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The effects of morphology, phylogeny and prey availability on trophic resource partitioning in an anuran community

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Abstract

Several factors influence the partitioning of trophic resources in ecological communities, such as morphology, evolutionary history, and resource availability. Although the effects of morphology, phylogeny, and resource availability on trophic ecology have long been explored by theoretical studies, little has been done to empirically test these relationships. Here, we tested whether phylogenetic and morphological distances correlate with trophic niche overlap using a path analysis of multiple partial regression of distance matrices. Also, we tested whether niche breadth is influenced by body size using Phylogenetic Generalized Least Squares analysis. Trophic niche overlap was better explained by morphology *per se* than by the phylogenetic distance. We also found that predator's body size influences niche breadth calculated considering prey traits and availability, but not when we do not include these availability data. Additionally, trophic niche breadth was usually smaller when we considered prey traits and availability, differently from niche overlap, whose values increased when we did not consider these data. Our findings show that the interpretation of trophic niche in communities changes if we consider availability data, affecting inferences about coexistence and trophic specialization. Our study contributes to understanding trophic specialization and emphasizes the importance of incorporating prey availability and their traits into diet analysis.

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Keywords: Niche overlap; Niche breadth; Consumer-resource interaction; Trophic ecology; Phylogenetic signal; Contemporary niche theory

Introduction

The diet of animals is usually associated with their morphological, physiological, and behavioral characteristics that influence the location, identification, capture, ingestion, and digestion of prey (Román-Palacios, Scholl & Wiens, 2019; Solé & Rödder, 2010). Morphology is a strong constraint of the diet of individuals, especially in size-limited predators (Wilbur, 1988). Size-limited predators are unable to capture prey larger than a critical body size, due to the failure to subdue prey (Costa-Pereira, Araújo, Olivier, Souza & Rudolf,

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2018). Thus, body size can play a key role in determining niche breadth and overlap of species (Woodward & Hildrew, 2002). Additionally, morphological differences between species can scale up to affect the partitioning of available resources in a community (Albertson, 2008), being a key factor to explain the relationship between organisms and the trophic resources they use (Ricklefs & Miles, 1994).

A given trait exhibits phylogenetic signal when closely related species are more similar to each other, than with species taken randomly in the phylogeny (Blomberg & Garland, 2002). When ecological relationships (e.g., climatic tolerances, density-dependent interactions) are determined by phenotypic traits (e.g., morphology) that are themselves conserved phylogenetically, closely related species tend to be ecologically similar (Pyron, Costa, Patten & Burbrink, 2015; Wiens et al., 2010). Community ecologists have increasingly used phylogenetic relationships to investigate ecological differences between species (reviewed in Swenson, 2019). Although linking morphology, phylogeny, and diet has been a subject of long-term interest in community ecology, few studies have tested empirically whether morphologically similar species have similar diets while controlling for phylogeny. Thus, using the phylogenetic relationships of species allows one to make inferences about processes involved in community assembly and dynamics (reviewed in Swenson, 2019), such as resource partitioning.

Resource availability plays a key role in classical theories of species diversity and resource partitioning (Tilman, 1980). However, few empirical studies include resource availability in diet analyses. In addition, previous studies often considered all prey equally similar in terms of their vulnerability to predators (De Cáceres, Sol, Lapiedra & Legendre, 2011). However, not all prey available in the environment are actually consumed due to differences in life history traits (e.g., presence of spines or a hard cuticle). As a result, predators may perceive prey with distinct traits differently (Colwell & Futuyma, 1971). Prey traits and their nutritional quality can affect handling time and determine prey choice by predators (Costa-Pereira et al., 2018). For example, frogs may perceive ants and termites as more similar to each other due to eusocial habits and high local abundance (Ceron et al., 2019), which can allow the intake of several individuals at the same time. Thus, niche indexes that do not consider this information can be biased by the subjectivity of taxonomic classification of resource categories (De Cáceres et al., 2011; Wilcox, Schwartz & Lowe, 2018). Conversely, prey availability is commonly confused with the amount of prey, but prey traits can be more important in determining their actual availability, especially when predators are size-limited (Costa-Pereira et al., 2018; Gawlik, 2002). Consequently, it is necessary to incorporate the functional and morphological aspects of prey that determine their vulnerability and nutritional content to understand if predators are responding to changes in either prey density *per se* or prey characteristics.

