



What is the diversity and pattern of network interactions parasite-host in amphibians (Anura) from Caatinga domain? – A meta-analysis

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Received: 25 August 2023 / Accepted: 22 May 2024 / Published online: 17 June 2024

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Abstract

The first records in the literature compiled on the parasitic fauna of amphibians in Northeastern Brazil date back to the 1990s. Since then, several new studies have been published on parasite-host relationships, parasite communities, and descriptions of new taxa. However, only in the last decade has there been a significant increase in these studies. Given this growth, we aim to provide a complete and updated compilation of helminth records associated with amphibians from the Brazilian Northeastern region and to analyse the dynamics and network structure formed between parasites and their hosts. Therefore, 33 studies were found in the specialized literature that addressed data from eight families, 15 genera, and 34 species of anuran amphibians, distributed mainly in areas of the morphoclimatic domain of the Caatinga and Atlantic Forest remnants in the Brazilian Northeast. These data correspond to 35% of the total known species of the Caatinga, with Leptodactylidae being the most representative taxon. Regarding helminths, 51 species were recorded, belonging to 20 families and 32 genera. To evaluate the structure of the network, we used measures of connectivity, nestedness, modularity, and centrality, that were considered to identify key species. The web presented 247 interactions with a highly connected structure formed by two parasite generalist species, non-nested and non-modular. We concluded that anuran amphibians from the Brazilian Northeast possess a high parasitic diversity, being Bufonidae and Leptodactylidae taxa considered fundamental for the network structure. Herein, we provided the first analysis of the global framework of parasite communities in amphibians from Brazilian Northeast, by using antagonistic network interactions.

Keywords Anuran · Checklist · Ecological network · Hosts · Northeastern · Parasites

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Introduction

The Caatinga morphoclimate domain (CMD) is located in the Brazilian Northeast and holds an area of approximately 912,000 Km² representing about 10% of the national territory. This region is characterized by a distinct seasonality with high temperatures, irregular rainfall with precipitation levels of 300–1000 mm annually and long drought periods (Ab'Saber 2003; Silvano and Segalla 2005; Queiroz et al. 2017). Despite being the only Brazilian natural region with limits restricted to the national territory, little attention has been given to the conservation of the Caatinga landscape and the diversity of its biota (Silva et al. 2004; Oliveira 2012).

The CMD presents the fourth greatest biological richness of Brazil, with a high degree of endemism. The Brazilian Caatinga presents 98 amphibian species, from which 20 are endemic and the remaining occur also in transition areas between the biomes Cerrado, Amazon Forest, and Atlantic Forest (Garda et al. 2017). The diversity of this group in the northeast region is distributed among 14 families, being Hylidae and Leptodactylidae the most representative taxa among anurans, with 39 and 28 species, respectively (Garda et al. 2017; Segalla et al. 2021).

Currently, Brazil has 1,188 amphibian species (Segalla et al. 2021), which represents 14.2% of the global diversity for this group (Frost 2024). The vast majority of the species are anurans, including 1,144 species (two exotic and invasive species) distributed in 20 families and 107 genera (Segalla et al. 2021). Considering the taxonomical diversity of amphibians, several studies have addressed aspects about their biology, ecology, taxonomy, behavior, and parasitism (Daszak et al. 2003; Cassiano-Lima et al. 2011; Roberto et al. 2013; Andrade et al. 2020; Sena et al. 2018; Madelaire et al. 2020).

Even though Brazil is well known worldwide regarding parasitological researches on anurans, the hidden diversity that these parasites represent is far from being completely unraveled. Less than 10% of the described amphibian species in Brazil have data on their helminthfauna (Campião et al. 2014). The first parasitological studies on Brazilian amphibians is from 1917 by Travassos (Vicente et al. 1991), and since then, the number of publications have been increasing (Nascimento et al. 2013; Silva et al. 2018; Oliveira et al. 2019; Silva-Neta et al. 2020).

Due to the richness of species, amphibians act as hosts to a great diversity of parasites, being infected by the main helminth groups like Nematoda, Digenea, Cestoda and Acanthocephala in larval and adult stages (Campião et al. 2014; Toledo et al. 2014). Furthermore, parasites are considered as bioindicators of environmental changes, providing information about the health and structure of

ecosystems and trophic interaction networks (Campião et al. 2009; Koprivnikar et al. 2012).

Therefore, in view of the above and considering the importance and megadiversity of helminth endoparasites of amphibians, we aim 1) to provide a checklist of associations between parasites and their anuran hosts from the northeast region of Brazil based on compiled literature data from 1990 to 2022, and 2) to describe the network pattern of parasite-host interaction that exists within this set and verify which helminth and anuran species are most important in structuring the dynamics of infection in these communities.

Material and methods

Collection of data

In order to carry out this checklist, literature was surveyed using the available databases: Scientific Electronic Library Online (SciELO), Google Scholar, Science Direct, Scopus, Medline (Pubmed), Web of Science, and CAPES Portal, using the following key-words combined: helminths, parasites, endoparasites, amphibians, anuran, infection, Brazil, and Northeastern. Data published in books, book chapters, and annals related to parasites were also included in the checklist. The criteria for inclusion of scientific production was the specific approach of infection of helminth endoparasites in amphibians in the Northeast of Brazil, published from 1990 to 2022.

Data analyses

To create the table of endoparasite species associated with amphibians, the following information was recorded and analyzed separately: host species, parasite, infection site and authors. The methods used for detection and identification of the hosts and parasites species in the literature cited were not taken into consideration. The data were also distributed and organized in graphics, presenting information on the anuran families.

Network analysis

We built a parasite-host interaction network from a binary matrix. The resulting matrix, with parasites as columns and hosts as rows, consisted of cells filled with 1 when interaction was recorded and 0 otherwise. To describe the structure of the web, we calculate the Connectivity, Nestedness and Modularity (Q). Connectance is provided by the ratio between the number of existing interactions and the total number of possible interactions in the network, measuring how much species are linked in the community (Jordano

et al. 2006). Nestedness measures how much the set of interactions of less connected vertices is a subset of interactions of more connected vertices. Thus, a network is more nestedness the more specialist species interact with species that belong to a subset of the species with which generalists interact (Delmas et al. 2018).

