INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

COMO FATORES AMBIENTAIS AFETAM A ABUNDÂNCIA E DISTRIBUIÇÃO DE DUAS ESPÉCIES DO MESMO GÊNERO DE RÃS DA AMAZÔNIA

ANTÔNIO EDUARDO SOARES MORENO

Manaus, Amazonas
Fevereiro, 2023

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de mestre em Biologia (Ecologia).

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ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 16 dias do mês de Setembro do ano de 2022, às 15h00min, por videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Igor Luis Kaefer**, da Universidade Federal do Amazonas – UFAM, o Dr. **Marcelo Gordo**, da Universidade Federal do Amazonas – UFAM e o Dr. **Mirco Solé Kienle**, da Universidade Estadual De Santa Cruz – UESC, tendo como suplentes o Dr. Rafael Filgueira Jorge, egresso do PPG-Ecologia do Instituto Nacional de Pesquisas da Amazônia – INPA e a Dra. Jussara Santos Dayrell, egressa do PPG-Ecologia do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do orientador, a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **ANTÔNIO EDUARDO SOARES MORENO**, intitulado: **"COMO FATORES AMBIENTAIS AFETAM A ABUNDÂNCIA E DISTRIBUIÇÃO DE DUAS ESPÉCIES DO MESMO GÊNERO DE RÃS DA AMAZÔNIA"**, orientado pelo Dr. William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia – INPA e co-orientado pelos Drs. Adrian Paul Ashton Barnett, do Instituto Nacional de Pesquisas da Amazônia – INPA e Miquéias Ferrão da Silva Junior, da Harvard University – Museum of Comparative Zoology.

Após a exposição, o discente foi arguido oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADO (A) ☐ REPROVADO (A)

☒ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

DR. IGOR LUIS KAEFER Igor Luis Kaefer

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DR. MIRCO SOLÉ KIENLE

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Sinopse:

Estudamos os efeitos de alguns gradientes ambientais sobre a abundância e distribuição de duas espécies de rãs da Amazônia ao longo da BR-319.

Palavras-chave: *Phyzelaphryne miriamae*, *Phyzelaphryne* sp., Simpatria, Anuros, Espécies Congenéricas, Heterogeneidade ambiental.

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RESUMO

Para testar a hipótese de que fatores ambientais podem atuar de maneiras diferentes na abundância e distribuição de espécies filogeneticamente relacionadas, amostramos duas espécies de anuros, *Phyzelaphryne miriamae* e *Phyzelaphryne* sp., ao longo de aproximadamente 600 km na Amazônia brasileira. A amostragem de dados foi realizada em 11 módulos de amostragem permanentes distribuídos ao longo de aproximadamente 600 km no Interflúvio Purús-Madeira entre 2013 e 2014. Usando modelos lineares generalizados mistos, descobrimos que as espécies podem ter associações ambientais distintas, o que pode estar permitindo que elas coexistam em simpatria. *Phyzelaphryne miriamae* foi mais frequente em ambientes com lençol freático profundo, características comuns a ambientes mais abertos, enquanto *P*. sp. não mostrou preferência por nenhuma variável ambiental avaliada. Devido ao seu maior tamanho corporal em relação a *P*. sp., *P. miriamae* pode ser mais resistente à desidratação e, portanto, capaz de ocupar ambientes mais secos. Nossos resultados estão de acordo com a ideia de que a evolução das características resultantes da seleção deve ter ocorrido de forma que a competição por recursos entre espécies próximas fosse reduzida, permitindo assim uma coexistência em simpatria.