Here, we tested the direct and indirect effects of morphology and evolutionary relationships on species diet composition to understand resource partitioning patterns in a Neotropical frog community. Differences in frog trophic niche are usually associated with biomechanics of the mouth, activity periods, body size, foraging strategy, and prey availability (Wells, 2007). Most previous studies on anuran diet focused on investigating diet composition (e.g., Ceron et al., 2018), or diet differences associated with sex, ontogeny, and seasonality (Maragno & Souza, 2011; Protázio, Albuquerque, Falkenberg & Mesquita, 2015). However, few studies (e.g., Protázio et al., 2015) tested the mechanisms that affect resource partitioning in anuran communities using niche breadth and overlap indices that consider prey availability data (but see Leite-Filho et al., 2017), and no study so far considered prey traits when calculating these indices. Specifically, we asked the following questions: (1) Does phylogeny influence trophic niche overlap directly or indirectly via morphology? We expect that morphology influences trophic niche overlap; morphologically similar species share more similarity in diet than morphologically divergent ones; and those morphological characteristics, which determine prey consumption, are conserved along the phylogeny. (2) We also tested whether body size influences niche breadth. Because anurans are size-limited predators, and most have a generalist diet, we expect to find a positive relationship between body size and niche breadth. (3) Does taking into account prey availability and traits change trophic niche breadth and overlap indices? We expect that niche breadth and overlap increase when taking resource availability and prey traits into account.

Materials and methods

Study area

We sampled a pond ca. 3358 m^2 in area and 2.5 m deep, next to a small forest fragment, surrounded by a soybean plantation at the Private Reserve Fazenda Santa Fé (−20.5131 S, −54.7277 W, 500 m a.s.l.), Campo Grande, Mato Grosso do Sul, central Brazil. The average temperature in the region is 22.8 °C and average annual rainfall is 1533 mm. The climate is tropical with two well defined seasons: a dry winter (April to August) and a humid summer (September to March) (Alvares, Stape, Sentelhas, Gonçalves & Sparovek, 2013). The pond is surrounded by shrubby and herbaceous vegetation. There is an inflow from a small stream bordered with palm trees. The soil is permanently muddy, located near a spring.

Frog survey and morphometry

We collected adult anurans during the rainy season between December 2017 and February 2018 in three field trips of five days each. Our sampling effort consisted of 4 h/person each day, for a total 60 h/person. We conducted surveys at the breeding site by walking slowly around the pond

searching for frogs (Crump & Scott, 1994). To avoid temporal variation in community composition and diet (Dias, Ortega, Gomes & Agostinho, 2017; Wells, 2007), samplings were concentrated in the rainy season because this is the period in which most tropical species are active (Wells, 2007). To avoid dietary differences due to ontogenetic stage and sexual dimorphism, we captured only adult males. After capture, all collected individuals were euthanized with 5% lidocaine, fixed in 10% formaldehyde, and preserved in 70% ethanol. We took linear measurements from each frog specimen that are known to influence the size of prey consumed (Emerson, 1985; Wells, 2007): snout-vent length (SVL), mouth width (MW), and head length (HL) following Watters, Cummings, Flanagan and Siler (2016). Measurements were made with a digital hand caliper to the nearest 0.01 mm. In the following analysis, we used the raw morphometric measurements without correcting for body size. All voucher specimens were deposited in the "Coleção Zoológica de Referência" of Universidade Federal do Mato Grosso do Sul" (ZUFMS) (Appendix A).

Prey availability

To assess prey availability in the environment, we installed 25 pitfall traps (500-mL plastic cups), with 300 mL of 70% ethanol and detergent drops to break the surface tension of the solution. Traps were buried at ground level and distributed around the pond to cover all available habitats (Solé & Rödder, 2010). We spread the traps around the pond with a distance of at least 3 m from each other. We kept traps open during sampling nights until the next morning (12 h). Complementarily, we used an entomological umbrella to catch arboreal and flying invertebrates, which we sampled during the afternoon and evening (30 min each) in each sampling day. We assumed that the frogs captured fed in the area surrounding the pond. This is a reasonable assumption because anurans are strongly dispersal-limited due to their physiological requirements and there were no other ponds nearby. Additionally, home range size of small-sized anurans averages approximately 40 m^2 (Wells, 2007).

