

Diet overlap of three sympatric species of *Leptodactylus* Fitzinger (Anura: Leptodactylidae) in a Protected area in the Brazilian Amazon

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ABSTRACT

Closely related species are often similar in morphological and ecological characters, which may lead them to compete when occurring in sympatry. In this sense, we analyzed trophic niche overlap among three *Leptodactylus* species, *Leptodactylus macrosternum*, *L. fuscus* and *L. aff. podicipinus*, in a floodplain environment from a Protected area in the Brazilian Amazon. In addition, we applied Network and Non-metric multidimensional scaling (NMDS) analysis. We found 18 prey categories, most of them belonging to Arthropoda (94.4%). Coleoptera, Isoptera, Diptera and Hymenoptera were the most abundant prey on the diet shared among the three species. The rarefaction curve of prey richness did not reach an asymptote, indicating that the diet composition may be higher by increase the sample. The species presented a broad niche breadth, however, no relationship between jaw width and prey size were found in the studied species. Despite the line-up in NMDS with Bray Curtis Index indicated that the species' diets are similar with few different attributes, with some food items overlapping among species (Stress= 0.00201), the niche overlap between the pair of species was not high ($O_{jk} < 0.7$). Therefore, we believe interactions such as competition would be better demonstrated addressing data on prey availability and microhabitat use patterns.

Key words: Trophic Niche; Overlapping; Similarity; Anurans.

RESUMEN

Las especies relacionadas filogenéticamente a menudo presentan similares en caracteres morfológicos y ecológicos, lo que puede llevarlos a competir cuando ocurren en simpatria. En este sentido, analizamos la superposición de nicho trófico entre tres especies simpátricas del género *Leptodactylus* (*Leptodactylus macrosternum*, *L. fuscus* y *L. aff. podicipinus*) en un entorno de planicie aluvial de una área protegida en la Amazonía brasileña. Además, aplicamos análisis de Network y Escalamiento multidimensional no métrico (NMDS). Encontramos 18 categorías de presas, la mayoría pertenecientes al orden de los artrópodos (94.4%). Coleoptera, Isoptera, Diptera e Hymenoptera fueron las presas más abundantes en la dieta compartida entre las tres especies. La curva de rarefacción de la riqueza de presas no alcanzó una asíntota, lo que indica que la composición de la dieta puede ser mayor al aumentar la muestra. Las especies presentaron una amplia amplitud de nicho, sin embargo, no se encontró relación entre el ancho de la mandíbula y el tamaño de la presa en las especies estudiadas. A pesar de que la alineación en NMDS con el Índice Bray Curtis indicó que las dietas de las especies son similares con pocos atributos diferentes y con algunos alimentos superpuestos entre especies (Estrés= 0.00201), la superposición de nicho entre el par de especies no fue alta ($O_{jk} < 0.7$). Por lo tanto, creemos que las interacciones como la competencia se demostrarían mejor abordando los datos sobre la disponibilidad de presas y los patrones de uso de microhabitat.

Palabras clave: Nicho trófico; Superposición; Similitud; Anuros.

Introduction

Ecological studies on trophic niche allow to make characterizations about the structure and dynamic

of a population or community (Putman, 1994). This niche dimension includes, among other factors, the

description of the diet composition and the use of food resource among the species (Schoener, 1974; Sih and Christensen, 2001). The way the species use the resources on environment strictly depends on intrinsic and extrinsic factors, such as foraging habits and nutritional demands, ontogenetic development, changes in resource availability and competition (Schoener, 1974; Putman, 1994). These factors affect the structure and coexistence patterns of communities and produces variation in the degree of overlap in resource use among species at a local scale (Schoener, 1974; Gordon, 2000). Also influences on the exchange of organisms and energy across ecosystem, affecting food web structure (Marczak *et al.*, 2007; McDonald-Madden *et al.*, 2016).

Measures of niche overlap are useful to quantify the degree to which two or more species overlap in their utilization of resources, being applied in studies of species interactions and community structure (Hurlbert, 1978). However, the food webs are also a important representation of the interactions between species in an ecosystem (McDonald-Madden *et al.*, 2016), which describe the trophic links between consumers, and can be a powerful tool not only in represent species interaction in a ecosystem but for the management of complex ecosystems in terms of conservation (May, 1974; Pimm *et al.*, 1991).

