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Disentangling the beta-diversity in anuran parasite communities

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Abstract

There is great heterogeneity in parasite communities among hosts, understanding the nature and drivers of such variations is still a great scientific quest. Here, we analyse the variation in parasite communities by addressing the following questions: (i) What is the beta-diversity component (nestedness or turnover) that most contributes to beta diversity in parasite communities among anuran species? (ii) Does the beta diversity of parasite communities follow a non-random pattern? (iii) Is the dissimilarity in composition of parasite communities related to the phylogenetic or functional dissimilarity among hosts? We found that turnover in parasite assemblages was the main component of beta diversity, but the variation observed both in the total beta diversity and in its components did not differ from the respective null models. The dissimilarity among parasite communities was not related to the phylogenetic species variability or functional dissimilarity among anuran species for most localities. In short, our findings may indicate a process of resource tracking by the parasite species, in which the resource may not necessarily be conserved phylogenetically in their hosts.

Introduction

Ecologists are always pursuing to unveil mechanisms that generate variations in the assemblage and functionality of biological communities. An ubiquitous pattern is the temporal and spatial shift in the composition and abundance of these communities, which can be described as beta diversity. Beta diversity may be decomposed into two components: nestedness and turnover. These components reflect mechanisms underneath the differences in species composition among communities (Harrison *et al*., 1992; Baselga *et al*., 2007; Baselga, 2017). Nestedness occurs when communities with a lower number of species are subsets of richer communities, and may reflect processes of species loss (Wright and Reeves, 1992; Ulrich and Gotelli, 2007; Baselga, 2010). Turnover implies the replacement of some species, and generally reflects species sorting by environmental or dispersal processes, stochastic events, geographic barriers or historical constraints (Qian *et al*., 2005; Baselga, 2010, 2012, 2017). Disentangling the components of beta diversity can help us understand the processes underlying the variation in community composition (Baselga, 2012, 2013*a*; Baselga and Leprieur, 2015).

Spatial and environmental determinants of beta diversity have been studied in a variety of communities, including plant (Condit *et al*., 2002; Svenning and Skov, 2007), and animal communities in terrestrial (Baselga, 2008; Maestri and Patterson, 2016; Maestri *et al*., 2017), marine (Thrush *et al*., 2010) and freshwater environments (Pool *et al*., 2014; Maestri *et al*., 2017). Parasite organisms have received less attention, although they represent a substantial proportion of global biodiversity (Poulin and Morand, 2000). Parasites are good models to study beta-diversity patterns because their habitat can be easily and discretely defined as a set of exploited hosts. Differences in host species characteristics such as habitat, geographic distribution, diet and body size, will be reflected in the extent they are exposed to different parasite species (e.g. Fontenot and Font, 1996; Lile, 1998; Campião *et al*., 2015). Thus, each host individual is considered a habitat patch for colonization by any species within the local pool of parasite species, and sympatric host species can represent a natural experiment, where the analysis of their characteristics may explain the differences among their parasite communities.

Similarity between parasite communities can result from both historical and contemporary determinants (Poulin and Morand, 2000). A shared evolutionary history among host species contributes to the similarities in the composition of parasite communities. This may reflect conservatism of specific traits tracked by parasite species and may create phylogenetic congruences in species interactions. However, species present traits that are not preserved phylogenetically, such as aspects of host ecology that are shared among non-related hosts may also explain the absence of phylogenetic patterns. Phylogenetically conserved or not, traits are related to essential aspects of the host's natural history, such as the feeding and reproduction strategies and habitat use, these traits act as filters for the establishment of parasites. Each host trait can affect parasite species differently, resulting in differences among communities. Understanding the influence of these host traits is essential to direct studies beyond the pure number of parasite species towards a more inclusive approach.

