

Spatial and Trophic Structure of Anuran Assemblages in Environments with Different Seasonal Regimes in the Brazilian Northeast Region

Francis L. S. Caldas¹, Adrian A. Garda², Lucas B. Q. Cavalcanti³, Edinaldo Leite-Filho³, Renato G. Faria¹, and Daniel O. Mesquita³

We investigated the roles of ecological and historical factors on the phylogenetic structure and spatial and trophic niches of anurans in Caatinga and Atlantic Forest in the Brazilian Northeast Region. We sampled specimens and ecological data using both active search and pitfall traps to sample sites for 15 days during dry and wet seasons. Assemblages from Caatinga were more structured on dietary niche than those from Atlantic Forest. Ecological factors had a higher effect on the trophic niche than on the spatial niche but were lower than historical factors, thus indicating past adaptations. The onset of the dry season usually increases the dietary structure of assemblages. Water restrictions in Caatinga affected prey abundance, increasing niche segregation. Differences between environments indicated that local factors exerted greater influence in Caatinga. We did not observe spatial niche structure in most assemblages, regardless of the environment, and we found strong evidence of niche conservatism in all assemblages. Phylogenetic effects detected in spatial niches reinforce the separation between arboreal and terrestrial/semi-aquatic lineages during the Cretaceous. Lastly, no niche complementarity was detected, despite the different structure patterns. No assemblage was phylogenetically structured, and the existence of a possible “ecological filter” in Caatinga did not lead to increased “phylogenetic clustering” in this environment.

Nós analisamos o efeito de fatores ecológicos e históricos sobre a estrutura filogenética e nichos espacial e trófico de anuros na Caatinga e Mata Atlântica da região Nordeste do Brasil. Nós coletamos espécimes e dados ecológicos utilizando busca ativa e pitfall traps e amostramos as localidades durante 15 dias durante as estações seca e chuvosa. As taxocenoses de Caatinga estiveram mais estruturadas em função da dieta que as de Mata Atlântica. Fatores ecológicos possuem maior influência sobre o nicho trófico do que no nicho espacial, mas tem menor efeito do que os fatores históricos, indicando ação de adaptações que ocorreram no passado. O início da estação seca geralmente aumenta a estrutura trófica das taxocenoses. As restrições hídricas da Caatinga afetam a disponibilidade de presas, contribuindo para a segregação dos nichos. As diferenças entre os ambientes indicam que fatores ecológicos exercem maior influência na Caatinga. Não observamos estrutura espacial na maioria das taxocenoses, independente do ambiente estudado e encontramos fortes evidências de conservatismo de nicho em todas elas. Efeitos filogenéticos detectados sobre os nichos espaciais reforçam a separação entre linhagens arbóreas e terrestres/semi-aquáticas que ocorreu durante o período Cretáceo. Por fim, não foi observada complementaridade de nicho apesar dos diferentes padrões de estrutura. Nenhuma taxocenose esteve filogeneticamente estruturada e a existência de um possível “filtro ecológico” na Caatinga não implicou num “agrupamento filogenético” nesse ambiente.

COMMUNITIES have been classified in several ways, and some definitions include the concept of a group of species occurring sympatrically and interacting, possibly forming an organized unit (Wilbur, 1972; McGill et al., 2006). This organization (structure) results from the effect of selective forces shaping species composition, richness, abundances, and resource-use patterns (Pianka, 1973; Winemiller and Pianka, 1990). In a structured community, species segregate niches at lower levels than expected by chance (Winemiller and Pianka, 1990).

However, communities are complex systems with many different organisms, leading researchers to study subdivisions based on trophic level or taxonomy, such as “guilds” and “assemblages” (Pianka, 1973). Assemblage structure may reflect recent events resulting from ecological interactions, although the effect of historical factors on the biology of species cannot be ignored (Losos, 1996; Vitt and Pianka, 2004). Therefore, comparisons among different assemblages considering phylogenetic relationships among species may help clarify the relative strength of these factors and, ultimately, help researchers understand how natural com-

munities are assembled (Mesquita et al., 2006a; Beaulieu et al., 2012).

From a historical perspective, the analysis of phylogenetic niche conservatism may help explain the composition of different assemblages according to their resources. This conservatism is expressed through ecological divergences and similarities among coexisting species (Wiens and Graham, 2005; Pyron et al., 2015). Thus, closely related species should have similar ecological traits, while distant lineages are expected to have more divergent traits (Richardson, 2001; Losos, 2008). Therefore, a key “phylogenetic effect” may account for the current organization of assemblages; that is, conserved traits would be crucial to the survival of organisms and their interactions, and current ecological functions would result from previous competitive pressures, or the “ghost of competition past” (Connell, 1980; Losos, 1992).

Access to phylogenetic data also enables the precise identification of which factors allow the co-occurrence of more- or less-related species (Whitfield et al., 2012; Chalmandrier et al., 2015). Extrinsic and intrinsic forces on assemblages may generate patterns in which either closely related (phylogenetic clustering) or distant (phylogenetic dispersion)

¹ Departamento de Biologia, Laboratório de Cordados, Universidade Federal de Sergipe, São Cristóvão, SE 49100-000, Brazil; Email: (FLSC) francisluis_bio@hotmail.com. Send reprint requests to FLSC.

² Departamento de Botânica e Zoologia, Laboratório de Anfíbios e Répteis-LAR, Universidade Federal do Rio Grande do Norte, Natal, RN 59078-900, Brazil.

³ Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, PB 58059-000, Brazil.

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species may coexist at ratios higher than expected by chance (Webb et al., 2002; Savage and Cavender-Bares, 2012). Hence, the existence of an “ecological filter” (e.g., tolerance to salinity and resistance to dry climates) can limit the occurrence of taxa, allowing those with similar traits to persist (Sobral and Cianciaruso, 2012; de Bello et al., 2013). Thus, the phylogenetic organization (structure) in an assemblage presumes a non-random taxonomic composition pattern relative to the regional species pool (Webb et al., 2002; Kraft et al., 2007). Conversely, based on ecological perspective, competition is treated as one of the main factors affecting assemblage structure (González-Romero et al., 1989; Vitt et al., 1999). Theoretically, if two or more species use the same limiting resource, they will rarely coexist, assuming the existence of a maximum limit of niche overlap (Gause, 1932; Ricklefs, 1987). However, resource use overlap may lead species to share resources, thereby ensuring coexistence and the maintenance of richness patterns (Vitt, 1981; Brown et al., 2002).

The dynamics of many seasonal ecological systems is partly controlled by resource availability (Toft and Duellman, 1979; Nowlin et al., 2008) and may be critical for species (Hussell, 1985; Abell et al., 2006). This situation is particularly important for amphibians because they are strongly dependent on water in their environment (Aichinger, 1987; Dayton and Fitzgerald, 2006). Indeed, temporal variation of resources is marked in situations of strong seasonality, with a period favoring foraging, growth, and reproduction and an unfavorable period during which species undergo stages of estivation (Roff, 1992; Williams and Middleton, 2008). Conversely, in humid tropical regions, regular water availability and the absence of severe drought periods allows water bodies to last longer and species to extend their reproductive activities and use trophic and spatial resources throughout the year (Hödl, 1990; Stebbins and Cohen, 1997).

The Caatinga is located in the Brazilian Northeast Region and has a semiarid tropical climate, with the predominance of two distinct characteristic seasons: a very dry and prolonged season and another with moderate and irregularly distributed rainfall (Chiang and Koutavas, 2004; Leal et al., 2005). Conversely, the Atlantic Forest spans an area from the coast of Rio Grande do Norte to Rio Grande do Sul, stretching far inland in some areas (Steinmetz, 2004; Prochnow et al., 2006), and has a high rainfall index resulting from moisture-laden ocean trade winds, which are pushed into continental regions against coastal mountain ranges, where rainfall occurs (Ab'Saber, 1977; Tonhasca-Júnior, 2005). Both environments occur in northeastern Brazil, thus enabling observations on anurans subjected to more limiting conditions in the Caatinga, which require adaptations of their traits (Navas et al., 2004; Pereira et al., 2007), and on those subjected to more stable situations in the Atlantic Forest (Hödl, 1990; Duellman, 1999).

Some studies evaluated the role of the ecological and historical components in the dynamics of anuran assemblages in the Neotropics, primarily using morphological, reproductive, and habitat-use data as comparative parameters (Zimmerman and Simberloff, 1996; Eterovick and Fernandes, 2001; Graham et al., 2012). In southeastern Brazil, historical factors had little effect on microhabitat use in anuran assemblages in five Atlantic Forest areas, where resource partition was better explained by recent environmental factors (Eterovick et al., 2010). Conversely, Protázio et al. (2014) showed a significant influence of phylogenetic

conservatism in the spatial niche of a Caatinga anuran assemblage, especially among Hylidae and Leptodactylidae.

In the present study, dietary and microhabitat data were used to evaluate the presence of resource-use patterns in anuran assemblages at four sites in the Brazilian Northeast Region with contrasting rainfall regimes (two Caatinga and two Atlantic Forest sites). We hypothesized that: 1) In the Caatinga, where the rainy season is short and resource availability is limited or nonexistent during the dry season, anuran assemblages would be more structured in resource use compared to the Atlantic Forest, where rainfall is abundant and resources continuously available. Furthermore, because amphibians are highly dependent on water, ecological factors are expected to have a stronger effect on the trophic component than historical factors, especially in the Caatinga. 2) Conversely, studies on microhabitat use indicate that anuran morphological adaptations are more closely related to the way amphibians exploit space (Cardoso et al., 1989; Prado and Pombal, 2005). This suggests that historical factors have a stronger effect on microhabitat use and that this relation is less affected by seasonality. 3) We also expect that even if some species become inactive with the approaching of the dry season, assemblage structure increases due to the scarcity in trophic resources, and this effect is stronger in the Caatinga. 4) Lastly, the strong seasonality in Caatinga may promote the existence of an environmental filter responsible for a phylogenetic structure in these areas by selecting lineages with some type of resistance to arid conditions (Webb et al., 2002; Losos, 2008). Thus, we expect that anurans from Caatinga will have higher phylogenetic clustering, in contrast to the Atlantic Forest, which would have higher phylogenetic dispersion.