Stomachal content analysis

We analyzed the diet of all individuals collected, which were: *Rhinella diptycha* (n = 10); *Boana albopunctata* (n = 16); *Boana punctata* (n = 10); *Dendropsophus jimi* (n = 15); *Dendropsophus minutus* (n = 17); *Dendropsophus nanus* (n = 6); *Scinax fuscomarginatus* (n = 41); *Scinax fuscovarius* (n = 13); *Scinax nasicus* (n = 8); *Leptodactylus chaquensis* (n = 39); *Leptodactylus furnarius* (n = 6); *Leptodactylus fuscus* (n = 19); *Leptodactylus podicipinus* (n = 9); *Physalaemus nattereri* (n = 13); and *Physalaemus cuvieri* (n = 8). We identified stomach contents under a stereomicroscope and classified the material to order level using taxonomic keys (Rafael, Melo, Carvalho, Casari & Constantino, 2012). Most of the material was partially digested, making identification to lower taxonomic levels impractical. To estimate prey biomass, we obtained wet masses of each item found in stomachs and those found in the environment using a digital scale (to the nearest 0.0001 g). We estimated wet masses of material lighter than the accuracy level of the scale by grouping 10–100 individuals of similar size from the same taxon and calculating the mean mass, following Lima and Moreira (1993).

Molecular phylogenetic inference

To build a community phylogenetic tree, we extracted genomic DNA from muscle samples of individuals from our study locality using standard phenol-chloroform protocol (Sambrook, Fritschi & Maniatis, 1989). We used the T3-AnF1/ T3-AnF1 primer pair of Lyra, Haddad and Azeredo-Espin (2017). The PCR cycling program was run as follows: initial denaturation step with 3 min at 95 °C, 35 cycles of denaturation for 20 s at 95 °C, annealing for 20 s at 50 °C and extension for 1 min at 60 °C, and final extension for 5 min at 60 °C (Lyra et al., 2017). We purified PCR products with Ethanol/Sodium Acetate and sequenced them on an ABI 3730XL DNA Analyzer (Applied Biosystems, Foster City, California). Resulting sequences were edited and aligned using Geneious v. 9.1.2 with the MUSCLE algorithm using default parameters (Edgar, 2004).

We aligned our COI sequences with COI sequences of *Lithobates catesbeianus* (MH034267) as outgroup, which were available in GenBank (Appendix B). We removed gaps and poorly aligned positions in the alignment using GBLOCKS v0.91b (Castresana, 2000) which is available online (http://molevol.cmima.csic.es/castresana/Gblocks_server.html). The final aligned dataset used in all analyzes comprised 421 base pairs (bp). We used the Bayesian Information Criterion in jModelTest (Darriba, Taboada, Doallo & Posada, 2012) to determine that HKY+I + G was the best model of nucleotide substitution.

We performed Bayesian phylogenetic analysis of using BEAST v1.8 (Drummond & Rambaut, 2007) for 30 million generations, sampling every 1000 steps using a Yule Process tree prior. We checked for stationarity by visually inspecting trace plots and ensuring that all values for effective sample size were above 200 in Tracer v1.5. We discarded the first 10% of sampled genealogies as burn-in and calculated the maximum clade credibility tree with median node ages in TreeAnnotator v1.8 (Drummond & Rambaut, 2007).

Data analysis

Trophic niche overlap

We used the framework proposed by De Cáceres et al. (2011) to calculate niche overlap and breadth. We built

three matrices: (1) matrix **U**, with prey biomass (columns) of each individual frog (rows); (2) Matrix **Q** with biomass of prey found in the environment; (3) Matrix **D** is the similarity matrix between prey given their traits; it starts by a squared matrix in which rows are prey categories and columns their life history traits. We included life history traits that may influence prey capture and handling by predators, such as wings (presence or absence), developmental stage (larval or adult), defensive morphological structures (presence or absence of elytra, spines, urticating bristles), and habit (solitary or colonial). From this matrix, we calculated a Jaccard distance matrix (**D**), since the matrix included presence/absence of each trait. To visualize the relationship between prey, we built a dendrogram with UPGMA (Fig. 1).

To calculate trophic niche overlap, we used the cosine of the angle between the two vectors of relative resource preference, considering the similarity between resource classes (De Cáceres et al., 2011). Then, we conducted a bootstrap resampling procedure to generate confidence intervals for each niche measure, which allows performing statistical inferences without null models. Resource categories found in the environment (e.g., acari), but not present in the stomach of any specimen were removed from the analysis, and so were the resource categories that were in the diet (e.g., Isoptera for *Physalaemus nattereri*), but absent in the environment (see Moroti, Soares, Pedrozo, Provete & Santana, 2020). Analysis was performed using 'nichevar' and 'nicheoverlap' functions from the package 'indicspecies' (De Cáceres & Legendre, 2009) of R v. 3.6.1 (R Core Team, 2020).

