Original Article

Helminth metacommunity structure of wild rodents in a preserved area of the Atlantic Forest, Southeast Brazil

Estrutura da metacomunidade de helmintos de roedores silvestres em uma área preservada da Floresta Atlântica, sudeste do Brasil

Thiago dos Santos Cardoso[1,2]; Caryne Aparecida de Carvalho Braga[3]; Carla Elizabeth Macabu[1]; Raquel de Oliveira Simões[1]; Sócrates Fraga da Costa-Neto[4,5]; Arnaldo Maldonado Júnior[1]; Rosana Gentile[1]*; José Luis Luque[6]

[1] Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz – FIOCRUZ, Rio de Janeiro, RJ, Brasil

[2] Programa de Pós-graduação em Ciências Veterinárias, Departamento de Parasitologia Animal, Universidade Federal Rural do Rio de Janeiro – UFRRJ, Seropédica, RJ, Brasil

[3] Núcleo de Pesquisa Ecológica de Macaé, Universidade Federal do Rio de Janeiro – UFRJ, Macaé, RJ, Brasil

[4] Fiocruz Mata Atlântica, Fundação Oswaldo Cruz – FIOCRUZ, Rio de Janeiro, RJ, Brasil

[5] Programa de Pós-graduação em Biodiversidade e Saúde, Instituto Oswaldo Cruz – FIOCRUZ, Rio de Janeiro, RJ, Brasil

[6] Departamento de Parasitologia Animal, Universidade Federal Rural do Rio de Janeiro – UFRRJ, Seropédica, RJ, Brasil

Abstract

The helminth fauna and metacommunity structure of eight sympatric sigmodontine rodents were investigated at the Serra dos Órgãos National Park, an Atlantic Forest reserve located in the State of Rio de Janeiro, southeast Brazil. Rodents of the species *Abrawayaomys ruschii*, *Akodon montensis*, *Blarinomys breviceps*, *Delomys dorsalis*, *Oligoryzomys flavescens*, *Oligoryzomys nigripes*, *Oxymycterus quaestor* and *Thaptomys nigrita* were found infected with helminths. *Akodon montensis* presented the highest total helminth species richness, with six different species of helminths. The nematode *Stilestrongylus lanfrediae* was the most abundant and prevalent helminth species observed. The host-parasite network analysis showed little interactions among host species. *Akodon montensis* seems to act as a keystone-species in the rodent community. This species shared the nematodes *Stilestrongylus aculeata* with *A. ruschii* and *Protospirura numidica criceticola* with *T. nigrita*, and the cestode *Rodentolepis akodontis* with *D. dorsalis*. The congeners host species *O. flavescens* and *O. nigripes* shared the nematodes *Guerrerostrongylus zetta* and *S. lanfrediae*. The rodents *B. breviceps* and *O. quaestor* did not share any helminths with other hosts. The helminth metacommunity showed a random pattern on both infracommunity and component community levels, indicating different responses by each helminth species to the environmental gradient.

Keywords: Elements of metacommunity structure, network analysis, parasitism, small mammals.

Resumo

Foram investigadas a helmintofauna e suas estruturas da metacomunidade em oito roedores sigmodontíneos simpátricos ao longo do Parque Nacional da Serra dos Órgãos, uma reserva de Mata Atlântica no estado do Rio de Janeiro, Brasil. Roedores das espécies *Abrawayaomys ruschii*, *Akodon montensis*, *Blarinomys breviceps*, *Delomys dorsalis*, *Oligoryzomys flavescens*, *Oligoryzomys nigripes*, *Oxymycterus quaestor* e *Thaptomys nigrita* foram infectados por helmintos. *Akodon montensis* apresentou a maior riqueza total de espécies de helmintos, com seis espécies. O nematoide *Stilestrongylus lanfrediae* foi a espécie de helminto com maior abundância e prevalência. A análise de rede parasito-hospedeiro mostrou poucas interações entre as espécies hospedeiras e *A. montensis* atuou como uma espécie-chave na comunidade de roedores. Esta espécie compartilhou os nematoides *Stilestrongylus aculeata* com *A. ruschii* e *Protospirura numidica criceticola* com *T. nigrita*, e o cestoide *Rodentolepis akodontis* com *D. dorsalis*. As espécies congêneres *O. flavescens* e *O. nigripes* compartilharam os nematoides *Guerrerostrongylus zetta* e *S. lanfrediae*. Os roedores *B. breviceps* e *O. quaestor* não compartilharam helmintos com outros hospedeiros. A metacomunidade de helmintos mostrou um padrão aleatório em ambos os níveis, comunidade componente e infracomunidade, indicando diferentes respostas de cada espécie de helminto ao gradiente ambiental.

Palavras-chave: Elementos de estrutura de metacomunidade, análise de rede, parasitismo, pequenos mamíferos.

