

**Title page**

Protozoan diversity in small mammals' network - a systematic review

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**Running title: Protozoan diversity in Small Mammals network****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.

**Keywords:** Didelphimorphia, Rodentia, Parasite, Host, Host-Parasite Interaction,

**Introduction**

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

34 Host-parasite associations are driven by complex ecological interactions that can be influenced by  
35 a variety of parasites (Daniels and Fish, 1990; Behnke et al., 2008), host (Jansen et al., 2018; Santos et al.,  
36 2019, 2021), climatic conditions (Jonas et al., 2015), intrinsic and extrinsic factors, such as host sex, age,  
37 study site, or study site (Bajer et al., 2014; Grzybek et al., 2014). Among these parasites, protozoan  
38 infections were traditionally studied as a dichotomous variable (i.e., individuals are classified as infected  
39 or uninfected) (Herrera et al., 2011; Nantes et al., 2021). An individual found infected is a host of a parasite,  
40 which may be part of a more complex reservoir system(Ashford, 1996),constitute not just a single mammal  
41 species, but a system that can include one or more host species responsible for the maintaining of the  
42 parasite in nature (Ashford, 1997; Roque and Jansen, 2014; Santos et al., 2019). Therefore, the detection of  
43 a parasite by molecular and/or serological tests is not enough to consider this species as a reservoir (Roque  
44 and Jansen, 2014).

45 Taking this in account, the knowledge about the structures of host-parasite interaction networks is  
46 still incipient, with studies mainly focused on the levels of the infracommunity (individual hosts) or  
47 component community (set of local infracommunities) (Poulin and Dick, 2007). Understanding these  
48 complex transmission networks one essential tool to describe the role in parasite maintenance and to be  
49 able to understand this host-parasite relationship in another level. Indeed, these host-parasite associations  
50 are generally more unstable than expected, resulting in complex association patterns (Jansen et al., 2018;  
51 Roque and Jansen, 2014). The possible explanations for these host changes are 'ecological fitting', which  
52 comprises mechanisms that allow organisms to colonize and persist in new hosts (Janzen 1985). These  
53 ecological approaches are fundamental to the study of infectious diseases, once that new host species can  
54 become new sources of infections. Through understanding the dynamics of biological cycles of parasites,  
55 we can gain a better knowledge of these dynamics (Johnson et al., 2015; Rynkiewicz et al., 2015; Seabloom  
56 et al., 2015). One tool that have been used to understand these interaction processes is network metrics, to

58 describe the processes and understand the dynamics of these interactions (Santos et al., 2021). We elected  
59 small mammals group to start with because it acts as ecological links in many complex transmission chains  
60 of parasites and zoonotic diseases (Han et al., 2015) for they can be found in almost all types of habitat (i.e.  
61 arboreal, terrestrial, semi-aquatic, and semi-fossorial). Different species can play different functional roles  
62 in the transmission of protozoan parasite networks between and within biomes. We hypothesize that most  
63 small mammals will maintain their functional and structural role in a biome-independent network because  
64 their biological characteristics remain constant regardless of habitat. With this analysis, we will focus on a  
65 general pattern for this relation between small mammals (host) and parasites. We used two distinct  
66 phylogenetic groups (i.e. Rodentia and Didelphimorphia), with similar ecological function and associating  
67 an environmental component (the biome). We also hope to identify some gaps in the studies of parasitology  
68 focused on small wild mammals.