MATERIALS AND METHODS

Study site.—The study was conducted in four Protected Areas (PAs) of the Brazilian Northeast Region (Fig. 1) located in environments with different seasonal regimes. The first was Seridó Ecological Station (Seridó ESEC), located in the southwestern region of the state of Rio Grande do Norte (06°35' to 06°40'S, 37°20' to 37°39'W), in the municipality of Serra Negra do Norte, totaling an area of approximately 1,166 ha (Velloso et al., 2002). This site is included in the Caatinga biome and is composed mostly of herbs and shrubs, predominantly *Amburana* (Fabaceae), *Ximania* (Olacaceae), *Luetzelburgia* (Fabaceae), *Mimosa* (Fabaceae), among others, and an endemic species, *Gossypium mustelinum* (Malvaceae; Velloso et al., 2002). The rainy season usually occurs from January to May (Santana and Souto, 2006).

The second PA was Aiuaba ESEC, located in the state of Ceará (06°36'01" to 06°44'35"S, 40°07'15" to 40°19'19"W), in the municipality of Aiuaba, totaling an area of 11,525 ha (Velloso et al., 2002). Aiuaba ESEC includes an arboreal Caatinga remnant with predominantly open vegetation formations with *Cnidioscolus-Bursera-Caesalpinia* (Euphorbiaceae, Burseraceae, Fabaceae, respectively; Andrade-Lima, 1981). The rainy season usually occurs from October to April. The Seridó and Aiuaba ESECs are located in the ecoregion called “Depressão Sertaneja Setentrional,” and their annual rainfall ranges from approximately 500 to 800 mm (Velloso et al., 2002).

The third PA studied was the Guaribas Biological Reserve (Reserva Biológica [REBIO] Guaribas), located in the state of Paraíba in the municipalities of Mamanguape (91.59%) and Rio Tinto (8.41%). The site totals approximately 4,321 ha and

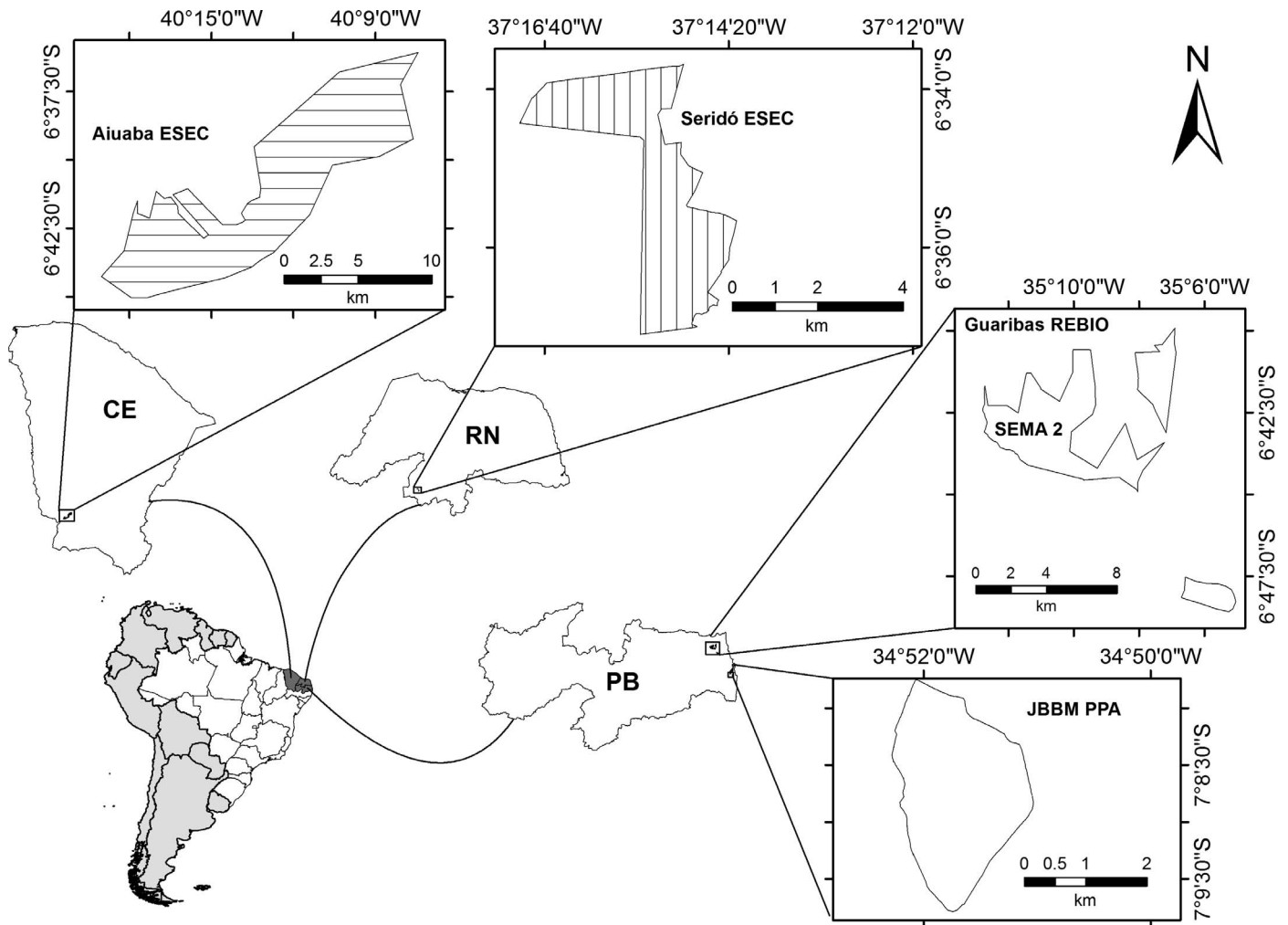


Fig. 1. Study sites: Aiuaba ESEC—Ceará (CE); Seridó ESEC—Rio Grande do Norte (RN); Guaribas REBIO—Paraíba (PB); and JBBM PPA—Paraíba (PB). The Caatinga areas are shown with horizontal (Aiuaba) or vertical (Seridó) lines, and the Atlantic Forest areas are shown with no lines.

encompasses discontinuous areas termed SEMA 01, 02, and 03. The study was developed at SEMA 2 ($06^{\circ}40'40''$ to $06^{\circ}44'59''$ S, $41^{\circ}12'47''$ to $41^{\circ}07'11''$ W), totaling approximately 3,378 ha (Barbosa et al., 2011). The Reserve, which is included in the Atlantic Forest, is highly heterogeneous, with tree formations and typical savannas of coastal restingas and an arboreal formation represented by semi-deciduous seasonal forest (Oliveira-Filho and Carvalho, 1993). The annual rainfall regime ranges from 1,750 to 2,000 mm (Nimer, 1979). The rainy season lasts from April to October (Aguar and Martins, 2002).

The fourth study site was the Permanent Protection Area (PPA) of the Benjamim Maranhão Botanical Garden (Jardim Botânico Benjamim Maranhão—JBBM), an Atlantic Forest remnant located in the urban area of João Pessoa, Paraíba ($07^{\circ}06'S$, $34^{\circ}52'W$). The area is transected by highway BR-230, resulting in a larger stretch of continuous forest with 471 ha (area of interest) and 11 small fragments located within Campus I of the Federal University of Paraíba. This is a typical coastal rainforest environment of the Brazilian Northeast, with secondary growth and flora consisting of trees, shrubs, and herbaceous plants with a low sub-canopy stratum and infrequent lianas (Dias et al., 2006). The rainfall regime ranges from 1,500 to 1,700 mm, and the rainy season lasts from March to August (Lima and Heckendorff, 1985).

Data collection.—Most of the study was conducted in 2013. We performed sample collections in the first three sites described above during the dry (January—Guaribas REBIO, September—Aiuaba ESEC, December—Seridó ESEC) and rainy (June—Guaribas REBIO, April—Aiuaba ESEC, May—Seridó ESEC) seasons, including 15 consecutive days of field work during each season, totaling 30 days per site and 90 days of sampling effort. The seasons were determined based on monthly rainfall distribution in each area over the years (Fig. 2).

The main sampling method was the active search for individuals (Crump and Scott, 1994), performed from 0600 to 2200 hrs, which consisted of searching for specimens by systematically surveying habitats. We tried to cover as many water bodies as possible based on their availability in the study areas: Guaribas REBIO—one lake, one perennial stream, and five temporary ponds; Aiuaba ESEC—one perennial lake and four temporary ponds; and Seridó ESEC—one perennial lake, one intermittent stream, and three temporary ponds. Because species in the region do not have riparian habits, and all but one (*Corythomantis greeningi*) reproduce in lentic habitats (Arzabe, 1999; Vieira et al., 2007; Santana et al., 2008), structural variation in water bodies among sites was not considered problematic. The second method was the use of pitfall traps (Cechin and Martins, 2000; Enge, 2001), which were used to supplement the

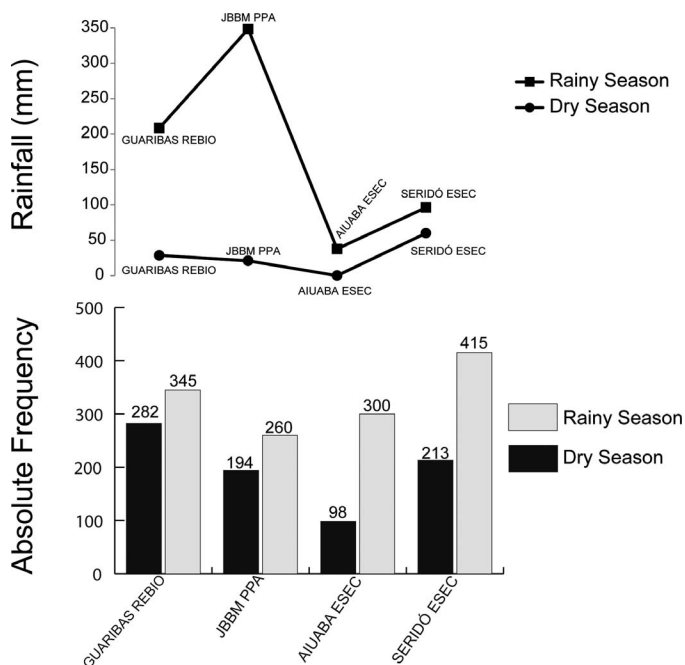


Fig. 2. Mean rainfall of the sampling seasons and absolute frequencies of the anurans collected per season. Rainfall data from the National Institute of Meteorology (Instituto Nacional de Meteorologia—INMET), Ceará Foundation for Meteorology and Water Resources (Fundação Cearense de Meteorologia e Recursos Hídricos—FUNCEME), and the Executive Agency for Water Management of the State of Paraíba (Agência Executiva de Gestão das Águas do Estado da Paraíba—AESAs).

number of individuals captured for diet analysis. We set up six Y-shaped pitfall traps, which consisted of four 30-liter buckets interconnected by 5-meter plastic drift fences. From all water bodies sampled on the different sites, we selected two with varying characteristics and set three trapping systems at the margins of each of the selected water bodies (Guaribas REBIO—one perennial stream and one temporary pond; Seridó ESEC—one perennial lake and one intermittent stream; and Aiuaba ESEC—one perennial lake and one temporary pond because no lotic waterbody was available). Traps were checked and cleaned twice a day for 15 days to avoid frogs from dying or feeding on animals inside the buckets.

