Research Paper

Metacommunity structure of the helminths of the black-eared opossum *Didelphis aurita* in peri-urban, sylvatic and rural environments in south-eastern Brazil

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Abstract

Among the Brazilian marsupials, the species of the genus *Didelphis* are the most parasitized by helminths. This study aimed to describe the species composition and to analyse the helminth communities of the Atlantic Forest common opossum *Didelphis aurita* at infracommunity and component community levels using the Elements of Metacommunity Structure Analysis, considering peri-urban, sylvatic and rural environments in the state of Rio de Janeiro, Brazil. Seventy-three specimens of *D. aurita* were captured during the study. Fourteen species of helminths were collected: nine of the phylum Nematoda (*Trichuris minuta*, *Trichuris didelphis*, *Globocephalus marsupialis*, *Heterostrongylus heterostrongylus*, *Travassostrongylus orloffi*, *Viannaia hamata*, *Aspidodera raillieti*, *Cruzia tentaculata* and *Turgida turgida*); four of the phylum Platyhelminthes (three species of Trematoda, *Duboisiella proloba*, *Brachylaima advena* and *Rhopalias coronatus*, and one species of the class Cestoda); and one species of the phylum Acanthocephala (*Oligacanthorhynchus microcephalus*). More than 95% of the animals were infected with parasites. The most abundant parasite species were *V. hamata*, *T. turgida*, *C. tentaculata* and *T. orloffi*. The nematodes *T. turgida*, *C. tentaculata* and *A. raillieti* were the most dominant species in the three environments. The analysis of the metacommunity structure indicated a structured pattern as a function of the environmental gradient, but only when all localities were considered together. At the infracommunity and component community levels, quasi-nested and nested structures with stochastic species loss were observed, respectively. The results indicate that the settlement of helminth species in the opossums can be attributed to the heterogeneity among individual hosts in relation to their exposure to parasites and to extrinsic factors, which vary among habitats, considering a regional scale. On a local scale, the characteristics of this host species may promote homogenization among individual hosts in terms of their exposure to the helminths. This study constitutes a new host record for the species *G. marsupialis* and *T. didelphis* and represents a pioneering investigation of the helminth metacommunity of a Neotropical marsupial.

Introduction

Conservation of biological diversity is a global concern. Ecosystems have experienced increasing anthropogenic disturbance in structure and function, resulting in alterations to species composition and abundance (Turner, 1996; Laurance, 1999; Scott *et al.*, 2006). The remnant natural environments in the Brazilian Atlantic Forest have been dramatically reduced, fragmented or isolated due to a continuous process of urbanization and development that has caused habitat changes. The Atlantic Forest is located in the most densely populated region in Brazil. This biome, considered a hotspot of biodiversity, is characterized by its habitat heterogeneity (Caramaschi *et al.*, 2000), its isolation from other ombrophilous forests and its high degree of fragmentation.

Within the Atlantic Forest biome, the state of Rio de Janeiro has a wide mammalian fauna (Rocha *et al.*, 2003), but in several localities the medium and large animals have disappeared or have very small populations. This decline has led to changes in ecological interactions, an abundance of generalist small mammal species, and an increase in the presence of many species around human dwellings, such as the black-eared opossum *Didelphis aurita* (Didelphimorphia, Didelphidae) (Fonseca and Robinson, 1990; Moura *et al.*, 2009).

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Human infection by the parasitic helminths of wild animals has been attributed to the increasing interface of urban or rural populations with sylvatic areas, where mammalian species may act as reservoirs of zoonosis (Gentile *et al.*, 2006; Simões *et al.*, 2014). Mammalian helminth infections may also occur in domestic, synanthropic and breeding animals (Prestwood *et al.*, 1977; Simões *et al.*, 2011; Brianti *et al.*, 2012).