Evolutionary related species often share morphological characteristics and similar ecological functions, as a resulting of sharing a common ancestor, and expected to exhibit little niche differentiation (Losos, 2008). In this sense, resource competition and niche partitioning may occur in closely related species when they share the same spatial habitat (Violle *et al.*, 2011; Schoener, 1974). Among amphibians, the anuran lineage is the most ecologically diverse (Duellman and Trueb, 1994). As predators of invertebrates, a rich taxonomic group, the anurans exhibit high diet plasticity and several degrees of specialization related to prey selection (Toft, 1980, 1995; Solé and Rödder, 2010); this makes them important test cases for studying mechanisms of diet segregation that facilitate species coexistence.

The Leptodactylidae is one of the most widely distributed anuran families in the world and comprise 218 species occupying a wide range of environments (Frost, 2020). Leptodactylids species usually consume invertebrate prey (Rodrigues *et al.*, 2004) but also can predate on anurans or other vertebrates (De-Sá *et al.*, 2014). This study evaluates the diet composition and trophic niche overlap among three

sympatric *Leptodactylus* species, namely *Leptodactylus* aff. *podicipinus*, *L. fuscus* and *L. macrosternum* from in a protected area in northern Brazil. In addition, we provide a network analysis to better understand the interactions between species in this study.

Materials and methods

The Rio Curiaú Environmental Protection Area (hereafter APA Curiaú) is located north of the Municipality of Macapá, Amapá state, Brazil. It is established in the Curiaú river basin which covers 40% of the 21,700 hectares of the area's extent. Vegetation is predominantly composed of *várzeas* forests, such as lowland marshes and swamps. APA Curiaú is composed of permanent and temporary lakes and foodplains, supporting a rich anuran community (Lima *et al.*, 2017). The region's climate is tropical monsoonal (Am from the Köppen Geiger system, see Peel *et al.*, 2007) and the rainy season last from January to June (Silva *et al.*, 2013).

The study took place in two areas where the three target species occur in sympatry within APA Curiaú, Fazenda Toca da Raposa (00° 09' 00.7"; 051° 02' 18.5") and Lago do Dezivaldo (00° 9' 12.4"; 51° 0' 53.9"), respectively Point 1 and Point 2 (Fig. 1). Both areas are characterized as floodplain environments dominated by typical floodplain vegetation, such as herbaceous and grasses, and surrounded by narrow bands of *várzea* forest composed of large and medium sized trees and shrubs (Lima *et al.*, 2017). The campaigns were conducted between July 2013 and June 2014. We collected the specimens for two nights in a row in each campaign, always starting early night (19:00 h) and lasting until 23:00 h. Three people in each sampling point participated of the collections and the search effort corresponded to 12 person-hours per day in each sampling point. We located the target species by using auditory and visual search (Heyer *et al.*, 1994) along all the floodplain and adjacent *várzea* forest.

We placed the captured specimens inside individual plastic bags for identification and posterior examination of dietary aspects. We measured the snout-vent length (SVL) of specimens using a digital caliper (0.01 mm precision) and, body mass using a Pesola dynamometer (0.1g precision). We collected frogs under permit number #41586-1 issued by SISBIO/ICMBio and housed all specimens in the Herpetological Collection of Universidade Federal do Amapá (Appendix 1).

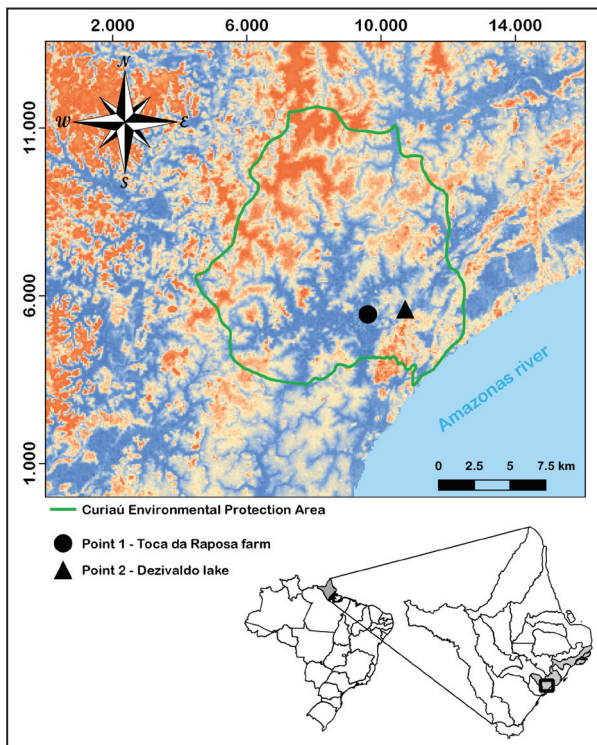


Figure 1. Rio Curiaú Environmental Protection Area, State of Amapá, Brazil, showing the two sampling points: Point 1 - Fazenda Toca da Raposa and Point 2 - Lake Dezivaldo.

