Diversity and Distributions WILEY

Habitat amount and ambient temperature dictate patterns of anuran diversity along a subtropical elevational gradient

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Abstract

Aim: Patterns of diversity along elevational gradients are driven by species characteristics but remain poorly understood. Filling this gap is imperative given the deteriorating conservation status of anurans worldwide. Here, we examine frog diversity and species composition along a sharp subtropical elevational gradient and assess the degree to which these are determined by environmental and spatial predictors.

Location: An extensive southern Brazilian Atlantic Forest elevational gradient ranging from 300 to 1,800 m above sea level.

Methods: We sampled 38 ponds and used structural equation modelling to examine the direct and indirect effects of area, climate, habitat amount, habitat complexity and productivity on frog species richness and abundance. We also applied joint species distribution models to investigate the importance of these predictors on frog species composition using species distribution and co-occurrence along the elevational gradient.

Results: We recorded 12,636 individuals of 41 frog species. Frog species richness was highest at intermediate elevations, showing a hump-shaped pattern. Frog abundance was highest at lowlands and decreased towards higher elevations. We found support for only the habitat amount hypothesis in explaining overall species richness. Although temperature had a positive influence on productivity and frog abundance, neither predictors were related to species richness. Species composition diverged markedly between lowland and highland frog assemblages, which was mainly attributed to differences in ambient temperature.

Main conclusion: Elevations containing more extensive natural habitat areas retained the most species-rich frog assemblages. The mid-elevational peak is likely attributed to lowland habitat (<800 masl) heterogeneity and extreme climatic conditions in highland areas (>1,400 masl). The entire elevational gradient is, however, critical in maintaining anuran species diversity as lowland assemblages are distinct from those at mid- to high elevations. Our study also shows that anthropogenic habitat loss has a decisive effect on montane frog diversity, reinforcing the need to effectively protect these areas.

1 | INTRODUCTION

Biodiversity heterogeneity along environmental gradients is a central topic in ecology and biogeography (Lomolino, 2001; Ricklefs, 2004). Over the last decades, considerable effort has been allocated to understanding diversity patterns along montane environmental gradients, which correspond to half of all global biodiversity hotspots (Elsen et al., 2018; Körner, 2004). Extensive reviews (e.g. Beck et al., 2017; McCain, 2005, 2010; McCain & Beck, 2016; Rahbek, 2005) and empirical studies on animal and plant communities across montane regions (e.g. Longino & Branstetter, 2018; Zu et al., 2019) recognize four major elevational patterns of species richness: (a) decreasing, (b) low plateau peak, (c) low plateau with mid-peak and (d) mid-elevation peaks. Nevertheless, the operational spatial scale and the causal mechanisms of these patterns remain unclear (Laiolo et al., 2018; McCain & Grytnes, 2010; McCain et al., 2018).

Proposed explanations generally invoke multiple drivers that can potentially act and interact at different scales (Szewczyk & McCain, 2019; Willing & Presley, 2016). Variation in contemporary climatic conditions, such as temperature and precipitation, may directly filter out organisms given their physiological tolerance, leading to changes in species richness and composition (i.e. a positive climate–diversity relationship; Fu et al., 2006; McCain, 2009). Warmer climates mostly lead to higher primary productivity, resulting in more available resources, which in turn ensure coexistence of more individuals (McCain, 2007). Therefore, productivity can indirectly promote diversity by maintaining more viable populations and reducing local extinction rates, also known as the more-individuals-hypothesis (MIH: Binkenstein et al., 2018; Srivastava & Lawton, 1998). Diversity also scales to the available habitat area, and montane regions covering larger areas or providing more available habitat should also harbour more species and individuals (Fahrig, 2013; Rosenzweig, 1995). This area–diversity relationship is based on the assumption that larger habitat areas reduce extinction rates and are more likely to encompass more habitat types (MacArthur & Wilson, 1967; Rosenzweig, 1995). Biotic processes such as competition, habitat complexity and habitat heterogeneity across ecotones have also been proposed to explain elevational patterns of diversity (Beck et al., 2017; McCain & Beck, 2016; McCain et al., 2018). However, the contribution of these factors to montane diversity remains unclear given the difficulty in measuring these processes along natural elevational gradients.

Montane regions of the Brazilian Atlantic Forest biome (hereafter, AF) harbour a remarkable diversity of endemic plants, arthropods, birds and frogs (e.g. Garey & Provet, 2016; Vale et al., 2018). However, the AF is a highly threatened global biodiversity hotspot with only 26% of its original forest cover remaining, most of which scattered across thousands of fragments <50 ha (Rezende et al., 2018; Ribeiro et al., 2009). Virtually all extensive tracts of AF are in montane regions, rendering them a conservation priority (Tabarelli et al., 2010). However, there have been few attempts to elucidate the elevational patterns of diversity throughout the AF (e.g. Almeida-Neto et al., 2006; Martinelli, 2007; da Silva et al., 2018).

Atlantic Forest anurans are especially diverse, with 625 recorded species, 85% of which are endemics (Rossa-Feres et al., 2017). This high level of diversity has been attributed to the exceptional heterogeneity of macro- and microhabitats, topography and climatic variation across this biome (Brown & Brown, 1992; Haddad & Prado, 2005). However, this frog diversity is threatened by the relentless impacts of habitat fragmentation, habitat loss, climate change and infectious diseases, all of which elevate anurans to the most threatened vertebrate taxon worldwide (Becker et al., 2007; IUCN, 2019; Stuart et al., 2004). Despite the vast remaining extent of montane AF habitat, investigations on the variation in frog diversity along elevational gradients remain scant, and available data are restricted to a few sites and narrow elevational ranges (350–750 masl; Giaretta et al., 1997; Giaretta et al., 1999; Goyannes-Araújo et al., 2015). Given the rapid pace of habitat conversion and degradation, basic information on AF frog diversity is therefore crucial to help develop evidence-based conservation strategies (Pereira et al., 2013).

Here, we investigate the patterns and potential drivers of frog diversity along an extensive subtropical elevational gradient in the southern Atlantic Forest. First, we describe how frog species richness and abundance changes with elevation. We expected mid-elevation peaks in frog diversity, which is consistent with the trend for all major vertebrate taxa (McCain & Grytnes, 2010). Second, we assess the role of environmental and spatial variables on frog species richness and abundance by simultaneously testing predictions from six major hypotheses of diversity: area, climate, habitat complexity, habitat amount, MIH and productivity (Table 1). Finally, we describe the compositional variation in frog assemblages along the elevational gradient and assess the contribution of environmental predictors and species relationships on the structure of these assemblages.

2 | METHODS

2.1 | Study area

The largest remaining AF montane forest habitat span the Serra do Mar, Serra da Mantiqueira and Serra Geral ridges of southeastern and southern Brazil, where elevations range from sea level to ~2,900 m (Gontijo-Pascutti et al., 2012). This study was carried out within the Serra Geral, a complex montane landscape formed

TABLE 1 Major hypotheses and predictors of frog diversity along elevational gradients considered in this study

Hypothesis	Theory	Predictor	Scale
Area	Diversity is positively related to area (MacArthur & Wilson, 1967; Rosenzweig, 1995)	Pond surface area (PSA)	Local
		Elevational band area (Area)	Landscape
Climate	Diversity is positively related to temperature (Allen et al., 2002)	Mean annual temperature (MAT)	Landscape
Habitat complexity	Diversity is positively related to habitat complexity (Rosenzweig, 1995)	Water surface cover (WSC)	Local
		Pond vegetation structure (PVS)	Local
Habitat amount	Diversity is positively related to total habitat amount (Fahrig, 2013)	Pond habitat amount (PHA)	Local
		Band habitat amount (BHA)	Landscape
More-individuals-hypothesis	Abundance is positively related to productivity, and therefore, species richness is positively related to abundance (Binkenstein et al., 2018; Srivastava & Lawton, 1998)	Frog abundance	Local
Productivity	Diversity is positively related to productivity (McCain, 2009)	Net primary productivity (NPP)	Landscape

mainly by Early Cretaceous lava flows, which are associated with the break-up of Gondwana, separating the modern continents of South America and Africa (Hartmann, 2014). The ~920,000 km^2 Serra Geral region extends from Argentina through Uruguay, Paraguay and southern to south-eastern Brazil (Frank et al., 2009). Specifically, we focused on the ~49,800 ha São Joaquim National Park (hereafter, SJNP), a strictly protected area located in the state of Santa Catarina, Brazil (Figure 1). The study area spans approximately 1,200 km^2 of dissected terrain and altitudes ranging from 200 to 1,822 masl (Vianna et al., 2015). The vegetation comprises of a mosaic of dense evergreen forest largely occurring up to 800 masl, replaced by mixed *Araucaria* forest and high-altitude grasslands at higher altitudes (IBGE, 2012). The climate is humid subtropical without a dry season with some variation depending on elevation: hot summers and mean annual temperature of 19°C below 800 masl, and cold winters with frequent frosts and a mean annual temperature of 13.5°C above 800 masl (Alvares et al., 2014).

2.2 | Sampling design

We sampled frogs along 38 discrete lentic aquatic environments (ponds, humid areas, marshes and small dams; hereafter, ponds) located between 312 and 1796 masl (Figure 1). We acknowledge that some specialist anuran species (i.e. ground-dwelling, stream-dwelling and bromeliad breeders) may have been undersampled, but ponds are considered suitable environments given that most AF frogs use them and their vicinities to reproduce and forage (Crump, 2015; Haddad et al., 2013). We employed the following steps to select survey ponds. We first subdivided the elevational gradient into eight 200-m elevational bands, from 200 to 1,800 masl, which ensured that pond selection was not biased for or against any single region of the elevational gradient (McCain & Grytnes, 2010). Using a complete map of all water bodies recorded for the state of Santa

Catarina (SIGSC; available at http://sigsc.sc.gov.br/sigaresc/), we searched for all perennial ponds within these bands, but up to 5 km from the boundaries of SJNP, corresponding to a planimetric area of ~7,854 km^2. The SIGSC contains spatially accurate geographic and elevational data derived from 70,000 high-resolution aerial photographs of the State of Santa Catarina (year 2012). We further validated pond locations based on the Shuttle Radar Topography Mission (SRTM) elevational data with 30-m or 1 arc-sec spatial resolution (Valeriano & Rossetti, 2012). We randomly selected five ponds for each elevational band that (a) were at least 1 km apart; (b) were surrounded by negligible anthropogenic habitat disturbance; and (c) were no farther than 5 km from the nearest access road. Prior to sampling, we visited all selected ponds to confirm their presence and accessibility. Due to restricted availability, only four ponds were selected between 1,000 and 1,200 masl and between 1,600 and 1,800 masl. A detailed description of each pond can be found in Appendix S1.1 in Supporting Information.