*Corresponding author: Rosana Gentile. Laboratório de Biologia e
Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz,
Fundação Oswaldo Cruz – FIOCRUZ, Avenida Brasil, 4365, CEP 21040-900,
Rio de Janeiro, RJ, Brasil. e-mail: rgentile@ioc.fiocruz.br

Introduction

Parasites have important ecological roles in ecosystems because they affect the fitness of their hosts, promote changes in their physiology and population dynamics, regulate host populations, mediate competition and predation, and influence diversity through a cascade effect (POULIN, 2007). The occurrence and distribution of parasites in host populations depend on several factors that include host and parasite attributes, such as phylogenetic relationships, host behavior, susceptibility to parasites (BROUAT et al., 2007; WOLINSKA & KING, 2009), as well as characteristics of the environment such as seasonality and habitat (WOLINSKA & KING, 2009; SIMÕES et al., 2010; CASTRO et al., 2017).

Due to their biological and ecological features, rodents and helminths are a good model for ecological studies of host-parasite interactions in different ecosystems (MALDONADO JR. et al., 2006; CARDOSO et al., 2016; SIMÕES et al., 2016). Rodents are the most diversified group of mammals (PATTON et al., 2015), may harbor a number of parasites and are reservoirs of several zoonoses (HAN et al., 2015). Helminths may show high biomass indices within a biological community (POULIN, 2007), and can be used as indicators of environmental changes (VIDAL-MARTÍNEZ & WUNDERLICH, 2017). In addition, many helminth species have complex life cycles in which rodents act as intermediate and / or definitive hosts (CHAISIRI et al., 2017).

Therefore, information on the occurrence, distribution and community structure of parasites are fundamental to understand the ecosystem dynamics, the host-parasite interactions, and are essential for the knowledge of biodiversity. In addition, studies of community ecology and network analysis helps to describe and evaluate the patterns of distribution, abundance, and interactions between animal species. These patterns occur at different spatial scales with local communities interacting and affecting each other on a regional scale (PRESLEY et al., 2010).

The metacommunity approach has been recently used in community ecology to understand how species are distributed in communities and how these species respond to ecological changes at different spatial scales (LEIBOLD & MIKKELSON, 2002; DÜMMER et al. 2016; BRAGA et al., 2017). A metacommunity is a set of local communities that potentially interact by species dispersal (LEIBOLD & MIKKELSON, 2002). The application of the metacommunity theory in parasite ecology helps to understand host-parasite interactions both on the infracommunity scale (host individuals) and on the component communities (populations of a host species) (DALLAS & PRESLEY, 2014).

Helminth communities of wild animals are still poorly understood, given the diversity of species that this group shows and their distinct patterns of host specificity and susceptibility (HUGOT et al., 2001; POULIN, 2007). Most of the studies about helminths of rodents in Brazil report helminth faunas or occurrences of specific parasites (MALDONADO JR. et al., 2010; PINTO et al., 2011; ARAUJO et al., 2014; WERK et al., 2016). Few studies reported the helminth community structure of wild small mammals (MALDONADO JR. et al., 2006; PÜTTKER et al., 2008; SIMÕES et al., 2010, 2011). Moreover, studies using the

metacommunity approach for this interaction are scant (COSTA, 2017; COSTA-NETO et al., 2018).

The present study is part of a research project on biodiversity and aimed at investigating the fauna of several taxa in areas of the Atlantic Forest, including taxonomic, evolutionary, ecological and parasitological aspects. Herein, we describe the helminth fauna of Sigmodontine rodents in Serra dos Órgãos National Park (PARNASO), State of Rio de Janeiro, southeast Brazil. Our study also aimed at understanding the pattern of the structure of the helminth communities in rodent hosts. Considering the environmental gradient at the infracommunity scale as host individuals and at the component community scale as host species, we tested the following hypotheses: 1) Host species with greater ecological and biological similarity tend to share parasite species, due to the evolutionary processes involving adaptation between parasites and hosts; 2) The helminth metacommunity is non-randomly structured (coherent structure) in both scales, as we expect more similar species of parasites within each host species and also a certain level of similarity in closely related species of hosts.

Materials and Methods

Study area

Rodent sampling was carried out at the PARNASO, Municipality of Petrópolis, which is a preserved forest with an area of 20,024 ha. This park is internationally recognized as a Biosphere Reserve and is one of the most important Atlantic Forest remnants in Brazil. The municipality of Petrópolis covers 43% of the area of the PARNASO which also comprises the municipalites of Teresópolis, Magé, and Guapimirim (ICMBIO, 2014). The study area presents continuous, dense, ombrophilous vegetation of Mountain Atlantic Forest. The climate of this region is highland mesothermic (Cwb), according to Köppen's classification, with mild temperatures, rainy summers, and a dry season between June and August (AYOADE, 1986). Trappings were conducted in three localities of the park: Bonfim (22º27'36.2"S 43º05'37"W; 1074 m height), Barragem do Caxambú (22°30'20"S 43°06'47.5"W; 1117 m height) and Uricanal (22º29'20.5"S 43º07'27.8"W; 1056 m height) in late spring 2014 (rainy season) and winter 2015 (dry season).

