Helminths of sigmodontine rodents in an agroforestry mosaic in the Brazilian Atlantic Forest: Patterns and processes of the metacommunity structure

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ABSTRACT

Phylogenetically or taxonomically related hosts may harbour similar parasite communities due to phylogenetic conservatism. In addition, host attributes may favour their exposure to parasites. This study aimed to characterize the helminth fauna of sigmodontine rodents in an Atlantic Forest area in northeastern Brazil and determine the pattern of the helminth metacommunity structure. The influence of host attributes and host taxonomy on the metacommunity structure was also investigated. The most abundant helminth species were *Raillietina* sp. and *Hassalstrongylus lauroi*. *Euryoryzomys russatus* was the most infected host species for helminth parasites, as approximately 81% (35/43) of the animals were infected by at least one helminth species. The helminth metacommunity structure was coherent at both the infracommunity and the component community scales, indicating that species responded to the same environmental gradient. A quasi-Clementsian pattern was observed for the infracommunities, indicating the occurrence of compartments of parasite species that were substituted along the environmental gradient, which was formed by host individuals. A quasi-Gleasonian pattern was found at the component community scale, showing random boundary clumping, which is consistent with the individualistic responses of parasite species to each host species. These patterns corroborated the high values of beta-diversity observed, indicating high species turnover among communities at both scales. Host taxonomic distance was the most important variable explaining the patterns of the helminth metacommunity structure.

1. Introduction

Parasites show different patterns of species diversity and distribution in their hosts (Poulin, 2007). A parasite community in a single host forms an infracommunity, and a parasite community in a host population, i.e., the summ of all infracommunities of a given host species, forms the component community (Bush et al., 1997). Thus, in the context of parasitism, species and/or specimens of hosts represent local communities (sites) that affect the transmission or establishment of the parasites (Poulin, 2007). Studies on parasite communities are essential to the knowledge of biodiversity, and they help to understand the mechanisms associated with the occurrence and distribution of parasites in their hosts at different spatial and temporal scales (Krasnov et al., 2006; Nieto-Rabiela et al., 2018; Richgels et al., 2013). Metacomunities are local communities linked by the dispersal of potentially interacting species or specimens (Leibold et al., 2004). The metacommunity theory may be suitable for the study of parasitic communities, given the fragmented nature of parasitic populations in their hosts (Mihaljevic, 2012;

Poulin, 2007). Thus, the parasite metacommunity is a set of infra-communities of a given host species or a set of component communities.

Two complementary approaches of investigation have been proposed to study metacommunities, one related to their structuring patterns and one related to their mechanisms. The pattern-based approach (Leibold and Mikkelson, 2002) evaluates the elements of meta-community structure (EMS). This approach investigates how local differences shape species distributions along environmental gradients. EMS analysis evaluates the species response to a given environmental gradient, the loss or replacement of species as a function of resource need, and the distribution limits of the species along the environmental gradient (Presley et al., 2010). In turn, the mechanistic approach is based on the mechanisms responsible for species diversity and community structuring (Cottenie, 2005; Leibold et al., 2004). In this way, the degree of similarity among local communities may depend on several factors (mechanisms), such as local and regional processes of species dispersion, biotic interactions, and environmental requirements (Leibold et al., 2004; Presley et al., 2010).

The mechanistic approach investigates the contribution of different factors to the metacommunity structure by decomposing the variance of a given set of factors (Dallas and Presley, 2014; Cardoso et al., 2020). Host attributes, for example (diet, body mass and abundance) are considered important predictors of host-parasite relationships (Cardoso et al., 2019, 2020, 2021; Dallas and Presley, 2014; Dallas et al., 2019; Kamiya et al., 2014). The host's diet can contribute to the acquisition of parasites because many parasites that have indirect life-cycles can be acquired by the consumption of their intermediate hosts (Leung and Koprivnikar, 2019). Hosts with higher body masses may have a greater number of potential niches for parasite colonization (Kamiya et al., 2014; Dallas et al., 2019). Hosts that are more abundant may have greater exposure to parasites in the environment than less abundant hosts (Cardoso et al., 2021; Dallas et al., 2020; Kamiya et al., 2014; Morand, 2015). In addition, the phylogeny of the host is related to the evolution of the host-parasite interaction (Dallas and Presley, 2014). Due to phylogenetic conservatism, phylogenetically (or taxonomically) related hosts may harbour similar parasite communities (Poulin, 2014).

Rodents constitute the most diverse mammalian order (Burgin et al., 2018) and harbour many helminth species (Carlson et al., 2020), some with zoonotic potential (Carvalho-Pereira et al., 2018). These organisms are hosts of several other parasites, such as bacteria, viruses and protozoa (Han et al., 2016). Despite this, there is still a large gap concerning the helminth community structure of wild rodents, as well as the mechanisms that influence the diversity of these parasites. In Brazil, recent studies on helminth metacommunities of wild rodents have been conducted in the Atlantic Forest (Boullosa et al., 2020; Cardoso et al., 2018) and in the Cerrado (Costa et al., 2019) using EMS analysis. The mechanistic approach was used in a helminth metacommunity of small mammals in the Brazilian Atlantic Forest (Cardoso et al., 2020); helminths of marsupials were also studied using the pattern-based approach in Brazil (Cirino et al., 2022; Costa-Neto et al., 2019). In addition, several studies on helminth metacommunities have been developed in different regions of the world, seeking to understand the patterns and processes of community structure in different hosts. Helminths of molluscs were investigated in lakes in the United States (Richgels et al., 2013); helminths of rodents in New Mexico (Dallas and Presley, 2014); benthic nematodes in lakes in Europe (Dümmer et al., 2016); helminths of amphibians in wetlands of the United States (Mihaljevic et al., 2018); and helminths of freshwater fishes in Brazil (Costa et al., 2021).

The aims of this study were to identify the helminth fauna of sigmodontine rodents (Rodentia: Sigmodontinae) in an area of the Atlantic Forest in northeastern Brazil and to determine the pattern of the metacommunity structure of these helminths and its related mechanisms, using both EMS and mechanistic analysis. The influence of host attributes and their taxonomic distance was investigated considering the infracommunity and component community scales. The following

hypotheses were tested: (1) The helminth metacommunity is characterized by a structuring pattern of greater species substitution than species loss along the environmental gradient due to the high variability of resource supply among host species depending on their characteristics, such as diet, body mass and abundance (Dallas and Presley, 2014; Poulin, 2007). (2) The host taxonomic distance influences the pattern of the helminth metacommunity because host-parasite interactions are constrained by phylogeny. Thus, a high degree of specificity of helminth species and, consequently, low sharing among host species is expected.

