Diversity and patterns of interaction of an anuran–parasite network in a neotropical wetland

K. M. CAMPIÃO[1]*, A. RIBAS[2] and L. E. R. TAVARES[3]

[1] *Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal Paraná, Curitiba, Brazil*
[2] *Faculdade de Computação, Universidade Federal do Mato Grosso do Sul, Brazil*
[3] *Departamento de Biologia, Universidade Federal do Mato Grosso do Sul, Brazil*

SUMMARY

We describe the diversity and structure of a host–parasite network of 11 anuran species and their helminth parasites in the Pantanal wetland, Brazil. Specifically, we investigate how the heterogeneous use of space by hosts changes parasite community diversity, and how the local pool of parasites exploits sympatric host species of different habits. We examined 229 anuran specimens, interacting with 32 helminth parasite taxa. Mixed effect models indicated the influence of anuran body size, but not habit, as a determinant of parasite species richness. Variation in parasite taxonomic diversity, however, was not significantly correlated with host size or habit. Parasite community composition was not correlated with host phylogeny, indicating no strong effect of the evolutionary relationships among anurans on the similarities in their parasite communities. Host–parasite network showed a nested and non-modular pattern of interaction, which is probably a result of the low host specificity observed for most helminths in this study. Overall, we found host body size was important in determining parasite community richness, whereas low parasite specificity was important to network structure.

Key words: network, nestedness, parasite, amphibian, helminth.

INTRODUCTION

Identifying which factors affect the diversity of parasite communities across hosts is one of the major quests in parasite ecology. The most common approach to untangle the processes behind the patterns is inferring which factors correlate with what we observe. For example, which host traits correlate with parasite diversity? When we observe different hosts exploring a given habit, how do we expect these hosts to be explored as habitats for the local pool of parasite species? Which host species are the most parasitized, and which traits favour high parasite exploitation? For some hosts groups, such as fishes and mammals, these questions have been studied extensively, and major advances in this field have occurred in the recent years, unveiling some mechanisms underlying long observed patterns (Poulin, 2007).

Body size is the best-studied host trait explaining parasite biodiversity, being positively related to parasite species richness (Kamiya *et al*. 2014). Large-bodied hosts may be easier to colonize because of the greater amounts of food they ingest, their large surface area, greater mobility, wider niche breadth and longer time of exposure to parasites (Poulin, 2007). Other host features, such as diet, behaviour and habit, might be equally important in determining parasite diversity and composition. Host habit may play an import role in parasite assembly because, all else being the same, variation in habitat used by hosts implies varying exposure to parasite infective stages (Poulin and Morand, 2004). Nonetheless, few studies have examined the influence of host habit on parasite communities (Aho, 1990; Hamann *et al*. 2013).

One promising way of studying parasite biodiversity is using the concepts of network theory (Proulx *et al*. 2005). Ecological networks are considered the building blocks of biodiversity, and an understanding of their structure is important to the understanding of the functioning of the whole ecosystem (Joppa and Williams, 2013). Network analysis provides a useful framework to identify, understand and predicting how parasites and hosts interact (Poulin, 2010; Lima *et al*. 2012; Krasnov *et al*. 2012; Bellay *et al*. 2015). These interactions are generally not random, and because of the intimacy between hosts and their parasites, a phylogenetic signal in network structure is expected to reflect the relatedness among hosts (Krasnov *et al*. 2012).

Two main patterns emerge when studying host–parasite networks, nestedness and modularity. Nested networks are those where generalist parasite species interact with other generalists as well as with specialists, while specialist parasite species tend to interact with generalists rather than other specialists (Ulrich *et al*. 2009). In such networks, the composition of parasite communities in hosts associated with few parasite species is a subset of those associated with many parasite species (Almeida-Neto

* Corresponding author: Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal Paraná, 81531-980, Curitiba, Brazil. E-mail: karla_mcamp@yahoo.com.br

and Ulrich, 2011). On the other hand, modular networks are composed of subgroups of hosts and parasites that interact more with each other than with other species within the network (Fortuna *et al.* 2010). Both the body size and habit of the hosts may influence network architecture. For instance, if hosts' habit is related to parasite community structure, we expect that host species of similar habit will form interaction modules with their parasites, resulting in a modular network.