## 69 **Materials and methods**

### 70 **Systematic Review: Relevant screening, inclusion, and exclusion criteria**

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

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

### 85 **Network structure**

87 The data collected through the systematic review were used to build a weighted incidence matrix of  
88 interactions ( $A \times B$ ), in which the lines correspond to the nodes hosts (i) and the columns to the nodes  
89 parasites (j). Each cell in the  $A_{ij}$  matrix contained values of interaction frequencies, that is, the number of  
90 times that a species of host was reported parasitized by a species of parasite j. We describe the structure of  
91 the studied network using three network-level metrics as proposed by Queiroz et al. (2020). The  
92 complementary specialization ( $H_2'$ ) is a measure of niche divergence between species and varies between  
93 0 and 1, higher values of  $H_2'$  indicate higher specialization (Blüthgen, 2010). Nestness is assessed using  
94 the WNODF metric, to describe the aggregate pattern of parasitic-host infections (few hosts have many  
95 parasites and most hosts have few species of parasites) (Almeida-Neto and Ulrich, 2011; Poulin and Dick  
96 2007), via a subset of interactions of species with more parasite descriptions. WNODF ranges from 0 (non-  
97 nested network) to 1 (perfectly nested network) (Beckett, 2016). Finally, we also tested a composite  
98 topology in the studied network -WNODA metric. A composite network can have a modular structure, but  
99 its modules can present a different type of internal structure, such as nesting with an aggregation pattern  
100 within the module (Queiroz et al., 2020). So, we calculated nestedness in the entire network, between its  
101 modules, and within its modules. A compound network is expected to show higher nestedness within its  
102 modules than between its modules and in the entire network. The significance of the network metrics was  
103 estimated through Monte Carlo procedures based on comparisons with randomized distributions generated  
104 with null models. We generated 1,000 randomized matrices based on the original weighted matrix using  
105 the algorithm proposed by (Vázquez et al., 2007) and (Pinheiro et al., 2019). Network structure was  
106 considered to significantly deviate from the null model when  $p < 0.05$ .

### 107 **Species roles**

108 To assess the relative importance of each host and parasite node to the network structure, we  
109 calculated a set of species-level metrics.. The centrality of a species was first measured by the normalized  
110 degree ( $n_k$ ) – the proportion of parasites with which a given host species interact concerning the total  
111 number of potential parasites available on the network (Freeman, 1979). A host connected to a higher  
112 proportion of parasites is more influential in the structure and dynamics of its network (Martín González et  
113 al., 2010). We also calculated betweenness centrality (BC), that is, the proportion of shortest paths that pass  
114 through a node (Freeman, 1977). A species positioned between several pairs are assumed to contribute  
115 more to connecting different regions of the network (Mello et al., 2015). Finally, we quantified node

117 specialization using Blüthgen's  $d'$  ( $d'$ ), which measures the specialization of a node to a set of other nodes  
118 (Blüthgen, 2010; Mello et al., 2019).

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

### 127 **Influence of host biotic characteristics with network metrics**

128 To assess what will be influencing the metrics at the species level of the hosts (normalized degree,  
129 betweenness centrality, specialization, and functional function) and modular structure, these species-level  
130 metrics were compared among the categories (habitats [Arboreal, Scansorial, Semi Aquatic, Semi Fossorial,  
131 and Terrestrial], order [Didelphimorphia and Rodentia] and diet [Frugivore, Frugivore/Omnivore,  
132 Herbivore, and Insectivore/Omnivore]) by adjusting generalized linear models (GLMs) (Queiroz et al.,  
133 2020). Significance was assessed using chi-square tests. The significance of the differences between pairs  
134 of metrics was assessed using t-tests after repetition. Networks were constructed with the packages 'igraph'  
135 (Csardi and Nepusz, 2006) and the incidence matrix of host-parasite interaction with the package 'Bipartite'  
136 (Dormann et al., 2021). All data were analyzed using R 3.5.0 (Team R Development Core, 2018). Due to  
137 unprecise identification of the host, we opted to do the analysis only those one which species is well defined  
138 in the study (genus identification were excluded).

## 139 **Results**

### 140 **Systematic Review**

141 The search strategies were conducted by two of the investigators (F.M.S., N.Y.S.). We defined a  
142 search to identify all papers published on the chosen topic. We identified 4527 potentially relevant  
143 references and finally included 41 papers (Supplementary material 1 and 2). Only original papers with a  
144 detailed methodology were retained; meta-analyses and systematic reviews were excluded, as they provide  
145 elements of other studies, and can be redundant by information. The 41 selected papers are presented in  
146

147 Table 1. We observed that the biome with the largest number of papers was the Atlantic Forest (n=10),  
148 followed by Cerrado (n=09), Pantanal (n=09), Caatinga (n=06), and Amazon (n=05). Three papers studied  
149 on two or more biomes (Amazon + Atlantic Forest + Caatinga + Cerrado + Pantanal [n=01] and Amazon  
150 + Atlantic Forest [n=01]). No paper was reported on Pampa (Table 1).