2. Materials and methods

2.1. Study area

This study is part of a comprehensive project that aimed to survey the biodiversity fauna and its parasites in several areas of the Brazilian Atlantic Forest. Helminths were collected from sigmodontine rodents at the Pratigi Environmental Protection Area (13°51′ S; 39°16′ W) in the municipality of Igrapiúna, state of Bahia, northeast Brazil. The area is covered by valleys and plains within the landholding of the Juliana Valley United Farms (Fazendas Reunidas Vale do Juliana). These farms comprise a set of agroforestry systems of rubber, cocoa, clove and peach palm production and include patchy areas of dense ombrophilous forest (OCT, 2019). The climate of the region is classified as wet equatorial (Af), according to the Köppen climate classification, which is characterized by high temperatures, high humidity and few seasonal variations, without dry seasons (Alvares et al., 2013).

2.2. Collection and identification of the helminths and hosts

The rodents were collected using Sherman® (Model XLK, (7.62 cm × 9.53 cm × 30.48 cm, Florida, USA) and Tomahawk (45 cm × 16 cm × 16 cm) live traps, which were placed on the ground and understorey along six linear transects composed of 15 capture points equidistant in 20 m, completing 35 traps in each transect. Pitfall traps were also installed using 60-L buckets along four additional linear transects with 20 capture points equidistant in 10 m, interconnected by a guide fence. Transects were spaced 500 m apart. All the traps were baited with a mixture of peanut butter, ripe bananas, oatmeal and sardines in soybean oil and replenished when consumed or every two days. Captures were carried out during ten consecutive nights in August 2014 and March 2015. The total sampling effort in the Pratigi Environmental Protection Area was 4,200 live traps-night and 1,600 pitfall buckets-nights. The rodents had their bionomic data recorded and were submitted to euthanasia for helminth recovery. The rodents were identified by external morphology, cranial morphology and cytogenetic analyses when necessary. The specimens were preserved using taxidermy and were housed as voucher specimens in the "Alexandre Rodrigues Ferreira" Mammal Collection at Santa Cruz State University (CMARF-UESC) (Supplementary Material).

Helminths were searched in the stomach, large and small intestine, lungs, liver and thoracic and abdominal cavities of the hosts. The nematodes were diaphanized in 0.5% lactophenol or 50% glycerol and mounted between a slide and a coverslip. Cestodes were stained with chlorhydric carmine, dehydrated in a graded alcohol series, cleared in methylsalicylate, and mounted in Canada balsam. The specimens were counted using a stereoscopic microscope and were identified under an optical microscope (Zeiss Axio Scope A1) that was coupled to an Axio Cam MRc digital camera for photomicrography. The species were identified according to Vicente et al. (1997) and Anderson et al. (2009) for nematodes, Rêgo (1967), Simões et al. (2017) and Guerreiro Martins et al. (2014) for cestodes, and other species descriptions. Voucher specimens were deposited at the Laboratory of Biology and Parasitology of Wild Mammal Reservoirs at Oswaldo Cruz Institute in Rio de Janeiro (Supplementary Material).

The animals were captured under authorization from the Brazilian

Government's Chico Mendes Institute for Biodiversity and Conservation (ICMBio; licence number 17131-4) and the Ethics Committee for Animal Use (CEUA) of the Oswaldo Cruz Foundation (licence LW-39/14) in collaboration with Santa Cruz State University (UESC). Biosafety techniques and personal safety equipment were used during all procedures involving animal handling and biological sampling (Lemos and D'Andrea, 2014).

2.3. Data analysis

Mean abundance, mean intensity and prevalence were calculated for each helminth species in each host species according to Bush et al. (1997). The mean abundance was calculated by dividing the total number of parasites by the total number of hosts. The mean intensity was considered the total number of parasites divided by the number of infected hosts. Prevalence was calculated by dividing the number of hosts infected by the total number of hosts and multiplying by 100. Species richness was considered the number of helminth species in each infracommunity.

The metacommunity structure of the helminths was investigated at the infracommunity level, considering each individual host as a site, and at the component community level, considering each host species as a site. The three elements of the metacommunity structure (EMS) (coherence, turnover and boundary clumping) were evaluated according to 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, i.e., sites where there was no record of the presence of a particular species between two sites where the species was recorded (interruptions in the distribution of species) on a species incidence matrix ordered by reciprocal averaging. The metacommunity is considered coherent when the element coherence is significant and positive, that is, the matrix has fewer embedded absences than expected by chance. In this case, the two other elements are analysed. Significant and negative coherence, i.e., more embedded absences than expected by chance, indicates a checkerboard pattern. This pattern is related to competitive exclusion between pairs of species as a structuring mechanism (Diamond, 1975). When coherence is not significant, that is, embedded absences do not differ from the expected by chance, a random pattern is observed, which indicates that the species do not respond to the same environmental gradient (Leibold and Mikkelson, 2002).

The turnover element determines whether the processes that structure the diversity lead to species substitution or loss along the gradient and is calculated by the number of species replacements in the incidence matrix. Significant and positive turnover, that is, higher turnover rate in relation to the average generated by chance, indicates species substitutions along the environmental gradient. Significant and negative turnover, i.e., lower turnover in relation to the average generated by chance, indicates loss of species resulting in nested structures (Patterson and Atmar 1986). When turnover is non-significant, the metacommunity patterns are called quasi-structures, which present the same assumptions as their idealized structures, but with less structuring strength (Presley et al., 2010). Then, the third element, boundary clumping, is calculated to determine the observed pattern.

Boundary clumping quantifies the overlap in the limits of species distribution along the environmental gradient (Leibold and Mikkelson, 2002). This element is based on the Morisita index, in which the expected value for the null model is 1 (Hoagland and Collins, 1997). When turnover is positive, three structures might be detected, which indicates more species replacements than species loss. A Clementsian pattern is found when boundary clumping is greater than 1. This pattern is characterized by species compartments, due to phylogenetic, ecological and/or biological similarities with each other, which replace each other (Clements, 1916). When the index is less than 1, an evenly spaced distribution is found, indicating competition between species (Tilman, 1982). A Gleasonian pattern is observed when the boundary clumping is

non-significant. This pattern indicates that species distributions are the result of their individualistic responses to the environmental gradient (Gleason, 1926). When turnover is negative, nested structures are observed, indicating more species loss than species replacements. These structures might be clumped with species loss, if boundary clumping is greater than 1, hyperdispersed with species loss if boundary clumping is less than 1, or random with species loss, if boundary clumping is non-significant (Leibold and Mikkelson, 2002).