Determinants of parasite species richness and the network patterns are still poorly understood for amphibian hosts. In this study, we investigate how body size and the differences in habitat used by anurans influence parasite community diversity, and how the local pool of parasites exploits sympatric host species. Specifically, we examine how parasite diversity varies across hosts of different size and habit, and test whether similarity among parasite communities correlates with host's phylogeny. We further investigate the interaction proprieties of this anuran–parasite network.

MATERIALS AND METHODS

This study was carried out with anurans collected in the farmland Fazenda Alegria (18°59′Se 56°39′W), Southeastern Pantanal, Brazil. Our field trips to collect the host species were conducted in the rainy seasons of 2011–2013. Anurans were hand-captured and taken to the laboratory, where they were euthanized with an overdose of sodium thiopental solution. We recorded their snout-vent length and examined their body cavity, digestive tract, accessory organs and musculature for helminth parasites. Parasites were collected and processed according to standard procedures (Goater and Goater, 2001), and then identified to the lowest taxonomic category possible. Voucher parasite specimens are deposited in the collection of the Universidade Federal de Mato Grosso do Sul (accession numbers: ZUFMS NEM00001 – ZUFMS NEM00028, ZUFMS PLA00001 – ZUFMS PLA00005, ZUFMS ACA00001).

We examined 229 host specimens, interacting with 32 helminth parasite taxa (one acanthocephalan cystacanth, 24 nematodes, six trematodes and an undetermined helminth cyst). A complete list of helminth taxa is provided in the Supplementary material. All helminth taxa are reported to describe parasite species richness, but only those that could be identified to species or morphospecies were used in the analyses. The term infracommunity refers to the helminth community in a single host (Bush *et al.* 1997).

We adopted two measures of parasite biodiversity: the number of helminth taxa per host (species richness) and taxonomic diversity. The latter accounts for the variety of parasite taxa, and thus, captures some of the phylogenetic diversity in parasite

community composition (Supplementary Table 1). The taxonomic diversity index takes both the abundance and phylogenetic relatedness (based on the distance of a classification tree) amongst species into account. We used parasite phylum, class, superfamily, family and genus to build the classification tree. This analysis was performed in R (R Development Core Team, 2013), with the functions '*tax2dist*' and '*taxondive*' of the '*vegan*' package (Oksanen *et al.* 2013) to calculate the taxonomic diversity for each infracommunity. We tested the relation of host traits (mean body size and habit) and parasite diversity (species richness and taxonomic diversity) with mixed effect models using the '*lme4*' package (Bates *et al.* 2014).

To test whether closely related hosts had more similar helminth communities, we compared distance matrices of host's phylogeny and parasite communities. We first reconstructed the amphibian's phylogenetic tree from Pyron and Wiens (2011) for our 11 anuran species with the '*ape*' package, and used the function '*cophenetic.phylo*' to compute the pairwise distances between the pairs of tips from the phylogenetic tree using branch lengths (Paradis *et al.* 2004). Pairwise distance measures among hosts based on the dissimilarity of their parasite communities (considering data on parasite presence/absence) were calculated with the Sorensen index. We then tested if the two distance matrices were correlated with a mantel test, with the Pearson coefficient and 1000 permutations in '*vegan*'.

The degree of nestedness of the network was evaluated using the NODF metric (Almeida-Neto *et al.* 2008). The randomness of matrix nestedness was assessed by the analysis of the row–column null model CE. The calculation of the NODF metric and the simulation of the CE null model (1000 randomizations) were calculated using the program ANINHADO (Guimarães and Guimarães, 2006). The detection of a modular pattern in network interactions was assessed with the program MODULAR (Marquitti *et al.* 2014). The program generates a value of modularity (M) for the interaction matrix, and verifies if the degree of modularity differs from those generated by random networks. We randomized 1000 matrices using 'null model 2' (see Marquitti *et al.* 2014). Network graphs were constructed with the packages '*igraph*' (Csardi and Nepusz, 2006) and '*RColourBrewer*' (Neuwirth, 2011), and the incidence matrix of host–parasite interaction with the packge '*Bipartite*' (Dormann *et al.* 2008), in R.