### 151 **Network structure**

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

161 Only the CN presented significant values ( $p < 0.01$ ), showing specialization in the interactions ( $H2'$   
162 = 0.36,  $Z = 2.74405$ ,  $p = 0.003$ ), although not too high (value ranging from 0 – 1, where higher values of  
163  $H2'$  indicate higher specialization). Our data show a modular pattern organized into six subgroups (Qw  
164 modularity = 0.36,  $Z = 3.12193$ ,  $p = 0.004$ ). Although, in the modules there is an aggregation pattern  
165 (network's nestedness), where the nesting within modules was almost three times larger (WNODA = 0.61)  
166 then between modules (WNODA = 0.22) and across the entire network (WNODA = 0.27) (Table 1) (Figure  
167 1).

### 168 **Species roles**

169 Most species of host occupied ultra-peripheral or peripheral roles (R1 [n=13] or R2 [n=21], 84%).  
170 Six species (*Akodon cursor*, *Clyomys laticeps*, *Didelphis albiventris*, *Marmosa demerarae*, *Monodelphis*  
171 *domestica*, and *Oligoryzomys nigripes*) were non-hub connector vertices, with many interactions to other  
172 modules. And the most important host species, *Gracilinanus agilis*, was assigned to R7 (kinless hubs).  
173 Among of parasites, most species also occupied ultra-peripheral or peripheral roles (R1 [n = 10] or R2  
174 [n=05], 84%). The three remaining species were classified as non-hub connector vertices (*Leishmania*  
175 *braziliensis*, *Toxoplasma gondii*, and *T. cruzi*) (Table 2; Figure 1).

### 176 **Influence of host biotic characteristics with network metrics**

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

## 187 Discussion

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

196 The gracile mouse opossum (*G. agilis*) was the only species host that connect various transmission  
197 cycles, for its assign to kinless hubs with interactions evenly distributed among all modules. Hubs are  
198 important elements in many types of complex networks (Albert and Barabási, 2000; Costa, 2004), including  
199 ecological ones (Martín González et al., 2010). As in facultative mutualism networks, species with few  
200 interactions tend to be preferentially connected to species with many interactions (Bascompte et al., 2003),  
201 the loss of hubs compared to non-hubs can lead to a greater number of secondary losses (Memmott et al.,  
202 2004). Guimerà and Amaral (2005) found that the loss of connectors can lead to major changes in the  
203 network structure, for example, fragmentation, especially in modular networks. One consequence is an  
204 ecological and evolutionary separation of subgroups, as the transmission of information throughout the  
205 system becomes more difficult of interactions (Guimarães et al., 2007).

207 Only three species of parasites (*L. braziliensis*, *T. gondii*, and *T. cruzi*) and six hosts (*Akodon cursor*,  
208 *Clyomys laticeps*, *Didelphis albiventris*, *Marmosa demerarae*, *Monodelphis domestica*, and *Oligoryzomys*  
209 *nigripes*) were classified as non-hub connector vertices with many interactions with other modules, these  
210 biological characteristics demonstrate that these parasites are distributed infecting a wide range of hosts,  
211 multi-host parasites, and the hosts have an importance in the maintenance of several species of parasites.  
212 We did not observe any relationship between the biological features of the hosts and the metrics at the  
213 species level and modular structure. But small mammals play an important role in the life cycle of several  
214 parasites as definitive hosts, but also can be paratenic host, connecting the parasite with the final host as in  
215 *T. gondii* infection. After getting infected in the environment for the ingestion of sporulate oocysts (Horta  
216 et al., 2018), the small mammal can act as one of the main sources of infection of domestic and wild cats  
217 through the trophic network (Dubey, 2010; Gennari et al., 2015).

