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Endoparasite community structure of an anuran assemblage in the Caatinga, Northeastern Neotropical Region

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Abstract

Amphibians are a widespread Chordata taxon and are important for maintaining the balance of both terrestrial and aquatic ecosystems. Brazil has a rich amphibian fauna; however, little is known about the role of their ecology and phylogenetic relationships during the assembly processes of associated endoparasite communities. Herein, we describe an endoparasite community in an anuran assemblage in the Caatinga, a unique biome of dry forests in north-eastern Brazil. We studied endoparasite diversity, as well as the effects of body length, body mass, body volume and sex on parasite abundance. We also investigated the influence of ecological and historical factors and anuran microhabitat use on endoparasite composition. We analysed individuals from 13 anuran species distributed across five families: Odontophrynidae (*Proceratophrys cristiceps*); Leptodactylidae (*Leptodactylus fuscus*, *Leptodactylus vastus*, *Leptodactylus macrosternum*, *Leptodactylus troglodytes* and *Physalaemus cuvieri*); Hylidae (*Pithecopus gonzagai*, *Scinax x-signatus*, *Boana raniceps* and *Dendropsophus nanus*); Bufonidae (*Rhinella diptycha* and *Rhinella granulosa*); and Microhylidae (*Dermatonotus muelleri*). We found nine species of endoparasites, including seven nematodes (*Aplectana membranosa*, *Cosmocerca* sp., *Oswaldocruzia mazzai*, *Raillietnema spectans*, *Rhabdias fuelleborni*, *Schrankiana* sp. and *Physaloptera* sp.), one species of Trematoda (*Glypthelmins pseudium*) and one non-identified cestode. There was no significant relationship between endoparasite abundance and host body length, body mass, body volume and sex. A phylogenetic principal component analysis showed that ecological factors had a greater influence on endoparasite assemblage than historical factors. Similarly, our results showed that ecological factors had a greater influence on anuran microhabitat use compared to historical factors, which contributed to the generalist characteristics presented by most of the sampled endoparasite species.

Introduction

The assembly rules for temporal and environmental gradients in biological communities are strongly influenced by evolutionary and ecological forces, which can also affect the composition of parasite communities (Morand *et al.*, 2002; Warburton *et al.*, 2018). Host–parasite relationships can be described based on complexity since, although hosts can be considered as habitats, they are not passive receivers of their parasites (Warburton *et al.*, 2018), raising the issue of which factors should be considered in order to better understand helminth composition in their hosts.

Some studies have shown that phylogenetic relatedness in fish and lizard communities was the most important variable for explaining parasitic community composition (Muñoz *et al.*, 2005; Brito *et al.*, 2014). These results illustrate that hosts which are phylogenetically closer are more likely to share the same set of parasites, which may be related to niche constraints (Lima *et al.*, 2012). Such patterns are shaped by coevolution, a complex process that mutually matches both host and parasite life cycles (Marcogliese, 2004).

When species share the same resources, competition can lead to segregation or exclusion (Gause, 1932; Winemiller & Pianka, 1990); thus, coexistence is only possible when the differential use of resources occurs (Vitt, 1981). Anurans commonly share resources due to phylogenetic limitations (Inger, 1969; Eterovick & Sazima, 2000; Toledo *et al.*, 2003; Prado & Pombal, 2005). Protázio *et al.* (2014) demonstrated the phylogenetic conservatism of spatial niches in an anuran taxocoenosis in the Caatinga biome, northeastern Brazil, dividing Hylidae and Leptodactylidae into arboreal and semiaquatic species. This pattern demonstrates that phylogenetic conservatism plays an important role in the actual functions displayed by the

species in a taxocoenosis (Webb et al., 2002; Cooper et al., 2010; Protázio et al., 2014). Therefore, we could expect that host traits would be reflected in parasitic species' compositions.

Anurans use a great variety of microhabitats all over the world, influencing the assembly patterns of their parasitic communities (Poulin & Morand, 2004). Aho (1990) and Bush et al. (1990) also highlighted the influence of aquatic environments on intensity of infection. According to Poulin (1995), parasite community compositions are a result of interactions between the evolutionary history and ecological characteristics of the hosts. Sympatric and phylogenetically closer hosts with similar ecologies, are expected to have more similar parasite communities compared to allopatric and phylogenetically distant hosts (Muñoz et al., 2005).

