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Commentary

Functional role of Small Mammals in protozoan transmission networks in Brazilian Biomes

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Abstract

Host-parasite associations are driven by complex ecological interactions that can be influenced by the parasite, the host, and the climatic conditions. Knowledge about the structures of host-parasite interaction networks is still incipient and studies mainly focused on the infracommunity levels. So, we conducted a systematic review using full-text articles to understand the relation between Brazilian small mammals and protozoan infections besides identify their functional roles in the network. We identified 4527 potentially relevant references and finally included 41 papers and considered 42 species of small mammals and 13 species of the protozoan. We found non-specificity of this relationship, with a modular network that is nestedness with low specialization values with most of the parasite and hosts occupying ultraperipheral or peripheral roles. Didelphids were homogeneously distributed among all modules, reinforcing the ancient relationship between this clade and the protozoan clade to spread infections. We also identify an isolated relation between the rodent *O. cleberi* and *T. dionisii*, a common bat protozoan highlighting that the environment and features of the parasites and hosts make these relationships more complex, and understanding these relationships can help to understand the dynamics of many infectious diseases.

Introduction

Parasitism is an ecological interaction that a host provides to another organism the nutrients and the physiological conditions required by the parasite reproduction and survival, a unilateral flow of energy resources (Levine, 1968). This relation must be approached as a host-parasite system, with a parasitic stage and a free-living stage (responsible to the infection on other hosts), that encompassing an extremely dynamic relationship with many points of stability and instability (Poulin and Morand, 2004). Parasite infection is not a random process, it is linked with several ecological features (Lindenfors et al., 2007; Hechinger and Lafferty, 2005).

Host-parasite associations are driven by complex ecological interactions that can be influenced by a variety of parasites (Daniels and Fish, 1990; Behnke et al., 2008), host (Jansen et al., 2018; Santos et al., 2019, 2021), climatic conditions (Jonas et al., 2015), intrinsic and extrinsic factors, such as host sex, age, study site, or study site (Bajer et al., 2014; Grzybek et al., 2015). Among these parasites, protozoan infections were traditionally studied as a dichotomous variable (i.e., individuals are classified as infected or uninfected) (Herrera et al., 2011; Nantes et al., 2021). An individual found infected is a host of a parasite, which may be part of a more complex reservoir system (Ashford, 1996), constitute not just a single mammal species, but a system that can include one or more host species responsible for the maintaining of the parasite in nature (Ashford, 1997; Roque and Jansen, 2014; Santos et al., 2019). Therefore, the detection of a parasite by molecular and/or serological tests is not enough to consider this species as a reservoir (Roque and Jansen, 2014).

Taking this in account, the knowledge about the structures of host-parasite interaction networks is still incipient, with studies mainly focused on the levels of the infracommunity (individual hosts) or component community (set of local infracommunities) (Poulin and Dick, 2007) one essential tool to describe the role in parasite maintenance and to be able to understand this host-parasite relationship in another level. Indeed, these host-parasite associations are generally more unstable than expected, resulting in complex association patterns (Jansen et al., 2018; Roque and Jansen, 2014). The possible explanations for these host changes are "ecological fitting", which comprises mechanisms that allow organisms to colonize and persist in new hosts (Janzen, 1985). These ecological approaches are fundamental to the study of infectious diseases, once that new host species can become new sources of infections. Through understanding the dynamics of biological cycles of parasites, we can gain a better knowledge of these dynamics (Johnson et al., 2015; Rynkiewicz et al., 2015; Seabloom et al., 2015). One tool that have been used to understand these interaction processes is network metrics, to describe the processes and understand the dynamics of these interactions (Santos et al., 2021). We elected small mammals group to start with because it acts as ecological links in many complex transmission chains of parasites and zoonotic diseases (Han et al., 2015) for they can be found in almost all types of habitat (i.e. arboreal, terrestrial, semi-aquatic, and semi-fossorial).

Different species can play different functional roles in the transmission of protozoan parasite networks between and within biomes. We hypothesize that most small mammals will maintain their functional and structural role in a biome-independent network because their biological characteristics remain constant regardless of habitat. With this analysis, we will focus on a general pattern for this relation between small mammals (host) and parasites. We used two distinct phylogenetic groups (i.e. Rodentia and Didelphimorphia), with similar ecological function and associating an environmental component (the biome). We also hope to identify some gaps in the studies of parasitology focused on small wild mammals.