We investigated the relative importance of host attributes and host taxonomic distance on the variation in helminth species abundance in the metacommunity. This analysis was performed for both the infracommunity and component community scales. For the infracommunity, the helminth abundance was considered the number of specimens of a given helminth species recovered in each single host, and for the component community, the helminth mean abundance in each host species was used. The host attributes considered were body mass, the abundance of a given host species (only at the infracommunity scale), host diet based on Paglia et al. (2012) (frugivorous/granivorous, frugivorous/omnivorous, frugivorous/seed predator and insectivorous/omnivorous), and helminth species richness for each infracommunity and component community. The host species abundance was estimated as the number of individuals of each species captured per transect. The mean body mass of each host species was considered for the analysis at the component community scale. Helminth species richness was considered the number of helminth species observed in each infracommunity or each component community. Taxonomic distance matrices were built using the taxa2dist function to quantify the taxonomic similarity among host species. As all host species belonged to the same subfamily, the rodent tribe was also used as a taxonomic level. This function generates a matrix of taxonomic distance indices between all possible pairs of species in the metacommunity. Scores were extracted from the first axis of a principal coordinate analysis (PCoA) of the matrix. These scores were used as the taxonomic variable in the following analyses.

The association of explanatory variables (host attributes and taxonomic variables) with the species abundance matrix was investigated using redundancy analysis (Rao, 1964). Before this analysis, species abundance matrices were transformed using the Hellinger distance method to adjust the data for the RDA (Legendre and Gallagher, 2001). Stepwise selection (forward stepwise selection) was performed from the global models (Blanchet et al., 2008) to identify which variables better explained the variation in helminth abundance. The significance of each model was obtained by ANOVA with 1000 permutations. Statistically significant models were used as components of the Variation Partitioning analysis performed using the "varpart" function. In this analysis, RDA and ANOVA were also used to run the models and test their significance, respectively, to calculate the variation attributable to each set of explanatory variables.

In addition, we calculated the multiple-site beta diversity for both infracommunity and component community scales and decomposed it into components of balanced variation in abundance (i.e., turnover of individuals) and abundance gradients (i.e., nestedness), according to Baselga (2017). The component of balanced variation will have the maximum value (1) when no species is present in more than one infracommunity or component community. In turn, the abundance gradient component will have the minimum value (0) when there are no species sharing among host individuals (infracommunity scale) or host species (component community scale). This analysis investigates whether diversity is driven by species loss or replacement in the metacommunity. This analysis was performed based on a dissimilarity matrix of the helminth species occurrence in each host species. This matrix was calculated using the Bray–Curtis index, considering the species abundance for each infracommunity and the mean species abundance for each component community (Cardoso et al., 2020).

A bipartite network analysis was carried out between the rodents and the helminth species to illustrate the interaction between the hosts and

their parasites (Poulin, 2010). This analysis was based on a matrix of the presence/absence of each helminth species in each host species.

The taxonomic distance matrices, ANOVA, RDA, and Variation Partitioning were performed using the vegan package (Oksanen et al., 2018), PCoA using the ape package (Paradis and Schliep, 2018), and beta diversity using the betapart package (Baselga et al., 2018). Bipartite network analysis was generated using the bipartite package (Dormann et al., 2008). The EMS analysis was performed using the metacom package (Dallas and Santini, 2020) in R software version 4.0.3 (R Core Team, 2020). The level of significance was 5% in all the analyses.

3. Results

3.1. Helminth fauna

One hundred seventy-two specimens of sigmodontine rodents belonging to eight species were captured and analysed for the presence of gastrointestinal helminths. The rodent species were *Akodon cursor* Winge, 1887, *Euryoryzomys russatus* (Wagner 1848), *Hylaeamys seuanezi* (Weksler, Geise and Cerqueira, 1999), *Nectomys squamipes* Brants, 1827, *Oecomys catherinae* Thomas, 1909, *Oxymycterus dasytrichus* (Schinz, 1821), *Rhipidomys mastacalis* (Lund, 1840) and *Oligoryzomys nigripes* Olfers, 1818. In total, 16 helminth species were recovered (Tables 1–5). The nematodes found were *Syphacia carlitosi* Robles and Navone, 2007, *Syphacia hugoti* Robles, Panisse and Navone, 2014, *Syphacia* sp. (Seurat 1916), *Stilestrongylus eta* (Travassos, 1937) Durette-Desset, 1971, *Stilestrongylus* sp., *Hassalstrongylus epsilon* (Travassos, 1937) Durette-Desset, 1971, *Hassalstrongylus lauroi* Costa et al., 2021, *Protospirura numidica criceticola* Quentin, Karimi and Rodriguez de Almeida, 1968, *Nematomystes scapteromi* (Ganzorig, Oku, Okamoto, Malgor and Kamiya, 1999) and *Physaloptera* sp. The cestodes found were *Raillietina* sp. Fuhrmann, 1920 and *Rodentolepis akodontis* Rêgo, 1967. Specimens of the family Hymenolepididae Railliet and Henry, 1909 and of the genus *Syphacia* were recovered but could not be identified at the species level.

Helminth species richness was low in all host species, ranging from four in *H. seuzanezi* to one in *O. catherinae* and *R. mastacalis* (Fig. 1; Tables 1–5).

The bipartite network indicated that there was little sharing of helminth species among rodent species (Fig. 1). *Hylaeamys seuanezi* shared *H. lauroi* with *O. dasytrichus*, and *Stilestrongylus* sp. and *Raillietina* sp. with *E. russatus* (Fig. 1). *Oligoryzomys nigripes, N. squamipes* and *O. catherinae* shared the nematode *H. epsilon* (Fig. 1). *Akodon cursor* and *R. mastacalis* did not share helminth species with other host species (Fig. 1). Considering the helminths, among the 16 species found, only four were observed in more than one host species (Fig. 1).

3.2. Helminth metacommunity structure and its mechanisms

The helminth metacommunity structure was coherent at both scales, infracommunities and component communities and indicated more

species turnover than species loss along the environmental gradient (Table 6). At the infracommunity scale, a quasi-Clementsian pattern was observed, which indicates that species distribution along the environmental gradient was more clumped than expected by chance and that their distribution boundaries were coincident (Fig. 2, Table 6). At the component community scale, a quasi-Gleasonian pattern was observed,

Table 2
Mean abundance, means intensity (±SD), prevalence (95% CI) and Importance Indices of the helminths of *Euryoryzomys russatus* (N = 43; number of infected hosts = 35) at Pratigi Environmental Protection area, state of Bahia. Brazil.