In the Caatinga biome, studies on helminth fauna associated with anurans are still scarce, comprising a few recent studies (e.g. Teles et al., 2014, 2015, 2018; Alcantara et al., 2018; Madelaire et al., 2020). Madelaire et al. (2020) evaluated the influence of seasonality on parasite community composition in three anuran species (Rhinella diptycha, Rhinella granulosa and Pleurodema diplolister), however no influence was detected. These authors also observed similarities between the parasite fauna of the studied hosts; however, their analyses did not elucidate the roles of host ecology and phylogeny on parasite composition. Therefore, there is a need to analyse the relative effect of ecological and/or historic factors on the assembly patterns of parasite communities. Thus, the main aim of this study was to describe the composition of endoparasites found in an anuran assemblage in the Caatinga biome and report their ecological data (e.g. abundance, prevalence and intensity of infection). Our study also aimed to verify the influence of host size, body mass, body volume and sex on parasite abundance, as well as the relative influence of host ecological and historical factors and microhabitat use on parasite community composition.

Material and methods

Study area

Anurans were collected in the municipality of Granjeiro, Ceará State, northeastern Brazil (06°53′S, 39°13′W). This area has a warm tropical and semi-arid climate, with an average rainfall of 1236.6 mm per year and a temperature of 24–26°C. The local vegetation is part of the Caatinga biome, which comprises dense shrub vegetation and thorny deciduous forest (Instituto de Pesquisa e Estratégia Econômica do Ceará, 2015).

Host sampling and microhabitat

Different anuran species were collected during two field trips performed in February and March 2018. The primary sampling method was active searching near temporary ponds, lakes and waterlogged areas, performed during the night from 18:00 to 22:00 h (Crump & Scott, 1994). Substrate type was recorded for every collected individual, such as exposed soil, perched on shrub, perched on grass, on a macrophyte, on rocks, on a fallen tree trunk, on leaf-litter, at the water's edge and in the water. We computed microhabitat niche breadths (B) using the inverse of Simpson's (1949) diversity index:

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

where p is the proportion of microhabitat category i and n is the number of categories.

The anurans were euthanized with a lethal dose of lidocaine hydrochloride 2%. The collection and use of frogs in the present study was authorized by the Instituto Chico Mendes de Conservação da Biodiversidade ICMBio (62017-1) and by the ethics committee of Universidade Regional do Cariri (00202/2018.2). The anurans were weighed and snout–vent length (SVL), body height and body width were measured with a digital caliper (accuracy ± 0.5 mm). To estimate body volume for each specimen, the volume formula of a parallelepiped was used, multiplying the SVL by body height and width. The specimens were fixed using 10% formalin and conserved in 70% ethanol. Voucher specimens were deposited in the Herpetological Collection of the Universidade Regional do Cariri.

Parasite sampling

The anuran specimens were dissected under a stereomicroscope, sexed and the respiratory, gastrointestinal and body cavities were surveyed for endoparasites. Parasites were mounted on slides with lactophenol and analysed under a light microscope (Zeiss, Imager M2). Parasite abundance (total number of parasites, regardless of species, in a single infected host), prevalence (total number of infected hosts divided by the total number of hosts in the sample × 100) and mean intensity of infection (total number of parasites found in a sample divided by the number of hosts infected with that parasite) were calculated according to Bush et al. (1997). All means appear as ± 1 standard deviation.

Statistical analyses

To investigate whether parasite abundance was related to SVL, body mass, body volume or host sex, two analyses using generalized linear mixed models (GLMMs) were performed. In the first model, SVL, body mass and body volume were included as fixed effects, and anuran species (this category allowed us to remove the ontogenetic effect of each anuran species, as well as the effect of anuran abundance) and sex (this category allowed us to remove the effect that host sex may exert on this model) were included as random effects. In the second model, the sex of the host was included as a fixed effect, while anuran species was included as a random effect. In both models, parasite abundance was tested with a Poisson distribution and log link function (Wilson & Grenfell, 1997). GLMMs were performed using the 'lme4' package (Bates et al., 2014) of R software.

