Influence of habitat heterogeneity on anuran diversity in Restinga landscapes of the Parnaíba River delta, northeastern Brazil

Kássio C. Araújo¹, Anderson Guzzi³, Robson W. Ávila¹,²

¹ Programa de Pós-Graduação em Ecologia e Recursos Naturais, Bloco 902, Centro de Ciências, Universidade Federal do Ceará – UFC, Campus do PICI, Av. Humberto Monte, s/n, 60455-760 Fortaleza, Ceará, Brazil
² Programa de Pós-Graduação em Bioprospeção Molecular, Universidade Regional do Cariri, Campus do Pimenta, Rua Cel. Antônio Luiz, 1161, Bairro do Pimenta, 63105-000, Crato, Ceará, Brazil
³ Curso de Ciências Biológicas, Centro de Ciências do Mar, Universidade Federal do Piauí – UFPI, Campus Ministro Reis Veloso, Av. São Sebastião, 2819, Planalto Horizonte, 64202-020, Parnaíba, Piauí, Brazil

Corresponding author: Kássio C. Araújo (kassio.ufpi@gmail.com)

Academic editor: A. Crottini  |  Received 28 October 2017  |  Accepted 9 April 2018  |  Published 10 May 2018

http://zoobank.org/C0F6C60D-24BD-4FCE-9533-7E76A2D0FB69

Citation: Araújo KC, Guzzi A, Ávila RW (2018) Influence of habitat heterogeneity on anuran diversity in Restinga landscapes of the Parnaíba River delta, northeastern Brazil. ZooKeys 757: 69–83. https://doi.org/10.3897/zookeys.757.21900

Abstract
Anurans have close associations with environmental conditions and therefore represent an interesting vertebrate group for examining how resource availability and environmental variables influence species diversity. Associations between habitat heterogeneity and anuran species diversity were tested in the Restinga landscapes of the Parnaíba River delta in northeastern Brazil. Twenty-one anuran species were sampled in the rainy season during monthly excursions (December 2015 to June 2016) into areas of Restinga on two islands in the Parnaíba River delta. The fourth highest anuran diversity was found in this type of environment in Brazil and is the third in northeastern Brazil. Microenvironments, characterized by a combination of vernal pools with different vegetational and physical structures, better explained anuran species composition in the Parnaíba River delta.

Keywords
Amphibians, heterogeneity, Parnaíba River delta
Introduction

Scientists have long attempted to explain species distribution patterns and species richness worldwide, and several ecological hypotheses and theories have been proposed (e.g., Hutchinson 1959, Pianka 1966, MacArthur and Wilson 1967, Huston 1979, Hubbell 2001, Tjørve et al. 2008), including the habitat heterogeneity hypothesis of MacArthur and MacArthur (1961), which proposed that heterogeneous environments improve species richness by allowing species coexistence.

The habitat heterogeneity hypothesis has since been used to explain distribution patterns and species richness throughout the world (e.g., Atauri and Lucio 2001, Tews et al. 2004, Bastazini et al. 2007, González-Megías et al. 2007, Vasconcelos et al. 2009, Silva et al. 2010, Jimenez-Alfaro et al. 2016). Several studies in Brazil have shown a close relationship between environmental heterogeneity and amphibian diversity, although those studies have been largely concentrated in the Amazon rain forest and Atlantic Forest (Keller et al. 2009, Vasconcelos et al. 2009, Silva et al. 2011). Studies in open formations in Brazil, such as in the morphoclimatic domains Tropical Atlantic, Caatingas, and Cerrados (see Ab’Sáber 1977 for definition of morphoclimatic domains), have been scarce (e.g., Bastazini et al. 2007, Xavier and Napoli 2011, Dória et al. 2015, respectively).

Although the habitat heterogeneity hypothesis of MacArthur and MacArthur (1961) is well understood, the measurement of this heterogeneity is difficult due to the close connection with resources variety and availability. Thus, resources such as size of water pond may be important to amphibian richness, as predicted by species-area relationship in the Islands Biogeography theory of MacArthur and Wilson (1967). In addition, duration and depth of water pond is important for amphibian reproductive success especially in regions with irregular rainfall (Becker et al. 2007).

Vegetation structure in and around water bodies is an important resource for local diversity of anurans (Bastazini et al. 2007, Dória et al. 2015) by providing conditions of more reproductive modes (Andrade et al. 2016). Amphibians are strongly influenced by environmental conditions (Duellman and Trueb 1994) and, therefore, represent an interesting vertebrate group to investigate how resource availability can influence species diversity.