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Materials and methods

Systematic Review: Relevant screening inclusion, and exclusion criteria

The systematic review was conducted according to Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Shamseer et al., 2015) to identify full-text articles reporting the occurrence of small mammals' infection for any parasite in the Brazilian Biome. The following databases were explored: (i) PubMed; (ii) SciELO; (iii) Jstor; (iv) Science Direct, (v) LILACS; and (vi) MEDLINE. We used the terms *Small Mammals*, *Amazon Forest*, *Cerrado*, *Atlantic Forest*, *Caatinga*, *Pampa*, and/or *Pantanal* and the combinations with *Parasite* and/or *Protozoan* applied in the title, abstract, and the keywords.

No restrictions were applied regarding language and date of publication (the last search was run on September 29, 2020). Duplicate references and reports outside Brazil were excluded. If the information of the abstract was not enough to assess the data, the full-text file of the publication was screened. The data was grouped according to: (i) year; (ii) latitude/ longitude; (iii) bioma; (iv) state; (v) city; (vi) species small mammals; (vii) abundance small mammals; (viii) prevalence small mammals' infection; (ix) species parasite; and (x) parasitic load. Reference information regarding the author's name and title were recorded in the data extraction file. We defined small mammals infected in any diagnosis method.

Network structure

The data collected through the systematic review were used to build a weighted incidence matrix of interactions (A×B), in which the lines correspond to the nodes hosts (i) and the columns to the nodes parasites (j). Each cell in the Aij matrix contained values of interaction frequencies, that is, the number of times that a species of host was reported parasitized by a species of parasite j. We describe the structure of the studied network using three network-level metrics as proposed by Queiroz et al. (2020). The complementary specialization (H2′) is a measure of niche divergence between species and varies between 0 and 1, higher values of $H2'$ indicate higher specialization (Blüthgen, 2010). Nestness is assessed using the WNODF metric, to describe the aggregate pattern of parasitic-host infections (few hosts have many parasites and most hosts have few species of parasites) (Almeida-Neto and Ulrich, 2011; Poulin and Dick, 2007), via a subset of interactions of species with more parasite descriptions. WNODF ranges from 0 (non-nested network) to 1 (perfectly nested network) (Beckett, 2016). Finally, we also tested a composite topology in the studied network-WNODA metric. A composite network can have a modular structure, but its modules can present a different type of internal structure, such as nesting with an aggregation pattern within the module (Queiroz et al., 2020). So, we calculated nestedness in the entire network, between its modules, and within its modules. A compound network is expected to show higher nestedness within its modules than between its modules and in the entire network. The significance of the network metrics was estimated through Monte Carlo procedures based on comparisons with randomized distributions generated with null models. We generated 1000 randomized matrices based on the original weighted matrix using the algorithm proposed by (Vázquez et al., 2007) and (Pinheiro et al., 2019). Network structure was considered to significantly deviate from the null model when $p<0.05$.

Species roles

To assess the relative importance of each host and parasite node to the network structure, we calculated a set of species-level metrics. The centrality of a species was first measured by the normalized degree (nk) — the proportion of parasites with which a given host species interact concerning the total number of potential parasites available on the network (Freeman, 1979). A host connected to a higher proportion of parasites is more influential in the structure and dynamics of its network (Martín González et al., 2010). We also calculated betweenness centrality (BC), that is, the proportion of shortest paths that pass through a node (Freeman, 1977). A species positioned between several pairs are assumed to contribute more to connecting different regions of the network (Mello et al., 2015). Finally, we quantified node specialization using Blüthgen's (d'), which measures the specialization of a node to a set of other nodes (Blüthgen, 2010; Mello et al., 2019).

The "ecological functional role" (Eltonian niche) of each species was assessed through its "network functional role" which classifies each node according to their position and importance in the network as (R1) "ultraperipheral vertices" with all interactions within their module, (R2) "peripheral vertices" with most interactions within their module, (R3) "non-hub connector vertices" with many interactions to other modules, (R4) "non-hub kinless vertices" with interactions evenly distributed among all modules, (R5) "provincial hubs" with most interactions within their module, (R6) "connector hubs" with many interactions to most of the other modules, and (R7) "kinless hubs" with interactions homogeneously distributed among all modules (Bezerra et al., 2012; Queiroz et al., 2020).

