Evolutionary and Ecological Factors Influencing an Anuran Community Structure in an Atlantic Rainforest Urban Fragment

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Many factors influence community structure, including stochastic, historical, or ecological factors. We test how phylogenetic relationships and morphology influence patterns of diet and microhabitat niche partitioning of an anuran community in the Atlantic forest in northeastern Brazil. We conducted fieldwork in an urban fragment of the Atlantic forest. Niche breadth for microhabitat use was low for all species pairs, whereas diet niche breadth was high for most. The main prey categories were Coleoptera and Orthoptera, and closely related species showed a distinct diet. We also found a non-random pattern of resource use for diet and microhabitats. Phylogenetic relationships influenced microhabitat, but not diet, use of hylids and leptodactylids. Morphological variability was not clustered in only one node, nor in a few nodes, and trait values were not skewed to the root or the tips of the phylogeny and appear to concur with phylogenetic relationships for microhabitat use. Therefore, phylogenetic relationships influenced microhabitat use, whereas ecological processes determined diet.

Muitos fatores influenciam a estrutura de uma comunidade, sejam de ordem estocástica, histórica ou ecológica. Nós testamos como as relações filogenéticas e a morfologia influenciam os padrões na partição de nicho da dieta e uso de microhabitat em uma comunidade de anuros de Mata Altântica do nordeste do Brasil. Nós conduzimos o estudo em um fragmento urbano de floresta atlântica no nordeste brasileiro. A largura de nicho de uso de microhábitat foi baixa para todos os pares de espécies, enquanto a de dieta foi alta para a maioria. As principais categorias alimentares foram Coleoptera e Orthoptera, sendo que espécies mais próximas filogeneticamente apresentaram dieta distinta. Nós também encontramos um padrão não aleatório no uso dos recursos de dieta e uso de microhábitat. O grau de parentesco influenciou o uso de microhábitat em hilídeos e leptodactilídeos, mas não a dieta. A variabilidade morfológica não foi agrupada em um nó, nem em poucos nós, e os valores dos atributos não estão enviesados em direção a raiz ou aos ramos terminais da filogenia, e, aparentemente, corrobora as relações filogenéticas para uso de microhábitat. Portanto, o parentesco filogenético influenciou o uso de microhábitat, enquanto a dieta foi mais influenciada por processos ecológicos.

MANY factors influence community structure, including stochastic, historical, or ecological ones, such as competition, predation, or parasitism (Cody and Diamond, 1975; Gee and Giller, 1990). Some factors can be used to test for patterns of resource partitioning in frog assemblages, such as species composition, diet, microhabitat use (of space), activity, and acoustic and morphometric aspects (e.g., Eterovick and Sazima, 2000; Santos et al., 2004; Protázio et al., 2015).

Competition has already been regarded as a primary process for structuring assemblages due to the competitive exclusion principle (Gause, 1934; Connell, 1961). However, this idea has been challenged by the contemporary coexistence theory, which states that maintenance of species diversity is related to a stable coexistence by equalizing species fitness or stabilizing the intra- and interspecific interactions via mechanisms like resource partitioning and environmental factors (Chesson, 2000; Chase and Leibold, 2003; HilleRisLambers et al., 2012). Some studies with anuran assemblages from arid environments showed that water availability plays a key role in structuring anuran assemblages, whereas resources such as microhabitats and food could not be limiting factors (Vieira et al., 2009; Protázio et al., 2015). In addition, assemblages from more mesic environments also appear to be unaffected by spatial competition (Afonso and Eterovick, 2007). Finally, these patterns clearly indicate that similar species can still coexist if their competitive ability is low or equivalent (HilleRisLambers et al., 2012).

Recently, more attention has been given to phylogenetic approaches in community assembly studies (Webb et al., 2002; Cavender-Bares et al., 2009; Ernst et al., 2012), suggesting that environmental and biotic filters, along with phylogenetic relations, are major forces in community assembly (Webb, 2000). Zimmerman and Simberloff (1996) showed that most amphibians in a "terra-firme" forest area in central Amazonia use lentic water bodies as breeding sites, whereas some lineages in Southeast Asia use riparian environments. The authors also showed that this phenomenon is related to ancestral characteristics.

However, few studies of anuran assemblages attempt to encompass ecological and phylogenetic aspects. Eterovick et al. (2010) studied five assemblages in the Atlantic forest, from larvae to adults, and found no relationship between phylogeny and microhabitat use for tadpoles and a weak relationship for adults, indicating that despite not exhibiting phylogenetic conservatism, microhabitat use might be interesting for investigating adaptation and natural selection in species.

Morphology is an interesting tool in the study of assemblages, since data can be easily obtained and can reflect ecological habits, like spatial and diet resource use, thus it is commonly used as a measure of niche dimension (see Ricklefs et al., 1981). Some studies have associated certain body measurements with the use of environmental resources, such as the relative leg length of lizards and the use of space (Pianka and Pianka, 1976) or frog head measurements with the consumed prey volume (Toft, 1981), indicating that these measures might be indirect indicators of species ecology, as a

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reflection of the phylogeny, allowing a given organism to explore a given resource (Losos, 2010).

In the present study, we test how phylogenetic relationships and morphology influence patterns of diet and microhabitat partitioning of an anuran community in the Atlantic forest in northeastern Brazil.

MATERIALS AND METHODS

Study site and sampling.—We conducted fieldwork from August 2011 to July 2012 in an artificial dam of the Jaguaribe River (7°08′42″S, 34°51′54″W), located at "Jardim Botânico Benjamim Maranhão," in João Pessoa, Paraíba state, an Atlantic forest fragment in northeastern Brazil. We sampled during a five-day period each month, for a total of 60 days of sampling. The study area has a 515 ha Atlantic forest fragment within the urban area of João Pessoa, adjacent to the Federal University of Paraíba. The climate of the study area is warm and wet, with rains in the winter (March to August), a mean annual temperature of about 25°C, a total annual rainfall from 1,500 to 1,700 mm, and a relative humidity of about 80%. The dry season is short, ranging from one to three months (Lima and Heckendorff, 1985). The herpetofauna of this area consists of 37 species of amphibians and reptiles (Santana et al., 2008).

We sampled adult anurans using visual and auditory surveys limited by time and to casual encounters (Scott et al., 1994). Visual surveys consisted of trips during the day, from 0800 h to 1200 h, and at night, from 1930 h to 2230 h. Visual searches consisted of walking along the margins of the river, as well as in the adjacent forested areas, including small pools formed by rain, trunks and fallen branches, shrubs, grasses, trees and leaf litter, always at the same points, covering approximately 50 ha. For the morphological and dietary analysis, we also used eight pitfall trap arrays with drift fences placed adjacent to the water body (Scott et al., 1994). Previous studies found that the diet of specimens collected with these traps did not differ statistically in composition and ingested volume from haphazardly collected individuals, since these traps can be checked daily (Costa et al., 2008). Each array consisted of four 40 L plastic buckets arranged in a "Y," with a central bucket connected to each of three peripheral buckets using a 5 m long plastic drift fence, forming three 120° angles. The collected specimens were euthanized with an injection of Tiopental, fixed in 10% formalin, and stored in 70% ethanol at the Coleção Herpetológica da Universidade Federal da Paraíba (CHUFPB). Since this study was part of a bigger project involving other studies, alternative non-lethal techniques were not possible. In the expeditions, no globally or locally endangered species (e.g., IUCN listed as threatened) were killed. We took into account the ethical guidelines provided by the American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists' League (HL), and the Society for the Study of Amphibians and Reptiles (SSAR). Finally, IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) and SUDEMA (Superintendência de Administração do Meio Ambiente) provided all necessary permissions to sample animals.