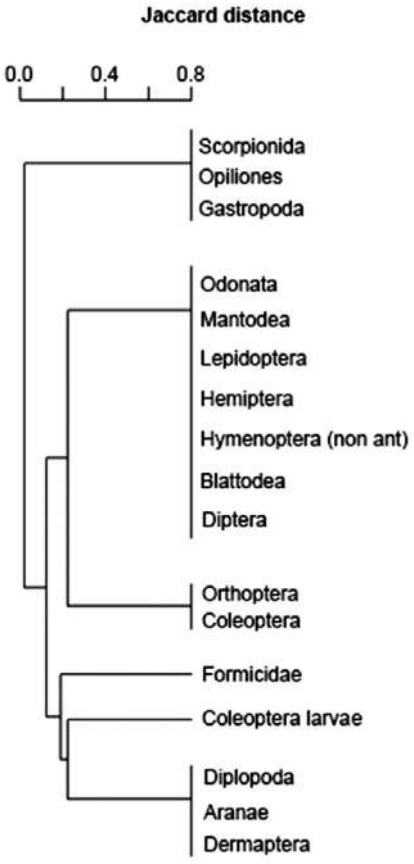

Fig. 1. Cluster analysis showing the Jaccard dissimilarity among prey given their life history traits that may influence capture and handling by anurans, such as wing (presence or absence), developmental stage (larva, pupa, adult), defensive morphological structures (presence of elytra, spines, urticating bristles), and habit (solitary or colonial).

Influence of morphometry and phylogeny on trophic niche overlap

To test whether phylogeny directly influences trophic niche overlap or indirectly through morphology, we used a series of simple and partial multiple regressions on distance matrices (MRM; Lichstein, 2007). We calculated a distance matrix from species diet using Euclidean distance. Similarly, we calculated a Euclidean distance matrix from the morphometric measurements. Moreover, we calculated a cophenetic distance from the phylogeny (Fig. 2). Then, we built four MRM models to test the direct and indirect effects of phylogeny and morphology on pair-wise species diet overlap calculated considering prey availability and traits. This analysis was carried out in the 'ecodist' package (Goslee & Urban, 2007).

To test whether body size (SVL; predictor variable) influences niche breadth (response variable), we used a Phylogenetic Generalized Least Squares (PGLS). We repeated this test for niche breath values calculated taking and not taking into account prey availability and traits. To control for phylogenetic autocorrelation in the residuals, we estimated the Pagel's λ parameter using restricted maximum likelihood, while also estimating model parameters (Revell, 2010). This analysis was carried out in the 'nlme' (Pinheiro, Bates, DebRoy & Sarkar, 2020) and ape packages (Paradis & Schliep, 2019).

Finally, we tested whether niche breadth values calculated incorporating and not incorporating prey availability and traits were different using a phylogenetic paired *t*-test (Lindenfors, Revell & Nunn, 2010). This analysis was carried out in the 'phytools' package (Revell, 2012). To test for differences between niche overlap values calculated with and without prey availability, we used a simple Mantel correlation (Legendre & Legendre, 2012) in the R package vegan (Oksanen et al., 2019). The data and R code used in the analysis are deposited at FigShare (Moroti et al., 2020).

Results

We analyze 230 anuran individuals from 14 species, of which 216 (94%) had stomach contents. There were 1817 prey items classified into 23 categories that resulted in a total of 61.441 g. The three prey items with the highest wet mass were Hemiptera (25.368 g), Diplopoda (11.203 g), and