Sample collections at the JBBM were performed from 2011 to 2012. We therefore selected the three rainiest (May, June, and July) and three driest (October, November, and December) months, which had mean rainfall similar to those of Guaribas REBIO in 2013 (Fig. 1), and sampled for a total of 15 days in each season, similarly to the other areas. The sampling methods were the same as above and were performed in a dammed stretch of the Jaguaribe River, which formed a large lentic water body (7°08'42"S, 34°51'54"W). Rainfall varied significantly between seasons in both environments, with higher rainfall in the Atlantic Forest (Fig. 2).

Microhabitat and diet.—We used information from specimens collected by active search and from other individuals sighted in the environment to compile microhabitat data. By considering the microhabitats of all sampled sites and the position of the animals in the microhabitats, we defined 13 categories (on macrophytes, perched on emergent vegetation, perched on grass, perched on a shrub, perched on a tree, partly submerged, in litter, on a rock, on dry soil, on wet soil, submerged in a hole, on a fallen tree trunk, and in a burrow).

The specimens were euthanized immediately after each collection with 2% lidocaine, then fixed in 10% formalin and preserved in 70% ethanol. In the laboratory, the stomachs and their contents were removed and analyzed with a stereoscopic microscope. We identified the prey consumed, usually to order, using specialized literature (Triplehorn and Johnson, 2011). We counted the prey consumed by anurans and measured the length and width of intact prey with a digital caliper (accurate to 0.01 mm). We estimated prey volume using the ellipsoid formula:

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

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

We then calculated the importance value index (IVI) for stomachs, which were clustered to assess how much each food item contributed to the diets of the different species, using the following equation:

$$IVI = \frac{F\% + N\% + V\%}{3},$$

where F , N , and V correspond to the frequency, number, and volume of prey consumed, respectively, all expressed as percentage.

We calculated the trophic (number and volume) and spatial (microhabitat) niche breadths using the inverse of Simpson's diversity index (1949):

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

where p is the proportion of the (trophic or spatial) resource category used, and i and n are the number of resource categories. B ranges from 1 (exclusive use of one resource type) to n (homogenous use of all types of resources). We examined whether there was a similarity in resource use by different species using the symmetrical overlap formula (Pianka, 1973):

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

using the same symbols as those mentioned above, although j and k represent different species. Values close to 0 indicate no similarity in resource use, whereas values close to 1 indicate similar resource use.

We used the EcoSim niche overlap module (Gotelli and Entsminger, 2004) to assess the presence of non-random patterns of trophic and spatial niche overlap. Thus, we used a matrix in which each species corresponds to a row and each prey category or microhabitat to a column, and the value in each cell is the proportion resource use of each category. The matrix was reformulated based on 30,000 randomizations, producing pseudo-communities, to simulate expected random patterns in the absence of assemblage structure. The presence of structure in the assemblage was evaluated when comparing the average observed and the simulated overlaps, adopting a 5% significance level. Meeting this assumption, the average observed overlap was lower than or equal to the simulated or randomly expected average in 95% of the resamplings.

We selected the options “Pianka’s niche overlap index” and “randomization algorithm 2” (“retained zero states” and “relaxed niche breadth” in the matrix) in the EcoSim niche overlap module. The analysis was performed for each season (dry and rainy) using the microhabitat and dietary data from the assemblages of each site. We performed the analysis twice: once considering all assemblage species and another excluding the rarest species ($n < 5$) to assess whether rare species could substantially affect the results. In the case of diet, we used the option “resource status,” entering the electivity data of each prey category based on the sum of prey volume values consumed by all species. If the assemblage is structured, the diet of each species is not a random sample of electivity; it indicates the selection of specific categories (increased specialization in resource use).

We used phylogenetic principal component analysis (pPCA), a multivariate method that seeks phylogenetic autocorrelation (Gittleman and Kot, 1990), i.e., the dependence of a trait on specific taxonomic groups, to detect the effect of ecological or historical factors on the trophic and spatial niches of the different communities. Species dietary (importance value indices of pooled stomachs of each prey category) and microhabitat (frequency of use of each microhabitat category) data are arranged in one matrix (X), and the species of each assemblage (with the respective phylogenetic distances in the cells—using data from Pyron and Wiens, 2011) are arranged in another, the phylogenetic matrix (W). High autocorrelation indicates similarity between nearby taxa for a given characteristic, and low autocorrelation indicates divergence between these taxa. These patterns are summarized by identifying principal components; that is, high positive values indicate a global (historical) effect, and low negative values indicate a local (ecological) effect (Jombart et al., 2010). The analysis was performed for each assemblage in the dry and rainy seasons.

Niche complementarity and phylogenetic structure.—We also analyzed the interrelations between the trophic and spatial components of the niches of all anuran species studied. For this purpose, we used a partial Mantel test, crossing the diet and microhabitat overlap matrices of the assemblages of each site in their respective season (dry and rainy). The test was performed using the phylogenetic distances available in the most recently published phylogeny for Anura (Pyron and Wiens, 2011).

Lastly, we tested the presence of non-random patterns of phylogenetic structure for both environments, constructing a phylogenetic tree with all anuran species of the Brazilian Northeast Region north of the São Francisco River, based on the most recent distribution data (Haddad et al., 2013; Garda et al., 2017) and adapted from the existing phylogeny (Pyron and Wiens, 2011). We assumed that this measure would not critically affect the results because larger evolutionary changes should occur at the most-basal nodes of the phylogenetic tree (Roelants et al., 2007). Subsequently, we estimated phylogenetic diversity (PD), mean phylogenetic distance (MPD), and mean nearest taxon distance (MNTD; Webb, 2000; Webb et al., 2002) for the Caatinga and Atlantic Forest (grouping the species from the sites of each biome sampled) by comparing these data with a null distribution of the above values (PD, MPD, and MNTD) generated through 10,000 randomizations.

All tests that used phylogenetic data (pPCA, Mantel, and phylogenetic structure) were performed in R software (R Core Team, 2016) for Windows using the respective software

packages: 1) pPCA: ade4 (Thioulouse et al., 1997), adephylo (Jombart and Dray, 2013), and ape (Paradis et al., 2004); 2) Mantel: vegan (Oksanen et al., 2007); and 3) phylogenetic structure: ape (Paradis et al., 2004) and picante (Kembel et al., 2010). We adopted a 5% significance level for all tests.

RESULTS

Species composition.—In the Atlantic Forest, we recorded 28 anuran species. We found seven (Bufonidae, Craugastoridae, Hylidae, Leptodactylidae, Microhylidae, Phyllomedusidae, and Ranidae) and five families (Craugastoridae, Hylidae, Leptodactylidae, Microhylidae, and Ranidae), respectively, at the Guaribas REBIO and JBBM. In the Caatinga, we collected 18 species. On both sites, we recorded six families (Bufonidae, Hylidae, Leptodactylidae, Microhylidae, Odontophrynidae, and Phyllomedusidae). The two environments share 34% of the species (Table 1), and in both some species become inactive during the dry season, mostly in the Caatinga, where the largest number of absences was recorded (Table 1). In the Atlantic Forest, Hylidae had the highest number of species, followed by Leptodactylidae, and the opposite was found in the Caatinga areas (Table 1). The abundance of individuals was also higher during the rainy season in both environments, although at higher proportions in the Caatinga (Fig. 2).

Microhabitat.—Niche breadth values were low, regardless of the study assemblage (Table 2). Overlap values ranged from 0 to 0.99 in most areas and seasons but were generally low. We found the lowest values in the dry season at Aiuaba ESEC. High overlap values were prevalent in both seasons in the Caatinga, especially among the Leptodactylidae, regardless of phylogenetic relationships. High overlap among hylids usually occurred in the Atlantic Forest (Supplemental Tables A–H; see Data Accessibility).

Pseudo-community analysis, in most sites and seasons, showed higher observed than simulated overlap means, indicating lack of structure in spatial resource sharing (Table 3). The only exception occurred during the dry season of an Atlantic Forest site (JBBM), where the observed mean was 0.10, significantly lower ($P < 0.0001$) than the simulated mean (0.16), indicating presence of assemblage structure based on spatial niche (Table 3). Both types of null model analysis (including and excluding rare species) showed similar and nonsignificant results, with the same exception reported above, indicating that rare species had no effect on the results.

Phylogenetic principal component analysis (pPCA) showed variable results according to the biome and season. Historical and ecological effects were detected in the use of microhabitats, regardless of the assemblage (Fig. 3). However, in most cases, historical effects were stronger than ecological effects, showing evidence of a greater effect of phylogenetic niche conservation (Fig. 3). In most situations, independent of the domain, the assemblages may be divided into guilds of “terrestrial/semi-aquatic” and “arboreal” organisms with phylogenetic signals, especially among the Hylidae and Leptodactylidae (Supplemental Spreadsheet A; see Data Accessibility).

Diet.—Coleoptera and Formicidae were the most important dietary items in most sites, regardless of species and season (Table 4). Moreover, plant material was the most consumed dietary category of some species found in the Atlantic Forest (Table 4).

Table 1. Richness and abundance of anurans collected in four protected areas. Data next to the names of the areas indicate local richness. Abundance values are shown for the rainy (without parentheses) and dry (in parentheses) seasons. The habit of anurans corresponds to: ter (terrestrial), arb (arboreal), sa (semi-aquatic).