Microhabitat.—We divided the microhabitats into 11 categories based on substrate, height, and distance from the water body in which the specimen occurred (adapted from Afonso and Eterovick, 2007): arbustive stratum in the water, arbustive stratum at the margin of the water body, arboreal stratum in the water, arboreal stratum at the margin of the water body, herbaceous stratum in the water, herbaceous stratum at the margin of the water body, rock in the water, rock on the water's edge, litter in the water, litter on the waterfront, and leaf litter. We measured the abundance of individuals for each species sampled in each category. The Simpson index (1949) was used to calculate the niche breadth:

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

where p_i is the proportion of individuals found using resource i, and n is the total number of categories. Values varied from 1.0 (use of only one microhabitat) to 11 (use of all microhabitats in the same proportion). We standardized these values to a known interval from 0 to 1.

We calculated the spatial niche overlap using the Pianka index (1973), which can vary from 0 (no overlap) to 1 (full overlap). The index is represented by the following equation:

$$O_{jk} = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2}}$$

where p_{ij} is the proportion of resource i used by species j, p_{ik} is the proportion of resource i used by species k, and n is the total resources used. We tested for significance of these indices using null models (Gotelli, 2000) with Ecosim software (Gotelli and Entsminger, 2004), based on 29,999 randomizations. We compared the observed mean overlap with the simulated mean overlap. Significance was reached when the mean observed overlap was 95% or less compared to the simulated one. We used "randomization algorithm RA2" ("zero state retained" and "niche breadth relaxed" [Winemiller and Pianka, 1990]). We performed this analysis both including all species and excluding the rarest species ($n < 5$) to avoid bias related to sample size. Since both analyses showed similar results, we will only include the analysis that used all species.

To evaluate the influence of phylogeny on microhabitat use, we performed a Canonical Phylogenetic Ordination (CPO; Giannini, 2003). This is an ordination method that promotes the orientation of a set of variables insomuch that a relationship with a second set of variables is maximized. The abundance of each captured species on each microhabitat category is the response matrix (Y), whereas the coded phylogeny is the predictor matrix (X), containing all monophyletic groups in the community. We used the Pyron and Wiens (2011) tree to code the phylogeny, so that each group is coded separately as a binary variable. The analysis consists of finding subsets (columns of X) that best explain the variation in Y, using correspondence analysis combined with Monte Carlo permutations. We performed this analysis using CANOCO 4.5 for Windows with the following settings: "symmetric scaling," "biplot scaling," "downweighting of rare species," "manual selection of environmental variables" (monophyletic groups), "9,999 permutations," and "unrestricted permutations" (Giannini, 2003). We performed two separate analyses: one with all species and another excluding rare species. Since both analyses showed similar results, we will only discuss the results for the CPO that used all species.

Diet.—We analyzed stomach contents using a stereoscopic microscope and identified up to the order level. We measured

the maximum length and width of each intact prey with a digital caliper (0.01 mm) and estimated its volume using an ellipsoid formula (see Solé et al., 2009):

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

where w is the prey width, and l is prey length.

We calculated dietary niche breadth using Simpson's index (1949). This value ranged from 1 (use of only one food category) to 28 (use of all categories in the same proportion). We standardized the niche breadth to a known interval from 0 to 1.

To infer the importance of each prey category in the species diet, we calculated the Importance Index for pooled stomachs using the following equation (see Solé et al., 2009):

$$I = (F\%)(N\% + V\%)$$

where F% is the percentage of occurrence, N% is the numeric percentage, and V% is the volumetric percentage.

To evaluate prey availability in the environment, we installed five pitfall traps (300 mL plastic cups) to collect soil invertebrates and one window trap for winged invertebrates at random locations close to sampling sites, covering all microhabitat categories. We filled traps with 70% ethanol and a few drops of detergent to break the surface tension (Leather, 2005). We preserved collected invertebrates in 70% glycerinated ethanol. We performed screening and identification of prey using a stereoscopic microscope and the literature (Triplehorn et al., 2005), as well as consultations with experts. We identified specimens to order level.

We calculated the dietary niche overlap using Pianka's index (1973), as described above for spatial niche. We also performed a null model analysis to test for significance in food resource partitioning. We defined each food prey weight *a priori* from the abundance of food in the environment. We also performed this analysis in two ways, either taking the whole assemblage into account or excluding the rarest species, as previously described.

To test the influence of phylogeny on diet, we used a CPO (Giannini, 2003), as described for microhabitat. Due to differences in sample size (microhabitat was not recorded for some species, since they were captured only in pitfall traps), we used two different trees: one for microhabitat and one for diet and morphometry.

Morphometry.—Following Napoli and Pimenta (2009), we measured 11 morphometric variables for each individual using a digital caliper (0.01 mm): snout–vent length (SVL), head length (HL), head width (HW), inter-orbit distance (IOD), eye–nostril distance (END), inter-nostril distance (IND), thigh length (ThL), tibia length (TiL), feet length (FL), eye diameter (ED), and inter-eye distance (IED; Appendix 1). To evaluate if the morphometry was a labile or conserved trait in the assemblage, we performed the analysis proposed by Pavoine et al. (2010), which takes into account the phylogenetic tree, the distribution of relative abundance (frequencies) of species, and a matrix of morphological variable distances among species. From this, we tested if the morphological variability of species was clustered in the phylogeny, so that only one (SN test) or a few nodes (FN test) expressed the most morphological diversity, and if the trait values are skewed to the root or the tips of the phylogeny (Ro test). The analysis was conducted in R software (R Core Team, 2015), using the packages *ape* and *ade4*.

RESULTS

Species composition.—We collected 887 individuals, totaling 16 species, including one Microhylidae (*Chiasmocleis alagoanus*), one Ranidae (*Lithobates palmipes*), six Leptodactylidae (*Adenomera marmorata*, *Leptodactylus latrans*, *Leptodactylus natalensis*, *Leptodactylus troglodytes*, *Leptodactylus vastus,* and *Physalaemus cuvieri*), seven Hylidae (*Dendropsophus branneri*, *Dendropsophus minutus*, *Dendropsophus oliveirai*, *Hypsiboas albomarginatus*, *Hypsiboas raniceps*, *Scinax nebulosus,* and *Scinax x-signatus*), and one Craugastoridae (*Pristimantis ramagii*).