The Parnaíba River delta in northeastern Brazil is dominated by Restinga coastal vegetation with sandy soils and open herbaceous, shrubby, and arboreal plant formations (Silva and Britez 2005, Santos-Filho et al. 2010, Santos-Filho et al. 2015, Serra et al. 2016) with approximately 363 known plant species belonging to 74 families (Santos-Filho et al. 2015) – indicating high local heterogeneity. The relationship of this presumed heterogeneity with anuran diversity in the Parnaíba River Delta, however, remains unknown (Andrade et al. 2016, Andrade et al. 2014, Andrade et al. 2012, Loebmann and Mai 2008). The present study aimed to test the influence of habitat heterogeneity on anurans diversity in the Restinga landscapes of the Parnaíba River Delta.
Materials and methods

Study area: The Parnaíba River Delta is contained within an Environmental Protection Area (EPA) created in August 1966, covering approximately 313,800 ha in the Brazilian states of Piauí, Maranhão, and Ceará (Fig. 1) (Brasil 2002). The region is composed of a transitional area between Caatinga and Cerrado formations and marine systems (Brasil 2002). The predominant physiognomy is the Restinga environment, quaternary habitats characterized by sandy soils with high salt concentrations covered predominantly by herbaceous and shrubby xerophytic vegetation (see Xavier et al. 2015 for the definition of a Restinga). Rainfall is concentrated mainly from January through May (IBAMA 1998).

Sampling: Amphibians were collected in areas of Restinga from two islands in the Parnaíba River Delta: Ilha Grande de Santa Isabel Island in the state of Piauí (2°52’27”S, 41°47’20”W, WGS84 datum, 5 m a.s.l.) and Canárias Island in the state of Maranhão (2°48’09”S, 41°52’19”W, WGS84 datum, 8 m a.s.l.). First we selected the areas of Restinga in Parnaíba River Delta according to the soil type (Embrapa Solos UEP Recife 2006). We then selected three Restinga landscapes covering approximately 10 km² from these areas. Using the ArcToolbox (Create Random Points) function from the software ARCGIS, version 9.3 (ESRI 2008), two plots of 1 km² were ran-
domly chosen in each landscape as sampling points. The three Restinga landscapes and the sampling points were marked using a C7 GPS, version 1.0.

Anuran sampling was undertaken monthly on consecutive days during the rainy season (from December 2015 to June 2016) employing visual searches (Crump and Scott Jr 1994). Our sampling effort was approximately 336 hours/4 researchers. Voucher specimens were deposited in the amphibians’ collection of the Universidade Regional do Cariri (URCA) and Universidade Federal do Piauí (UFPI) (Appendix 1). Anuran nomenclature follows Frost (2017). The species were identified according to literature and comparisons of specimens deposited in the amphibians’ collection of URCA and UFPI.

Habitat heterogeneity was quantified using seven environmental descriptors adapted from Santos et al. (2007). Values from 1 to 4 were ascribed for each environmental descriptor, being 4 the highest heterogeneity local indicator. The habitat heterogeneity of each sampling point was then quantified using the mean values of environmental descriptors (Table 1). The mean value was used to give the same importance for each environmental descriptor.

Species distributions and associations with Brazilian morphoclimatic domains (Ab’Sáber 1977) were obtained from literature records (Bastazini et al. 2007, Valdujo et al. 2012, Roberto et al. 2013, Gondim-Silva et al. 2016). Species that occurs in the four Brazilian morphoclimatic domains were considered of wide distribution (Appendix 1).

Statistical analyses: the SHANNON-WIENER diversity index and EQUITY OF PIELOU (Krebs 2000) were used to measure anuran diversity; the estimator CHAO 1, which uses the number of rare species to estimate species richness of a community (Chao 1984, Colwell and Coddington 1994), was used to estimate the expected richness of amphibians. The BERGER-PARKER index (d) was used as a measure of species dominance, using Vegan package (Oksanen et al. 2016). We then produced sample-

### Table 1. Main characteristics of the six sampling points in the Parnaíba River Delta: duration (in months) of the water pond (MWP), size (in meters) of water pond (SWP), depth (in centimeters) of water pond (DWP), approximate percentage of vegetation cover on water surface (PVC), types of vegetation within water (TVI), number of types of marginal vegetation (TMV) and types of margin (TM). Types of vegetation: herbaceous and macrophytes (HM), shrub (SH), and arboreal (AB). Types of margin: plans (MP), inclined (MI), and plan and inclined (MPI). Locality (LC) of the sampling points: Ilha Grande de Santa Isabel Island (ILG) and Canárias Island (ILC). In parentheses, the value of each environmental descriptors (1–4). Mean (Mean values of environmental descriptors).