Parameters/Species	*Syphacia* sp. 3	*Stilestrongylus* sp.1	*Raillietina* sp.
Total Mean Abundance	0.14 ± 0.68	1.72 ± 4.90	8.51 ± 12.26
Male hosts	0	1.54 ± 4.93	7.25 ± 10.49
Female hosts	0.32 ± 0.98	1.95 ± 4.87	10.11 ± 13.93
Total Mean Intensity	3.00 ± 1.41	8.22 ± 8.11	12.62 ± 13.11
Male hosts	0	9.25 ± 9.54	10.24 ± 11.21
Female hosts	3.00 ± 1.41	7.40 ± 7.83	16.00 ± 15.27
Total Prevalence	4.65 (4.64–4.66)	20.93 (20.88–20.98)	67.44 (67.32–67.56)
Male hosts	0	16.67 (16.60–16.73)	70.83 (70.70–70.97)
Female hosts	10.53 (10.51–10.54)	26.32 (26.25–26.39)	63.16 (62.96–63.36)
Importance Indices	0.11	5.90	94.00
Category	Codominant	Dominant	Dominant

Table 3
Mean abundance, means intensity (±SD), prevalence (95% CI) and Importance Indices of the helminths of *Oligoryzomys nigripes* (N = 23; number of infected hosts = 5) at Pratigi Environmental Protection area, state of Bahia, Brazil.

Parameters/Species	*Syphacia* sp. 2	*Hassalstrongylus epsilon*	*Stilestrongylus eta*
Total Mean Abundance	0.87 ± 2.38	1.22 ± 4.55	0.57 ± 2.15
Male hosts	0.73 ± 1.94	0.47 ± 1.81	0.87 ± 2.64
Female hosts	1.13 ± 3.18	2.63 ± 7.42	0.00
Total Mean Intensity	6.67 ± 2.08	14.00 ± 9.90	6.50 ± 4.95
Male hosts	5.50 ± 0.71	7.00	6.50 ± 4.95
Female hosts	9.00	21.00	0.00
Total Prevalence	13.04 (13.01–13.07)	8.70 (8.64–8.76)	8.70 (8.67–8.72)
Male hosts	13.33 (13.30–13.36)	6.67 (6.64–6.70)	13.33 (13.29–13.38)
Female hosts	12.50 (12.43–12.57)	12.50 (12.34–12.66)	0
Importance Indices	42.25	39.44	18.31
Category	Dominant	Dominant	Dominant

Table 1
Mean abundance, means intensity (±SD), prevalence (95% CI) and Importance Indices of the helminths of *Hylaeamys seuanezi* (N = 50; number of infected hosts = 26) at Pratigi Environmental Protection area. state of Bahia, Brazil.

Parameters/Species	*Syphacia* sp. 1	*Hassalstrongylus lauroi*	*Stilestrongylus* sp.1	*Raillietina* sp.
Total Mean Abundance	2.00 ± 7.97	7.12 ± 16.70	0.58 ± 4.10	0.50 ± 2.62
Male hosts	1.96 ± 9.80	5.84 ± 16.50	1.16 ± 5.80	0.24 ± 0.83
Female hosts	2.04 ± 5.79	8.40 ± 17.13	0.00	0.76 ± 3.67
Total Mean Intensity	20.00 ± 18.10	16.95 ± 22.54	29.00	5.00 ± 7.38
Male hosts	49.00 ± 0.00	16.22 ± 25.05	29.00	2.00 ± 1.73
Female hosts	12.75 ± 9.29	17.50 ± 21.60	0.00	9.50 ± 12.02
Total Prevalence	10.00 (9.93–10.07)	42.00 (41.85–42.15)	2.00 (1.96–2.04)	10.00 (9.98–10.02)
Male hosts	4.00 (3.88–4.12)	36.00 (35.79–36.21)	4.00 (3.93–4.07)	12.00 (11.99–12.01)
Female hosts	16.00 (15.93–16.07)	48.00 (47.79–48.21)	0.00	8.00 (7.95–8.05)
Importance Indices	6.15	91.96	0.36	1.54
Category	Dominant	Dominant	Codominant	Dominant

Table 4

Mean abundance, mean intensity (±SD), prevalence (95% CI) and Importance Indices of the helminths of *Akodon cursor* (N = 17; number of infected hosts = 5) at Pratigi Environmental Protection area, state of Bahia, Brazil.

Parameters/Species	*Syphacia carlitosi*	*Rodentolepis akodontis*
Total Mean Abundance	1.82 ± 4.63	0.06 ± 0.24
Male hosts	1.08 ± 2.81	0.08 ± 0.28
Female hosts	4.25 ± 8.50	0
Total Mean Intensity	7.75 ± 7.27	1.00
Male hosts	4.67 ± 4.51	1.00
Female hosts	17.00	0
Total Prevalence	23.53 (23.46–23.60)	5.88 (5.88–5.89)
Male hosts	23.08 (23.03–23.13)	7.69 (7.69–7.70)
Female hosts	25.00 (24.73–25.27)	0
Importance Indices	99.20	0.80
Category	Dominant	Codominant

indicating randomly distributed boundaries and nonsignificant boundary clumping (Fig. 2, Table 6).

Regarding the mechanisms related to the observed structures, both host attributes and host taxonomic distance were significant, explaining the variation in helminth abundance at the infracommunity scale in the a priori analysis (Table 7). However, no influence of the tested variables was observed at the component community scale (Table 7).