Microhabitat.—We recorded microhabitats for 795 individuals (89% of total). We found most hylids in arbustive and herbaceous strata, while leptodactylids and *L. palmipes* were found in horizontal microhabitats associated with water, like ground, rocky areas, or leaf litter. We found *Pristimantis ramagii* more often in leaf litter far from the water body, in contrast to the other species (Table 1).

Niche breadth was low for all species (Table 1). Hylids had the largest niche breadths, especially for *S. x-signatus* and species of *Dendropsophus*. Leptodactylids had an even lower niche breadth, with *L. vastus* showing the greatest niche breadth among species of the genus (1.96). Although *L. palmipes* occurred in most microhabitat categories, it showed a low niche breadth (2.09) because most individuals occurred at the river margin and in aquatic herbs. *Pristimantis ramagii* was the most specialized species regarding microhabitat use, with a spatial niche of 1.87, since most individuals used leaf litter. Niche overlap was low except for hylids (Table 2). The observed mean (0.255) was lower ($P = 0.004$) than was the simulated mean (0.323), indicating a non-random use of space.

Phylogeny influenced microhabitat use for hylids (clades B and E) and leptodactylids (clades I and J; Table 3; Fig. 1A), dividing species into two main guilds: arboreal and terrestrial. The basal node, with groups B (Hylidae and *P. ramagii*) and I (Leptodactylidae; Fig. 1A), corresponded to 44.89 and 32.34%, respectively, of the total variation (Table 3).

Diet.—We analyzed the stomach contents of 887 individuals, totaling 1,886 prey (Table 4). For most species, Coleoptera and Orthoptera were the most important categories, followed by Formicidae, Araneae, and Hemiptera. The proportion of empty stomachs was 22%.

Niche breadth was high for half of the species that showed at least four prey categories in the diet, whereas *L. palmipes* was the most generalist (0.50). Other species, such as *L. natalensis* and *P. ramagii,* also had a more generalized diet (Table 4).

Niche overlap varied from 0 to 0.997 (Table 2). *Chiasmocleis alagoanus* and *L. vastus* showed low niche overlap compared to other species, while *P. ramagii* showed a high dietary overlap with *H. albomarginatus* and *H. raniceps*. *Lithobates palmipes* showed a high niche overlap only with *D. oliveirai* and *L. latrans*. Hylids usually did not show a high overlap among them. The observed mean (0.198) was lower ($P < 0.001$) compared to the simulated mean (0.356), indicating a non-random use of food resources. There was no significant effect of phylogeny on diet (Table 3; Fig. 1B).

Morphology.—Morphological variability is not clustered in only one node (SN test = 0.40), nor in a few nodes (FN test = 0.12), and trait values are not skewed to the root or the tips of the phylogeny (Ro test = 0.32). However, a detailed inspection of the decomposition of the morphological diversity among the nodes of the phylogenetic tree indicates that most diversity (e.g., phenotypic variation) is clustered in the nodes with all species of *Leptodactylus* and *Dendropsophus*, indicating that these species showed similar morphological traits among each other, but were different from others (Fig. 2).

DISCUSSION

Microhabitat.—Hylids had the greatest niche breadth and generally used more microhabitats along the vertical stratum, such as trees and shrubs. This pattern is common for species of this family (Wells, 2007) and seems to be a conserved trait. Their wide spatial distribution is due to the presence of adhesive discs on fingers and toes, which confers an adaptive advantage for inhabiting arboreal strata (Wells, 2007). Conversely, leptodactylids had a narrower niche breadth. Most species occurred at the margin of the water body, similar to other studies (Cardoso and Andrade, 1989; Moreira et al., 2008; Vieira et al., 2009), indicating a strong influence of phylogeny on microhabitat use. The use of aquatic environments by *L. palmipes* has a phylogenetic influence as well, since this behavior has also been observed in most species of this family (Wilbur, 1972; Given, 1990; Gorman et al., 2009).

The strong spatial structure does not necessarily indicate that the species are avoiding competition. Spatial structure seems to be influenced by phylogeny (Losos, 1996), as indicated by the CPO. In addition, species were divided into two guilds: arboreal species, composed of the hylids, and ground-dwelling species, comprising the remaining families that mainly use the horizontal stratum. This fact has been documented in other assemblages of tropical forests (Vitt and Caldwell, 1994; Parmelee, 1999) and in dry tropical areas (Protázio et al., 2015) and may be explained by an adaptive radiation triggered by evolution of a trait that allowed the utilization of new resources that was not possible before (ecological opportunity; see Losos, 2010). In a general way, hylids show morphological adaptations (e.g., enlarged toepads) that allow them to exploit resources along the vertical stratum (Wells, 2007). In fact, hylids have a high overall diversity (Wiens et al., 2011) and were the most diverse family for this study (seven species). Eterovick et al. (2010) suggested that microhabitat use is a plastic and variable trait for amphibians. However, the statistical test used (Mantel test) did not account for possible non-stationary effects.

Diet.—The numeric niche breadth confirms that most species have generalist and opportunistic habits. However, the volumetric niche breadth, which was smaller than was the numeric breadth for almost all species, indicated that species fed on prey with similar volumes. Some studies documented a positive relationship between frog head size and prey volume (Toft, 1980, 1981; Dietl et al., 2009), which might allow species to eat more prey items (regardless of size), promoting the increase in niche breadth. However, this was not the case in this study.

Chiasmocleis alagoanus had a specialized diet of Formicidae and Isoptera, reflecting a strong conservation in the diet

Table 1. Frequency of microhabitat use (percentage in parentheses) of an anuran assemblage in an Atlantic rainforest fragment in the easternmost point of Neotropical region.

Categories	*D. b.*	*D. m.*	*D. o.*	*H. a.*	*H. r.*	*Pr. r.*	*L. l.*	*A. m.*	*L. n.*	*L. t*	*L. v.*	*Li. p.*	*S. n.*	*S. x.*
Shrub water	48 (29.6)	9 (22.5)	40 (41.4)	7 (26.9)	10 (58.8)	–	–	–	–	–	–	1 (0.5)	28 (71.8)	4 (28.6)
Shrub margin	33 (20.4)	17 (42.5)	31 (32.0)	–	1 (5.9)	1 (0.7)	–	–	–	–	–	–	1 (2.6)	3 (21.4)
Tree water	–	3 (7.5)	–	14 (53.8)	1 (5.9)	–	–	–	–	–	–	–	–	1 (7.1)
Soil margin	2 (1.2)	–	–	–	–	3 (2.0)	–	3 (30.0)	3 (7.7)	–	3 (42.9)	129 (66.1)	–	–
Herb water	71 (43.8)	11 (27.5)	10 (10.3)	4 (15.4)	4 (23.5)	2 (1.4)	1 (100)	–	–	–	–	34 (17.4)	10 (25.6)	6 (42.8)
Herb margin	4 (2.5)	–	16 (16.4)	–	–	–	–	–	–	–	–	–	–	–
Rock water	–	–	–	–	1 (5.9)	–	–	–	1 (2.6)	–	4 (57.1)	2 (1.0)	–	–
Rock margin	–	–	–	–	–	–	–	–	–	–	–	12 (6.1)	–	–
Litter water	–	–	–	–	–	–	–	–	28 (71.8)	–	–	3 (1.5)	–	–
Litter margin	4 (2.5)	–	–	1 (3.9)	–	99 (67.3)	–	7 (70.00)	7 (17.9)	1 (100)	–	14 (7.2)	–	–
Litter woods	–	–	–	–	–	42 (28.6)	–	–	–	–	–	–	–	–
N	162	40	97	26	17	147	1	10	39	1	7	195	39	14
NB_n	3.1	3.2	3.2	2.6	2.4	1.9	1.0	1.7	1.8	1.0	2.0	2.1	1.7	3.2
SNB_n	0.3	0.3	0.3	0.2	0.2	0.2	0.1	0.2	0.2	0.1	0.2	0.2	0.2	0.3