ABSTRACT

To test the hypothesis that environmental factors would act in different ways on the abundance and distribution of phylogenetically related species, we sampled two anuran species, *Phyzelaphryne miriamae* and *Phyzelaphryne* sp., along approximately 600 km in the Brazilian Amazonia. Data sampling was carried out in 11 permanent sampling modules distributed along ~600 km in the Purús-Madeira Interfluve between 2013 and 2014. Using mixed generalized linear models, we found that the species have distinct environmental associations, which may be enabling them to coexist in sympatry. *Phyzelaphryne miriamae* was more frequent in environments with deep water-table, characteristics common to more open environments, while *P*. sp. showed no preference for any evaluated environmental variable. Due to its larger body size in respect to *P*. sp., *P. miriamae* may be more resistant to dehydration, and therefore able to occupy drier environments. Our results are in concordance with the idea that the evolution of characteristics resulting from selection must have occurred in a way that the competition for resources between closely related species was reduced, thus allowing a coexistence in sympatry.

SUMÁRIO

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Ferrão, M.; Lima, A. P.; Magnusson, W. E.

How environmental factors affect the abundance and distribution
of two congeneric species of Amazonian frogs.

Manuscrito em revisão: Biotropica

How environmental factors affect the abundance and distribution of two congeneric species of Amazonian frogs

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ABSTRACT

In this study, we test the hypothesis that, at a fine-scale, environmental variables influence differently sister-species that live in sympatry and are phylogenetically closely related. We sampled two Amazonian anuran species, *Phyzelaphryne miriamae* and *Phyzelaphryne* sp., in 11 permanent sampling modules distributed across ~600 km in the Purus-Madeira Interfluve between 2013 and 2014. Using mixed generalized linear models, we found that the species have distinct environmental associations, which may be enabling them to coexist in sympatry. *Phyzelaphryne miriamae* was more frequent in environments with low precipitation, suggesting this species is better adapted to live in drier places. In contrast, *Phyzelaphryne* sp. appeared to be a generalist regarding to habitat and resource use. These patterns are in accordance with the hypothesis that environmental variables influence sister-species differently on a fine-scale. It is possible that natural selection may favor individuals of *Phyzelaphryne miriamae* allowing them to use resources not used by the other species. *Phyzelaphryne miriamae* is larger than *Phyzelaphryne* sp., which may make it more resistant to dehydration, allowing it to explore drier environments. In conclusion, our results are in concordance with the hypothesis that the evolution of characteristics resulting from selection must have occurred in a way that the competition for resources between closely related species was reduced, thus allowing a coexistence in sympatry.

Keywords: anurans, congeneric species, environmental heterogeneity, *Phyzelaphryne miriamae*, *Phyzelaphryne* sp., sympatry.

INTRODUCTION

It is commonly expected that the closer species are phylogenetically, the more similar are their environmental requirements (Darwin 1859, Inger & Greenberg, 1966). Such needs can, in many cases, make the individuals of these species compete for the limiting resources (Utida 1953, Duré & Kehr 2004, Luiselli 2006). The stronger the competition, the less likely these species will co-occur in the same environment, leading to the exclusion by competition of one or more species that are less efficient in using and obtaining resources (Lotka, 1934; Zaret & Rand, 1971). However, if resources are not limiting, species with similar requirements may co-occur in the same area (Levine & HilleRisLambers 2009, Palomares *et al.* 2016).

On a finer scale, it is common to presume that competition will make congeneric species unable to coexist in the same places (e.g. Duré & Kehr 2004). However, due to evolutionary factors that may shape the needs of each species in different ways, this pattern of competition may not be found in all groups, thus enabling the coexistence of closely related species (Pianka 1974, Menin *et al.* 2005, Corrêa Nogueira *et al.* 2019). For example, at local scales, the influence of soil clay content on anuran abundance differs between two closely-related species of anurans with direct reproduction, being positive in the semi-arboreal *Pristimantis fenestratus* and negative in the arboreal *P. ockendeni* (Menin *et al.* 2007). However, how environmental factors influence on the distribution and abundance of most sympatric closely-related species of Amazonian frogs remains unknown, especially for those with terrestrial habits.

