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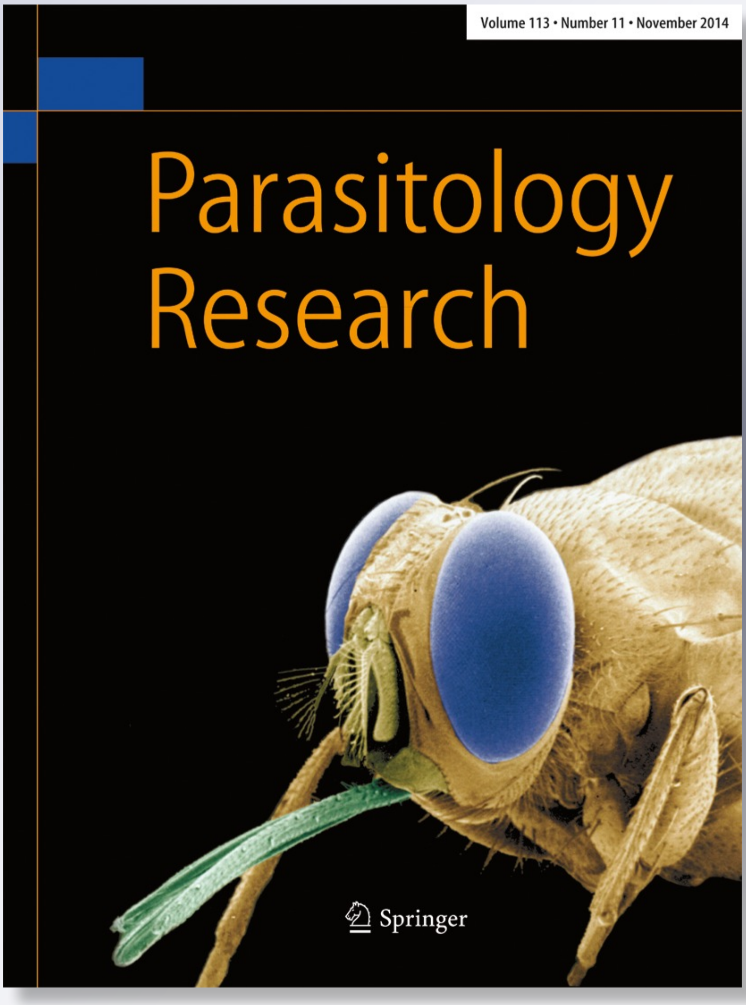

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ORIGINAL PAPER

Phylogeny and micro-habitats utilized by lizards determine the composition of their endoparasites in the semiarid Caatinga of Northeast Brazil

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Abstract Trophic networks can have architectonic configurations influenced by historical and ecological factors. The objective of this study was to analyze the architecture of networks between lizards, their endoparasites, diet, and micro-habitat, aiming to understand which factors exert an influence on the composition of the species of parasites. All networks showed a compartmentalized pattern. There was a positive relation between diet and the diversity of endoparasites. Our analyses also demonstrated that phylogeny and the use of micro-habitat influenced the composition of species of endoparasites and diet pattern of lizards. The principal factor that explained the modularity of the network was the foraging strategy, with segregation between the "active foragers" and "sit-and-wait" lizards. Our analyses also demonstrated that historical (phylogeny) and ecological factors (use of micro-habitat by the lizards) influenced the composition of parasite communities. These results corroborate other studies with ectoparasites, which indicate phylogeny and micro-habitat as determinants in the composition of parasitic fauna. The influence of phylogeny can be the result of coevolution between parasites and lizards in the Caatinga, and the influence of micro-habitat should be a result of adaptations of species of parasites to occupy the same categories of micro-habitats as hosts, thus favoring contagion.

Keywords Parasitism · Neotropical region · Semiarid · Trophic networks

Introduction

Trophic networks demonstrate the flow of energy within and between ecosystems, and understanding the pattern of these networks and the possible factors behind this organization is one of principal challenges in ecology (Lafferty et al. 2006; Rezende et al. 2009). Moreover, studies on trophic networks can help understand the impacts of the introduction or extinction of a species in an assemblage or understand the consequences of environmental changes on the composition of species of a particular locality (Guimarães Jr et al. 2006; Pascual and Dunne 2006).

There are a large number of studies emphasizing the structure of food networks, between organisms with mutualistic interactions (Olesen and Jordano 2002; Bascompte et al. 2003; Vazquez and Aizen 2004) as well as between organisms that interact in an antagonistic way, such as predator–prey (Allesina and Pascual 2007), parasitoid–host (Cohen et al. 2005), and parasite–host (Vazquez et al. 2005; Genini et al. 2011; Krasnov et al. 2012).