Modularity assesses the extent to which species form subgroups with a higher density of internal than external interaction. Modularity analysis can provide information on the level of specialization in communities concerning the affinities of interactions (Vázquez et al. 2009). The DIRTL-PAb + binary modularity maximization algorithm was used (Beckett 2016), and estimated with the computeModules() function in the Bipartite package in the R program.

As network metrics can be affected by intrinsic characteristics, such as the number of species that interact and sampling from different studies (Vizentin-Bugoni et al. 2016) the significance of the observed modularity was evaluated by comparing it with a null model. We used the Shuffles.web binary null model, similar to the one proposed by Vázquez et al. (2005), which limits the connectance and marginal totals of the matrices. The 95% confidence interval for the modularity metric (DIRTL-PAb+) was estimated from 1000 simulated values, with a metric value considered significant if the confidence intervals do not overlap (0.025–0.975).

To assess the role of species in the network following centrality metrics were used: Degree and mean degree, which analyzes how much a species is interacting with another in the network (number of interactions), contributing to examining the influence of the species on other species in the network, that is, the higher the degree of a species, the more potential influence it has on other species in the network; and Closeness which measures the proximity of a species to all other species in the network, indicating how quickly/efficiently a node is likely to influence the overall network (Delmas et al. 2018).

Results

Thirty-three studies published from 1990 to 2022 were selected, from which 16 are articles, 14 scientific notes, one dissertation and two monographs. Sixteen scientific journals were identified and listed in order of the largest number of publications related to helminth fauna of anurans in Northeastern Brazil, with *Herpetology Notes* ($n=5$) being the most representative journal, followed by *Herpetological Review* ($n=4$), *Zootaxa* and *Neotropical Helminthology* ($n=3$), *Acta Parasitologica*, *Brazilian Journal of Biology* and *Journal of Parasitology* ($n=2$) and *Parasitology Research*, *Biota Neotropica*, *Journal of Natural History*, *Brazilian Journal of Veterinary Parasitology*, *Helminthologia*, *Comparative Parasitology*, *Cuadernos de Herpetología*, *Revista*

Brasileira de Zoologia e Biologia ($n=1$), respectively. An interval of ten years was considered to observe the number of publications related to this topic. In the two first intervals, only one study was found, however, in the last decade, there was an increase of studies related to parasitology of anurans in the Brazilian Northeast, with the publication of thirty-one studies from 2010 to 2022 (Fig. 1).

These studies recorded data on parasitism in eight families, 15 genera and 35 species of amphibians, all of Anura, in terrestrial, arboreal, semi-aquatic and fossorial niches, distributed in the habitats from Caatinga and remains of Atlantic Forest in the Brazilian Northeastern region, corresponding to approximately 35% of the known species from Caatinga domain. The anuran family with the highest number of records was Leptodactylidae with 13 host species infected, followed by Hylidae with 11, Bufonidae and Odontophrynidae with three, Microhylidae with two, and Phyllomedusidae, Eleutherodactylidae, and Ranidae with only one species recorded. Regarding helminths, a total of 82 endoparasites were reported, belonging to 20 families and 32 genera. These total, 59 are nematodes, nine digeneans, six cestodes, six acanthocephalans, one monogenean, and one pentastomid. Among those, 51 were identified at species level (42 nematodes, five digeneans, one cestodes, two acanthocephalans, and one pentastomid) The remaining taxa were identified only at order, family or genus level. (Table 1, Online resource).

Network analysis

The parasite-host interaction network showed a low nestedness pattern (NODF = 18.09), that is, a large number of species with a small number of interactions (specialists), while a small number of species with a greater number of interactions (generalists) interacted with each other (Fig. 2). The network was represented by 82 species of helminths and

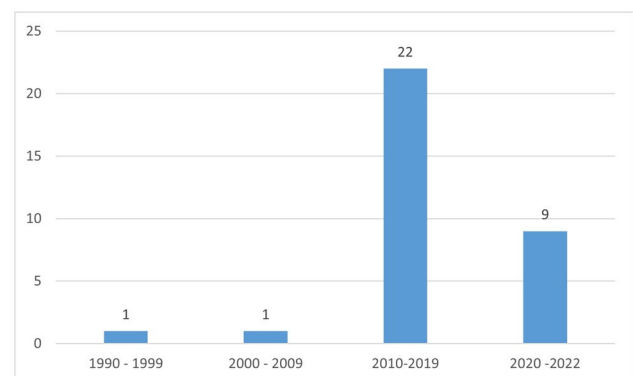


Fig. 1 Number of publications related to endoparasite helminths infecting anurans in the Brazilian northeastern region between 1990 and 2022

Table 1 Data on the literature of parasitism in anuran amphibians in the Brazilian Northeastern region recorded from 1990 to 2022

