ORIGINAL ARTICLE

Effects of environmental factors on the ecology and survival of a widespread, endemic Cerrado frog

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Abstract

Understanding the mechanisms that affect habitat use by vertebrates is critical for understanding how species are distributed across landscapes and how they cope with habitat change. The Brazilian Savanna (the Cerrado) has vegetation ranging from grassland to woodland savannas and harbors a rich and diverse amphibian fauna impacted by accelerated habitat loss. Here, we test the influence of vegetation type (from grassy scrubland to woodland) and distance from breeding sites (ephemeral water bodies) on body size, abundance, and survival of the frog *Physalaemus nattereri* in a natural metapopulation system of south-central Brazil. We also test whether body size is a significant predictor of population abundance. We found that the abundance of *P. nattereri* varies according to the mean snout–vent length of each metapopulation (sampling unit), as well as a higher estimated mortality rate in woodlands compared with typical Cerrado. Furthermore, we found no difference in estimated mortality among sampling units located far or close to ephemeral water bodies. Thus, our results highlight variable responses of *P. nattereri* metapopulations to environmental factors, despite the observed high heterogeneity among sampled habitats and the importance of ephemeral water bodies for reproduction. These findings highlight that land cover and availability of breeding sites might not always interact to explain population persistence of Cerrado frogs.

KEYWORDS
amphibians, habitat, mark–recapture, savanna, vegetation heterogeneity

1 | INTRODUCTION

The study of population dynamics depends on ecological and natural history data, such as habitat use, recruitment timing, and reproductive requirements (e.g., Bionda et al., 2013; Faggioni et al., 2020). These data are vital for species distribution modeling and the reconstruction of species' life history, thus being useful for assessing extinction risk and designing management actions for declining or endangered species (IUCN, 2001; Lindenmayer & Burgman, 2005). However, comprehensive life-history information is often unavailable for most species of tropical vertebrates (Greene, 2005). Amphibians have been historically considered a key taxon in life-history studies due to their developmental shift from an aquatic larval stage to a terrestrial adult, and their strong responses to disturbances and spatial connectivity across aquatic and terrestrial habitats (Barbault, 1984; Becker et al., 2007). Additionally, the myriad diversity of anuran reproductive modes (Duellman & Trueb, 1986; Haddad & Prado, 2005; Nunes-de-Almeida et al., 2021) often leads to great variation in terms of habitat and microhabitat use as both are intrinsically related to reproduction (see Haddad & Prado, 2005; Nunes-de-Almeida et al., 2021). Given the relevance of environmental heterogeneity shaping amphibian populations (e.g., Silva et al., 2011; Vasconcelos et al., 2009), studies aiming to unravel and disentangle mechanisms of habitat use in complex landscapes, such as those in Cerrado (see below), are complex but can offer invaluable estimates of population viability.

In the Cerrado ecoregion of South America, open formations such as grassy scrubland and/or grassy scrubland with scattered trees, locally called *campo sujo* and *campo cerrado*, respectively, harbor greater biodiversity than nonopen vegetation types such as typical Cerrado (*cerrado strictu* sensu), cerrado woodland (*cerradão*), and gallery forests (Abreu et al., 2017; Araujo et al., 2013; Fiorillo, 2020; Fiorillo & Martins, 2021; Sawaya et al., 2008). A recent study provided additional support for amphibian diversity decreasing across a woody density gradient of a Cerrado fragment in southeastern Brazil (Thomé et al., 2021). Moreover, Thomé and colleagues found that species dominance at the community level significantly varied among Cerrado vegetation types, with distinct species identities being dominant in different vegetation types (e.g., *Physalaemus* spp. gr. *cuvieri* was the dominant species in *campo cerrado* while *Rhinella ornata* was the dominant species in *cerradão*).

In addition to the effect of Cerrado vegetation type, the spatial distribution of water bodies is expected to affect amphibian species diversity and composition (Moreira et al., 2010). This environmental feature is often a strong predictor of population-level fitness (Becker et al., 2007) and consequently a proxy for community structure, depending on species life history, behavioral and physiological strategies, and reproductive modes (e.g., Díaz-Ricaurte et al., 2020; Haddad & Prado, 2005; Moreira et al., 2010). Survival and reproductive strategies are usually associated and may synergistically affect the development of anurans. For instance, some species breeding in temporary water bodies (e.g., family Bufonidae) are constrained by a trade-off between development and growth rates (Richter-Boix

et al., 2011). Breeding in temporary water bodies is supposedly related to predator-avoidance during the larval phase, increasing larval survival probability (Kats et al., 1988; Richter-Boix et al., 2011; Woodward, 1983). Regardless of the trade-off between time to metamorphosis and growth, tadpoles that develop faster may metamorphose at a reduced size (Merilä et al., 2000). During the next phase, when juveniles are leaving wetlands, they may become highly susceptible to predation (Wassersug & Sperry, 1977) and desiccation especially, if they are small (mainly due to their high surface-to-volume ratio; Schmid, 1965). It has been shown that juvenile survival in terrestrial habitats is critical for population growth (Biek et al., 2002; Vonesh & De la Cruz, 2002).

Anurans are especially vulnerable during the aquatic larval stage, being exceptionally prone to predation, competition (which can lead to negative density-dependent responses due to reduced food availability linked to malnutrition and starvation), and being constantly exposed to the widespread chytrid fungus and other waterborne diseases (Densmore & Green, 2007). Higher mortality during the aquatic larval period may also reduce competition among tadpoles and result in more individuals successfully transitioning into terrestrial habitats, that is, a density-dependent response (Cabrera-Guzmán et al., 2013; Harper & Semlitsch, 2007; Smith, 1983). In a manipulative study with *Pseudacris maculata*—a hylid species that breeds in ephemeral and permanent water bodies—tadpoles developed faster in permanent than in ephemeral ponds, likely to escape predation in the aquatic environment (Amburgey et al., 2012). Thus, studies estimating population viability throughout the development of individual frogs provide important information for the management and conservation of species (Barrile et al., in press).