Influence of host biotic characteristics with network metrics

To assess what will be influencing the metrics at the species level of the hosts (normalized degree, betweenness centrality, specialization, and functional function) and modular structure, these species-level metrics were compared among the categories (habitats [Arboreal, Scansorial, Semi Aquatic, Semi Fossorial, and Terrestrial], order [Didelphimorphia and Rodentia] and diet [Frugivore, Frugivore/Omnivore, Herbivore, and Insectivore/Omnivore]) by adjusting generalized linear models (GLMs) (Queiroz et al., 2020). Significance was assessed using chi-square tests. The significance of the differences between pairs of metrics was assessed using t-tests after repetition. Networks were constructed with the packages `igraph` (Csardi and Nepusz, 2006) and the incidence matrix of host-parasite interaction with the package `Bipartite` (Dormann et al., 2008). All data were analyzed using R 3.5.0 (R Core Team, 2018). Due to unprecise identification of the host, we opted to do the analysis only those one which species is well defined in the study (genus identification were excluded).

Results

Systematic review

The search strategies were conducted by two of the investigators (F.M.S., N.Y.S.). We defined a search to identify all papers published on the chosen topic. We identified 4527 potentially relevant references and finally included 41 papers (Supplemental materials S1 and S2). Only original papers with a detailed methodology were retained; meta-analyses and systematic reviews were excluded, as they provide elements of other studies, and can be redundant by information. The 41 selected papers are presented in Tab. 1. We observed that the biome with the largest number of papers was the Atlantic Forest (n=10), followed by Cerrado (n=9), Pantanal (n=9), Caatinga (n=6), and Amazon (n=5). Three papers studied on two or more biomes (Amazon + Atlantic Forest + Caatinga + Cerrado + Pantanal [n=1] and Amazon + Atlantic Forest [n=1]). No paper was reported on Pampa (Tab. 1).

Network structure

We compiled a set of networks for different Brazilian biomes (except Pampa — because there is no data on infection by protozoa in small mammals) and a Complete Network (CN). Amazon showed the smallest biological richness for hosts (n=9) and protozoans (n=3) and the Cerrado biome showed the highest richness for the host (n=18) and protozoans (n=9). There were in total 42 species of small mammals of 30 genera (highlighting the genus *Thrichomys* with four species), and 13 species of protozoan of eight genera (highlighting the genus *Trypanosoma* with six species). The most widespread host species has been *Didelphis albiventris* and *Monodelphis domestica*, which occurred in four biomes, followed by *Gracilinanus agilis*, which occurred in three

Table 1 – Network-level metrics of parasites-host interaction in Brazilian biome.

	Amazon	Atlantic Forest	Caatinga	Cerrado	Pantanal	Full
Host (number of Hosts detected)	8	15	13	18	12	42
Parasite (number of Parasites detected)	3	8	3	9	6	18
Network's specialization	0.27	0.24	0.34	0.43	0.11	0.36*
Network's modularity	0.36	0.47	0.22	0.47	0.14	0.36*
Modules (number of Modules formed)	3	5	3	5	3	6
Network's nestedness	0.10	0.13	0.26	0.11	0.43	0.21
The network shows the following scores of nestedness:						
Entire network	0.24	0.14	0.34	0.18	0.67	0.27*
Between the modules	0.21	0.11	0.25	0.09	0.63	0.22*
Within the modules	0.31	0.23	0.56	0.56	0.79	0.61*

*$p<0.05$

biomes. Among protozoans, the most widespread species, *Trypanosoma cruzi* and *Leishmania braziliensis* occurred in five and three biomes, respectively.

Only the CN presented significant values ($p<0.01$), showing specialization in the interactions ($H2'=0.36$, Z=2.74405, $p=0.003$), although not too high (value ranging from 0–1, where higher values of $H2'$ indicate higher specialization). Our data show a modular pattern organized into six subgroups (Qw modularity=0.36, Z=3.12193, $p=0.004$). Although, in the modules there is an aggregation pattern (network's nestedness), where the nesting within modules was almost three times larger (WNODA=0.61) then between modules (WNODA=0.22) and across the entire network (WNODA=0.27) (Tab. 1, Fig. 1).