2.3 | Frog survey

We quantified frog species richness and abundance at each pond based on 10 monthly samples from September 2017 to August 2018, except for December 2017 and April 2018. We combined visual and acoustic encounter surveys, within a 5-m buffer along the pond perimeter and recorded all frogs on the water surface, above and underneath any vegetation, rocks and logs (Scott-Jr & Woodward, 1994). A 5-m survey buffer was selected do maximize visual and acoustic anuran detectability, avoiding double counting. Sampling initiated at least one hour after dusk (17:30 hr–19:18 hr) and ended no later than 01:00 hr. Sampling effort was standardized by one person-hour per pond per month. Each pond therefore accumulated a sampling effort of 10 person-hours, amounting to an overall effort of 380 person-hours of active search time. Up
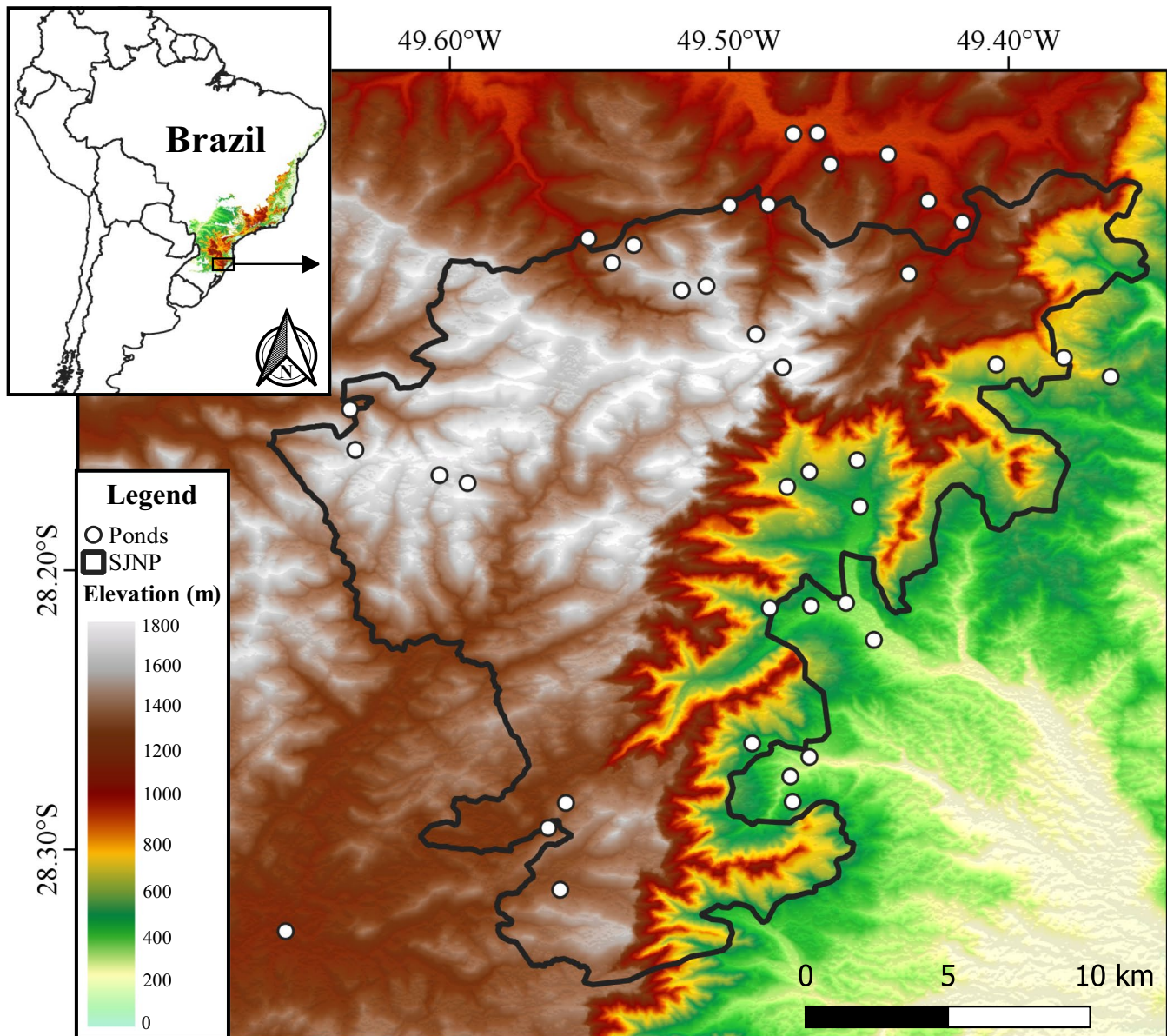
FIGURE 1 Altitudinal variation of the Brazilian Atlantic Forest, showing the study region of the ~49,800-ha São Joaquim National Park (SJNP) and surrounding areas within the state of Santa Catarina, Brazil (inset map). Open circles indicate the location of the 38 perennial ponds surveyed in this study

to four ponds were surveyed each night, and the pond survey sequence was randomized across months to minimize any bias related to nocturnal sampling schedules. We collected two voucher individuals per species per pond using a research permit previously granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, permit #59223-1). All vouchers were deposited at the Herpetological Collection of the Universidade Federal de Santa Catarina (CHUFSC), Brazil.

2.4 | Environmental and spatial predictors

We measured environmental and spatial variables at both local and landscape scale. Ponds and their immediate surroundings

(within a 500-m radial buffer) were defined as the local scale. At the landscape scale, we opted for a different approach from most previous altitudinal gradient studies because our sampling protocol was not restricted to a single survey site per evenly spaced elevational band. We therefore followed Peters et al. (2016) in quantifying predictors at the landscape scale and considered the entire area within an elevation range of + 50 m above and –50 m below the elevation centroid of each pond. This approach mirrors the 100-m elevation band typically used in elevational gradient studies (McCain & Beck, 2016; McCain & Grytnes, 2010). We hereafter refer to the landscape scale as the elevational band. Additionally, boundaries of elevational bands were delimited by the 50-km radius from the highest mountain top across the entire study region as suggested by McCain (2007).

Habitat complexity was measured at the local scale, using two widely used proxies based on previous studies on neotropical frog diversity (e.g. Melchior et al., 2017; da Silva et al., 2012). The first was the proportion of pond water surface covered by aquatic and/or emergent vegetation (WSC). The second was the proportion of pond margins covered by shrubs and/or trees, which we used as a proxy of pond vegetation structure (PVS), with higher values indicating more complex habitats. WSC and PVS values were determined using aerial photographs (summer 2018) taken by a rotary-wing drone (Phantom 3 Standard, DJI, China) and subsequently analysed using the ImageJ software (Rasband, 1997). Habitat amount was considered as the percentage of natural vegetation cover measured at both the pond (PHA) and the elevational band (BHA) scales. We included these predictors because even though SJNP is a protected area, private agricultural landholdings are still active inside the park boundaries. Additionally, some ponds were also located outside the SJNP area and had been exposed to some anthropogenic activities. PHA and BHA values were obtained using previously classified, georeferenced 30-m resolution land cover data available from MapBiomas, the Brazilian Annual Land Use and Land Cover Mapping Project (collection 3.1; year 2017; http://mapbiomas.org/).

Pond water surface area (PSA) was defined as a local area predictor and measured in the field using a GPS Garmin Oregon 550® considering the maximum flood level. Total area of elevational bands was calculated using the SRTM 30-m digital elevation model available in TOPODATA (http://www.dsr.inpe.br/topodata). We used mean annual temperature (MAT), mean observed temperature during surveys (MOT) and mean annual cumulative precipitation (MAP) as proxies of contemporary climatic conditions. Values of MAT and MAP were extracted from the WorldClim database (~1 km^2 spatial resolution; 1970–2000 temporal resolution; Fick & Hijmans, 2017). Ambient temperature was measure at the beginning and at the end of each survey at each pond using an Inconterm 7,664® digital thermometer. As a measure of ecosystem productivity, we extracted the mean net primary productivity (NPP) estimates produced by the moderate resolution imaging spectroradiometer (MODIS) monthly product (MOD17A3; 30 arc-sec or ~1-km^2 resolution temporal extent 2000–2015; http://www.ntsg.umt.edu/project/modis/mod17.php). MAT, MAP and NPP were calculated by averaging values within each elevational band, and values of MOT were calculated by averaging values across all 10 monthly surveys.

All GIS analyses were performed using the Albers Equal Area Conic projection in QGIS v3.4 (QGIS Development Team, 2019). Hydroperiod was not considered because only four of the 38 ponds became almost dry in three of the 10 sampling sessions. We do not include predictions concerning the mid-domain effect because the lower boundaries of our study landscape are not constrained, and species ranges could extend for over 70 km to the eastern coastline (Rana et al., 2019).

2.5 | Data analysis

Species were assumed to occur at all elevations between the lowest and highest elevations at which they were detected, a common range interpolation approach in elevational gradient studies (Rowe & Lidgard, 2009). This can be considered the most realistic approach to understand diversity patterns as species tend to be distributed continuously (Rowe & Lidgard, 2009). We also used total species richness and abundance based on all surveys at each pond, given that overall sampling effort was equal at each pond. We acknowledge that local diversity may change through time and data pooling may lead to overestimated species richness and abundance. However, few individuals are usually found more than once in a reproductive event, which is associated with the generally low recapture rates within year compared to between years (e.g. Nomura et al., 2012; Tucker, 1995). Therefore, we considered this a valid approach in representing frog diversity at the pond scale, and any temporal variation in frog diversity will be investigated elsewhere.