|        | Point I | Point II | Point III | Point IV | Point V | Point VI |
|--------|---------|----------|-----------|----------|---------|----------|
| LC     | ILG     | ILG      | ILG       | ILG      | ILC     | ILC      |
| MWP    | 5–8 (2) | 5–8 (2)  | 5–8 (2)   | 1–5 (1)  | 1–5 (1) | 1–5 (1)  |
| SWP    | 300 (2) | 700 (3)  | 400 (2)   | 300 (2)  | 300 (2) | 400 (2)  |
| DWP    | > 61 (3)| > 61 (3) | > 61 (3)  | 31–50 (2)| 31–50 (2)| > 61 (3) |
| PVC    | 76–100 (4)| 76–100 (4)| 31–50 (2)| 31–50 (2)| 31–50 (2)| 31–50 (2)|
| TVI    | HM (2)  | HM (2)   | HM (2)    | HM (2)   | HM (2)  | HM (2)   |
| TMV    | AB (3)  | AB (3)   | AB (3)    | AB (3)   | AB (3)  | AB (3)   |
| TM     | MPI (2) | MPI (2)  | MPI (2)   | MPI (2)  | MPI (2) | MPI (2)  |
| Mean   | 2.57    | 2.71     | 2.28      | 1.85     | 2       | 2.14     |
Influence of habitat heterogeneity on anuran diversity in Restinga landscapes...

based accumulation curves with 1000 sampling randomizations, using ESTIMATE S VERSION 9.1 software (Colwell 2013) to verify if the sampling effort was sufficient to adequately represent the species community.

The normal distribution assumption was tested for both diversity and habitat heterogeneity data using the SHAPIRO-WILK test (Shapiro and Wilk 1965), at each sampling point, and was not rejected (diversity p-value = 0.5653 and habitat heterogeneity p-value = 0.8006). A linear regression analysis was used to test the influence of habitat heterogeneity (independent variable) on anurans diversity (dependent variable) (null hypothesis of no association between anuran diversity and habitat heterogeneity). All statistical analyses were performed in R software (R Development Core Team 2011), using Vegan package (Oksanen et al. 2016).

**Results**

1822 anuran specimens were recorded, belonging to six families (Bufonidae, Hylidae, Leptodactylidae, Microhylidae, Odontophrynidae, and Phyllomedusidae), 12 genera, and 21 species (see Appendix 1 and 2).

The most abundant species belonged to the families Leptodactylidae and Hylidae (Fig. 2), and they also showed the highest BERGER-PARKER dominance values (d): *Pseudopaludicola mystacalis* (d = 0.14), *Leptodactylus macrosternum* (d = 0.13), *Pleurodema diplomister* (d = 0.12), *Leptodactylus fuscus* (d = 0.11), and *Dendropsophus nanus* (d = 0.10). The CHAO 1 species richness estimator was 21.5 ± 3 species in the Parnaíba River Delta; 18 ± 1 species in Ilha Grande de Santa Isabel Island and 14 ± 3 species in Canárias Island (Tab. 2).

*Figure 2. Abundance of anurans species obtained in Ilha Grande de Santa Isabel Island and Canárias Island, Parnaíba River Delta, Northeastern Brazil.*
Table 2. Anuran diversity in the Parnaíba River Delta (PRD), Ilha Grande de Santa Isabel Island (ILG) and Canárias Island (ILC), with data on species richness (CHAO 1 species richness estimator), dominant species (BERGER-PARKER index) and evenness (PIEUOU’s index J’).

|                | PRD   | ILG   | ILC   |
|----------------|-------|-------|-------|
| Number of individuals | 1822  | 1465  | 357   |
| Species richness (observed) | 21    | 18    | 14    |
| Species richness (estimated) | 21.5 ± 3 | 18 ± 1 | 14 ± 3 |
| Dominant species | *P. mystacalis* | *P. mystacalis* | *L. fuscus* |
| Dominance observed | 14%   | 14%   | 19%   |
| Shannon - Wiener (H’) | 2.485 | 2.476 | 2.185 |
| Pielou’s index J’ | 0.8165 | 0.8569 | 0.8282 |

The sample-based accumulation curve tended asymptote (Fig. 3), which suggests that the sampling effort was sufficient to adequately represent the species community in Parnaíba River Delta, northeastern Brazil.

The species richness at the six sampling points varied from 8 to 17 (Tab. 2). The highest values of species diversity were recorded at points II, I and III, respectively, while point IV had the lowest diversity value. The highest values of habitat heterogeneity were observed at points II, I, and III, respectively, all located in Ilha Grande de Santa Isabel Island. Points V and VI showed intermediated values, while point IV had the lowest habitat heterogeneity value (Tab. 3). The combination of all environmental descriptors is the reason for different heterogeneity indexes in present study.
The linear regression analysis evidenced that the habitat heterogeneity of the Restinga environment in the Parnaíba River Delta is able to explain the anuran diversity ($R^2 = 0.9204$, $p = 0.0015$) (Fig. 4).