Species	Habit	Number of specimens			
		Guaribas REBIO (27)	JBBM PPA (15)	Aiuaba ESEC (16)	Seridó ESEC (17)
Craugastoridae					
<i>Pristimantis ramagii</i>	ter/arb	7(19)	8(67)	—	—
Bufoidea					
<i>Rhinella granulosa</i>	ter	—	—	13(0)	47(19)
<i>Rhinella jimi</i>	ter	15(17)	—	15(0)	32(7)
Hylidae					
<i>Boana albomarginata</i>	arb	22(0)	25(1)	—	—
<i>Boana faber</i>	arb	10(1)	—	—	—
<i>Boana raniceps</i>	arb	7(1)	3(2)	6(10)	5(28)
<i>Corythomantis greeningi</i>	arb	—	—	—	7(4)
<i>Dendropsophus branneri</i>	arb	45(44)	24(56)	—	—
<i>Dendropsophus elegans</i>	arb	3(0)	—	—	—
<i>Dendropsophus minutus</i>	arb	57(0)	40(0)	—	—
<i>Dendropsophus nanus</i>	arb	5(17)	—	64(32)	15(45)
<i>Dendropsophus oliveirai</i>	arb	15(9)	14(16)	—	—
<i>Scinax cretatus</i>	arb	11(0)	—	—	—
<i>Scinax eurydice</i>	arb	9(2)	—	—	—
<i>Scinax fuscomarginatus</i>	arb	6(0)	—	—	—
<i>Scinax nebulosus</i>	arb	18(29)	13(3)	—	—
<i>Scinax x-signatus</i>	arb	9(0)	14(0)	12(1)	10(4)
Leptodactylidae					
<i>Adenomera</i> sp.	ter/sa	0(3)	8(0)	—	—
<i>Leptodactylus fuscus</i>	ter/sa	0(4)	—	5(0)	26(3)
<i>Leptodactylus macrosternum</i>	ter/sa	13(28)	0(1)	70(15)	49(30)
<i>Leptodactylus natalensis</i>	ter/sa	9(14)	68(3)	—	—
<i>Leptodactylus troglodytes</i>	ter/sa	4(5)	—	5(0)	60(12)
<i>Leptodactylus vastus</i>	ter/sa	25(5)	0(1)	16(3)	8(2)
<i>Physalaemus albifrons</i>	ter/sa	—	—	4(0)	1(1)
<i>Physalaemus cicada</i>	ter/sa	—	—	6(0)	27(13)
<i>Physalaemus cuvieri</i>	ter/sa	10(4)	1(0)	13(0)	—
<i>Pleurodema diplolister</i>	ter/sa	6(29)	—	—	25(4)
<i>Pseudopaludicola mystacalis</i>	ter/sa	6(4)	—	—	—
<i>Pseudopaludicola pocoto</i>	ter/sa	—	—	56(37)	36(40)
Microhylidae					
<i>Chiasmocleis alagoana</i>	ter	—	5(0)	—	—
<i>Dermatonotus muelleri</i>	ter	1(0)	—	1(0)	31(0)
Odontophrynidae					
<i>Proceratophrys cristiceps</i>	ter	—	—	2(0)	18(1)
Phyllomedusidae					
<i>Pithechopus nordestinus</i>	arb	18(0)	—	12(0)	18(0)
Ranidae					
<i>Lithobates palmipes</i>	ter/sa	14(48)	37(44)	—	—

Niche breadths were narrow in both environments, ranging from 1 to 3 for most species (Table 2). Trophic niche overlap values ranged from 0 to 0.99 in most areas and seasons and were usually low. We found the lowest values at Aiuaba ESEC in the dry season (Caatinga). In both environments, the high overlaps varied widely between seasons and sites and involved species with different phylogenetic proximities (Supplemental Tables A–H; see Data Accessibility).

Pseudo-community analysis generated observed overlap means lower than the simulated overlap means in all sites and seasons, with highly significant results ($P < 0.0001$), indicating structure based on trophic niche (Table 3). The relation found between the observed and simulated means was up to threefold lower in the Caatinga than in the

Atlantic Forest in the dry season and onefold lower in the rainy season (Table 3). Both analyses (including and excluding rare species) showed similar and significant results, indicating that rare species had no effect on the results.

Phylogenetic principal component analysis (pPCA) showed variable results depending on the biome and season. In both Caatinga and Atlantic Forest sites, historical and ecological effects on the diet were detected, regardless of the season (Fig. 4). However, in most cases, the historical effects were stronger than the ecological effects, although the differences were small. Nevertheless, the ecological effects on trophic niches were stronger than the spatial effects and more-recent effects were stronger in the rainy season at JBBM (Atlantic Forest) and in both seasons at Seridó ESEC (Caatinga; Fig. 4).

Table 2. Species niche breadths of all assemblages. The trophic niche breadth values are shown in bold font, and the spatial niche breadth values are shown in regular font.

Species	Spatial and trophic niche breadth							
	Guaribas REBIO		JBBM PPA		Aiuaba ESEC		Seridó ESEC	
	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy
Craugastoridae								
<i>Pristimantis ramagii</i>	3.8/5.2	1.4/2.3	1.1/5.0	1.0/3.5	—	—	—	—
Bufonidae								
<i>Rhinella granulosa</i>	—	—	—	—	—	2.0/1.8	4.3/1.6	1.0/1.9
<i>Rhinella jimi</i>	2.4/2.2	1.8/1.7	—	—	—	3.3/2.6	2.2/1.6	2.3/1.6
Hylidae								
<i>Boana albomarginata</i>	—	3.7/2.0	1.0/2.3	2.5/2.9	—	—	—	—
<i>Boana faber</i>	1.0/1.0	1.5/2.0	—	—	—	—	—	—
<i>Boana raniceps</i>	1.0/—	1.7/1.9	1.0/1.8	1.8/2.3	2.6/2.3	1.8/2.6	2.3/4.2	3.5/3.8
<i>Corythomantis greeningi</i>	—	—	—	—	—	—	1.0/—	2.0/1.8
<i>Dendropsophus branneri</i>	1.2/3.9	1.7/3.2	1.5/5.0	1.0/2.2	—	—	—	—
<i>Dendropsophus elegans</i>	—	1.8/1.0	—	—	—	—	—	—
<i>Dendropsophus minutus</i>	—	2.0/2.2	—	2.0/3.1	—	—	—	—
<i>Dendropsophus nanus</i>	1.0/2.9	1.0/1.7	—	—	1.1/2.6	2.8/4.1	1.5/3.0	1.0/1.7
<i>Dendropsophus oliveirai</i>	1.0/1.5	1.7/3.0	1.3/4.7	1.3/2.8	—	—	—	—
<i>Scinax cretatus</i>	—	3.3/1.0	—	—	—	—	—	—
<i>Scinax eurydice</i>	1.0/2.9	4.2/1.6	—	—	—	—	—	—
<i>Scinax fuscomarginatus</i>	—	1.0/1.4	—	—	—	—	—	—
<i>Scinax nebulosus</i>	2.1/3.4	1.3/2.2	1.0/1.8	1.0/2.2	—	—	—	—
<i>Scinax x-signatus</i>	—	4.8/1.0	—	2.3/1.9	—	2.1/1.0	1.4/1.8	4.3/4.3
Leptodactylidae								
<i>Adenomera</i> sp.	1.0/2.0	—	—	1.9/4.3	—	—	—	—
<i>Leptodactylus fuscus</i>	1.0/1.0	—	—	—	—	1.8/3.2	1.0/1.0	2.6/1.9
<i>Leptodactylus macrosternum</i>	1.4/3.6	2.0/4.3	1.0/2.0	—	2.6/2.4	2.7/5.5	2.0/4.0	2.7/2.0
<i>Leptodactylus natalensis</i>	2.8/4.6	2.0/2.3	1.0/1.5	1.5/6.0	—	—	—	—
<i>Leptodactylus troglodytes</i>	1.0/2.3	1.8/2.4	—	—	—	1.0/2.4	4.0/1.6	1.0/2.8
<i>Leptodactylus vastus</i>	2.9/4.3	1.8/2.6	1.0/2.7	—	2.3/2.6	4.0/2.4	1.0/1.4	3.8/3.7
<i>Physalaemus albifrons</i>	—	—	—	—	—	4.0/1.9	—	1.0/—
<i>Physalaemus cicada</i>	—	—	—	—	—	1.5/1.0	1.0/1.4	1.0/1.8
<i>Physalaemus cuvieri</i>	1.8/3.0	2.6/1.5	—	−/1.1	—	1.4/1.1	—	—
<i>Pleurodema diplolister</i>	1.1/3.2	2.0/1.8	—	—	—	—	1.0/1.0	1.4/3.2
<i>Pseudopaludicola mystacalis</i>	1.0/3.2	1.0/2.9	—	—	—	—	—	—
<i>Pseudopaludicola pocoto</i>	—	—	—	—	1.8/5.2	1.8/4.8	3.0/2.3	2.5/5.7
Microhylidae								
<i>Chiasmocleis alagoana</i>	—	—	—	−/1.2	—	—	—	—
<i>Dermatonotus muelleri</i>	—	−/1.0	—	—	—	1.0/1.3	—	2.0/1.0
Odontophrynidae								
<i>Proceratophrys cristiceps</i>	—	—	—	—	—	1.0/2.8	—	1.6/1.8
Phyllomedusidae								
<i>Pithecopus nordestinus</i>	—	2.6/2.2	—	—	—	1.0/4.0	—	2.1/2.9
Ranidae								
<i>Lithobates palmipes</i>	4.3/5.2	4.6/7.5	2.6/9.4	2.8/7.2	—	—	—	—

Niche complementarity and phylogenetic structure.—Using the Mantel test, we found no evidence of spatial and trophic niche complementarity in most assemblages, regardless of the season: Guaribas REBIO (rainy season: $r = 0.08$, $P = 0.08$; dry season: $r = 0.09$, $P = 0.14$), Aiuaba ESEC (rainy season: $r = -0.08$, $P = 0.76$; dry season: $r = -0.26$, $P = 0.83$), and Seridó ESEC (rainy season: $r = 0.03$, $P = 0.34$; dry season: $r = 0.09$, $P = 0.22$). Evidence was only found during the rainy season at JBBM PPA, despite the low correlation value (rainy season: $r = 0.26$, $P = 0.04$; dry season: $r = 0.11$, $P = 0.21$).

Phylogenetic structure analysis indicated a lack of structuring based on the PD, MPD, and MNTD indices, in both the Caatinga and Atlantic Forest, with the different sites clustered by biome: Caatinga ($n = 18$)—PD (observed =

4.38, $Z = 0.07$, $P = 0.51$), MNTD (observed = 0.31, $Z = -0.34$, $P = 0.37$), MPD (observed = 0.58, $Z = -0.93$, $P = 0.17$); Atlantic Forest ($n = 28$)—PD (observed = 6.19, $Z = 0.40$, $P = 0.66$), MNTD (observed = 0.28, $Z = -0.01$, $P = 0.50$), MPD (observed = 0.67, $Z = 0.41$, $P = 0.65$).