We assessed our data reliability by evaluating sample completeness by means of sample coverage (Chao et al., 2014). We also estimated asymptotic species richness using the species abundance data at each pond using the *iNEXT* R package (Hsieh et al., 2016). We then used Pearson correlations to examine observed and estimated species richness values.

Prior to analysis, we examined a predictor correlation matrix to reduce issues of multicollinearity. Mean annual temperature, observed temperature and precipitation were highly correlated (Pearson r = +0.93, –0.98 and –0.90, respectively; Appendix S2.1) so we opted to retain the former as a proxy of climatic conditions. Precipitation values are relatively high along the SJNP elevational gradient (range = 1,463–1,817 mm/yr; see Appendix S1.1 for predictor values along the elevational gradient), and given the marked precipitation aseasonality (absence of a dry season), we assumed that rainwater is not a limiting factor in the study region. Additionally, MAT was also highly negatively correlated with PHA and BHA (r = –0.75 and r = –0.81, respectively; Appendix S2.1), but we opted to retain MAT and both habitat amount variables in order to assess the purposed hypotheses.

We examined the distribution of frog species richness and abundance along the elevational gradient using generalized additive models (GAMs), which incorporate more flexible smoothing functions in modelling nonlinear relationships compared to generalized linear models (Hastie & Tibshirani, 1990). We used a thin plate regression spline on elevation, set the data family to Poisson for richness and negative binomial for abundance (to account for overdispersion) and allowed scaling parameters to be estimated in model fitting. Smoothing parameters were estimated using restricted maximum likelihood (REML) and basis dimension (k) set to five to prevent overparameterization (Peters et al., 2016). GAMs were computed using the *mgcv* R package (Wood, 2011). The presence of any residual spatial autocorrelation in both species richness and abundance was tested using Moran's eigenvector maps based on 42 different spatial weighting matrices (Bauman et al., 2018), but none could be found (see details in Appendix S3).

We used structural equation modelling (SEM; Grace, 2006) to simultaneously test the direct and indirect effects of multiple hypothesized predictors of frog species richness and abundance. SEM

constructs a network of causal relationships, where pathways and their directions indicate previously formulated hypotheses (Grace et al., 2010). Using this framework, we developed an initial full model encompassing the hypothetical a priori causal relationships among the measured predictors and response variables (Appendix S4.2). First, we hypothesized that productivity (NPP) would be directly and positively influenced by temperature (MAT). We would also expect that frog abundance was directly influenced positively by habitat complexity (WSC and PVS), area (PSA and Area), habitat amount (PHA and BHA) and productivity, but also via a direct or indirect effect of temperature (mediated by productivity). Lastly, we expected that these same predictors would directly influence positively frog species richness, but also indirectly, via indirect abundance-mediated effects.

SEM was applied in a Bayesian framework with local estimation of parameters to account for specific error distribution on each response variable using the *brms* R package (Carpenter et al., 2017). Therefore, productivity, abundance and species richness were modelled with gamma, negative binomial and Poisson error distribution (all log link), respectively. For each model, we ran four chains with 50,000 iterations each, with the first 25,000 discarded as burn-in and the remaining thinned by 100, so that 1,000 samples from the posterior distributions were retained for analysis. We used *brms* default weekly informative priors for parameters estimate (Lemoine, 2019). Chains convergence was assessed by ensuring that potential scale reduction factor (Rhat) values were less than or equal to 1.01 for all parameters (Bürkner, 2017). We considered relationships important when predictors' highest 95% posterior density intervals (HPDIs) exclude zero. In addition to raw estimates, we also computed paths coefficients standardized on relative ranges (Grace et al., 2018) and calculated the Bayesian R^2 for each response variable (Gelman et al., 2019).

Classic approaches to analyse multivariate species data do not account for proper mean–variance relationships of abundance, nor provide sufficient quantitative information on the contributions of different community assembly processes, which may lead to misleading interpretations (Hui et al., 2015; Warton et al., 2012). Therefore, we employed a joint species distribution model (JSDM; Pollock et al., 2014) with the inclusion of latent variables (LVs) to simultaneously describe the pattern of compositional variation and estimate the contribution of predictors on assembly processes. JSDMs extend multivariate generalized linear models by using LVs, which ensure separating species co-occurrences given (dis)similar responses to known environmental predictors (e.g. environmental filtering), to unexplained species associations ("residual correlation"; Ovaskainen et al., 2017; Warton et al., 2015). These residual correlations can either represent responses to unmeasured predictors or the outcome of biotic interactions (D'Amen et al., 2018; Warton et al., 2015).

We fitted JSDMs using the *boral* R package (Hui, 2016), which uses Bayesian Markov chain Monte Carlo (MCMC) sampling to estimate model parameters. First, we fitted a pure latent variable model (LVM) including only two LVs, which can be understood as

a model-based unconstrained ordination (Hui et al., 2015; Warton et al., 2015). From this model, we extracted the posterior median LVs values and used as unconstrained ordination axis coordinates to visualize the variation in species composition across ponds. We then fitted a second model by adding the same covariates used to model species richness and abundance (MAT, NPP, BHA, PHA, PVS, Area, WSC and PSA), but also included vegetation type (either dense evergreen forest or mixed *Araucaria* forest) where ponds were located, plus two LVs. We also extracted the posterior median LVs values to visualize pond-scale species composition after controlling for environmental predictors (residual ordination). We then quantified correlations in frog species' abundance due to shared environmental responses and their respective residual correlations (responses to unknown covariates or biotic interactions) (Ovaskainen et al., 2016; Warton et al., 2015). Lastly, we performed variation partitioning among the included predictors to quantify their relative contribution in structuring frog assemblages (Ovaskainen et al., 2017).

Predictors were centred and standardized prior to inclusion into JSDMs. For this analysis, we only included species that occurred in at least three ponds to avoid misinterpretations (*n* = 28; Warton et al., 2015). We ran models using the default uninformative normal priors for model parameters. The number of iterations on MCMC chains was set to 200,000 with a 100,000 burn-in period and a thinning factor of 100. A negative binomial error distribution was used to account for overdispersion in modelling species abundance simultaneously. We also included a site random effect to account for any possible spatial autocorrelation (Hui, 2016). Model convergence was assessed using a combination of the Geweke diagnostic (Geweke, 1992) and visualization of trace plots, while Dunn–Smyth residuals plots were used to inspect violation of model assumptions (Hui, 2016). Correlations were considered important whenever their corresponding 95% HPDIs excluded zero.

3 | RESULTS

We recorded a total of 12,636 frogs across the 38 surveyed ponds, representing 41 species and nine families (Appendix S5.3). Some species, such as *Boana bischoffi* (*n* = 3,022 individuals), *Leptodactylus latrans* (*n* = 1,357) and *Sphaenorhynchus surdus* (*n* = 353), virtually occurred along the entire elevational gradient (Figure 2). In contrast, *Scinax tymbamirim* (*n* = 801) and *Phyllomedusa distincta* (*n* = 97) were restricted to lowland ponds (<800 m), whereas *Boana joaquini* (*n* = 209) and *Scinax squalirostris* (*n* = 52) were only found at high-elevation ponds (>800 m) (Figure 2). We also recorded 10 individuals of the alien bullfrog species *Lithobates catesbeianus*, all of which within a single pond at 1,139 masl, but these were excluded from subsequent analyses.

Frog species richness showed a hump-shaped pattern at intermediate elevations (Figure 3a). We observed a maximum richness peak at around 620 masl (25 species), followed by similarly high values up to ~1,450 masl, where numbers of species began to decrease until the highest altitudes (deviance explained = 81.8%,
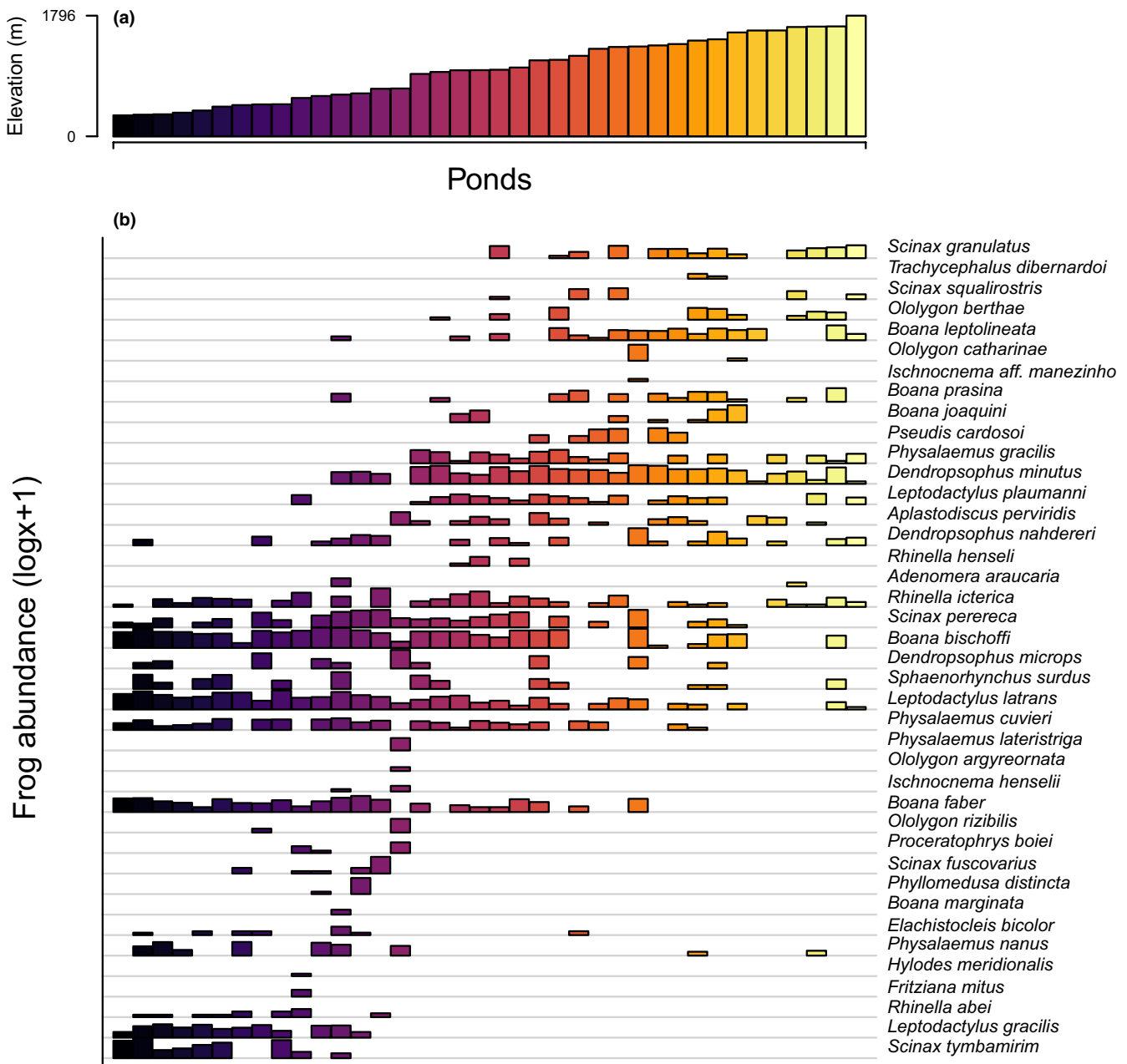
FIGURE 2 Anuran occurrence and population abundance in perennial ponds distributed along the entire SJNP elevational gradient and surrounding areas in the state of Santa Catarina, Brazil. (a) Upper panel shows the elevation distribution of ponds, and (b) lower panel shows the observed species abundance (log $x + 1$ for better visualization) at each pond