Host	Helminth	Species	Sites of infection	Phytophysiognomy	References
Bufonidae <i>Rhinella granulosa</i> (Spix, 1824)	Acanthocephala	Cystacanth	SI	CA	Madelaire et al. (2020); Müller et al. (2018); Silva-Neta et al. (2020); Teles et al. (2018a, b)
	Cestoda	<i>Cylindrotaenia americana</i> (Jewell, 1916) Unidentified cestode	LI		
	Digenea	<i>Plagiorchis rangeli</i> (Artigas and Zerpa, 1961)	LI		
	Nematoda	<i>Aplectana membranosa</i> (Schneider, 1866)	LI		
		<i>Aplectana</i> sp.	LI		
		Cosmocercidae	LI		
		<i>Oswaldocruzia mazzai</i> (Travassos, 1935)	SI		
		<i>Oswaldocruzia</i> sp.	SI		
		<i>Physaloptera</i> sp.	L		
		<i>Parapharyngodon</i> sp.	LI		
		<i>Raillietinema spectans</i> (Gomes, 1964)	LI		
		<i>Raillietinema</i> sp.	L		
		<i>Rhabdias androgyna</i> (Kloss, 1971)	L		
	<i>Rhinella diptycha</i> (Cope, 1862)	<i>Rhabdias breviensis</i> (Nascimento et al. 2013)	L		
		<i>Rhabdias</i> sp.	L		
		<i>Schrankiana</i> sp.	L		
Cestoda	<i>Cylindrotaenia americana</i> (Jewell, 1916)	SI			
	Digenea	<i>Gorgoderina rochamillae</i> (Pereira and Cuocolo, 1940)			
		<i>Plagiorchis rangeli</i> (Artigas and Zerpa, 1961)			
	<i>Rauschiella linguatula</i> (Travassos, 1924)				
Nematoda	<i>Aplectana membranosa</i> (Schneider, 1866)				
	<i>Aplectana</i> sp.				
	Cosmocercidae	SI/LI			

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References
		Nematode cyst	SI		
		<i>Oswaldo cruzia lopesi</i> (Fretas and Lent, 1938)	SI/S		
		<i>Oswaldocruzia mazzai</i> (Travassos, 1935)	SI		
		<i>Oswaldocruzia subauricularis</i> (Rudolphi, 1819)	I		
		<i>Parapharyngodon</i> sp.	SI/LI/S		
		<i>Physaloptera</i> sp.	S		
		<i>Raillietnema spectans</i> (Gomes, 1964)	LI		
		<i>Rhabdias fuelleborni</i> (Travassos, 1926)	L		
		<i>Rhabdias sphaerocephala</i> (Goodey, 1924)	L		
		<i>Rhabdias</i> sp.	L		
		<i>Aplectana vellardi</i> (Travassos, 1926)			
		Nematode larvae			
		<i>Ochoterenella</i> sp.			
		<i>Oswaldo cruzia</i> sp.			
		<i>Rhabdias pseudosphaerocephala</i> (Kuzmin et al., 2007)			
	Pentastomida	<i>Railliettiella mottiae</i> (Almeida et al., 2008)			Vicente et al. (1991)
<i>Rhinella marina</i> (Linnaeus, 1758)			L		
	Nematoda	<i>Rhabdias fuelleborni</i> (Travassos, 1926)			
Eleutherodactylidae					
<i>Adelophryne maranguapensis</i> (Hoogmoed et al., 1994)				AF	Oliveira et al. (2022)
	Nematoda	Ascarididae gen. sp.			
		<i>Aplectana</i> sp.			
		<i>Parapharyngodon</i> sp.			
		<i>Physaloptera</i> sp.			
Hyliidae					
<i>Boana albomarginata</i> (Spix, 1824)				AF	Martins-sobrinho et al. (2017)
	Acanthocephala	<i>Centrothynicus</i> sp.	GT		
	Nematoda	<i>Brevimulticaecum</i> sp.	GT		
		<i>Cosmocerca parva</i> (Travassos, 1925)	I		
		<i>Cosmocerca</i> sp.	I		

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References
<i>Boana multifasciata</i> (Günther, 1859)		<i>Oswaldo cruzia</i> sp.	I		
		<i>Physaloptera</i> sp.	S	AF	Machado et al. (2021)
	Acanthocephala	<i>Pseudoacanthocephalus lutzii</i> (Hamann, 1891)	SI		
	Digenea	<i>Glythelminis</i> sp.	SI		
	Nematoda	<i>Cosmocerca brasiliense</i> (Travassos, 1925)	SI/LI		
		<i>Physalopteroides venancioi</i> (Lent, Freitas and Proença, 1946)	E		
		<i>Physaloptera</i> sp.	LI		
		<i>Rhabdias</i> sp.	L		
		Cosmocercidae	SI/LI		
	<i>Boana raniceps</i> (Cope, 1862)				AF
<i>Dendropsophus branneri</i> (Cochran, 1948)	Acanthocephala	<i>Pseudoacanthocephalus lutzii</i> (Hamann, 1891)			
	Digenea	<i>Lophosicyadiplostomum</i> sp.			
	Nematoda	<i>Rhabdias pseudosphaerocephala</i> (Kuzmin et al., 2007)	L		
		<i>Aplectana travassosi</i> (Gomes and Motta, 1967)			
		<i>Cosmocerca brasiliense</i> (Travassos, 1925)			
		<i>Cosmocerca parva</i> (Travassos, 1925)			
		<i>Cosmocerca paraguayensis</i> (Moravec and Kaiser, 1994)			
		<i>Oswaldo cruzia mazzai</i> (Travassos, 1935)			
		<i>Rhabdias</i> sp.			
		<i>Centrorhyncus</i> sp.			
Acanthocephala	<i>Centrorhyncus</i> sp.	GT	AF	Martins-Sobrinho et al. (2017)	
Nematoda	<i>Aplectana</i> sp.	I			
	<i>Cosmocerca parva</i> (Travassos, 1925)	I			
	<i>Cosmocerca</i> sp.	I			
	<i>Porrocaecium</i> sp.	GT			
	<i>Centrorhyncus</i> sp.	GT			
<i>Dendropsophus decipiens</i> (Lutz, 1925)	Acanthocephala	<i>Centrorhyncus</i> sp.	GT	AF	Martins-Sobrinho et al. (2017)
	Nematoda	<i>Aplectana</i> sp.	I		
		<i>Cosmocerca parva</i> (Travassos, 1925)	I		
		<i>Cosmocerca</i> sp.	I		