RESULTS

Helminth species richness varied across hosts (Fig. 1). Semi-terrestrial frogs had more complex associations with parasites, being more explored by the local pool of helminth species (Fig. 1). The
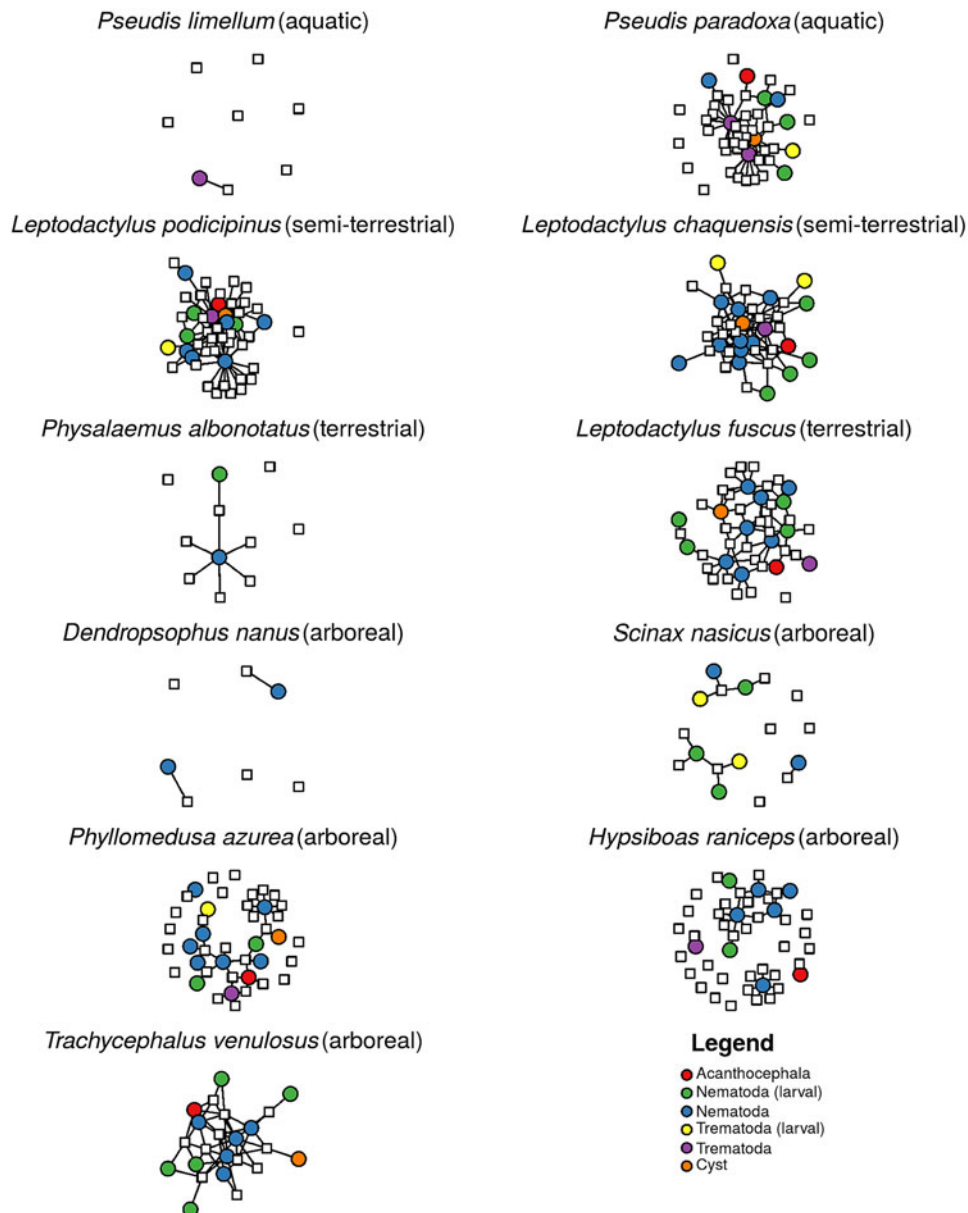
Fig. 1. Interaction between host individuals of 11 anuran species (squares) of different habits and their helminth parasites (circles).

frog *Leptodactylus chaquensis* had the highest values of helminth diversity, followed by the treefrog *Trachycephalus typhonius*. Leptodactylids had higher parasite biodiversity than hylids of similar size. Among the median-sized hylids, the aquatic frog *Pseudis platensis* had the highest taxonomic diversity. In general, small anurans had low parasite diversity, despite their habit and taxonomy (Table 1). The mixed effect models indicated anuran body size, but not the habit, as a determinant of parasite species richness (Table 2). Variation on taxonomic diversity on the other hand, was not significantly correlated to host size or habit (Table 2). Similarity in parasite communities did not correlate with host phylogeny (Fig. 2) (Mantel statistic r: 0·03 575, $P = 0.43\,956$).