To better study potential influences of ecological/historical factors and host microhabitat use on endoparasite composition, a phylogenetic principal component analysis (pPCA) was performed (Jombart et al., 2017) using the Adephylo package (Jombart et al., 2017) in R software (R Core Team, 2018). For this analysis, species with $n < 5$ individuals were excluded (Proceratophrys aridus and Leptodactylus troglodytes). The pPCA is a multivariate method that tests phylogenetic autocorrelation (Gittleman & Kot, 1990). To perform this test, two matrices (X and W) were built. The X matrix containing p quantitative traits measured (endoparasite prevalence and amphibian microhabitat niche breadth) on n taxa, and a matrix W disposed the phylogenetic matrix with the sampled host species (with the respective phylogenetic distances in the cells).

The aim of this analysis is to find combinations of life history traits that exhibit a high level of variance and exhibit global or

local structures (Jombart *et al.*, 2010). Global structures result in patterns of trait similarity between related taxa which, according to ecological niche theory, indicates the prevalence of historical factors in assemblage structure (Winemiller & Pianka, 1990). In the pPCA the presence of global structures is represented by positive eigenvalues (Jombart *et al.*, 2010). On the other hand, local structures are consequences of relatively recent events that result in the divergence of evolutionary strategies between closely related taxa, indicating the greater importance of ecological factors in assemblage structure (Winemiller & Pianka, 1990). In the pPCA the presence of local structures is represented by negative eigenvalues (Jombart *et al.*, 2010). To perform this analysis, we used one of the most recent phylogenetic distances for anurans (fig. 1; Pyron & Wiens, 2011). Taxa occurring in this geographical delimitation which were not included in the respective phylogeny were replaced with close relatives, assuming that adequacy does not influence the results, since more marked evolutionary changes must occur in the most basal nodes of the tree (Roelants *et al.*, 2007).

Results

A total of 288 individuals from 13 anuran species and five families (table 1) were collected, of which 110 were parasitized (4447 specimens of parasites), with an overall prevalence of approximately 38% and a mean infection intensity of 40 ± 38.6 parasites. The observed nematodes belong to seven different families and were identified as: *Aplectana membranosa* Miranda, 1924 ($n = 1196$); *Cosmocerca* sp. Travassos, 1925 ($n = 56$); *Raillietnema spectans* Gomes, 1964 ($n = 119$); *Rhabdias fuelleborni* Travassos, 1926 ($n = 998$); *Oswaldocruzia mazzai* Travassos, 1935 ($n = 541$); *Schrankiana* sp. Strand, 1942 ($n = 4$); and larvae of *Physaloptera* sp. (Pinto *et al.,* 1994). Additionally, the digenean species, *Glypthelmins pseudium* Mañé-Garzón & Holcman-Spector, 1967 ($n = 4$) and a non-identified cestode ($n = 70$) were found. The prevalence and mean intensity of infection values were calculated according to Bush *et al.* (1997), as shown in table 1.

The GLMMs indicated that SVL ($Z = 1.34$; $R^2 = 0.99$; $P = 0.17$), body mass ($Z = 1.39$; $R^2 = 0.996$; $P = 0.16$), body volume ($Z = 1.258$; $R^2 = 0.996$; $P = 0.2$) and host sex ($Z = -0.35$; $R^2 = 0.99$; $P = 0.73$) did not alter parasite abundance.
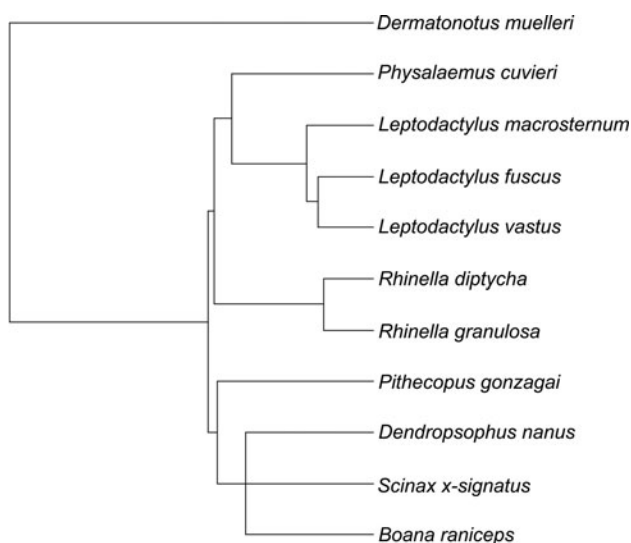

Fig. 1. Phylogenetic tree of the studied anuran assemblage, obtained from Pyron & Wiens (2011).