$p < .001$; Figure 3a). Frog abundance showed the highest levels at low altitudes, with a maximum at around 320 masl (919 individuals), followed by a monotonic decrease through high elevations (DE = 30.7%, $p < .001$; Figure 3b). Estimated and observed species richness were highly correlated ($r = 0.94$, $p < .001$), and sample coverage values indicated sufficient sampling effort and reliability in our estimates (all values ≥0.95; Appendix S6.4).

In the mechanistic SEM proposed with the direct effects of temperature, productivity, area, habitat amount and habitat complexity on frog species richness, plus their indirect effects though frog abundance, only the proportion of natural habitat remnants within elevational bands (BHA) was considered an important

predictor of richness (i.e. 95% HPDIs excluded zero; Figure 4). Standardized path coefficient indicates that local frog species richness increases in 45% of its observed range values when moving from areas with minimum to maximum BHA (observed range: 57% - 99%). Similarly, mean annual temperature (MAT) was the only important predictor of frog abundance (Figure 4). Moving from colder to hotter areas (range: 11.7°C – 18.5°C), frog abundance increases by 43% of its observed range. Lastly, even though we found that mean annual temperature positively influences net primary productivity, our data provide no support for the more-individuals-hypothesis. Neither the direct nor indirect effect of productivity through abundance was important in predicting local
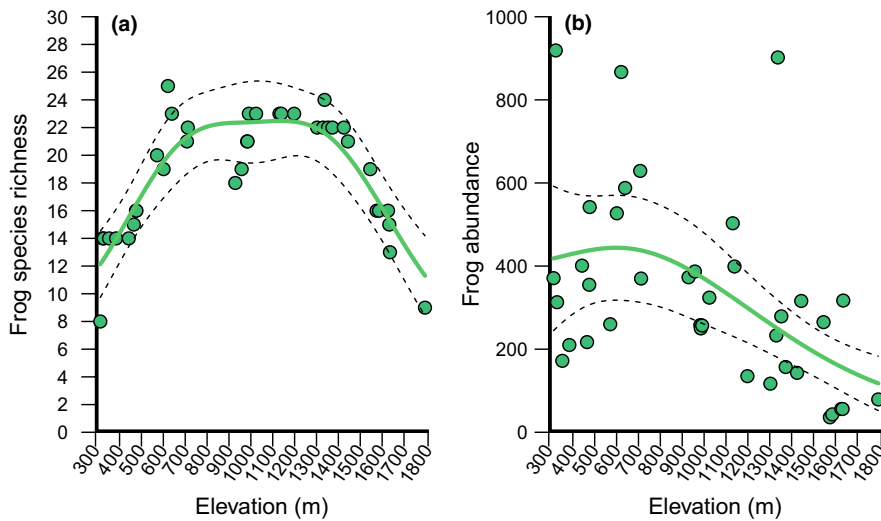
FIGURE 3 Patterns of (a) frog species richness and (b) abundance along the elevational gradient at SJNP and surrounding areas. Dots represent values for each of the 38 ponds. Solid lines represent trends and dashed lines the respective 95% credible intervals computed using a generalized additive model
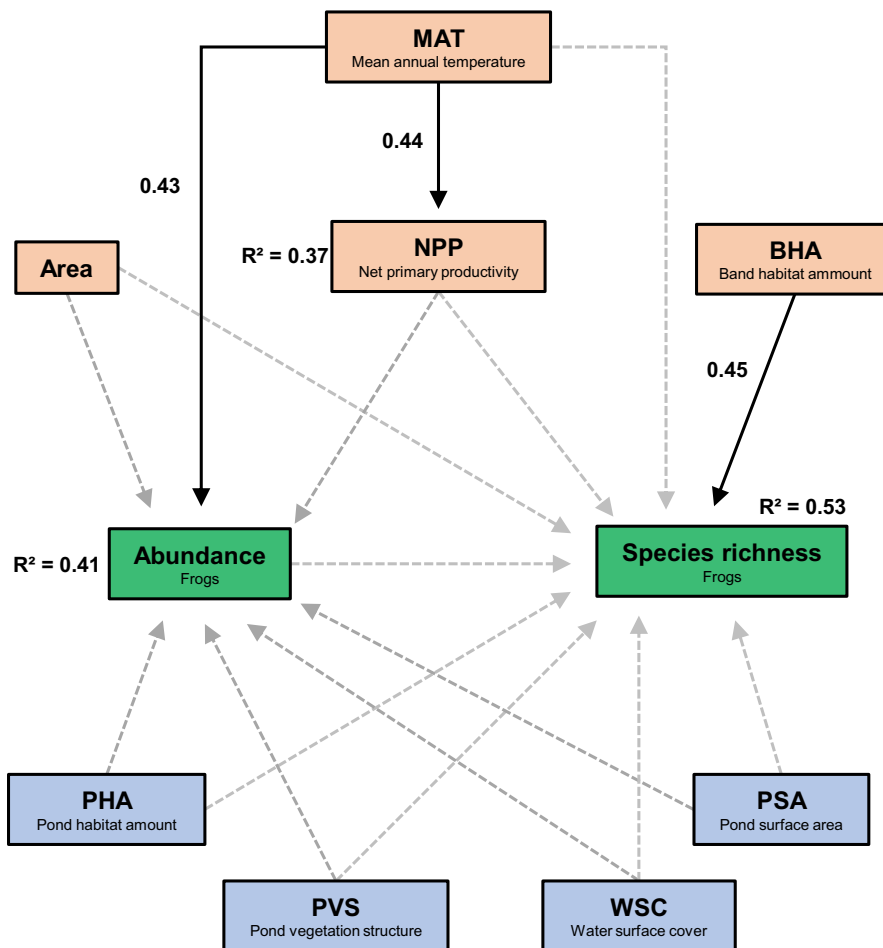

FIGURE 4 Path models showing the direct and indirect effects of hypothesized predictor variables on frog species richness and abundance along the SJNP elevational gradient and surrounding areas. Important (i.e. 95% high posterior density interval exclude zeros) and unimportant predictors are depicted with solid and dashed arrows, respectively. Numbers on path arrows represent relevant range standardization coefficients for important predictors and the relative amount of prediction capacity (Bayesian R^2) is given for response variables. All relationships were hypothesized to be positive

frog species richness. Predictors´ raw path coefficient estimates, HPDIs, convergence and estimated sample size can be found in Appendix S7.5.

Pond sites showed a clear elevational gradient in species composition (Figure 5a). The unconstrained ordination showed a separation along the second latent variable axis, with a tight cluster of ponds at the bottom left and another sparser cluster spanning the top along the first latent variable. The first cluster was formed mainly by ponds