The heterogeneous landscape of the Purus-Madeira Interfluve (PMI) is ideal for evaluating the role of environmental factors on the abundance of sympatric Amazonian congeneric species. Its northern portion is covered by tropical lowland rainforest with emergent canopy over silty soils and has less seasonal temperature and a shorter dry season than the southern portion, which is covered mainly by more open rainforest with abundant palms over clayey soils, and has strongly seasonal temperatures and a prolonged dry season (IBGE 1997, Emilio 2007, Cintra *et al.* 2013, Martins *et al.* 2014).

The interfluve harbors the sister species *Phyzelaphryne miriamae* and *Phyzelaphryne* sp., both of which have wide distributions in the interfluve, and inhabit leaf litter of unflooded forests in the PMI. As with other Amazonian anurans (Jorge *et al.* 2016), they could respond in different ways to small differences in essential factors for their survival.

In this study, we show that *Phyzelaphryne miriamae* and *Phyzelaphryne.* sp. tended to be associated with different environmental conditions (i.e. divergences in habitat and resource use), which can lead to a reduction in the competition and allow them to occur in the same locations.

METHODS

Study species

Phyzelaphryne miriamae (Figure 1A) has a wide distribution in the Amazon (Fouquet *et al.* 2012, Simões *et al.* 2018), and is commonly found in the litter of primary forests and in different degrees of disturbance, including regrowth. The species reaches approximately 20 mm in length, males are territorial and vocalize mainly between 18:00 and 20:00 on decaying logs or litter clusters. *Phyzelaphryne* sp. (Figure 1B) is an undescribed species measuring approximately 15 mm, and its distribution in the Amazon appears to be more restricted than that of *P. miriamae* (Fouquet et al., 2012). The species occurs along the entire PMI and adjacent areas, where it was observed vocalizing in the litter early in the morning (5:00–9:00) and the late afternoon (16:00–18:00). Reproductive activity occurs in the rainy season. Females of both species lay their directdeveloping eggs in wet leaf litter; the embryos develop completely inside the eggs without a free-living aquatic stage. Details about their natural history are based on field observations by A. P. Lima and M. Ferrão, authors of the present study.

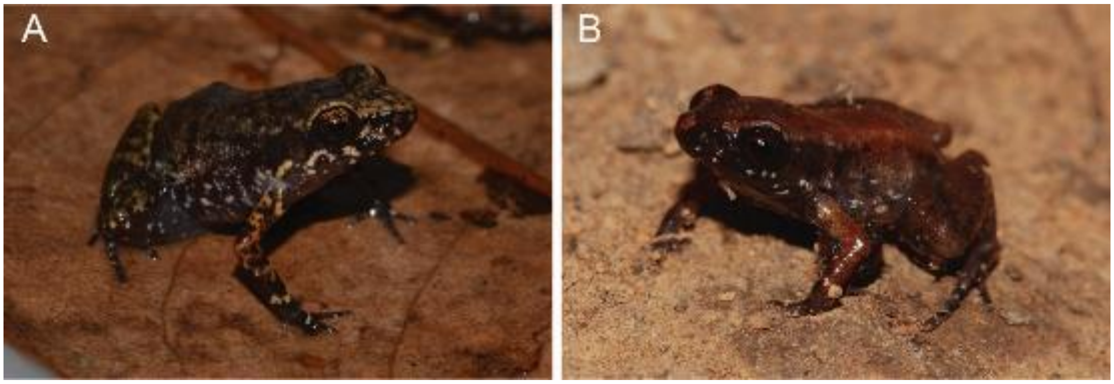

Figure 1. Adult males of *Phyzelaphryne miriamae* (A) and *Phyzelaphryne* sp. (B), Purus-Madeira Interfluve, Brazil.