Both global and local phylogenetic structures were found by pPCA in the endoparasite and microhabitat data. For the former, the local structure (recent/ecological factors) was identified as having a greater influence on the organization of the infection patterns observed in amphibians, since the negative eigenvalues (-384.7) were much greater than the positive eigenvalues (125.2) (fig. 2B). Regarding the first global component, the frog species *R. diptycha* and *R. granulosa*, had the most negative scores compared to the rest of the tree (taxa with positive scores or close to zero), while the species *Boana raniceps* had the least similar life history values (fig. 2A). Among the other species, *Leptodactylus macrosternum* was also distinguished by its negative score. The loadings of the analyses (fig. 2C) showed that the endoparasite species *A. membranosa* and *R. fuelleborni,* exerted greater influence on the global negative axis, where the frog species *R. diptycha* was primarily associated with *R. fuelleborni*. The unidentified species of Cestoda exerted an intermediate influence in relation to the negative axis, presenting a historical association mainly with *R. granulosa*. On the other hand, the global positive axis was mainly influenced by the nematode *O. mazzai*, presenting a close association with the frog species *B. raniceps*.

Regarding the first local component, the frog species *R. diptycha* and *B. raniceps* presented the highest negative scores, while *R. granulosa*, *Dendropsophus nanus* and *Dernatonotus muelleri* presented opposite ecological values (low or intermediately positive scores) (fig. 2A). The loadings of the analyses (fig. 2C) showed that the nematodes *O. mazzai*, *R. fuelleborni* and *Physaloptera* sp., exerted the greatest influence on the local negative axis (closer to the axis and far from zero), where the former two species showed a close association with the frog species *R. diptycha* and the latter was associated with *B. raniceps*. The positive local axis was moderately influenced by the taxa *Schrankiana* sp. and Cestoda, presenting ecological associations with *Scinax x-signatus* and *R. granulosa*, respectively.

For microhabitat use, the global structure (historical factors/ phylogeny) was identified as having a greater influence on the spatial organization (microhabitat) of the studied amphibian assemblage, since the positive eigenvalues (0.006) were greater than the negative eigenvalues (-0.002) (fig. 3B). Regarding the first global component, the species *D. nanus* and *D. muelleri* had intermediately negative scores as opposed to the life history value of the species *R. granulosa*, which presented the highest positive score in the tree (fig. 3A).

The loadings of the analyses (fig. 3C) showed that the microhabitats 'on a macrophyte' (**F**) and 'perched on shrub' (**G**) exerted greater influence on the global negative axis composition, where the species *D. nanus* was the most historically affected by these two categories of spatial use. In contrast, the global positive axis was mainly influenced by the category 'exposed soil' (**I**), where the species *R. granulosa* was the most historically affected by this category of spatial use.

Regarding the first local component, the frog species *R. granulosa* presented the highest negative score. In contrast, the species *S. x-signatus* had a low local positive score (fig. 3A). The loadings of the analyses (fig. 3C) showed that the use of the microhabitat 'exposed soil' (**I**) exerted a greater influence on the local negative axis composition, where the species *R. granulosa* was the main species affected by this category of spatial use. In addition, the positive local axis was moderately influenced by the category 'on leaf litter' (**A**), where *D. nanus* and *D. muelleri* were the main species affected by this category of spatial use.

Table 1. Endoparasites recorded in individuals of an anuran assemblage from Granjeiro, Ceará state, north-eastern Brazil.