The host attributes, represented by their body mass, diet and abundance, and the host taxonomic distance were significant in explaining the variation in helminth abundance when analysed either separately or together at the infracommunity scale (Table 8). The host taxonomic distance was represented by the first five PCoA vectors, which quantified approximately 80% of the taxonomic data variation. In relation to the variance partitioning analysis, the host attributes and the host taxonomic distance quantified 50.54% of the variation in the helminth species abundance (Table 8). Among these variables, taxonomic
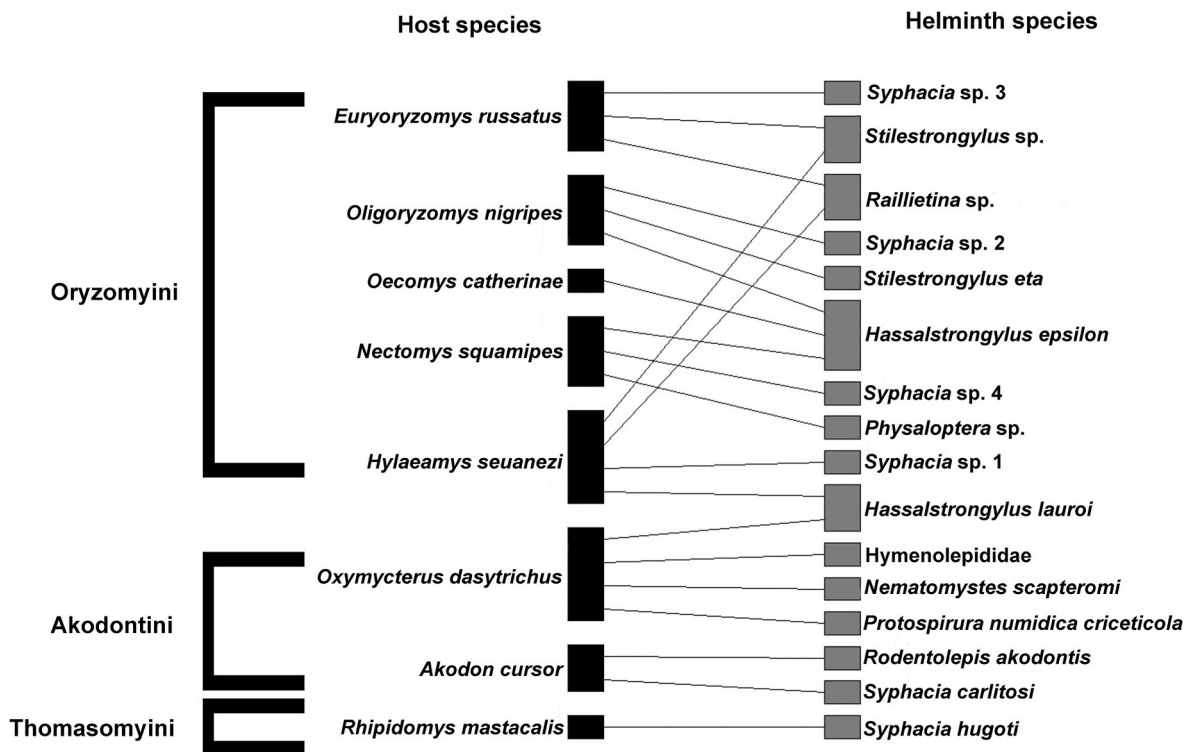
Table 5

Mean abundance, mean intensity (±SD), prevalence (95% CI) and Importance Indices of the helminths of *Nectomys squamipes* (N = 10; number of infected hosts = 6). *Oecomys catherinae* (N = 1; number of infected hosts = 1). *Oxymycterus dasytrichus* (N = 24; number of infected hosts = 12) and *Rhipidomys mastacalis* (N = 4; number of infected hosts = 1) at Pratigi Environmental Protection area, state of Bahia, Brazil.

Host species/Helminth species	Mean abundance ± Standard deviation	Mean intensity ± Standard deviation	Prevalence (95% CI)	Importance index	Category
Nectomys squamipes					
Syphacia sp. 4	4.50 ± 10.49	22.50 ± 13.44	20.00 (19.79–20.21)	14.48	Dominant
Hassalstrongylus epsilon	9.10 ± 15.52	18.20 ± 18.29	50.00 (49.69–50.31)	83.33	Dominant
Phisaloptera sp.	0.10 ± 0.32	1.00	10.00 (9.99–10.01)	1.00	Dominant
Oecomys catherinae					
Hassalstrongylus epsilon	16,00	16,00	100,00	100,00	Dominant
Oxymycterus dasytrichus					
Hassalstrongylus lauroi	0.46 ± 2.25	11.00	4.17 (4.14–4.20)	1.28	Dominant
Nematomystes scapteromi	0.50 ± 1.79	6.00 ± 2.83	8.33 (8.31–8.36)	2.79	Dominant
Protospirura numidica	4.33 ± 10.89	14.86 ± 16.49	29.17 (29.03–29.31)	84.75	Dominant
Hymenolepidiade 1	1.00 ± 2.93	6.00 ± 5.10	16.67 (16.63–16.70)	11.18	Dominant
Rhipidomys mastacalis					
Syphacia hugoti	1,75 ± 3,50	7,00	25,00 (24,89 ± 25,11)	1,00	Dominant

Fig. 1. The bipartite network analysis illustrating the rodent–helminth association at Pratigi Environmental Protection Area, municipality of Igrapiúna, state of Bahia, northeast Brazil. The brackets separate the rodent tribes.

Table 6

Elements of the helminths metacommunity structure (EMS) of sigmonontine rodents, at the infracommunity and component community scales, at Pratigi Environmental Protection area, state of Bahi, Brazil. Abs = embedded absences. Rep = observed replacements. IMI = Morisita's Index. Mean = average of randomly generated matrices. SD = standard deviation and *P* = significance.

EMS	Infracommunities	Component communities
Coherence		
Abs	41	4
P	<0.01	<0.01
Mean	658.66	41.75
SD	71.62	6.92
Turnover		
Rep	6960	160
P	0.13	0.42
Mean	5642.91	152.13
SD	874.67	9.78
Boundary clumping		
MI	2.25	1.06
P	<0.01	0.27
Metacommunity structure	**quasi-Clementsian**	**quasi-Gleasonian**

distance accounted for most of the variation in helminth abundance when analysed separately from the host attributes (23.93%) (Table 8).

The total beta diversity among infracommunities was 0.98, and among component communities, it was 0.94 indicating low sharing of parasites between hosts. Considering each component of beta diversity, the helminth metacommunity showed greater turnover than nestedness

at both the infracommunity and component community scales (infracommunity: turnover = 0.95 and nestedness = 0.03; component community: turnover = 0.90 and nestedness = 0.04), indicating more species replacement than loss along the environmental gradient.

4. Discussion

4.1. Helminth fauna

This study contributes to filling a large gap concerning the patterns and processes of the structure of helminth metacommunities of sigmodontine rodents. It also registered new hosts and geographic records for

Table 7

Analysis of Variance of the Redundancy analysis of the association of host attributes and host taxonomic distance with the species abundance matrix of the helminth metacommunity at Pratigi Environmental Protection area, state of Bahia, Brazil.