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References
<i>Dendropsophus elegans</i> (Wied-Neuwied, 1824)	Acanthocephala	<i>Centrothyncus</i> sp.	GT	AF	Martins-Sobrinho et al. (2017)
	Nematoda	<i>Brevimulticaecum</i> sp.	GT		
		<i>Cosmocerca</i> sp.	I		
<i>Dendropsophus haddadi</i> (Bastos and Pombal, 1996)	Acanthocephala	<i>Centrothyncus</i> sp.	GT	AF	Martins-Sobrinho et al. (2017)
	Nematoda	<i>Brevimulticaecum</i> sp.	GT		
		<i>Cosmocerca</i> sp.	I		
<i>Dendropsophus minutus</i> (Peters, 1872)	Acanthocephala	<i>Centrothyncus</i> sp.	GT	AF	Martins-Sobrinho et al. (2017)
	Nematoda	<i>Brevimulticaecum</i> sp.	GT		
		<i>Cosmocerca parva</i> (Travassos, 1925)	I		
<i>Scinax auratus</i> (Wied-Neuwied, 1821)		<i>Cosmocerca</i> sp.	I	AF	Martins-Sobrinho et al. (2017)
	Acanthocephala	<i>Centrothyncus</i> sp.	GT		
	Nematoda	<i>Cosmocerca parva</i> (Travassos, 1925)	I		
<i>Scinax x-signatus</i> (Spix, 1824)		<i>Cosmocerca</i> sp.	I	AF	Martins-Sobrinho et al. (2017)
	Acanthocephala	<i>Centrothyncus</i> sp.	GT		
	Nematoda	<i>Brevimulticaecum</i> sp.	GT		
<i>Trachycephalus typhonius</i> (Linnaeus, 1758)		<i>Rhabdias</i> sp.	Cav	CA	Benício et al. (2022)
	Nematoda	<i>Aplectana yellardi</i> (Travassos, 1926)	LI		
		Nematode larvae	S		
Leptodactylidae <i>Leptodactylus fuscus</i> (Schneider, 1799)	Cestoda	Hexacante		CA	Lins (2016); Müller et al. (2018); Silva-Neta et al. (2020)
	Digenea	<i>Glythelmins linguatula</i> (Rudolphi, 1819)			
	Nematoda	Diplostomidae <i>Aplectana membranosa</i> (Schneider, 1866) Cosmocerciidae <i>Falcaustra mascula</i> (Rudolphi, 1819) <i>Ochoterenella</i> sp.			

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References		
<i>Leptodactylus latrans</i> (Steffen, 1815)	Nematoda	<i>Oswaldocruzia lopesi</i> (Fretas and Lent, 1938)					
		<i>Oswaldocruzia mazzai</i> (Travassos, 1935)					
		<i>Oxyascaris necopinus</i> (Freitas, 1958)					
		<i>Raillietinema spectans</i> (Gomes, 1964)					
		<i>Rhabdias</i> sp.	L				
		<i>Rhabdias breviensis</i> (Nascimento et al., 2013)	L				
		<i>Schrankiana formusula</i> (Freitas, 1959)					
		<i>Oswaldocruzia subauricularis</i> (Rudolphi, 1819)	L/SI	CA	Vicente et al. (1991)		
		<i>Raillietinema spectans</i> (Gomes, 1964)	SI	CA	Campião et al. (2014); Felix-Nascimento et al. (2020) Müller et al. (2018); Silva-Neta et al. (2020); Teles et al. (2017a); Teles et al. (2018a)		
		<i>Leptodactylus macrosternum</i> (Miranda-Ribeiro, 1926)	Nematoda	<i>Cosmocerca podicipinus</i> (Baker and Vaucher, 1984)			
<i>Oxyascaris oxyascaris</i> (Travassos, 1920)							
<i>Foleyella convoluta</i> (Molin, 1858)							
<i>Rhabdias</i> cf. <i>stenocephala</i> (Kuzmin et al., 2016)							
<i>Rhabdias</i> sp.							
<i>Oswaldocruzia mazzai</i> (Travassos, 1935)							
<i>Oxysonatium petrolinensis</i> (Felix-Nascimento et al., 2020)	LI						
<i>Oxyascaris caatingae</i> (Felix-Nascimento et al., 2020)	SI						
<i>Leptodactylus mystaceus</i> (Spix, 1824)	Nematoda			<i>Raillietinema spectans</i> (Gomes, 1964)			
				<i>Aplectana crucifer</i> (Travassos, 1925)			
		<i>Aplectana meridionalis</i> (Lent and Freitas, 1948)					
		<i>Aplectana lopesi</i> (Silva, 1954)					
		<i>Cosmocerca brasiliense</i> (Travassos, 1925)					
		<i>Cosmocerca paraguayensis</i> (Moravec and Kaiser, 1994)					
		<i>Cosmocerca parva</i> (Travassos, 1925)					
		<i>Cosmocerca</i> sp.					

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References
<i>Leptodactylus pentadactylus</i> (Laurenti, 1768)	Nematoda	<i>Cosmocerca travassosi</i> (Rodrigues and Fabio, 1970)		CA	Vicente et al. (1991)
		<i>Cosmocercidae</i>			
		<i>Multicaecum</i> sp.			
		<i>Ochoterenella</i> sp.			
		<i>Oxyascaris oxyascaris</i> (Travassos, 1920)			
		<i>Rhabdias</i> sp.			
		<i>Falcaustra mascula</i> (Rudolphi, 1819)	LI		
		<i>Oswaldo cruzia subauricularis</i> (Rudolphi, 1819)	I		
		<i>Rhabdias fuelleborni</i> (Travassos, 1926)	L		
		<i>Schrankiana freitasi</i> (Baker, 1982)	LI		
<i>Leptodactylus syphax</i> (Bokermann, 1969)	Nematoda	<i>Schrankiana inconspicua</i> (Freitas, 1959)	LI		
		<i>Schrankiana larvata</i> (Vaz, 1933)	LI		
		<i>Schrankiana schranki</i> (Travassos, 1925)	LI		
		<i>Schrankiana brasili</i> (Travassos, 1927)	LI	CA	Lins et al. (2017)
		Cystacanth	CAV		
		<i>Lophosicyadiplostomum</i> sp.	KID		
		<i>Aplectana membranosa</i> (Schneider, 1866)	SI/LI		
<i>Leptodactylus vastus</i> (Lutz, 1930)	Nematoda	<i>Schrankiana formusula</i> (Freitas, 1959)	LI		
		<i>Physaloptera</i> sp.	S		
		Unidentified larvae	CAV		
		<i>Gorgoderina parvicava</i> (Travassos, 1922)	B		
		<i>Aplectana membranosa</i> (Schneider, 1866)	LI		
<i>Leptodactylus vastus</i> (Lutz, 1930)	Nematoda	<i>Falcausta mascula</i> (Rudolphi, 1819)	LI		
		<i>Ochoterenella</i> sp.	Cav		
		<i>Oswaldo cruzia mazzai</i> (Travassos, 1935)	SI/LI		
		<i>Oswaldo cruzia subauricularis</i> (Rudolphi, 1819)	I		
<i>Leptodactylus vastus</i> (Lutz, 1930)	Nematoda	<i>Raillietinema spectans</i> (Gomes, 1964)			
		<i>Rhabdias fuelleborni</i> (Travassos, 1926)	L		