Species roles

Most species of host occupied ultra-peripheral or peripheral roles (R1 [n=13] or R2 [n=21], 84%). Six species (*Akodon cursor*, *Clyomys laticeps*, *Didelphis albiventris*, *Marmosa demerarae*, *Monodelphis domestica*, and *Oligoryzomys nigripes*) were non-hub connector vertices, with many interactions to other modules. And the most important host species, *Gracilinanus agilis*, was assigned to R7 (kinless hubs). Among of parasites, most species also occupied ultra-peripheral or peripheral roles (R1 [n=10] or R2 [n=5], 84%). The three remaining species were classified as non-hub connector vertices (*Leishmania braziliensis*, *Toxoplasma gondii*, and *T. cruzi*) (Tab. 2; Fig. 1).

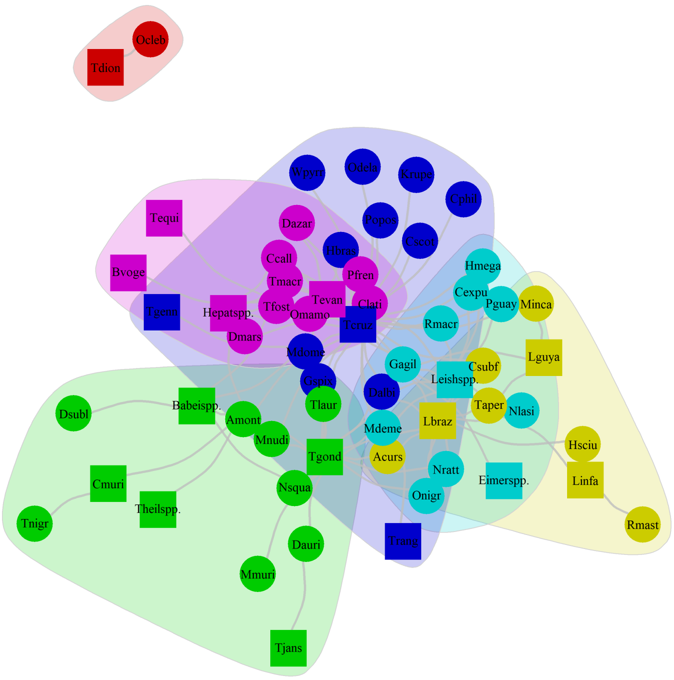

Figure 1 – Host-parasite networks of the interactions between small mammals (circles) and Protozoan parasites (square), using presence of parasite species in each host species. Color polygons around groups of nodes represent the interaction modules identified with the Beckett modularity detection algorithm.

Influence of host biotic characteristics with network metrics

We did not observe any relationship between the biological features of the hosts and the species level metrics and modular structure. The host species with the highest normalized degree values were *Gracilinanus agilis* (*nk*=0.39), *Akodon montensis* (*nk*=0.33), and *Thrichomys fosteri* (*nk*=0.33); and betweenness centrality were *G. agilis* (BC=0.29), *Monodelphis domestica* (BC=0.23), and *Didelphis albiventris* (BC = 0.21). Among the parasite, the highest normalized degree values were *Trypanosoma cruzi* (*nk*=0.73), *Toxoplasma gondii* (*nk*=0.30), and *Leishmania* spp. (*nk*=0.25); and betweenness centrality were *T. cruzi* (BC=0.65), *T. gondii* (BC=0.20), and *Trypanosoma evansi* (BC=0.10). The species of host and parasite with the highest specialization value was *Oecomys cleberi* (d'=1), which showed infection only *Trypanosoma dionisii* (d'=1), a parasite described only in this host.

Discussion

We found a modular network with a nested profile between modules only in the Complete Network. We found no significant values when analyze the biome networks separately. The network specialization values were very low with most of the parasite and hosts occupying ultraperipheral or peripheral roles (Lewinsohn et al., 2006), showing the non-specificity of this relationship that can also be found in mutualistic networks (Fortuna et al., 2010; Mello et al., 2011). This relatively high proportion of vertices with few connections may be related to a free-scale (power law) or large-scale (truncated power-law) (Barabási, 2009) distribution of interactions also found in mutualistic networks (Barabási, 2009; Jordano et al., 2003).