Scales	Variables					
	Host attributes			Taxonomic distance		
	DF	F	P	DF	F	P
Infracommunity	5	7.52	0.001	5	16.62	0.001
Component community	4	0.991	0.517	5	0.74	0.893

DF, degrees of freedom; F, Variation between sample means/variation within the samples; *P, p* value.
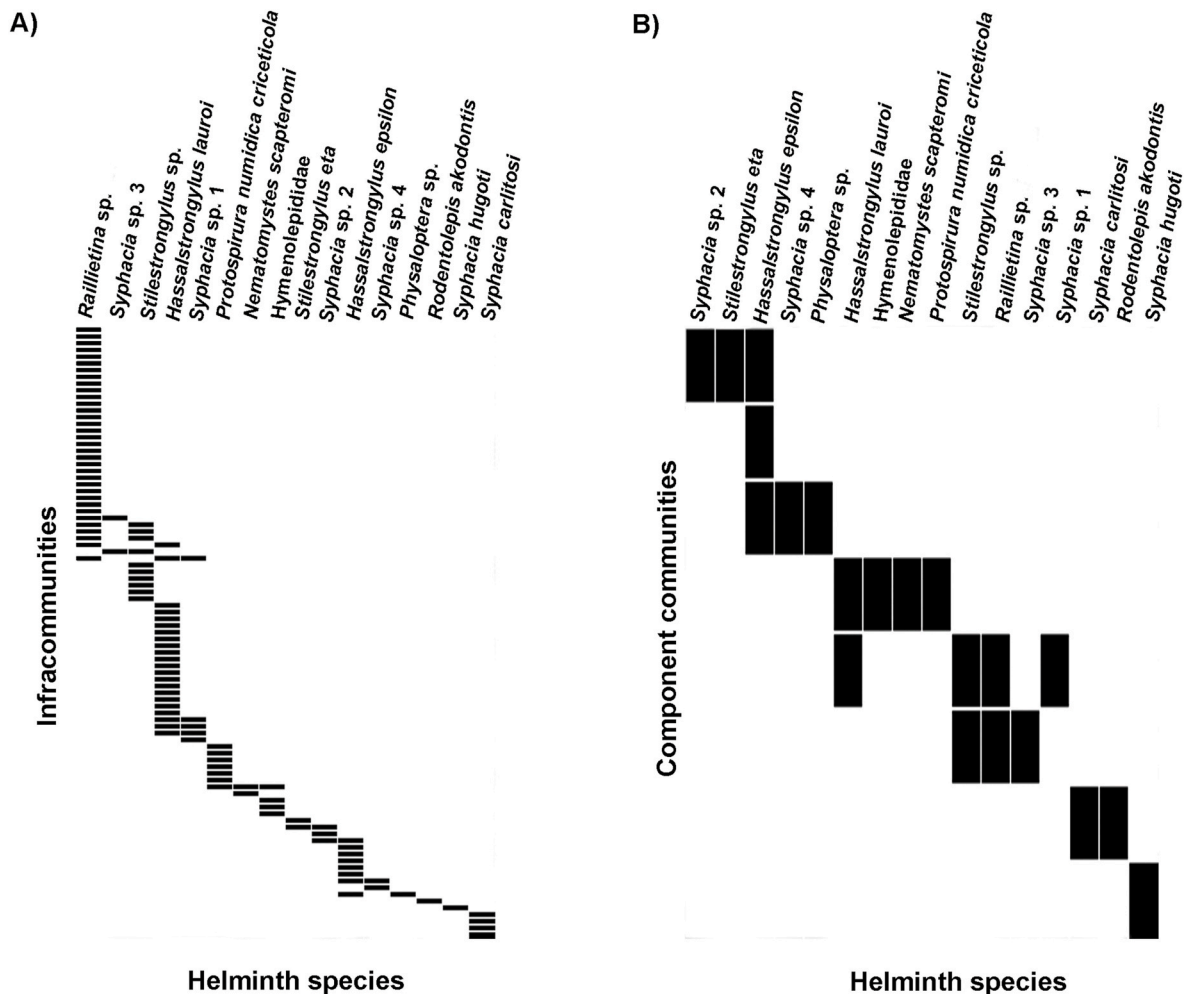

Fig. 2. Ordinated matrices for the helminths metacommunity at Pratigi Environmental Protection Area, municipality of Igrapiúna, state of Bahia, northeast Brazil. A) Infracommunities and B) Component Communities.

Table 8
Variance Partitioning analyses based on the redundancy analysis in order to determine the variation in helminth species abundance at Pratigi Environmental Protection area. state of Bahia, Brazil.

Scale	Partition	Variables	DF	Explained variation (%)	F	P
Infracommunity	Host attributes only	Host diet, Host body mass and host abundance	5	4.07	2.40	0.003
	Host taxonomic distance only	PCoA1, PCoA2, PCoA3, PCoA4 and PCoA5	5	23.93	9.22	0.001
	Host attributes + Host taxonomic distance (Total variation)		10	50.54	10.20	0.001
	Residuals (unexplained variation)			49.46		

several helminth species. *Euryoryzomys russatus* and *H. seuanezi* are new hosts for the cestode *Raillietina* sp. . *Oecomys catherinae* is a new host for *H. epsilon. Rhipidomys mastacalis* is a new host for *S. hugoti. Hylaeamys seuanezi* is a new host for the genus *Stilestrongylus. Oxymycterus dasytrichus* is a new host for *Nematomystes scapteromi.* This is the first report of the helminth fauna of the rodents *Oxymycterus dasytrichus* and *Oecomys catherinae.* It is also a new geographic record in the state of Bahia for *P. numidica criceticola, Raillietina* sp.*, R. akodontis,* and *Nematomystes scapteromi.* Moreover, this study also contributes to the helminth fauna of sigmodontine rodents in an agroforestry mosaic area in the Brazilian Atlantic Forest. Only one study of the helminth fauna of mammals has been carried out in agroforestry areas in Brazil, also in the state of Bahia (Kersul et al., 2020). In addition to that study, reports of helminths in rodents in the state of Bahia registered the presence of *Schistosoma mansoni* in the water rat *N. squamipes* (Silva and Andrade, 1989) and the helminth community of the common rat *Rattus norvegicus* in urban areas (Carvalho-Pereira et al., 2018).

