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ORIGINAL ARTICLE

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 facilitate their coexistence in sympatry. *Phyzelaphryne miriamae* was more frequent in environments with low precipitation and low water tables, 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. *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 may have reduced competition for resources between closely related species, thus facilitating coexistence in sympatry.

Abstract in Portuguese is available with online material.

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

1 | 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 (Duré & Kehr, 2004; Luiselli, 2006; Utida, 1953). 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 (Corrêa Nogueira et al., 2019; Menin et al., 2005; Pianka, 1974). 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 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 (Cintra et al., 2013; Emilio, 2007; IBGE, 1997; Martins et al., 2014).

The sister species *Phyzelaphryne miriamae* and *Phyzelaphryne* sp. have wide distributions along the Purus-Madeira Interfluve and inhabit leaf litter of unflooded forests in this region. To test whether environmental factors influence these species differently, we examined whether the abundance distributions of these sister species respond differently to minor variations in soil, vegetation, and precipitation variables (e.g., Jorge et al., 2016). We also investigated whether this response is independent of the presence of a sister species. Our results showed that only *Phyzelaphryne miriamae* tended to be associated with different levels of precipitation (i.e., divergences in habitat). This suggest that, at a finer scales, a species' response to environmental factors could enable congeneric species to co-occur in the same locations. While such differences would not avoid competition at locations, sites with higher precipitation and shallower water tables could provide a refuge for the smaller species and enable them to co-occur in the region.

2 | METHODS

2.1 | 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 with different degrees of disturbance, including regrowth. The species reaches approximately 20 mm in snout-urostyle length, and 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 Purus-Madeira Interfluve 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 direct-developing 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.

2.2 | Study area and sample design

The Purus-Madeira Interfluve (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 PMI, 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 2800 mm in the northern portion to 2100 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.

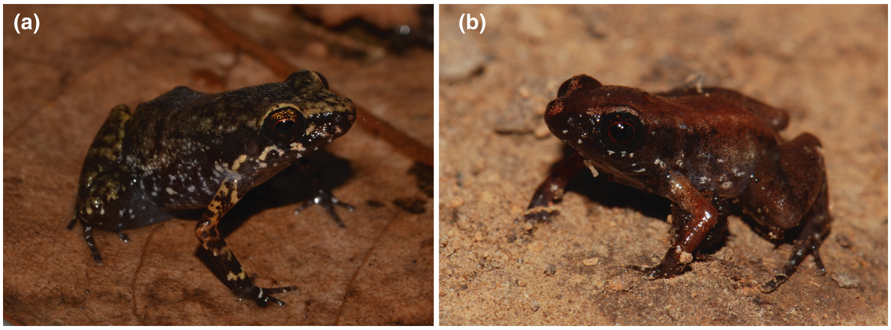

FIGURE 1 Adult males of *Phyzelaphryne miriamae* (a) and *Phyzelaphryne* sp. (b), Purus-Madeira Interfluve, Brazil. The *Phyzelaphryne miriamae*'s photograph is credited to Rafael de Fraga.