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The architecture of an interaction network can be influenced by various factors, such as phylogeny (Cattin et al. 2004), restrictions of habitat, seasonality (Pimm and Lawton 1980; Winemiller 1990; Tylianakis et al. 2007), behavior of species that interact (Ings et al. 2009), or even morphometric characteristics (e.g., body size; Cohen et al. 2005; Woodward et al. 2005; Brose et al. 2006). In the case of interactions between parasites and hosts, most studies of networks do not emphasize the factors that contribute to their architecture. Usually, interaction networks marked by antagonistic relations tend to be more modular, while mutualistic interaction networks are biased to nestedness (Olesen and Jordano 2002; Bascompte et al. 2003). Both nested and modular structures do not have random architectures; in the modular structure, there are groups of species that interact more strongly with each other, forming cliques. On the other side, nested networks are mainly constituted by generalist species that interact more strongly with specialist ones (Olesen and Jordano 2002; Bascompte et al. 2003).

The ways in which parasites infect their hosts are generally related to diet (Martin et al. 2005), where common species of hosts with similar diets also have a large similarity in the species of associated parasites. In addition, phylogeny is considered an important aspect in the exploitation of the host, expecting that parasites exploit host species that are phylogenetically close (Clayton et al. 2004; Brooks et al. 2006). Networks between parasites and hosts are less studied than other types of antagonistic interactions, but a compartmentalized (modular) pattern is expected to be found in this type of relation. Phylogeny is a determinant factor for a modular structure in networks between parasites and hosts, since phylogenetic proximity is reflected in phenotypic similarity, so that certain lineages of parasites are more likely to exploit particular lineages of hosts. Thus, the formation of modules consisting of groups of hosts and parasites that are intimately related is possible (Krasnov et al. 2012).

The micro-habitat in which part of a community is situated can also influence the architecture of the interactions between species (Krause et al. 2003), where species that share the same habitats would be grouped in the same modules. However, there are not many studies on interaction networks investigating the role of the micro-habitat. The influence of spatial structure on the compartmentalized pattern in networks between species of marine fishes was observed by Rezende et al. (2009). There are no studies indicating that the type of environment utilized by the host influences the architecture of the network of its parasites, although the micro-habitat has an important role in determining the composition of species of parasites in some species of vertebrates (Kerr and Bull 2006), especially in the semiarid Caatinga of Northeast Brazil. The Caatinga is a Brazilian biome that covers around 800,000 km^2, with a semiarid climate, where rainfall usually does not reach 750 mm annually (Andrade-Lima 1981). The Caatinga harbors many vegetation types, usually deciduous, xerophitic, and thorny, varying according to soil type, altitude, and rainfall level (Velloso et al. 2001). In view of the above facts, the principal objective of this study was to analyze the architecture of interaction networks between the species of lizards in the Caatinga, relating them to their food items, categories of micro-habitats, and species of endoparasites associated with them.

Materials and methods

Lizards were collected in four different localities in the Brazilian Caatinga (Fig. 1). The lizards were captured with the help of pitfall traps with drift fences and by means of active searches. All micro-habitats utilized by each lizard species were recorded when they were first sighted. After the collection, all specimens were fixed in 10 % formalin and preserved in 70 % alcohol, and they were deposited in the herpetological collection of the Universidade Federal da Paraíba—CHUFPB. In the laboratory, the respiratory and gastrointestinal tracts of each individual were removed to determine the endoparasites present. The food items present in the stomach were collected and later identified to the order level, except for *Iguana iguana*, which is an herbivore; in this case, we used only the category “plant material.” The parasites obtained were counted and identified. The foraging mode of the lizards was categorized according to Perry (1999). Basically, most Iguania and Gekkota are sit-and-wait foragers, while most Autarchoglossa are active foragers.

Parasites

Hosts were necropsied, and their gastrointestinal tracts and body cavities were examined under a stereomicroscope for the presence of helminths. Nematodes were preserved in 70 % ethanol and identified according to Vicente et al. (1993). They were cleared with lactophenol and examined using the Leica Qwin Lite 2.5 computerized system.

Networks

Three networks were constructed from the biological data. All networks had 12 species of lizards in common. The bipartite networks were formed by the species of parasites, categories of food items, and micro-habitats of lizards sampled in the Caatinga. Examining network modularity among lizards, their diet, micro-habitat, and parasites is an interesting way to evaluate in a group of species (assemblage) how they interact more with each other, and less with species from other network compartments. In addition, network modularity could reveal critical scales for connectivity in ecology and evolution (Fletcher et al. 2013).