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References
		<i>Rhabdias cf. stenocephala</i> (Kuzmin et al., 2016)	L		
		<i>Schrankiana freitasi</i> (Baker, 1982)	LI		
		<i>Schrankiana inconspicata</i> (Freitas, 1959)	LI		
		<i>Schrankiana larvata</i> (Vaz, 1933)	LI		
		<i>Schrankiana schranki</i> (Travassos, 1925)	LI		
		<i>Schrankiana brasili</i> (Travassos, 1927)	LI		
		<i>Cosmocerca podicipinus</i> (Baker and Vaucher, 1984)	LI		
		Nematode cyst	VM		
		Nematode larvae	S/CAV		
		<i>Ochoterenella digiticauda</i> (Caballero, 1944)	CAV		
		<i>Oswaldocruzia lopesi</i> (Fretas and Lent, 1938)	S		
		<i>Oxyascaris oxyascaris</i> (Travassos, 1920)	SI		
		<i>Rauschiella linguatula</i> (Rudolphi, 1819)	SI	CA	Vicente et al. (1991); Campião et al. (2014); Teles et al. (2015); Madelaire et al. (2020); Silva-Neta et al. (2020)
<i>Pleurodema diplolister</i> (Peters, 1870)					
	Acanthocephala	<i>Oligacanthorhynchus</i> sp.			
	Cestoda	<i>Cylindrotaenia americana</i> (Jewell, 1916)			
		Plerocercoid			
	Nematoda	<i>Aplectana membranosa</i> (Schneider, 1866)			
		<i>Aplectana</i> sp.			
		Cosmocercidae			
		<i>Falcaustra mascula</i> (Rudolphi, 1819)			
		<i>Oswaldocruzia mazzai</i> (Travassos, 1935)			
		<i>Oxyascaris oxyascaris</i> (Travassos, 1920)			
		<i>Raillietnema spectans</i> (Gomes, 1964)			
<i>Physalaemus albifrons</i> (Spix, 1824)					
	Acanthocephala	Cystacanth	CAV/S		Oliveira et al. (2019); Silva-Neta et al. (2020)
	Nematoda	<i>Aplectana membranosa</i> (Schneider, 1866)			
		<i>Oswaldocruzia mazzai</i> (Travassos, 1935)	SI		
		<i>Physaloptera</i> sp.	S		
		<i>Raillietnema spectans</i> (Gomes, 1964)	LI/SI		
		<i>Rhabdias cf. brevienis</i> (Nascimento et al., 2013)	L		

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References		
<i>Physalaemus cicada</i> (Bokermann, 1966)	Acanthocephala	Cystacanth	S	CA	Oliveira et al. (2019); Silva-Neta et al. (2020)		
	Cestoda	<i>Cylindrotaenia americana</i> (Jewell, 1916)	SI				
	Nematoda	<i>Cosmocerca parva</i> (Travassos, 1925)	SI				
		<i>Oswaldocruzia mazzai</i> (Travassos, 1935)	I				
		<i>Oxyascaris oxyascaris</i> (Travassos, 1920)	SI				
		<i>Raillietinema spectans</i> (Gomes, 1964)	SI/LI				
		<i>Rhabdias</i> sp.	L				
		<i>Schrankiana schranki</i> (Travassos, 1925)	LI				
		Acanthocephala	Cystacanth	Cav		CA	
		<i>Acanthocephalus cf. saopaulensis</i> Smales, 2007	LI				
<i>Oswaldocruzia cf. mazzai</i> (Travassos, 1935)	SI						
<i>Physalaemus cuvieri</i> (Fitzinger, 1826)	Nematoda	<i>Physaloptera</i> sp.	S		Oliveira et al. (2019); Silva-Neta et al. (2020)		
		<i>Raillietinema spectans</i> (Gomes, 1964)	LI				
		<i>Schrankiana schranki</i> (Travassos, 1925)	SI				
	Nematoda	<i>Physaloptera</i> sp.		CA			
		<i>Physaloptera</i> sp.		CA			
	<i>Pseudopaludicola mystacalis</i> (Cope, 1887)	Acanthocephala	Cystacanth				Silva et al. (2018); Ávila et al. (2017); Morais et al. (2020)
		Nematoda	<i>Brevimulticaecum</i> sp.				
			<i>Cosmocerca parva</i> (Travassos, 1925)	SI			
			Nematode unidentified				
			<i>Oxyascaris oxyascaris</i> (Travassos, 1920)				
<i>Physaloptera</i> sp.							
<i>Rhabdias pocoto</i> (Morais et al., 2020)			L				
<i>Spiroxys</i> sp.							
<i>Cosmocerca ornata</i> (Dujardin, 1845)			I	AF			
<i>Pseudopaludicola pocoto</i> (Magalhães et al., 2014)		Nematoda	<i>Cosmocerca ornata</i> (Dujardin, 1845)		CA		
	<i>Cosmocerca ornata</i> (Dujardin, 1845)			CA			
Microhylidae	<i>Chiasmocleis capixaba</i> (Cruz et al., 1997)				Sluys et al. (2006)		
<i>Dermatonotus muelleri</i> (Boettger, 1885)					Bezerra et al. (2012); Araújo-Filho et al. (2015); Alcantara et al. (2018)		