Physalaemus nattereri is an endemic, widely distributed anuran species in the Cerrado ecoregion (Valdujo et al., 2012), which shows a seasonal and explosive reproductive pattern (Rodrigues et al., 2004). It is often classified as a habitat generalist species, being able to occupy natural and disturbed habitats with open and closed vegetation (Díaz-Ricaurte et al., 2020; Fiorillo et al., 2019), reproducing mostly in ephemeral water bodies (Brasileiro et al., 2005; Silva & Rossa-Feres, 2010). Despite its wide distribution and the knowledge on some aspects of its natural history and thermal ecology (Díaz-Ricaurte et al., 2020), it remains elusive how environmental factors affect the abundance and survival of *P. nattereri* populations. Here, we tested the influence of natural landscapes of the Cerrado and distance from ephemeral water bodies on body size, abundance, and survival of *P. nattereri* in a metapopulation system in southern Brazilian Cerrado. Given the high habitat generalism of our focal species, we predicted that the type of natural Cerrado vegetation would not affect body size, abundance or survival of *P. nattereri*. However, considering the explosive breeding nature of *P. nattereri*, we expected that distance from ephemeral water bodies would be a good predictor of local variations in body size, abundance, and survival. We also tested whether body size is a good predictor of abundance. Given that anurans can control larval development (and thus time to metamorphosis) in ephemeral ponds, we expected to find an inverse relationship between body size and abundance. Understanding how

environmental factors affect populations of Cerrado frogs may help predict their responses to the extensive habitat loss and disturbance that is ongoing in this ecoregion during the last decades (e.g., Françoso, 2014; Rausch et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was carried out at Santa Bárbara Ecological Station (SBES), municipality of Águas de Santa Bárbara, state of São Paulo, south-central Brazil (−22.800000°, −49.216667°; Datum WGS84; 600–680m a.s.l; Figure 1a). The mean precipitation is 1454.2mm and temperature averages 17°C in the coldest months and 24°C in the warmest months (data for 1995–2014 at Manduri, SP, 20.3 km from our study area; CIIAGRO, 2021). The SBES has a total area of 3223ha (Melo & Durigan, 2011) and harbors different Cerrado

vegetation types: *campo sujo* (CS; grassy scrubland), *campo cerrado* (CC; grassy scrubland with scattered trees), *cerrado* sensu stricto (SS; dense savanna), and *cerradão* (CD; cerrado woodland), as well as some small areas of semideciduous forests (Figure 1a; see more details about each vegetation type of the study area in Fiorillo et al., 2021). The distance between sampling units and floodable areas where ephemeral ponds (the breeding habitat of *P. nattereri*) appear in the wet season (October to March) was obtained in QGIS (QGIS, 2021) based on a detailed land cover classification including the category of floodable areas (Figure 1b). These floodable areas were all validated in the field during the wet season.

2.2 | Sampling

Sampling was performed monthly for 10days, from August 2016 to July 2018, for a total of 24 field campaigns and 240days of fieldwork. At each sampled vegetation type (*campo cerrado*, *campo sujo*,
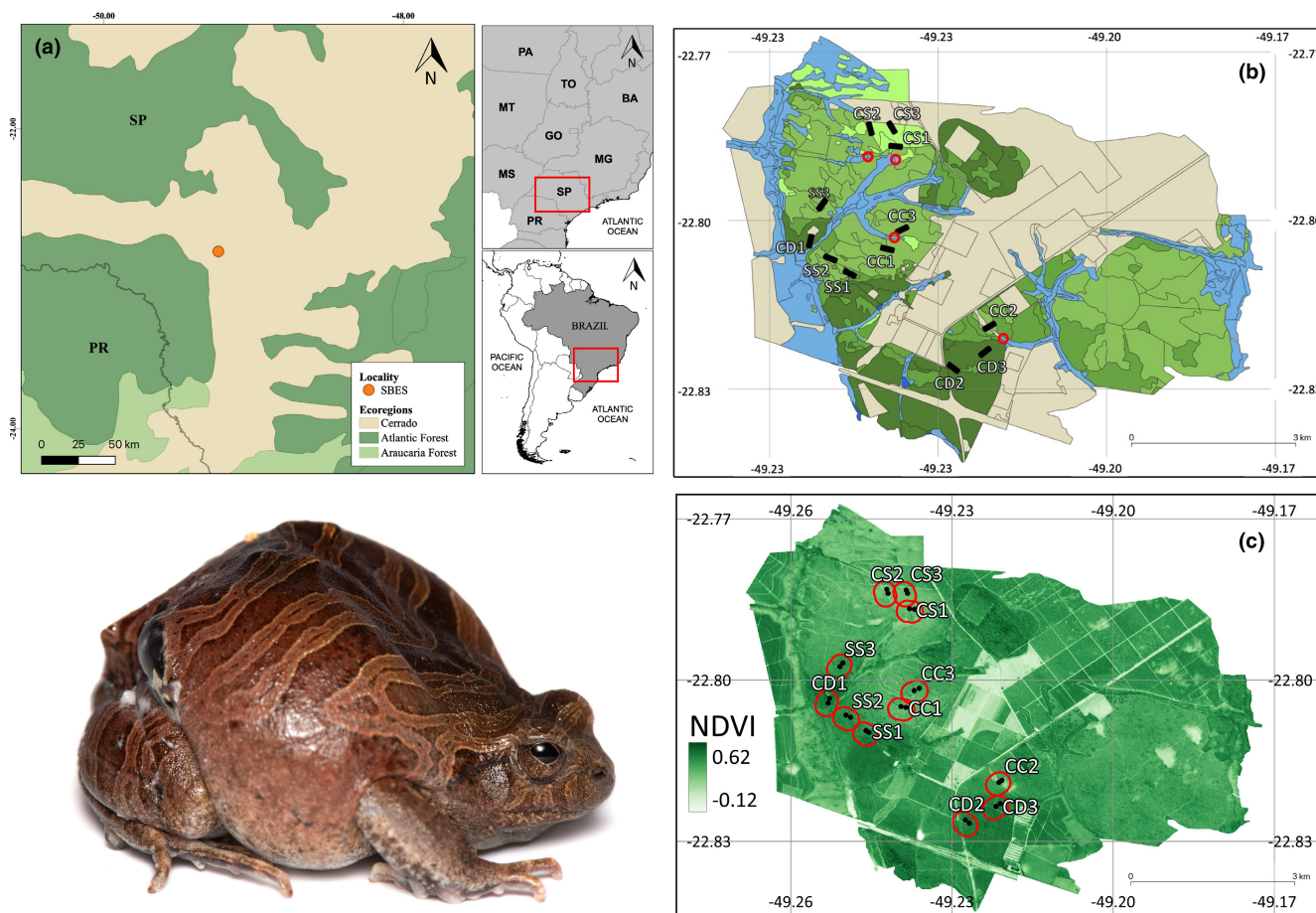