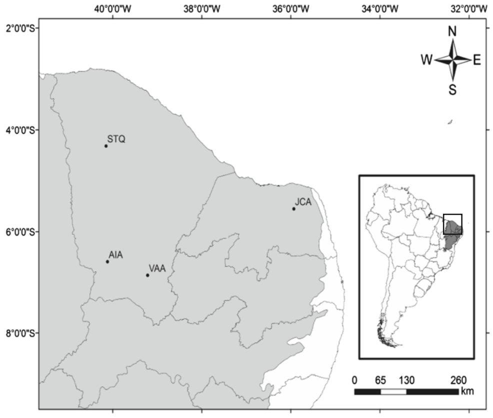


Fig. 1 Sampling sites—AIA (Estação Ecológica de Aiuaba-CE), JCA (Fazenda Cauaçu, João Câmara-RN), STQ (Santa Quitéria-CE), and VAA (Várzea Alegre-CE)

A network with the micro-habitat data was constructed using a presence/absence matrix based on observations of micro-habitat types utilized by the lizards in the Caatinga as follows: 1—stone (St), 2—tree trunk (Tt), 3—litter (Li), 4—bare soil (Bs), 5—canopy (Ca), 6—fallen trunk (Fl), and 7—sandy soil (Ss). For the construction of networks related to lizards and their diet, we identified the food items present in the stomach of species of lizards collected during the study. We recorded 16 orders of arthropods, besides molluscs and plant material, and built a presence/absence matrix of all food items recorded for each lizard species. In addition, to construct the network between the lizards and their endoparasites, we used a presence/absence matrix based on 15 endoparasite species identified in lizards' gastrointestinal tract and body cavities.

An analysis of modularity of networks was carried out with the R program (R 2012), using the bipartite package (Dormann et al. 2008). The modules formed were not altered when the number of algorithm interactions went from 50,000 to 100,000, indicating the reliability of the technique used in the determination of modular structure. The bipartite package available in R is based on Newman's algorithm (Newman 2004) for estimating modular compartments.

Historical effects

A canonical phylogenetic ordination analysis was performed to determine the influence of historical factors (phylogeny) and use of micro-habitat on the composition of parasite species (Giannini 2003). The analysis was carried out with Monte Carlo permutations (9,999), in the software CANOCO 4.5 for Windows (Ter Braak and Smilauer 1998). Accordingly, two matrices were constructed, one containing the comparative ecological data of all species of lizards sampled and the second matrix containing all phylogenetic groups, where this matrix was obtained from the cladogram shown in Fig. 2, with each group separately coded ("0" for absence and "1" for presence).

Ecological effects

To determine the overlap value between the species of lizards relative to the species of parasites, we utilized Pianka's index of niche overlap (Pianka 1973). In this analysis, a matrix was constructed with the proportions (%) of each parasite species found in each lizard species. The analysis was performed using Ecosim (Gotelli and Entsminger 2001).

Finally, to see if the species with the highest diversity of food items consumed also had the highest richness of species of associated parasites, we utilized a simple linear regression, in which the number of *links* with food items and with species of endoparasites was counted for all species of lizards.

Results

A total of 1,077 lizards (12 species) were collected, from the four study areas (Table 1), and 7,588 parasite specimens (15 species) were found. We calculated the prevalence and mean intensity of infection (*Sensu* Bush et al. 1997) for each species of endoparasite found (Table 2).

Networks

The analyses of interaction networks of lizards and their parasites, food items, and micro-habitat categories showed a pattern that tended to be compartmentalized (modular) (Figs. 3, 4, and 5).

In relation to the network between the lizards and the their micro-habitats, the foraging strategy was determinant in the separation of compartments, where the "sit-and-wait"-type lizards were grouped in a single compartment, with only one exception, *G. geckoides* (Gg), which was grouped with the active foragers. Lizards of the foraging type were divided into two compartments, where the lizards of the family Teiidae were grouped in one compartment and the other foragers in a different compartment. The species *I. iguana* (Ii), which occupied a specific micro-habitat, essentially arboreal, and without overlap of micro-habitat use with the other species of lizards in the Caatinga, was isolated in a specific module (Fig. 5).

