T = -5.360, P < 0.001) on the anuran community structure (NMS-1 axis). In contrast, species richness (T = 2.541, P = 0.021) and species abundance (T = 4.452, P = 0.0003) were affected by the density of tank-bromeliads (Fig. 3). Other variables did not affect the response variables (Appendix 3). Regarding Akaike's information criterion for all variables, only the models with "LLD and temperature" and "temperature" were interpreted as having the most

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substantial support in explaining the anuran community structure. In contrast, tank-bromeliads plus leaf litter depth and cover were also interpreted as having significant support to explain the anurans' abundance besides tank-bromeliads' density (Table 2).

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We also observed that the altitudinal gradient plays an important role in explaining the anuran composition ($r^2 = 0.763$, $P < 0.001$), abundance ($r^2 = 0.378$, $P < 0.001$), and richness ($r^2 = 0.169$, $P < 0.05$) in the Serra Bonita RPPN complex (Fig. 4). Additionally, we found a significant influence of the optimal altitude of each anuran species on their range-size distribution considering both Stevens's midpoint method ($F = 21.84$, r^2 (adj.) $= 0.788$, $P = < 0.0001$) and the Specimen method ($F = 13.62$, r^2 (adj.) $= 0.726$, $P = < 0.0001$). Therefore, anurans with optimal altitudes in the highlands exhibited a lower range-size distribution (Fig. 5).

Discussion

Most herpetofaunistic studies on anurans have focused on areas near ponds, where most species rely on water for reproduction (*Wells, 2007*). However, anurans depend on forested environments for essential resources such as food and shelter (*Duellman & Trueb, 1994*). We sampled in forested environments of the Serra Bonita RPPN complex almost half of the anurofauna known for this mountain (*Dias et al., 2014*). In addition, the anurans' species richness found in this study aligns with that reported in other checklists for forested environments of the Atlantic Forest (*Rojas-Padilla et al., 2020; Protázio et al., 2021; Lima et al., 2021; Siqueira et al., 2022*), highlighting the critical role of natural forests in maintaining anuran diversity.

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The highest abundance of Terrarana frogs, such as brachycephalids, craugastorids, and strabomantids, might be associated with the fact that direct-developing frogs usually lay eggs on the forest floor (*Nunes-de-Almeida et al., 2021*), and thus are independent of water bodies. In addition, these species were generally more abundant in the highland areas, where lentic ponds are scarce. The milder temperature and higher humidity should ensure additional protection against desiccation of their eggs deposited in the environment, contributing to the increased reproductive success of these species at higher altitudes. In contrast, leptodactylids and microhylids had one species registered for each. Some anurans in the Atlantic Rainforest (e.g., leptodactylids) build foam nests close to ponds to deposit and incubate egg clutches, which will hatch into tadpoles and then metamorphose into frogs (*Haddad & Prado, 2005*). At the same time, other species (e.g., microhylids) present explosive reproduction, fossorial or semi-fossorial behavior, and low dispersal capacity in the environment, characteristics that make it difficult to sample adults in the field (*Peloso et al., 2014; De Sá et al., 2019*). Thus, perhaps this might be the reason for the low abundance of leptodactylids and microhylids that were restricted to lowland areas, as well as most of the species that use lentic ponds for breeding. The steepness of the terrain may hinder the formation of lentic ponds along the altitudinal gradient, decreasing the availability of suitable sites for the species that breed in these environments. Lastly, Hylidae was the most diverse family along the range, which is a typical pattern for Neotropical anuran communities (*Duellman, 1988*), including several studies on anuran communities in the Atlantic

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Forest (e.g., *Dias et al., 2014; Mira-Mendes et al., 2018*). The dominance of hylids might be associated with mountain streams or aerial aquatic habitats (e.g., tank-bromeliads) for developing eggs and tadpoles. Once the reproductive modes are essential to understand how anurans are distributed in altitudinal environments (*Siqueira et al., 2021*), our sampling design might be strictly linked to these results.

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We observed that the anuran composition was influenced by the altitudinal gradient in which some frogs were found at specific altitudes. For instance, *Rhinella hoogmoedi*, *Dendropsophus novaisi*, *Trachycephalus nigromaculatus*, and *Physalaemus erikae* were restricted to the lowest altitudinal bands; *Chiasmocleis crucis* and *Bahius bilineatus* occurred just at mid-altitudes; and *Brachycephalus pulex*, *Ischnocnema verrucosa*, *Pristimantis* sp. 1, *Gastrotheca pulchra*, *Aplastodiscus ibirapitanga*, *A. weygoldti*, *Bokermannohyla lucianae*, and *Scinax strigilatus* occurred only at higher altitudes. Other species were found throughout the altitudinal range. Species composition changes in anuran communities in response to altitudinal gradients have already been reported for different mountains worldwide (e.g., *Hu et al., 2011; Zancolli et al., 2014; Matavelli et al., 2022*). Environmental conditions in montane ecosystems vary across the range (*Lomolino, 2001; Tito et al., 2020*), and therefore, different environmental filters might influence the species composition. In this sense, we observed that colder altitudinal strata with low leaflitter depth had the highest species turnover.