We euthanized the collected frogs with cream anesthetic 2% Lidocaine (applying through the animal's skin), and fixed them in 10% formaldehyde for posterior preservation in alcohol at 70%. Afterwards, we dissected the specimens and removed stomach contents through a ventral longitudinal incision and gathered carefully all contents into plastic tubes filled with 70% ethanol to interrupt continued digestion. The stomach contents were analyzed under stereo microscopes and identified to the lowest possible taxonomic level, with the aid of dichotomy keys (Borror and DeLong, 2011; Rafael *et al.*, 2012). Larval forms of insects were placed in different categories from the adults. Some non-insect invertebrates were difficult to identify in the level of order and, therefore, were placed into major taxonomic categories.

For each food item, we measured the length and the width using digital calipers (0.01 mm precision) and prey volume (mm³) was estimated using the formula for ellipsoid bodies (Griffiths and Mylotte, 1987). Where *V* represents prey volume, *l* = item length e *w* = item width:

$$V = \frac{4}{3} \pi \left(\frac{l}{2}\right) \times \left(\frac{w}{2}\right)^2$$

For each prey category we applied the Importance Value Index (IVI) described by Gadsden and Palácios-Orona (1997) using the sum of the percentages of number (*N%*), frequency (*F%*) and volume (*V%*).

$$IVI = \left(\frac{F\% + N\% + V\%}{3}\right)$$

We measured trophic niche breadth of the three sympatric frog species using the Levins index (*B*) described by Pianka (1986). Where *B* = Levins index (trophic niche breadth); *i* = prey category; *n* = number of categories; *p_i* = numerical or volumetric proportion of the category of prey *i* in the diet:

$$B = 1 / \sum_{i=1}^n p_i^2$$

We calculated standardized measure of Levin's index (*L_{st}*) which limits the value on a scale from 0 to 1 according to the formula (Hurlbert, 1978): *L_{st}* = (*B* - 1)/(*n* - 1), where *n* represents the number of resources (prey categories) registered and *B* represents the Levin's measure of niche breadth. Values closer to 0 we attributed to a more specialist diet, while values closer to 1 we considered a more generalist diet (Krebs, 1989).

We used the absolute number of each prey item (*N*) to calculate the dietary overlap between *L. aff. podicipinus*, *L. fuscus* and *L. macrosternum* in the study area by applying Pianka's index equation, in which the value ranges from 0 (no overlap) to 1 (complete overlap) (Pianka, 1973). The Pianka's index was calculated using the following equation, where *p_{ij}* (or *p_{ik}*) is the absolute frequency of food item *i* in diet *j* (or *k*).

$$o_{jk} = \sum_i^n p_{ij} p_{ik} / \sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}$$

We performed a Spearman correlation test to determine the existence of correlation between jaw-width (JW) and the volume of the largest prey for each specimen. Statistical tests were performed using Bio-Estat 5.0 software (Ayres *et al.*, 2007). Analyzes used to quantify the amplitude of the ecological niche and

niche overlap of the species were carried out in the program Ecosim 7.0 (Gotelli and Entsminger, 2001).

The network of associations were formed through the number of species collected in the two sampling areas and correlated with the number of prey consumed by the specimens. This analysis considers the prey predator relationship and was performed in the R (R core team 2017) statistical software, using the bipartite package that focuses on the definition of patterns in webs (Dormann *et al.*, 2009).

To analyze the sampling size and taxonomic richness of prey consumed by the three frog species we plotted rarefaction curves based on the number of specimens and food items using ESTIMATES 9.1 (Gotelli and Colwell, 2001). Non-metric multidimensional scaling (NMDS) with Bray-Curtis similarity distances were used to assess the similarity pattern between species using the abundance data for each species. In this analysis, we used the R statistical environment (R core team 2017) and the "Vegan" library (Oksanen *et al.*, 2017).

Results

We collected 107 individuals from the three *Leptodactylus* species, the number of individuals collected in each sampling point are reported in Table 1. The contents found in the stomachs of *Leptodactylus macrosternum*, *L. fuscus* and *L. aff. podicipinus* from the two sites are reported, respectively, in Table 2, Table 3 and Table 4. All identifiable prey items were placed in 18 Orders, comprising terrestrial invertebrates most of them belonging to Arthropoda (94.4%) (Table 1). The rarefaction curve did not reach the asymptote and indicated the higher taxonomic richness in the diet of *L. macrosternum* (Fig. 2).