Sampling and examination of rodents

Samplings consisted of 10 linear transects, each set for 10 consecutive days. Six of these transects had 15 points with two live traps on the ground, one Tomahawk trap (40.64 cm × 12.70 cm × 12.70 cm) and one Sherman trap (7.62 cm × 9.53 cm × 30.48 cm), and six additional traps in the understorey, three of each type intercalated. These traps were baited with a mixture of peanut butter, banana, oats and bacon. Four transects had 20 points, with pitfall traps spaced 10 m apart. Rodents were euthanized and necropsied, and their bionomic data recorded (age, gender, reproductive activity, body mass and external measurements). Rodents were identified based on their external features, cranial morphology and cytogenetics analysis (diploid number).

Animals were captured under authorization of the Brazilian Government's Chico Mendes Institute for Biodiversity and Conservation (ICMBIO, license number 45839- 1). All procedures followed the guidelines for capture, handling and care of animals of the Ethical Committee on Animal Use of the Oswaldo Cruz Foundation (CEUA license number LW – 39/14). Biosafety techniques and personal safety equipment were used during all procedures involving animal handling and biological sampling.

Nematodes, trematodes and cestodes were recovered from the lungs, bile ducts, stomach, small intestine and cecum, and thoracic and abdominal cavities and washed in saline solution (NaCl 0.85%). Some of the specimens were fixed in AFA (acetic acid 2%, formaldehyde 3% and ethanol 95%) and some were stored in 70% ethanol for further molecular analysis. Nematodes were cleared in lactophenol. Trematodes and cestodes were stained with chlorhydric carmine. Taxonomic identification of these parasites was carried out based on Travassos (1937), Yamaguti (1961), Khalil et al. (1994), Vicente et al. (1997) and Bray et al. (2008). Voucher specimens of the rodents were deposited at the National Museum of Rio de Janeiro, Brazil. Voucher specimens of helminths were deposited at the Helminthological Collection of the Oswaldo Cruz Institute, in Rio de Janeiro, Brazil (CHIOC numbers 38556, 38557, 38558, 38559, 38560, 38561, 38562 and 38563).

Data analysis

Parasitological parameters were calculated for each species of helminth according to Bush et al. (1997) for infracommunities (communities within an individual host) and component communities (communities including the entire host population). Mean abundance was considered as the total number of helminths recovered divided by the number of rodents examined. Prevalence of each species was calculated as the proportion of the infected rodents for a given helminth species in relation to the total number of analysed rodents. Confidence intervals of prevalence were calculated based on the standard deviation considering $\alpha = 95\%$. Importance indexes of species of helminths (each component community) were calculated according to Thul et al. (1985), considering the number of infected hosts and the total abundance of each helminth species. Each species of helminth was classified in the community as dominant species ($I \geq 1.0$) representing the most abundant and prevalent species in the community, co-dominant ($0.01 \leq I < 1.0$), which contributed significantly to the community but in a lesser degree than the dominant species, and subordinate ($0 < I < 0.01$), which occurred infrequently.

The analysis of ecological networks was carried out to verify the interactions between hosts and helminth species. The analysis was based on a matrix of presence / absence of each helminth species in each host. A bipartite network was built between rodent species and helminth species. This type of network indicates the connectance between two different sets - in this case the connectance between hosts and parasites (POULIN, 2010).

The metacommunity structure of the helminths found in the sigmodontine rodents was investigated at the level of infracommunity, considering each individual host as a site, and at the component community level as well, considering each host species as a site.

According to this analysis, sites with no species occurrence must not be included in the species incidence matrix (LEIBOLD & MIKKELSON, 2002). The three elements of metacommunity structure (EMS) (coherence, turnover and boundary clumping), were evaluated according to the method described by Leibold and Mikkelson (2002) and Presley et al. (2010). The coherence element tests whether species respond to the same environmental gradient, quantifying the number of embedded absences (absences localized between two species occurrences) on a species incidence matrix ordered by Reciprocal Averaging. When the coherence element is significant, the turnover and boundary clumping are also assessed. The turnover element determines whether the processes that structure the diversity lead to substitution or loss of species along the gradient, and is calculated by the number of species replacements in the incidence matrix. Boundary clumping is the third element and quantifies the overlap of species distribution limits in the environmental gradient, which can be clumped (when the index value is greater than 1), hyperdispersed (when the index is less than 1) or random (when boundary clumping is not statistically significant) (PRESLEY et al., 2010; BRAGA et al., 2017).

The network analysis was performed in RStudio software version 1.0.136 using the bipartite package. The host-parasite interaction matrix was visualized using 'plotweb' function (DORMANN et al., 2008). The analysis of Metacommunity structure was performed in Matlab R2018a software (MathWorks) using the EMS Script (HIGGINS, 2008). The significance level was 5% in all the analyses.