**Table 3.** Habitat heterogeneity, SHANNON-WIENER diversity index, evenness (Pielou’s index $J'$) and habitat heterogeneity value for each sampling point in the Parnaíba River Delta.

| Sampled points | Diversity index | Pielou’s index $J'$ | Heterogeneity |
|----------------|-----------------|---------------------|---------------|
| Point I        | $H' = 2.279$    | $J' = 0.8637$       | $He = 2.57$   |
| Point II       | $H' = 2.467$    | $J' = 0.8708$       | $He = 2.71$   |
| Point III      | $H' = 2.220$    | $J' = 0.8935$       | $He = 2.28$   |
| Point IV       | $H' = 1.768$    | $J' = 0.8502$       | $He = 1.85$   |
| Point V        | $H' = 1.815$    | $J' = 0.7881$       | $He = 2$      |
| Point VI       | $H' = 2.052$    | $J' = 0.8557$       | $He = 2.14$   |

**Figure 4.** Association between anurans’ species diversity (SHANNON-WIENER diversity index) and habitat heterogeneity in the Parnaíba River Delta, Northeastern Brazil ($R^2 = 0.9204$, $p$-value = 0.0015). Computation of the habitat heterogeneity index is explained in Material and methods.

The linear regression analysis evidenced that the habitat heterogeneity of the Restinga environment in the Parnaíba River Delta is able to explain the anuran diversity ($R^2 = 0.9204$, $p = 0.0015$) (Fig. 4).
Discussion

The Restinga of the Parnaíba River Delta have the fourth highest anuran richness in this type of environment in Brazil and the third in northeastern Brazil (21 species). The Restinga areas with the highest anuran diversity were encountered in the municipalities of Mata de São João (34 species; Bastazini et al. 2007, Oliveira and Rocha 2015, Xavier et al. 2015) and Conde (33 species; Gondim-Silva et al. 2016), both in the state of Bahia, and in the municipality of Grumari, Rio de Janeiro state (22 species; Telles et al. 2012).

The anuran species composition of the Parnaíba River Delta was similar to that reported by Borges-Leite et al. (2014) and Gondim-Silva et al. (2016) for the municipalities of São Gonçalo do Amarante and Conde, in the Brazilian states of Ceará and Bahia, respectively. The aforementioned study in the Ceará state was carried out in an ecotonal environment with floristic elements of Caatinga, Cerrado and Restinga (Borges-Leite et al. 2014) and the study in Bahia state included only “Open Restinga” (Gondim-Silva et al. 2016). The similarity between the present work and these studies could be explained by the presence of floristic elements of Caatinga, Cerrado and Restinga in our open Restinga area studied.

Nevertheless the Restinga of the Parnaíba River Delta differed greatly from Restinga sites in southeastern Brazil (states of São Paulo, Rio de Janeiro and Espírito Santo; Rocha et al. 2008, Silva et al. 2008, Vilela et al. 2011, Telles et al. 2012) and other regions of the state of Bahia (municipalities of Prado, Trancoso and Mata de São João; Bastazini et al. 2007, Rocha et al. 2008, Narvaes et al. 2009). These studies included lowland forests that can be very important for explaining the differences in anuran composition between them. The high habitat heterogeneity in Restinga environments (Gomes et al. 2016), however, could also account for those differences.

Increased habitat structural complexity results in greater species diversity (MacArthur and MacArthur 1961), with homogeneous areas showing less microhabitat availability, which hampers species coexistence and resource partitioning (Macarthur and Levins 1967). Highly heterogeneous environments promote higher species richness by promoting the coexistence, persistence, and diversification of species at different spatial and temporal scales (Stein and Kreft 2014).

Positive relationships between habitat heterogeneity and anuran diversity have been recorded in different morphoclimatic domains in Brazil, as well in the present study. Habitat heterogeneity has been shown to influence anuran diversity in Restinga areas in northeastern Brazil (Bastazini et al. 2007), in “Campo rupestre” vegetation in the Caatinga (Xavier and Napoli 2011), and in Cerrado vegetation with a predominance of semi-deciduous seasonal forest (Dória et al. 2015). A clear relationship between habitat heterogeneity and anuran diversity was recorded in the Atlantic Forest (Lop et al. 2012, Santos et al. 2012) as did Silva et al. (2011) in pasture areas, both in southeastern Brazil. Some studies, however, could not identify relationships between habitat heterogeneity and anuran diversity (Eterovick 2003, Vasconcelos and Rossa-Feres 2005, Santos et al. 2007), and more studies will consequently be necessary to elucidate the importance of environment heterogeneity to species diversity.
Anuran populations from the Restinga of the Parnaíba River Delta are influenced by habitat complexity and the variety of available microhabitats, in agreement with Bastazini et al. (2007) who highlighted the importance of shrub formations and bromeliad densities to explain changes in anuran composition in Restinga environments.

Earlier studies highlighted the importance of pond size and edge vegetation to anuran diversity (Parris and McCarthy 1999, Burne and Griffin 2005, Bastazini et al. 2007, Vieira et al. 2007, Xavier and Napoli 2011, Dória et al. 2015, Gonçalves et al. 2015). Furthermore, microenvironments composed of vernal pools with different edge vegetation structures and percentage of vegetation cover on water surface better explained the different compositions of anuran communities in Parnaíba River Delta.