at lower elevations (300–800 masl), whereas the second consisted of mid- to high-elevation ponds (>800–1,800 masl), thereby reflecting the observed altitudinal gradient (Figure 5a). The residual ordination indicates that most of the variability among ponds were no longer detected once the environmental predictors were included (Figure 5b). Therefore, it was not possible to identify any distinct clusters based on elevational differences, but a few ponds remained more segregated from the core of the ordination (Figure 5b).
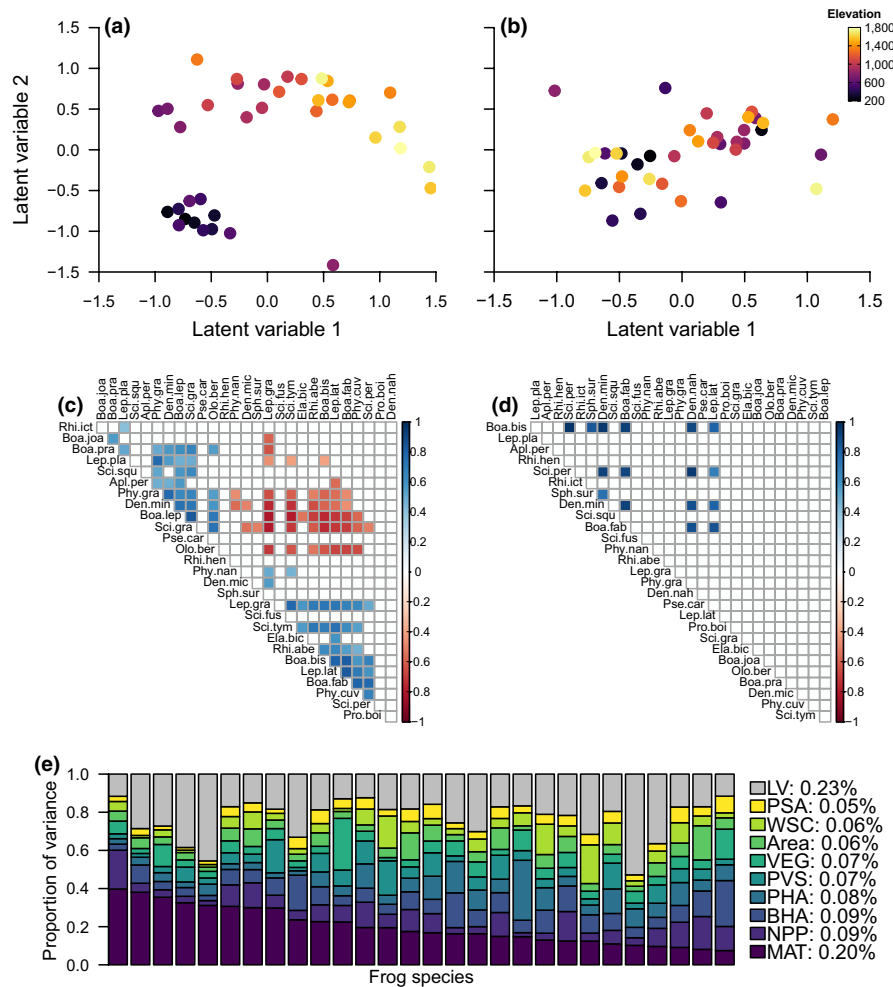
FIGURE 5 Influence of predictors on the community composition, species correlation and variation in frog species abundance within ponds along the SJNP elevational gradient, Santa Catarina, Brazil. The first two panels show (a) the model-based unconstrained ordination based on the pure latent variable model and (b) the residual ordination based on the inclusion of measured predictors, with pond colour codes representing their elevation values (included variables detailed in panel (e)). Panel (c) shows the covariation estimates among frog species abundance due to similar response to measured predictors, and panel (d) shows the respective residual correlations after controlling for effects of predictors estimated by the joint species distribution model. Correlations range from negative (red), to neutral (white), to positive (blue), and are based on 95% high posterior density intervals that exclude zeros. Codes represent species abbreviations whose full names are given in Appendix S4.2. Panel (e) shows the relative proportions of variance attributed to mean annual temperature (MAT), net primary productivity (NPP), percentage of natural vegetation within elevational bands (BHA), percentage of natural vegetation at pond surrounds (PHA), pond vegetation structure (PVS), vegetation type (VEG), total area within elevational bands (Area), water surface cover (WSC), pond surface area (PSA), and to the latent variables (LV) in frog species abundance. Bars show species-specific responses (species ordered by the highest proportion attributed to mean annual temperature) where legend indicates species averages. See Appendix S8.6 for specific values of each predictor for each species

We detected both positive and negative important correlations (i.e. 95% HPDIs exclude zero; $n = 106$) due to similar responses to measured predictors for several species (Figure 5c), indicating that environmental filtering was important in producing correlations in species abundance. Of these, 57% were positive ($n = 60$) and 43% ($n = 46$) were negative, indicating that observed correlations in species abundance were mostly attributed to convergences rather than divergences in species-specific responses to predictors. In contrast, we observed a greatly reduced small set of important residual correlations after accounting for environmental predictors ($n = 16$), all of which were positive (Figure 5d). The joint species distribution model indicated that all measured predictors combined accounted for 77% of the variation in species abundance (averaged over species; Figure 5e). Of these, mean annual temperature was most influential in frog species composition, as on average 22% of the variance in species abundance was attributed to this covariate (Figure 5e). Other predictors contributed individually to less than 10% of the variance.

4 | DISCUSSION

To the best of our knowledge, this is the first comprehensive study documenting transitions in anuran diversity along a steep elevation

gradient (range of 1,500 m) of the Brazilian Atlantic Forest that simultaneously tests multiple hypotheses explaining these patterns. In this study, frog species richness showed a hump-shaped distribution while frog abundance was high in the lowlands but decreased at mid- to high elevations. The variation in frog species richness was best explained by the available area of natural habitats within elevational bands, whereas changes in mean annual temperature best explained frog abundance along the elevational gradient. In addition, we observed marked compositional divergence between frog assemblages from lowland to mid-to-high-elevation sites, which was also best explained by changes in temperature.

The mid-elevational peak in species richness we found here is consistent with previous studies on vertebrate elevational ranges, for which this pattern is considered to be the most pervasive (e.g. Gebert et al., 2019; McCain, 2010; McCain & Grytnes, 2010). In terms of anurans, most elevational gradients worldwide show a curvilinear relationship between species richness and elevation for these ectotherm vertebrates (McCain & Sanders, 2010). However, subtropical mountain ranges have been poorly sampled, and our study provides new support for the mid-elevational richness peak, suggesting that this can also be a more universal pattern for frogs. In addition, our results are at odds with the only other anuran study conducted along an AF elevational gradient (Ilha Grande island tropical coastal forests; narrower range of 750 m), which found a richness peak at low elevations (Goyannes-Araújo et al., 2015). These results reinforce that emergent patterns may vary within a single taxonomic group (McCain & Grytnes, 2010) and highlight the need for more rigorous surveys to be carried out along other tropical and subtropical elevational gradients.

Yet, there is still no consensus on the operational mechanisms promoting this pattern, which appears to be driven by a complex interplay of different predictors (Beck et al., 2017; Lomolino, 2001). We evaluated the support for most frequently proposed hypotheses explaining elevational patterns of species richness (e.g. Laiolo et al., 2018; McCain et al., 2018; Wu et al., 2013). Surprisingly, frog species richness was positively related to only landscape-scale habitat amount. This indicates that ponds located in areas containing more native vegetation should also harbour more frog species. This provides direct support for the habitat amount hypothesis (HAH; Fahrig, 2013), rather than the more general species–area relationship. The HAH was also found to be important in predicting taxonomic diversity in small mammals and functional diversity in frogs in highly fragmented Atlantic Forest landscapes (Almeida-Gomes et al., 2019; Vieira et al., 2018).

Areas corresponding to more extensive natural vegetation are more likely to harbour a higher diversity of suitable (micro)habitats and thereby confer a higher chance of accommodating habitat specialist species (Henneron et al., 2019; Leibold et al., 2004). Many frog species are considered habitat specialists and their local occupancy depends exclusively on some environmental conditions. For instance, *Ischnocnema henselii* exhibits direct development and depends on moist leaf-litter to lay their eggs (Haddad & Prado, 2005). Similarly, *Fritziana mitus* is found in epiphytic bromeliads, which

they use for shelter, foraging, ovipositing and raising their tadpoles (Walker et al., 2018). At SJNP, these two species were only found where their specific microhabitat requirements were present. This highlights the strict dependence of some species on specific microhabitat types, which can partly explain the mid-elevational species richness peak documented here. At the elevational band scale, overall natural vegetation cover ranged from 57% to 99% (mean = 70±12%, *SD*; Appendix S1.1) and was positively correlated with elevation ($r = 0.81$, $p < .001$). This positive effect therefore indicates sufficiently strong environmental filtering in excluding species from unsuitable habitat areas along the elevation gradient. Like most topographically dissected landmasses worldwide, lowland Atlantic Forest areas succumbed to the heaviest impacts of agricultural land use, particularly compared to adjacent high-elevation forest lands (Tabarelli et al., 2010), and this reflects the strong positive relationship uncovered here between elevation and primary habitat amount. Moreover, we cannot rule out the possibility that lowland areas in the past retained higher anuran species diversity. For instance, water body density (e.g. ponds) throughout the entire 785,400-hectare planimetric area of our study region decreases at increasingly higher elevations (see Appendix S9.3). Water body density can also be seen as proxy of suitable habitat conditions for anurans, given that many species use them to reproduce (Crump, 2015; Haddad et al., 2013). We would therefore expect that higher lowland density of water bodies could also lead to higher species packing. Wachlevski et al. (2014) recorded twice as many frog species ($n = 32$) within similar lowland ranges (240 m - 490 masl) at Serra do Tabuleiro State Park, a protected area ~75 km east of our study landscape. Serra do Tabuleiro is one of the largest AF remnants in southern Brazil and most of its lowlands still remain relatively intact (MMA, 2000). In this context, historical land use trajectories—that are stacked against the integrity of contemporary lowland habitats—likely contribute to the observed pattern of frog species richness.

Habitat patch area is widely considered a major determinant of vertebrate species richness (Belmaker & Jetz, 2015; Rosenzweig, 1995). In general, larger areas tend to harbour more individuals, thereby reducing local extinction rates, and promote higher levels of habitat diversity and heterogeneity (Rosenzweig, 1995). However, habitat area per se (i.e. pond size and area of elevational bands) was a poor predictor of frog species richness, which is consistent with montane regions in China (Fu et al., 2006; Hu et al., 2011; see also Bueno et al. (2019) for a recent discussion on island species–area relationships). We found no support for the habitat complexity hypothesis even by taking into account many distinct montane habitats spanning a broad spectrum of habitat complexity (Figure 4; Table S1.1). Although local habitat complexity was not an important predictor of frog diversity, previous studies have found that higher local habitat complexity promotes species diversity, which is attributed to greater numbers of suitable sites for anuran egg-laying, vocal activity and shelter against predators (e.g. Vasconcelos et al., 2014). Species inhabiting low-complexity habitats may exhibit temporal segregation in pond use (Vasconcelos & Rossa-Feres, 2005), and this resource partitioning could partly explain the co-occurrence of similar frog

diversity compared to more complex habitats. In summary, local habitat complexity seems to be species and/or system dependent and is not an essential element for pond-dwelling frog diversity along the elevational gradient.

Our data also indicate that neither temperature nor a proxy of habitat productivity was important predictors of frog species richness. This implies that, although anurans exhibit a critical thermal minimum lower than other ectothermic vertebrates (Buckley et al., 2012), their physiological limitations do not necessarily restrict their distribution along the elevational gradient. Indeed, some subtropical Brazilian frog species are known to be reproductively active all year-round, even showing physiological and behavioural adaptations to exploit cold environments (Kiss et al., 2008; Rossa-Feres & Jim, 1994). Should these limitations hold true, we would expect a monotonic upslope decline in frog species richness, which does not reflect our data. Productivity was high at low elevations but was not followed by a monotonic upslope decline, even though ~40% of the variance in productivity was explained by ambient temperature. This suggests that available potential energy may not be limiting along the elevation gradient, which could lead to similar levels of food availability for frogs. In addition, freshwater pond environments are likely to buffer upslope declines in local productivity and none of the ponds we surveyed ever freeze even during severe winters, even though widespread frosts are common above 800 masl. We acknowledge that we did not quantify food resource availability directly. However, both arthropod species richness and abundance, which comprise the bulk of anuran diets (Carvalho-Rocha et al., 2018; Solé & Rödder, 2010), are positively related to productivity (Schuldt et al., 2019), which may support this hypothesis. Frog species richness was apparently decoupled from frog abundance and productivity, lending little if any support to the "more-individuals-hypothesis" in our study system, although further studies on food availability along elevational gradients are needed.