We found a nested (NODF = 44·93, P (CE) = 0·02), but not modular ($M = 0.25$, $P = 0.99$) pattern in the host–parasite network (Fig. 3). Among all parasite species, 14 were associated with a single host and 11 were associated with five or more.

DISCUSSION

The complexity of host–parasite associations varied among hosts of different size and habit. In general, frog species of *Leptodactylus* had the richest parasite communities, with higher taxonomic diversity. *L. chaquensis* was the host with greatest parasite biodiversity. Indeed, semi-terrestrial anurans, such as *L. chaquensis* and *Leptodactylus podicipinus*, are susceptible to acquiring parasites whose infective stages

Table 1. Number of specimens (N), mean body size (mm), habit, total helminth species richness (THR), mean and standard deviation of helminth species richness (MHR ± S.D.), and taxonomic diversity (Δ+) of the helminth parasites of eleven anuran species

	Host traits			Parasite diversity		
Host species	N	Size (mm)	Habit	THR	MHR ± S.D.	Δ+
Hylidae						
Dendropsophus nanus	5	21·4	Ar	2	0·4 ± 0·49	0
Hypsiboas raniceps	36	57·6	Ar	11	0·9 ± 0·93	12·7 ± 28·9
Phyllomedusa azurea	29	37·2	Ar	12	0·9 ± 1·40	16·7 ± 33·9
Pseudis limellum	7	17·7	Aq	2	0 ± 0·45	0
Pseudis paradoxa	37	36·7	Aq	11	1·7 ± 1·25	34 ± 42·9
Scinax nasicus	11	31·1	Ar	6	1·0 ± 1·14	19 ± 40·5
Trachycephalus typhonius	10	69·5	Ar	12	4·3 ± 1·30	76 ± 0·8
Leptodactylidae						
Leptodactylus chaquensis	20	63·8	ST	19	4·6 ± 1·89	74 ± 11·9
Leptodactylus fuscus	30	41·1	T	13	2·0 ± 1·20	39 ± 36·8
Leptodactylus podicipinus	35	32·1	ST	14	2·6 ± 2·02	43 ± 42·6
Physalaemus albonotatus	9	26·3	T	3	0·1 ± 0·82	6·9 ± 20·8

Habit: Ar, Arboreal; Aq, Aquatic; ST, Semi-terrestrial; T, Terrestrial.

Table 2. Mixed effect models of host traits on helminth infracommunity diversity

	Random effect variable			Fixed effect variable				
Response variable	Parameter	V[a]	SE[b]	Parameter	Estimate	SE[b]	Z	P
Infracommunity species richness	Host species	1·99	1·41	Intercept	0·3374	1·02	0·33	0·74
				Body size	0·033	0·00	28·90	0·001
				Habit Ar[c]	0·2539	1·20	0·211	0·833
				Habit St[c]	2·403	1·42	1·682	0·09
Infracommunity taxonomic diversity	Host species	114·8	10·7	Intercept	7·6725	9·53	0·805	0·454
				Body size	0·0953	0·15	0·629	0·533
				Habit Ar[c]	−0·9726	10·2	−0·095	0·929
				Habit St[c]	18·855	11·9	1·583	0·194
				Habit T[c]	−0·723	11·8	−0·06	0·954

[a] Variance.
[b] Standard error.
[c] Habit: Ar, Arboreal; Aq, Aquatic; ST, Semi-terrestrial; T, Terrestrial.

are both in the water (such as trematodes) and soil (direct life-cycle nematodes). Among the tree frogs, *T. typhonius* harboured the richest helminth community and had the highest value of taxonomic diversity. The parasite communities of these anurans are composed mostly by parasites transmitted through the ingestion of the infective stages. This is probably due to the arboreal habit of *T. typhonius*, which might reduce the chances of acquiring trematodes and directly transmitted nematodes, respectively, through water and soil. The high taxonomic diversity may be related to the wide range of prey they consume (including Coleoptera, Diptera, Hemiptera, Hymenoptera, Orthoptera, Pseudoescorpionida and Aranae) (Sabagh *et al*. 2010), once several invertebrate species act as intermediate hosts for different parasite taxa (Anderson, 2000).

Differences in foraging strategy may also underlie some of the differences we observed among hosts.