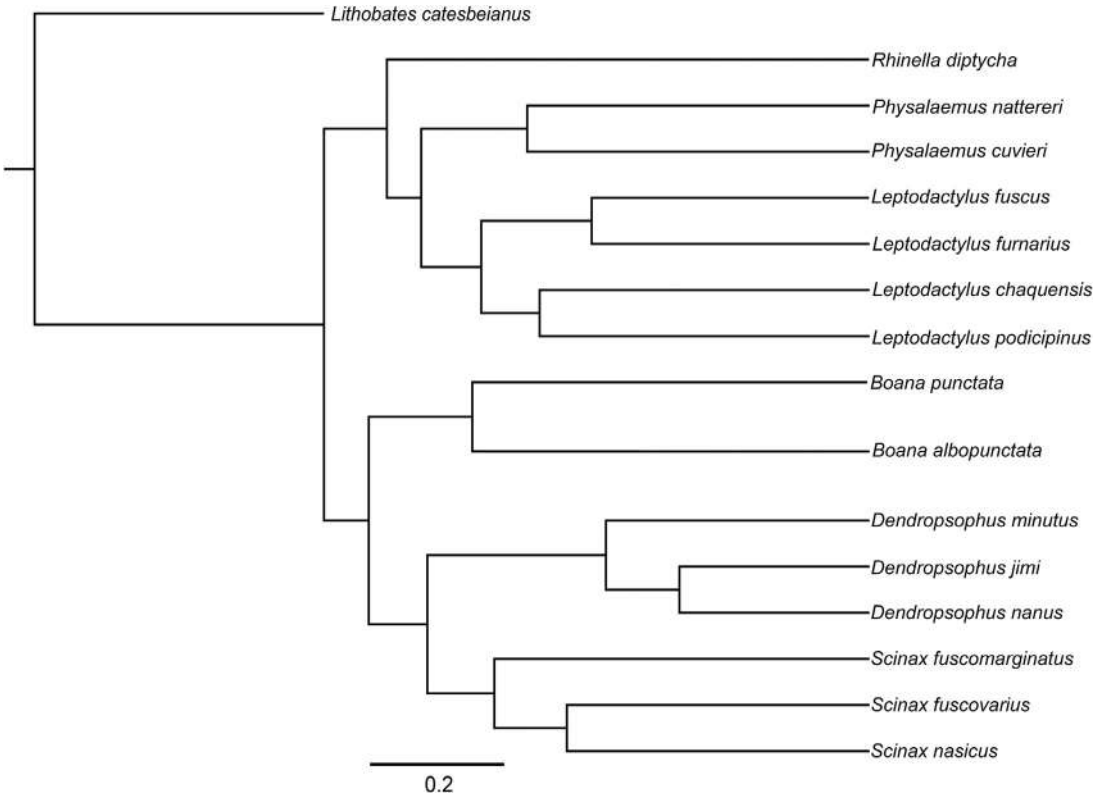

Fig. 2. Molecular phylogeny inferred with mitochondrial COI gene for frog species occurring in the study area. The phylogeny is rooted with COI sequences of *Lithobates catesbeianus* as outgroup. Legend bar indicates the number of substitutions per site.

Coleoptera (9.667 g). We found the same prey items in the environment, resulting in a total of 23.719 g. As in the stomachs, the items with the greatest mass in the field were Hemiptera (4.115 g), Diplopoda (3.218 g), and Coleoptera (2.856 g). Acari was present in the environment, but not in the stomachs analyzed.

Morphological distance was positively related with niche overlap (slope = 0.0096; R^2 = 0.42; P = 0.03). There was a weak relationship between phylogenetic distance and niche overlap (slope = 0.2766; R^2 = 0.04; P = 0.01), but the strength of the correlation increased when taking morphology into account (slope = 0.0094; R^2 = 0.43; P = 0.03). Phylogenetic distance was weakly correlated with morphological distance (slope = 0.0020; R^2 = 0.03; P = 0.01; Fig. 3). Body size was positively related (slope= 0.0015) to niche breadth when it was calculated considering prey availability and traits (λ= 1.016; $F_{1,13}$ = 6.967; P = 0.02), but this relationship does not when we did not hold consider prey availability and traits (λ= −0.496; $F_{1,13}$ = 0.106; P = 0.74).

Trophic niche breadth differed when we considered prey availability and traits (phylogenetic mean difference= −0.164 [95% CI= −0.213373, −0.114612], t = −6.50917, df = 12, P <0.001). The niche breadth is, on average, smaller when considering prey availability data than when we do not consider these data. The analysis not considering prey availability shows that the niche breadth values ranged from 0.12 to 0.39 (mean= 0.24 ± 0.10), while the analysis considering prey availability shows that niche breadth values ranged from 0.08 to 0.19 (mean= 0.08 ± 0.05) (Fig. 4). Similar to niche breath, niche overlap values calculated considering availability and traits were only slightly correlated with those not considering them (r_M= 0.347, P = 0.014). Niche overlap values when we considered prey availability and traits ranged from 0.40 to 0.99. The mean observed overlap was 0.834 ± 0.015 with most species pairs (95.9%) having overlap higher than 0.60. Conversely, when we did not consider prey availability and traits, overlap values ranged from 0 to 0.99. The mean overlap observed was 0.394 ± 0.033 with most species pairs (87.7%) having less than 0.60 of overlap (Fig. 5).

Discussion

Trophic niche overlap was better explained by morphology alone than by phylogenetic distance. This relationship still holds when we controlled for phylogeny on morphological distance. We also found that the body size influences niche breadth calculated with prey availability and traits, but this relationship does not hold when niche breadth did not include prey availability and trait data. In addition, trophic niche overlap changed considerably when prey availability and traits are considered.