The gracile mouse opossum (*G. agilis*) was the only species host that connect various transmission cycles, for its assign to kinless hubs with interactions evenly distributed among all modules. Hubs are important elements in many types of complex networks (Albert and Barabási, 2000; Costa, 2004), including ecological ones (Martín González et al., 2010). As in facultative mutualism networks, species with few interactions tend to be preferentially connected to species with many interactions (Bascompte et al., 2003), the loss of hubs compared to non-hubs can lead to a greater number of secondary losses (Memmott et al., 2004). Guimerà and Amaral (2005) found that the loss of connectors can lead to major changes in the network structure, for example, fragmentation, especially in modular networks. One consequence is an ecological and evolutionary separation of subgroups, as the transmission of information throughout the system becomes more difficult of interactions (Guimarães et al., 2007). Only three species of parasites (*L. braziliensis*, *T. gondii* and *T. cruzi*) and six hosts (*Akodon cursor*, *Clyomys laticeps*, *Didelphis albiventris*, *Marmosa demerarae*, *Monodelphis do-*

Table 2 – Species-level metrics and network functional role of parasites-host interaction in Brazilian biomes.

Species	Abbreviation	Vertice Type	nk	BC	p	Network functional role	Biome
Gracilinanus agilis	Gagil	Host	0.39	0.29	0.09	kinless hub	Caatinga, Cerrado and Pantanal
Monodelphis domestica	Mdome	Host	0.28	0.23	0.14	non-hub connector vertex	Atlantic Forest, Caatinga, Cerrado and Pantanal
Didelphis albiventris	Dalbi	Host	0.28	0.21	0.19	non-hub connector vertex	Amazon, Atlantic Forest, Caatinga and Cerrado
Clyomys laticeps	Clati	Host	0.17	0.03	0.17	non-hub connector vertex	Cerrado and Pantanal
Akodon cursor	Acurs	Host	0.17	0	0.16	non-hub connector vertex	Atlantic Forest, Caatinga and Cerrado
Marmosa demerarae	Mdeme	Host	0.17	0	0.10	non-hub connector vertex	Amazon and Atlantic Forest
Oligoryzomys nigripes	Onigr	Host	0.17	0	0.23	non-hub connector vertex	Atlantic Forest and Cerrado
Akodon montensis	Amont	Host	0.33	0.13	0.35	peripheral vertex	Atlantic Forest and Cerrado
Thrichomys apereoides	Taper	Host	0.22	0.06	0.42	peripheral vertex	Caatinga and Cerrado
Oecomys mamorae	Omamo	Host	0.17	0.04	0.18	peripheral vertex	Pantanal
Thrichomys fosteri	Tfost	Host	0.33	0.02	0.22	peripheral vertex	Pantanal
Nectomys squamipes	Nsqua	Host	0.11	0	0.45	peripheral vertex	Atlantic Forest and Caatinga
Calomys callosus	Ccall	Host	0.17	0	0.07	peripheral vertex	Pantanal
Thylamys macrurus	Tmacr	Host	0.17	0	0.07	peripheral vertex	Pantanal
Calomys expulsus	Cexpu	Host	0.11	0	0.11	peripheral vertex	Cerrado
Cerradomys subflavus	Csubf	Host	0.11	0	0.21	peripheral vertex	Atlantic Forest and Cerrado
Dasyprocta azarae	Dazar	Host	0.11	0	0.06	peripheral vertex	Amazon and Pantanal
Didelphis marsupialis	Dmars	Host	0.11	0	0.36	peripheral vertex	Amazon
Galea spixii	Gspix	Host	0.11	0	0.08	peripheral vertex	Caatinga
Holochilus brasiliensis	Hbras	Host	0.11	0	0.05	peripheral vertex	Pantanal
Hylaeamys megacephalus	Hmega	Host	0.11	0	0.11	peripheral vertex	Amazon
Marmosops incanus	Minca	Host	0.11	0	0.45	peripheral vertex	Cerrado
Metachirus nudicaudatus	Mnudi	Host	0.11	0	0.10	peripheral vertex	Amazon and Atlantic Forest
Necromys lasiurus	Nlasi	Host	0.11	0	0.48	peripheral vertex	Caatinga and Cerrado
Nectomys rattus	Nratt	Host	0.11	0	0.36	peripheral vertex	Atlantic Forest and Cerrado
Philander frenatus	Pfren	Host	0.11	0	0.12	peripheral vertex	Pantanal
Proechimys guayannensis	Pguay	Host	0.11	0	0.11	peripheral vertex	Amazon