Acknowledgments

We are grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for the research grant awarded to R.W.A (PQ # 303622/2015-6); Tássia G. P. Lima, Ocivana A. Pereira, and Arthur S. N. Ribeiro for their assistance during fieldwork and Marcelo F. Napoli for the valuable comments on the manuscript. We are grateful to the CNPq/FUNCAP/CAPES for financial support (PROTAX – Processes 440511/2015-1; 5574685/2017; 88882.156872/2016-01); and ICMBio for the collection license (Permit: ICMBio 7770-1, process: 29613). This study was approved by the Animal Ethics Committee of the Universidade Regional do Cariri (Comissão de experimentação e Uso de Animais – CEUA/URCA: process 00026/2015.2).

References

Ab’Sáber AN (1977) Os domínios morfoclimáticos da América do Sul. Primeira Aproximação. Geomorfologia 53(1): 1–52.
Andrade EB, Leite JRSA, Andrade GV, Macedo RG (2012) Diversidade de Anfíbios do Delta do Parnaíba. In: Guzzi A (Org.). Biodiversidade do Delta do Parnaíba. EDUFPI, Parnaíba, 209–269.
Andrade EB, Leite JRSA, Andrade GV (2014) Anurans from the municipality of Ilha Grande, Parnaíba River Delta, Piauí, northeastern Brazil. Herpetology Notes 7: 219–226.
Andrade EB, Leite JRSA, Andrade GV (2016) Diversity and distribution of anuran in two islands of Parnaíba River Delta, Northeastern Brazil. Journal of Biodiversity and Environmental Sciences 8(2): 74–86.
Atauri JA, Lucio JV (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. Landscape Ecology 16: 147–159. https://doi.org/10.1023/A:1011115921050
Bastazini CV, Munduruca JFV, Rocha PLB, Napoli MF (2007) Which environmental variables better explain changes in anuran community composition? A case study in the restinga of Mata de São João, Bahia, Brazil. Herpetologica 63(4): 459–471. https://doi.org/10.1655/0018-0831(2007)63[459:WEVBEC]2.0.CO;2
Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI (2007) Habitat split and the global decline of amphibians. Science 318(1): 1775–1777. https://doi.org/10.1126/science.1149374

Brasil (2002) Zoneamento Ecológico-Econômico do Baixo Parnaíba: primeira aproximação. MMA, Brasília. [CD-ROM]

Borges-Leite ML, Rodrigues JFM, Borges-Nojosa DM (2014) Herpetofauna of a coastal region of northeastern Brazil. Herpetology notes 7(1): 405–413.

Burne MR, Griffin CR (2005) Habitat associations of poolbreeding amphibians in eastern Massachusetts, USA. Wetlands Ecology Management 13(3): 247–259. https://doi.org/10.1007/s11273-004-7519-4

Chao A (1984) Nonparametric estimation of the number of classes in a population. Scandinavian Journal of Statistics 11(4): 265–270.

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London. Series B 345(1): 101–118. https://doi.org/10.1098/rstb.1994.0091

Colwell RK (2013) Estimates: statistical estimation of species richness and shared species from samples. Version 9.3. User’s Guide and application published at: http://viceroy.eeb.uconn.edu/estimates

Crump ML, Scott Jr NJ (1994) Visual encounter surveys. In: Measuring and Monitoring Biological Diversity – Standard Methods for Amphibians. Heyer, WR, Donnelly MAR, McDiarmid W, Hayek LAC, Foster MS (Eds.), Smithsonian Institution Press, Washington, 84–91.

Dória TAF, Klein W, Abreu RO, Santos DC, Cordeiro MC, Silva LM, Bonfim VMG, Napoli MF (2015) Environmental variables influence the composition of frog communities in riparian and semi-deciduous forests of the Brazilian Cerrado. South American Journal of Herpetology 10(2): 90–103. https://doi.org/10.2994/SAJH-D-14-00029.1

Duellman WE, Trueb L (1994) Biology of Amphibians. The Johns Hopkins University Press, Baltimore, 670 pp.

Embrapa Solos UEP Recife (2006) Electronic Database accessible at: http://www.uep.cnps.embrapa.br/solos/index.html [Access on: 10 Jan of 2017]

ESRI (2008) ArcGIS Desktop: version 9.3. Redlands, CA: Environmental Systems Research Institute. Electronic Database accessible at: http://www.esri.com/software/arcgis/index.html [Access on: 10 Jan of 2017]

Eterovick PC (2003) Distribution of anuran species among montane streams in southeastern Brazil. Journal of Tropical Ecology 19: 219–228. https://doi.org/10.1017/S0266467403003250

Frost DR (2017) Amphibian Species of the World: an Online Reference. Version 6.0 (10 Jan of 2017). Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA.