For example, leptodactilids are active foragers, while most hylids are sit-and-wait predators. Such differences in foraging behaviour may explain why leptodactilids had higher parasite diversity. Among hylids, the aquatic *Pseudis paradoxa* had more diverse parasite communities than the arboreal anurans of similar size. This is not surprising though, once aquatic hosts generally have more diverse parasite fauna than their terrestrial counterparts (Poulin and Morand, 2004).

Our results confirmed host size as a determinant of helminth species richness in anuran hosts (Kamiya *et al*. 2014). Large anuran species always had the most diverse parasite communities, while the small ones had the least diversity. Nonetheless, it is important to consider that the diversity of parasites in small anurans might be higher than observed here if they are targeted with higher sampling effort (Poulin and Morand, 2004). Despite the differences
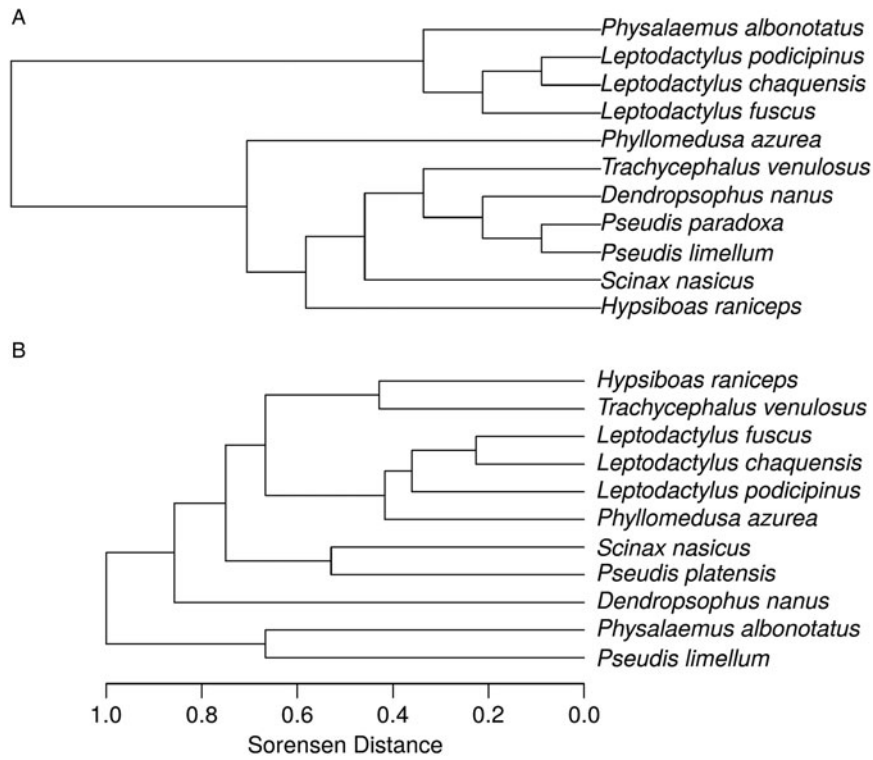
Fig. 2. A. Phylogeny of 11 anuran species adapted from Pyron and Wiens (2011). B. Dendrogram of the similarity among 11 anuran species based on the Sorensen distance of their helminth communities.
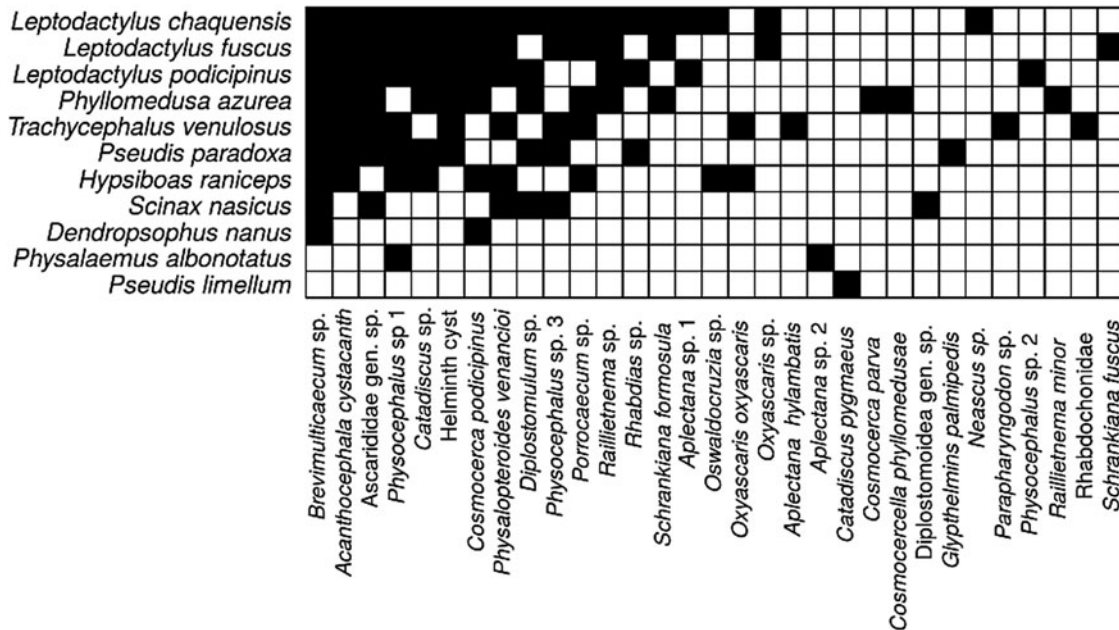