FIGURE 1 Maps showing (a) the location of our focal sampling site: the Santa Bárbara Ecological Station (orange point) in São Paulo state, southeastern Brazil (Ecoregions in the detailed map are from Dinerstein et al., 2017); (b) the distribution of sampling units at Santa Bárbara Ecological Station (paired black dots) (the lighter the green, the more open the vegetation). Cream areas are commercial tree plantations, pastures, and other disturbed areas; wet areas are shown in blue; red circles indicate floodable areas where ephemeral ponds (the breeding habitat of *P. nattereri*) appear in the wet season; and (c) variation in Normalized Difference Vegetation Index (shades of green, indicating variation in vegetation complexity), sets of pitfall trap lines, and buffers of 200m used to extract average values around sampling units. CS: *campo sujo*, CC: *campo cerrado*, SS: *cerrado* sensu stricto, CD: *cerradão*.

cerrado sensu stricto, and *cerradão*), three units of pitfall traps with drift fences were installed (Figure 1b). Each unit corresponded to two 40-m trap lines, 60 m apart. Each trap line had four 100-L plastic buckets every 10 m, connected by a plastic drift fence 60 cm tall (see Fiorillo et al., 2021). Buckets were punctured on the bottom to avoid the accumulation of rainwater. Drift fence was buried 10 cm into the soil and attached to wooden stakes (see Cechin & Martins, 2000; Sawaya et al., 2008). To reduce the risk of dehydration in captured animals, we placed a piece of styrofoam ($20 \times 20 \times 5$ cm) supported by wooden posts and a small water plate inside each bucket to provide shelter and moisture (Sawaya et al., 2008). We installed a total of 12 sampling units (each one was composed of a pair of pitfall trap lines, totaling 24 lines, 96 buckets, and 960 m of fences), and pitfalls were kept in operation for ten consecutive days every month. There was a single *campo sujo* site within SBES; thus, we had to adjust the distances among sampling units to be proportional to those included within this area (maximum of 400 m distance between sampling units). Thus, pitfall sampling took place during 240 nonconsecutive days, corresponding to 23,040 bucket-days. All captured individuals were measured (snout–vent length was recorded using a Mitutoyo analogical caliper to the nearest 0.01 mm), photographed (using digital cameras), and released.

2.3 | Vegetation complexity

We extracted vegetation complexity information for our study area using the Normalized Difference Vegetation Index (NDVI), as NDVI increases with increasing foliage-height diversity and horizontal vegetation structure (see Wood et al., 2012). To generate this index, the satellite image corresponding to the perimeter of the SBES was extracted from the Planet imagery base. The image extracted refers to the year 2017 (4/29/2017) obtained from the 4-BandPlanetScopecom satellite, with a spatial resolution of 3 m. The image was processed using the QGIS software (QGIS Development Team, 2021). To generate the NDVI, only images in "tif" format were used, corresponding to the red and infrared spectrum bands. The images were submitted to an arithmetic calculation using the raster calculator function. We obtained NDVI using the following formula (Jensen & Lulla, 1996):

$$NDVI = \frac{Infra\ Red\ band - Red\ band}{Infra\ Red\ band + Red\ band}$$

The product obtained is a raster with continuous values ranging from −1 to 1, where higher values correspond to greater chlorophyll activity. We extracted the centroid of the 24 pitfall trap lines and then generated buffers of 200 m around each centroid using the buffer calculator function. Then, average NDVI was calculated for each buffer at different spatial scales. We submitted buffer maps (Figure 1c) to the zonal statistics function to obtain the average NDVI for each buffer pair (corresponding to a sampling unit). The 200 m scale showed just a slight overlap between buffers from different

sampling units; therefore, we assumed that this overlap would not affect our results.