DISCUSSION

Microhabitat.—Higher niche overlap occurred mostly between congeners, mainly within the clades Leptodactylidae and Hylidae. Interactions within leptodactylids, within bufonids, and between them prevailed in the Caatinga, and higher overlaps within Hylidae were observed in the Atlantic Forest. These patterns reflect the predominance of interac-

Table 3. Results of the pseudo-community analysis of each studied assemblage. Observed mean (Obs mean) and simulated mean (Sim mean) niche overlap and corresponding significance values (P) for each site and season. Values in bold indicate increased trophic structure in the dry season, calculated by the difference between the two means.

Site	Diet		Microhabitat	
	Rainy	Dry	Rainy	Dry
Guaribas REBIO	Obs mean: 0.11 Sim mean: 0.28 $P < 0.0001$	Obs mean: 0.16 Sim mean: 0.34 $P < 0.0001$	Obs mean: 0.25 Sim mean: 0.26 $P: 0.34$	Obs mean: 0.25 Sim mean: 0.22 $P: 0.96$
JBBM PPA	Obs mean: 0.17 Sim mean: 0.35 $P < 0.0001$	Obs mean: 0.09 Sim mean: 0.24 $P < 0.0001$	Obs mean: 0.37 Sim mean: 0.30 $P: 0.95$	Obs mean: 0.10 Sim mean: 0.16 $P < 0.0001$
Aiuaba ESEC	Obs mean: 0.08 Sim mean: 0.34 $P < 0.0001$	Obs mean: 0.06 Sim mean: 0.55 $P < 0.0001$	Obs mean: 0.23 Sim mean: 0.24 $P: 0.27$	Obs mean: 0.13 Sim mean: 0.19 $P: 0.09$
Seridó ESEC	Obs mean: 0.15 Sim mean: 0.35 $P < 0.0001$	Obs mean: 0.06 Sim mean: 0.35 $P < 0.0001$	Obs mean: 0.25 Sim mean: 0.23 $P: 0.85$	Obs mean: 0.20 Sim mean: 0.21 $P: 0.42$

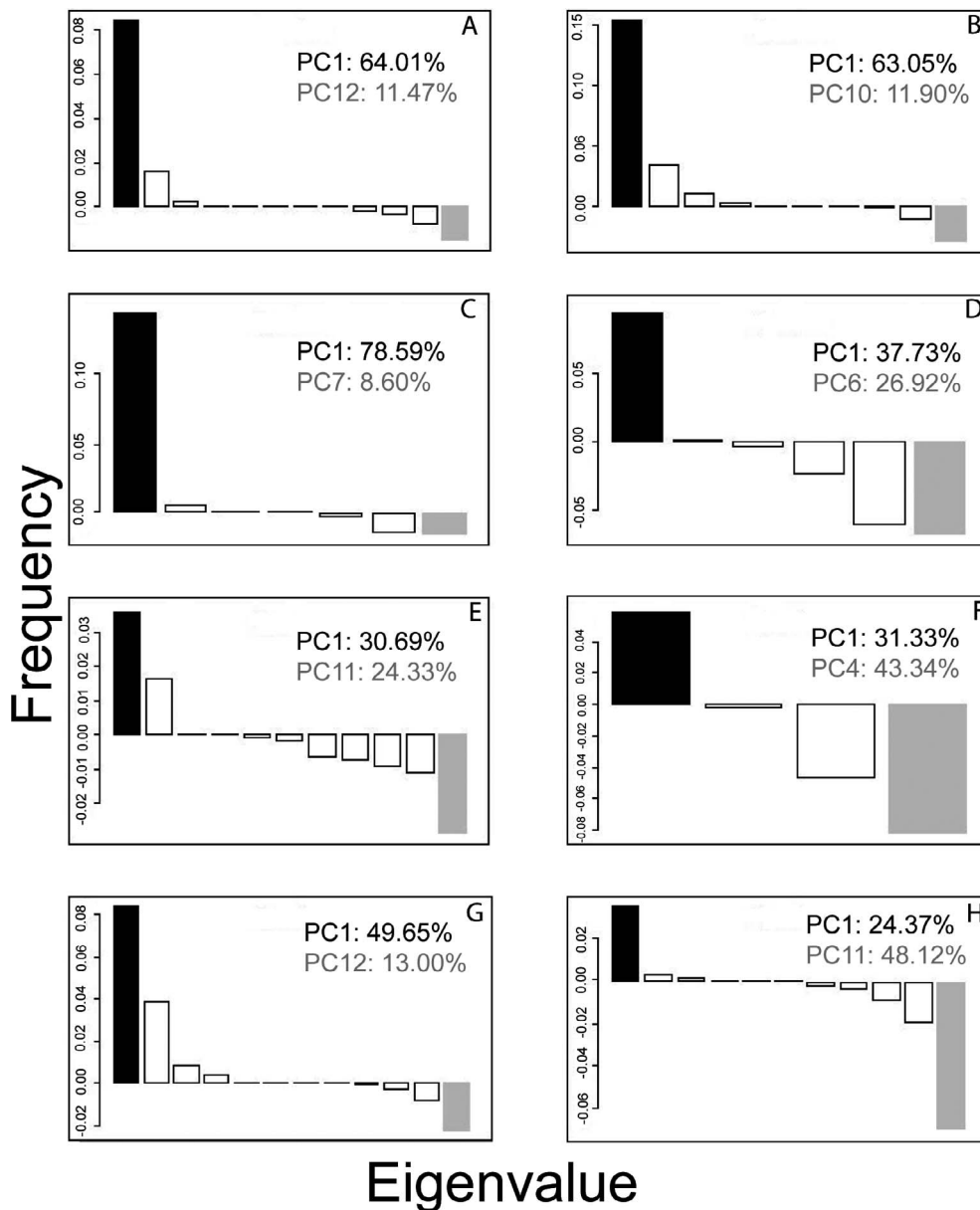


Fig. 3. Results of the phylogenetic principal component analysis (pPCA) for microhabitat use. The most important eigenvalues related to global (historical) and local (ecological) components are represented by black and gray bars, respectively. Guaribas REBIO—Atlantic Forest (A: rainy season, B: dry season); JBBM PPA—Atlantic Forest (C: rainy season, D: dry season); Aiuaba ESEC—Caatinga (E: rainy season, F: dry season); and Seridó ESEC—Caatinga (G: rainy season, H: dry season). The two highest principal component (PC) scores are shown in each graph.

Table 4. Most important prey categories for the diet of species from the four assemblages studied based on the importance value index (IVI). Dashes correspond to absence of the species from that particular condition or site or a lack of dietary data. Acarina, Aca; Anura, Anu; Araneae, Ara; Blattaria, Bla; Coleoptera, Col; Diptera, Dip; Formicidae, For; Hemiptera, Hem; Hymenoptera, Hym; Insect larvae, IL; Insect nymph, IN; Isoptera, Iso; Orthoptera, Ort; Plant material, PM.

Species	Most important food items (IVI)							
	Guaribas REBIO		JBBM PPA		Aiuaba ESEC		Seridó ESEC	
	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy
Craugastoridae								
<i>Pristimantis ramagii</i>	Col	Ara	Hem	Ort	—	—	—	—
Bufonidae								
<i>Rhinella granulosa</i>	—	—	—	—	—	For	Iso	For
<i>Rhinella jimi</i>	For	For	—	—	—	For	Col	Col
Hylidae								
<i>Boana albomarginata</i>	—	IL	Col	Ort	—	—	—	—
<i>Boana faber</i>	Bla	Col	—	—	—	—	—	—
<i>Boana raniceps</i>	—	Ort	Ara	Ort	Bla	Ort	Col	Hem
<i>Corythomantis greeningi</i>	—	—	—	—	—	—	—	IL
<i>Dendropsophus branneri</i>	Hym	Col	Dip	Col	—	—	—	—
<i>Dendropsophus elegans</i>	—	Col	—	—	—	—	—	—
<i>Dendropsophus minutus</i>	—	Ort	—	For	—	—	—	—
<i>Dendropsophus nanus</i>	Ara	Hym	—	—	Bla	Bla	IN	For
<i>Dendropsophus oliveirai</i>	Col	Hem	IL	Ort	—	—	—	—
<i>Scinax cretatus</i>	—	PM	—	—	—	—	—	—
<i>Scinax eurydice</i>	Ort	PM	—	—	—	—	—	—
<i>Scinax fuscomarginatus</i>	—	Ara	—	—	—	—	—	—
<i>Scinax nebulosus</i>	Ort	Hem	PM	Aca	—	—	—	—
<i>Scinax x-signatus</i>	—	Ara/PM	—	Iso	—	For	Col	Col
Leptodactylidae								
<i>Adenomera</i> sp.	Ara	—	—	Iso	—	—	—	—
<i>Leptodactylus fuscus</i>	Ara	—	—	—	—	Col	Col	IL
<i>Leptodactylus macrosternum</i>	Col	Col	Ort	—	For	Col	Ort	IL
<i>Leptodactylus natalensis</i>	IL	Col	For	Iso	—	—	—	—
<i>Leptodactylus troglodytes</i>	PM	Ara	—	—	—	Col	For	IL
<i>Leptodactylus vastus</i>	PM	For	Dip	—	Col	Col	Anu	Col
<i>Physalaemus albifrons</i>	—	—	—	—	—	IL	—	—
<i>Physalaemus cicada</i>	—	—	—	—	—	Iso	For	For
<i>Physalaemus cuvieri</i>	For	IL	—	For	—	Iso	—	—
<i>Pleurodema diplolister</i>	For	Ort	—	—	—	—	Ara	IL
<i>Pseudopaludicola mystacalis</i>	For	IL	—	—	—	—	—	—
<i>Pseudopaludicola pocoto</i>	—	—	—	—	Ort	IL	Ort	Col
Microhylidae								
<i>Chiasmocleis alagoana</i>	—	—	—	Iso	—	—	—	—
<i>Dermatonotus muelleri</i>	—	Iso	—	—	—	For	—	Iso
Odontophrynidae								
<i>Proceratophrys cristiceps</i>	—	—	—	—	—	IL	—	Col
Phyllomedusidae								
<i>Pithecopus nordestinus</i>	—	IL	—	—	—	—	—	IL
Ranidae								
<i>Lithobates palmipes</i>	Col	Col	IL	Bla	—	—	—	—

tions within clades with higher species richness (Leptodactylidae and Hylidae), which shifted between environments. This suggests the influence of historical factors on these assemblages because more overlap in microhabitat use occurred among the phylogenetically closer taxa, which share more traits and are thus more likely to compete (Wiens and Graham, 2005; Mesquita et al., 2006b). On the other hand, it is important to highlight that ecological effects were higher in Caatinga during dry season.