In the network between the lizards and the food items consumed, the type of foraging strategy also exerted an influence on the type of prey consumed, where the "sit-and-wait" species were concentrated in the first compartment, with the exception of *Brasiliscincus heathi* (Bh), which is an "active forager" (Fig. 4). Foragers were concentrated in the second compartment, with the exception of *Phyllopezus periosus*

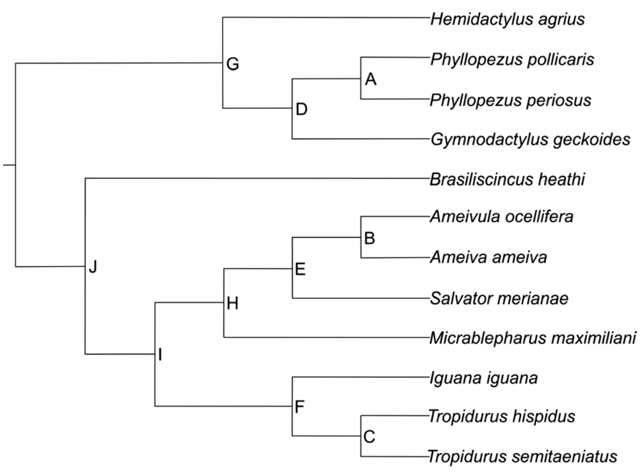


Fig. 2 Phylogenetic tree of species of lizards collected in the Caatinga, obtained from Giugliano et al. (2007), Gamble et al. (2011), Sites Jr et al. (2011), and Wiens et al. (2012). The *letters* in the clade represent the taxa: **a** genus *Phyllopezuz*, **b** Teiinae**, c** family Tropiduridae, **d** family Phyllodactyllidae, **e** family Teiidae, **f** Iguania, **g** Gekkota, **h** Teoidea, **i** Episquamata, **j** Unidentata

(Pz), which is a sit-and-wait species. *I. iguana* (Ii), like in the other networks constructed, was isolated (Figs. 3. 4, and 5), since this lizard is exclusively vegetarian, in contrast to the other species which are insectivores. In the network between the lizards and their parasites, the tropidurid lizards Th and Ts were grouped together with Gg (Fig. 3). Despite not being phylogenetically close, the tropidurids and Gg feed on many similar items, including those grouped in the same compartment in the network between lizards and food items (Fig. 4). The lizards of the family Teiidae were all grouped in a single compartment with *H. agrius* (Ha). The compartment formed between the species *M. maximiliani* (Mm) and *B. heathi* (Bh), with respect to species of parasites, was also repeated when the network between lizards and micro-habitat was observed, and thus the use of habitat and phylogeny were determinants in the composition of species of parasites for these lizards.

Phylogeny was determinant in the formation of the module with the lizards of the family Phyllodactylidae, where the two members of this family (Ps and Pz), besides being phylogenetically close, share the same micro-habitat categories.

Historical effects

On analyzing the phylogeny of the lizards sampled (Fig. 2), we found a strong indication of the influence of historical factors (phylogeny) on the composition of species of parasites of the lizards in the Caatinga (Table 3), where the more related species of lizards such as the tropidurids (Th and Ts), teids (Aa and Sm), and Phyllodactylidae (Ps and Pz) showed greater overlap of species of endoparasites between them than when compared with lizards of other lineages (Table 4).

Table 1 Lizards collected at the sampling sites—AIA (Estação Ecológica de Aiuaba-CE), JCA (Fazenda Cauaçu, João Câmara-RN), STQ (Santa Quitéria-CE), and VAA (Várzea Alegre-CE)

	AIA		JCA		STQ		VAA	
	N	SVL±SD	*N*	SVL±SD	*N*	SVL±SD	*N*	SVL±SD
Family Teiidae								
Ameiva ameiva	3	118.3±40.2	8	60.2±28.8	–	–	32	61.7±23.7
Ameivula ocellifera	58	58.2±11.6	100	68.9±18.7	42	67±19	101	53.4±12.4
Salvator merianae	–	–	–	–	2	114.4±2.8	3	181.3±118
Family Tropiduridae								
Tropidurus hispidus	96	66.5±18.7	57	70.5±17.2	76	55.4±17.3	59	58.1±14
Tropidurus semitaeniatus	–	–	59	63±15.2	16	70.6±15.1	45	63.7±11.2
Family Gekkonidae								
Gymnodactylus geckoides	17	38.5±4	–	–	–	–	30	38.9±6.3
Hemidactylus agrius	6	46.3±6.4	–	–	1	47±0	17	48.1±9.1
Phyllopezus pollicaris	66	61.8±14	–	–	–	–	28	72.3±12.4
Phyllopezus periosus	–	–	6	110±15.8	–	–	–	–
Family Scincidae								
Brasiliscincus heathi	6	58.3±13.4	–	–	2	60±1.3	8	58.5±9.5
Family Gymnophthalmidae								
Micrablepharus maximiliani	–	–	–	–	9	44.4±2.2	121	38±4.8
Family Iguanidae								
Iguana iguana	–	–	1	200±0	2	105.6±3.6	–	–

SVL mean snout-vent length, *SD* standard deviation

Table 2 Endoparasites collected in the taxocene of lizards in the Caatinga. Prevalence (*P*) (%) of hosts infected by parasite species; intensity (I), mean intensity of infection, for the hosts infected