Study area and sample design

The PMI is bounded to the north by the Amazon River, to the west by the Purus River and to the east by the Madeira River, and covers approximately 15.4 million hectares (Fearnside *et al.* 2009, Figure 2). The water table is predominantly shallow (Schietti *et al.* 2016). Soils are mainly gleisols and plinthsols, characterized by poor drainage and predominantly consist of silt and clay (Cintra *et al.* 2013, Martins *et al.* 2014). In the northern portion of the IPM, tropical lowland rainforest with emergent canopy predominates, while in the southern portion there is predominance of open rainforest lowlands with palms (Emilio 2007). Average annual rainfall varies from 2,800 mm in the northern portion to 2,100 mm in the south (Alvares *et al.* 2013, Fick & Hijmans 2017). On a regional scale, the topography is flat and the elevation varies from 27 m above sea level in the north to 80 m in the south.

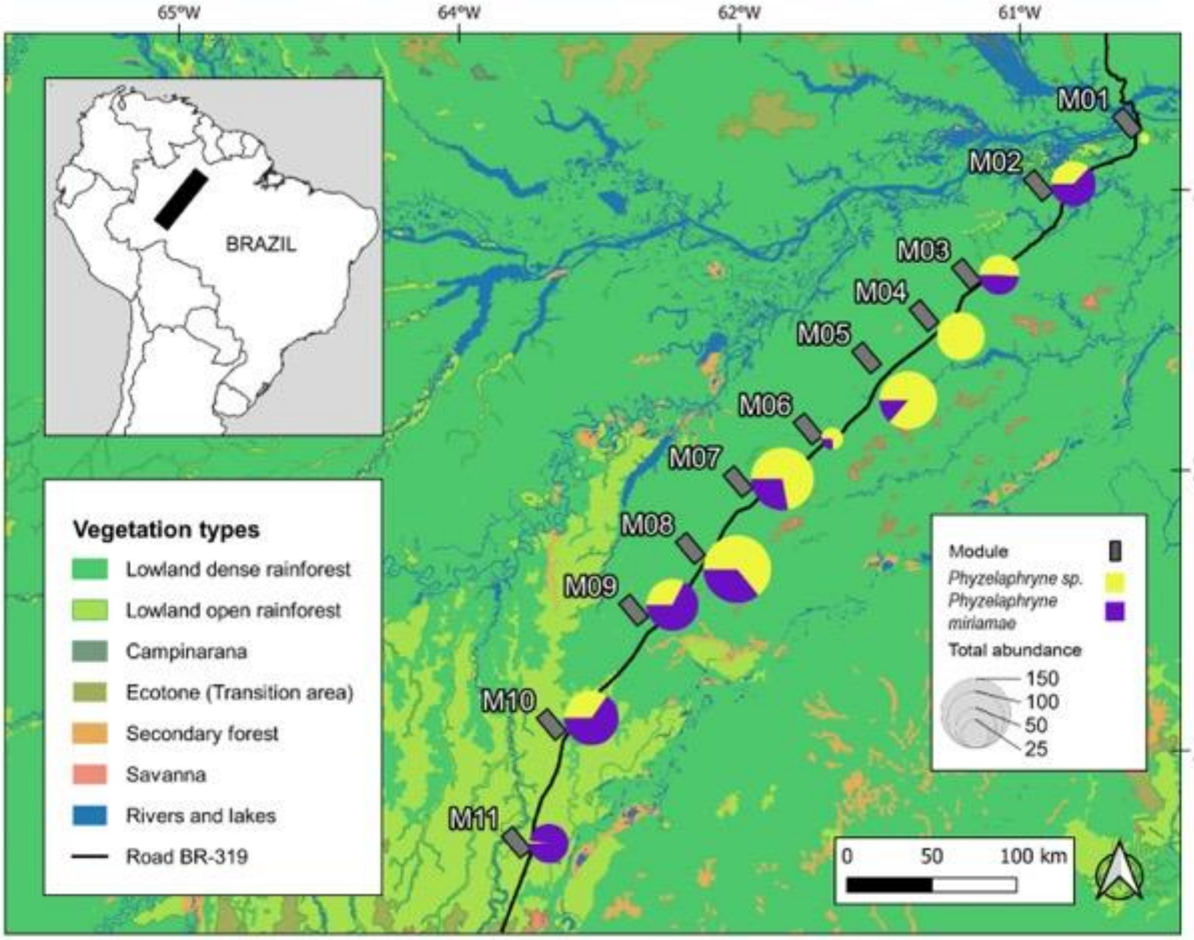

Figure 2. Distribution and relative abundance of *Phyzelaphryne miriamae* and *Phyzelaphryne* sp. in 11 permanent sampling modules (M1–M11) in the Purus-Madeira Interfluve. (More information about sample sites and design in BR-319 is available in https://ppbio.inpa.gov.br/en/Sites/BR319).

Data were collected in 11 RAPELD permanent sampling modules (Magnusson et al., 2013) distributed along approximately 600 km in the MPI. Modules are located approximately every ~60 km along the BR-319, a federal highway that run through the interfluve from north to south. They are positioned perpendicular to the highway and have two parallel tracks of 5 km long separated by 1 km. A 250 m long plot is distributed every 1 km along each trail (Figure S1), totaling 5 plots per track and 10 plots per module. Sampling of focal species was carried out in the rainy seasons (October–March) of 2013 and 2014 through auditory and visual sampling during their afternoon activity period (16–19h). Plots were sampled once in each of two field campaigns.

Environmental variables