2.4 | Photo identification

Dorsal marks of individual frogs were recorded using digital cameras (Figure S1). Then, we performed a computer-assisted matching method, using the Wild-ID program (Java 1.5; Bolger et al., 2012; see Caorsi et al., 2012, Díaz-Ricaurte et al., 2019). This software detects recaptures based on an algorithm of Scale Invariant Feature Transform (SIFT; Lowe, 2004), which extracts and combines the distinctive features in the image, regardless of size and orientation.

2.5 | Structural equation modeling

Considering that differences in capture rates and annual growth could affect our results, before generating the structural equation models, we computed Tukey Honest Significant Differences between models that incorporated the proportion of individuals captured in each sampling unit in each year ($p = .99$) and the mean SVL of each sampling unit in each year ($p = .70$) using the "stats" package (R Core Team, 2020). These results were not significant, and thus, we ignored the annual variation.

To evaluate potential causal structures connecting abundance (count), snout–vent length (SVL), distance to ephemeral ponds (dist), vegetation type (veg.cat), and NDVI, we performed piecewise structural equation models (SEMs; Appendix S1). We used SEMs to investigate three different groups of causal networks. The first two groups of causal networks were composed of generalized linear models (GLM). While group 1 included the four categories of vegetation type (*campo sujo*, *campo cerrado*, *cerrado* sensu stricto, and *cerradão*) as a categorical variable (veg.cat), group 2 included vegetation complexity (NDVI) instead (Figures S4 and S5). Group 3 was composed of generalized linear mixed models (GLMM), where NDVI was included as a fixed predictor, such as in group 2, but with veg. cat added as a random variable (Figure S6). Each group consisted of three distinct structures representing alternative hypotheses about the expected relationship between SVL and count (A: SVL –> count; B: count –> SVL; C: SVL <–> count; Figures S4–S6). Regardless of model structure, dist, veg.cat, and NDVI were included as exogenous variables. Count and SVL, however, were added as endogenous or exogenous according to alternative hypotheses.

We used Gaussian error distribution and checked residuals' normality visually in the first group of models. Because we detected residual overdispersion in all paths that considered abundance as the response variable using Poisson distribution, we obtained parameter estimates with a negative binomial error distribution. For paths that considered continuous response variables (SVL), we used Gaussian error distribution. We estimated model parameters using maximum likelihood in the "stats" (R Core Team, 2020), "piecewiseSEM" (Lefcheck, 2016), and "lme4" (Bates et al., 2014),

and checked residuals' dispersion in the "hnp" package (Moral et al., 2016). Residuals autocorrelation test was performed using Moran's Test (*testSpatialAutocorrelation* function) on the simulation of residuals generated by fitting the model (*simulateResiduals* function) in DHARMa (Hartig, 2019). We also calculated the goodness-of-fit statistics of each SEM in the "piecewiseSEM" package (Lefcheck, 2016). We conducted all analyses in R (R Core Team, 2020).

We used the Akaike Information Criteria adjusted sample size (AICc) in model selection to compare and rank models according to the number of parameters and likelihood (Burnham et al., 2011). We considered models with ΔAICc ≤2 to be of equally good support (Burnham & Anderson, 2002) and therefore suitable for inference and estimation. We were confident of a covariate effect if 95% of the confidence interval (95% CI) of the estimated regressors did not encompass zero (Faggioni et al., 2020). We compared and explored models using the function *AIC* with argument *aicc* as true in the "piecewiseSEM" package (Lefcheck, 2016) in R (R Core Team, 2020). The R script and data used in SEM analyses are available as Appendix S1.

2.6 | Survival rate and vegetation type

To investigate how vegetation type and categorical distance from ephemeral ponds (close vs far from ephemeral water bodies) affect the survival rate (comparing different postmetamorphic individuals in juvenile to adult stages), we used Bayesian survival trajectory analyses from the R package BaSTA (Colchero & Clark, 2012; Colchero et al., 2012; Appendix S2). We established the two categories of distance from ephemeral ponds based on Ficetola et al. (2009). This method estimates parametric survival functions using Markov chain Monte Carlo (MCMC) simulations. Specifically, BaSTA is an appropriate tool to fit an age-specific mortality function on capture–mark–recapture data (e.g., Boonekamp et al., 2014; Cayuela et al., 2020), which considers imperfect detection and unknown birth and death date. We explored age-specific survival rates through four mortality functions (exponential, Gompertz, Weibull, and logistic) and three potential shapes (simple, Makeham, and bathtub) implemented in BaSTA. We then performed a model selection approach based on the lowest deviance information criterion (DIC) to seek the most parsimonious model (Colchero et al., 2012; Spiegelhalter et al., 2002). The best-fitting model consists of six parameters: (i) two alpha parameters (*a0* and *a1*) that describe an exponential decline observed early in life, (ii) a constant *c* that describes the lowest point of the mortality function, (iii) *b0* that is the age-independent mortality (i.e., baseline mortality), (iv) *b1* that describes the initial exponential increase in mortality with age, and (v) *b2* that describes the degree of deceleration in mortality with age. We interpreted the outputs of the best-supported model by inspecting mean estimates and 95% credible intervals (Amrhein et al., 2019). Moreover, model parameters were compared using Kullback–Leibler discrepancy criterion (KLDC), which is used to evaluate the extent of overlap of posterior distributions of parameter estimates (Kullback & Leibler, 1951;

McCulloch, 1989). The KLDC varies between 0.5 (complete overlap) and 1.0 (no overlap) and allows the determination of the magnitude of the effect of vegetation type on mortality trajectories. We considered a KLDC value in a more conservative manner (i.e., >0.85) to test for a substantial difference between the two posterior distributions that are compared. Markov chain Monte Carlo (MCMC) optimizations were performed using three parallel simulations, each consisting of 1,000,000 iterations using a thinning interval of 200 and 20% of samples discharged as burn-in. The setups used were appropriate to reach convergence of model parameters (see Figures S1 and S2).