The lack of structure identified in the pseudo-community analysis suggests that competition has limited effect on the organization of most communities studied herein, regardless

of biome and season. In addition, results from the phylogenetic principal component analysis (pPCA) indicate, in all cases, the separation of arboreal (represented by Hylidae) and terrestrial/semi-aquatic (herein mainly represented by Leptodactylidae) lineages, thereby corroborating the differentiation between these two morphological clusters of Hyloidea, which originated in the Cretaceous (Roelants et al., 2007; Báez et al., 2009). The close relationship between microhabitat use and the presence of specific morphological adaptations (Crump, 1971; Hödl, 1977) reinforces that spatial resource use reflects the phylogenetic relationships among taxa, even under different seasonal conditions.

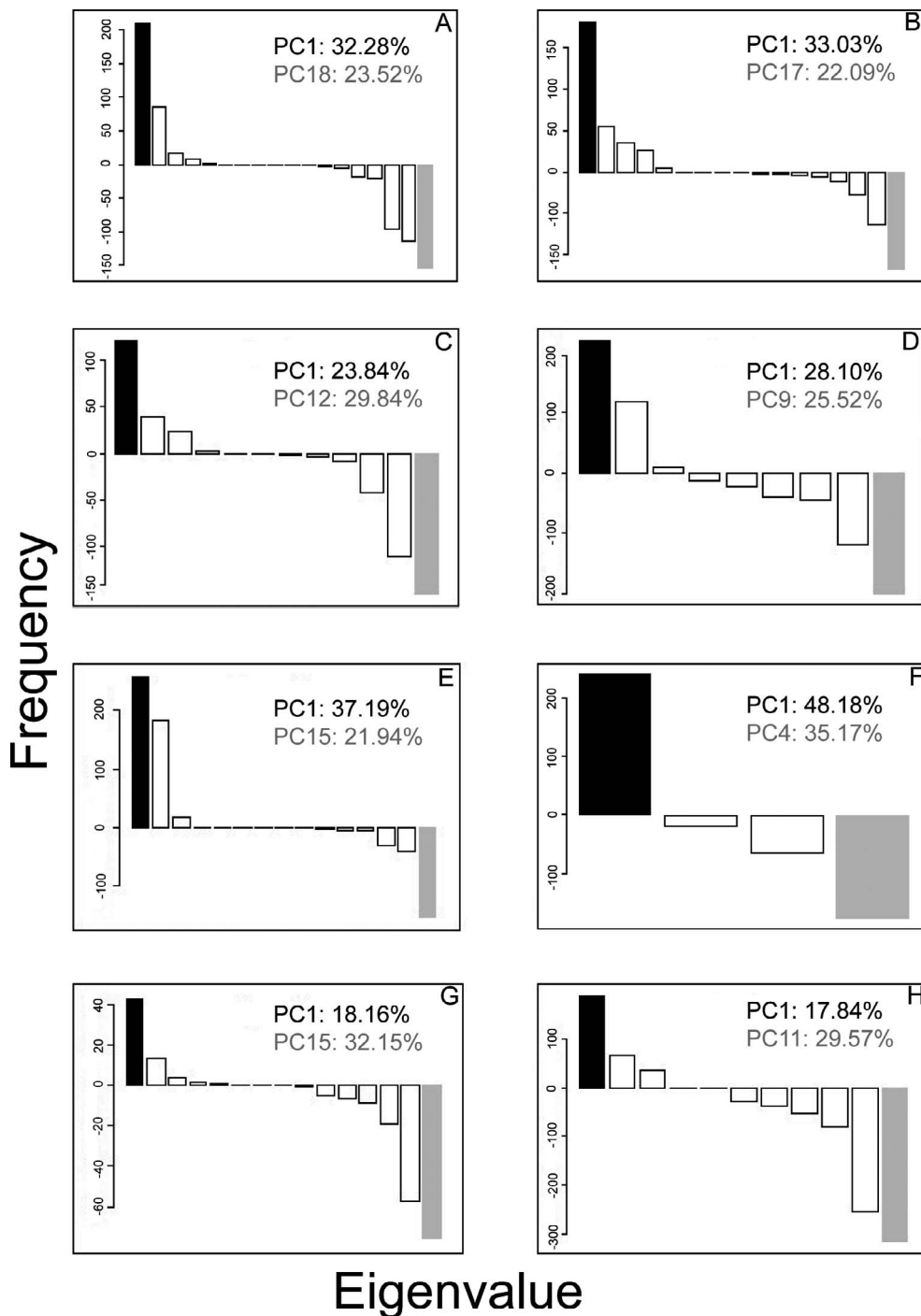


Fig. 4. Results of the phylogenetic principal component analysis (pPCA) for diet. The most important eigenvalues related to global (historical) and local (ecological) components are represented by black and gray bars, respectively. Guaribas REBIO—Atlantic Forest (A: rainy season, B: dry season); JBBM PPA—Atlantic Forest (C: rainy season, D: dry season); Aiuaba ESEC—Caatinga (E: rainy season, F: dry season); and Seridó ESEC—Caatinga (G: rainy season, H: dry season). The two highest principal component (PC) scores are shown in each graph.

Phylogenetic relationships have been shown to shape resource-sharing patterns in tropical anuran communities (Inger, 1969; Eterovick and Fernandes, 2001; Leite-Filho et al., 2017). Indeed, phylogenetic relationships affected adult anuran assemblages in the Brazilian Southeast Atlantic Forest (Eterovick et al., 2010). Likewise, an anuran community in the Brazilian semi-arid Caatinga was not structured in microhabitat use but showed a significant phylogenetic effect differentiating arboreal from terrestrial lineages (Protázio et al., 2014). Accordingly, our results corroborate a prominent role of phylogeny in amphibian community structure.

Limited or compromised spatial resources can increase competitive interactions, causing species to segregate their niches (Hutchinson, 1957; Tilman, 1982), especially during

dry seasons, when water availability is reduced (Dayton and Fitzgerald, 2005; Wells, 2007). Accordingly, the anuran assemblage at JBBM (Atlantic Forest) was structured regarding space use during the dry season, supporting a stronger effect of ecological factors in contrast to other sites. Notably, this is an urban forest fragment with clear signs of anthropogenic effects. Urban density tends to affect assemblage structure by promoting habitat loss (Pillsbury and Miller, 2008; Purrenhage et al., 2009).

Space sharing among anurans results from a series of complex interactions that depend on the synergy between current biotic and abiotic factors, as well as the effects of past interactions (Duellman and Trueb, 1994; Ernst and Rödel, 2006). Although the lack of structure based on microhabitat use occurred in most sites, the pPCA showed the existence of

ecological and historical factors affecting all assemblages, and the latter were stronger in most cases. Microhabitat availability may be high in both environments, even if the animals use a limited number of categories. Thus, the notion that “open vegetation” would be less heterogeneous and would promote microhabitat overlap between species (Cardoso et al., 1989; Pombal, 1997) may not apply to all cases. Variation in the abundance of males vocalizing during the reproductive period may explain the high spatial niche overlap observed (Santos et al., 2007). The occurrence of anurans in different environments may also reflect specific reproductive preferences, the dispersal and colonization potential of each species, stochasticity, or even tolerance to arid conditions and estivation (the last two in the Caatinga), without necessarily resulting in competitive pressures (Navas et al., 2004; Kopp and Eterovick, 2006; Afonso and Eterovick, 2007).

Diet.—Anurans are considered generalist predators with opportunistic foraging behavior (Duellman and Trueb, 1994; Solé and Rödder, 2009). Their diets basically consist of arthropods, reflecting the abundance of such prey in the environment (Teixeira and Coutinho, 2002; Almeida-Gomes et al., 2007). Conversely, groups with trophic specialization have been detected in the Amazon segregating into two guilds: ant specialists and generalists (Toft, 1980). The diet of a species is usually related to morphological, physiological, and behavioral characteristics that facilitate the location, identification, and capture of prey (Pough et al., 2004; Maragno and Souza, 2011). Therefore, foraging must meet a cost-benefit condition, combining prey quality (size and energy gain) with the predator needs and, therefore, with time and difficulty to access it (Toft, 1980; Biavati et al., 2004). Morphological and physiological adaptations, preserved in the form of phylogenetic traits over time should not be discarded from this understanding because they may affect the specialization needed to consume some prey (Toft, 1985; Darst et al., 2005).

In the present study, Formicidae and Coleoptera were usually the most important items in bufonid diets, corroborating other studies (Batista et al., 2011; Sabagh et al., 2012) and showing evident signs of trophic niche conservation. These signs are even clearer when observing the presence of Isoptera and Formicidae in the diets of microhylids, as also found in other studies (Solé et al., 2002; Berazategui et al., 2007). Conversely, *L. palmipes*, found only in the Atlantic Forest sites, has the most generalist diet of the anuran assemblages, similar to other ranids (Guidali et al., 2000; Leivas et al., 2012), which may also indicate the presence of a historical trait in its trophic niche.

When resources are limited in time, species niches tend to segregate to avoid increased interspecific competition (Vitt, 1995; Dayton and Fitzgerald, 2001). Arthropod population abundances change considerably through the year (Janzen and Schoener, 1968; James, 1991), especially in xeric environments (Karr, 1976; Lister and Aguayo, 1992). Sites experiencing severe droughts have a much higher food supply for anurans during the rainy season (Holenweg and Reyer, 2000; Kovács et al., 2007). Resource-use patterns detected herein suggest niche segregation to avoid harmful interactions, given that Caatinga assemblages were more structured than the Atlantic Forest assemblages in all cases. Furthermore, the ecological component had a stronger effect on trophic structuring compared to microhabitat, although in most cases the historical effect was still stronger,

indicating that a phylogenetic constraint affects diet, at least in some clades. Although a clear synergy exists between these factors, historical effects are usually predominant in assemblage organization (Losos, 1996; Mesquita et al., 2006b). When analyzing trophic resources, the Caatinga assemblages were more structured than the Atlantic Forest assemblages in all cases. This pattern may be related to the effect of seasonality on prey abundance.

The comparison between seasons of all sites shows that in most cases assemblage structure increased even further as the dry season progressed. In the Caatinga sites, water availability during the dry season was limited to the presence of perennial water bodies used for human supply. Although some cases show a marked decrease in the number of active anuran species (Aiuaba ESEC), this condition may have been accompanied by a limitation in prey availability, aggravated by rainfall and moisture constraints (Parker and Courtney, 1983; Odum and Barrett, 2007). This situation could contribute to niche segregation in response to environmentally unfavorable periods. This did not occur at the Guaribas REBIO (Atlantic Forest), thereby corroborating the effect of more regular water availability on prey abundance (Duellman and Trueb, 1994; Anu et al., 2009). However, an effect similar to that in the Caatinga was noted in the dry season at the JBBM (Atlantic Forest), which exhibited a higher degree of assemblage structure based on diet composition and was also the only assemblage with structured microhabitat use. However, because this Atlantic Forest site is included in an urban environment, anthropogenic effects may compromise the resource quality and enhance niche segregation (Ernst and Rödel, 2005; Parris, 2006).