Gomes VSM, Vecchi MB, Loisselle BA, Missagia CCC, Alves MAS (2016) Heterogeneity of bird communities in a mosaic of habitats on a resting ecosystem in southeast Brazil. Zoologia 33(5): 1–13. https://doi.org/10.1590/S1984-4689zool-20150205

Gonçalves DS, Crivellari LB, Conte CE (2015) Linking environmental drivers with amphibian species diversity in ponds from subtropical grasslands. Annals of the Brazilian Academy of Sciences 87(3): 1751–1762. https://doi.org/10.1590/0001-3765201520140471
Influence of habitat heterogeneity on anuran diversity in Restinga landscapes...

Gondim-Silva FAT, Andrade ARS, Abreu RO, Nascimento JS, Corrêa GP, Menezes L, Trevisan CC, Camargo SS, Napoli MF (2016) Composition and diversity of anurans in the Restinga of the Conde municipality, northern coast of the state of Bahia, northeastern Brazil. Biota Neotropica 16(3): 1–16. https://doi.org/10.1590/1676-0611-BN-2016-0157

González-Megias A, Gómes JG, Sánchez-Piñero F (2007) Diversity-habitat heterogeneity relationship at different spatial and temporal scales. Ecography 30: 31–41. https://doi.org/10.1111/j.0906-7590.2007.04867.x

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, New Jersey, 396 pp.

Huston MA (1979) General hypothesis of species diversity. The American Naturalist 113(1): 81–101. https://doi.org/10.1086/283366

Hutchinson GE (1959) Homage to Santa Rosalia or why are there so many kind of animals? The American Naturalist 93(870): 145–159. https://doi.org/10.1086/282070

IBAMA (1998) Proteção e controle de ecossistemas costeiros: manguezais da Baía de Babitonga/Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis. Coleção meio ambiente. Série estudos – pesca, 25. Brasília, 145 pp.

Jimenez-Alfaro B, Chytrý M, Mucina L, Grace JB, Rejmánek M (2016) Disentangling vegetation diversity from climate-energy and habitat heterogeneity for explaining animal geographic patterns. Ecology and Evolution 6(5): 1515–1526. https://doi.org/10.1002/ece3.1972

Keller A, Rodel MO, Linsenmair KE, Grafe TU (2009) The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs, Journal of Animal Ecology 78: 305–314. https://doi.org/10.1111/j.1365-2656.2008.01457.x

Krebs CJ (2000) Ecological Methodology. 2 ed. Harper and Row Publishers, New York.

Loebmann D, Mai ACG (2008) Amphibia, Anura, Coastal Zone, Piauí state, Northeastern Brazil. Check List 4: 161–170. https://doi.org/10.15560/4.2.161

Lop S, Caldart VM, Santos TG, Cechin SZ (2012) What is the role of heterogeneity and spatial autocorrelation of ponds in the organization of frog communities in Southern Brazil? Zoological Studies 51(7): 1094–1104.

Macarthur RH, Macarthur JW (1961) On bird species diversity. Ecology 42: 594–598. https://doi.org/10.2307/1932254

Macarthur RH, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101(921): 377–385. https://doi.org/10.1086/282505

Macarthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, NJ, 215 pp.

Narvaes P, Bertolucci J, Rodrigues MT (2009) Species composition, habitat use and breeding seasons of anurans of the resting forest of the Estação Ecológica Juréia-Itatins, Southeastern Brazil. Biota Neotropica 9(2): 117–123. https://doi.org/10.1590/S1676-06032009000200011

Oliveira JCF, Rocha CFD (2015) A review on the anurofauna of Brazil’s sandy coastal plains. How much do we know about it? Journal of Coastal Conservation 19: 35–49. https://doi.org/10.1007/s11852-014-0354-8

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O’Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2016) Vegan: Community Ecology Package. R package version 2.3-3. https://CRAN.R-project.org/package=vegan [Last access in 15/12/2017]
Parris KM, McCarthy MA (1999) What influences the structure of frog assemblages at forest streams? Austral Journal of Ecology 24(5): 495–502. https://doi.org/10.1046/j.1442-9993.1999.00989.x

Pianka ER (1966) Latitudinal gradients in species diversity: A review of concepts. The American Naturalist 100(910): 33–46. https://doi.org/10.1086/282398

R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/

Roberto IJ, Ribeiro SC, Loebmann D (2013) Amphibians of the state of Piauí, Northeastern Brazil: a preliminary assessment. Biota Neotropica 13(1): 322–330. https://doi.org/10.1590/S1676-06032013000100031

Rocha CFD, Hatano FH, Vrcibradic D, Van Sluys M (2008) Frog species richness, composition $\beta$-diversity in coastal Brazilian restinga habitats. Brazilian Journal of Biology 68(1): 101–107. https://doi.org/10.1590/S1519-69842008000100014