We analyzed 53 stomachs from *Leptodactylus macrosternum* and found 16 prey categories. Diet of both populations was composed mostly of arthropods, including both larval and adult forms. At sampling point 1 the most important prey in the diet of *L. macrosternum* were Isoptera (IVI= 15.66)

and larval forms of Diptera (13.03); other prey such as Coleoptera (IVI= 12.84) and Acari (IVI= 11.22) also were representative in the diet of the species. We identified six prey categories in the diet of *L. macrosternum* at sampling point 2, in which the most important prey categories were larval Lepidoptera (IVI= 24.31) and Chilopoda (IVI= 22.14). In terms of number, however, the most abundant prey in the diet of *L. macrosternum* were Coleoptera (28.57%) and Hymenoptera (21.43%) (Table 2). The niche breadth was slightly broader in sampling point 2 population ($L_{st} = 0.84$), than in sampling point 1 population ($L_{st} = 0.76$) and intermediate ($L_{st} = 0.48$) considering both sampling sites. There were no significant correlation between the highest volumetric prey and frog jaw width (JW) for *L. macrosternum* ($rs = -0.0626$, $p = 0.7471$).

The diet composition of *Leptodactylus fuscus* consisted of only two prey categories at both sampling sites. Individuals primarily consumed Coleoptera, comprising 85.71% of the prey consumed at sampling point 1 and it was the only prey found in the stomachs of individuals at sampling point 2 (Table 3). Considering both populations, the niche of *L. fuscus* was broad ($L_{st} = 0.74$). As expected, no significant correlation between the highest volumetric prey and frog jaw width (JW) were found for *L. fuscus* ($rs = -0.4524$, $p = 0.2603$).

With regards to prey richness in the diet of *Leptodactylus aff. podicipinus*, we found 11 prey categories. Individuals from sampling point 1 consumed primarily Coleopterans (IVI= 31.47), followed by Blattaria (IVI= 25.29) and Orthoptera (IVI=9.38). At sampling point 2 the diet of *L. aff. podicipinus* consisted of six prey categories and was dominated by Lepidoptera (IVI= 22.19), Orthoptera (IVI= 20.2) and Coleoptera (IVI= 19.96). Niche breadth was narrower in sampling point 1 ($L_{st} = 0.52$), broader in sampling point 2 ($L_{st} = 0.91$) and intermediate at both sampling sites ($L_{st} = 0.66$). We found no significant relationship between the highest volumetric prey and frog jaw width (JW) for *L. aff. podicipinus* ($rs = 0.2508$, $p = 0.2266$).

Table 1. Species, total number of specimens collected (N), Number of species collected at Point 1 - Toca da Raposa farm and Point 2 - Dezivaldo Lake, total richness of prey consumed and of the two sampled points, and dominant prey category in anurans collected in Rio Curiaú Environmental Protection Area.

Species	N	Point 1	Point 2	Richness of prey consumed	Dominant prey category
<i>Leptodactylus macrosternum</i>	53	43	10	15	Hymenoptera
<i>Leptodactylus fuscus</i>	16	14	2	2	Coleoptera
<i>Leptodactylus aff. podicipinus</i>	38	30	8	11	Coleoptera

Table 2. Prey categories found in the stomachs of *Leptodactylus macrosternum* in two locates (Point 1 - Toca da Raposa farm and Point 2 - Dezivaldo Lake) at Rio Curiaú Environmental Protection Area. N = number of items consumed; F = frequency of items; V = prey volume (mm³); IVI = Index of Value Importance.

Prey Category	Point 1							Point 2						
	N	N%	F	F%	V	V%	IVI	N	N%	F	F%	V	V%	IVI
Acari	25	27.17	2	6.45	0.17	0.02	11.22	-	-	-	-	-	-	-
Aranae	4	4.35	4	12.9	32.82	3.98	7.08	-	-	-	-	-	-	-
Blattaria	1	1.09	1	3.23	54.57	6.62	3.64	-	-	-	-	-	-	-
Coleoptera	10	10.87	7	22.58	41.82	5.07	12.84	4	28.57	3	25	157.72	8.87	20.81
Diptera	2	2.17	2	6.45	3.85	0.47	3.03	-	-	-	-	-	-	-
Diptera larvae	4	4.35	1	3.23	160.58	19.47	13.03	-	-	-	-	-	-	-
Haplotaxida	2	2.17	1	3.23	277.95	33.7	9.01	-	-	-	-	-	-	-
Hemiptera	1	1.09	1	3.23	184.03	22.31	8.87	-	-	-	-	-	-	-
Hymenoptera	7	7.61	7	22.58	19.01	2.3	10.83	3	21.43	3	25	11.57	0.65	15.69
Isoptera	34	36.96	3	9.68	2.88	0.35	15.66	-	-	-	-	-	-	-
Lepidoptera larvae	1	1.09	1	3.23	45.51	5.52	3.28	3	21.43	2	16.67	619.31	34.82	24.31
Neuroptera	1	1.09	1	3.23	1.62	0.2	1.5	-	-	-	-	-	-	-
Opilione	-	-	-	-	-	-	-	2	14.29	2	16.67	18.81	1.06	10.67
Orthoptera	-	-	-	-	-	-	-	1	7.14	1	8.33	65.08	3.66	6.38
Chilopoda	-	-	-	-	-	-	-	1	7.14	1	8.33	905.94	50.94	22.14
Total	92	100	31	100	822.52	100	100	14	100	12	100	1778.43	100	100