The community structure of parasites is usually studied at the infracommunity (individual hosts) and component-community (set of local infracommunities) levels (Poulin and Dick, 2007). A recent approach to the study of community structure uses metacommunity analysis (Winegardner *et al.*, 2012). A metacommunity can be defined as a set of local communities potentially linked by the dispersal of multiple species on a larger spatial scale (Gilpin and Hanski, 1991; Leibold *et al.*, 2004). The analysis of the Elements of Metacommunity Structure (EMS hereafter) evaluates three elements. Coherence is a measure that tests whether species respond to the same environmental gradient, that is, the degree to which a pattern can be grouped into a single dimension, and is quantified by the number of interruptions in the occurrence of a species (embedded absences) in an incidence matrix. The second element, species turnover, represents the number of species replacements in this dimension. The boundary clumping element represents how the limit of occurrence of each species is distributed between the sites along the environmental gradient (Leibold and Mikkelson, 2002). Six idealized basic structures can be identified: checkerboard, nested, Clementsian, Gleasonian, evenly spaced and random distributions (Leibold and Mikkelson, 2002). This is a promising approach for studies of parasite communities (Richgels *et al.*, 2013) or zoonotic diseases (Suzán *et al.*, 2015) due to the fragmented nature of the populations of these organisms, where each individual host comprises an infracommunity.

Previous studies on the helminths of *D. aurita* have primarily been taxonomic descriptions and records of occurrence (Thatcher, 2006; Chagas-Moutinho *et al.*, 2014). There have been a few studies on helminth community structure in marsupial species (Antunes, 2005; Jiménez *et al.*, 2011; Byles *et al.*, 2013). This study describes the species composition and analyses the structure of the helminth metacommunities of *D. aurita* at both infracomunity and component community levels. We compare the abundance, intensity, prevalence and richness of the helminth species in peri-urban, sylvatic and rural habitats in the state of Rio de Janeiro and investigate the parasitological parameters for the most abundant species. We hypothesized that, for this host, the helminth metacommunity across infracommunities and component communities on a regional scale would have a coherent pattern of species distribution. In this way, species would be non-randomly distributed along the environmental gradient formed by hosts and the external habitats of each area due to the heterogeneity in the host exposure to helminth species among habitats.

Material and methods

Study area

This study was carried out in three habitat types within the Atlantic Forest in the state of Rio de Janeiro: peri-urban, sylvatic and rural. The peri-urban environment comprised localities of the Fiocruz Atlantic Forest Campus (CFMA) (22°56′18.00″S, 43° 24′10.13″W) and the Pedra Branca State Park (PBSP) subunit Pau-da-Fome (22°56′55.32″S, 43°26′36.66″W) in the Municipality of Rio de Janeiro. The CFMA partially overlaps with the PBSP, and both are adjacent to an expanding urban region in the Jacarepaguá Basin that encompasses preserved areas. The PBSP is considered the largest forest reserve located within an urban environment in the Americas, covering 12,492 hectares. The predominant vegetation is ombrophilous dense forest. This area was previously occupied by sugar cane mills and coffee farms. During the last decade, the area began to suffer greater anthropogenic pressure as a result of an increasing population, the expansion of low-sanitation communities, the implementation of major infrastructure projects and the expansion of road networks. All samplings were conducted near dwellings and in disturbed forest areas.

The sylvatic environment comprised three localities in the Serra dos Órgãos National Park (PARNASO), Bonfim (22°27′50.53″S, 43°05′17.78″W), Uricanal (22°29′04.99″S, 43°07′02.50″W) and Barragem-do-Caxambú (22°30′09.46″S, 43°07′12.33″W) in the municipality of Petrópolis. PARNASO encompasses 20,024 hectares and is located in the mountain region of the state of Rio de Janeiro, *c.* 80 km from the city of Rio de Janeiro. It includes four municipalities (Teresópolis, Petrópolis, Magé and Guapimirim). The present study was carried out in the municipality of Petrópolis. The park is one of the most important Atlantic Forest remnants in the state of Rio de Janeiro and is internationally recognized as a Biosphere Reserve. Samplings were conducted in areas of preserved dense ombrophilous montane forest in Uricanal and Barragem-do-Caxambú. Bonfim is also within a preserved ombrophilous forest, but it is located closer to human lodgings.

The rural environment comprised the localities of Pamparrão (22°01′47.03″S, 42°39′13.46″W) and Porteira Verde (22°02′20.57″S, 42°39′23.53″W) in the municipality of Sumidouro, in the mountain region of the state of Rio de Janeiro, *c.* 160 km from the city of Rio de Janeiro. Since the 19th century, the economy of this region has been based on agriculture and livestock. Currently, agriculture is the main income source in the region, especially vegetable cultivation and milk production. The area still has some Atlantic Forest remnants of dense ombrophilous forest, mostly in the high mountain ranges. Anthropogenic activities have transformed the landscape into a matrix of agricultural plots and pastures, with small fragments of forest remnants. Samplings were carried out in plantations, pastures and along shrub vegetation.