Santos TG, Rossa-Feres DC, Casatti L (2007) Diversidade e distribuição espaço-temporal de anuros em um ambiente com pronunciada estação seca no sudeste do Brasil. Iheringia Série Zoologia 97(1): 37–49. https://doi.org/10.1590/S0073-47212007000100007

Santos-Filho FS, Almeida Jr EB, Soares CJRS, Zickel CS (2010) Fisionomias das restings do Delta do Parnaíba, Nordeste, Brasil. Revista Brasileira de Geografia Física 3: 218–227. https://doi.org/10.26848/rbgf.v3i3.232605

Santos TG, Vasconcelos TS, Haddad CFB (2012) The role of environmental heterogeneity in maintenance of anuran amphibian diversity of the Brazilian Mesophytic Semideciduous Forest. Tropical Forests 1: 119–138. https://doi.org/10.5772/31241

Santos-Filho FS, Almeida Jr EB, Lima PB, Soares CJRS (2015) Checklist of the flora of the restings of Piauí state, Northeast Brazil. Check List 11(2): 1–10. https://doi.org/10.15560/11.2.1598

Serra FCV, Lima PB, Almeida Jr EB (2016) Species richness in restinga vegetation on the eastern Maranhão State, Northeastern Brazil. Acta Amazonica 46(3): 271–280. https://doi.org/10.1590/1809-4392201504704

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52(3–4): 591–611. https://doi.org/10.1093/biomet/52.3-4.591

Silva SM, Britez RM (2005) A vegetação da planície costeira. In: Marques MCM, Britez RM (orgs.). História Natural e Conservação da Ilha do Mel. Curitiba: Ed. UFPR, 49–84.

Silva HR, Carvalho ALG, Bittencourt-Silva GB (2008) Frogs of Marambaia: a naturally isolated Restinga and Atlantic Forest remnant of southeastern Brazil. Biota Neotropica 8(4): 167–174. https://doi.org/10.1590/S1676-06032008000400017

Silva RJ, Diniz S, Vaz-de-melo FZ (2010) Heterogeneidade do habitat, riqueza e estrutura da assembléia de besouros rola-bostas (Scarabaeidae: Scarabaeinae) em áreas de Cerrado na Chapada dos Parecis, MT. Neotropical Entomology 39(6): 934–940. https://doi.org/10.1590/S1519-566X2010000600014

Silva RA, Martins IA, Rossa-Feres DC (2011) Environmental heterogeneity: anuran diversity in homogeneous environments. Zoologia 28(5): 610–618. https://doi.org/10.1590/S1984-46702011000500009
Telles FBS, Menezes VA, Maia-Carneiro T, Dorigo TA, Winck GR, Rocha CFD (2012) Anurans from the “Restinga” of Parque Natural Municipal de Grumari, state of Rio de Janeiro, southeastern Brazil. Check List 8(6): 1267–1273. https://doi.org/10.15560/8.6.1267

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jetlsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31: 79–92. https://doi.org/10.1046/j.0305-0270.2003.00994.x

Tjørve E, Kunin WE, Polce C, Tjørve KMC (2008) Species-area relationship: separating the effects of species abundance and spatial distribution. Journal of Ecology 96: 1141–1151. https://doi.org/10.1111/j.1365-2745.2008.01433.x

Valdujo PH, Silvano DL, Colli G, Martins M (2012) Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. South American Journal of Herpetology 7(2): 63–78. https://doi.org/10.2994/057.007.0209

Vasconcelos TS, Rossa-Feres DC (2005) Diversidade, distribuição espacial e temporal de anfíbios anuros (Amphibia, Anura) na região noroeste do estado de São Paulo, Brasil. Biota Neotropica 5(2): 137–150. https://doi.org/10.1590/S1676-06032005000300010

Vasconcelos TS, Santos TG, Rossa-Feres DC, Haddad CFB (2009) Influence of the environmental heterogeneity of breeding ponds on anuran assemblages from southeastern Brazil. Canadian Journal of Zoology 87(8): 699–707. https://doi.org/10.1139/Z09-058

Vieira WLS, Arzabe C, Santana GG (2007) Composição e distribuição espaço-temporal de anuros no Cariri paraibano, Nordeste do Brasil. Oecologia Brasiliensis 11(3): 383–396. https://doi.org/10.4257/oeco.2007.1103.08

Vilela VMFN, Brassaloti RA, Bertoluci J (2011) Anuran fauna of the restinga forest of the Parque Estadual da Ilha do Cardoso, southeastern Brazil: species composition and breeding site utilization. Biota Neotropica 11(1): 83–93. https://doi.org/10.1590/S1676-06032011000100008

Xavier AL, Napoli MF (2011) Contribution of environmental variables to anuran community structure in the Caatinga Domain of Brazil. Phyllomedusa 10(1): 45–64. https://doi.org/10.11606/issn.2316-9079.v10i1p45-64