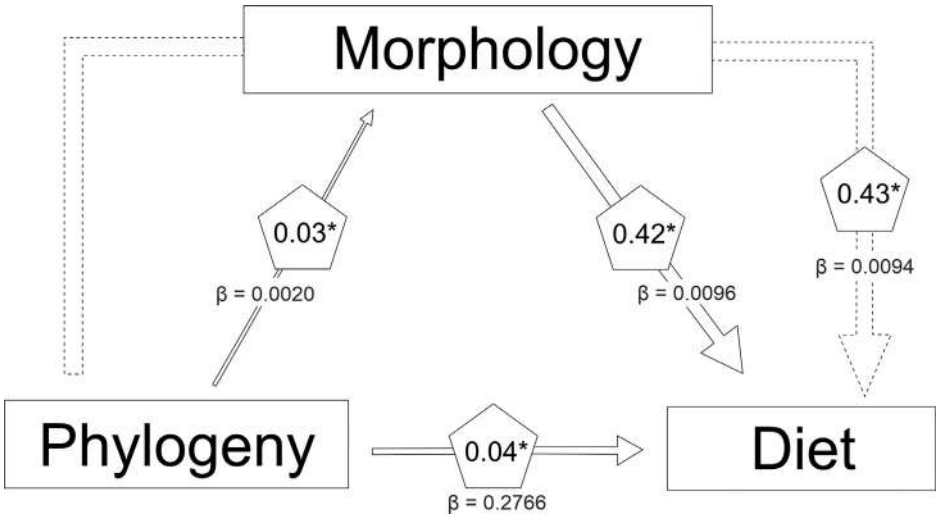

Fig. 3. Path analysis of multiple regression of distance matrices showing that phylogeny influences trophic niche overlap, directly (continuous lines) and indirectly (dotted lines) via morphology. In addition, morphology (controlling for species phylogenetic relationships) influences diet overlap. There is also a slight influence of phylogeny on morphology (phylogenetic signal). Arrow thickness indicates the strength of the relationship between distance matrices. Numbers inside pentagons are R^2, the slope (β) of the multiple regression is shown below each pentagon. * indicates $P < 0.05$.

As predicted, our results demonstrate an association between trophic niche overlap and species morphology, in which more morphologically distinct species also have a more distinct diet. It is widely known that frog body size is positively related with prey volume (Emerson, 1985; Parmelee, 1999; Toft, 1980) and size (Costa-Pereira, Araújo, Souza & Ingram, 2019). This pattern is predicted by the optimal diet theory (MacArthur & Pianka, 1966), in which larger predators tend to maximize their energy intake by consuming large prey. Nonetheless, larger predators can still consume small items, but the diet of small predators is often limited to small prey (Costa-Pereira et al., 2018; Diaz, 1994). Consequently, previous studies have indeed found a positive relationship between body size and trophic niche breadth in birds (Brändle & Brandl, 2008), herbivorous insects (Novotny & Basset, 1999), and lizards (Amorim et al., 2017). Our results are consistent with the fact that small frogs tend to have more specialized diets, preying only on small arthropods, while larger frogs tend to have more generalist