Note: *D. b.: Dendropsophus branneri, D. m.: Dendropsophus minutus, D. o.: Dendropsophus oliveirai, H. a.: Hypsiboas albomarginatus, H. r.: Hypsiboas raniceps, Pr. r.: Pristimantis ramagii, L. l.: Leptodactylus latrans, A. m.: Adenomera marmorata, L. n.: Leptodactylus natalensis, L. t.: Leptodactylus troglodytes, L. v.: Leptodactylus vastus, Li. p.: Lithobates palmipes, S. n.: Scinax nebulosus, S. x.: Scinax x-signatus,* NB_n: numeric niche breadth, SNB_n: standardized numeric niche breadth.

Table 2. Niche overlap for diet and microhabitat use (italic) of an anuran assemblage in an Atlantic rainforest fragment in the easternmost point of Neotropical region.

	C. a.	*D. b.*	*D. m.*	*D. o.*	*H. a.*	*H. r.*	*Pr. r.*	*Li. p.*	*L. l.*	*A. m.*	*L. n.*	*L. t.*	*L. v.*	*P. c.*	*S. n.*	*S. x.*
C. a.	—	0.085	0.880	<0.001	0.003	0.000	0.000	0.000	0.000	0.440	0.226	<0.001	<0.001	0.012	0.180	0.997
D. b.	—	—	0.120	0.368	0.073	0.173	0.375	0.044	0.006	0.095	0.065	0.314	<0.001	<0.001	0.564	0.090
D. m.	—	*0.862*	—	0.203	0.413	0.419	0.313	0.012	0.043	0.394	0.276	0.230	<0.001	0.216	0.225	0.902
D. o.	—	*0.748*	*0.825*	—	0.410	0.441	0.604	0.575	0.592	0.272	0.162	0.592	<0.001	0.006	0.267	0.027
H. a.	—	*0.419*	*0.412*	*0.366*	—	0.950	0.684	0.019	0.100	0.004	0.173	0.466	0.000	0.000	0.103	0.063
H. r.	—	*0.794*	*0.631*	*0.799*	*0.566*	—	0.736	0.026	0.100	0.018	0.178	0.548	0.000	0.000	0.289	0.061
Pr. r.	—	*0.058*	*0.016*	*0.009*	*0.061*	*0.008*	—	0.094	0.071	0.241	0.327	0.640	<0.001	0.015	0.422	0.048
Li. p.	—	*0.224*	*0.127*	*0.052*	*0.072*	*0.101*	*0.127*	—	0.875	0.147	0.276	0.098	0.212	0.003	0.048	0.001
L. l.	—	*0.771*	*0.492*	*0.185*	*0.247*	*0.367*	*0.020*	*0.252*	—	0.000	0.018	0.048	0.000	0.000	0.008	0.006
L. m.	—	*0.048*	*0.000*	*0.000*	*0.057*	*0.000*	*0.856*	*0.472*	*0.000*	—	0.293	0.089	<0.001	0.008	0.169	0.439
L. n.	—	*0.013*	*0.000*	*0.000*	*0.015*	*0.003*	*0.225*	*0.146*	*0.000*	*0.262*	—	0.576	0.276	0.004	0.100	0.237
L. t.	—	*0.043*	*0.000*	*0.000*	*0.062*	*0.000*	*0.920*	*0.104*	*0.000*	*0.919*	*0.241*	—	<0.001	0.009	0.482	0.029
L. v.	—	*0.130*	*0.000*	*0.000*	*0.000*	*0.070*	*0.016*	*0.586*	*0.000*	*0.236*	*0.090*	*0.000*	—	0.004	0.000	0.000
P. c.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.000	0.000
S. n.	—	*0.762*	*0.570*	*0.779*	*0.490*	*0.989*	*0.006*	*0.092*	*0.336*	*0.000*	*0.000*	*0.000*	*0.000*	—	—	0.187
S. x.	—	*0.354*	*0.326*	*0.486*	*0.230*	*0.516*	*0.024*	*0.793*	*0.000*	*0.325*	*0.085*	*0.000*	*0.494*	—	*0.521*	—

Note: *C. a.: Chiasmocleis alagoanus*, *P. c.: Physalaemus cuvieri*. The abbreviations for other species are the same as in Table 1.

niche of the Microhylidae (Das, 1996; Parmelee, 1999; Solé et al., 2002; Wells, 2007). Despite a generalist feeding behavior, *P. ramagii* also showed a diet similar to that of closely related species, indicating a strong relationship with this major microhabitat and the kinds of prey found in leaf litter (Dietl et al., 2009).

Many studies suggest that species belonging to the family Ranidae have generalist habits and are highly influenced by food availability (Hedeen, 1972; Popovic et al., 1992; Aszalós et al., 2005), confirming the pattern found for *L. palmipes*, which showed the most generalist diet of the assemblage. Only *A. marmorata* and *L. natalensis* among leptodactylids had diverse food habits, differing from the generalist habits reported elsewhere (Parmelee, 1999). The distinct feeding habits of *L. vastus* can be explained by its opportunistic habits that are highly related to prey size; it selects larger prey, including some vertebrates (Gouveia et al., 2009; Fonseca et al., 2012), although it also feeds on prey items that are similar to other Leptodactylidae, such as Formicidae and Coleoptera (França et al., 2004). Hylids showed the most distinct diet pattern—they usually eat larger prey (Orthoptera and Lepidoptera) in small amounts (Toft, 1981; Wells, 2007). However, some species showed the opposite pattern, such as *S. x-signatus* and *S. nebulosus*, for which Isoptera was one of the main prey items, and *D. minutus*, which had Formicidae as its main prey item, contrasting with other studies (Van Sluys and Rocha, 1998; Santos et al., 2004; Solé et al., 2005).

Distantly related species, such as *S. x-signatus*, *C. alagoanus,* and *P. ramagii,* showed a high overlap, whereas most species showed a low overlap. These results, coupled with the lack of influence of phylogeny, suggest that food could be a limiting resource. This is reflected in the feeding ecology of the species, which tends to change their habits (Winemiller and Pianka, 1990; Vitt, 1995). However, studies that take into account the accumulation of fat bodies in these individuals would help to confirm this hypothesis.