Taxa	Host (n)	P	MII	S
Nematoda				
Cosmocercidae				
Aplectana membranosa	*Dermatonotus muelleri* (36)	8.2%	1	SI
	Leptodactylus fuscus (14)	7.1%	1	SI
	Leptodactylus macrosternum (30)	16.6%	51.2	SI, LI
	Leptodactylus troglodytes (2)	100%	32.5	SI
	Leptodactylus vastus (9)	11.1%	4	SI
	Pithecopus gonzagai (31)	3.2%	1	SI
	Scinax x-signatus (33)	6%	1.5	SI
	Rhinella diptycha (32)	3.1%	1	IG
	Rhinella granulosa (32)	40.6%	41.8	S, SI, LI
	Proceratophrys aridus (1)	100%	235	SI
Cosmocerca sp.	*S. x-signatus*	21.2%	7.8	SI, LI
	R. diptycha	3.1%	1	LI
Raillietnema spectans	*L. troglodytes*	50%	67	LI
	R. diptycha	6.2%	2.5	SI
	R. granulosa	3.1%	32	LI
	Pithecopus gonzagai	3.2%	15	SI
Molineidae				
Oswaldocruzia mazzai	*Boana raniceps* (27)	91.6%	11.2	S, SI, LI
	L. macrosternum	30%	7.8	S, SI, LI
	L. vastus	11.1%	1	SI
	P. gonzagai	6.4%	2	SI, LI
	Physalaemus cuvieri (24)	16.6%	1.2	SI, LI
	R. diptycha	59.3%	9.2	SI, LI
	R. granulosa	3.1%	2	SI
Physalopteridae				
Physaloptera sp. larvae	*B. raniceps*	16.6%	1.5	S
	P. cuvieri	8.3%	1	S, SI
	R. granulosa	9.3%	3.3	S
	R. diptycha	53.1%	13	S, SI, LI
	S. x-signatus	6%	1.5	LI
	Dendropsophus nanus (32)	3.1%	1	SI
	L. vastus	33.3%	8.3	S
	L. macrosternum	3.3%	1	S
Rhabdiasidae				
Rhabdias fuelleborni	*D. nanus*	3.1%	1	L
	B. raniceps	8.3%	1	L
	L. macrosternum	40%	2.1	L
	P. cuvieri	12.5%	1.6	L
	R. diptycha	96.8%	30.9	L
	R. granulosa	6.2%	3	L
	S. x-signatus	6%	1	L

(Continued)

Table 1. (*Continued.*)

Taxa	Host (n)	P	MII	S
Schrankianidae				
Schrankiana sp.	*R. granulosa*	3.1%	2	LI
	S. x-signatus	6%	1	SI, LI
Trematoda				
Glypthelminthidae				
Glypthelmins pseudium	*L. vastus*	11.1%	4	SI
Cestoda				
non-identified cestode	*R. granulosa*	12.5%	17.2	SI
	R. diptycha	3.1%	1	LI

Abbreviations: P, prevalence; MII, mean intensity of infection; IS, infection sites; SI, small intestine; LI, large intestine; S, stomach; L, lungs.
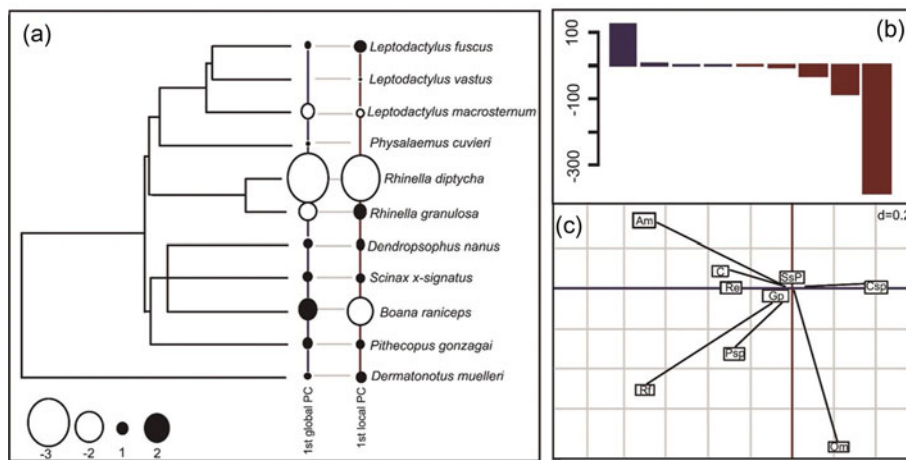

Fig. 2. Phylogenetic principal component analysis for the endoparasites of an anuran assemblage from the Caatinga. On the left is the phylogenetic tree built for the assemblage with the 1st global principal component (PC) and 1st local PC. Negative and positive scores were indicated for the white and black circles, respectively. Circle size is proportional to the values of the scores. On the right are the loadings of the first historical (blue) and ecological (red) components. Endoparasites studied: *Aplectana membranosa* (Am), *Cosmocerca* sp. (Csp), *Physaloptera* sp. (Psp), *Schrankiana* sp. (Ssp), *Rhabdias fuelleborni* (Rf), *Raillitnema spectans* (Re), *Oswaldocruzia mazzai* (Om), *Glypthelmins pseudium* (Gp) and Cestoda (C).