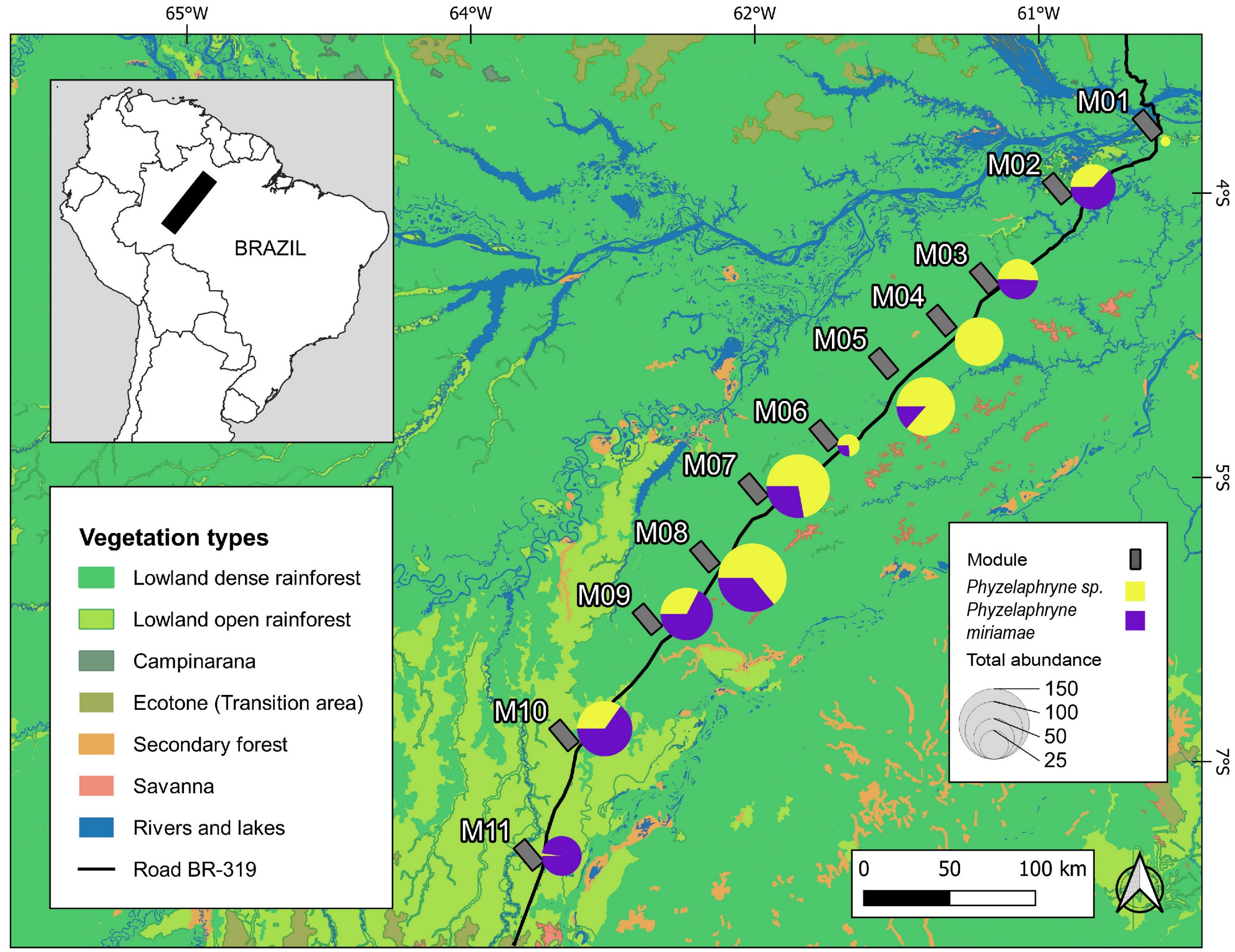

FIGURE 2 Distributions and abundances of *Phyzelaphryne miriamae* and *Phyzelaphryne* sp. in 11 permanent sampling modules (M1–M11) in the Purus-Madeira Interfluve (More information about sample sites and design in BR-319 is available in https://ppbio.inpa.gov.br/en/Sites/BR319).

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 runs through the interfluve from north to south. They are positioned perpendicular to the highway and have two parallel 5-km tracks of separated by 1 km. A 250 m long plot is located every 1 km along each trail (Figure S1), totaling 5 plots per track and 10 plots per module. Sampling of the 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 (16–19 h). Plots were sampled once in each of two field campaigns.

Frogs were detected by visual and auditory surveys, but almost all detections of the focal species in this study were by auditory cues, which are much less affected by vegetation clutter than visual records. Each 250-m plot was divided in 10-m segments, and the presence or absence of the species was recorded in each segment, giving an abundance index varying from 0 to 25.

2.3 | 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 & 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., Ferrão et al., 2018; Ferreira et al., 2018; Menin et al., 2007). (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 (Dayrell et al., 2021; Greenberg et al., 2017). (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 × 1 m (~0.025 ha), counting all stems with diameter at breast height (DBH) ≥1 cm; (2) in a strip 250 × 20 m (~0.5 ha), counting all stems with DBH ≥10 cm; and (3) in a strip 250 × 40 m (~1 ha), counting all stems with DBH ≥30 cm (Magnusson et al., 2005).

Water table depth in each plot was based on the mean of seven measurements of distance to free water from the surface 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 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.

2.4 | Data analyses

To investigate the variation in the indices of abundance of the two species along environmental gradients, we used generalized linear mixed models (GLMMs). In each model, the 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 of 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 counts per plot followed a negative binomial distribution. The sample size used for this analysis consisted of 51 sample units, each of which represents a 250-m plot located at 1 km intervals along a 5-km trail extending perpendicularly from the highway. To avoid multicollinearity in our models, we checked the variance inflation factor (VIF) and the Pearson's correlation. There was no significant multicollinearity (Tables S1 and S2).

As the number of segments with a species was low in most plots, we used the sum of records in the two campaigns to represent the abundances of the species in each plot. This enabled us to use a negative binomial distribution in analyses, which would not have been possible with the mean. Individual counts for each sampling occasion are given in Table S3 of Data S1. 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).