218 An isolated duo of host-parasite was *Oecomys cleberi* ( $d' = 1$ ), that showed infection only by  
219 *Trypanosoma dionisii* ( $d' = 1$ ) and vice-versa (this parasite was described only in this host), highlighting as  
220 the highest specialization value in the complete network. It is interesting to note that the only protozoan  
221 infection that this arboreal rodent show is *T. dionisii*, a species known for its strong relationship with bats  
222 (Austen et al., 2020; Dario et al., 2017b; Gardner and Molyneux, 1988; Santos et al., 2019; Wang et al.,  
223 2019). Although the vector of *T. dionisii* is unknown, Gardner and Molyneux (1988) reported experimental  
224 infection in arthropods of the Cimicidae family, and Dario et al. (2017a) observed *Triatoma vitticeps*  
225 infected by *T. dionisii*. Thus, this infection of rodents by *T. dionisii* may be related to the feeding of these  
226 infected arthropods (Demoner et al., 2019). Taking this into account, a possible form of infection of this  
227 rodent may be occurring due to its ecological features (Camargo et al., 2016; Paglia et al., 2012). This  
228 arboreal habitat may be favoring a possible sharing of a habitat with possible vectors related to bat  
229 infections. Also, several studies have been described small mammals as important reservoirs of different  
230 trypanosomatids such as *T. cruzi* and *Leishmania* spp. and showed the importance of these hosts in  
231 maintaining the sylvatic cycle of these groups (Brandão et al., 2019; Herrera et al., 2011; Jansen et al.,  
232 2018; Lopes et al., 2018; Nantes et al., 2021; Quaresma et al., 2011; Santos et al., 2019; Tonelli et al.,  
233 2017). Besides that, our data show a low number of species with high specialization indices ( $d'$ ) - indicating  
234 that most observed hosts are generalists, infected by more than one species of parasite - which provided us  
235 with a less specialized interaction network (Blüthgen, 2010; Blüthgen et al., 2006).



237 The most prominent positions in the network belong to the following didelphids: *G. agilis*, *M.*  
238 *domestica* and *D. albiventris* for the high values of normality and centrality. Didelphimorphia is considered  
239 to be one of the oldest hosts for Trypanosomatidae and is considered as bioaccumulators (Jansen et al.,  
240 2018; Lopes et al., 2018; Nantes et al., 2021; Roque and Jansen, 2014). The scansorial habitat also could  
241 favor this position in some environments (Lammers et al., 2006; Sano et al., 2021), once that this ability to  
242 go in multiples vertical strata increases the chance of vector encounters. We highlight here the didelphids  
243 host *G. agilis* for presenting high normality and centrality values in addition to having a functional role of  
244 kinless hubs with interactions homogeneously distributed among all modules. In addition, *G. agilis* select  
245 positively hemipteran arthropod in its diet (de Camargo et al., 2014) that can influence protozoan infection  
246 via a trophic transmission (Herrera et al., 2011).

247 Despite the extensive literature review that was performed using the six main bibliographic  
248 databases (we identified 4,527 potentially relevant references and finally included 41 articles), some  
249 underreporting of our study may be occurring. Our result reveals a bias towards protozoa of importance in  
250 human health (*L. braziliensis*, *T. cruzi*, and *T. gondii*) which consequently have a greater financial support.  
251 This does not reflect the diversity of parasites that infect these groups of hosts, but aware us about this gap.  
252 Despite the contrast between hosts/protozoan more and less explored, our results may show important  
253 aspects of the interactions between small mammals and parasites that are essential for Brazilian  
254 biodiversity.

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

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

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

\*p &lt; 0.05.