Discussion

The present study recorded nine helminth species. The observed species richness was lower than previously recorded in other anuran communities studied in South America (Bursey *et al.*, 2001; Toledo *et al.*, 2018). Most of the parasites found in this study were nematodes. The higher nematode prevalence seems to be a common trait in parasite communities associated with anurans (Aho, 1990; Campião *et al.*, 2014).

The parasites recorded herein showed low specificity, occurring in two or more host species (except the species *G. pseudium*), which may be related to sampling season, since sampling was only carried out during the rainy season at the beginning of the year. Our data corroborate Poulin *et al.* (2006), who attributed low species specificity to small mammalian parasites due to fluctuations in host populations, where the instability of the resource (host population) tends to produce a community of generalist parasites.

In terms of the biotic factors related to the studied anurans, parasite abundance was not influenced by any of the tested variables (SVL, body mass, body volume and sex). These findings differ from other studies on Brazilian anurans, which found a significant influence of host size, body mass and sex on parasite abundance (e.g. Santos & Amato, 2010; Santos *et al.*, 2013; Toledo *et al.*, 2018). These contrasting results highlight the need

for further studies on the parasites of anuran communities in the Caatinga biome in northeastern Brazil. We highly recommend that future studies approach this topic using the same analytical method utilized in the present study. GLMMs can study the effect of a factor without the interference of other variables and/or pseudoreplication (Bates *et al.*, 2014).

According to Vieira *et al.* (2009), the mating strategy of anurans in the Caatinga biome is adapted to rainfall patterns in the area, which occurs over the course of a few months. As a result, anurans must aggregate in both time and space, increasing their chances of becoming infected and sharing the same pool of parasite species. This situation also contributes to the use of similar microhabitats by individuals of different species, which can be seen in the case of *D. nanus* and *D. muelleri*. According to our results, both species are ecologically influenced by the category 'on leaf litter', although in this study, they did not share infections. Furthermore, in a study on lizards in the Caatinga, Brito *et al.* (2014) showed that the use of microhabitats can influence the composition of endoparasites associated with these hosts, which may represent a pattern for this biome.

In general, anurans are associated with two types of environments (aquatic and terrestrial), allowing a great diversity of parasites to settle in these animals (Chandra & Gupta, 2007). The way

Fig. 3. Phylogenetic principal component analysis for anuran microhabitat use in the Caatinga. On the left is the phylogenetic tree built for the analysed anuran assemblage, with the 1st global principal component (PC) and 1st local PC. Negative and positive scores were indicated for the white and black circles, respectively. The size of the circle is proportional to values of the scores. On the right are the loadings of the first historical (blue) and ecological (red) components. Microhabitat categories: A – on leaf litter; B – at the water's edge; C – on a fallen tree trunk; D – on the rocks; E – in a water body; F – on a macrophyte; G – perched on shrub; H – perched on grass; and I – exposed soil.
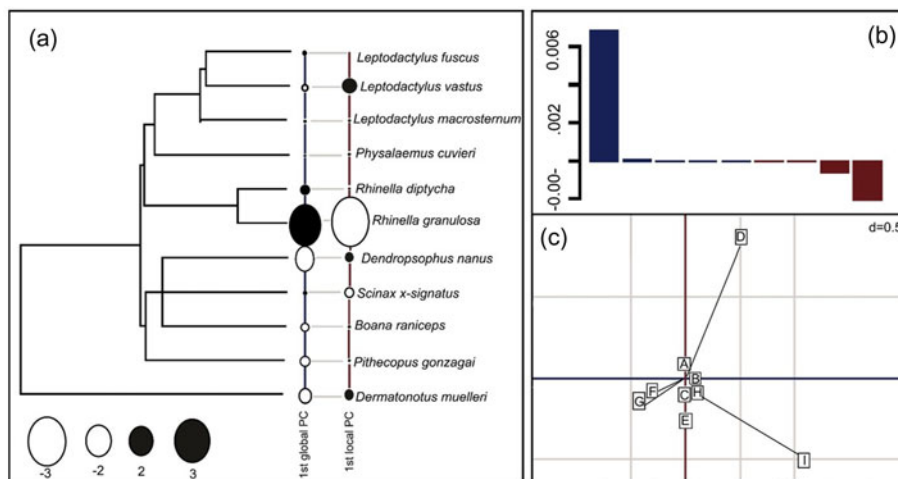
in which hosts explore their habitats can also explain the richness and diversity of associated parasites (Poulin & Morand, 2004). The microhabitats used by hosts is an important factor for determining the composition of parasite communities. The specialization of parasites for the same microhabitat as their hosts, leads to an increased likelihood of encounters between the parasites and their hosts, facilitating infection (Kerr & Bull, 2006).