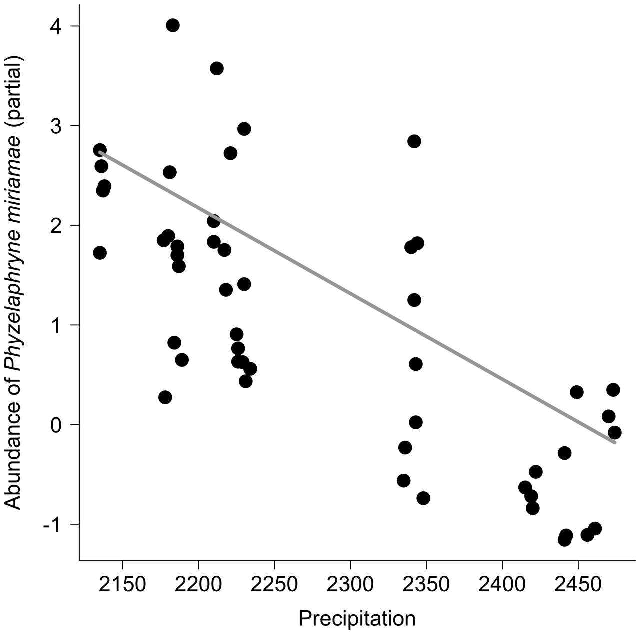

FIGURE 3 Graphs showing the direct effects of precipitation on the abundance of *Phyzelaphryne miriamae* along the Purus-Madeira Interfluve. The *y*-axis shows partial residuals to control for remaining predictors. Each point represents one sampling plot. The line represents model predictions.

3 | 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, $p = .0009$), and there was evidence of a positive relationship with deeper water tables (Figure S1, b = −0.56, $p = .064$), 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 habitat; its abundance was not related to any of the environmental characteristics used in our analyses (Table 1 and Figure S2).

4 | DISCUSSION

Due to similarities in resource use, competition is expected to be greater between phylogenetically close species and that this process

TABLE 1 Summary of generalized mixed linear models examining the effects of environmental variables and the abundance indices of one species on the abundance index of the other (sample size = 51).

	Abundance of *Phyzelaphryne* sp.			Abundance of *Phyzelaphryne miriamae*		
Predictors	**Estimates**	***SE***	***p***	**Estimates**	***SE***	***p***
Abundance of *Phyzelaphryne miriamae*	0.006	0.02	.761	***	***	***
Abundance of *Phyzelaphryne* sp.	***	***	***	−0.02	0.02	.3488
Water table level	−0.02	0.25	.933	**−0.56**	**0.31**	**.0674**
Precipitation	0.24	0.37	.509	**−0.97**	**0.29**	**.0009**
Clay content	0.02	0.26	.928	0.02	0.37	.9544
Silt content	−0.22	0.26	.401	−0.04	0.28	.8686
Tree basal area	0.38	0.33	.249	0.47	0.29	.1105
Variance explained by the entire model	$R^2 = 0.48$			$R^2 = 0.37$		

Bold values within the table highlight the most important variables in the models.

Abbreviation: *SE*, standard error; and *p*, probability value.

will lead to congeneric species generally not occurring in sympatry (Violle et al., 2011; Webb et al., 2002). However, some studies have questioned this prediction, showing that in some groups, closely related species occur in sympatry (Gambale et al., 2020; Moser et al., 2018; Zainudin et al., 2017). 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, only *Phyzelaphryne miriamae* responded to environmental variables we tested, which indicates association with precipitation. Although our data and tests do not directly address this issue, the association of *Phyzelaphryne miriamae* with places with low precipitation and deep-water tables (i.e., dry conditions) means that it is less common in wetter places than *Phyzelaphryne* sp. Although we can only speculate, ecological character displacement (Slatkin, 1980) may have contributed to the tolerance of *Phyzelaphryne* sp. to these conditions. Other sympatric anurans also show differences in use of environmental gradients 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* (Ferrão et al., 2018), 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* sp. with traits that allowed them to exploit environments not used by *Phyzelaphryne miriamae* as has been suggested for other taxa (Komine et al., 2019; Nakano et al., 2020; Simberloff et al., 2000). *Phyzelaphryne miriamae* is larger than *Phyzelaphryne* sp., which may make it more resistant to dehydration, allowing it to exploit drier environments (Chown & Gaston, 1999; McKechnie & Wolf, 2010; Van Berkum et al., 1982). 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, there is evidence of males of both species calling 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 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), but the strong overlap between the two species and the lack of a negative relationship between the abundances of them after taking into account the environmental variables do not support this hypothesis.

In conclusion, despite being closely related phylogenetically and having broadly overlapping distributions, *Phyzelaphryne miriamae* responded to environmental characteristics, which may explain the lack of evidence of a negative relationship with the abundance indices of the *Phyzelaphryne* sp. 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), especially if wider tolerance for environmental conditions provides a refuge for the weaker competitor, or they may segregate spatially due to ecological drift and/or dispersal rather than competitive exclusion (Hubbell, 2001; Vellend, 2016).

AUTHOR CONTRIBUTIONS

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, Co-supervision. **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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CONFLICT OF INTEREST STATEMENT

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.

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.w0vt4b8zc

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