To investigate the role of the environment on the distribution and abundance of *Phyzelaphryne miriamae* and *Phyzelaphryne* sp., we sampled four groups of environmental variables: (1) Soil physical parameters (clay and silt content), which were selected for retaining more moisture than sandy soils (Juo SR & Franzluebbers 2003), considering that both species lay eggs in the litter that is in constant contact with the soil, and soil characteristics often influence the abundance of Amazonian anurans (e.g. Menin *et al.* 2007, Ferrão *et al.* 2018, Ferreira *et al.* 2018). (2) Forest structure (using basal area data as a proxy), selected because it is related to the entry of light, heat and wind inside the forest, which may influence the incidence of sunlight and air circulation in the surface layer of the litter, affecting the hydration capacity of frogs and their eggs; an example of how forest structure influences anuran abundance is given in Ferreira *et al.* 2018. (3) Depth of water table, selected because, although they are animals sensitive to dehydration, terrestrial frogs need ideal conditions for the development of their eggs, and a very shallow water table can result in saturation and waterlogging, impairing embryo development (Greenberg *et al.* 2017, Dayrell *et al.* 2021). (4) Average annual precipitation, which is also related to water availability. The first three variables were collected in situ, and precipitation data were obtained from the WorldClim database (Fick & Hijmans 2017) using ~1 km^2 resolution.

Soil samples were collected with an auger to a depth of 10 cm every 50 m along the central transect of each plot, giving six samples per plot. After collection, the samples were kept in sealed plastic bags for 2 to 5 days, dried at room temperature and later mixed to form a composite sample for each plot (Cintra *et al.* 2013). Applying a standard total dispersion protocol (Donagema *et al.* 2011), the percentage of sand in the soil was estimated using a sieve with a mesh size of 0.053 mm, that of clay was determined by isolating 20 mm particles from other smaller particles, and proportion of silt was determined by the difference from clay plus sand values.

The forest structure was represented by the total basal area of trees and palms (Schietti *et al.* 2016) sampled in three size classes: (1) in a strip (on the left side of the central line) of 250 x 1 m (~0.025 ha), counting all stems with diameter at breast height (DBH) ≥ 1 cm; (2) in a strip 250 x 20 m (~0.5 ha), counting all stems with DBH ≥ 10 cm; and (3) in a strip 250 x 40 m (~one ha), counting all stems with DBH ≥ 30 cm (Magnusson *et al.* 2005).