3 | RESULTS

3.1 | Sampling and photo identification

We captured a total of 298 individuals of *P. nattereri* during our two-year sampling period (Mean$_{SU}$ = 24.84 ± 18.93; Mean$_{year}$ = 149.00 ± 36.77), of which 77 were captured in *campo cerrado* (Mean$_{SU}$ = 25.67 ± 25.42; Mean$_{year}$ = 38.50 ± 13.44), 75 in *campo sujo* (Mean$_{SU}$ = 25.00 ± 5.29; Mean$_{year}$ = 37.50 ± 9.19), 36 in *cerrado sensu stricto* (Mean$_{SU}$ = 12.00 ± 6.08; Mean$_{year}$ = 18.00 ± 4.24), and 110 in *cerradão* (Mean$_{SU}$ = 36.67 ± 28.29; Mean$_{year}$ = 55.00 ± 18.38). Although the number of individuals captured in *cerradão* was higher than in other vegetation types, 67 out of 110 individuals (~61% of the total observed) were captured by a single sampling unit (CD3). This sampling unit was located near a *campo cerrado* sampling unit (CC2), which had the second largest number of individuals captured (N = 55; ~71% of all individuals captured in this vegetation type); note that these sampling units were the most distant from ephemeral ponds at SBES (Figure 1b).

The accuracy of computer-assisted ID matching using photography was high, with 100% of the hits classified in all the first elections. Only four individuals were recaptured during our field study (~1.3%); three of them at the same sampling unit of the first capture, in subsequent days. One individual (ID327) was recaptured three times after the first capture at the same sampling unit in three consecutive days. Another individual (ID180) was first captured in *cerradão* (CD3) and recaptured in another sampling unit in *campo cerrado* (CC2), about 500 m apart, 19 days later.

3.2 | Structural equation modeling

All structural equation models (Figures S4–S6) had *p* > .05 in their independence claim tests (Table S1), indicating good support for the designed structures. The most parsimonious structural equation model (AICc = −339.88; Figure 2) contained four specified paths: (1) vegetation type (veg.cat) -> count; (2) distance from ephemeral ponds (dist) -> count; (3) SVL -> count; and (4) veg.cat -> SVL. Sites with larger individuals had smaller frog abundances (*p* = .009; Point estimate = −0.126; 95% CI −0.2280 to −0.0258; Table 1, Figure 3).

The Moran's test indicated no spatial autocorrelation in three of the four paths: (1) vegetation type (veg.cat) –> count ($p = .12$), (3) SVL –> count ($p = .91$), and (4) veg.cat –> SVL ($p = .06$). However, the path dist –> count had significant distance-based autocorrelation ($p = .006$).

3.3 | Survivorship rates

Based on deviance information criterion (DIC) comparisons, age-specific survival and mortality patterns associated with vegetation type were best described by a logistic function with a bathtub shape (Table S2). Overall, modeling age-specific survival and mortality patterns in BaSTA uncovered an increase in estimated mortality with age across the four vegetation types (Figure 4, Table S3). Nevertheless,
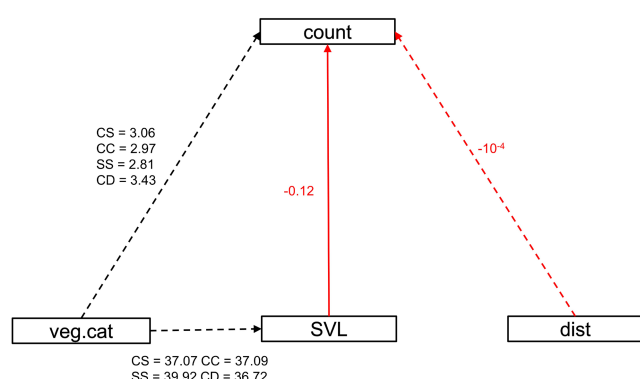

FIGURE 2 Path diagram of the most parsimonious structural equation model (AICc = −302.78) evaluating the effect of vegetation type, *P. nattereri* abundance, average SVL, and distance from ephemeral ponds. Arrows start at the predictor and point to response variables, where solid and dashed lines represent significant and nonsignificant relationships, respectively. The red arrows' colors represent a negative relationship between variables. Numbers are coefficients of the estimate of each model.

our analyses revealed some contrasting patterns of age-specific survival and mortality among individuals of *P. nattereri* from natural Cerrado habitats with different degrees of vegetation complexity. More specifically, a significantly faster increase in estimated mortality with age (from juvenile stage) was identified in *cerradão* when compared to *cerrado* sensu stricto (Figure 4, Table 2). Individuals from the *cerrado* sensu stricto had indeed substantially lower initial acceleration in estimated mortality rate (i.e., smaller early-life acceleration parameter b1) than from *cerradão* (KLDC = 0.934, Table 2). By contrast, there was no detectable difference in estimated mortality between *campo sujo*, *campo cerrado*, and *cerradão* (Figure 4, Table 2), with a high degree of overlap between posterior distributions (KLDC <0.85, Table 2). Collectively, the findings for these three vegetation types indicate a similar spectrum of response to habitat complexity.

Regarding the categorical distance from ephemeral ponds (close vs far from ephemeral water bodies), age-specific survival and mortality patterns were best described by a logistic function with a simple shape (Table S2). For both types of environments, we observed an increase in estimated mortality with age (Figure 4, Table S3). However, our analyses did not reveal significant differences in estimated mortality between the two environments (KLDC <0.85, Table 2), indicating a similar spectrum of response of *P. nattereri* to environments far and close to ephemeral ponds.