Despite all evidence related to the effect of ecological factors on assemblage structure, a considerable historical effect was present in all assemblages. Some species showed signs of conservatism in their diets, especially related to the presence of Formicidae in the diets of bufonids and microhylids. Ants are a very important resource for some Dendrobatidae, a historical constraint, and are directly related to the need for the acquisition of alkaloids related with dendrobatid toxins (Caldwell, 1996; Mebs et al., 2010). This constraint may be occurring in Caatinga and Atlantic Forest assemblages, as evidenced by the presence of current bufonid differentiation from an ancestral myrmecophagy and due to adaptations to myrmecophagy within the Microhylidae (Vences et al., 1998). However, studies focusing on physiology and experimental approaches, among others, are needed for more-specific conclusions.

The presence of plant material was found in the diet of species from all assemblages. The intake of this item is considered accidental by some researchers, who argue that animals may swallow plant fragments by catching prey on them (Brandão et al., 2003; Kovács et al., 2007). The inclusion of plant parts in the diet in all situations, along with acquisition of minerals, could also provide volume to the stomachs, thereby helping to macerate the exoskeletons of arthropods (Evans and Lampo, 1996). In the present study, we observed that plants were the most important item for some congeners from different families found in the Atlantic Forest (Hylidae—*Scinax cretatus*, *Scinax eurydice*, *Scinax nebulosus*, and *Scinax x-signatus*; Leptodactylidae—*Leptodactylus troglodytes* and *Leptodactylus vastus*). Thus, at least in these cases, the plant material intake may be non-random and related to some physiological need (Anderson et al., 1999). The presence of plant material in the diet as an important source of water has already been reported in some studies and

could be essential in environments with drastic seasonality (Silva et al., 1989; Protázio et al., 2015). However, because only leptodactylids used this category during the dry season and in an environment with more regular water availability (Atlantic Forest), this behavior may be promoted for other reasons, or even accidentally. Our findings show that a significant number of congeners fed on plants, and this behavior may correspond to the effect of historical factors, thereby requiring further examination.

Niche complementarity and phylogenetic structure.—The comparison of all anuran faunas suggests an inversely proportional relation between trophic and spatial niches: the former is usually structured, whereas the latter is not. Niche complementarity occurs when two or more species exploit a resource with higher intensity, increasing the overlap in a niche dimension and, therefore, reducing the effect of interactions on an alternative resource (Schoener, 1974; Huey, 1979). However, this effect was not significant in most cases, which may suggest that it requires a longer time scale to affect assemblages (Fargione et al., 2007; Lanari and Coutinho, 2010). Furthermore, the possibility exists that spatial resources may not be limiting in most cases and may be highly available in both environments, thereby promoting high niche overlap values (Pianka, 1973; Toft, 1980). Thus, niche complementarity would not be necessary as an ecological factor minimizing competition.

From a phylogenetic standpoint, more adverse seasonal conditions, as observed in the Caatinga, could be acting as ecological filters, directly affecting the phylogenetic structure of assemblages from this biome, thereby favoring lineages with some type of resistance to the drastic seasonal regime. Such adaptations are known to exist in some species typical of this environment, allowing them to primarily seek to avoid water loss or to ensure their tolerance to high temperatures (Navas et al., 2004; Pereira et al., 2007). In this case, selection pressures could favor the coexistence of taxa with similar ecological traits (Savage and Cavender-Bares, 2012; de Bello et al., 2013). The assumption would be that only more closely related species, and therefore with more similar traits, would persist in the Caatinga, thereby forming a more defined phylogenetic cluster than in the Atlantic Forest (Webb et al., 2002; Vamosi et al., 2009). However, we found no signals of phylogenetic structure in either environment, which could be explained by their time of origin and establishment. Sasa and Bolaños (2004) state that species occurring in semiarid formations in Costa Rica are a remnant fraction of the anuran fauna previously existing in more humid environments. We know that the Caatinga is more recent than the Atlantic Forest (Prado and Gibbs, 1993; Behling et al., 2000). Thus, Caatinga anuran fauna could correspond to subgroups previously adapted to more mesic conditions, and the environment would still be directing specific selective pressures that would result in the phylogenetic structure of the assemblages over time.

The present findings reinforce the notion that anuran assemblages are affected by a complex synergy between ecological and historical factors (Ernst and Rödel, 2006; Eterovick et al., 2010; Dias-Terceiro et al., 2015). Limiting the discussion of different niche aspects exclusively to effects may hinder the understanding of interactions between these animals and the environment, and the refinement of a hypothesis and phylogenetic analysis may contribute to an understanding of both (ecological and historical) characteristics as equally important factors. Furthermore, applying this

approach to other aspects, either stochastic or deterministic, may provide the necessary grounds to clarify the patterns affecting anuran faunas at regional and local scales.

MATERIAL EXAMINED

Institutional abbreviations follow Sabaj (2019).

Adenomera sp.: (11) Brazil, Paraíba, JBBM PPA: CHUFPB 10125–10126, 10557–10559, 10653, 10762, 10775; Guaribas REBIO: CHUFPB 4084, 4114, 4259.

Boana albomarginata: (48) Brazil, Paraíba, JBBM PPA: CHUFPB 3535, 8343–8346, 10597–10607, 10628–10637; Guaribas REBIO: CHUFPB 8012–8013, 8018, 8073–8075, 8117–8118, 8149–8151, 8198–8200, 8211, 8257–8263.

Boana faber: (11) Brazil, Paraíba, Guaribas REBIO: CHUFPB 4269, 8100–8104, 8185–8186, 8229–8231.

Boana raniceps: (62) Brazil, Paraíba, JBBM PPA: CHUFPB 4633–4634, 8359, 10652, 10763; Guaribas REBIO: CHUFPB 4197, 8076–8077, 8209–8210, 8291, 8307–8308; Ceará, Aiuaba ESEC: CHUFPB 3071–3074, 3087, 3150, 3203, 3295, 5109–5110, 5123, 5176–5177, 5189, 6339, 6340; Rio Grande do Norte, Seridó ESEC: CHUFPB 4888–4893, 4904, 4907–4911, 4936–4940, 4958–4963, 5363, 5724, 5792, 5853–5854, 6713–6715, 6758, 6782.

Chiasmocleis alagoana: (5) Brazil, Paraíba, JBBM PPA: CHUFPB 10107, 10109–10112.

Corythomantis greeningi: (11) Brazil, Rio Grande do Norte, Seridó ESEC: CHUFPB 5452–5454, 5543, 6116–6117, 6200, 6752, 6763–6764, 6768.

Dendropsophus branneri: (169) Brazil, Paraíba, JBBM PPA: CHUFPB 3495, 3498, 3534, 3541–3542, 3624–3632, 4494–4495, 4497, 4499, 4553–4559, 4625–4627, 4636–4657, 4659–4664, 10156–10179; Guaribas REBIO: CHUFPB 4034–4037, 4039, 4048, 4052–4053, 4081, 4102–4103, 4126, 4156–4158, 4180–4185, 4189–4191, 4112, 4213–4217, 4244–4246, 4255–4256, 4270–4276, 4282–4283, 8039–8043, 8056–8059, 8071, 8087–8092, 8112–8113, 8137–8138, 8165, 8170–8171, 8201–8202, 8206–8207, 8215–8216, 8226, 8241–8243, 8248–8249, 8267, 8288–8290, 8296, 8300–8303, 8305.

Dendropsophus elegans: (3) Brazil, Paraíba, Guaribas REBIO: CHUFPB 8126–8127, 8153.

Dendropsophus minutus: (97) Brazil, Paraíba, JBBM PPA: CHUFPB 10114–10120, 10136–10145, 10617–10627, 10638–10649; Guaribas REBIO: CHUFPB 8011, 8022–8038, 8049–8052, 8055, 8082–8086, 8160–8164, 8184, 8196–8197, 8217, 8219–8224, 8264–8266, 8268–8270, 8297–8298, 8304, 8344–8348.

Dendropsophus nanus: (178) Brazil, Paraíba, Guaribas REBIO: CHUFPB 4186–4188, 4206–4211, 4239–4243, 4254, 4277, 4284, 8283–8285, 8306, 8339; Ceará, Aiuaba ESEC: CHUFPB 3075, 3079, 3082–3086, 3144–3149, 3206–3210, 3235–3240, 3272–3277, 3296, 6341, 5012–5013, 5016–5023, 5039, 5054–5060, 5073–5078, 5093–5096, 5157, 5160–5165, 5183–5188, 5210–5214, 5225–5229, 5240–5242, 5245–5248, 5267–5269,

5285–5287; Rio Grande do Norte, Seridó ESEC: CHUFPPB 4895–4899, 4914–4923, 4928–4935, 4972–4976, 4998–5000, 5319–5328, 5364, 5729–5732, 6706–6709, 6753–6757, 6777–6781.

Dendropsophus oliveirai: (54) Brazil, Paraíba, JBBM PPA: CHUFPPB 3494, 3499, 3536, 3539, 4492, 4498, 4551–4552, 4622–4624, 4628, 4658, 6875–6877, 8355–8357, 10146–10155, 10565; Guaribas REBIO: CHUFPPB 4082–4083, 4095–4101, 8044–8048, 8093, 8208, 8218, 8295, 8349–8354.

Dermatonotus muelleri: (33) Brazil, Paraíba, Guaribas REBIO: CHUFPPB 8078; Ceará, Aiuaba ESEC: CHUFPPB 5254; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5477, 5591, 5633–5634, 5636, 5659–5660, 5662–5664, 5690, 5706–5707, 5711, 5761, 5771, 5811–5815, 5866–5869, 5922–5925, 5939–5940.

Leptodactylus fuscus: (38) Brazil, Paraíba, Guaribas REBIO: CHUFPPB 4058, 4111–4112, 4152; Ceará, Aiuaba ESEC: CHUFPPB 5086–5088, 5178, 5281; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5392, 5399, 5427–5428, 5437, 5441, 5443, 5525, 5623, 5640, 5675, 5680, 5693–5695, 5704, 5760, 5855–5856, 5865, 5929, 5937, 6002–6003, 6008, 6016, 6744–6745, 6769.