In the present study, hosts that used the same microhabitats had similar parasite compositions; for example, *Cosmocerca* sp. was found only in *S. x-signatus* and *R. diptycha*, which explored rock microhabitats. Bufonids were found mainly on exposed soil and shared five parasite taxa (*A. membranosa*, *Physaloptera* sp. larvae, *O. mazzai*, *R. fuelleborni* and *R. spectans*). Anurans of the Hylidae family, which are usually arboreal species, were found in various microhabitats and followed the pattern of helminthic infection of terrestrial species (Bolek & Coggins, 2003). Most of the helminth species found in Hylidae (*R. fuelleborni* and *Cosmocerca* sp.) were direct cycle and active infection species (Anderson, 2000). Therefore, similar microhabitat use by related species is directly reflected in endoparasite composition.

Additionally, the present study corroborates Campião *et al.* (2015) and Toledo *et al.* (2018), who found that ecological (contemporary) factors are determinant for the structuring of parasitic communities associated with amphibians. In such cases, ecological adjustment events, such as host switching, parasite dispersal and colonization of new habitats (new types of hosts) can generate inconsistencies regarding host phylogeny (Nuismer & Thompson, 2006). Thus, these parasite life history traits are explained by the frequent alternation between strains of related and unrelated hosts (Krasnov & Shenbrot, 2002; Zietara & Lumme, 2002; Johnson *et al.*, 2011). Therefore, by showing a smaller effect of host phylogeny in relation to ecology, our results may be consistent with these views.

Host ecological traits may act as selective barriers against parasites and therefore, each ecological variable may affect parasite species in different ways, thus shaping their communities (Holmes, 1987). Anuran parasites tend to be generalists (Aho, 1990) and are exposed to similar ecological conditions. In the present study, the parasite *A. membranosa* was present in ten of the 13 host species analysed. This result is consistent with the hypothesis that the anurans of the Caatinga biome are exposed to ecological pressures similar to those previously reported for other species in temporary ponds from other arid environments, resulting in similar mating systems and patterns of parasitism (Sullivan, 1989). Therefore,

anuran reproductive behaviour facilitates the contact of potential hosts with the same infective larvae. Furthermore, as anurans from the Caatinga biome have similar diets (Protázio *et al.*, 2015), they may have ingested the same parasites through intermediate hosts, thus strengthening our hypothesis about *Physaloptera* sp. (indirect life cycle) infecting most species in the area.

Finally, another factor that may explain the greater ecological influence on the parasite community organization studied here is time of community formation. According to Brooks & Mclennan (1993) and Losos (1996), communities with different ages may reflect historical adjustments in their organization since the longer the establishment time, the longer the coexistence between the competing taxa and the greater the possibility of resource segregation adjustments, thereby allowing greater structuring, including phylogenetic structuring. As the Caatinga is an environment that presents a high level of climatic unpredictability and constantly suffers from high anthropic interference intensity (Rito *et al.*, 2017), it is expected that ecological values exert greater influence on the organization of communities contained in these places.

Conflicts of interest. None.

Ethical standards. All authors gave their consent to participation in the study. The Instituto Chico Mendes de Conservação da Biodiversidade provided the licence to collect the animals and the ethics committee of the Universidade Regional do Cariri approved this study.

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