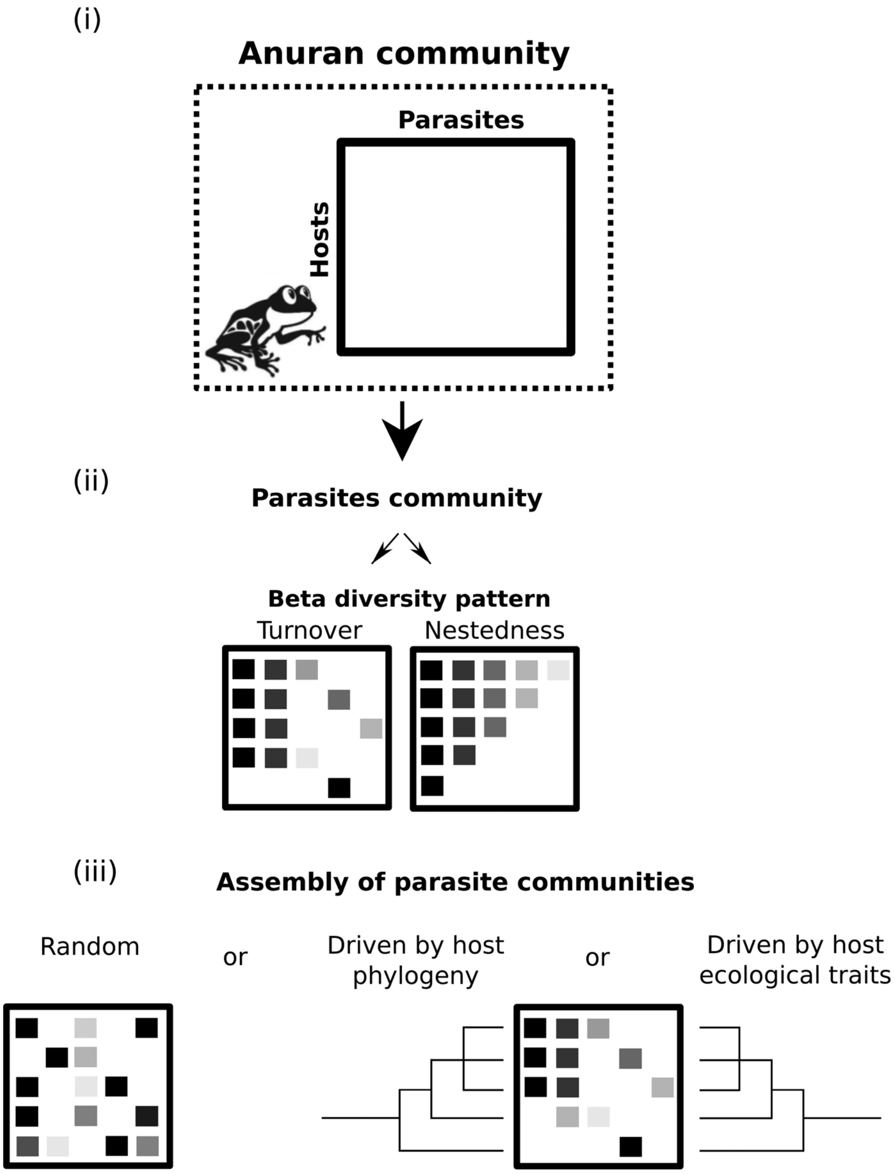

Fig. 1. Schematic representation of our study hypothesis, where we analysed the anuran host community (dotted box) and the local pool of parasite species: (i) each host species (lines) is a habitat patch for colonization by the local pool of parasite species (columns); (ii) there is a variation in the composition of parasite communities among host species, that can be partitioned into two components: turnover and nestedness; (iii) the dissimilarity in the composition of parasite communities among host species may be random or determined by the phylogenetic or functional dissimilarity of anurans host species.

In this study, we analysed the variation in the parasite communities (Fig. 1) by addressing the following questions: (i) What is the beta-diversity component (nestedness or turnover) that most contribute to beta diversity in parasite communities among anuran species? (ii) Does the beta diversity of parasite communities follow a non-random pattern? (iii) Is the dissimilarity in composition of parasite communities related to the phylogenetic or functional dissimilarity among hosts?

Materials and methods

Data on parasites and anuran host species composition

We compiled data on parasite species of anuran hosts from published surveys. All possible combinations with key-words 'amphibians', 'parasites', 'helminth' and 'Anura' were used to search for anuran-parasite empirical studies conducted from 1 January 1925 to 20 April 2020. These data were collected using online database platforms such as BioOne, Isi JSTOR, PubMed, SciELO, Scopus and Web of Science. We updated the amphibian's nomenclature according to Frost (2020). Parasite communities included species of the phyla Acanthocephala, Nematoda and Platyhelminthes (monogenean, digenean trematodes and monogenean). It is known that the composition of parasite species may be inaccurate for small samples (Poulin, 2007). Therefore, we used data from the surveys that (i) examined at least six individuals for each species of host, and (ii) at least six host species in each anuran community. Details on each selected study are given in Table 1 and Supplementary material S1.