Frog abundance was also decoupled from productivity but was positively affected by temperature. Lower temperatures may impose prohibitive limitations on anuran reproductive success, even in cold-adapted species (Kiss et al., 2008; Navas et al., 2013), which may result in small populations at high-elevation sites. For instance, lower temperatures can impose changes in species phenology and restrict breeding seasons to shorter periods, but can also increase the time to complete larval metamorphosis and affect tadpole survival (Amat & Meiri, 2017; Bernal & Lynch, 2013). While these mechanisms can explain the lower frog abundance at lower temperatures, we highlight that more physiological and behavioural studies are needed to help us better understand the mechanisms behind these patterns.

The latent variable model showed that lowland frog assemblages were very distinct compared to those in the highlands. Differentiation among frog assemblages along the elevational gradient was also observed in palaeotropical montane areas in Tanzania (Zancolli et al., 2014), China (Hu et al., 2011) and Borneo (Menegon & Salvidio, 2005). This observed segregation is consistent with variation in vegetation macromosaics across our study region. This suggests that each vegetation formation retains its own pool of species

adapted to local environmental conditions and exploiting specific microhabitats (Crump, 2015; Haddad & Prado, 2005). Thus, it is likely that environmental filters may operate in promoting differentiation among frog assemblages, mirroring what we found for species richness.

Our results confirm that local abiotic conditions, mainly temperature, play an important role in predicting frog assembly composition. For example, *Scinax tymbamirim*, *Leptodactylus gracilis* and *Rhinella abei* were common sympatric species at warmer sites (lower altitudes; Figure 2) and were strongly positively correlated with one another and this climatic predictor. These species were also negatively correlated with species that are also typically sympatric at cold, high-elevation sites, such as *Boana leptolineata*, *S. granulatus* and *Physalaemus gracilis* (Figure 2). We detected just a few positive relationships between frog species that could be associated with positive interactions. Competition among frog species, specially noncongeners, is often acknowledged to be rare (Cloyed & Eason, 2017; Duellman, 1999), and general assembly process is more related to responses to environmental conditions (e.g. Ernst & Rödel, 2006; Indermaur et al., 2010), corresponding to a Gleasonian community worldview (Gleason, 1926). This strongly suggests that frog assemblages along the SJNP elevational gradient are formed by species with similar thresholds of thermal tolerance.

Although frog species richness and assemblages were associated with their own key predictors, both were conditional on effects of environmental filtering, providing further evidence that this process is the main driver of different levels of frog diversity (Werner et al., 2007). Several studies have shown that climatic gradients are important drivers of the spatial distribution of neotropical anurans at large biogeographic scales (Luiz et al., 2016; Silva et al., 2014; Vasconcelos et al., 2014). However, we have shown that steep climatic variation imposed by elevational settings is also important in shaping frog assemblages, even at a relatively narrow spatial scale.

5 | CONCLUSIONS

Patterns of heterotherm diversity along tropical elevational gradients remain poorly explored. Our study shows that different components of anuran species diversity are influenced by mechanisms related to environmental filtering along the elevational gradient. Specifically, frog species richness was strongly associated with the proportion of natural habitats remaining within each elevational zone, while frog abundance was highly associated with mean annual temperature. This reinforces the detrimental effects of the widespread historical degradation of lowland areas in the Atlantic Forest, which is directly associated with the leading cause of declines in frog diversity worldwide. Climatic conditions were strong determinants of frog assemblage structure along the elevational gradient. Lowland assemblages clearly diverge from those at mid- to high elevations, leading to two distinct groups of frog species. Nonetheless, future studies considering species functional traits and phylogenetic relationships may help elucidate if climatic

restrictions are due to niche conservatism or species-specific environmental filtering operating on life history characteristics. Lastly, the entire elevational gradient we studied was clearly important in retaining the overall regional scale (gamma) diversity. This indicates that anthropogenic habitat disturbance has exerted an enormous overarching influence on montane frog diversity, reinforcing the need for effectively protected areas that are well distributed across all elevational zones.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13187.

DATA AVAILABILITY STATEMENT

The raw data are provided in Appendix S1.1 and S5.3.

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REFERENCES

Allen, A. P., Brown, J. H., & Gillooly, J. F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science, 297*, 1545–1548. https://doi.org/10.1126/science.1072380

Almeida-Gomes, M., Vieira, M. V., Rocha, C. F. D., & Melo, A. S. (2019). Habitat amount drives the functional diversity and nestedness of anuran communities in an Atlantic Forest fragmented landscape. *Biotropica, 51*, 874–884. https://doi.org/10.1111/btp.12687

Almeida-Neto, M., Machado, G., Pinto-da-Rocha, R., & Giaretta, A. A. (2006). Harvestman (Arachnida: Opiliones) species distribution along three Neotropical elevational gradients: An alternative rescue effect to explain Rapoport's rule? *Journal of Biogeography, 33*, 361–375. https://doi.org/10.1111/j.1365-2699.2005.01389.x

Alvares, C. A., Stape, J. L., Sentelhas, P. C., Gonçalves, J. L. M., & Sparovek, G. (2014). Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift, 22*, 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Amat, F., & Meiri, S. (2017). Geographical, climatic and biological constraints on age at sexual maturity in amphibians. *Biological Journal of the Linnean Society, 123*, 34–42.

Bauman, D., Drouet, T., Fortin, M. J., & Dray, S. (2018). Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. *Ecology, 99*, 2159–2166. https://doi.org/10.1002/ecy.2469

Beck, J., McCain, C. M., Axmacher, J. C., Ashton, L. A., Bärtschi, F., Brehm, G., Choi, S.-W., Cizek, O., Colwell, R. K., Fiedler, K., Francois, C. L., Highland, S., Holloway, J. D., Intachat, J., Kadlec, T., Kitching, R. L., Maunsell, S. C., Merckx, T., Nakamura, A., … Novotny, V. (2017). Elevational species richness gradients in a hyperdiverse insect taxon: A global meta-study on geometrid moths. *Global Ecology and Biogeography, 26*, 412–424. https://doi.org/10.1111/geb.12548

Becker, C. G., Fonseca, C. R., Haddad, C. F. B., Batista, R. F., & Prado, P. I. (2007). Habitat split and the global decline of amphibians. *Science, 318*, 1775–1777. https://doi.org/10.1126/science.1149374

Belmaker, J., & Jetz, W. (2015). Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters, 18*, 563–571. https://doi.org/10.1111/ele.12438

Bernal, M. H., & Lynch, J. (2013). Thermal tolerance in anuran embryos with different reproductive modes: Relationship to altitude. *The Scientific World Journal, 2013*, 1–7. https://doi.org/10.1155/2013/183212

Binkenstein, J., Klein, A.-M., Assmann, T., Buscot, F., Erfmeier, A., Ma, K., Pietsch, K. A., Schmidt, K., Scholten, T., Wubet, T., Bruelheide, H., Schuldt, A., & Staab, M. (2018). Multi-trophic guilds respond differently to changing elevation in a subtropical forest. *Ecography, 41*, 1013–1023. https://doi.org/10.1111/ecog.03086

Brown, K. S., & Brown, G. G. (1992). Habitat alteration and species loss in Brazilian forests. In T. C. Whitmore, & J. A. Sayer (Eds.), *Tropical deforestation and species extinction* (pp. 119–142). Chapman and Hall.

Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography, 21*, 873–885. https://doi.org/10.1111/j.1466-8238.2011.00737.x

Bueno A. S., Masseli G. S., Kaefer I. L., Peres C. A. (2019). Sampling design may obscure species–area relationships in landscape-scale field studies. *Ecography, 43*(1), 107–118. http://dx.doi.org/10.1111/ecog.04568

Bürkner, P. C. (2017). Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software, 80*, 1–28.

Carpenter, B., Gelman, A., Hoffman, M., Lee, D., Goodrich, B., Betancourt, M., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software, 76*, 1–32.

Carvalho-Rocha, V., Lopes, B. C., & Neckel-Oliveira, S. (2018). Interindividual patterns of resource use in three subtropical Atlantic Forest frogs. *Austral Ecology, 43*, 150–158. https://doi.org/10.1111/aec.12552

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs, 84*, 45–67. https://doi.org/10.1890/13-0133.1

Cloyed, C. S., & Eason, P. K. (2017). Niche partitioning and the role of intraspecific niche variation in structuring a guild of generalist anurans. *Royal Society Open Science, 4*, 170060. https://doi.org/10.1098/rsos.170060

Crump, M. L. (2015). Anuran reproductive modes: evolving perspectives. *Journal of Herpetology, 49*, 1–16. https://doi.org/10.1670/14-097

da Silva, F. R., Gibbs, J. P., & Rossa-Feres, D. C. (2012). Breeding habitat and landscape correlates of frog diversity and abundance in a

tropical agricultural landscape. *Wetlands*, 31, 1079–1087. https://doi.org/10.1007/s13157-011-0217-0

da Silva, P. G., Lobo, J. M., Hensen, M. C., Vaz-de-Mello, F. Z., & Hernández, M. I. M. (2018). Turnover and nestedness in subtropical dung beetle assemblages along an elevational gradient. *Diversity and Distributions*, 24, 1277–1290. https://doi.org/10.1111/ddi.12763

D'Amen, M., Mod, H. K., Gotelli, N. J., & Guisan, A. (2018). Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. *Ecography*, 41, 1233–1244. https://doi.org/10.1111/ecog.03148

de Vianna, L. F. N., da Silva, E. B., Massignam, A. M., & Neckel Oliveira, S. (2015). Aplicação de descritores de heterogeneidade ambiental na seleção de áreas para sistemas de parcelas amostrais: Um estudo de caso para a determinação de hotspots potenciais de biodiversidade. *Geografia*, 40, 211–239.