Fig. 3. Incidence matrix of the network of 11 anuran species (rows) and 32 helminth parasites (columns). A filled square represents interaction, and an empty square indicates that no interaction occurs.

we observed in parasite diversity across hosts of different life styles, habit was not significantly related to helminth species richness. It is possible that host habit is more influential to parasite community composition, or to the diversity of certain parasite groups (see Hamann *et al.* 2013), rather than to overall helminth species richness. Similarly, parasite taxonomic diversity did not

correlate to host size or habit. This is different from what we expected, since the taxonomic diversity of parasite assemblages can be more sensitive to the influence of host traits than parasite species richness (Luque and Poulin, 2008).

Hosts that are closely related phylogenetically may have more similar parasite communities than unrelated hosts (Lima *et al.* 2012; Krasnov *et al.* 2012;

Brito *et al.* 2014). We expect that because host switching is probably more frequent among closely related hosts. Assuming phylogenetic trait conservatism, related hosts probably offer the same set of resources to parasites, and are expected to share physiological and behavioural constraints. Thus, such hosts may have the chances of being exposed to the same parasite infective stages (Poulin, 2007). Notwithstanding, our results showed that closely related anurans did not necessarily have more similar parasite communities. Two processes mainly explain this outcome, one is that parasite network may be strongly influenced by contemporary factors that are not directly related to historical factors. The other is the low specificity observed in most parasite species may play an important role in increasing the similarity in parasite communities.

Low parasite specificity was also important to network structure. The nested pattern of interaction observed between anuran and their helminth parasites indicates that specialist parasites tend to interact more often with generalists than to other specialists (Poulin, 1996, 2010). Thus, specialist helminth species generally occurred in anurans with the richest parasite communities, and species poor parasite communities were subsets of those. This result is consistent with several other studies that investigated nestedness in host–parasite networks (Vázquez *et al.* 2005; Graham *et al.* 2009; Joppa *et al.* 2010; Bellay *et al.* 2011; Lima *et al.* 2012). The mechanisms underlying nestedness in interacting networks are not well understood, but are probably related to species abundance and co-evolutionary constrains (McQuaid and Britton, 2013). In the network accessed in this study, all host species are similarly very abundant, but the differences in body size among them might have influenced the interaction pattern, especially because of the effect of body size on parasite species richness.

Different from what we expected, anuran species did not form interacting modules with their parasites. First, we expected modularity because of the general high degree of intimacy and adaptation between species in a host–parasite network (Guimarães *et al.* 2007; Olesen *et al.* 2007; Fortuna *et al.* 2010). Second, we expected that the different habits amongst host species (aquatic, arboreal, semi-terrestrial and terrestrial) could favour the formation of modules. Ecological and phylogenetic groups of related host species could promote modularity, and the similarity (either phylogenetic, ecological or functional) is higher among species within the same module (Guimarães *et al.* 2007; Olesen *et al.* 2007; Bellay *et al.* 2011; 2013; Lima *et al.* 2012; Krasnov *et al.* 2012), and would be higher among species with the same habit. This has been observed in several host–parasite networks (Fortuna *et al.* 2010; Bellay *et al.* 2011, 2013; Lima *et al.* 2012; Krasnov *et al.* 2012). For instance, Brito *et al.* (2014) observed

that lizard species of similar microhabitat and diet form modules of interaction with their parasites, highlighting the importance of historical and ecological processes to network structure.