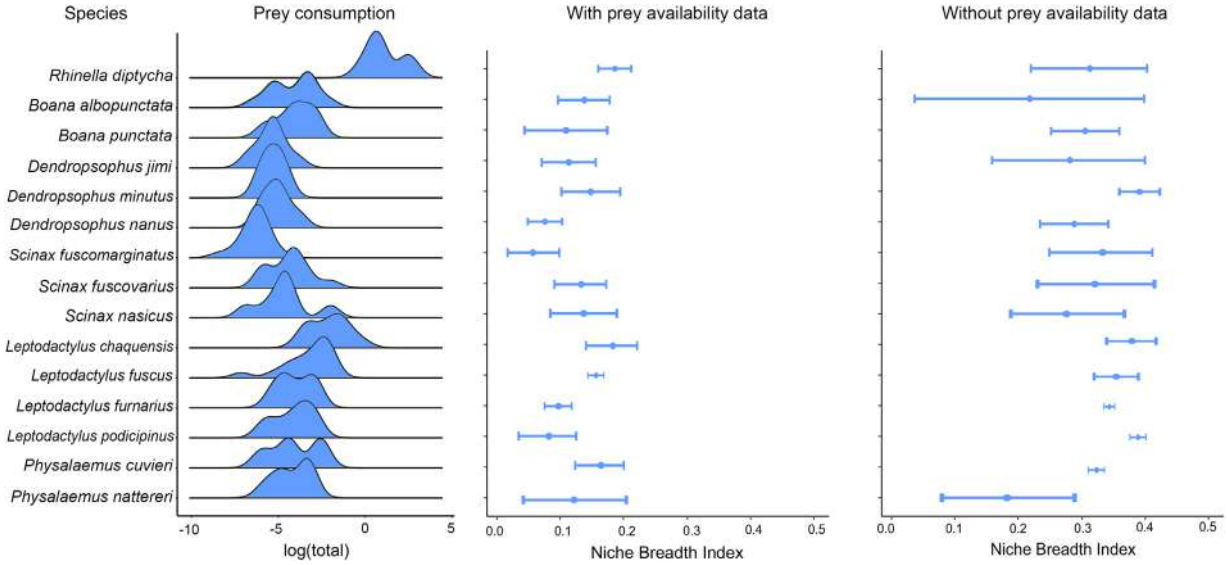

Fig. 4. Prey biomass (log of total grams) consumed by each species along with their respective niche breadth values calculated with and without prey availability and trait data. Niche breadth values were lower on average when considering prey availability and traits. The analysis not considering prey availability shows that the niche breadth values ranged from 0.12 to 0.39 (mean= 0.24 ± 0.10), while the analysis considering prey availability shows that the niche breadth values ranged from 0.08 to 0.19 (mean= 0.08 ± 0.05). The error bars show 95% confidence intervals.

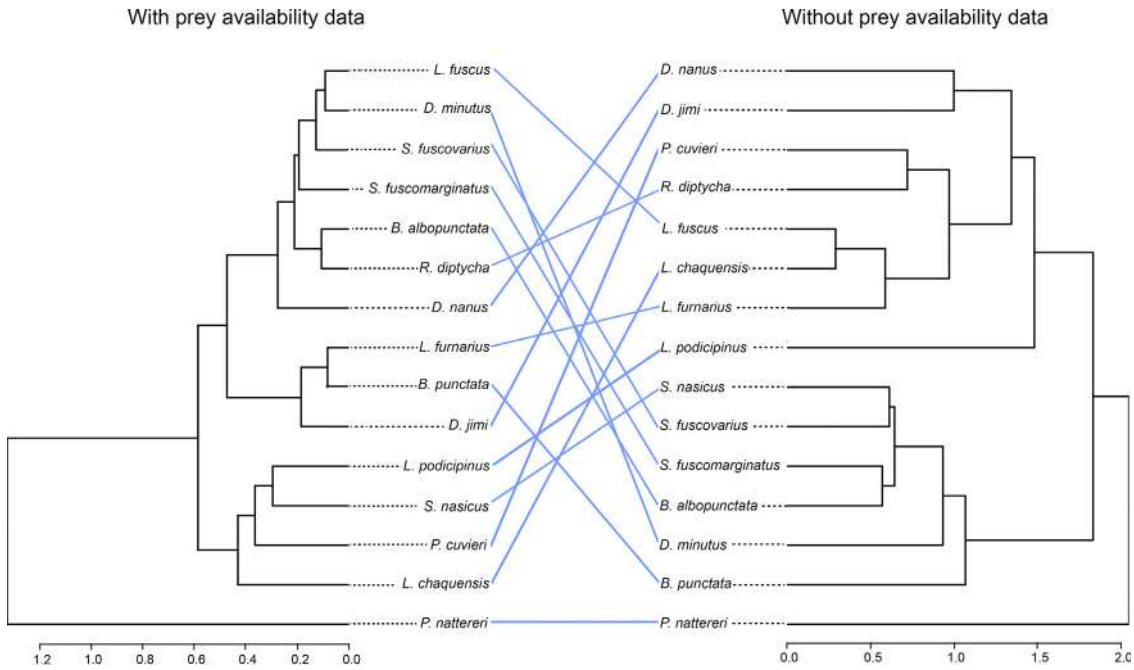

Fig. 5. Cluster analysis of the pair-wise niche overlap matrix calculated considering (left) and not considering (right) prey availability and similarity. Notice that the pattern of diet overlap between species changes radically depending on the type of niche overlap metric used, except for *Physalaemus nattereri*.

diets, consuming a wider range of prey (Costa-Pereira et al., 2018). This suggests that larger predator species may overlap not only with predators of similar sizes, but also partially with small ones, which would explain the high niche overlap values between all species pairs. However, large predators may be less efficient in capturing and handling small prey (Costa, Vitt, Pianka, Mesquita & Colli, 2008). This fact could explain why we found a higher overlap between pairs of species with similar morphologies. Taken together, these results support the fact that body size constraints play a key role in trophic resource partitioning (Wilbur, 1988; Woodward & Hildrew, 2002), especially in communities of size-limited predators.