Parasite	Host	*P* (%)	*I*
Nematoda			
Family Heterakidae			
Strongyluris oscari (Sos)	*Tropidurus hispidus* (Th)	25	5.26
	Tropidurus semitaeniatus (Ts)	15.9	6.28
	Gymnodactylus geckoides (Gg)	0.6	4
	Ameivula ocellifera (Ao)	0.32	1
Family Molineidae			
Oswaldocruzia sp. (Osw)	*Brasiliscincus heathi* (Bh)	6.25	9
Family Onchocercidae			
Oswaldofilaria sp. (Osf)	*Tropidurus hispidus*	1	2
Family Pharyngodonidae			
Aleuris sp. (Ale)	*Iguana iguana* (Ii)	33.3	1,235
Ozolaimus cirratus (Oza)	*Iguana iguana*	33.3	2,430
Pharyngodon sp. (Pha)	*Ameivula ocellifera*	12.13	19.05
	Tropidurus hispidus	1.7	13.2
Parapharyngodon alvarengai (Pal)	*Tropidurus hispidus*	27	3.67
	Tropidurus semitaeniatus	25.9	8.68
	Phyllopezus pollicaris (Ps)	2.72	2.66
	Phyllopezus periosus (Pz)	16.6	58
	Gymnodactylus geckoides	14	1.68
	Brasiliscincus heathi	25	2.25
	Ameiva ameiva (Aa)	18.6	2.3
	Ameivula ocellifera	0.65	2
	Hemidactylus agrius (Ha)	16.6	1.75
Spauligodon okxcutzcabiensis (Sok)	*Phyllopezus pollicaris*	41.81	13.2
	Phyllopezus periosus	83.3	34
	Ameivula ocellifera	0.65	21.5
Spauligodon sp. (Spa)	*Micrablepharus maximiliani* (Mm)	18.18	4.23
Family Physalopteridae			
Physaloptera lutzi (Plu)	*Tropidurus hispidus*	29.5	6.71
	Tropidurus semitaeniatus	2	9.7
	Gymnodactylus geckoides	1.82	1.33
	Ameivula ocellifera	3.27	4.66
	Ameiva ameiva	18.6	1.8
	Hemidactylus agrius	8.33	2.5
	Micrablepharus maximiliani	2.27	3.6
	Salvator merianae (Sm)	20	13
Family Rabdiasidae			
Rhabdias sp. (Rha)	*Tropidurus hispidus*	1	3
Family Kathlaniidae			
Cruzia sp. (Cru)	*Salvator merianae*	40	6
	Ameiva ameiva	9.3	15.2
	Ameivula ocellifera	0.32	22
Pentastomida			
Family Raillietiellidae			
Raillietiella mottae (Rmo)	*Tropidurus hispidus*	1	1.3
	Tropidurus semitaeniatus	0.51	1
	Phyllopezus pollicaris	3.63	1.75

Table 2 (continued)

Parasite	Host	*P* (%)	*I*
	Phyllopezus periosus	50	2.66
Cestoda			
Family Linstowiidae			
Oochoristica sp. (Ooc)	*Tropidurus hispidus*	1.38	3
	Tropidurus semitaeniatus	1.55	2
	Gymnodactylus geckoides	0.6	1
	Brasiliscincus heathi	12.5	1.5
	Ameivula ocellifera	1.96	1.16
	Ameiva ameiva	6.97	1.33
	Micrablepharus maximiliani	9.1	2.1
Achanthocephala			
Family Oligacanthorhynchidae			
Oligacanthorhynchus sp. (Oli)	*Tropidurus hispidus*	0.69	3.5
	Tropidurus semitaeniatus	0.51	1

The use of micro-habitat also demonstrated an important role in the determination of composition of species of parasites in an assemblage of lizards, as demonstrated by the species *I. iguana* (Ii), which segregated in relation to the use of habitat of the other species of lizards and did not show overlap with any other species of lizard in relation to the presence of parasites. On the contrary, the lizards with the "sit-and-wait" strategy (Gg, Ha, Th, and Ts), which shared the same micro-habitats, showed high values of overlap of parasites (Tables 3 and 4).

In relation to richness of parasites, the lizards that consumed a greater variety of prey also showed a greater richness of endoparasites ($F_{1,12}=13.53$; $R^2=0.53$; $P<0.005$) (Fig. 6). (In this case, diet explained 53 % of the distribution of parasites).