The lack of modularity, and the nested pattern of interaction observed in the network of sympatric anurans and their parasites are probably the result of low host specificity observed amongst most helminth taxa. No host species had a unique parasite community, and several parasite species were shared among different hosts. Even some helminth species that were associated to a single host in this study (*Aplectona hylambatis, Cosmocerca parva, Cosmocercella* cf. *phyllomedusae, Glypthelmins palmipedis* and *Raillietnema minor*) are reported as parasites of a wide range of hosts (Campião *et al.* 2014). Notwithstanding, parasites may be specialists to a particular resource provided by the host, and not to a particular host taxon. If this resource is either widespread amongst hosts or is a result of hosts convergent evolution, then parasites could track this resource despite host's taxonomic boundaries (Brooks *et al.* 2006). Low host specificity was especially evident among larval nematodes. Indeed, parasites in larval stages may increase the connectivity in host–parasite networks, because they tend to be more generalist (Bellay *et al.* 2013). Our results agree with that, as we observed parasites in larval stages interacting with host species of different habits and long phylogenetic distances.

Overall, we found that host attributes, such as body size, were important in determining parasite community richness, whereas parasite attributes (specificity) were important to network structure.

REFERENCES

Aho, J. M. (1990). Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and process. In *Parasite Communities Patterns and Process* (eds. Esch, G. W., Bush, A. O. and Aho, J. M.), pp. 157–190. Chapman and Hall, London, UK.

Almeida-Neto, M. and Ulrich, W. (2011). A straightforward computational approach for measuring nestedness using quantitative matrices. *Environmental Modelling and Software* **26**, 173–178.

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Jr, Loyola, R. D. and Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* **117**, 1227–1239.

Anderson, R. M. (2000). *Nematode Parasites of Vertebrates: Their Development and Transmission*, 2nd Edn. CABI Publishing, Wallingford, Oxon, UK. 650 pp.

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1–6. http://CRAN.R-project.org/package=lme4.

Bellay, S., Lima, D. P., Takemoto, R. M. and Luque, J. L. (2011). A host–endoparasite network of neotropical marine fish: are there organizational patterns? *Parasitology* **138**, 1945–52.

Bellay, S., De Oliveira, E. F., Almeida-Neto, M., Lima Junior, D. P., Takemoto, R. M. and Luque, J. L. (2013). Developmental stage of parasites influences the structure of fish–parasite networks. *PLoS ONE* **8**, e75710.

Bellay, S., De Oliveira, E. F., Almeida-Neto, M., Mello, M. A. R., Takemoto, R. M. and Luque, J. L. (2015). Ectoparasites and endoparasites of fish form networks with different structures. *Parasitology* **142**, 901–909.

Brito, S. V., Corso, G., Almeida, A. M., Ferreira, F. S., Almeida, W. O., Anjos, L. A., Mesquita, D. O. and Vasconcellos, A. (2014). Phylogeny and micro-habitats utilized by lizards determine the composition of their endoparasites in the semiarid Caatinga of Northeast Brazil. *Parasitology Research* **113**, 3963–3972.

Brooks, D. R., León-Règagnon, V., Mclennan, D. A. and Zelmer, D. (2006). Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology* **87**, 76–85.

Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.

Campião, K. M., Morais, D. H., Dias, O. T., Aguiar, A., Toledo, G., Tavares, L. E. R. and da Silva, R. J. (2014). Checklist of helminth parasites of amphibians from South America. *Zootaxa* **30**, 1–93.

Csardi, G. and Nepusz, T. (2006). The igraph software package for complex network research. International journal of complex systems 1695. http://igraph.sf.net.

Dormann, C. F., Gruber, B. and Fründ, J. (2008). Introducing the bipartite package: analysing ecological networks. *R News* **8**, 8–11.

Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, B. R., Poulin, R. and Bascompte, J. (2010). Nestedness *vs* modularity in ecological networks: two side of the same coin? *Journal of Animal Ecology* **79**, 811–817.

Goater, T. M. and Goater, C. P. (2001). Ecological monitoring and assessment network: protocols for measuring biodiversity: parasites of amphibians and reptiles Available at website http://www.emanrese.ca/eman/ecotools/protocols/terrestrial/herpparasites/intro.htm.

Graham, S. P., Hassan, H. K., Burkett-Cadena, N. D., Guyer, C. and Unnasch, T. R. (2009). Nestedness of ectoparasite-vertebrate host networks. *PLoS ONE* **4**, 1–8.