Table 1 (continued)

Host	Helminth	Species	Sites of infection	Phytophysiology	References
Phyllomedusidae <i>Pithecopus gonzagai</i> (Andrade et al., 2020)	Acanthocephala	<i>Centrorhynchus</i> sp.	S	CA	Martins-Sobrinho et al. (2017); Sena et al. (2018); Silva-Neta et al. (2020); Vicente et al. (1991)
		Centrorhynchidae			
	Nematoda	<i>Brevimulticaecum</i> sp.	GT		
		Cosmocercidae gen. sp.	I		
		<i>Cosmocerca parva</i> (Travassos, 1925)	I		
		<i>Cosmocercella phyllomedusae</i> (Baker and Vaucher, 1983)	I		
		<i>Oxyascaris caudacutus</i> (Freitas, 1958)	S/SI		
		<i>Raillietema minor</i> (Freitas and Dobbin Junior, 1961)	LI		
		<i>Raillietema spectans</i> (Gomes, 1964)	I		
		<i>Rhabdias</i> sp.	Cav		
Ramidae <i>Lithobates palmipes</i> (Spix, 1824)	Nematoda	<i>Subulascaris falcaustriformis</i> (Freitas and Dobbin Junior, 1957)	LI	CA	Vicente et al. (1991)

Infection sites: B = bladder; Cav = body cavity; S = stomach; GT = gastrointestinal tract; I = intestine; SI = small intestine; LI = large intestine; L = lungs; K = kidneys; SAT = subcutaneous abdominal tissue. Phytophysiology: CA = Caatinga domain; AF = Atlantic Forest domain

anurans (Silva et al. 2018), where most of the nematodes found have a monoxenic life cycle with their larvae being found in the soil, which makes infection possible through penetration of their host's skin. About 60% of the hosts that had their helminth fauna inventoried have terrestrial or semi-aquatic habits and life history and ecological strategies that contribute to the encounter of these with their parasites.

Digeneans tends to be the second largest group in parasite diversity (Cribb et al. 2002), often with infections in amphibians being more related to aquatic and semiaquatic frog clades (Machado et al. 2021). Diplostomidae, Glyptelmidae, Macroderoididae, and Plagiorchiidae were the digenetic taxa associated with anuran hosts in the Caatinga, divided into four genera (*Glyphelmis*, *Lophosicyadiplostomum*, *Plagiorchis* and *Rauschiella*) and three species (*G. linguatula* (Rudolphi, 1819), *P. rangeli* Artigas and Zerpa, 1961 and *R. linguatula* (Rudolphi, 1819)). The genus *Lophosicyadiplostomum* is a parasite of birds that uses anurans as intermediate hosts (Hamann and González 2009). *Glyphelmis* is a cosmopolitan genus of amphibian parasites, which currently has eight species formally recognized based on molecular and morphological evidence and forms a sister group with the genus *Haematoloechus* (Razo-Mendivil et al. 2006). Species of this genus have a heteroxenic life cycle with two hosts in their life cycle, an invertebrate as an intermediate host and a vertebrate as the definitive host (Hamann 2006). Regarding the Monogenea and Pentastomida taxa, both had only one record, which demonstrates that potentially these parasitic groups have difficulties establishing themselves or using the anuran species recorded here as hosts in their life cycles.

Of the total taxon surveyed in this study, 31 was unidentified at a specific level. Poulin (2018) reiterates the importance of identifying the species of parasites, therefore contributing to a better measurement of the existing diversity of parasites between different communities, and avoiding errors of underrated of parasite richness, imprecise estimates of diversity, or overestimation of parasites, parasitic similarities between different communities. Thus, we reinforce that the identification of parasitic species is not easy, requires time and taxonomic knowledge, and when possible, molecular techniques for species-specific identification are implemented (Müller et al. 2018; Morais et al. 2020).

Regarding the remarkable growth of research in the last decade, we believe that it can be justified by both political and scientific issues. In the first half of the last decade, there were broad investments in public education through financial resources and research incentives in Brazil. Therefore, investing such resources in public universities boosted the development of basic and applied research in the most diverse fields of scientific knowledge (Marques 2019). Another factor that contributed to these results has been the consolidation of regionalized research groups in different universities in the Northeast that have concentrated their

research and explored the diversity of different taxonomic groups of both parasites and hosts in environments of the Caatinga domain (Teles et al. 2015, 2018a, b; Silva et al. 2018, 2019; Oliveira et al. 2019; Felix-Nascimento et al. 2020) and Atlantic Forest domain (Martins-Sobrinho et al. 2017; Sena et al. 2018; Silva-Neta et al. 2020; Mascarenhas et al. 2021; Oliveira et al. 2022).

As for the parasitic diversity associated with the taxon Bufonidae, the reunion of data from Brazilian Northeast began with the study of Vicente et al. (1991), that reported the nematodes *Oswaldocruzia subauricularis* (Rudolphi, 1819), *Rhabdias fuelleborni* Travassos, 1926, and *Rhabdias sphaerocephala* Goodey, 1924, parasitizing *Rhinella icterica* (Spix, 1824) (= *Bufo marinus*). However, only from 2008 onwards that other helminthfauna studies for *Rhinella granulosa* and *Rhinella diptycha* (= *R. jimi*) were published (Anjos et al. 2008; Müller et al. 2018; Teles et al. 2018a; Amorim et al. 2019; Madelaire et al. 2020; Lima et al. 2021). Among the species of Bufonidae, *R. diptycha* is the only species with a record of infection by trematode (Benício et al. 2022).