Phylogenetic and functional variables

To analyse anuran communities, similarities among anuran species were considered in the phylogenetic and functional dimensions. The relatedness among anuran species in each community was analysed with the phylogeny proposed by Jetz and Pyron (2018) (Supplementary material S2). We calculated the phylogenetic species variability (PSV) of each anuran community by using the phylogenetic distance among the host species (Helmus *et al.*, 2007). PSV quantifies the decrease in phylogenetic relatedness according to similarities shared by all species in a community, regardless of the number of species (Helmus *et al.*, 2007). Values of PSV range from 0 to 1, where 1 indicates that the sampled species are maximally unrelated (overdispersed).

The ecological variation among anurans was described by four different traits that represent different aspects of their life history. We calculated the functional diversity (FD) considering anuran body size, type of habitat used and aspects of the reproductive behaviour. Anuran habitat was classified as terrestrial, arboreal, aquatic, cryptozoic, fossorial and rheophilic. The reproductive

Table 1. Description of the anuran host communities analysed.

Location	Latitude	Longitude	PSV host	FD host	*P*	Host species richness	Host sample size	Parasite species richness	Parasite sample size	Reference
ANC	−45.05	−23.75	0.76	1.11	0.33	8	194	8	2058	Aguiar *et al.* (2014)
CAS	−49.94	−9.36	0.17	0.63	0.98	6	107	8	363	Goldberg *et al.* (2009)
DIN	−22.60	−52.87	0.61	0.52	0.07	6	140	15	–	da Graça *et al.* (2017)
PAN	−56.65	−18.98	0.47	0.78	0.12	11	229	16	–	Campião *et al.* (2016)
PER	−35.19	−8.04	0.36	0.57	0.03	9	218	11	781	Martins-Sobrinho *et al.* (2017)
PAR	−45.31	−23.22	0.48	0.69	0.35	13	168	12	1422	Toledo *et al.* (2018)

Legend: Locations- ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; and PAR, Paraitinga. Description of the phylogenetic species variability (PSV) and functional diversity (FD) of hosts. *P* value refers to the observed functional diversity (FD) compared with random expectations.

behaviour was described based on the oviposition site for tadpole development, which can be aquatic with or without a nest, terrestrial with or without a nest (Haddad and Prado, 2005; Haddad *et al*., 2013; Crump, 2015) (Supplementary material S3). In addition to describing the FD of anuran communities, these characteristics reflect different levels of exposure to the parasitic infective stages and can act as filters in the assembly of parasite communities.

Data analyses

We tested whether the variables used to describe anuran communities were collinear by calculating pairwise differences between host species richness and PSV, and FD. For these comparisons, we used the Kruskal–Wallis test, once our data did not meet all assumptions of parametric tests.

Using the approach proposed by Baselga (2010, 2013*a*, *b*) we calculated total beta diversity (β) among host populations for each local community and then partitioned it into turnover and nestedness components. Total beta diversity is calculated by using the Sorensen dissimilarity measure (β_{SOR}), whereas the Simpson dissimilarity measure (β_{TUR}) calculates the turnover component; nestedness (β_{NES}) is calculated by subtracting total beta diversity and turnover (R Core Team, 2020). We used a resampling procedure computing 1000 random samples and calculated the average, standard deviation and *P* values for each local community (Baselga, 2017).

To test the relation between both phylogenetic and functional distances among host species and the similarity of their parasite communities we used a Mantel test (*r*) with the Spearman method. After that, for each location we generated 10 000 matrices to create a null sampling distribution of the Mantel statistic, and calculated a *Z*-score. This was calculated as $Z_{\text{score}} = [r_{\text{obs}} - \text{mean}(r_{\text{sim}})]/\sigma(r_{\text{sim}})$, where r_{obs} is the observed value of correlation and r_{sim} represents the values of correlation in the randomized matrices. We report correlation coefficients (*r*), *Z*-score and *P* value.

All statistical analyses were performed using R software (R Core Team, 2020), with the 'betapart' (Baselga *et al*., 2018), 'picante' (Kembel *et al*., 2010) and 'vegan' (Oksanen *et al*., 2019) packages. For all tests, we assumed significance of $P < 0.05$.