Xavier AL, Guedes TB, Napoli MF (2015) Biogeography of anurans from the poorly known and threatened coastal sandplains of eastern Brazil. PloS One 10(6): 1–18. https://doi.org/10.1371/journal.pone.0128268
Appendix 1

Anuran species obtained at the Restinga of the Parnaíba River delta, northeastern Brazil. Morphoclimatic domains (Ab’Sáber 1977): Caatingas (CA), Cerrados (CE), Tropical Atlantic (AT), and Equatorial Amazonian (AM). Species that occur in the four Brazilian morphoclimatic domains were considered as having a wide distribution (WD). Species without voucher specimens were represented by photography.

| Taxon | Voucher specimens | Sampling points (I–VI) | Morphoclimatic domains |
|-------|-------------------|------------------------|------------------------|
| *Bufonidae* | | | |
| Rhinella granulosa (Spix, 1824) | Photographed | I, II | CA, AT |
| Rhinella jimii (Stevaux, 2002) | Photographed | All sampling points | CA, AT |
| Rhinella mirandaribeiroi (Gallardo, 1965) | Photographed | V | CE |
| *Hylidae* | | | |
| Dendropsophus minusculus (Rivero, 1971) | URCA-H12120 | I, II, V, VI | WD |
| Dendropsophus nanus (Boulenger, 1889) | CZDP473 | I, II, III, V, VI | WD |
| Hypsiboas raniceps (Cope, 1862) | URCA-H12115 | I, II, III, V | WD |
| Scinax sp. (gr. ruber) | URCA-H12123 | II | No information |
| Scinax x-signatus (Spix, 1824) | Photographed | All sampling points | WD |
| *Leptodactylidae* | | | |
| Adenomera cf. hylaedactyla (Cope, 1868) | URCA-H12125 | V | AM, CE, AT |
| Leptodactylus fusus (Schneider, 1799) | Photographed | All sampling points | WD |
| Leptodactylus macrosternum Miranda-Ribeiro, 1926 | Photographed | All sampling points | WD |
| Leptodactylus punctatus (Peters, 1870) | URCA-H12126 | II | CE |
| Leptodactylus troglodytes Lutz, 1926 | CZDP485 | II, IV | CA, CE, AT |
| Leptodactylus vittatus Lutz, 1930 | Photographed | I, II, III | CA, CE, AT |
| Physalaemus albifrons Spix, 1824 | Photographed | I, II, III, IV, VI | CA, CE, AT |
| Physalaemus cuvieri Fitzinger, 1826 | CZDP470 | II | WD |
| Pleurodeina diploister Peters, 1870 | Photographed | I, II, III, IV, VI | CA, CE, AT |
| Pseudopaludicola mystacalis (Cope, 1887) | URCA-H12118 | I, II, III, V | WD |
| *Microhylidae* | | | |
| Elachistocleis piuianenses Caramaschi and Jim, 1983 | URCA-H12124 | I, III, VI | CA, CE |
| *Odontophrynidae* | | | |
| Proceratophrys caramaschii Cruz, Nunes and Juncá, 2012 | Photographed | VI | CA |
| *Phyllomedusidae* | | | |
| Pithecopus nordestinus (Caramaschi, 2006) | Photographed | I, II, III, IV | CA, CE, AT |
Appendix 2

Anurans recorded at the Restinga of the Parnaíba River Delta, Northeastern Brazil. In brackets, the voucher specimen with the acronym of the scientific collection followed by the respective institutional registration number and specimen snout-vent length (SVL) in millimeters. Some species only have photographic records. (A) *Rhinella granulosa*, (B) *R. jim*, (C) *R. mirandariheiroi*, (D) *Dendropsophus minusculus* (URCA-H12120, SVL 18.4), (E) *D. nanus* (CZDP473, SVL 19.2), (F) *Hypsiboas raniceps* (URCA-H12115, SVL 62.6), (G) *Scinax* sp. (gr. *rubra*) (URCA-H12123, SVL 20.1), (H) *S. x-signatus*, (I) *Adenomera cf. hylaedactyla* (URCA-H12125, SVL 15.8), (J) *Leptodactylus fuscus*, (K) *L. macrosternum*, (L) *L. pustulatus* (URCA-H12126, SVL 41.2), (M) *L. troglodytes* (CZDP485, SVL 43.3), (N) *L. vastus*, (O) *Physalaemus albifrons*, (P) *P. cuvieri* (CZDP470, SVL 24.5), (Q) *Pleurodema diplolisters*, (R) *Pseudopaludicola mystacalis* (URCA-H12118, SVL 11.9), (S) *Elachistocleis piauiensis* (URCA-H12124, SVL 30.2), (T) *Proceratophrys caramaschii*, (U) *Pithecopus nordestinus*. Photographs: Kássio C. Araújo and Ocivana A. Pereira.