Hylidae is the taxon with the greatest species occurrence in the Brazilian Northeast, being largely represented in herpetofauna surveys and species description (Roberto et al. 2017; Orrico et al. 2018), phylogeography (Menezes et al. 2016), evolution, ecology, and physiology (Jared et al. 2015; Leite-Filho et al. 2017). However, there is only one study on the helminth fauna of hylid anurans for CMD with the host *Trachycephalus typhonius* (Linnaeus, 1758) (Benício et al. 2022). Most of the records for hylids anurans are from humid forest vegetation and Atlantic Forest (Nascimento et al. 2013; Martins-Sobrinho et al. 2017; Machado et al. 2021). The development of more research in the semi-arid region is necessary to better understand the host-parasite dynamics between hylid species, identify the parasite species associated with these hosts, and broaden the records of the geographic distribution of their helminths in the Northeastern region. These studies contribute to the understanding of parasitic relationships and highlight the importance of the use of molecular tools for parasite identification since the findings of larvae and females hinder identification and limit discussions on parasite specificity.

Leptodactylidae was represented in the studies about endoparasites by 13 species, belonging to four genera: *Leptodactylus*, *Physalaemus*, *Pseudopaludicola*, and *Pleurodema* (Vicente et al. 1991; Campião et al. 2014; Teles et al. 2014, 2015, 2017a, b; Lins 2016; Lins et al. 2017; Müller et al. 2018; Silva et al. 2018; Oliveira et al. 2019; Madelaire et al. 2020; Silva-Neta et al. 2020; Soares et al. 2020). The literature presents a diverse parasitic fauna for hosts from *Leptodactylus* genus (Camião et al. 2014; Teles et al. 2017a; Müller et al. 2018; Silva-Neta et al. 2020). While studies for the *Physalaemus* genus are scarce (Oliveira et al. 2019; Silva-Neta et al. 2020).

Interaction networks

The network of parasite-host interactions between helminths and anurans from Brazilian Northeastern region did not show a nestedness pattern, which makes it possibly less resistant to anthropic disturbances. Dehling (2018) explains that nestedness structure of a network increases its stability and makes well-connected generalist species more resistant against extinction. Fortuna and Bascompte (2006) studying the structure of real networks and simulated networks in response to habitat loss, observed that real networks lose species faster than simulated networks. However, due to their high degree of nesting and heterogeneity, they resist for longer time to disturbance. In nestedness networks, specialist species are the first to be extinct because they have a smaller number of interactions, thus causing them to be replaced by generalist species that have a greater number of interactions and that, due to the robustness of the interaction between other high-level generalist species, degree of interaction are the last to be extinguished (Rodrigues et al. 2016).

The low nesting and modular value can make the network more susceptible to anthropic disturbances (Dehling 2018). Modularity, like nesting, increases the robustness of the network against disturbances in the system, which makes it difficult to spread negative effects to other modules. Thus, non-nestedness or low-nesting networks may be characteristic of agonistic interactions in host-parasite networks. Furthermore, we can observe a large number of peripheric species of helminths with several isolated records of specific bindings with one to three hosts (Fig. 2). This characteristic contributed the non-nestedness and not modular structuring of the network agonistic.

Most interactions between helminths and their anuran hosts that occurred comprise very specifically and unique links, such as the sympatric occurrence of the species *Aplectana crucifer*, *A. lopesi*, *A. meridionalis*, *A. travossosi*, and *Cosmocerca travossosi* in *L. mystaceus*, *P. silvo* in *D. muelleri* and, in particular, several taxa of digenetic trematodes and cestodes occurring singly in different anuran host species (Table 1, Online resource).

Another fundamental issue is how the data were used in this work. In this study, unequal factors such as collection methodologies, sampled location, the type of landscape (the Caatinga domain or Atlantic Forest domain), the collection effort employed, and especially the temporality in which these works passed and have been developed may have influenced the descriptive parameters of the network (Pilosof et al. 2013; Runghen et al. 2021). Therefore, future studies with a well-designed sample developed only in a morphoclimatic domain may come to corroborate or refute the network pattern presented in this work.

Network analyses enable to record interactions amongst the components of those system, the way that communities

are organized, and the complexity of these interactions (Bascompte and Jordano 2007; Metz et al. 2007; Schreiber 2008; Bellay et al. 2013; Mello et al. 2015). Recently, studies on ecological networks have been encompassing mutualistic plant-pollinator and plant-seed-disperser and antagonist relationships (Lewinsohn et al. 2006; Bascompte and Jordano 2007; Mello 2010; Francisco et al. 2019). Specifically, antagonistic interactions benefit only one of the involved species, such as herbivory and parasitism (Schowalter 2011; Souza et al. 2015; Lopes et al. 2020).

The network analysis identified the anuran and parasite core species that have higher interaction frequency aiming at verifying what are the most important species that structure and balance the host-parasite interaction network in this study. *Raillietnema spectans* (Cosmocercidae) and *O. mazzai* (Molineidae) are core parasite species and could be considered generalists, given the number of host species parasitized. Besides, they configure as the most important parasite species for the structure of network. However, other species also had a relatively high frequency of interactions in the network, such as species from the taxa Cosmocercidae, Physalopterae, and Rhabdiasidae.

Aplectana membranosa and *C. parva* are common, generalist species that occur widely in amphibians in the northeast as well as in other geographic locations (Gonçalves et al. 2002; Luque et al. 2005; Silva et al. 2018; Oliveira et al. 2019; Silva-Neta et al. 2020; González et al. 2021; Mascarenhas et al. 2021). Both are monoxenic nematodes that infect their hosts through ingestion of larvae or penetration through the skin (Anderson 2000) and that can also be considered important in structuring the parasite community of their hosts. *Physaloptera* is a diverse genus that infects all classes of terrestrial vertebrates, and rarely fishes (Teles et al. 2018a). Although, among amphibians, there are only two species described *Physaloptera amphibia* Linstow, 1889 and *Physaloptera tigrinae* Ali and Farooqui, 1969, using these as definitive hosts in the Palearctic and Oriental region, respectively (Pereira et al. 2012). For the Neotropical region, the taxon *Physaloptera* sp. is usually found in the larval stage in different anuran taxa, which makes it possible to infer that this parasite uses anuran hosts as paratenic hosts to reach its definitive hosts (Mascarenhas et al. 2021).