Results

Characterization of host communities

We found six studies on anuran communities that met the criteria for analyses. These communities were distributed in different ecosystems in Brazil, which included forested areas in the northern and southern Atlantic Forest (ANC – Anchieta, DIN – Diamante do Norte, PER – Pernambuco, PAR – Paraitinga), Cerrado areas – i.e. the Brazilian savanna (CAS – Caseara) and wetland areas (PAN – Pantanal) (Table 1). A total of 48 anuran species belonging to eight families were sampled: 22 species of Hylidae, 14 Leptodactylidae, three Bufonidae, three Microhylidae, two Brachycephalidae, one Craugastoridae, one Hemiphractidae, one Odontophrynidae and one Phyllomedusidae. The number of anuran species studied in each local community ranged from 6 to 13 (Table 1), and these communities varied in PSV and FD.

Anuran communities from CAS and DIN were the least diverse, with six anuran species and the lowest values of PSV and FD (Table 1). The anuran community in PAN had the highest species richness, but showed intermediate values of PSV and FD. The anuran community of ANC had the most diverse anuran community in the phylogenetic and functional dimensions, even though their taxonomic species richness was not the highest. There was no significant relationship between the observed PSV and species richness (Kruskal–Wallis chi-squared = 2.57, df = 3, *P* value = 0.46), neither between observed anuran FD and species richness (Kruskal–Wallis chi-squared = 3.71, df = 4, *P* value = 0.44).

Characterization of the parasite communities and their beta diversity

The six anuran communities comprised 54 helminth taxa and included four undetermined acanthocephalans, 37 nematodes and 12 platyhelminthes (11 digenetic trematodes and 1 monogenean). Parasite species richness was the highest in PAN, followed by DIN (Table 1). For all the parasite compound communities (all host species combined) the total beta diversities varied between 0.68 in PER and 0.90 in CAS (Table 2). The variation in the composition of the parasite among anurans for all the communities indicated the turnover (β_{TUR}) as the component with a greater contribution than nestedness (Table 2 and Fig. 2). The variation observed both in the total beta diversity and in its components did not differ from the respective null models (Table 2, $P > 0.05$ in all cases), except for the PER community, where the difference between the observed total parasite beta diversity and the null models was marginally significant (Table 2). In short, for all parasite communities, turnover contributes more to the observed beta diversity, and the differences in the parasite communities among anuran species did not differ from random distributions.

Relationship between parasite communities and host traits

To investigate deterministic factors that could drive parasite occurrence among hosts, we tested whether host phylogeny and

Table 2. Beta diversity of parasite communities in six communities of anuran hosts

			Null model		
Location	Beta diversity	Obs	Mean	SD	*P*
ANC	β_{SOR}	0.64	0.44	0.27	0.28
	β_{TUR}	0.44^{a}	0.25	0.34	0.36
	β_{NES}	0.20	0.18	0.15	0.43
CAS	β_{SOR}	0.70	0.23	0.23	0.32
	β_{TUR}	0.48^{a}	0.38	0.38	0.45
	β_{NES}	0.22	0.62	0.23	0.34
DIN	β_{SOR}	0.90	0.92	0.13	0.73
	β_{TUR}	0.84^{a}	0.85	0.27	0.73
	β_{NES}	0.06	0.06	0.15	0.20
PAN	β_{SOR}	0.88	0.79	0.23	0.51
	β_{TUR}	0.82^{a}	0.68	0.36	0.38
	β_{NES}	0.06	0.10	0.17	0.51
PER	β_{SOR}	0.68	0.38	0.17	0.06
	β_{TUR}	0.56^{a}	0.26	0.21	0.12
	β_{NES}	0.12	0.11	0.09	0.47
PAR	β_{SOR}	0.70	0.54	0.21	0.31
	β_{TUR}	0.38^{a}	0.12	0.23	0.18
	β_{NES}	0.32	0.42	0.28	0.59

Legend: Locations - ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; PAR, Paraitinga. β_{SOR}, stands for the overall beta diversity; β_{TUR}, for turnover; β_{NES}, for nestedness. Obs, refers toobserved. sd, refers to standard deviation. *P* value refers to the observed beta diversity (β) compared with random expectations.
[a]Major component.

life-history traits could be related to the variation in parasite community composition by comparing distance matrices. For most anuran communities, the dissimilarity in the composition of parasite communities did not relate to the phylogenetic or functional dissimilarity among anuran species (Table 3). However, for the anuran community from PAR, there was a significant correlation between parasite community dissimilarity and the phylogenetic distance among their hosts (Mantel statistic $r = 0.32$, $Z\text{-score} = 2.14$, $P = 0.01$).