Table 3. Prey categories found in the stomachs of *Leptodactylus fuscus* in two locates (Point 1 - Toca da Raposa farm and Point 2 - Dezivaldo Lake) at Rio Curiaú Environmental Protection Area. N = number of items consumed; F = frequency of items; V = prey volume (mm³); IVI = Index of Value Importance.

Prey Category	Point 1							Point 2						
	N	N%	F	F%	V	V%	IVI	N	N%	F	F%	V	V%	IVI
Coleoptera	12	85.71	6	75	8.99	44.77	68.49	1	100	1	100	1.19	100	100
Hymenoptera	2	14.29	2	25	11.09	55.23	31.51	-	-	-	-	-	-	-
Total	14	100	8	100	20.08	100	100	1	100	1	100	1.19	100	100

Table 4. Prey categories found in the stomachs of *Leptodactylus* aff. *podicipinus* in two locates (Point 1 - Toca da Raposa farm and Point 2 - Dezivaldo Lake) at Rio Curiaú Environmental Protection Area. N = number of items consumed; F = frequency of items; V = prey volume (mm³); IVI = Index of Value Importance.

Prey Category	Point 1							Point 2						
	N	N%	F	F%	V	V%	IVI	N	N%	F	F%	V	V%	IVI
Aranae	3	8.57	3	11.11	40.06	7.8	9.16	-	-	-	-	-	-	-
Blattaria	1	2.86	1	3.7	355.9	69.3	25.29	-	-	-	-	-	-	-
Coleoptera	17	48.57	12	44.44	7.09	1.38	31.47	2	28.57	2	28.57	2.06	2.75	19.96
Diptera	3	8.57	3	11.11	4.13	0.8	6.83	1	14.29	1	14.29	1.89	2.52	10.36
Haplotaxida	1	2.86	1	3.7	2.68	0.52	2.36	-	-	-	-	-	-	-
Hemiptera	3	8.57	3	11.11	13.92	2.71	7.46	-	-	-	-	-	-	-
Isoptera	4	11.43	1	3.7	2.61	0.51	5.21	-	-	-	-	-	-	-
Lepidoptera	-	-	-	-	-	-	-	1	14.92	1	14.29	28.47	37.99	22.19
Mantodea	-	-	-	-	-	-	-	1	14.92	1	14.92	16.21	21.63	16.73
Odonata	1	2.86	1	3.7	3.02	0.59	2.38	1	14.29	1	14.29	2.31	3.08	10.55
Orthoptera	2	5.71	2	7.41	84.14	16.38	9.38	1	14.29	1	14.29	24	32.02	20.2
Total	35	100	27	100	513.54	100	100	7	100	7	100	74.94	100	100

Table 5. Trophic niche overlap between the three *Leptodactylus* species collected at Point 1 - Toca da Raposa and Point 2 - Lake Dezivaldo at Rio Curiaú Environmental Protection Area.

	Point 1		Point 2	
	<i>L. fuscus</i>	<i>L. aff. podicipinus</i>	<i>L. fuscus</i>	<i>L. aff. podicipinus</i>
<i>L. macrosternum</i>	0.49	0.52	0.48	0.35
<i>L. fuscus</i>	-	0.64	-	-

When analyzing trophic niche overlap for pairs of species, we found the lowest overlap between *L. macrosternum* and *L. aff. podicipinus* at sampling point 2 ($O_{jk} = 0.35$) and the highest overlap between *L. fuscus* and *L. aff. podicipinus* at sampling point 1 ($O_{jk} = 0.64$). Overall, none of the species showed high overlap values to consider overlap in the use of resource ($O_{jk} > 0.7$) (Table 5).

We found association of 14 prey categories in the diet of the three *Leptodactylus* species, showing Coleoptera, Isoptera, Diptera and Hymenoptera as the most abundant prey on the diet shared among the three species at sampling point 1, exhibiting more than one association in network analysis (Fig. 3A). At sampling point 2, we verified 11 prey categories with Coleoptera and Orthoptera showing more than one association between species, representing important items on the diet of the three frog species (Fig. 3B). The line-up in NMDS with Bray Curtis Index indicated that the species' diets are similar with few different attributes, with some food items overlapping among species (Stress= 0.00201) (Fig. 4).