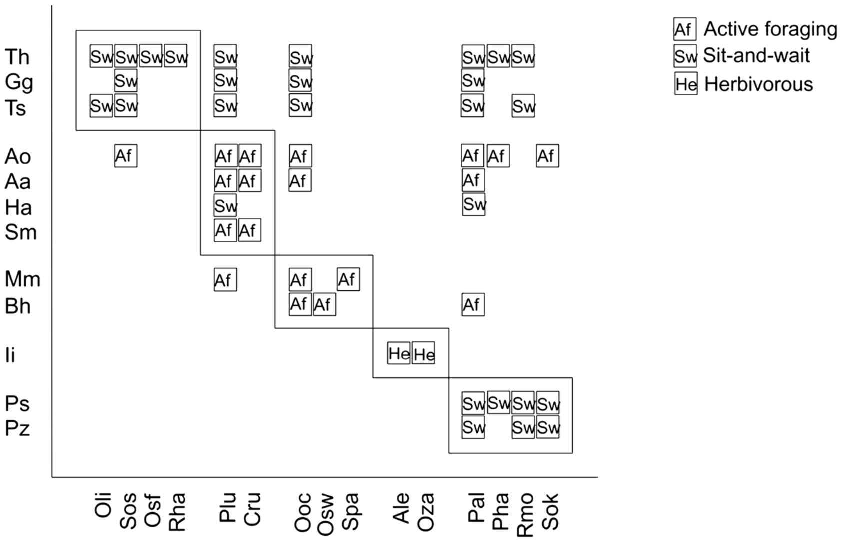
Discussion

Compartmentalization

All bipartite networks demonstrated a compartmentalized configuration; this pattern is the most expected when antagonistic interactions between species are analyzed (Bascompte 2010; Thebault and Fontaine 2010). Species that are placed in the same compartment can effectively have a similar niche and live in similar environments as well as be phylogenetically close (Lewinsohn et al. 2006; Rezende et al. 2009).

The structure of the network of interactions between the lizards and their diet was influenced by phylogeny together with the type of foraging strategy of the lizards, where there was a separation between the active foragers and sit-and-wait

Fig. 3 Bipartite network between the species of lizards on the *Y*-axis and species of parasites on the *X*-axis. The *codes* refer to each species of parasites and lizards found in Table 1



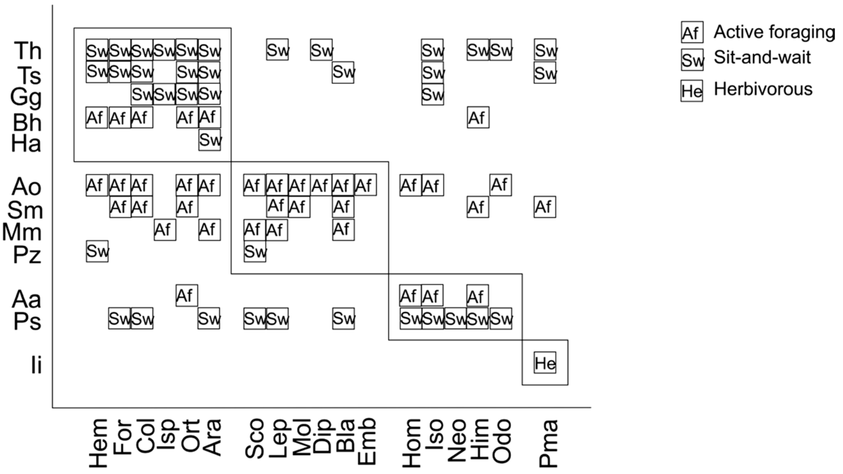


Fig. 4 Bipartite network between the species of lizards on the *Y*-axis and the categories of food items on the *X*-axis; (Hem) Hemiptera, (For) Formicidae, (Col) Coleoptera, (Isp) Isopoda, (Ort) Orthoptera, (Ara) Araneae, (Sco) Scorpiones, (Lep) Lepidoptera, (Mol) Mollusca, (Dip) Diptera, (Bla) Blattodea, (Emb) Embioptera, (Hom) Homoptera, (Iso) Isoptera, (Neo) Neoptera, (Him) Hymenoptera, (Odo) Odonata, (Pma) plant material

lizards. Besides, there was some incongruence as in the case of *B. heathi* (Bh), which is an active forager that grouped more with sit-and-wait species, and the species *P. periosus* (Pz), which is a sit-and-wait animal, grouped more with the foraging lizards. These incongruences can occur due to the fact that there are species of lizards that are errant foragers, having an intermediate foraging activity between active foraging and sit-and-wait (Pough et al. 2003). McLaughlin (1989) and Perry (1999) also suggest that the two foraging modes are not always clearly distinct, where they are probably part of a continuum. Basically, some species could be very plastic in their foraging mode, according to prey availability (McLaughlin 1989; Perry 1999). Similarly, the network between the lizards and their parasites, where the groups formed, tended to form between species more phylogenetically related or with uses of similar micro-habitats.