Discussion

We described beta-diversity patterns in parasite communities and examined underlying factors that could drive the helminth parasite assemblages of anurans. Our analyses demonstrate that the turnover component had a greater contribution in the variation of the composition of parasite community among species of sympatric anurans. However, the beta-diversity pattern observed in parasite communities seems random, as it did not differ from the null model expectations. Also, the taxonomic dissimilarity among parasite communities was not related to the host PSV or host FD. We found only one anuran community with a significant correlation between the dissimilarity in the composition of the parasite communities and the phylogenetic among their hosts.

The turnover in parasite species, as we observed here, may reflect patterns of parasite species dispersion, and additionally, how these species recognize the available hosts as resources. Local environmental filters may have selected a very heterogeneous pool of host species, which, in addition to parasite resource specialization, may constrain the interactions. Indeed, helminth species have environmental tolerances that restrict their spatial distribution, and often specialize on a subset of available host species (Cooper *et al*., 2012). In other words, this pattern may be a result of the parasites tracking and exploiting specific resources within the available pool of hosts.

The pattern of parasite beta diversity observed in this study did not differ from that expected by null models, which assumes that species are ecologically equivalent (Hubbell, 2001; Ulrich and Gotelli, 2007). This non-differentiation indicates that the parasite species can be randomly assembled from the local pool to the communities analysed here. This pattern can occur when the abundance of species is the most important factor driving the association (Hubbell, 2001; Mouritsen and Poulin, 2002; Poulin, 2004). When a species is more abundant, it is more likely to colonize and establish itself in a new environment. Particularly, due to the low specificity observed in many species of parasites, being abundant would be enough for the establishment of the interaction. As we did not have data on the abundance of species, we suggest that this relationship needs to be verified in future studies. The random pattern in assemblies of parasites is commonly observed at local scales, in which species are probably more susceptible to stochastic factors (Korallo-Vinarskaya *et al*., 2013; Van Der Mescht *et al*., 2016). However, studies on larger scales may reveal a non-random pattern, describing the mechanisms we are searching for.

The composition of parasite communities was not related to the host PSV or host FD. Distantly related hosts can provide the same resource for parasites if this resource is any characteristic that evolved in parallel. In this case, the interaction can be mediated by factors such as contact opportunity. For example, two terrestrial frog species that are phylogenetically distant but share the same habitat would have similar parasite communities. This has been frequently observed in many host–parasite systems, including anurans, where we see the same parasite species associated with host species that are very distant phylogenetically (Aguiar *et al*., 2014; Campião *et al*., 2016). The commonness of these 'not expected' host–parasite associations confound predictions based on species phylogenies.

Anuran species have considerable diversity in ways of life (terrestrial, arboreal, aquatic, cryptozoic, fossorial and rheophilic), and may promote differential infection opportunity by several parasites. The similarities in the biological attributes of the hosts may predict similarity in the composition of their parasite communities. Thus, our results are surprising since we expected that the higher the phylogenetic and functional similarity among hosts, the lower the taxonomic dissimilarity in parasite species (Krasnov *et al*., 2012; Campião *et al*., 2015; Cuthill and Charleston, 2019).

A limitation in our study is that the anuran communities, as well as the phylogenetic and functional trees in each location, are not complete, as there were species present in the environment that were not studied, and could change the results if they had been included. In this sense, our findings could be affected by the reduced statistical power of small host sampling size in each community. Still, we were able to observe some congruences among communities in the different localities analysed. Moreover, studies on parasite communities, as those we analysed here, generally target the most common and abundant host species, and may therefore be helpful models to access community assembly patterns.

In summary, our study supports the idea that a parasite is likely to be tracking specific resources. This would indicate that the assembly of the parasite species depends on the type of resource that the parasite can use. The influence of host traits and evolutionary history on parasite community composition