Leptodactylus macrosternum: (206) Brazil, Paraíba, JBBM PPA: CHUFPPB 3639; Guaribas REBIO: CHUFPPB 4003, 4040–4043, 4049, 4079, 4085–4087, 4115, 4150–4151, 4154, 4192–4194, 4232, 4260–4264, 4266–4267, 4280–4281, 4289, 8194–8195, 8239–8240, 8278–8282, 8310–8313; Ceará, Aiuaba ESEC: CHUFPPB 3017–3020, 3202, 3204–3205, 3241, 3243, 3271, 3293, 3343–3344, 5001–5009, 5024–5035, 5043–5053, 5066–5072, 5089–5092, 5113–5114, 5136–5137, 5158–5159, 5168–5169, 5179–5180, 5201–5209, 5216–5221, 5243–5244, 6338, 6360; Rio Grande do Norte, Seridó ESEC: CHUFPPB 4900–4903, 4912–4913, 4926–4927, 4952–4957, 4977–4981, 4988–4993, 5318, 5370, 5389–5391, 5393, 5395, 5397, 5411, 5418, 5420, 5425, 5438, 5444, 5448, 5511, 5514–5515, 5518, 5588–5590, 5592–5596, 5598, 5625–5627, 5630–5632, 5635, 5643–5644, 5649–5652, 5668, 5671–5672, 5709, 5713–5714, 5752, 5974, 6710–6711, 6728–6730.

Leptodactylus natalensis: (94) Brazil, Paraíba, JBBM PPA: CHUFPPB 3543, 3606–3607, 8329, 8331–8340, 8347–8350, 10081, 10088–10106, 10124, 10132–10135, 10182–10185, 10573–10596; Guaribas REBIO: CHUFPPB 4005, 4015–4016, 4044, 4076–4078, 4110, 4123, 4153, 4155, 4161–4162, 4238, 8062–8063, 8068–8069, 8144–8145, 8233–8234, 8341.

Leptodactylus troglodytes: (86) Brazil, Paraíba, Guaribas REBIO: CHUFPPB 4001, 4011, 4116–4117, 4144, 8008, 8079, 8225, 8332; Ceará, Aiuaba ESEC: CHUFPPB 5124–5128; Rio Grande do Norte, Seridó ESEC: CHUFPPB 4925, 4966, 5405–5408, 5474, 5582, 5599, 5601–5604, 5611–5612, 5614–5615, 5629, 5638, 5645, 5681–5683, 5696, 5699, 5757–5758, 5765–5768, 5795–5799, 5804, 5862, 5870, 5880–5884, 5886, 5913, 5920–5921, 5926–5927, 5932–5936, 5944, 5946–5948, 5950–5951, 5954, 6712, 6747–6751, 6770–6773.

Leptodactylus vastus: (60) Brazil, Paraíba, JBBM PPA: CHUFPPB 6869; Guaribas REBIO: CHUFPPB 4088, 4092–4094, 4278, 8128, 8156–8158, 8187–8188, 8232, 8274–8275, 8323–8338; Ceará, Aiuaba ESEC: CHUFPPB 3028, 3294, 3341, 5010, 5036–5037, 5040, 5042, 5083–5084, 5121–5122, 5156, 5181–5182,

5215, 5256–5257, 5280; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5315–5317, 5358, 5624, 5734–5735, 5908, 6766, 6792.

Lithobates palmipes: (143) Brazil, Paraíba, JBBM PPA: CHUFPPB 3490–3493, 3531–3533, 3635–3638, 4491, 4513–4520, 4560–4573, 4615–4616, 4629–4632, 6870–6873, 8351–8354, 10068–10079, 10082–10087, 10108, 10128–10131, 10180–10181, 10556, 10566–10572; Guaribas REBIO: CHUFPPB 4006–4008, 4017, 4045–4046, 4050, 4108, 4118–4122, 4124, 4164–4179, 4218–4229, 4248–4251, 4257–4258, 8060–8061, 8146–8148, 8193, 8235–8238, 8255, 8276–8277, 8342.

Physalaemus albifrons: (6) Brazil, Ceará, Aiuaba ESEC: CHUFPPB 5112, 5139, 5141, 5302; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5446, 6776.

Physalaemus cicada: (46) Brazil, Ceará, Aiuaba ESEC: CHUFPPB 5279, 5303–5307; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5527, 5560–5574, 5661, 5676, 5776–5777, 5807, 5879, 5931, 5938, 5952–5953, 5979, 6759–6762, 6783–6789, 6793–6794.

Physalaemus cuvieri: (28) Brazil, Paraíba, JBBM PPA: CHUFPPB 10113; Guaribas REBIO: CHUFPPB 4018, 4021, 4075, 4198, 8019–8021, 8054, 8067, 8108–8110, 8169, 8256; Ceará, Aiuaba ESEC: CHUFPPB 5131, 5142–5147, 5174–5175, 5190, 5276–5277, 5301.

Pithecopus nordestinus: (48) Brazil, Paraíba, Guaribas REBIO: CHUFPPB 8014–8016, 8094–8095, 8119–8120, 8154, 8203–8205, 8227–8228, 8271–8273, 8299, 8355; Ceará, Aiuaba ESEC: CHUFPPB 5079, 5097, 5250–5253, 5270–5274, 5282; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5314, 5789–5791, 5901, 5995–6000, 6027–6033.

Pleurodema diplolister: (64) Brazil, Paraíba, Guaribas REBIO: CHUFPPB 4059–4070, 4132–4143, 4145–4149, 8105–8107, 8131–8133; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5545, 5548, 5552–5558, 5608–5609, 5756, 5762, 5800, 5806, 6060, 6062, 6071–6072, 6133, 6136, 6141, 6164, 6169–6170, 6774–6775, 6795–6796.

Pristimantis ramagii: (101) Brazil, Paraíba, JBBM PPA: CHUFPPB 3496–3497, 3500, 3537–3538, 3540, 3544–3550, 3597–3605, 3608–3623, 4493, 4496, 4500–4512, 4574–4581, 4617–4621, 6874, 8330, 8342, 8358, 10080, 10127, 10562–10564; Guaribas REBIO: CHUFPPB 4012–4014, 4104–4107, 4199–4205, 4233–4237, 8009, 8080–8081, 8166–8167, 8320–8321.

Proceratophrys cristiceps: (21) Brazil, Ceará, Aiuaba ESEC: CHUFPPB 5111, 5132; Rio Grande do Norte, Seridó ESEC: CHUFPPB 5447, 5528, 5583, 5648, 5689, 5712, 5820, 5858–5861, 5914, 5919, 5941–5942, 5977, 5978, 6015, 6790.

Pseudopaludicola mystacalis: (10) Brazil, Paraíba, Guaribas REBIO: CHUFPPB 4113, 4286, 4252–4253, 8121–8125, 8155.

Pseudopaludicola pocoto: (169) Brazil, Ceará, Aiuaba ESEC: CHUFPPB 3013–3014, 3109–3138, 3345, 3348–3349, 5061–5065, 5080–5082, 5098–5100, 5115–5119, 5138, 5148, 5191–5194, 5199–5200, 5230–5239, 5259–5266, 5275, 5278, 5289–5300, 6332, 6342; Rio Grande do Norte, Seridó ESEC:

CHUFPP 4942–4951, 4967–4971, 4994–4997, 5451, 5500–5508, 5578–5781, 5832–5842, 5844–5847, 5850–5851, 5902, 5904–5907, 6696–6705, 6717–6727.

Rhinella granulosa: (79) Brazil, Ceará, Aiuaba ESEC: CHUFPP 5014, 5038, 5149–5154, 5170–5173, 5258; Rio Grande do Norte, Seridó ESEC: CHUFPP 4941, 4965, 4983–4987, 5356, 5533–5534, 5536–5539, 5579, 5653, 5669, 5684–5686, 5691–5692, 5697, 5700, 5717, 5726, 5755, 5759, 5763, 5764, 5770, 5801–5803, 5808–5809, 5871, 5878, 5885, 5887–5891, 5910–5911, 5917–5918, 5928, 5930, 5946, 5955, 5330, 5331, 6716, 6734–6739, 6741–6743, 6767–6768.

Rhinella jimi: (86) Brazil, Paraíba, Guaribas REBIO: CHUFPP 4002, 4004, 4009, 4022, 4047, 4051, 4089–4091, 4109, 4125, 4163, 4195–4196, 4231, 4265, 4279, 8001–8007, 8064–8066, 8212, 8253–8254, 8292, 8343; Ceará, Aiuaba ESEC: CHUFPP 5011, 5041, 5085, 5106–5108, 5120, 5140, 5155, 5167, 5195, 5222, 5223, 5249, 5255; Rio Grande do Norte, Seridó ESEC: CHUFPP 4924, 4964, 4982, 5371, 5401–5404, 5423–5424, 5429, 5431, 5473, 5475–5476, 5520–5523, 5577–5578, 5639, 5641–5642, 5646, 5665, 5687–5688, 5716, 5737, 5769, 5810, 5864, 5909, 5313, 6731, 6732–6733, 6791.

Scinax cretatus: (11) Brazil, Paraíba, Guaribas REBIO: CHUFPP 8096–8099, 8168, 8172–8173, 8175, 8179, 8213–8214.

Scinax eurydice: (11) Brazil, Paraíba, Guaribas REBIO: CHUFPP 4010, 4230, 8017, 8159, 8174, 8177–8178, 8180–8183.

Scinax fuscomarginatus: (6) Brazil, Paraíba, Guaribas REBIO: CHUFPP 8293–8294, 8317–8319, 8340.

Scinax nebulosus: (63) Brazil, Paraíba, APP JBBM: CHUFPP 3633–3634, 4635, 10560–10561, 10764–10774; Guaribas REBIO: CHUFPP 4023–4033, 4054–4057, 4071–4074, 4127–4131, 4159–4160, 4268, 4287–4288, 8070, 8134–8136, 8139–8143, 8244–8247, 8250–8252, 8286–8287.

Scinax x-signatus: (50) Brazil, Paraíba, APP JBBM: CHUFPP 10121–10123, 10608–10616, 10650–10651, Guaribas REBIO: CHUFPP 8010, 8072, 8111, 8114–8116, 8130, 8152, 8176; Ceará, Aiuaba ESEC: CHUFPP 3278, 5015, 5101–5105, 5129–5130, 5166, 5224, 5283–5284; Rio Grande do Norte, Seridó ESEC: CHUFPP 4894, 4906, 5362, 5421, 5773–5775, 5900, 5994, 6026, 6291, 6305, 6740, 6752.

DATA ACCESSIBILITY

Supplemental material is available at <https://www.copeiajournal.org/ch-18-109>.

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