Duellman, W. E. (1999). *Patterns of distribution of amphibians: A global perspective*. The Johns Hopkins University Press.

Elsen, P. R., Monahan, W. B., & Merenlender, A. M. (2018). Global patterns of protection of elevational gradients in mountain ranges. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 6004–6009. https://doi.org/10.1073/pnas.1720141115

Ernst, R., & Rödel, M.-O. (2006). Community assembly and structure of tropical leaf-litter anurans. *Ecotropica*, 12, 113–129.

Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663. https://doi.org/10.1111/jbi.12130

Fick, S. E., & Hijmans, R. J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. https://doi.org/10.1002/joc.5086

Frank, H. T., Gomes, M. E. B., & Formoso, M. L. L. (2009). Review of the aerial extent and the volume of the Serra Geral Formation, Paraná Basin, South America. *Pesquisas Em Geociências*, 36, 49–57.

Fu, C.-Z., Hua, X., Li, J., Chang, Z., Pu, Z.-C., & Chen, J.-K. (2006). Elevational patterns of frog species richness and endemic richness in the Hengduan Mountains, China: Geometric constraints, area and climate effects. *Ecography*, 29, 919–927. https://doi.org/10.1111/j.2006.0906-7590.04802.x

Garey, M. V., & Provete, D. B. (2016). Species composition, conservation status, and sources of threat of anurans in mosaics of highland grasslands of southern and southeastern Brazil. *Oecologia Australis*, 20, 94–108. https://doi.org/10.4257/oeco.2016.2002.07

Gebert, F., Njovu, H. K., Treydte, A. C., Steffan-Dewenter, I., & Peters, M. K. (2019). Primary productivity and habitat protection predict elevational species richness and community biomass of large mammals on Mt. Kilimanjaro. *Journal of Animal Ecology*, 88, 1860–1872. https://doi.org/10.1111/1365-2656.13074

Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for bayesian regression models. *The American Statistician*, 73, 307–309. https://doi.org/10.1080/00031305.2018.1549100

Geweke, J. (1992). Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In J. M. Bernardo, J. O. Berger, A. P. David, & A. F. M. Smith (Eds.), *Bayesian statistics* (pp. 169–193). Oxford University.

Giaretta, A. A., Facure, K. G., Sawaya, R. J., de Meyer, J. H. M., & Chemin, N. (1999). Diversity and abundance of litter frogs in a montane forest of Southeastern Brazil: Seasonal and altitudinal changes. *Biotropica*, 31, 669–674.

Giaretta, A. A., Sawaya, R. J., Machado, G., Araújo, M. S., Facure, K. G., de Medeiros, H. F., & Nunes, R. (1997). Diversity and abundance of litter frogs at altitudinal sites at Serra do Japi, southeastern Brazil. *Revista Brasileira De Zoologia*, 14, 341–346.

Gleason, H. A. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, 53, 7–26. https://doi.org/10.2307/2479933

Gontijo-Pascutti, A. H. F., Hasui, Y., Santos, M., Soares-Jr., A. V., & Souza, I. A. (2012). As serras do Mar e da Mantiqueira. In Y. Hasui, C. D. R. Carneiro, F. F. M. Almeida, & A. Bartorelli (Eds.), *Geologia do Brasil* (pp. 549–571). Beca.

Goyannes-Araújo, P., Siqueira, C. C., Laia, R. C., Almeida-Santos, M., Guedes, D. M., & Rocha, C. F. D. (2015). Anuran species distribution along an elevational gradient and seasonal comparisons of leaf litter frogs in an Atlantic Rainforest area of southeastern Brazil. *Herpetological Journal*, 25, 75–81.

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge University Press.

Grace, J. B., Anderson, T. M., Olff, H., & Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, 80, 67–87. https://doi.org/10.1890/09-0464.1

Grace, J. B., Johnson, D. J., Lefcheck, J. S., & Byrnes, J. E. K. (2018). Quantifying relative importance: Computing standardized effects in models with binary outcomes. *Ecosphere*, 9(6), e02283. https://doi.org/10.1002/ecs2.2283

Haddad, C. F. B., & Prado, C. P. A. (2005). Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. *BioScience*, 55, 207–217. https://doi.org/10.1641/0006-3568(2005)055[0207:RMIFAT]2.0.CO;2

Haddad, C. F. B., Toledo, L. F., Prado, C. P. A., Loebmann, D., Gasparini, J. L., & Sazima, I. (2013). *Guia dos Anfíbios da Mata Atlântica: Diversidade e Biologia/Guide to the Amphibians of the Atlantic Forest: Diversity and Biology*. Anolis Books.

Hartmann, L. A. (2014). A história natural do Grupo Serra Geral desde o Cretáceo até o recente. *Ciência E Natura*, 36, 173–182. https://doi.org/10.5902/2179460X13236

Hastie, T. J., & Tibshirani, R. J. (1990). *Generalised additive models*. Chapman and Hall.

Henneron, L., Sarthou, C., de Massary, J.-C., & Ponge, J.-F. (2019). Habitat diversity associated to island size and environmental filtering control the species richness of rock-savanna plants in neotropical inselbergs. *Ecography*, 42, 1536–1547. https://doi.org/10.1111/ecog.04482

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for interpolation and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456.

Hu, J., Xie, F., Li, C., & Jiang, J. (2011). Elevational patterns of species richness, range and body size for Spiny frogs. *PLoS One*, 6(5), e19817. https://doi.org/10.1371/journal.pone.0019817

Hui, F. K. (2016). boral – Bayesian ordination and regression analysis of multivariate abundance data in R. *Methods in Ecology and Evolution*, 7, 744–750.

Hui, F. K., Taskinen, S., Pledger, S., Foster, S. D., & Warton, D. I. (2015). Model based approaches to unconstrained ordination. *Methods in Ecology and Evolution*, 6, 399–411. https://doi.org/10.1111/2041-210X.12236

IBGE (Instituto Brasileiro de Geografia e Estatística) (2012). *Manual Técnico da Vegetação Brasileira: sistema fitogeográfico, inventário das formações florestais e campestres, técnicas e manejo de coleções botânicas, procedimentos para mapeamentos*. Diretoria de Geociências.

Indermaur, L., Shaub, M., Jokela, J., Tockner, K., & Schmidt, B. (2010). Differential response to abiotic conditions and predation risk rather than competition avoidance determine breeding site selection by anurans. *Ecography*, 33, 887–895. https://doi.org/10.1111/j.1600-0587.2010.06150.x

IUCN (2019). *The IUCN Red List of Threatened Species. Version 2019–3*. Retrieved from http://www.iucnredlist.org. Downloaded on February 2019

Kiss, A. C. I., de Carvalho, J. E., Navas, C. A., & Gomes, F. R. (2008). Seasonal metabolic changes in a year-round reproductively active subtropical tree-frog (*Hypsiboas prasinus*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 152(2), 182–188.

Körner, C. (2004). Mountain biodiversity, its causes and function. *Ambio Special Report*, *13*, 11–17.

Laiolo, P., Pato, J., & Obeso, J. R. (2018). Ecological and evolutionary drivers of the elevational gradient of diversity. *Ecology Letters*, *21*, 1022–1032. https://doi.org/10.1111/ele.12967

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, *7*, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lemoine, N. P. (2019). Moving beyond noninformative priors: Why and how to choose weakly 2 informative priors in Bayesian analyses. *Oikos*, *128*, 912–928.

Lomolino, M. V. (2001). Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, *10*, 3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

Longino, J. T., & Branstetter, M. G. (2019). The truncated bell: An enigmatic but pervasive elevational diversity pattern in Middle American ants. *Ecography*, *42*, 272–283. https://doi.org/10.1111/ecog.03871

Luiz, A. M., Leão-Pires, T. A., & Sawaya, R. J. (2016). Geomorphology drives amphibian beta diversity in Atlantic Forest Lowlands of southeastern Brazil. *PLoS One*, *11*, e0153977. https://doi.org/10.1371/journal.pone.0153977

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.

Martinelli, G. (2007). Mountain biodiversity in Brazil. *Revista Brasileira De Botânica*, *30*, 587–597. https://doi.org/10.1590/S0100-84042007000400005

McCain, C. M. (2005). Elevational gradients in diversity of small mammals. *Ecology*, *86*, 366–372. https://doi.org/10.1890/03-3147

McCain, C. M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, *16*, 1–13. https://doi.org/10.1111/j.1466-8238.2006.00263.x

McCain, C. M. (2009). Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. *Ecology Letters*, *12*, 550–560. https://doi.org/10.1111/j.1461-0248.2009.01308.x

McCain, C. M. (2010). Global analysis of reptile elevational diversity. *Global Ecology and Biogeography*, *19*, 541–553. https://doi.org/10.1111/j.1466-8238.2010.00528.x

McCain, C. M., & Beck, J. (2016). Idiosyncratic species turnover on elevational gradients. *Global Ecology and Biogeography*, *25*, 299–310.

McCain, C. M., & Grytnes, J. A. (2010). Elevational gradients in species richness. Robert Baxter In *Encyclopedia of life sciences* (pp. 1–10). Chichester: John Wiley & Sons, Ltd. https://doi.org/10.1002/9780470015902.a0022548

McCain, C. M., King, S. R. B., Szewczyk, T., & Beck, J. (2018). Small mammal species richness is directly linked to regional productivity, but decoupled from food resources, abundance, or habitat complexity. *Journal of Biogeography*, *45*, 2533–2545. https://doi.org/10.1111/jbi.13432

McCain, C. M., & Sanders, N. J. (2010). Metabolic theory and elevational diversity of vertebrate ectotherms. *Ecology*, *91*, 601–609. https://doi.org/10.1890/09-0704.1

Melchior, L. G., Rossa-Feres, D. C., & Silva, F. R. (2017). Evaluating multiple spatial scales to understand the distribution of anuran beta diversity in the Brazilian Atlantic Forest. *Ecology and Evolution*, *7*, 2403–2413. https://doi.org/10.1002/ece3.2852

Menegon, M., & Salvidio, S. (2005). Amphibian and Reptile Diversity in the Southern Udzungwa Scarp Forest Reserve, South-Eastern Tanzania. In: B. A. Huber, B. J. Sinclair, & L. Karl-Heinz (Eds.) *African biodiversity* (pp. 205–212). Springer. https://link.springer.com/chapter/10.1007/0-387-24320-8_18.