Guimarães, P. R., Jr. and Guimarães, P. (2006). Improving the analyses of nestedness for large sets of matrices. *Environmental Modelling and Software* **21**, 1512–1513.

Guimarães, P. R., Rico-Gray, V., Oliveira, P. S., Izzo, T. J., Dos Reis, S. F. and Thompson, J. N. (2007). Interaction intimacy affects structure and co-evolutionary dynamics in mutualistic networks. *Current Biology* **17**, 1797–1803.

Hamann, M. I., Kehr, A. I. and González, C. E. (2013). Biodiversity of trematodes associated with amphibians from a variety of habitats in corrientes province, argentina. *Journal of Helminthology* **87**, 286–300.

Joppa, L. N. and Williams, R. (2013). Modeling the building blocks of biodiversity. *PLoS ONE* **8**, e56277.

Joppa, L. N., Montoya, J. M., Solé, R., Sanderson, J. and Pimm, S. L. (2010). On nestedness in ecological networks. *Evolutionary Ecology Research* **12**, 35–46.

Kamiya, T., O'Dwyer, K., Nakagawa, S. and Poulin, R. (2014). What determines species richness of parasitic organisms? a meta-analysis across animal, plant and fungal hosts. *Biological Reviews* **89**, 123–134.

Krasnov, B. R., Fortuna, M. A., Mouillot, D., Khokhlova, I. S., Shenbrot, G. I. and Poulin, R. (2012). Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *American Naturalist* **179**, 501–511.

Lima Jr, D. P., Giacomini, H. C., Takemoto, R. M., Agostinho, A. A. and Bini, L. M. (2012). Patterns of interactions of a large fish–parasite network in a tropical floodplain. *Journal of Animal Ecology* **81**, 905–913.

Luque, J. L. and Poulin, R. (2008). Linking ecology with parasite diversity in neotropical fishes. *Journal of Fish Biology* **72**, 189–204.

Marquitti, F. M. D., Guimarães, P. R., Pires, M. M. and Bittencourt, L. F. (2014). MODULAR: software for the autonomous computation of modularity in large network sets. *Ecography* **37**, 221–224.

Mcquaid, C. F. and Britton, N. F. (2013). Coevolution of resource trade-offs driving species interactions in a host–parasite network: an exploratory model. *Theoretical Ecology* **6**, 443–456.

Neuwirth, E. (2011). RColorBrewer: ColorBrewer palettes. http://CRAN.R-project.org/package=RColorBrewer.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H. (2013). *Vegan: community ecology package*. R package version 2. 0–6. http://CRAN.R-project.org/package=vegan.

Olesen, J. M., Bascompte, J., Dupont, Y. L. and Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 19891–19896.

Paradis, E. *et al.* (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290.

Poulin, R. (1996). Richness, nestedness, and randomness in parasite infracommunity structure. *Oecologia* **105**, 545–551.

Poulin, R. (2007). *Evolutionary Ecology of Parasites from Individuals to Communities*, 2nd Edn. Princeton University Press, NJ, USA.

Poulin, R. (2010). Network analysis shining light on parasite ecology and diversity. *Trends in Parasitology* **26**, 492–498.

Poulin, R. and Morand, S. (2004). *Parasite Biodiversity*, Smithsonian Institution Books, Washington, D.C., USA.

Proulx, S. R., Promislow, D. E. L. and Phillip, P. C. (2005). Network thinking in ecology and evolution. *Trends in Ecology and Evolution* **20**, 345–353.

Pyron, A. and Wiens, J. (2011). A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* **61**, 543–583.

R Development Core Team (2013). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. http://www.r-project.org/.

Sabagh, L. T., Ferreira, V. L. and Rocha, C. F. D. (2010). Living together, sometimes feeding in a similar way: the case of the syntopic hylid anurans *Hypsiboas raniceps* and *Scinax acuminatus* (Anura: Hylidae) in the Pantanal of Miranda, Mato Grosso do Sul State, Brazil. *Brazilian Journal of Biology* **70**, 955–959.

Ulrich, W., Almeida-Neto, M. and Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos* **118**, 3–17.

Vázquez, D. P., Poulin, R., Krasnov, B. R. and Shenbrot, G. I. (2005). Species abundance and the distribution of specialization in host – parasite interaction networks. *Journal of Animal Ecology* **74**, 946–995.