4 | DISCUSSION

We found differences in body size of *P. nattereri* metapopulations, as well as a higher estimated mortality rate in *cerradão* compared with *cerrado sensu stricto*. Contrary to our predictions, we found no differences in estimated mortality among sampling units located far or close to ephemeral water bodies (close: ≤400 m from water bodies; far: >400 m from ponds). Overall, our results suggested variable responses of *P. nattereri* metapopulations to the environmental factors addressed, despite the high heterogeneity among our focal Cerrado

Parameters	Abundance (count)		SVL	
	Estimate ± SE	95% CI	Estimate ± SE	95% CI
SVL	−0.125 ± 0.05	−0.228–−0.028	–	–
Dist. eph. ponds	$-10^{-4} \pm 6 \cdot -10^{-4}$	−0.001–0.001	–	–
Vegetation type				
CS (intercept)	3.065 ± 0.31	4.368–11.530	37.067 ± 2.24	32.665–41.468
CC	2.968 ± 0.33	−0.800–0.605	37.093 ± 2.24	−6.200–6.251
SS	2.812 ± 0.37	−1.313–0.799	39.920 ± 2.24	−3.371–9.078
CD	3.433 ± 0.29	−0.489–1.252	36.720 ± 2.24	−5.571–6.880

The header "Response variable" spans the Abundance and SVL columns.

TABLE 1 Parameters from the best-fit structural model (ΔAICc ≤2) formulated to investigate the effects of snout–vent length (SVL), distance to ephemeral ponds (Dist. eph. ponds), and vegetation type on abundance of *Physalaemus nattereri* in Santa Bárbara Ecological Station, SP, Brazil.
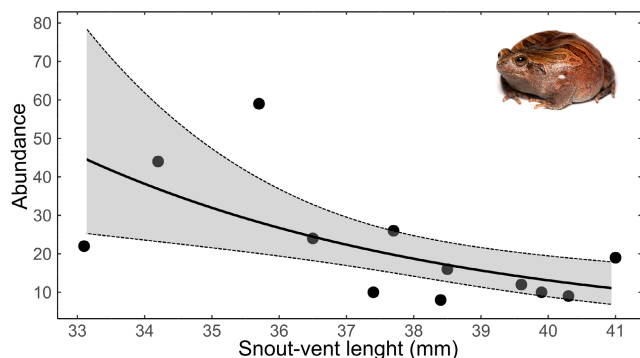
Abbreviations: SE: standard error; 95% CI: 95% confidence interval.

Note: Abbreviations of vegetation types as in Figure 1. We obtained 95% CI for each model nested in each SEM to look whether it included zero or not. Thus, point estimates obtained for each SEM (column Estimate) are not, necessarily, included in the 95% CI.

FIGURE 3 Relationship between snout–vent length (SVL) and abundance (count) of *P. nattereri* in our study site.

habitats (from grassy scrubland to cerrado woodland) and the importance of ephemeral ponds for reproduction.

As predicted, we recorded a very low number of recaptures, and most recaptures happened in the same sampling site. Thomé et al. (2021) marked over 1400 individuals of 13 species (including *P. nattereri*) in an area of Cerrado near our study site and yet did not record any recaptures. Thus, low recapture rates could be common among Cerrado frogs. Adult anurans are a major food resource for several vertebrate species, particularly snakes (Zipkin et al., 2020), and a large fraction of the snake community at SBES feeds on anurans (Fiorillo et al., 2021). Thus, high rates of predation on *P. nattereri* could help explain the observed low number of recaptures. Not a single individual captured during the first sampling year was recaptured in year 2, which could also indicate that *P. nattereri* has a relatively short lifespan and is functionally semelparous (see Hurme, 2015). Although the observed low number of recaptures in our study could widen confidence intervals of our models, our large sampling effort and our systematic and rigorous recapture assessments bring ecological realism to our results.

Only one individual was recaptured away from the initial capture site (about 500 m), after a relatively short period of time (19 days later). These findings may suggest that our focal species does not normally embark on long-distance dispersal. Even larger species than *P. nattereri*, which are thought to have larger home ranges (Miguet et al., 2016), may not disperse through long distances (e.g., *Leptodactylus labyrinthicus* is known to travel distances of up to 60 m in three days; Tozetti & Toledo, 2005). Moreover, being a habitat generalist species, *P. nattereri* can thrive in different environments, without the need to travel long distances. Conversely, recent studies using radiotelemetry show that the use of space by anurans can be highly variable and may encompass a larger area than previously thought (e.g., Henrique & Grant, 2019; Lemckert, 2004; Pitt et al., 2017). We suggest that future studies address the spatial ecology of *P. nattereri* through refined methodologies for the detection of dispersal such as radiotelemetry for a more ecologically realistic estimation of spatiotemporal habitat use by the species.

Vegetation types did not affect the abundance of *P. nattereri* in the study area. Our result looking at abundance vs. vegetation type agrees with those from Díaz-Ricaurte et al. (2020) in which this species is similarly abundant in open and nonopen Cerrado vegetation. The ability of *P. nattereri* to occupy open habitats (which would supposedly have higher temperatures and lead to a higher risk of desiccation) might be related to its burying behavior (burying in the soil allows for a rapid reduction of body temperature; Brasileiro et al., 2005; Díaz-Ricaurte et al., 2020; Giaretta & Facure, 2006; Pianka, 1986). Moreover, this species appears to be primarily nocturnal (e.g., Araujo et al., 2013; Brasileiro et al., 2005), which may contribute to avoid extreme daytime temperatures (Tozetti & Toledo, 2005), despite having a higher thermal tolerance compared with a sympatric species that is more associated to open areas in the Cerrado (*Physalaemus cuvieri*, Díaz-Ricaurte et al., 2020). Likewise, Díaz-Ricaurte et al. (2020) found that thermal tolerance of *P. nattereri* varies between day and night, suggesting that this species might still cool down slower than congeneric *P. cuvieri* when exposed to high temperatures, which might reflect its frequent use of cooler environments such as forests. Nevertheless, the difference in their daytime and nighttime thermal tolerance, and their implications on population dynamics deserves further investigation.