Water-table depth was measured during the months of March, July and November of 2011, March, August, October and December of 2012 and March of 2013. The mean of the seven measurements for was used to represent the depth of the water table in that plot. Positive water-table depth indicates that the water level was above ground.

Data analyses

To investigate the variation in the relative abundance of the two species along environmental gradients, we used Generalized Linear Mixed Models (GLMMs). In each model, the relative abundance of the species was modeled in relation to the abundance of its congeneric species (indicator of potential biotic interaction) and to environmental factors (clay, silt, precipitation, basal area and water table depth) as fixed factors and module as a random factor to take into account the non-independence between samples (Zuur *et al.* 2009). We excluded from the analysis the plots for which we did not have data on all environmental variables, and we assumed that species abundances (counts per plot) followed a negative binomial distribution. To avoid multicoleneariy in our models, we checked the variance inflation factor (VIF); and the Pearson´s correlation. There was no significant multicollinearity (Table S1 and S2).

As the number of individuals recorded was low in most plots, we used the sum of individuals recorded in the two campaigns to represent the relative abundance of *Phyzelaphryne miriamae* and *Phyzelaphryne* sp. in each plot. Statistical analyses were undertaken in the R 4.0.5 statistical platform (R Core Team, 2021). To build the model, we used the "lme4" package (Bates *et al.* 2015). Maps were produced with QGis (QGIS Development Team, 2022).

RESULTS

The *Phyzelaphryne* species were associated with different environmental conditions, in accordance with the hypothesis that environmental variables influence sister-species differently at a fine-scale. The abundance of *Phyzelaphryne miriamae* was negatively associated with precipitation (Figure 3, b = - 0.97, P = 0.0009), and there was evidence of a positive relationship with deeper water tables (Figure S1, b = -0.56, P = 0.064); suggesting that this species tends to be found in places that do not flood in drier areas (the relationships with other environmental variables are shown in Figure S1). In contrast, *Phyzelaphryne* sp. appeared to be a generalist regarding to habitat and resource use; its abundance was not related to any of the environmental characteristics used in our analyses (Table 1 and Figure S2).

Table 1. Summary of Generalized Mixed Linear Models examining the effects of environmental variables and the relative abundance of one species on the relative abundance of the other.

Predictors	**Abundance of *Phyzelaphryne* sp.**			**Abundance of *Phyzelaphryne miriamae***		
	Estimates	SE	P	Estimates	SE	P
Abundance of *Phyzelaphryne miriamae*	0.006	0.02	0.761	***	***	***
Abundance of *Phyzelaphryne* sp.	***	***	***	-0.02	0.02	0.3488
Water table level	-0.,02	0.25	0.933	-0.56	0.31	0.0674
Precipitation	0.24	0.37	0.509	**-0.97**	**0.29**	**0.0009**
Clay content	0.02	0.26	0.928	0.02	0.37	0.9544
Silt content	-0.22	0.26	0.401	-0.04	0.28	0.8686
Tree basal area	0.38	0.33	0.249	0.47	0.29	0.1105
Variance explained by the entire model	$R^2 = 0.48$			$R^2 = 0.37$		