Results

Eight species of sigmodontine rodents were infected with helminths: *Abrawayaomys ruschii* Cunha & Cruz, 1979 (n = 2), *Akodon montensis* Thomas, 1913 (n = 62), *Blarinomys breviceps* (Winge, 1887) (n = 4), *Delomys dorsalis* (Hensel, 1872) (n = 8), *Oligoryzomys flavescens* (Waterhouse, 1837) (n = 2), *Oligoryzomys nigripes* (Olfers, 1818) (n = 43), *Oxymycterus quaestor* Thomas, 1903 (n = 4) and *Thaptomys nigrita* (Lichtenstein, 1829) (n = 4) (Rodentia: Cricetidae) (in parenthesis are the number of animals analysed). The host species that presented the highest total helminth species richness was *A. montensis*. However, *O. flavescens* and *T. nigrita* presented the highest mean species richness (Table 1).

Akodon montensis was infected with six helminth species: the nematodes *Protospirura numidica criceticola* (Quentin, Karimi & Rodrigues De Almeida, 1968), *Stilestrongylus aculeata* (Travassos, 1918), *Stilestrongylus eta* (Travassos, 1937) and *Trichofreitasia lenti* Sutton & Durette-Desset, 1991, the trematode *Canaania obesa* (Travassos, 1944), and the cestode *Rodentolepis akodontis* (Rêgo, 1967). The most prevalent and abundant species in this rodent was *S. aculeata* (Tables 1 and 2). *Delomys dorsalis* was parasitized by two helminth species only: the nematode *Alippistrongylus* sp. and *R. akodontis*, both showing mid-term prevalence and low abundance (Tables 1 and 2). Three nematode species occurred in *T. nigrita*: *P. n criceticola*, *Pterygodermatites* sp. and *Stilestrongylus* sp. (Tables 1 and 2). *Oligoryzomys nigripes* and *O. flavescens* had two helminth species with high prevalence: the nematodes *Guerrerostrongylus zetta* (Travassos, 1937) Sutton and

Table 1. Prevalence (%) with 95% confidence limits and helminth species mean richness of sigmodontine rodents from Serra dos Órgãos National Park, Petrópolis, State of Rio de Janeiro, southeast Brazil. Total number of hosts captured and number of infected hosts are in parentheses.

Helminth species \ Rodent species	A. ruschii	A. montensis	B. breviceps	D. dorsalis	O. flavescens	O. nigripes	O. quaestor	T. nigrita
	2(1)	62(19)	4(1)	8(2)	2(2)	43(23)	4(1)	4(2)
Mean richness	0.5	0.45	0.25	0.25	1.5	0.69	0.25	1
Alippistrongylus sp.	-	-	-	12.5 (10.1-14.8)	-	-	-	-
G. zetta	-	-	-	-	50.0 (46.8-53.1)	20.9 (17.3-24.5)	-	-
Litomosoides sp.	-	-	-	-	-	-	25 (0-87.7)	-
P. n. criceticola	-	4.8 (1-13.5)	-	-	-	-	-	50 (39.6-60.3)
Pterygodermatites sp.	-	-	-	-	-	-	-	25 (21.8-28.1)
S. aculeata	50 (40.5-59.4)	17.7 (9.2-29.5)	-	-	-	-	-	-
S. eta	-	6.5 (1.8-15.7)	-	-	-	-	-	-
S. lanfrediae	-	-	-	-	100 (71.0-128.2)	48.8 (15.1-82.5)	-	-
Stilestrongylus sp.	-	-	-	-	-	-	-	25 (23.4-26.5)
T. lenti	-	4.8 (1-13.5)	-	-	-	-	-	-
R. akodontis	-	6.5 (1.8-15.7)	-	12.5 (11.7-13.2)	-	-	-	-
Cestoda	-	-	25 (23.4-26.5)	-	-	-	-	-
C. obesa	-	4.8 (1-1.35)	-	-	-	-	-	-

Table 2. Mean abundance followed by standard error of helminth species of sigmodontine rodents from Serra dos Órgãos National Park, Petrópolis, State of Rio de Janeiro, southeast Brazil. Total number of hosts captured and infected are in parentheses.

Helminth species / Rodent species	A. ruschii 2(1)	A. montensis 62(19)	B. breviceps 4(1)	D. dorsalis 8(2)	O. flavescens 2(2)	O. nigripes 43(23)	O. quaestor 4(1)	T. nigrita 4(2)
Alippistrongylus sp.	-	-	-	0.37 ± 1.06	-	-	-	-
G. zetta	-	-	-	-	0.50 ± 0.57	1.16 ± 3.77	-	-
Litomosoides sp.	-	-	-	-	-	-	10.00 ± 20.00	-
P. n. criceticola	-	0.06 ± 0.30	-	-	-	-	-	2.25 ± 3.30
Pterygodermatites sp.	-	-	-	-	-	-	-	0.50 ± 1.00
S. aculeata	1.50 ± 2.12	8.27 ± 33.97	-	-	-	-	-	-
S. eta	-	2.19 ± 14.47	-	-	-	-	-	-
S. lanfrediae	-	-	-	-	13.50 ± 6.36	19.41 ± 35.21	-	-
Stilestrongylus sp.	-	-	-	-	-	-	-	0.25 ± 0.50
T. lenti	-	0.04±0.21	-	-	-	-	-	-
R. akodontis	-	0.11 ± 0.48	-	0.12 ± 0.35	-	-	-	-
Cestoda	-	-	0.25 ± 0.50	-	-	-	-	-
C. obesa	-	0.25 ± 1.41	-	-	-	-	-	-

Durette-Desset, 1991 and *Stilestrongylus lanfrediae* Souza, Digiani, Simões, Luque, Rodrigues-Silva & Maldonado Jr., 2009, the later with larger abundance (Tables 1 and 2).