Discussion

We hypothesized that the three *Leptodactylus* species would consume the same types of prey given that morphological and ecological traits associated with feeding mechanisms are presumably similar in closely related species, driving species into resource competition and niche overlap. However, there is

no strong evidence supporting high overlap among the food resources consumed by the three species at both sampling sites. On the other hand, the three species exhibited broad niche breadth, which can be indication of a generalist feeding habit and variation in the use of resources.

It has been stated that populations with broader niche are likely to exhibit generalist behavior related to greater variation and diversification in the use of food resource among individuals in comparison to populations of specialist species with a narrower niches (Toft, 1980, 1995; Bolnick *et al.*, 2007). This variation can be related to extrinsic factors, including shifts in resource availability and interspecific competition (Schoener, 1974; Sih and Christensen, 2001). An appreciation on studies about the diet of *Leptodactylus* species reveals a generalist and opportunistic feeding behavior pattern (e.g. Rodrigues *et al.*, 2004; Sanabria *et al.*, 2005; Solé *et al.*, 2009). We suggest that the studied species, except for *L. fuscus* (due to the small sample found in the stomachs), exhibited a generalist behavior with a consumption of many different prey categories, with none of the food resources accounting more than 50% of the diet, which reflects in a broader niche breadth compared to specialists (Toft, 1980, 1995; Bolnick *et al.*, 2007; Solé and Rödder, 2010).

It would be expected a positive correlation between predator size and prey volume or prey length in *Leptodactylus*, given that this species usually feed on fewer but larger prey items (Rebouças and Solé, 2015). However, it contrasts with most studies on *Leptodactylus* species, which reported a lack of relationship between predator and prey size (Solé *et al.*, 2018; Sanabria *et al.*, 2005; Sugai *et al.*, 2012; Teles *et al.*, 2018). We believe lack of correlation between predator and prey size in our study, as well in other studies with *Leptodactylus* species, is probably related to the lack of juveniles in our sample and to the small sample obtained, which would consistently improve analysis.

We observed through NMDS analysis, similarities between the items consumed by the studied species. These data indicate that relative high overlap

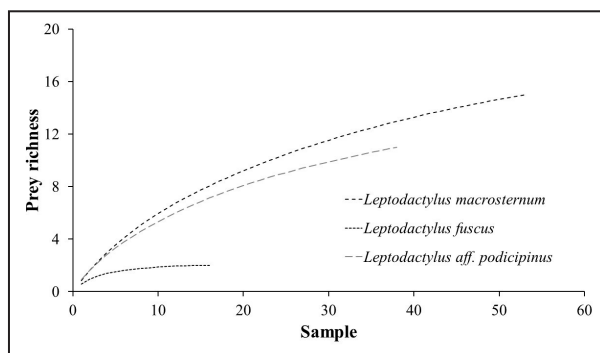


Figure 2. Rarefaction curves of the three *Leptodactylus* species diet, relating taxonomic richness to the number of individuals sampled.