Abbreviation: *SE*, standard error; and P, probability value

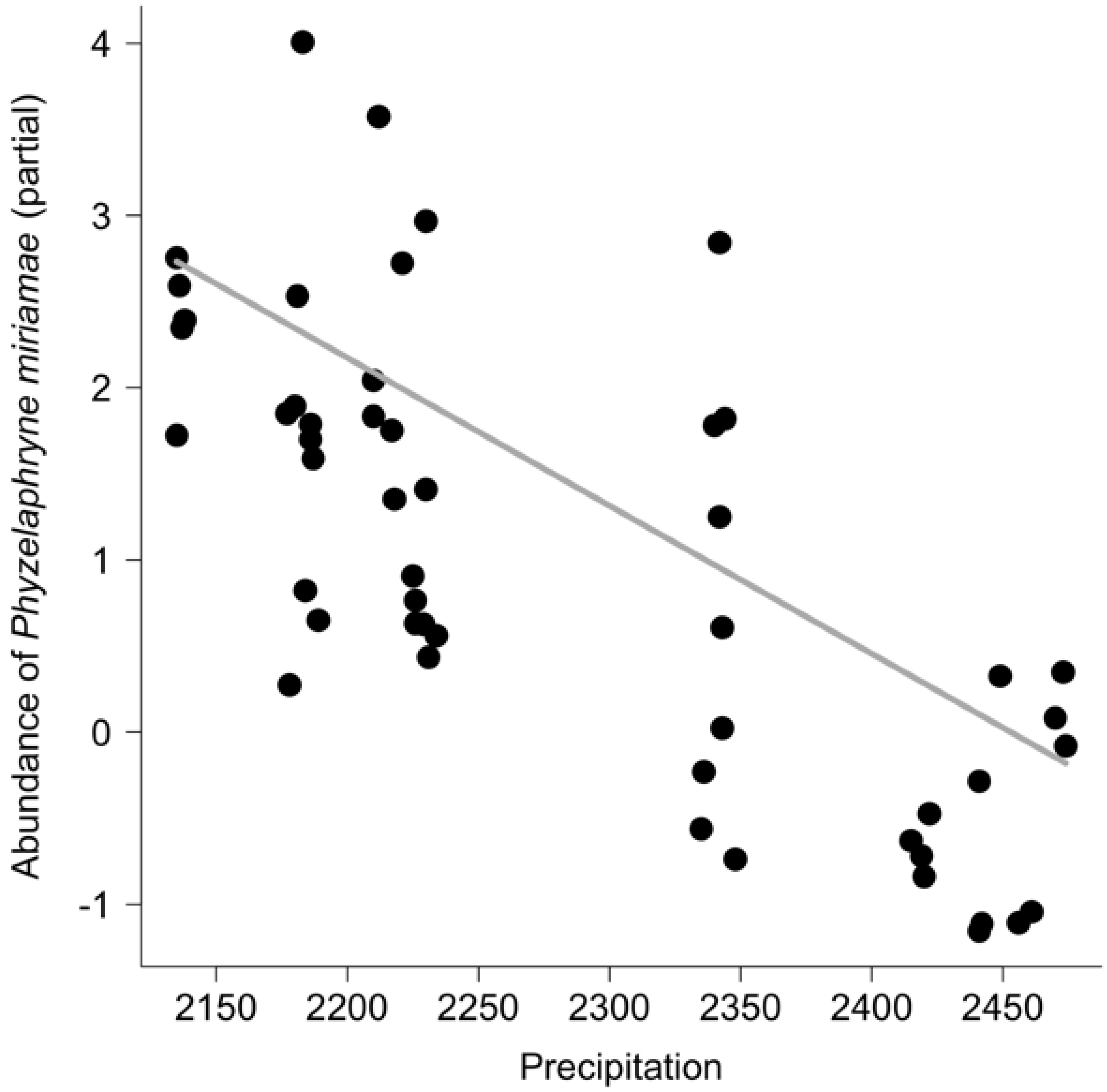

Figure 3. Graphs showing the direct effects of precipitation on the abundance of *Phyzelaphryne miriamae* along the Purus-Madeira Interfluve. The Y-axis shows partial residuals to control for remaining predictors. Each point represents one sampling plot. The line represents model predictions.

DISCUSSION

Due to similarities in resource use, competition is expected to be greater between phylogenetically close species and that this process will lead to congeneric species generally not occurring in sympatry ((Webb *et al.* 2002, Violle *et al.* 2011). However, some studies have questioned this pre-established pattern, showing that in some groups, closely related species occur in sympatry (Zainudin *et al.* 2017, Moser *et al.* 2018, Gambale *et al.* 2020). Although niche overlap increases interspecific competition, competitive exclusion depends on species differences in fitness-related traits (HilleRisLambers *et al*. 2012, Letten *et al*. 2017), and niche-related and fitness-related traits may not depend strongly on phylogenetic relatedness (Godoy *et al*. 2014).