Abrawayaomys ruschii, *O. quaestor* and *B. breviceps* had the lowest helminth richness, with only one species in each component community: *S. aculeata*, *Litomosoides* sp. and a cestode, respectively, all of them with only one infected specimen (Tables 1 and 2).

Some helminths could not be identified to the species level. The specimen of the genus *Pterygodermatites* was not identified to specific level because only one female specimen was recovered. For the genus *Stilestrongylus* and *Alippistrongylus,* only one male specimen was recovered from each host species. The only specimen of cestode recovered from *B. breviceps* was not well preserved.

### Helminth community structure

Except for the component communities that presented only one species, the ones for *A. ruschii*, *B. breviceps* and *O. quaestor*, no helminth species was considered dominant in any of the other component communities examined (Table 3). In *A. montensis*, *S. eta* and *S. aculeata* were co-dominant species and the other species were subordinate. In the other hosts, all helminth species were considered co-dominants (Table 3).

The host-parasite network analysis showed little interactions among rodent species regarding helminth metacommunity (Figure 1). *Akodon montensis* shared three helminth species with other hosts: *S. aculeata* with *A. ruschii*, *R. akodontis* with *D. dorsalis* and *P. n. criceticola* with *T. nigrita* (Figure 1). *Oligoryzomys nigripes*

and *O. flavescens* shared the two helminth species found: *G. zetta* and *S. lanfrediae* (Figure 1). *Blarinomys breviceps* and *O. quaestor* did not share any helminths with other hosts (Figure 1).

The helminth metacommunity structure was random on both levels (with no significant coherence), considering the infracommunities
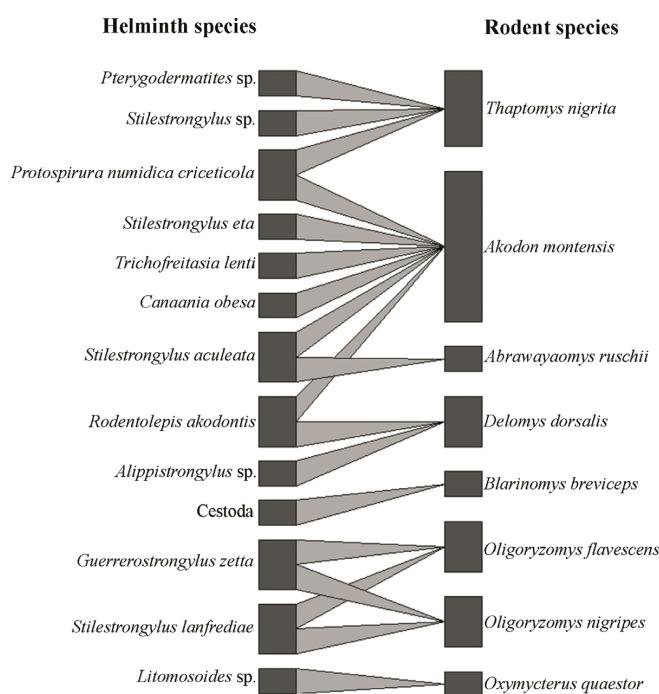
Figure 1. The bipartite network analysis illustrates the rodent–helminth association in Serra dos Órgãos National Park, Petrópolis, State of Rio de Janeiro, southeast Brazil.

(Embedded absences = 71, p = 0.27, mean = 155.75, standard deviation = 77.23) or component communitites (Embedded absences = 12, p = 0.71, mean = 9.83, standard deviation = 5.97), according to the EMS analysis. This pattern is characterized by independent responses of each species to the environmental gradient, *i.e.,* helminth species distribution are independent of each other. Figure 2 shows the occurrence of each helminth species in each rodent specimen, which represent the infracommunities (A), and in each rodent species, which represent the component communities (B), indicating that helminth species are randomly distributed along both gradients.

Discussion

Rodent helminth fauna

The highest total helminth species richness in *A. montensis* (six) in comparison with other rodents corroborates the results from other surveys which also found greater richness in this host (PÜTTKER et al., 2008; PANISSE et al., 2017). However, the total helminth species richness found for this rodent was lower than those reported in other studies; Püttker et al. (2008) observed seven morphotypes in a study in the State of São Paulo, Brazil; Panisse et al. (2017) reported eight helminth species for this rodent in Misiones Province, Argentina. In a previous study carried out in a different locality in PARNASO (Teresópolis) and in forest fragments on its surroundings, Simões et al. (2011) reported twelve helminth species in *A. montensis*, considering 13 localities. Regarding the mean helminth species richness, although *A. montensis* was the most abundant species in the present study, other host species (*O. flavescens* and *T. nigrita*) also showed higher mean

Table 3. Importance indices for the helminths that occur in sigmodontine rodents from Serra dos Órgãos National Park, Petrópolis, State of Rio de Janeiro, southeast Brazil.