MMA (Ministério do Meio Ambiente). (2000). *Avaliação de ações prioritárias para a conservação da biodiversidade da Mata Atlântica e Campos Sulinos.* Conservation International do Brasil, Fundação SOS Mata Atlântica, Fundação Biodiversitas, Instituto de Pesquisas Ecológicas, Secretaria do Meio Ambiente do Estado de São Paulo, SEMAD/Instituto Estadual de Florestas-MG. https://www.mma.gov.br/estruturas/sbf_chm_rbbio/_arquivos/Sumario%20Mata%20Atlantica.pdf.

Navas, C. A., Carvajalino-Fernández, J. M., Saboyá-Acosta, L. P., Rueda-Solano, L. A., & Carvajalino-Fernández, M. A. (2013). The body temperature of active amphibians along a tropical elevation gradient: Patterns of mean and variance and inference from environmental data. *Functional Ecology*, *27*, 1145–1154. https://doi.org/10.1111/1365-2435.12106

Nomura, F., Maciel, N. M., Pereira, E. B., & Bastos, R. P. (2012). Anura diversity (Amphibia) in recovered areas of mining activity in Cerrado and *Eucalyptus urophyla* planting in central Brazil. *Bioscience Journal*, *28*, 312–324.

Ovaskainen, O., Abrego, N., Halme, P., & Dunson, D. (2016). Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods in Ecology and Evolution*, *7*, 549–555. https://doi.org/10.1111/2041-210X.12501

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, *20*, 561–576. https://doi.org/10.1111/ele.12757

Pereira, H. M., Ferrier, S., Walters, M., Geller, G. N., Jongman, R. H. G., Scholes, R. J., Bruford, M. W., Brummitt, N., Butchart, S. H. M., Cardoso, A. C., Coops, N. C., Dulloo, E., Faith, D. P., Freyhof, J., Gregory, R. D., Heip, C., Hoft, R., Hurtt, G., Jetz, W., ... Wegmann, M. (2013). Essential biodiversity variables. *Science*, *339*, 277–278. https://doi.org/10.1126/science.1229931

Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S. W., Frederiksen, S. B., Gebert, F., Haas, M., Helbig-Bonitz, M., Hemp, C., Kindeketa, W. J., Mwangomo, E., Ngereza, C., Otte, I., Röder, J., Rutten, G., ... Steffan-Dewenter, I. (2016). Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications*, *7*, 13736. https://doi.org/10.1038/ncomms13736

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., & McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*, 397–406.

QGIS Development Team (2019). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. Retrieved from http://qgis.osgeo.org

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, *8*, 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Rana, S. K., Gross, K., & Price, T. D. (2019). Drivers of elevational richness peaks, evaluated for trees in the east Himalaya. *Ecology*, *100*, e02548. https://doi.org/10.1002/ecy.2548

Rasband, W. S. (1997). *ImageJ*. National Institutes of Health.

Rezende, C. L., Scarano, F. R., Assad, E. D., Joly, C. A., Metzger, J. P., Strassburg, B., Tabarelli, M., Fonseca, G. A., & Mittermeier, R. A. (2018). From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. *Perspectives in Ecology and Conservation*, *16*, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, *142*, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, *7*, 1–15. https://doi.org/10.1046/j.1461-0248.2003.00554.x

Rosenzweig, M. (1995). *Species diversity in space and time*. Cambridge University Press.

Rossa-Feres, D. C., Garey, M. V., Caramaschi, U., Napoli, M. F., Nomura, F., Bispo, A. A., & Haddad, C. F. B. (2017). Anfíbios da Mata Atlântica: Lista de espécies, histórico dos estudos, biologia e conservação. In E. L. A. Monteiro-Filho, & C. E. Conte (Eds.), *Revisões em Zoologia: Mata Atlântica* (pp. 237–314). Editora UFPR.

Rossa-Ferres, D. C., & Jim, J. (1994). Distribuição sazonal em comunidade de anfíbios anuros na região de Botucatu, São Paulo (Amphibia, Anura). *Revista Brasileira De Zoologia*, *54*, 323–334.

Rowe, R. J., & Lidgard, S. (2009). Elevational gradients and species richness: Do methods change pattern perception? *Global Ecology and Biogeography*, *18*, 163–177. https://doi.org/10.1111/j.1466-8238.2008.00438.x

Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N., Durka, W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L. R., Klein, A.-M., Roscher, C., Schaller, J., von Oheimb, G., Weigelt, A., Weisser, W., Wirth, C., … Eisenhauer, N. (2019). Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communication*, *10*, 1460. https://doi.org/10.1038/s41467-019-09448-8

Scott, N. Jr, Woodward, B. D. et al (1994). Surveys at breeding sites. In W. R. Heyer (Ed.), *Measuring and monitoring biological diversity, standard methods for amphibians*. Smithsonian Institution Press.

Silva, F. R., Almeida-Neto, M., & Arena, M. V. N. (2014). Amphibian beta diversity in the Brazilian Atlantic Forest: Contrasting the roles of historical events and contemporary conditions at different spatial scales. *PLoS One*, *9*, e109642. https://doi.org/10.1371/journal.pone.0109642

Solé, M., & Rödder, D. (2010). Dietary Assessments of adult amphibians. In C. K. Dodd (Ed.), *Amphibian ecology and conservation: A handbook of techniques* (pp. 167–184). Oxford University Press.

Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *The American Naturalist*, *152*, 510–529. https://doi.org/10.1086/286187

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, *306*, 1783–1786. https://doi.org/10.1126/science.1103538

Szewczyk, T. M., & McCain, C. M. (2019). Disentangling elevational richness: A multi-scale hierarchical Bayesian occupancy model of Colorado ant communities. *Ecography*, *42*, 977–988. https://doi.org/10.1111/ecog.04115

Tabarelli, M., Aguiar, A. V., Ribeiro, M. C., Metzger, J. P., & Peres, C. A. (2010). Prospects for biodiversity conservation in the Atlantic Forest: Lessons from aging human-modified landscapes. *Biological Conservation*, *143*, 2328–2340. https://doi.org/10.1016/j.biocon.2010.02.005

Tucker, J. K. (1995). Early post-transformational growth in the Illinois chorus frog (*Pseudacris streckeri illinoensis*). *Journal of Herpetology*, *29*, 314–316. https://doi.org/10.2307/1564577

Vale, M. M., Tourinho, L., Lorini, M. L., Rajão, H., & Figueiredo, M. S. L. (2018). Endemic birds of the Atlantic Forest: Traits, conservation status, and patterns of biodiversity. *Journal of Field Ornithology*, *89*, 193–206. https://doi.org/10.1111/jofo.12256

Valeriano, M. M., & Rossetti, D. F. (2012). Topodata: Brazilian full coverage refinement of SRTM data. *Applied Geography*, *32*, 300–309.

Vasconcelos, T. S., Prado, V. H. M., Silva, F. R., & Haddad, C. F. B. (2014). Biogeographic distribution patterns and their correlates in the diverse frog fauna of the Atlantic Forest hotspot. *PLoS One*, *9*(8), e104130. https://doi.org/10.1371/journal.pone.0104130

Vasconcelos, T. S., & Rossa-Feres, D. C. (2005). Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do estado de São Paulo, Brasil. *Biota Neotropica*, *5*, 1–14. https://doi.org/10.1590/S1676-06032005000300010

Vieira, M. V., Almeida-Gomes, M., Delciellos, A. C., Cerqueira, R., & Crouzeilles, R. (2018). Fair tests of the habitat amount hypothesis require appropriate metrics of patch isolation: An example with small mammals in the Brazilian Atlantic Forest. *Biological Conservation*, *226*, 264–270. https://doi.org/10.1016/j.biocon.2018.08.008

Wachlevski, M., Erdtmann, L., & Garcia, P. (2014). Anfíbios anuros em uma área de Mata Atlântica da Serra do Tabuleiro, Santa Catarina. *Biotemas*, *27*, 97–107. https://doi.org/10.5007/2175-7925.2014v27n2p97

Walker, M., Wachlevski, M., Nogueira-Costa, P., Garcia, P. C. A., & Haddad, C. F. B. (2018). A new species of Fritziana Mello-Leitão 1937 (Amphibia: Anura: Hemiphractidae) from the Atlantic Forest, Brazil. *Herpetologica*, *74*, 329–341. https://doi.org/10.1655/0018-0831.329

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology and Evolution*, *30*, 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Warton D. I., Wright S. T., Wang Y. (2012). Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, *3*(1), 89–101. http://dx.doi.org/10.1111/j.2041-210x.2011.00127.x

Werner, E. E., Skelly, D. K., Relyea, R. A., & Yurewicz, K. L. (2007). Amphibian species richness across environmental gradients. *Oikos*, *116*, 1697–1712. https://doi.org/10.1111/j.0030-1299.2007.15935.x

Willig, M., & Presley, S. (2016). Biodiversity and metacommunity structure of animals along altitudinal gradients in tropical montane forests. *Journal of Tropical Ecology*, *32*, 421–436. https://doi.org/10.1017/S0266467415000589

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, *73*, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wu, Y., Colwell, R. K., Rahbek, C., Zhang, C., Quan, Q., Wang, C., & Lei, F. (2013). Explaining the species richness of birds along a subtropical elevational gradient in the Hengduan Mountains. *Journal of Biogeography*, *40*, 2310–2323. https://doi.org/10.1111/jbi.12177

Zancolli, G., Steffan-Dewenter, I., & Rödel, M.-O. (2014). Amphibian diversity on the roof of Africa: Unveiling the effects of habitat degradation, altitude and biogeography. *Diversity and Distributions*, *20*, 297–308. https://doi.org/10.1111/ddi.12161

Zu, K., Luo, A., Shrestha, N., Liu, B., Wang, Z., & Zhu, X. (2019). Altitudinal biodiversity patterns of seed plants along Gongga Mountain in the southeastern Qinghai-Tibetan Plateau. *Ecology and Evolution*, *9*, 9586–9596.

BIOSKETCH

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SUPPORTING INFORMATION

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