Phyzelaphryne miriamae and *Phyzelaphryne* sp. are phylogenetically close relatives (Fouquet *et al.*, 2012) and often occur syntopically; on average, they differ in their responses to environmental variables, which indicates divergence in habitat and resource use. The differences between the two species that allow them to occur in the same locations and to explore different resources, may be due to ecological character displacement (Slatkin 1980). Due to this mechanism, the evolution of characteristics resulting from selection may have occurred to reduce competition for resources between species, thus acting on characteristics associated with resource use (Simberloff *et al.* 2000, Komine *et al.* 2019, Nakano *et al.* 2020). These patterns are qualitatively similar to other anuran species studies on a fine scale. For example, stream water discharge in the forests positively influences the abundance of the terrestrial *Atelopus manauensis* but negatively *Allobates sumtuosus* (Jorge *et al.*, 2016). Soil silt content in the Purus-Madeira Interfluve positively influences the distribution and abundance of the *Scinax* *ruberoculatus*, but has a negative effect on the abundance of *Allobates femoralis* (Ferreira *et al.*, 2018).

In this context, it is possible that natural selection may favor individuals of *Phyzelaphryne miriamae* with traits that allowed them to use that resource not used by another species (Simberloff *et al.* 2000, Komine *et al.* 2019, Nakano *et al.* 2020). *Phyzelaphryne miriamae* is larger than *Phyzelaphryne* sp., which may make it more resistant to dehydration, allowing it to exploit drier environments (Van Berkum *et al.* 1982, Chown & Gaston 1999, McKechnie & Wolf 2010). However, this species is less abundant in areas with high rainfall and in locations subject to waterlogging and flooding.

Other factors may be involved in the co-occurrence of the two species. For example, males of both species call during twilight, but those of *Phyzelaphryne miriamae* call more frequently between 18:00 and 20:00 hours and generally exposed on perches on the ground, whereas males of *Phyzelaphryne* sp. call hidden within the leaf litter, and more frequently from early in the morning (5:00–9:00) and mid-afternoon to early twilight (16:00–18:00). Preference for different times for vocalization is a fundamental factor to avoid unfavorable acoustic overlap between species of frogs (Krause 1993, Santos Protázio *et al.* 2015).

In conclusion, despite being closely related phylogenetically and having broadly overlapping distributions, *Phyzelaphryne miriamae* and *Phyzelaphryne* sp. differ in their responses to environmental characteristics, which may explain the lack of evidence of competitive exclusion. Although the species differ in their degree of response to environmental variables, they are frequently found in the same plots. While competition theory predicts that one of two competing species will be eliminated in the long term, populations are finite and environmental and demographic conditions change regularly, so that species may co-occur in some locations for a long time despite their coexistence being unstable (Schreiber *et al*. 2023), or they may segregate spatially due to ecological drift and/or dispersal rather than competitive exclusion (Hubbell 2002, Vellend 2016).

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTION STATEMENT

Eduardo Moreno: Conceptualization, Data curation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Pedro Pequeno:** Formal analysis, Writing - original draft, Writing – review & editing. **Sergio Santorelli Junior:** Formal analysis, Writing - original draft, Writing – review & editing. **Miquéias Ferrão:** Conceptualization, Data acquisition, Data curation, Investigation, Writing - original draft, Writing – review & editing, Cosupervision. **Albertina Pimentel Lima:** Conceptualization, Funding Acquisition, Methodology, Resources, Investigation, Writing – review & editing. **William E. Magnusson:** Conceptualization, Methodology, Formal Analysis, Resources, Investigation, Writing – original draft, Writing – review & editing, Supervision, Funding Acquisition. All authors contributed critically to the drafts and gave final approval for publication.

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