Morphometry.—Despite morphology being a labile trait in this assemblage, species of *Leptodactylus* and *Dendropsophus* showed similar traits among themselves (Fig. 2). This concurs with the results for microhabitat use, which suggest that the morphology in these two groups of species in the assemblage could be adapted to each microhabitat use, since both genera occur in different habitats—one is strictly

Table 3. Results of canonical phylogenetic ordination for microhabitat and diet data, based on Monte Carlo permutations. Total percentage of explained variance for each group, *F* and *P* values for each variable. See Figure 1 for identification of each group.

Group	Variation	Variation (%)	*F*	*P*
Microhabitat				
B	0.791	44.89	4.840	0.0006
I	0.570	32.34	3.103	0.0070
J	0.568	32.23	3.092	0.0073
E	0.512	29.05	2.713	0.0070
L	0.385	21.85	1.921	0.0969
K	0.314	17.82	1.517	0.1411
F	0.307	172.42	1.480	0.1236
H	0.294	16.68	1.410	0.1751
G	0.247	14.01	1.160	0.2788
A	0.230	13.05	1.072	0.3108
C	0.210	11.91	0.970	0.4478
D	0.160	9.08	0.22	0.6894
Diet				
M	0.273	23.82	2.429	0.0899
D	0.194	16.92	1.651	0.1665
C	0.169	14.64	1.418	0.1245
J	0.157	13.70	1.301	0.1488
L	0.148	12.91	1.225	0.2368
K	0.145	12.65	1.191	0.2560
A	0.133	11.60	1.087	0.3550
B	0.133	11.60	1.087	0.3455
H	0.121	10.55	0.980	0.3688
F	0.106	9.24	0.857	0.6332
G	0.086	7.50	0.687	0.7191
I	0.079	6.89	0.627	0.7749
E	0.071	6.89	0.561	0.7647
N	0.056	4.88	0.442	0.8851

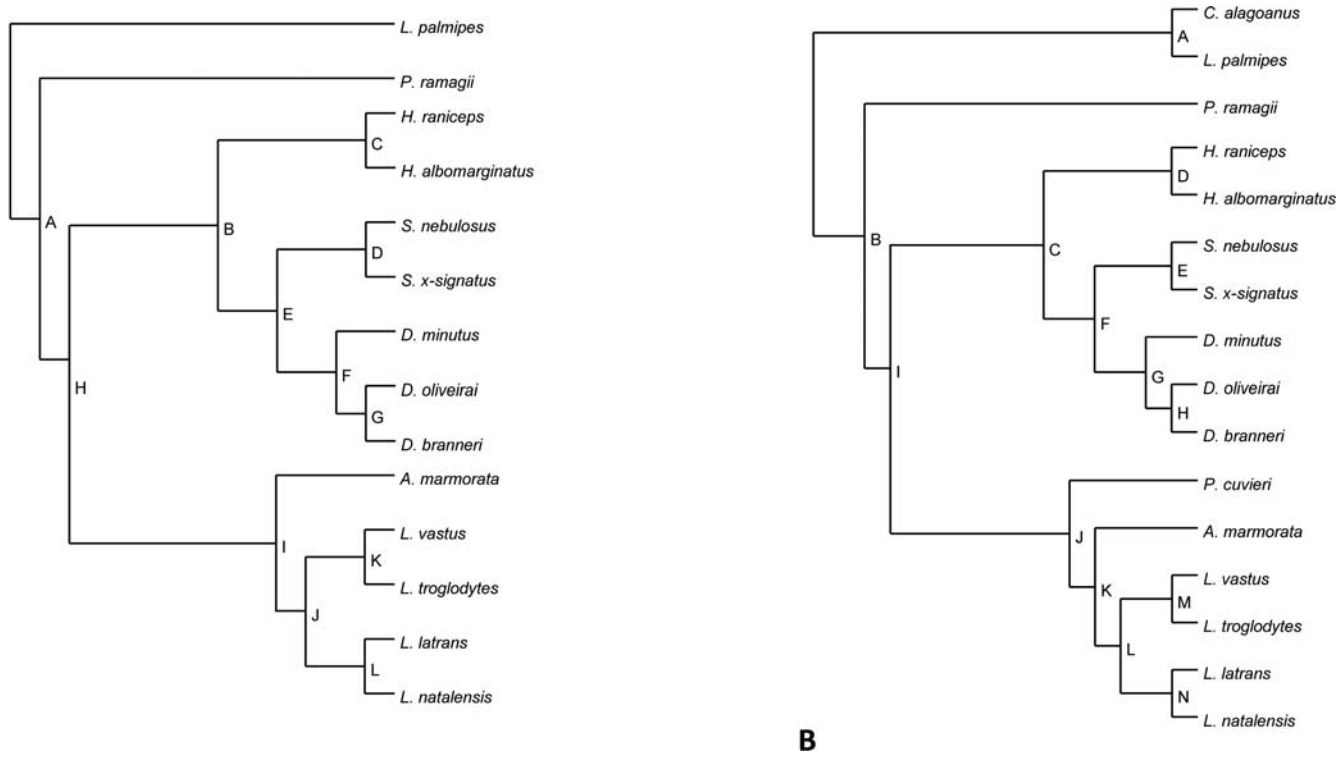

Fig. 1. Phylogenies used in Canonical Phylogenetic Ordination, based on Pyron and Wiens (2011). Microhabitat (A) and diet (B).

arboreal (*Dendropsophus* spp.) and the other is associated with more terrestrial habits (*Leptodactylus* spp.). This is supported by the presence of similar ecological traits in other closely related species from other areas (Eterovick and Sazima, 2000; Conte and Machado, 2005; Vieira et al., 2009; Protázio et al., 2015). In fact, the way that resources are used and the evolutionary history of the species are connected, either convergent evolution or natural selection is plausible (Losos, 2011). The morphology of the species of *Dendropsophus* allows them to use the vertical microhabitat strata. On the other hand, the morphology of species of *Leptodactylus* allows them to be associated with more terrestrial habits. Studies with other taxonomic groups also corroborate this idea (Losos, 1990; Mesquita et al., 2006; França et al., 2008), highlighting the importance of morphological components in determining patterns of resource use in assemblages.

MATERIAL EXAMINED

All from João Pessoa, Paraíba, Brazil.

Adenomera marmorata: (11) CHUFPB 2145, 6975, 9414, 10125, 10126, 10557–10559, 10653, 10762, 10775.

Chiasmocleis alagoanus: (6) CHUFPB 7270, 10107, 10109–10112.

Dendropsophus branneri: (152) CHUFPB 2142, 2143, 2155, 3495, 3498, 3534, 3541, 3542, 3624–3632, 4494, 4495, 4497, 4499, 4553–4559, 4625–4627, 4636–4657, 4659–4664, 4839, 4840, 4956, 4973, 5027, 5028, 6859, 6860, 6863, 6864, 6958–6963, 6965–6974, 6984–6996, 7018, 7262–7267, 8374–8377, 8388–8391, 8965, 8989–8993, 9443–9457, 9468–9471, 10156–10179.