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

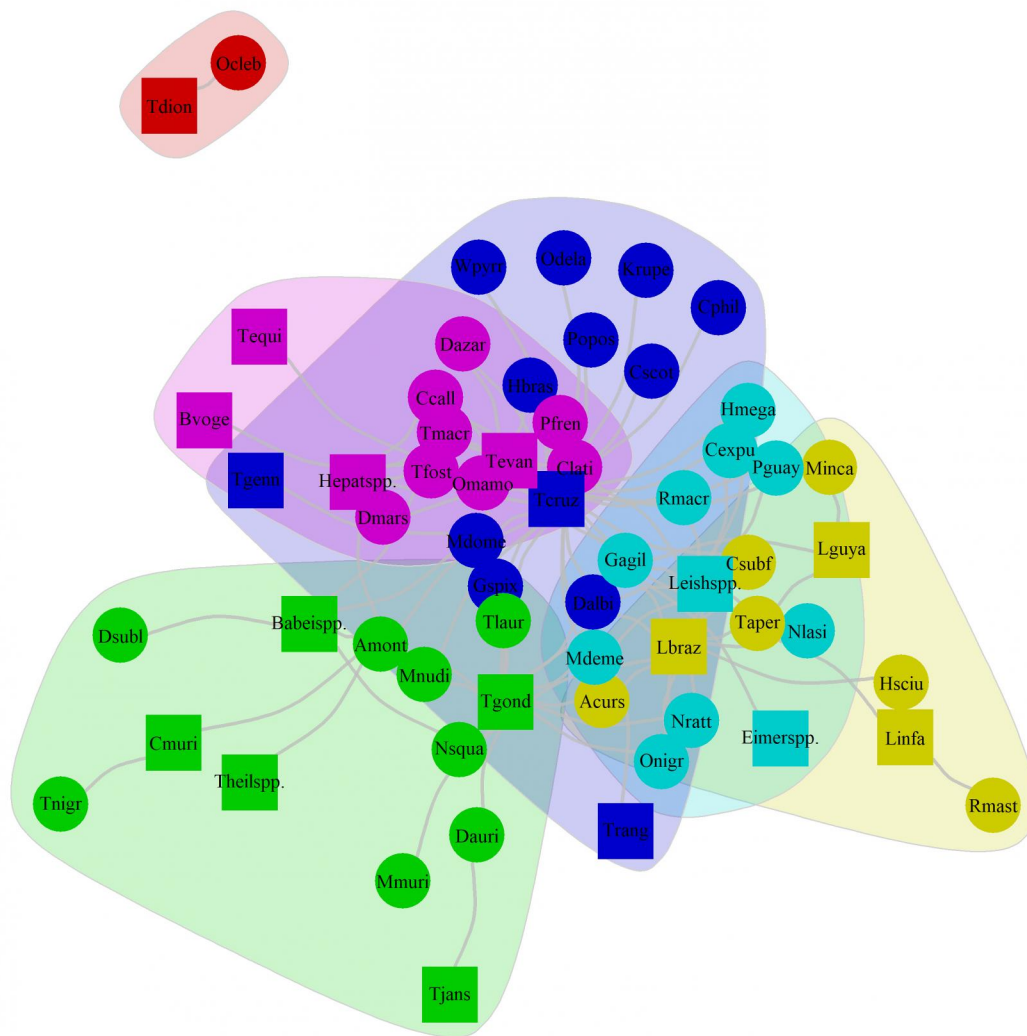
477	<b>Specie</b>	<b>Abbreviation</b>	<b>Vertice Type</b>	<b>nk</b>	<b>BC</b>	<b>p</b>	<b>Network functional role</b>	<b>Biome</b>
478	<i>Gracilinanus agilis</i>	Gagil	Host	0.39	0.29	0.09	kinless hubs	Caatinga, Cerrado and Pantanal
479	<i>Monodelphis domestica</i>	Mdome	Host	0.28	0.23	0.14	non-hub connector vertice	Atlantic Forest, Caatinga, Cerrado and Pantanal
480	<i>Didelphis albiventris</i>	Dalbi	Host	0.28	0.21	0.19	non-hub connector vertice	Amazon, Atlantic Forest, Caatinga and Cerrado
481	<i>Clyomys laticeps</i>	Clati	Host	0.17	0.03	0.17	non-hub connector vertice	Cerrado and Pantanal
482	<i>Akodon cursor</i>	Acurs	Host	0.17	0	0.16	non-hub connector vertice	Atlantic Forest, Caatinga and Cerrado
483	<i>Marmosa demerarae</i>	Mdeme	Host	0.17	0	0.10	non-hub connector vertice	Amazon and Atlantic Forest
484	<i>Oligoryzomys nigripes</i>	Onigr	Host	0.17	0	0.23	non-hub connector vertice	Atlantic Forest and Cerrado
485	<i>Akodon montensis</i>	Amont	Host	0.33	0.13	0.35	peripheral vertices	Atlantic Forest and Cerrado
486	<i>Thrichomys apereoides</i>	Taper	Host	0.22	0.06	0.42	peripheral vertices	Caatinga and Cerrado
487	<i>Oecomys mamorae</i>	Omamo	Host	0.17	0.04	0.18	peripheral vertices	Pantanal