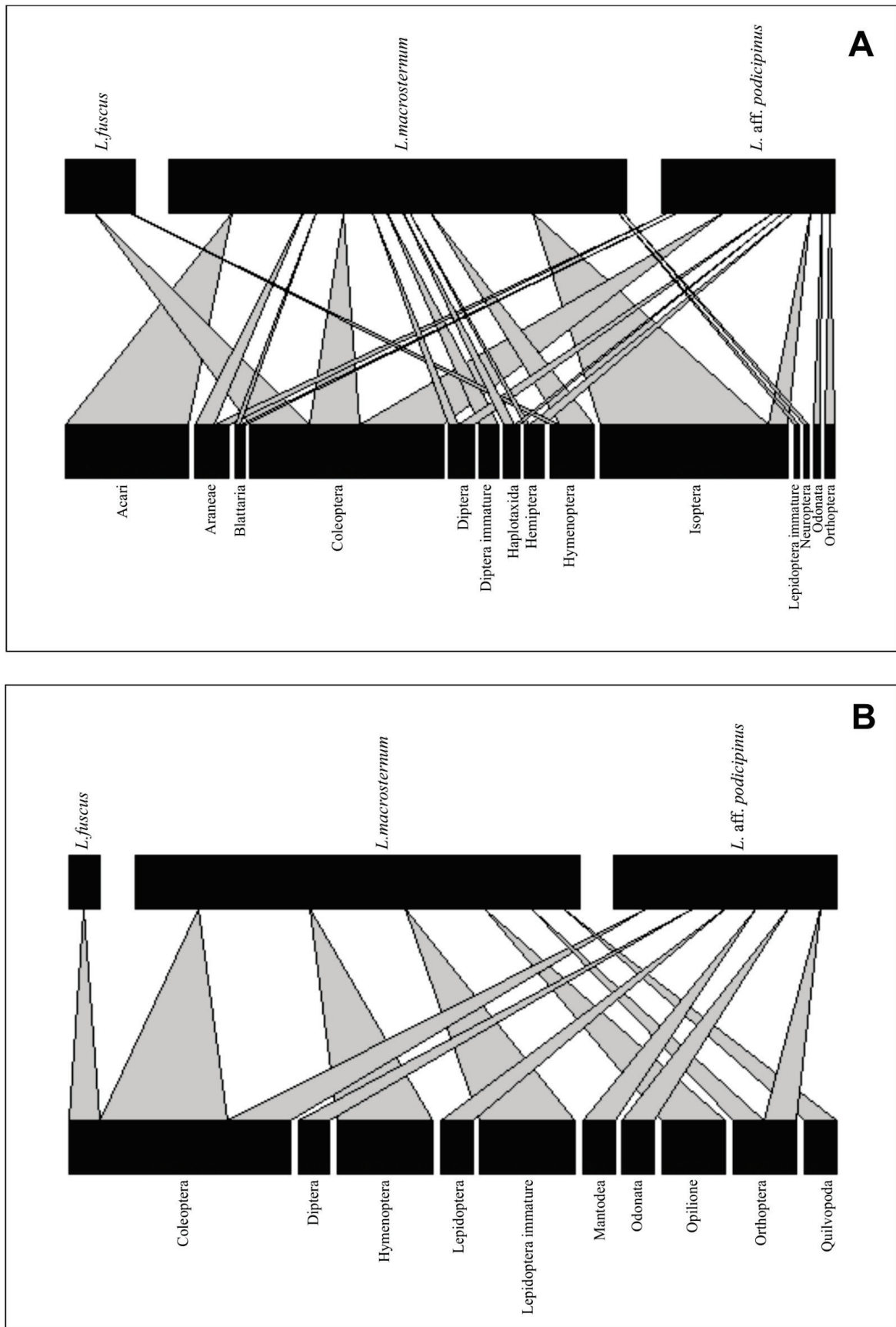


Figure 3. Network of interactions between prey and predators of *Leptodactylus* species for the two sampling points, (A) Point 1 - Toca da Raposa Farm and (B) Point 2 - Lake Dezivaldo in Rio Curiaú Environmental Protection Area.