The ability of *P. nattereri* to occupy several vegetation types in the Cerrado and a higher site philopatry to *cerrado sensu stricto* may be a shared feature among anuran species at SBES. A recent unpublished study in the same area found a relatively higher abundance of terrestrial anurans in the *campo sujo* (~50% of all individuals captured through pitfall traps), whereas the *cerrado sensu stricto* had the second largest in number of captures (20% of all individuals), with 93% of all recorded species. This indicates that the *cerrado sensu stricto* might harbor a representative sample of the regional Cerrado amphibian diversity, but also reinforces the importance of maintaining the mosaic of native Cerrado vegetation types to buffer and preserve a high diversity of organisms (see Durigan et al., 2020).

Contrary to our hypothesis, the distance from ephemeral ponds did not seem to affect the abundance of *P. nattereri*. This may also be partially related to *P. nattereri*'s ability to avoid desiccation and behavioral adaptations (burying behavior, foam nests). Rodrigues et al. (2004) showed that the reproductive activity of *P. nattereri* is related to the wettest period of the year, and takes place in small temporary ponds, such as wildlife footprints. We observed choruses of a large number of individuals (N ~ 30), amplexus, and spawning in a nearby disturbed area outside SBES (unpaved road) after heavy rains. The formation of these puddles was unpredictable (any time during the wet season), and they drained quickly. Such features also suggest certain adaptability of the species for reproduction in nearby disturbed environments (see Richter-Boix et al., 2006).

Our results indicate that the abundance of *P. nattereri* was associated with its average SVL, where sites with larger individuals also had smaller population abundances. Márquez-García et al. (2009) examined life-history traits of *Rhinella spinulosa* in ponds with different desiccation regimes and found, respectively, positive and negative effects of desiccation rate on metamorphosis timing and the size of newly metamorphosed individuals. Richter-Boix et al. (2006) measured the duration of the metamorphosis and size
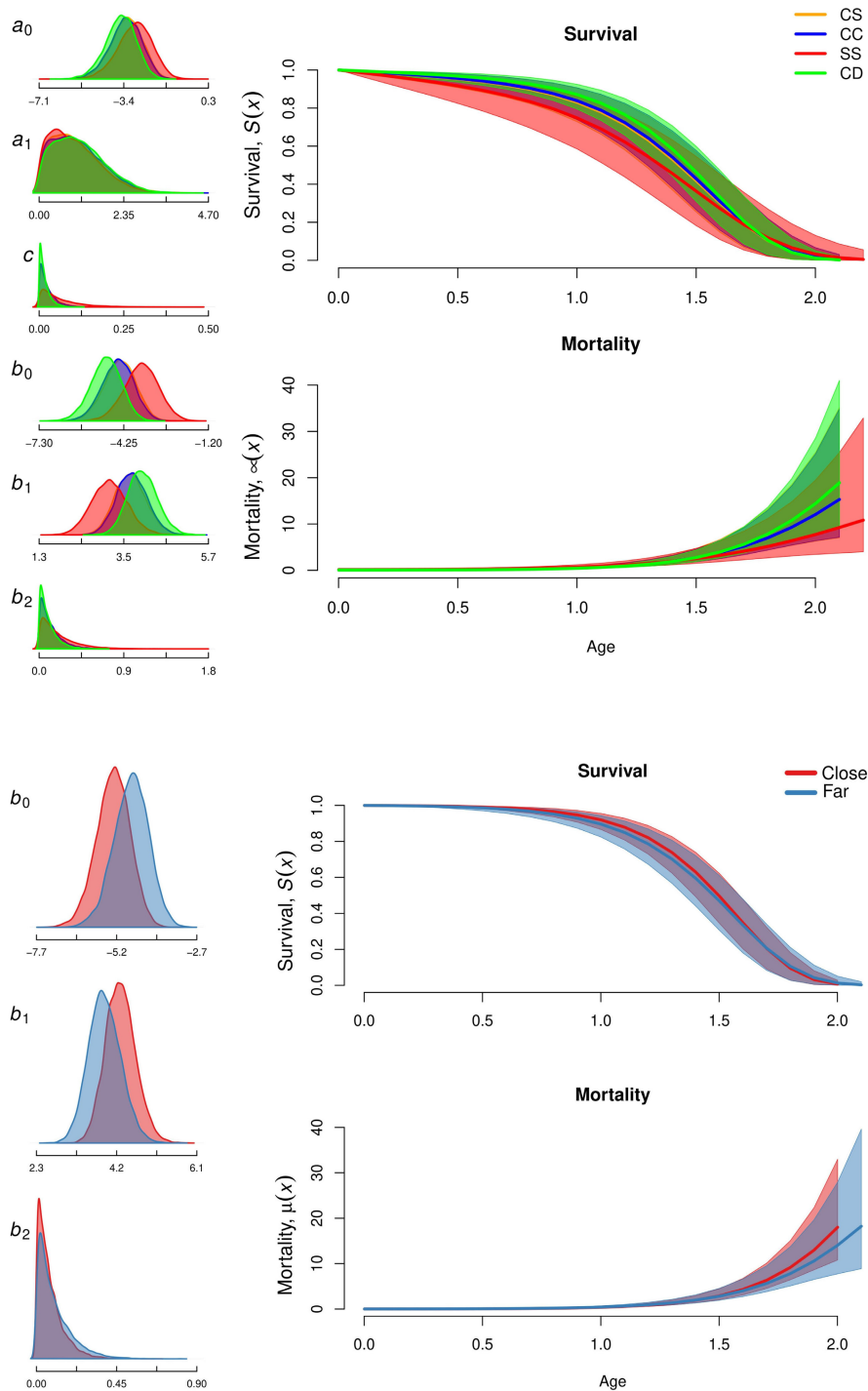
FIGURE 4 Age-specific mortality and survival trajectories for *P. nattereri* in each vegetation type (CC: *campo cerrado*; CS: *campo sujo*; SS: *cerrado sensu stricto*; CD: *cerradão*) and distance category from ephemeral pond (close: ≤400 m from water bodies; far: >400 m from ponds). Population-specific survival and mortality curves were estimated from the best-fitting model (vegetation types: logistic model with a bathtub shape; distance from ephemeral ponds: logistic model with a simple shape). The shaded areas surrounding the curves represent the 95% confidence intervals. Posterior distributions are shown for the model parameters in the left panels (see Table S3).