Dendropsophus minutus: (39) CHUFPB 10114–10120, 10136–10145, 10617–10627, 10638–10649.

Dendropsophus oliveirai: (89) CHUFPB 2122–2125, 2144, 2153, 2154, 3494, 3499, 3536, 3539, 4492, 4498, 4551, 4552, 4622–4624, 4628, 4658, 4841–4846, 4953–4955, 4971, 4972, 5024–5026, 6854–6858, 6875–6877, 6964, 6983, 7002–7017, 7083, 7084, 7239–7241, 8355–8357, 8366–8373, 8378–8382, 8994, 10146–10155, 10565.

Hypsiboas albomarginatus: (26) CHUFPB 3535, 8343–8346, 10597–10607, 10628–10637.

Hypsiboas raniceps: (17) CHUFPB 2129, 2130, 4633, 4634, 6853, 7242, 8359–8362, 8383, 8976, 8980, 8981, 9416, 10652, 10763.

Leptodactylus latrans: (1) CHUFPB 3639.

Leptodactylus natalensis: (106) CHUFPB 2119, 2146, 3543, 3606, 3607, 4974, 5009, 7271–7280, 8329, 8331–8340, 8347–8350, 8963, 8977–8979, 9392–9396, 9403–9413, 9435, 10081, 10088–10106, 10124, 10132–10135, 10182–10185, 10573–10596.

Leptodactylus troglodytes: (7) CHUFPB 2131, 2147, 6954, 7074, 7269, 8341, 8968.

Leptodactylus vastus: (7) CHUFPB 2120, 2121, 6869, 8969, 8970, 9419, 9420.

Lithobates palmipes: (215) CHUFPB 2106–2118, 2132–2136, 2149–2152, 3490–3493, 3531–3533, 3635–3638,

Table 4. Importance index of prey categories for an anuran assemblage in an Atlantic rainforest fragment in the easternmost point of Neotropical region.

Cat.	*C. a.*	*D. b.*	*D. m.*	*D. o.*	*H. a.*	*H. r.*	*P. r.*	*Li. p.*	*L. l.*	*A. m.*	*L. n.*	*L. t.*	*L. v.*	*P. c.*	*S. n.*	*S. x.*
Aca	19.6	10.8	—	41.3	—	158.7	36.9	1.4	—	116.5	7.6	—	—	—	27.1	—
Ann	—	—	—	—	—	—	—	1.0	—	—	—	—	—	—	—	—
Ara	—	395.9	293.2	38.8	393.4	2031.1	194.6	160.8	—	97.4	25.7	172.5	—	—	1171.1	—
Bla	—	—	—	7.1	—	—	—	41.8	4541.7	—	1.5	—	—	—	—	—
Col	—	33.7	303.0	11.2	169.3	97.4	180.4	115.0	—	30.1	218.8	60.6	32.5	—	24.1	790.2
Coll	—	35.1	—	14.6	—	—	223.8	0.2	—	12.7	—	—	—	2117.6	—	—
Der	—	—	—	—	102.9	—	—	—	—	—	—	—	—	—	—	—
Chi	—	—	—	—	—	—	—	3.5	—	—	0.9	—	55.8	—	—	—
Dip	—	—	—	—	—	—	—	11.8	—	—	0.2	—	3643.6	—	—	—
Dipt	—	1586.4	17.4	753.5	—	—	9.7	8.3	—	41.1	22.3	—	—	—	13.7	—
Esc	—	—	—	—	—	—	—	—	—	—	0.2	27.5	—	—	—	—
Gas	—	—	38.0	—	—	—	2.3	70.5	—	171.5	6.2	—	—	—	—	—
Hem	—	791.2	—	355.4	190.4	79.4	531.9	61.0	—	19.2	197.0	—	32.5	—	301.2	421.0
For	3487.9	11.7	2347.3	102.9	—	—	342.3	112.2	—	666.9	514.4	362.4	563.4	9098.1	270.3	—
Hym	—	26.9	—	39.0	—	—	7.5	112.6	—	—	4.0	—	—	—	13.5	—
Iso	—	—	—	4.4	—	—	1.5	4.6	—	168.4	71.2	—	—	—	—	—
Isop	3931	22.1	291.9	—	366.3	—	2.9	0.5	—	597.1	156.0	—	—	—	709.2	4061.0
Lar	—	136.4	23.6	795.2	—	—	181.3	182.3	—	130.6	228.7	932.2	—	—	178.7	—
Lep	—	32.2	—	35.1	—	—	9.1	1.2	—	—	1.3	—	—	—	13.5	—
Odo	—	—	—	—	—	79.4	—	99.6	—	—	0.2	—	—	—	—	—
Opi	—	—	—	—	—	—	3.9	14.9	—	—	169.9	220.4	—	—	—	—
Ort	—	45.8	250.3	110.9	3472.3	2260.7	249.6	101.6	5458.3	—	131.4	788.4	32.5	—	123.6	221.1
Pha	—	—	—	—	—	—	—	0.1	—	—	—	—	—	—	—	—
Pse	—	—	—	—	—	—	1.7	—	—	—	—	—	—	—	—	—
Thy	—	—	—	0.7	—	—	0.2	—	—	—	—	—	—	—	—	—
Tri	—	—	—	—	—	—	—	0.1	—	—	—	—	—	—	—	—
Fis	—	—	—	—	—	—	—	168.7	—	—	—	—	—	—	—	—
Ver	—	—	—	—	—	—	—	5.1	—	—	—	—	717.7	—	—	—
N	6	155	39	98	26	13	146	219	1	11	105	8	6	2	38	14
NB_n	2.1	6.1	3.1	6.7	5.3	3.6	8.3	13.6	2.0	5.6	7.8	2.1	2.9	2.0	5.7	1.5
SNB_n	0.1	0.2	0.1	0.2	0.2	0.1	0.3	0.5	0.1	0.2	0.3	0.1	0.1	0.1	0.2	0.1
NB_v	1.3	6.0	2.9	3.7	1.3	1.3	4.5	8.6	1.9	4.1	6.5	3.6	2.5	1.8	3.2	1.8
SNB_v	0.1	0.2	0.1	0.1	0.1	0.1	0.2	0.3	0.1	0.2	0.2	0.1	0.1	0.0	0.1	0.1

Note: Cat: Categories, Aca: Acari, Ann: Annelida, Ara: Araneae, Bla: Blattaria, Col: Coleoptera, Coll: Collembola, Der: Dermaptera, Chi: Chilopoda, Dip: Diplopoda, Dipt: Diptera, Esc: Escorpionida, Gas: Gastropoda, Hem: Hemiptera, For: Hymenoptera (Formicidae), Hym: Hymenoptera (others), Iso : Isopoda, Isop: Isoptera, Lar: insect larvae, Lep: Lepidoptera, Odo: Odonata, Opi: Opilionida, Ort: Orthoptera, Pha: Phasmatodea, Pse: Pseudoescorpionida, Thy: Thysanoptera, Tri: Tricoptera, Fis: Vertebrata (fish), Ver: Vertebrata (others), NB_n: numeric niche breadth, SNB_n: standardized numeric niche breadth, NB_v: volumetric niche breadth, SNB_v: standardized volumetric niche breadth. Species abbreviations are the same as in Table 2.