The study by Kersul et al. (2020) also recorded the greatest helminth species richness for the rodent *H. seuanezi* when compared to the other rodents. However, the authors observed five morphotypes in this host, including the nematodes *Hassalstrongylus* sp. (posteriorly identified as *H. lauroi* by Costa et al. (2021), *S. alata, Syphacia* sp., *Physloptera* sp. and cestode specimens of the family Hymenolepididae (Kersul et al., 2020).

Considering the occurrence of the genus *Stilestrongylus* in *E. russatus*, four species of this genus were reported for this host, *S. rolandoi, S. lanfrediae, S. kaaguyporai* and *S. evaginata* (Boullosa et al., 2019; Panisse and Digiani, 2018). The genus *Syphacia* was observed for this host by Kuhnen et al. (2012). Other helminth species reported for this host were *Guerrerostrongylus zetta* (Travassos 1937), *Guerrerostrongylus gomesae, Guerrerostrongylus ulysi, Hassalstrongylus luquei, Raillietina guaricana, Syphacia* sp.*, Tapinorema coronatum,* and the subfamily Nipostrongylinae (Boullosa et al., 2020; Costa et al., 2014; Kersul et al., 2020; Panisse et al., 2017).

The species *Hassalstrongylus epsilon* and *Stilestrongylus eta* have already been recorded in the rodent *O. nigripes* (Gomes et al., 2003; Kersul et al., 2020; Panisse et al., 2017; Simões et al., 2011). Other helminth species reported for this host were *Avellaria* sp., *S. aculeata, S. lanfrediae, Syphacia kinsellai, T. lenti, Litomosoides odilae, C. obesa, Cysticercus faciolaris, Railletina* sp. and *R. akodontis* in Serra dos Órgãos National Park and in fragmented areas of the Brazilian Atlantic Forest (Simões et al., 2011). In addition, *Trichuris travassosi* was reported in the state of Rio Grande do Sul, Brazil (Gomes et al., 1992), and *Echinoparyphium scapteromae, Litomosoides bonaerensis, Litomosoides navonae, Stilestrongylus flavescens, Hassalstrongylus epsilon* and *T. coronatum* were registered in Argentina in this host (Navone et al., 2009; Panisse et al., 2017).

Concerning the helminth fauna of the rodent *Akodon cursor*, Simões et al. (2011) previously reported the helminths *Syphacia carlitosi* and *Rodentolepis akodontis,* as well as *Angiostrongylus* sp, *S. lanfrediae, S. aculeata, S. eta, Syphacia* carlitosi in the state of Rio de Janeiro. Kersul et al. (2020) reported *Syphacia alata, Syphacia* sp. and *Stilestrongylus aculeata* in the State of Bahia. Recently, Lucio et al., (2021) reported the occurrence of *P. numidica criceticola, P. (Paucipectines) zygondontomis, M. necromysi, S. aculeata, S. eta, S. freitasi, T. navonae* and *S. alata* in *A. cursor*

in a matrix area of the Brazilian Atlantic Forest in the state of Rio de Janeiro.

Oxymycterus dasytrichus was infected by four species, including *Nematomystes scapteromi.* This species was previously reported in the rodent *Scapteromys tumidus* Waterhouse, 1837 (Jiménez-Ruiz and Gardner, 2003).

Hassalstrongylus epsilon was previously reported in the water-rat *N. squamipes* (Gomes et al., 2003; Kersul et al., 2020). Species of the genera *Syphacia* and *Phisaloptera* have also been reported for this rodent (Gomes et al., 2003; Kersul et al., 2020; Maldonado et al., 2006). Other records for this host include *Hassalstrongylus* sp.*, L. carinii, L. chagasfilho, Raillietina* sp.*, S. mansoni, T. travassosi* and *L. navonae* (Gomes et al., 2003; Kuhnen et al., 2012; Maldonado et al., 2010).

Usually, the report of helminths in sigmondotine rodents indicates that trematodes occur in low prevalence rates. It is possible that environmental conditions that affect the geographic distribution of intermediate hosts influence the distribution of the trematodes. Thus, intermediate hosts containing the infective phase of these parasites may not have been consumed by these hosts. More studies on the diet and microhabitat of the hosts in the region will be necessary to clarify these aspects.

4.2. Metacommunity structure

The patterns of the helminth species distribution along the metacommunity showed a coherent structure at both scales, the infracommunity and the component community, indicating that species responded to the same environmental gradient (Leibold and Mikkelson, 2002). The metacommunity structure showed higher turnover than nestedness rates at both scales, infracommunity and component community, corroborating the first hypothesis. A greater replacement than loss of parasite species along the environmental gradient suggests that the resources required for the occurrence of parasites are less variable among individuals within a given host species than among host species. Thus, compartments of host specimens of the same host population were observed at the infracommunity scale. Regarding the component community scale, random limits of distribution of the helminth species were observed.

The quasi-Clementsian pattern observed for infracommunities indicates that species are clumped in clusters that are replaced along their hosts. Each cluster may consist of similar species of helminths due to interdependent ecological relationships or a shared evolutionary history. In this case, given the high parasite specificity and a low level of parasite sharing among host species observed, which corroborate our first hypothesis, clusters between infracommunities were formed by parasite species that co-occurred in the same infracommunity, suggesting the influence of processes related to host-parasite coevolution. Similarly, Dallas and Presley (2014) reported a Clementsian pattern for the helminth metacommunity of rodents in New Mexico, attributing the occurrence of this pattern to the high parasite specificity observed in their study. Costa et al. (2021) also recorded a Clementsian pattern for helminths of neotropical fishes, which may have been influenced by host attributes, such as body length and body mass.

In turn, the quasi-Gleasonian pattern, recorded at the component

community scale, indicates idiosyncratic responses of helminth species to the environmental gradient and random responses to one another (Presley et al., 2010). In this case, species coexistence is due to random similarities in environmental requirements. Thus, the parasite species were individually distributed along the host species but presented environmental requirements (e.g., intrinsic and extrinsic to their hosts) that were coincident throughout the metacommunity (Dallas and Presley, 2014). Cirino et al. (20212) reported a quasi-Gleasonian structure for helminths of the marsupial *Didelphis albiventris* in the Atlantic Forest, which might be related to intrinsic responses of each helminth species to the environmental gradient.