488	<i>Thrichomys fosteri</i>	Tfost	Host	0.33	0.02	0.22	peripheral vertices	Pantanal
489	<i>Nectomys squamipes</i>	Nsqua	Host	0.11	0	0.45	peripheral vertices	Atlantic Forest and Caatinga
490	<i>Calomys callosus</i>	Ccall	Host	0.17	0	0.07	peripheral vertices	Pantanal
491	<i>Thylamys macrurus</i>	Tmacr	Host	0.17	0	0.07	peripheral vertices	Pantanal
492	<i>Calomys expulsus</i>	Cexpu	Host	0.11	0	0.11	peripheral vertices	Cerrado
493	<i>Cerradomys subflavus</i>	Csubf	Host	0.11	0	0.21	peripheral vertices	Atlantic Forest and Cerrado
494	<i>Dasyprocta azarae</i>	Dazar	Host	0.11	0	0.06	peripheral vertices	Amazon and Pantanal
495	<i>Didelphis marsupialis</i>	Dmars	Host	0.11	0	0.36	peripheral vertices	Amazon
496	<i>Galea spixii</i>	Gspix	Host	0.11	0	0.08	peripheral vertices	Caatinga
497	<i>Holochilus brasiliensis</i>	Hbras	Host	0.11	0	0.05	peripheral vertices	Pantanal
498	<i>Hylaeamys megacephalus</i>	Hmega	Host	0.11	0	0.11	peripheral vertices	Amazon
499	<i>Marmosops incanus</i>	Minca	Host	0.11	0	0.45	peripheral vertices	Cerrado
500	<i>Metachirus nudicaudatus</i>	Mnudi	Host	0.11	0	0.10	peripheral vertices	Amazon and Atlantic Forest
501	<i>Necromys lasiurus</i>	Nlasi	Host	0.11	0	0.48	peripheral vertices	Caatinga and Cerrado
502	<i>Nectomys rattus</i>	Nratt	Host	0.11	0	0.36	peripheral vertices	Atlantic Forest and Cerrado