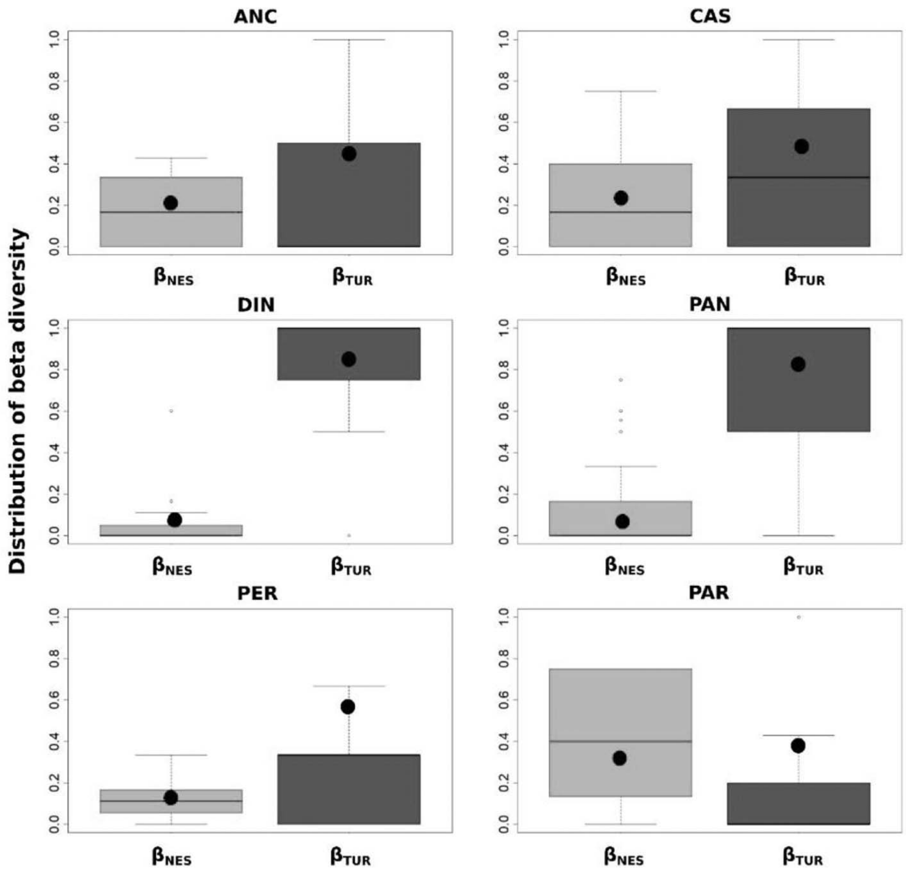

Fig. 2. Simulated and observed values of the two beta-diversity (β) components calculated for parasite communities of six communities of anuran hosts (Locations: ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; PAR, Paraitinga). The black dots represent the observed values and the boxplots show the null model distributions, where the light grey box is the nestedness component (β_{NES}) and the dark grey box is the turnover (β_{TUR}) component. The smaller grey dots correspond to the outliers, and the bars to the standard error of the null models.

Table 3. Results of Mantel tests used to test whether the taxonomic dissimilarity of parasite communities is more related to the phylogenetic or functional dissimilarity of the anuran hosts

Location	Correlation	Mantel statistic, *r*	Z_{score}	*P*
ANC	Taxonomic – phylogenetic	0.03	0.10	0.43
	Taxonomic – functional	−0.35	−1.38	0.91
CAS	Taxonomic – phylogenetic	−0.17	−0.59	0.68
	Taxonomic – functional	0.06	0.25	0.41
DIN	Taxonomic – phylogenetic	0.26	0.92	0.17
	Taxonomic – functional	0.05	0.20	0.45
PAN	Taxonomic – phylogenetic	−0.11	−0.85	0.80
	Taxonomic – functional	−0.04	−0.30	0.57
PER	Taxonomic – phylogenetic	0.24	0.99	0.17
	Taxonomic – functional	−0.09	−0.47	0.65
PAR	Taxonomic – phylogenetic	0.32	2.14	**0.01**
	Taxonomic – functional	0.27	1.85	**0.02**

Legend: Locations - ANC, Anchieta; CAS, Caseara; DIN, Diamante do Norte; PAN, Pantanal; PER, Pernambuco; PAR, Paraitinga. We report on the correlation coefficient (*r*), the Z_{score} of the comparison between the observed correlation and that of the null model, and the associated significant *P* (*P* value) for each location.

may be masked by other forces structuring communities, but most certainly influences community structure to some degree. Our study integrates different approaches from ecology and parasitology, and may also contribute to understanding the structure of parasites among populations of hosts in other antagonistic systems. The analysis of different dimensions of diversity, which is a tradition in the study of free-living organisms, has become an important baseline to the understanding of parasite assemblages, and in this sense our study adds data to this increasing body of evidence.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0031182020002061.

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Author contributions. Conceived and designed the experiments: EDB and KMC. Performed the experiments: EDB. Analysed the data: EDB and KMC. Wrote the paper: EDB and KMC.

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Conflict of interest. The authors declare that they have no conflict of interests.

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