Niche breadth values were lower on average when considering prey availability and traits. This suggests that species may actively select diet items from those available in the environment. The metric we used also considers the traits between resource categories. Dividing a similar resource category into subcategories can artificially alter niche breadth and overlap metrics, since commonly used indices (e.g., Pianka's O_{kj}) treat resource categories as independent (De Cáceres et al., 2011). Predator and prey characteristics are widely known to influence the likelihood of trophic interactions (Cohen, 1977), such as prey encounter rate, handling time, defensive mechanisms, and prey size (Chang, Teo, Norma-Rashid & Li, 2017; Costa-Pereira et al., 2019; Uiterwaal, Mares & DeLong, 2017). For example, ants and termites have eusocial habits and predators usually feed on many individuals at once. Another important aspect is the role in microhabitat use as a stabilizing mechanism promoting species coexistence (Chesson, 2000). For example, terrestrial frogs consume different prey categories than arboreal species (Ceron et al., 2019). In addition, individual specialization can play a key role in the trophic structure of communities (Costa-Pereira et al., 2019). Thus, combining predator and prey traits with resource availability can potentially change our conclusions about ecological specialization in anurans, since species seem to be more specialized when we consider resource availability in the environment.

Niche overlap values were higher for all species pairs when considering prey availability and trait data. This pattern holds even for distantly related species pairs. This same pattern has been observed in previous studies that measured trophic niche overlap in frog communities (Leite-Filho et al., 2017; Protázio et al., 2015). High overlap values can be explained by the type of prey anurans consume, which are usually arthropods (see Vignoli & Luiselli, 2012; Wells, 2007). Phenotypic traits have been increasingly used in community ecology to understand competitive interactions as a way to go beyond taxonomic identities (Wilcox et al., 2018). Trophic resources can share similarities due to their life history traits that influence predator decision making. Thus, the approach we use is in line with recent developments in theoretical community ecology to foster our understanding of resource-consumer interactions.

We did not find a significant relationship between phylogeny and either niche overlap or morphology. Some explanations for this pattern include the small phylogenetic extent of our study, which included only 15 species from three families. Phylogenetic scale directly influences the probability of detecting non-random patterns in ecological communities (Cadotte, Davies & Peres-Neto, 2017). Other studies that considered a small species

pool also found little or no phylogenetic signal in ecologically relevant traits (e.g., Parmentier et al., 2014; Silvertown, Dodd, Gowing, Lawson & McConway, 2006). Conversely, studies that used a larger phylogenetic scale or a specific lineage detected a phylogenetic signal (reviewed in Cavender-Bares, Kozak, Fine & Kembel, 2009). Another possible explanation is that the mode of evolution of traits we measured, which are involved in feeding, do not follow a simple Brownian Motion model, implicitly assumed by our analyzes. Phylogenetic signal is low when ecologically relevant traits are under divergent selection (Revell, Harmon & Collar, 2008) or are under strong stabilizing selection. Divergent selection occurs when co-occurring species diverge rapidly, so that closely related species differ substantially (Cadotte et al., 2017; Lankau, 2011). Another reason why species relatedness had little effect might be related to species coexistence mechanisms. For example, most species pairs had a high niche overlap. When there is little niche difference (high overlap of trophic niche; Letten, Ke & Fukami, 2017), stable coexistence requires a decrease in fitness difference (absence of competitive hierarchy; Chesson, 2000). But if phenotypic traits related to fitness differences (e.g., relative mouth width, body size; Kraft, Godoy & Levine, 2015) are not conserved along the phylogeny, which was our case since we did not find a strong phylogenetic signal, species relatedness will not be useful for understanding niche overlap patterns (see also HilleRisLambers, Adler, Harpole, Levine & Mayfield, 2012).

Conclusion

In conclusion, morphology and not phylogenetic relationship is more important to explain trophic niche overlap at a single site scale. Measures such as mouth width, body size, and head size determine the amount of prey frogs can consume and are probably related to fitness. As such, they are key to understand resource partitioning in communities, but prey size is also important for size-limited predators (Amorim et al., 2017; Costa-Pereira et al., 2018, 2019). Although our data are limited, since we only have wet biomass, future studies should include prey size as a trait to test how it influences resource partitioning (but see Costa-Pereira et al., 2018). Similarly, ontogenetic changes in size may exceed taxonomic differences, but are rarely included in dietary analyzes (Woodward & Hildrew, 2002). Another important implication of our results is that the interpretation of trophic niche overlaps in frog communities changes if we consider prey availability and traits, affecting inferences about coexistence and trophic specialization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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