504	<i>Philander frenatus</i>	Pfren	Host	0.11	0	0.12	peripheral vertices	Pantanal
505	<i>Proechimys guayannensis</i>	Pguay	Host	0.11	0	0.11	peripheral vertices	Amazon
506	<i>Rhipidomys macrurus</i>	Rmacr	Host	0.11	0	0.16	peripheral vertices	Caatinga and Cerrado
507	<i>Trichomys laurentinus</i>	Tlaur	Host	0.11	0	0.14	peripheral vertices	Atlantic Forest and Caatinga
508	<i>Didelphis aurita</i>	Dauri	Host	0.11	0	0.63	ultraperipheral vertices	Atlantic Forest
509	<i>Caluromys philander</i>	Cphil	Host	0.06	0	0.00	ultraperipheral vertices	Cerrado
510	<i>Cerradomys scotti</i>	Cscot	Host	0.06	0	0.08	ultraperipheral vertices	Pantanal
511	<i>Delomys sublineatus</i>	Dsubl	Host	0.06	0	0.65	ultraperipheral vertices	Atlantic Forest
512	<i>Holochilus sciureus</i>	Hsciu	Host	0.06	0	0.34	ultraperipheral vertices	Caatinga
513	<i>Kerodon rupestris</i>	Krupe	Host	0.06	0	0.00	ultraperipheral vertices	Caatinga
514	<i>Marmosa murina</i>	Mmuri	Host	0.06	0	0.34	ultraperipheral vertices	Atlantic Forest
515	<i>Oecomys cleberi</i>	Ocleb	Host	0.06	0	1.00	ultraperipheral vertices	Cerrado
516	<i>Oxymycterus delator</i>	Odela	Host	0.06	0	0.00	ultraperipheral vertices	Cerrado
517	<i>Philander opossum</i>	Popos	Host	0.06	0	0.08	ultraperipheral vertices	Amazon
518	<i>Rhipidomys mastacalis</i>	Rmast	Host	0.06	0	0.84	ultraperipheral vertices	Cerrado
519	<i>Thaptomys nigrita</i>	Tnigr	Host	0.06	0	0.85	ultraperipheral vertices	Atlantic Forest
520	<i>Wiedomys pyrrhorhinos</i>	Wpyrr	Host	0.06	0	0.00	ultraperipheral vertices	Caatinga
521	<i>Trypanosoma cruzi</i>	Tcruz	Parasite	0.73	0.65	0.16	non-hub connector vertice	Amazon, Atlantic Forest, Caatinga, Cerrado and Pantanal
522	<i>Toxoplasma gondii</i>	Tgond	Parasite	0.30	0.2	0.45	non-hub connector vertice	Atlantic Forest and Caatinga
523	<i>Leishmania sp.</i>	Leishspp.	Parasite	0.25	0	0.51	peripheral vertices	Amazon and Cerrado
524	<i>Trypanosoma evansi</i>	Tevan	Parasite	0.23	0.1	0.39	peripheral vertices	Pantanal
525	<i>Leishmania braziliensis</i>	Lbraz	Parasite	0.23	0.05	0.49	non-hub connector vertice	Atlantic Forest, Caatinga and Cerrado
526	<i>Hepatozoon sp.</i>	Hepatspp.	Parasite	0.14	0	0.37	peripheral vertices	Amazon, Atlantic Forest and Pantanal
527	<i>Babesia sp.</i>	Babeispp.	Parasite	0.11	0	0.41	peripheral vertices	Atlantic Forest and Pantanal
528	<i>Leishmania guyanensis</i>	Lguya	Parasite	0.07	0	0.53	peripheral vertices	Cerrado
529	<i>Cryptosporidium muris</i>	Cmuri	Parasite	0.05	0	0.65	ultraperipheral vertices	Atlantic Forest
530	<i>Leishmania infantum</i>	Linfa	Parasite	0.05	0	0.74	ultraperipheral vertices	Cerrado
531	<i>Babesia vogeli</i>	Bvoge	Parasite	0.02	0	0.01	ultraperipheral vertices	Pantanal

533	<i>Theileria equi</i>	Tequi	Parasite	0.02	0	0.01	ultraperipheral vertices	Pantanal
534	<i>Trypanosoma gennarii</i>	Tgenn	Parasite	0.02	0	0.06	ultraperipheral vertices	Cerrado
535	<i>Trypanosoma rangeli</i>	Trang	Parasite	0.02	0	0.07	ultraperipheral vertices	Cerrado
536	<i>Eimeria sp.</i>	Eimerspp.	Parasite	0.02	0	0.00	ultraperipheral vertices	Cerrado
537	<i>Theileria sp.</i>	Theilspp.	Parasite	0.02	0	0.31	ultraperipheral vertices	Atlantic Forest
538	<i>Trypanosoma janseni</i>	Tjans	Parasite	0.02	0	0.49	ultraperipheral vertices	Atlantic Forest
539	<i>Trypanosoma dionisii</i>	Tdion	Parasite	0.02	0	1.00	ultraperipheral vertices	Cerrado

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



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