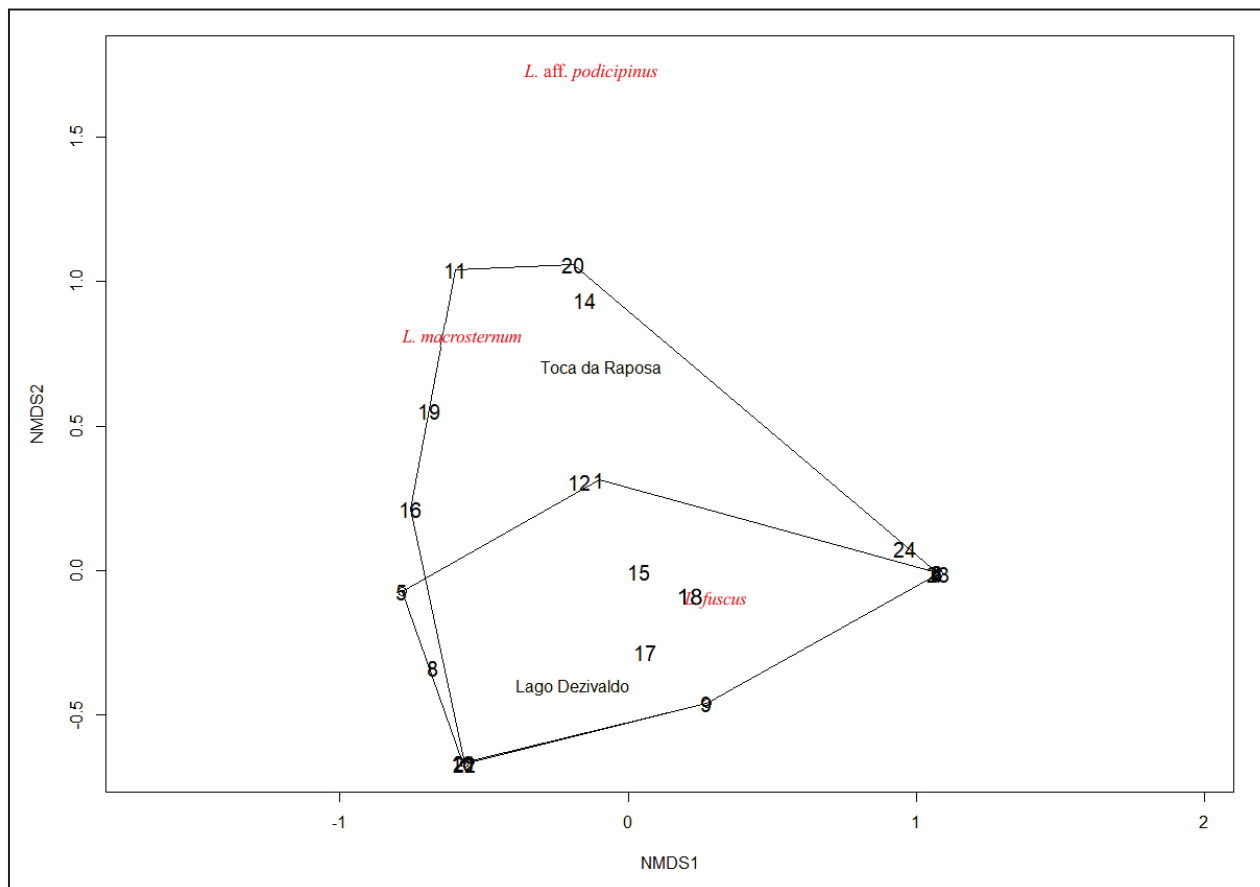


Figure 4. Non-metric multidimensional scaling (NMDS) for *Leptodactylus* species according to food items at two sampling points: Point 1 - Toca da Raposa Farm and Point 2 - Lake Dezivaldo in a Rio Curiaú Environmental Protection Area. Sequence of food item codes: 1 - Coleoptera, 2 - Diptera, 3 - Hymenoptera, 4 - Lepidoptera, 5 - Lepidoptera immature, 6 - Mantodea, 7 - Odonata, 8 - Opilione, 9 - Orthoptera, 10 - Chilopoda, 11 - Acari, 12 - Araneae, 13 - Blattaria, 14 - Coleoptera, 15 - Diptera, 16 - Diptera immature, 17 - Haplplotaxida, 18 - Hemiptera, 19 - Hymenoptera, 20 - Isoptera, 21 - Lepidoptera immature, 22 - Neuroptera, 23 - Odonata, 24 - Chilopoda.

between *L. aff. podicipinus* and *L. fuscus* at sampling point 1 may be related to the consumption of Coleoptera, which was the most important prey on the diet for both species (IVI = 68.49, 31.47; respectively). Although measures of niche breadth and niche overlap and other particular metrics are useful in studies estimating competition, the taxonomic level that the prey resources are identified has an important effect on the results obtained (Greene and Jaksić, 1983). A more refined taxonomic identification of prey items would probably give better results on niche measures, since anuran species are not only able to discriminate prey by size, but also taxonomically (Toft, 1980, 1995; Solé and Rödder, 2010).

Although phylogenetic-based argument is relevant, there are several factors influencing resource sharing among sympatric anurans, including differences in size, prey availability (Sabagh *et al.*, 2010), variation in feeding strategies (Toft, 1980; 1981) and different patterns of microhabitat use

(Van Sluys and Rocha, 1998). Also, the low degree of overlap observed between the three species may be an artifact of sample size of our study, as shown in the rarefaction curve the taxonomic prey richness is still underestimated, and more specimens sampled may reveal the presence of additional categories in the diet of the studied species. Furthermore, a more complex analysis, including availability of resources and microhabitat use patterns, would improve our conclusions about how these three frog species coexist in floodplain environment in Area de Proteção Ambiental Rio Curiaú, northern Brazil.

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Appendix 1

CECCAMPOS number collection – *Leptodactylus* aff. *podicipinus*: 7, 9, 10, 14-16, 18, 22-26, 30, 31, 38, 42, 57, 59, 65, 72, 77, 88, 90, 94, 101, 104, 105, 107, 109, 134, 139, 140, 230, 233, 240, 268-270; *Leptodactylus fuscus*: 55, 89, 91, 92, 95, 96, 99, 106, 113, 115, 117, 119, 129, 155, 184, 221; *Leptodactylus macrosternum*: 2-4, 11-13, 19-21, 29, 40, 41, 45, 58, 70, 71, 74, 82-84, 97, 108, 111, 118, 120, 123, 125, 136, 151-154, 162, 170, 174, 178, 179, 193, 220-228, 241, 242, 248, 256, 260, 267.

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