Other studies, however, recorded different patterns from those found in the present study. Cardoso et al. (2018) and Boullosa et al. (2020) recorded random distribution patterns of helminth species in sigmodontine rodents in the Atlantic Forest at both infracommunity and component community scales, suggesting that the helminths did not respond to the same environmental gradient. Costa et al. (2019) studied the helminth metacommunity of the sigmodontine rodent *Necromys lasiurus* in rural areas of the Brazilian Cerrado. The authors recorded a checkerboard pattern at the infracommunity scale, suggesting competitive exclusion between parasite species, and a quasi-nested pattern with random species loss at the component community scale, indicating that some localities had richer helminthic communities than others. Richgels et al. (2013) also recorded a quasi-nested pattern with random species loss for the trematode metacommunity of a mollusc in California lagoons. Costa-Neto et al. (2019) investigated the structure of the helminth metacommunity of the marsupial *Didelphis aurita* in different localities, recording patterns characterized by a greater species loss than species turnover at both scales, infracommunity and component community. However, when the localities were studied separately, random and checkerboard patterns were recorded for infracommunities, indicating that increasing spatial scale resulted in parasite species loss along the communities.

The high values of beta-diversity observed corroborated the pattern of the metacommunity structure. The larger rates for the turnover component compared to the nestedness component at both scales indicate that there is more species replacement than species loss among the hosts. This can be attributed to host-parasite coevolution processes, resulting in high host specificity and, consequently, low levels of helminth sharing in most species (Dallas and Presley 2014; Cardoso et al., 2020). As observed by the bipartite host-parasite interaction network, only four of 16 helminth species were recorded coinfecting different host species.

The sharing of *Stilestrongylus* sp. and *Raillietina* sp. between *H. seuanezi* and *E. russatus* may be associated with the taxonomic similarity between these hosts, as they both belong to the same tribe (Oryzomyini). Likewise, *O. nigripes*, *N. squamipes* and *O. catherinae* belong to the tribe Oryzomyini, which may have contributed to the sharing of *H. epsilon* among them. The sharing of *H. lauroi* between *H. seuanezi* and *O. dasytrichus*, which belong to different tribes (Oryzomyini and Akodontini, respectively), may be due to other host or parasite attributes. *H. lauroi* was one of the most abundant and prevalent helminths, which may have increased the chances of encountering hosts in the environment. Moreover, the high abundance of *H. seuanezi* may have promoted the sharing of *H. lauroi* with *O. daytrichus*. Hosts with high population sizes may have a greater contribution to parasite dispersal than hosts with small population sizes (Johnson et al., 2020).

Host attributes and host taxonomic distance were also important to explain the variation in helminth abundance on the infracommunity scale, partially corroborating our second hypothesis, given that no influence of the tested variables on the helminth metacommunity at the component community scale was observed. Host attributes explained only 4.07% of the variation in helminth species abundance at the infracommunity scale. However, host body mass and feeding habits are considered some of the main determinants of the variation in parasite species richness or abundance (Cardoso et al., 2020; Dallas and Presley,

2014; Kamiya et al., 2014). Recently, Cardoso et al. (2021) pointed out that small mammal hosts with a high abundance, frugivorous/omnivorous diet and terrestrial locomotor habits were more vulnerable to infection by helminth parasites in a natural environment. Dallas et al., 2019, using a global database of parasite sharing between mammals, reported that the population density of the hosts was an important predictor of the host-parasite interaction. In turn, the host body size or body mass can be interpreted from the perspective of species-area relationships, so that hosts with larger body sizes can provide more resources (potential niches) for the establishment of parasites than smaller hosts (Kamiya et al., 2014). In addition, larger hosts may have a higher rate of exposure to parasites in the environment due to greater food consumption than hosts with smaller body sizes.

Dallas and Presley (2014) and Cardoso et al. (2020) also demonstrated that host attributes (e.g., body mass and trophic status or diet) were important factors related to the distribution of helminths of rodents. Similarly, Martínez-Salazar et al. (2016) suggested that the presence of rodents with different diet types contributed to the observed helminth diversity, given the occurrence of species with direct and indirect life cycles. In the present study, the presence of hosts with Frugivore/Granivore, Frugivore/Omnivore, Frugivore/Seed and Insectivore/Omnivore diets influenced the diversity of helminths. This may have contributed to the occurrence of 10 species of helminths with direct life-cycles (*S carlitosi, S. hugoti*, four species of the genus *Syphacia, H. lauroi, H. epsilon, Stilestrongylus* sp. and *S. eta*), and six species with indirect life-cycles (*Raillietina* sp., *R. akodontis, Nematomystes* sp., *P. criceticola, Physaloptera* sp. and a species of Hymenolepididae).

The host taxonomic distance explained most of the variation in helminth abundance across infracommunities (20.84%) in the present study. In fact, some studies of mammalian parasites have shown the importance of host phylogeny or taxonomy in parasite diversity. Wells et al. (2019), studding helminths, and Dáttilo et al. (2020), studding ectoparasites, showed that phylogenetically and taxonomically close mammals had more similar parasite communities than taxonomically distant mammalian hosts. Contrary to the results of the present study, Dallas and Presley (2014) did not find a high contribution of host phylogeny to helminth diversity, despite having observed high parasite specificity. Likewise, Cardoso et al. (2021) found no influence of host taxonomy on parasite sharing in a small mammal-helminth interaction network, raising new discussions about the effect of phylogenetic signals on host-parasite interactions.

The residual variation observed in the variance partitioning analysis at the infracommunity scale and the absence of significant variables at the component community scale indicate that other factors may have influenced the parasite distribution in the hosts. Parasite attributes (e.g., life cycle and infection niche), number of sites, and climatic variables (such as temperature and precipitation) are some of those factors.

The quasi-Clementsian and quasi-Gleasonian distribution patterns observed for the helminth metacommunity indicated larger species replacement than loss, corroborating the high values of beta-diversity and turnover. The quasi-Clementsian pattern found at the infracommunity scale indicated the occurrence of compartments of similar helminth species within each host species. The quasi-Gleasonian structure recorded at the component community scale indicated that the helminth species were independently distributed along the infracommunities, which is attributed to the intrinsic responses of each helminth species to the environmental gradient. The low parasite sharing among host species might be related to the existence of distinct conditions for the establishment of parasites among rodent species, promoting few overlapping distribution limits between shared helminths (*e.g, H. epsilon, H. lauroi, Stilestrongylus* sp. and *Raillietina* sp.). In addition, the host taxonomic distance was shown to be more important than the host attributes on helminth abundance along the environmental gradient. These results and the low level of helminth sharing among hosts are in accordance with the processes of host-parasite coevolution, as taxonomically close hosts may have similarities in their parasite

communities.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2022.04.008.

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