Host species and helminths	Importance Indices	Classification
Akodon montensis		
Canaania obesa	0.007	Subordinate
Protospirura numidica criceticola	0.001	Subordinate
Rodentolepis akodontis	0.004	Subordinate
Stilestrongylus aculeata	0.897	Co-dominant
Stilestrongylus eta	0.086	Co-dominant
Trichofreitasia lenti	0.001	Subordinate
Delomys dorsalis		
Alippistrongylus sp.	0.750	Co-dominant
Rodentolepis akodontis	0.250	Co-dominant
Oligoryzomys nigripes		
Guerrerostrongylus zetta	0.025	Co-dominant
Stilestrongylus lanfrediae	0.974	Co-dominant
Oligoryzomys flavescens		
Guerrerostrongylus zetta	0.018	Co-dominant
Stilestrongylus lanfrediae	0.981	Co-dominant
Thaptomys nigrita		
Stilestrongylus sp.	0.047	Co-dominant
Protospirura numidica criceticola	0.857	Co-dominant
Pterygodermatites sp.	0.095	Co-dominant
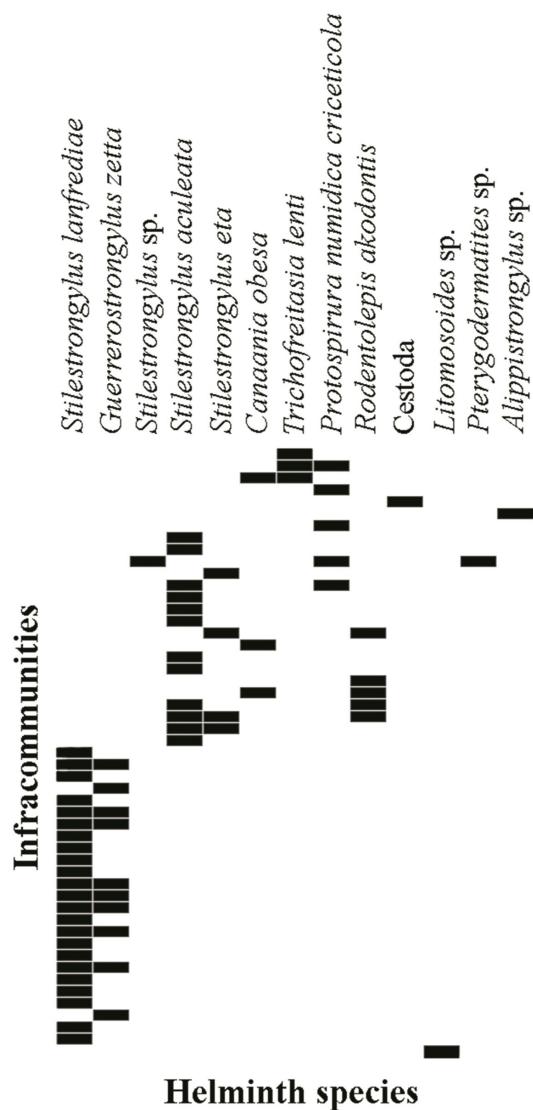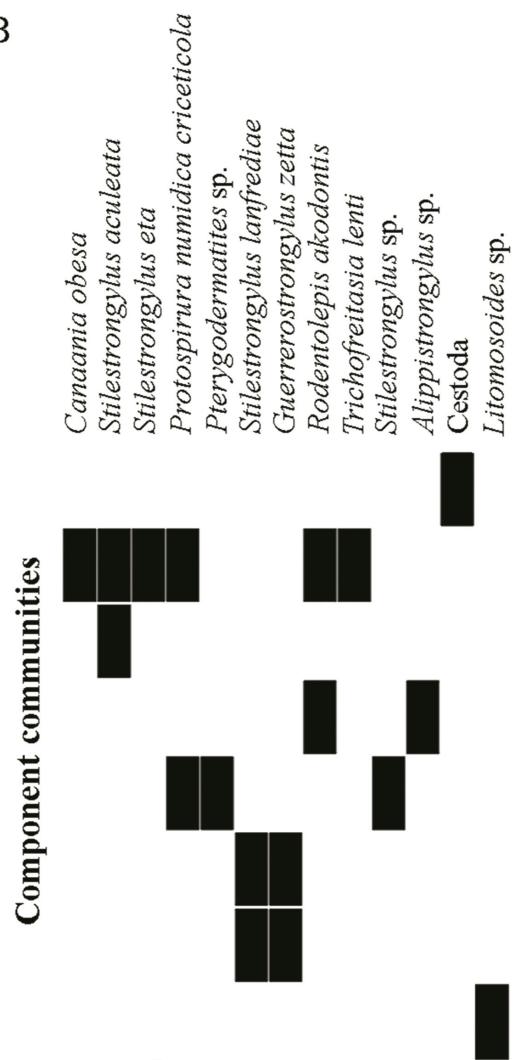
Figure 2. Ordinated matrices for the helminths metacommunities in Serra dos Órgãos National Park, Petrópolis, State of Rio de Janeiro, southeast Brazil: A) infracommunities and B) component communities.

richness. These findings suggest a greater susceptibility of their infracommunities to infection and may reflect co-occurrence between their helminth species.