Rhipidomys macrurus	Rmacr	Host	0.11	0	0.16	peripheral vertex	Caatinga and Cerrado
Thrichomys laurentinus	Tlaur	Host	0.11	0	0.14	peripheral vertex	Atlantic Forest and Caatinga
Didelphis aurita	Dauri	Host	0.11	0	0.63	ultraperipheral vertex	Atlantic Forest
Caluromys philander	Cphil	Host	0.06	0	0.00	ultraperipheral vertex	Cerrado
Cerradomys scotti	Cscot	Host	0.06	0	0.08	ultraperipheral vertex	Pantanal
Delomys sublineatus	Dsubl	Host	0.06	0	0.65	ultraperipheral vertex	Atlantic Forest
Holochilus sciureus	Hsciu	Host	0.06	0	0.34	ultraperipheral vertex	Caatinga
Kerodon rupestris	Krupe	Host	0.06	0	0.00	ultraperipheral vertex	Caatinga
Marmosa murina	Mmuri	Host	0.06	0	0.34	ultraperipheral vertex	Atlantic Forest
Oecomys cleberi	Ocleb	Host	0.06	0	1.00	ultraperipheral vertex	Cerrado
Oxymycterus delator	Odela	Host	0.06	0	0.00	ultraperipheral vertex	Cerrado
Philander opossum	Popos	Host	0.06	0	0.08	ultraperipheral vertex	Amazon
Rhipidomys mastacalis	Rmast	Host	0.06	0	0.84	ultraperipheral vertex	Cerrado
Thaptomys nigrita	Tnigr	Host	0.06	0	0.85	ultraperipheral vertex	Atlantic Forest
Wiedomys pyrrhorhinos	Wpyrr	Host	0.06	0	0.00	ultraperipheral vertex	Caatinga
Trypanosoma cruzi	Tcruz	Parasite	0.73	0.65	0.16	non-hub connector vertex	Amazon, Atlantic Forest, Caatinga, Cerrado and Pantanal
Toxoplasma gondii	Tgond	Parasite	0.30	0.2	0.45	non-hub connector vertex	Atlantic Forest and Caatinga
Leishmania sp.	Leishspp.	Parasite	0.25	0	0.51	peripheral vertex	Amazon and Cerrado
Trypanosoma evansi	Tevan	Parasite	0.23	0.1	0.39	peripheral vertex	Pantanal
Leishmania braziliensis	Lbraz	Parasite	0.23	0.05	0.49	non-hub connector vertex	Atlantic Forest, Caatinga and Cerrado
Hepatozoon sp.	Hepatspp.	Parasite	0.14	0	0.37	peripheral vertex	Amazon, Atlantic Forest and Pantanal
Babesia sp.	Babeispp.	Parasite	0.11	0	0.41	peripheral vertex	Atlantic Forest and Pantanal
Leishmania guyanensis	Lguya	Parasite	0.07	0	0.53	peripheral vertex	Cerrado
Cryptosporidium muris	Cmuri	Parasite	0.05	0	0.65	ultraperipheral vertex	Atlantic Forest
Leishmania infantum	Linfa	Parasite	0.05	0	0.74	ultraperipheral vertex	Cerrado
Babesia vogeli	Bvoge	Parasite	0.02	0	0.01	ultraperipheral vertex	Pantanal
Theleria equi	Tequi	Parasite	0.02	0	0.01	ultraperipheral vertex	Pantanal
Trypanosoma gennarii	Tgenn	Parasite	0.02	0	0.06	ultraperipheral vertex	Cerrado
Trypanosoma rangeli	Trang	Parasite	0.02	0	0.07	ultraperipheral vertex	Cerrado
Eimeria sp.	Eimerspp.	Parasite	0.02	0	0.00	ultraperipheral vertex	Cerrado
Theileria sp.	Theilspp.	Parasite	0.02	0	0.31	ultraperipheral vertex	Atlantic Forest
Trypanosoma janseni	Tjans	Parasite	0.02	0	0.49	ultraperipheral vertex	Atlantic Forest
Trypanosoma dionisii	Tdion	Parasite	0.02	0	1.00	ultraperipheral vertex	Cerrado

mestica and *Oligoryzomys nigripes*) were classified as non-hub connector vertices with many interactions with other modules, these biological characteristics demonstrate that these parasites are distributed infecting a wide range of hosts, multi-host parasites, and the hosts have an importance in the maintenance of several species of parasites. We did not observe any relationship between the biological features of the hosts and the metrics at the species level and modular structure. But small mammals play an important role in the life cycle of several parasites as definitive hosts, but also can be paratenic host, connecting the parasite with the final host as in *T. gondii* infection. After getting infected in the environment for the ingestion of sporulate oocysts (Horta et al., 2018), the small mammal can act as one of the main sources of infection of domestic and wild cats through the trophic network (Dubey, 2010; Gennari et al., 2015).