in anurans of different families and tested for differences in developmental plasticity using two treatments (constant water level and drying treatment) in the laboratory. This experiment showed that habitat generalists, which are usually associated with temporary ponds in the wild, showed greater plasticity (tended to reduce the larval period and had smaller newly metamorphosed individuals) than those commonly associated with constant and more predictable habitats. Given the high spatiotemporal stochasticity of ephemeral ponds, such a relationship (metamorphosis timing vs. metamorph size) could explain why abundance is inversely related

to body size in *P. nattereri*. Although we did not detect a significant effect of distance from ephemeral ponds on *P. nattereri* survival, our study only dealt with juvenile and adult stages, and the possible effects of this variable on the larval stage are still unknown. Besides survival, density dependence can also affect anuran development (e.g., Bardier et al., 2020; Harper & Semlitsch, 2007; Travis & Trexler, 1986). This might explain why *cerrado* sensu stricto (vegetation type with the lowest abundance; *N* = 36) not only had on average larger individuals, but also smaller estimated mortality rates than *cerradão* (highest abundance; *N* = 113). We are

TABLE 2 Values of the Kullback–Leibler divergence calibration (KLDC) obtained for *P. nattereri*.

	a0	a1	c	b0	b1	b2
CC-CS	0.5010	0.5003	0.5027	0.5033	0.5019	0.5000
SS-CS	0.5631	0.5015	0.8511	0.7926	0.7748	0.6743
SS-CC	0.5754	0.5032	0.8677	0.8224	0.8012	0.6699
CD-CS	0.5361	0.5028	0.6556	0.6632	0.6303	0.5403
CD-CC	0.5255	0.5012	0.6221	0.6291	0.6080	0.5432
CD-SS	0.6662	0.5084	0.9260	**0.9548**	**0.9348**	0.7996
Far-Close	–	–	–	0.7129	0.7019	0.5591

Note: This procedure compares parameter posterior distributions from the best-fitting model (logistic model with bathtub shape). Specifically, the values above a threshold (KLDC >0.85) indicate parameters that are substantially different between the four types of vegetation. Abbreviations of vegetation types as in Figure 1.

aware of the potentially confounding effect of sexual dimorphism on body size, although it is very likely that the vast majority of our captures corresponded to males (see Rodrigues et al., 2004). Still, the spatial variation in breeding sites by land cover type would not support differences in sex ratio among habitat types, because in the present study we showed that P. nattereri probably is not a long-distance traveler, and thus, it seems unlikely that males and females are separated by different landscapes.

Although *cerrado sensu stricto* and *cerradão* are relatively similar in terms of their environmental features (e.g., vegetation complexity, soil cover), we found that *cerrado sensu stricto* had significantly lower initial acceleration in estimated mortality rate than *cerradão*. These were the most contrasting recorded abundances (N = 36 individuals of P. nattereri in *cerrado* sensu stricto and N = 110 in *cerradão*), suggesting that survival of both adults and juveniles may be heavily controlled by density-dependent forces. Kissel et al. (2020) analyzed two populations of *Pseudacris maculata* and found a negative effect of population density on adult survival in the smaller one, suggesting that a larger population would have its growth rate decreased, thus contributing to keeping this population stable. As the *cerradão* had the largest metapopulation of SBES, it makes sense that, when compared to the smallest one (*cerrado sensu stricto*), there was a higher estimated mortality rate pushing this metapopulation to autoregulation.

Our results highlight that neither vegetation type nor proximity to ephemeral ponds affect habitat use by P. nattereri at SBES. Nonetheless, there is lower initial acceleration in estimated mortality rate in *cerrado sensu stricto* than in *cerradão*, suggesting that although abundance and individual body size are not directly affected by vegetation type, our findings indicate that these two variables should affect survival probabilities. The fact that metapopulations with individuals with smaller body size had higher average abundances also suggests that the use of ephemeral ponds (preferred by this species for reproduction) may reduce the time to metamorphosis without having a negative impact on population viability, which offers an opportunity for future experimental studies looking at ontogenetic development and growth of P. nattereri tadpoles. Our results help close an important knowledge gap in habitat use and

life-history adaptation in an ecologically important and iconic frog from the Brazilian Cerrado.

CONFLICT OF INTEREST STATEMENT
No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.m37pvmd6d (Fiorillo et al., 2023).

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SUPPORTING INFORMATION

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