Considering the helminth fauna of *A. montensis,* all helminth species found in the present study were previously reported (MALDONADO Jr. et al., 2010; SIMÕES et al., 2011; PANISSE et al., 2017). Other genera and species already registered for this host include *Angiostrongylus lenzii, S. lanfrediae, Syphacia carlitosi, Litomosoides silvai, Trichuris* sp., *Echinostoma luisreyi* in Brazil (SIMÕES et al., 2011; GRESSLER et al., 2017), *Eucoleus* sp., *Platynosomoides* sp., *Tapironema coronatum* and *Trichuris navonae* in Argentina (ROBLES, 2011; PANISSE et al., 2017).

For the rodent *O. nigripes,* the helminths *S. lanfrediae* and *G. zetta* were already registered in this host (SOUZA et al., 2009; SIMÕES et al., 2011; WERK et al., 2016; PANISSE et al., 2017). Other helminth species reported for *O. nigripes* are *Avellaria* sp., *S. aculeata, S. eta, S. lanfrediae, Syphacia kinsellai, T. lenti, Litomosoides*

odilae, C. obesa, Cysticercus fasciolaris, Railletina sp. and *R. akodontis* at PARNASO (SIMÕES et al., 2011), *Echinoparyphium scapteromae, Litomosoides bonaerensis, Litomosoides navonae, Stilestrongylus flavescens, Hassalstrongylus epsilon* and *T. coronatum* in Argentina (NAVONE et al., 2009; PANISSE et al., 2017) and *Trichuris travassosi* in the State of Rio Grande do Sul, Brazil (GOMES et al., 1992).

Similarly, *O. flavescens* was infected only by *S. lanfrediae* and *G. zetta.* This a novel finding for this host. Sutton & Lunaschi (1990) reported the occurrence of *Urotrema scabridum* in *O. flavescens* (syn. *Oryzomys flavescens*) in Uruguay. Sutton & Durette-Desset (1991) recorded *T. lenti* and *Stilestrongylus oryzomisi* in Argentina and *Guerrerostrongylus uruguayensis* and *S. flavescens* in Uruguay in this host species. Navone et al. (2009) reported in this rodent the occurrence of *E. scapteromae, L. bonaerensis, P. n. criceticola, S. flavescens, Syphacia* sp. and *Stilestrongylus* sp. in Argentina.

Litomosoides sp. was the only helminth to infect the semifossorial rodent *O. quaestor. Litomosoides legerae* was recorded in *O. quaestor*

in Teresópolis, Brazil (BAIN et al., 1980), *Litomosoides oxymycteri* was observed in *Oxymycterus rufus* (NOTARNICOLA et al., 2000; NAVONE et al., 2009) and *Litomosoides anguyai* in *Oxymycterus misionalis* (NOTARNICOLA et al., 2002), both in Argentina. *Litomosoides nasuti* was recorded in *Oxymycterus nasutus* in Uruguay (NOTARNICOLA & NAVONE, 2009). In addition to these helminth species, Navone et al. (2009) also observed *E. scapteromae*, *Levinseniella (Monarrhenos) cruzi*, *Zoonorchis oxymycterae*, *Rodentolepis* sp., *Pseudocapillaria* sp., *Nematomystes rodentiphilus* and *Suttonema* sp. in *O. rufus* in Argentina. Jiménez-Ruiz & Gardner (2003) recorded three nematode species infecting *Oxymycterus paramensis* in Bolivia, *Caroloxyuris boliviensis, N. rodentiphilus* and *P. numidica*.

The helminth fauna of *T. nigrita* was previously described by Panisse et al. (2017). These authors reported the occurrence of a new species of the genus *Stilestrongylus* in Argentina. In the present study, the only specimen of *Stilestrongylus* found in *T. nigrita* seems to be the same species that was found by Panisse et al. (2017) based on the morphological characteristic observed. However, the authors did not provide further information. The nematodes *T. navonae* and *Syphacia alata* were also reported in this rodent in Argentina (ROBLES, 2010; ROBLES & NAVONE, 2014; PANISSE et al., 2017).

The helminth fauna of *D. dorsalis* is largely unknown. The study conducted by Digiani & Kinsella (2014) described a new genus and species of helminth, *Alippistrongylus bicaudatus*, in this rodent. In the present study, specimens found in *D. dorsalis* presented the same diagnostic characteristics of the genus *Alippistrongylus* (DIGIANI & KINSELLA, 2014).