An isolated duo of host-parasite was *Oecomys cleberi* (d'=1), that showed infection only by *Trypanosoma dionisii* (d'=1) and vice-versa (this parasite was described only in this host), highlighting as the highest specialization value in the complete network. It is interesting to note that the only protozoan infection that this arboreal rodent show is *T. dionisii*, a species known for its strong relationship with bats (Austen et al., 2020; Dario et al., 2017b; Gardner and Molyneux, 1988; Santos et al., 2019; Wang et al., 2019). Although the vector of *T. dionisii* is unknown, Gardner and Molyneux (1988) reported experimental infection in arthropods of the Cimicidae family, and Dario et al. (2017a) observed *Triatoma vitticeps* infected by *T. dionisii*. Thus, this infection of rodents by *T. dionisii* may be related to the feeding of these infected arthropods (Demoner et al., 2019). Taking this into account, a possible form of infection of this rodent may be occurring due to its ecological features (Camargo et al., 2016; Paglia et al., 2012). This arboreal habitat may be favoring a possible sharing of a habitat with possible vectors related to bat infections. Also, several studies have been described small mammals as important reservoirs of different trypanosomatids such as *T. cruzi* and *Leishmania* spp. and showed the importance of these hosts in maintaining the sylvatic cycle of these groups (Brandão et al., 2019; Herrera et al., 2011; Jansen et al., 2018; Lopes et al., 2018; Santos et al., 2021; Quaresma et al., 2011; Santos et al., 2019; Tonelli et al., 2017). Besides that, our data show a low number of species with high specialization indices (d') — indicating that most observed hosts are generalists, infected by more than one species of parasite — which provided us with a less specialized interaction network (Blüthgen, 2010; Blüthgen et al., 2006).

The most prominent positions in the network belong to the following didelphids:*G. agilis*, *M. domestica* and *D. albiventris* for the high values of normality and centrality. Didelphimorphia is considered to be one of the oldest hosts for Trypanosomatidae and is considered as bioaccumulators (Jansen et al., 2018; Lopes et al., 2018; Santos et al., 2021; Roque and Jansen, 2014). The scansorial habitat could favor this position in some environments (Lammers et al., 2006; Sano et al., 2021), once that this ability to go in multiple vertical strata increases the chance of vector encounters. We highlight here the didelphids host *G. agilis* for presenting high normality and centrality values in addition to having a functional role of kinless hubs with interactions homogeneously distributed among all modules. In addition, *G. agilis* selects positively hemipteran arthropod in its diet (de Camargo et al., 2014) that can influence protozoan infection via a trophic transmission (Herrera et al., 2011).

Despite the extensive literature review that was performed using the six main bibliographic databases (we identified 4527 potentially relevant references and finally included 41 articles), some underreporting of our study may be occurring. Our result reveals a bias towards protozoa of importance in human health (*L. braziliensis*, *T. cruzi* and *T. gondii*) which consequently have a greater financial support. This does not reflect the diversity of parasites that infect these groups of hosts, but aware us about this gap. Despite the contrast between hosts/protozoan more and less explored, our results may show important aspects of the interactions between small mammals and parasites that are essential for Brazilian biodiversity.

The host-parasite network between small mammals and protozoa shows difference only when we disregard biome characteristics by showing a modular pattern. This can be reinforced by the fact that widespread host species are the most important hubs in this network, like *G. agilis* and *D. albiventris*. But inside the modules are aggregation pattern inside the modules, where few hosts are more connected with parasites and many hosts occupying ultraperipheral or peripheral roles. Understanding infection pattern are essential because host-parasite relationships are complex involving several roles (e.g. final host, paratenic host, vector and parasite), and understanding these relationships can help to prevent many infectious diseases.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

S1 Coordinates of samples used in the analysis.

S2 Geographic distribution of data collection and references.