There was a strong influence of historical factors (phylogeny) on the composition of species of parasites. The compartmentalized pattern in a network can provide greater stability (Krause et al. 2003; Teng and McCann 2004), because such structuration of the community would be a way of reducing the effects of competition (Rezende et al. 2009).

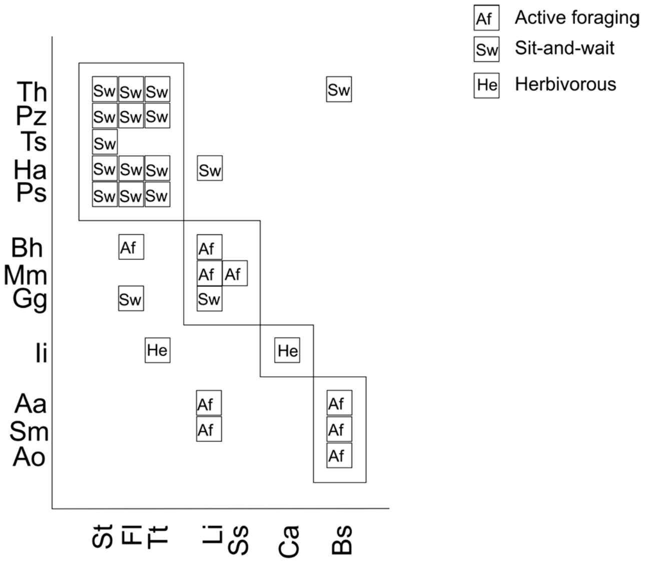


Fig. 5 Bipartite network between the species of lizards and categories of micro-habitat utilized by them. The *Y*-axis represents the species of lizards. On the *X*-axis are the categories of micro-habitat as follows: 1—stone (St), 2—tree trunk (Tt), 3—litter (Li), 4—bare soil (Bs), 5—canopy (Ca), 6—fallen trunk (Fl), and 7—sandy soil (Ss)

Table 3 Historical effects on the composition of parasite species in lizards in the Caatinga. Results of Monte Carlo permutation tests in individual groups (Fig. 2) for the composition matrices of parasite species and use of micro-habitat. Percentage of variation explained (in relation to the total variation without restrictions) and the values of *P* and *F* for each variable are given (with the utilization of 9,999 permutations) for each principal matrix. A–F in the table represent the taxa in the clade of Fig. 2

Groups	Variation	Variation (%)	*F*	*P*
Canopy	1	20.242	8.974	0.0001
F	0.895	18.117	7.876	0.0001
Stone	0.874	17.692	7.661	0.0001
Sandy soil	0.860	17.408	7.525	0.0001
I	0.856	17.327	7.484	0.0001
H	0.852	17.246	7.439	0.0001
A	0.851	17.226	7.434	0.0001
Bare soil	0.850	17.206	7.420	0.0001
D	0.849	17.186	7.414	0.0001
E	0.847	17.145	7.390	0.0001
J/G	0.844	17.064	7.356	0.0001
Fallen trunk	0.807	16.336	6.987	0.0001
Tree trunk	0.803	16.255	6.951	0.0001
Litter	0.793	16.052	6.849	0.0001
B	0.780	15.789	6.726	0.0001
C	0.588	11.902	4.889	0.0001
SVL	0.160	3.238	1.240	0.3791
Season	0.013	0.263	0.098	0.9723

SVL snout-vent length of lizards

Table 4 Overlap (Pianka's index of niche overlap) of lizard species according to the presence of endoparasites

	Ts	Ao	Aa	Sm	Mh	Gg	Ii	Po	Mm	Pe	Ha
Th	0.609	0.148	0.277	0.562	0.314	0.517	0.000	0.014	0.081	0.124	0.758
Ts		0.014	0.261	0.061	0.748	0.962	0.000	0.001	0.001	0.298	0.800
Ao			0.049	0.074	0.007	0.014	0.000	0.086	0.009	0.062	0.046
Aa				0.804	0.222	0.284	0.000	0.004	0.037	0.084	0.346
Sm					0.000	0.078	0.000	0.011	0.007	0.000	0.427
Mh						0.803	0.000	0.000	0.043	0.261	0.657
Gg							0.000	0.002	0.017	0.319	0.866
Ii								0.000	0.000	0.000	0.000
Po									0.002	0.946	0.009
Mm										0.000	0.058
Pe											0.262

Another aspect is that in antagonistic interactions, there is a greater level of specialization (coevolution) as emphasized by the Red Queen hypothesis (Van Valen 1973). In contrast to relations between mutualistic organisms, this constant arm race leads to a compartmentalized architecture. On the basis of the assumption that compartmentalization is the fruit of community structuration, our study is in line with various other works with lizards in South America that point out segregation by diet, time of foraging, and micro-habitat, besides combinations of these factors (e.g., Vitt 1991, 1995; Vitt and Carvalho 1995).