The genus *Rhabdias* occurs throughout the world and are lung parasites of amphibians and reptiles (Tkach et al. 2014). Recent studies of the phylogeny of this genus with Neotropical species revealed the monophyly of Rhabdiasidae as well as the existence of an infection pattern of *Rhabdias* species associated with the phylogeny of their hosts (see Müller et al. 2018). In our study, *Rhabdias* sp. treated here as a single taxon in our analysis may represent about five possible new species of the genus considering their occurrence records by different hosts of the taxa Bufonidae, Hylidae, Leptodactylidae, Odontophrynidae, and Phyllomedusidae.

The hidden diversity of *Rhabdias* in the Neotropics is evident and the presence of cryptic species occurring in different host taxa requires studies that use molecular techniques to identify these parasites as well as for a better understanding of these systematic and host-parasite relationships (Müller et al. 2018).

The host species *Rhinella diptycha* and *R. granulosa* (Bufonidae) and Anuran leptodactylids like *L. fuscus*, *L. mystaceus* and *L. vastus* presented the highest degree of interaction, from which some are common to the host species of each genus. The data corroborate previous studies, reinforcing that phylogenetically close hosts tend to present similar parasitic faunas when compared with non-related hosts (Bellay et al. 2011; Bellay et al. 2013; Krasnov et al. 2012; Lima et al. 2012). We assume that these host species present more interactions due to the phylogenetic proximity, their sympatric occurrence, and their similar generalist habits, ingesting a great variety of prey. Thus, because they harbor greater helminth diversity shared, we can consider the species cited above key-species relative importance in structure network.

Chiasmocleis capixaba and *Lithobates palmipes* interacted with only one parasite each, which did not interact with any other amphibian. Parasite species with high specificity to establish their interactions are selective regarding their host choice, which is reflected in the high modularity of the analyzed network (Lopes et al. 2020). Svensson-Coelho et al. (2014) stated that highly specialized associations are indicative of the existence of species groups that interact more among themselves, possessing functional traces that are compatible among the species. Thus, the antagonistic networks and high phylogenetic proximity among parasite lineages are highlighted, as well as their host specialization.

About half of the helminth species ($n = 42$, 51.2%) listed in this study maintain a single interaction with one host or with up to three anuran hosts (see Fig. 2 and supplementary material), which makes it possible for parasite species that have higher specialization are more prone to be affected by the removal of a host species from the network if there are no records of other hosts. Such fact stresses the importance of host species that are considered generalists for the establishment of the network (Burgos et al. 2007; Lopes et al. 2020). Moreover, according to Lopes et al. (2020), the establishment of the networks are key mechanisms for the maintenance of interactions and might be considered important in an evolutionary context of host-parasite relationships.

Studies analyzing the network structure of biological communities allow us to better understand the processes and complexity of ecosystems by being able to extract the properties of an ecological system according to the number and distribution of links between interacting organisms (Runghen et al. 2021). We concluded that anuran amphibians from the Brazilian Northeastern region present a high

parasitic diversity. Some hosts of generalist habits are infected by several helminths, being considered important for the network structure, as observed for some Bufonidae and Leptodactylidae. Even, more specialized species retain a smaller number of interactions, which is valid for both parasites and hosts, in a way that extremely specific interactions do not interact with the network itself and are presented as a weak point considering its specificity. On the other hand, although we have evidenced the existence of a great diversity of macroendoparasite helminths associated with these hosts, within this diversity there is a high percentage of taxa yet to be described and identified at a specific level, making it necessary to implement greater efforts in the field knowledge of this yet unidentified diversity.

The present study provided the first analysis of the global structure of parasite communities in amphibians from the Brazilian Northeastern region, by using antagonistic network interactions. Despite the increase in the number of studies in the last decade, the growing number of descriptions of new anuran species and the high diversity of endoparasitic helminths for this vertebrate host group, the development of more research is imperative. Such studies must aim taxonomical and ecological approaches of parasites in amphibians, mostly nematodes that are the most common, as well as assess host-parasites interactions and life-cycle of these parasites. It is thus expected that with the increase of sampling efforts, new records of interactions will emerge and unravel the hidden diversity of amphibian parasites.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11756-024-01717-2>.

Authors' contributions The manuscript in question was developed from the monograph of Ednalva da Silva Santos, supervised by Charles de Sousa Silva and co-supervised by Drausio Honorio Morais. All people who meet criteria of article authorship are listed as authors, and all authors are sufficiently at work to assume responsibility for its content, including participation in the concept, analysis, writing or revision of the manuscript, as detailed below.

Conceptualization and study design: Ednalva da Silva Santos and Charles de Sousa Silva; Methodology: Ednalva da Silva Santos; Acquisition and compilation of data: Ednalva da Silva Santos; Analysis, interpretation of data: Ednalva da Silva Santos, Isabela Hevily Silva Torquato and Charles de Sousa Silva; Construction of images: Ednalva da Silva Santos and Isabela Hevily Silva Torquato; Writing the manuscript: Ednalva da Silva Santos, Isabela Hevily Silva Torquato, Drausio Honorio Morais and Charles de Sousa Silva; Critical revision of paper: Paulo Cascon and Charles de Sousa Silva.

Funding Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES. [88887.888289/2023–00; 88887.738154/2022–00].

Data availability Data supporting the results of this study are available for free consultation and use as 'supplementary files' on the website of the journal *Biologia*.

Declarations

Ethical approval Not applicable.

Competing interests Not applicable.

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