In our survey, the other hosts captured, *A. ruschii* and *B. breviceps*, which had very low abundance, are considered rare in small mammal inventories when compared to other rodents such as *A. montensis* (PEREIRA et al., 2008; CERBONCINI et al., 2014; MACHADO et al., 2016). Thus, for these species, there are no records of helminth infection published in the literature. Therefore, the occurrence of *S. aculeata* in *A. ruschii* represent a new host for this helminth.

Helminth community structure

Among the four co-dominant helminth species with the highest values of importance, two belong to the genus *Stilestrongylus, S. aculeata* in *A. montensis* and *S. lanfrediae* in *O. flavescens* and *O. nigripes*. Species of the genus *Stilestrongylus* are common among rodents, as 21 species among 23 in this genus have been reported to infect rodents of the families Cricetidae, Muridae and Echimyidae (BOULLOSA et al., 2018). The co-dominance of the species *P. n. criceticola* and *R. akodontis* in their respective hosts, *T. nigrita* and *D. dorsalis*, and subordinate in *A. montensis* may be due to the lower helminth species richness in the former hosts. In fact, parasites may show greater abundances in infracommunities with few helminth species when compared to rich species infracommunities (POULIN, 1997, 2007). The latter, in turn, may present species saturation or negative interactions among the parasites such as competition, which might have reduced the parasite load of each species (POULIN, 1997; MORAND et al., 1999).

Ecological networks represent a useful tool to further our understanding of the various host-parasite interactions (POULIN, 2010; DALLAS et al., 2017). They may be used to identify potential routes of parasite transmission among hosts and keystone species in a community (POULIN, 2010; BELLAY et al., 2015; CHAISIRI et al., 2017), and also to investigate host-parasite specificity and the consequences of species losses (BELLAY et al., 2015). In the present study, the bipartite network analysis of the rodent-helminth interactions suggests that *A. montensis* acts as a keystone species in the rodent community sharing parasites with other species. Parasite sharing is more likely to occur among biologically, ecologically or phylogenetically related host species (DALLAS & PRESLEY, 2014; BELLAY et al., 2015).

Akodon montensis, which belongs to the Akodontini tribe (LEITE et al., 2014), is a terrestrial and opportunistic species in relation to habitat occupation (MELO et al., 2013; CARDOSO et al., 2016), and insectivorous (PAGLIA et al., 2012). *Thaptomys nigrita* and *D. dorsalis*, which shared helminth species with *A. montensis*, also have terrestrial habits. The former also belongs to the Akodontini tribe (LEITE et al., 2014) and have an insectivorous / omnivorous diet (PAGLIA et al., 2012), while the latter is frugivorous / granivorous (PAGLIA et al., 2012), and although it is *incertae sedis* (VILELA et al., 2014), it is also a sigmodontine. These similar ecological characteristics allow these rodents to explore resources in the environment in a pattern similar to the one of *A. montensis*, which may have facilitated the infection by the same helminth species. Although *A. ruschii* has a semifossorial habit (PAGLIA et al., 2012), the only species, *S. aculeata*, found in this rodent, which was also present in *A. montensis*, presents a direct life cycle. Helminth eggs are found in the soil (URQUHART et al., 1998), which favours the infection of both host species. *Oligoryzomys nigripes* and *O. flavescens*, which shared helminths only among themselves, are both of the Oryzomyini tribe (VILELA et al., 2014) and the only scansorial species of the host community studied (PAGLIA et al., 2012).

Metacommunities formed by parasites may respond coherently to the environmental gradient if hosts present similar suitable conditions, within and among host species, for the establishment, development and reproduction of the parasite populations. The random patterns observed for the helminths infracommunities and component communities indicate that species distributions are associated with different gradients, which may be related to the occurrence of helminth species with different environmental requirements and habitat heterogeneity (DALLAS & PRESLEY, 2014; PRESLEY et al., 2010). The low number of parasite species shared among hosts and the presence of helminth species with different life cycles (direct and indirect) support the random pattern found in this study. However, we should also take into account that when the hosts have few helminth species richness and the number of host examined (number of sites) is limited, as in our study, the random pattern is likely to occur.

The present report is a novel study on helminth metacommunity structure of sigmodontine rodents in Brazil. This is the first report of a bipartite network analysis for Brazilian rodents and their helminth fauna. The first hypothesis was valid as rodent species with the greatest ecological and biological similarity were those that shared more helminth species such as *A. montensis* with *T. nigrita*,

A. ruschii and *D. dorsalis*, and *O. nigripes* with *O. flavescens*. The findings on the helminth metacommunity structure of the sigmodontine rodents for the locality analysed contradict in part our second hypothesis, as we observed a random structure with different species responses to the environmental gradient (hosts) in both scales. It is probable that the few number of helminth species shared among rodent species has resulted in the random pattern for the helminth metacommunity studied, because local differences in the species composition of helminths among hosts may provide different responses to the environmental gradient.

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