In relation to the compartmentalized structure demonstrated by the parasites, various factors deserve special mention, including the specificity between the parasites and their hosts. This type of relation generally has a high-degree specialization, and thus, it is expected that interaction networks between endoparasites and hosts show a compartmentalized pattern. This pattern cannot be the same as that found in networks that involve other varieties of parasitism, such as ectoparasites and their hosts, as demonstrated by Graham et al. (2009), who attributed nested architecture to the networks between ectoparasites and vertebrates. In fact, ectoparasitism and endoparasitism differ greatly in the degree of intimacy of relation between the species, since endoparasites are more dependent on their hosts, consequently showing a higher degree of intimacy compared with ectoparasites (Price 1980), and thus influencing the architecture of the network.

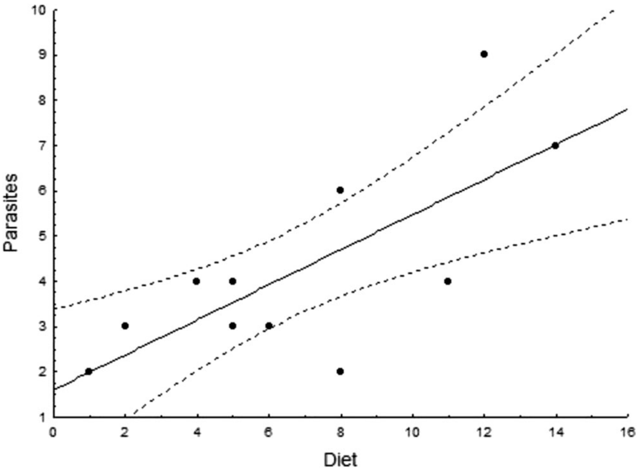


Fig. 6 Relation between the number of species of parasites and richness of food items of each species of lizard sampled. The *dotted lines* represent the 95 % confidence interval

Historical effects on composition of species of parasites in lizards

The majority of studies focusing on the ecology of parasites examine only the abundance patterns of the parasites in their respective hosts (Pedersen and Fenton 2007). In the present study, we demonstrated the role of historical and ecological factors in the determination of composition of species of parasites present in the taxocenes of lizards in the semiarid Caatinga. The historical effects (phylogeny) are considered one of the principal factors in the determination of species of parasites of vertebrates (Lima Jr et al. 2012), while diet in many cases can influence the presence of parasites, mainly with regard to taxocenes of species of heteroxenous parasites (which utilize intermediate hosts).

There was also a strong influence of the use of micro-habitat on the composition of parasites, but there are few available data in the literature that cite this relation (Marcogliese 2002). However, this has been observed in ectoparasites present on the lizard *Tiliqua rugosa* in Australia (Kerr and Bull 2006). The specialization for the same micro-habitat of the host can lead to an increase in the probability of having an encounter between the parasites and their hosts, favoring contagion (Kerr and Bull 2006). Parasites that are in the same places (micro-habitat or refuges) as their hosts can be indirectly transmitted between the hosts that frequently utilize these places (Leu et al. 2010). In addition, the fact that the species of parasites exploit the same micro-habitat categories as their hosts can represent an ecological adaptation that favors efficiency in the transmission to hosts.

Relation between diversity of diet and diversity of parasites

Our results demonstrated a positive relation between diversity of prey and diversity of endoparasites in lizards in the Caatinga, corroborating the work of Chen et al. (2008), which indicated that the species of hosts with greatest diversity of parasites are those that consume the largest diversity of food items. In fact, other reasons could also support this relation, especially the fact that lizards with more diversified diets in certain ways can be more exposed to parasites, due to the consumption of more intermediate hosts. Another factor that can be related to this observation is the fact that lizards that consume more food items could have a larger body mass, allowing them to host more parasites (Morand 2000).

Conclusions

This study supports the notion that networks of antagonistic interactions between lizards and their parasites, food items, and micro-habitat utilized assume a pattern of compartmentalized architecture, where this structure tends to be mainly determined by the phylogeny and foraging strategy of lizards. In addition, we conclude that phylogeny and the type of micro-habitat utilized by the hosts determine the composition of species of endoparasites in the Caatinga. With respect to the diversity of endoparasites, this work showed that their diversity is directly related to the diversity of food items consumed by the lizards.

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