4491, 4513–4520, 4560–4573, 4615, 4616, 4629–4632, 4829–4833, 4933–4936, 4957–4963, 4994–5008, 6839–6852, 6862, 6870–6873, 6955, 6982, 6997–7001, 7075–7077, 7229–7233, 7268, 8351–8354, 8363–8365, 8951–8962, 8966, 8967, 8971–8975, 8982–8988, 9397–9402, 9421–9426, 9458–9467, 10068–10079, 10082–10087, 10128–10131, 10180, 10181, 10108, 10556, 10566–10572.

Physallaemus cuvieri: (2) CHUFPB 6861, 10113.

Pristimantis ramagii: (150) CHUFPB 2126–2128, 2137–2141, 2148, 3496, 3497, 3500, 3537, 3538, 3540, 3544–3550, 3597–3605, 3608–3623, 4493, 4496, 4500–4512, 4574–4581, 4617–4621, 4834–4952, 4964–4970, 5010–5023, 6874, 6976, 7078–7082, 7234–7238, 8330, 8342, 8358, 8964, 9415, 9417, 9418, 9427–9434, 10080, 10127, 10562–10564.

Scinax nebulosus: (39) CHUFPB 3633–4635, 6956, 6957, 6977–6981, 7257–7261, 8384–8387, 9436–9442, 10560, 10561, 10764–10774.

Scinax x-signatus: (14) CHUFPB 10121–10123, 10608–10616, 10650, 10651.

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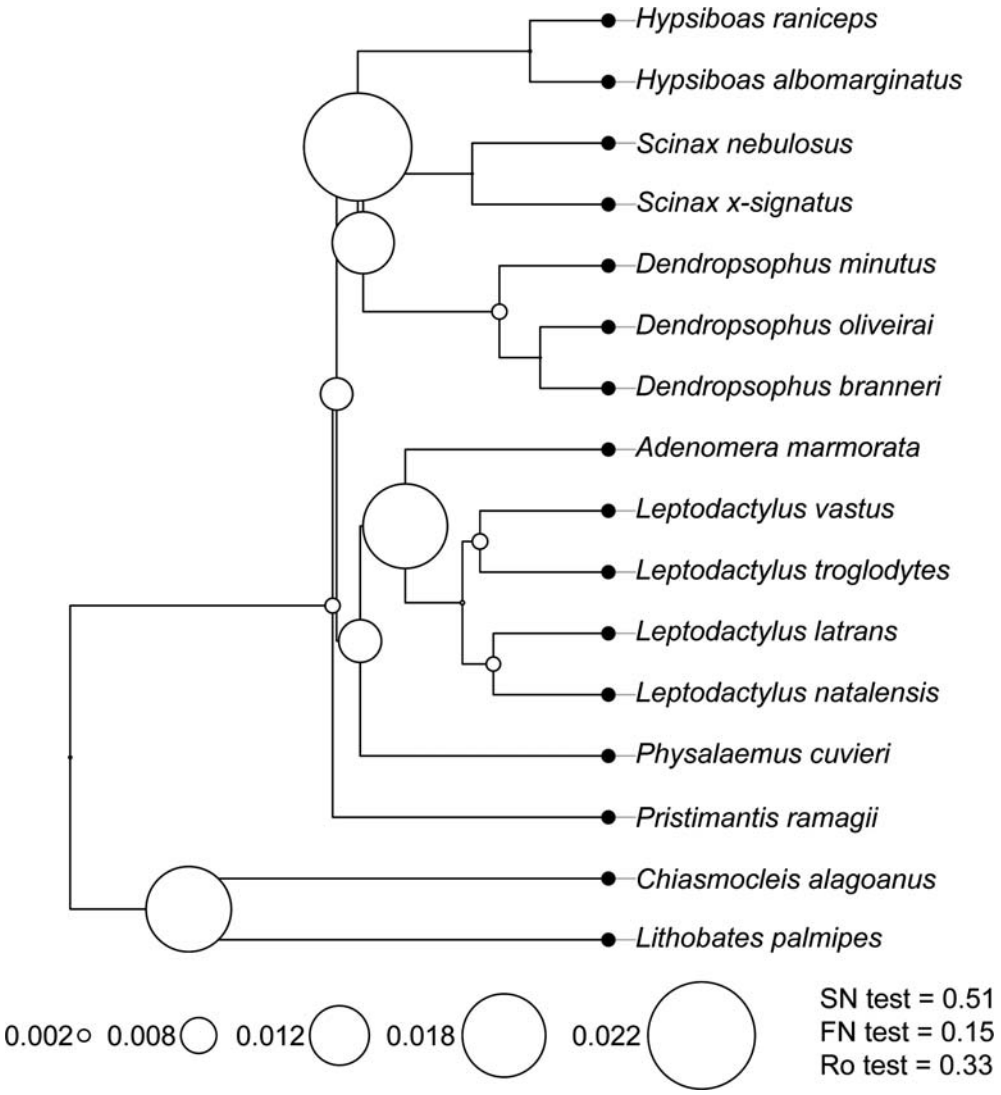

Fig. 2. Decomposition of the morphological diversity among the nodes of the anuran phylogenetic tree. Circles at nodes provide the contribution of nodes to morphological diversity. The scale is given below. The size of the circle represents the degree of trait diversity in that node. Results of the permutation tests are given at the bottom: SN, single-node skewness test; FN, few-nodes skewness test; Ro, root/tips skewness test (two sided).

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Appendix 1. Mean, standard deviation (±), maximum and minimum values of 11 morphometric variables of an anuran assemblage in an Atlantic rainforest fragment.