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Once anurans are sensitive to environmental changes (*Hopkins, 2007*), variables such as temperature might influence the community structure. It is consensus that tropical areas harbor the highest anuran species diversity due to environmental conditions such as productivity, humidity, and temperature (*Duellman & Trueb, 1994*). Therefore, as these animals need water or humidity to reproduce (*Crump, 2015*), milder climates are related to the highest species richness, consequently affecting the community structure. Some studies have already reported the influence of temperature in anuran communities from montane areas (*e.g., Matavelli et al., 2022; Carvalho-Rocha et al., 2023*), and our results reinforce this variable as an important driver for the community structure of frogs.

Similarly, we found a positive and significant altitudinal gradient effect on species richness and abundance, with the highlands hosting the greatest species diversity. Although some studies show greater richness and abundance in the middle ranges of the altitudinal gradient (e.g., *Carvalho-Rocha et al., 2021; Matavelli et al., 2022; Dahl et al., 2024*) or indicate a monotonic decrease in diversity with increasing elevation (e.g., *Zancolli et al., 2014; Khatiwada et al., 2019; Siqueira et al., 2021*), a reverse pattern has also been reported, as in the present study (e.g. *Naniwadekar & Vasudevan, 2006*). This pattern may be more common than previously reported in the literature for mountains below 1000 m in elevation. Most studies that have analyzed larger altitudinal ranges, typically finding a hump-shaped distribution for anurans, report an increase in diversity with altitude up to approximately 1000 m, with a decline occurring only at higher elevations (*Carvalho-Rocha et al., 2021; Matavelli et al., 2022; Dahl et al., 2024*). Up to this altitudinal range, we hypothesize that anuran communities still benefit from milder temperatures and high humidity, reducing physiological stress and promoting greater frog abundance and richness. However, a comprehensive meta-analysis may shed more light on this issue in the future.

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In the Atlantic Forest, different mountains are considered hotspots of anuran diversity (e.g., *Forlani et al., 2010; Dias et al., 2014; Roberto & Loebmann, 2016*), but little is known about the main drivers of the anuran communities. The density of tank-bromeliads plays an important role in anuran richness and abundance. The physical structure of some bromeliads enables rainwater to accumulate in the central tank and leaves axils, creating an important microhabitat for some anuran species (*Peixoto, 1995; Juncá & Borges, 2002; Lehtinen, 2004*). In addition, some species live throughout their entire lifecycle in bromeliads (*Peixoto, 1995*), such as *Phyllodytes* species, of which six species of the genus were found in the present study. The role of bromeliads' density in the anuran community was already highlighted in other studies (e.g., *Bastazini et al., 2007; Silva et al., 2011*). The highest species richness and abundance at high elevational strata might be strictly associated with tank-bromeliads' density because the sampling transects with the highest anuran densities was in the highest strata.

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Our results did not corroborate Rapoport's altitudinal rule, in which range sizes increased with altitude (*Stevens, 1992*). Instead, we observed an inverse pattern where anurans, with their midpoints at lower elevations, tend to cover broader elevational range sizes. Although supported in some studies (*Chen et al., 2020; Matavelli et al., 2022*), the anurans' distribution in altitudinal gradients seems to be inconsistent with the original predictions of Rapoport's rule (*e.g., Goyannes-Araújo et al., 2015; Khatiwada et al., 2019; Siqueira et al., 2021, Dahl et al., 2024*). Our results suggest that species with optimal altitudes in the highlands exhibit a lower range-size distribution. In particular, this may reflect a habitat specialization or microendemism at higher altitudes (*Siqueira et al., 2021*). In addition, anurans' occurrence and abundance might be associated with environmental characteristics (*Almeida-Gomes et al., 2016; Araújo et al., 2018; Pereira-Ribeiro et al., 2020, this study*). However, considering local and global scales, further studies are still needed to understand the principal filters driving anuran distribution in montane ecosystems.

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Conclusions

The drivers of anuran distribution in Neotropical forests are influenced by regional factors. Our study area has a high bromeliads abundance at higher elevations, and our analyses returned them as important diversity drivers. Most areas of the Atlantic Forest reveal a much lower bromeliad diversity, which could be why they have yet to be pointed out as the main diversity drivers in other areas (*Paz et al., 2020*). In addition, inventories with efforts directed only at forest environments can evidence a high species diversity and reveal the presence of little-known species and restricted endemics (e.g., *Brachycephalus pulex*, *Pristimantis* spp., *Ischnocnema* spp.). Understanding anurans' distribution and diversity patterns along altitudinal gradients is essential to establish effective and targeted actions for conserving this taxonomic group. In the mountainous complex of Serra Bonita, any conservation initiative should prioritize habitat protection in both lowland and highland areas, as each altitudinal stratum has a unique species composition.

Acknowledgements

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