	SVL	HL	HW	IOD	END	IND	ThL	Til	FL	ED	IED
C. a. (6)	23.59±3.36	5.65±0.95	6.52±0.47	2.88±0.29	2.05±0.14	1.62±0.23	6.58±0.85	8.06±0.88	2±1.11	1.54±0.26	3.42±0.19
	(28.3–20.16)	(6.93–4.27)	(7.04–6.06)	(3.27–2.54)	(2.28–1.86)	(2.01–1.34)	(7.52–1.34)	(9.3	(15.21–12.49)	(1.98–1.23)	(3.65–3.14)
D. b. (152)	17.33±3.22	5.17±0.69	5.47±0.74	2.14±0.34	1.69±0.21	1.58±0.25	7.86±1.17	8.53±1.36	12.30±1.70	2.08±0.27	3.63±0.39
	(48.03–9.50)	(9.26–3.15)	(7.57–1.25)	(3.29–1.00)	(2.50–1.00)	(2.21–0.94)	(11.20–4.50)	(11.95–1.98)	(16.61–6.25)	(2.72–1.36)	(4.96–2.36)
D. m. (39)	22.40±0.91	6.41±0.66	7.34±0.36	2.85±0.26	2.19±0.16	1.66±0.16	9.25±1.42	10.90±0.54	16.89±0.94	2.79±0.46	4.56±0.26
	(24.42–20.49)	(7.16–2.69)	(8.08–6.05)	(3.35–2.34)	(2.78–1.93)	(2.08–1.26)	(11.36–1.57)	(12.37–9.70)	(18.94–14.92)	(5.20–2.14)	(5.13–4.02)
D. o. (89)	16.47±2.43	5.08±0.63	5.29±0.70	2.04±0.34	1.65±0.26	1.55±0.22	6.98±1.07	7.67±1.16	10.94±1.73	1.97±0.26	3.46±0.52
	(20.60–9.56)	(6.46–3.58)	(6.60–3.02)	(2.72–1.04)	(2.06–0.48)	(1.93–0.95)	(9.17–4.43)	(10.70–4.70)	(13.37–5.87)	(2.70–1.21)	(4.60–0.82)
H. a. (26)	47.19±3.14	14.11±0.87	16.17±1.15	5.88±0.64	5.45±0.48	3.26±0.32	22.81±1.22	25.17±1.78	32.60±2.80	5.12±0.36	9.63±0.64
	(51.88–35.20)	(15.6–11.00)	(17.71–11.80)	(6.99–4.30)	(6.16–4.00)	(3.90–2.75)	(25.27–20.50)	(29.73–20.40)	(36.05–21.92)	(5.71–4.20)	(10.52–7.30)
H. r. (17)	67.95±7.62	19.34±2.77	21.07±2.75	6.41±0.78	7.03±0.78	5.26±0.75	34.98±3.87	38.03±3.83	49.83±5.64	6.26±1.13	12.60±2.39
	(84.36–51.77)	(28.81–16.11)	(28.88–16.90)	(7.68–5.10)	(8.29–5.07)	(6.84–4.05)	(45.60–28.25)	(48.90–32.00)	(62.09–41.16)	(8.47–3.88)	(16.41–5.35)
Pr. r. (150)	21.11±4.20	7.38±1.46	7.29±1.52	2.39±0.49	2.88±0.59	2.02±0.40	10.10±2.20	11.34±2.35	15.24±3.18	2.75±0.50	4.55±0.84
	(31.58–11.90)	(11.43–4.21)	(10.70–3.72)	(3.79–1.42)	(4.42–1.58)	(3.29–1.23)	(15.20–5.10)	(16.51–6.00)	(22.48–7.67)	(4.20–1.72)	(6.93–2.44)
Li. p. (215)	62.39±14.16	21.53±5.49	23.41±6.03	5.81±1.18	6.70±1.36	5.76±1.13	29.25±7.73	31.27±7.78	45.42±11.06	7.96±1.56	12.53±2.45
	(103.71–31.98)	(40.41–12.70)	(58.98–13.90)	(9.24–3.82)	(10.61–4.25)	(9.12–3.52)	(48.08–8.39)	(52.35–15.36)	(72.29–14.85)	(12.26–4.72)	(19.54–7.87)
L. l. (1)	75.18	21.95	27	3.81	7.83	5.7	37.4	39.8	58	4.9	7.1
A. m. (11)	20.57±3.15	6.78±0.94	7.32±1.04	2.08±0.22	2.15±0.38	2.41±1.82	7.35±1.52	9.16±1.48	16.32±2.38	2.30±0.34	3.47±0.63
	(24.70–14.28)	(8.00–4.88)	(8.43–5.40)	(2.29–1.61)	(2.63–1.47)	(2.86–1.47)	(9.52–4.85)	(10.71–5.78)	(19.79–11.09)	(2.99–1.72)	(4.38–2.17)
L. n. (106)	36.94±6.60	11.23±1.31	12.64±1.54	3.13±0.50	3.91±0.49	3.02±0.44	14.12±2.01	15.46±1.89	25.91±3.34	4.12±0.63	6.69±0.90
	(59.99–16.09)	(13.85–5.65)	(15.63–6.70)	(4.19–1.68)	(4.80–1.95)	(4.15–1.91)	(20.00–7.79)	(18.88–6.95)	(37.93–10.93)	(5.33–1.86)	(8.63–3.20)
L. t. (7)	43.19±5.54	14.67±0.97	14.23±3.78	3.52±0.72	4.73±0.70	4.20±0.33	16.74±1.76	17.92±1.27	27.66±1.79	4.97±0.60	8.01±1.20
	(50.28–34.45)	(16.31–13.44)	(16.71–6.18)	(4.58–2.74)	(5.81–3.88)	(4.73–3.85)	(18.80–14.34)	(19.22–15.83)	(29.00–24.53)	(5.99–4.16)	(9.39–6.01)
L. v. (7)	136.29±10.68	45.40±5.44	58.04±5.14	12.59±3.36	12.95±1.34	10.45±0.89	57.72±6.56	56.87±6.63	87.31±8.10	13.73±1.32	24.76±2.19
	(148.75–116.35)	(52.94–37.35)	(65.70–48.36)	(19.35–9.00)	(14.54–11.11)	(11.76–9.06)	(65.70–46.78)	(66.25–46.12)	(97.11–74.76)	(16.01–11.69)	(27.56–21.21)
P. c. (2)	21.81±6.36	6.52±2.17	7.09±1.72	2.18±0.62	2.39±0.45	1.64±0.43	8.54±1.06	9.92±2.06	15.78±3.73	2.50±0.45	4.27±0.62
	(26.30–17.31)	(8.05–4.98)	(8.30–5.87)	(2.61–1.74)	(2.70–2.07)	(1.94–1.33)	(9.29–7.79)	(11.38–8.46)	(18.42–13.14)	(2.81–2.18)	(4.71–3.83)
S. n. (39)	26.71±3.93	9.30±2.25	8.54±1.40	3.02±0.49	3.85±0.57	2.04±0.44	11.50±1.73	12.97±2.05	18.29±2.41	2.69±0.42	5.41±0.77
	(40.05–20.43)	(21.27–6.47)	(12.90–6.14)	(4.25–2.27)	(5.32–2.28)	(3.70–1.53)	(16.19–8.08)	(19.80–9.56)	(27.01–14.00)	(3.82–2.13)	(7.85–4.11)
S. x. (14)	34.47±1.68	9.82±0.49	10.65±0.67	3.45±0.29	4.00±0.30	2.42±0.19	11.38±0.54	13.83±0.89	20.19±0.79	3.75±0.22	6.32±0.47
	(37.06–31.84)	(10.46–8.57)	(11.84–9.84)	(3.90–2.95)	(4.43–3.39)	(2.76–2.12)	(12.45–10.37)	(15.85–12.65)	(22.07–18.92)	(4.14–3.43)	(6.87–5.24)

Note: Species abbreviations are the same as in Table 4.