Host captures

The marsupials were collected in Tomahawk® live-traps (16 × 5 × 5 inches). The collections were made between 2012 and 2015 in wet and dry seasons in forested areas. Each sampling was conducted for five consecutive days in the peri-urban and rural areas and for ten days in the sylvatic area. The traps were placed on the ground in transects of 20 points. All traps were baited with a mixture of peanut butter, banana, oatmeal and bacon. The capture effort included 4560 trap-nights in the peri-urban environment, 2160 trap-nights in the sylvatic area and 1330 trap-nights in the rural area, for a total of 8050 trap-nights.

The animals were captured under the authorization of the Brazilian Government's Chico Mendes Institute for Biodiversity and Conservation (ICMBio, license numbers 13373 and 45839-1) and the Environmental Institute of Rio de Janeiro State (INEA, license number 020/2011). All procedures followed the guidelines for capture, handling and care of animals from

the Ethical Committee on Animal Use of the Oswaldo Cruz Foundation (CEUA license numbers L-049/08, LW-81/12 and LW-39/14). Biosafety techniques and personal safety equipment were used during all procedures involving animal handling and biological sampling.

Helminth recovery and identification

The viscera, thoracic and abdominal cavities, pelvis and musculature of the marsupials were examined for helminths. The helminths were separated in Petri dishes with saline (0.85% NaCl) and dissected under a stereoscopic microscope. The helminths were fixed in AFA solution (93 parts 70% ethanol, 5 parts 0.4% formol and 2 parts 100% acetic acid) and heated to 65°C. Some specimens were stored in 70% ethanol for further molecular analysis. The trematodes were fixed in the same solution under compression, and the cestodes and acanthocephals were kept in distilled water for relaxation of the musculature (Amato *et al.*, 1991). Some of the nematode specimens were diaphanized with lactophenol or glycerinated alcohol. Some of the trematodes, cestodes and acanthocephals were stained with Langeron's carmine or Delafield's haematoxylin, differentiated with 0.5% hydrochloric acid, dehydrated in a crescent alcoholic series, diaphanized in methyl salicylate and fixed in Canada balsam for a permanent preparation (Amato *et al.*, 1991). Subsequently, the specimens were analysed with a light microscope (an Axio Scope.A1-Zeiss coupled to an Axio Cam MRc digital camera) for photomicrography. The specimens were counted and identified using morphological aspects according to Travassos (1937), Yamaguti (1961), Khalil *et al.* (1994), Vicente *et al.* (1997), Gibson *et al.* (2002), Jones *et al.* (2005), Anderson *et al.* (2009) and other articles of species description.

Voucher specimens of the opossums were deposited at the National Museum of Rio de Janeiro, and specimens of the helminths were deposited at the Helminthological Collection of the Oswaldo Cruz Institute (38321, 38322, 38323, 38571, 38572, 38573, 38574, 38575, 38576, 38577, 38578, 38579).

Data analysis

Parasitological parameters were calculated for each helminth species according to Bush *et al.* (1997). The mean abundance was considered as the total number of helminths of a certain species divided by the number of hosts analysed. The mean intensity was calculated as the total number of helminths of a species divided by the number of animals infected by the species. Prevalence was calculated as the proportion of infected animals in relation to the total number of animals analysed. The spatial distribution of the helminths in the host populations was calculated using the variance-to-mean ratio of the abundance of each helminth species, but only for species with prevalence > 10%. The mean species richness was calculated for each municipality as the mean number of species infracommunities for each area.

The abundance, intensity and prevalence rates were compared for the most abundant species according to the habitat type where the host was captured (peri-urban in the municipality of Rio de Janeiro, rural in the municipality of Sumidouro and sylvatic in the municipality of Petrópolis), the host gender (male or female) and the season (dry or rainy). Prevalence, intensity and abundance were compared using generalized linear models (GLM), when the data were available. The best models were chosen using the corrected Akaike information criterion (AICc), which

considered a model plausible if it had $\Delta AICc \leq 2$. Only the models with significant effects were considered.

Synergism or segregation between helminth pairs of species was investigated using the Spearman correlation only for the most abundant species that had similarities in their life cycles and sites of infection in the host, indicating similar niches. An importance index was calculated according to Thul *et al.* (1985) to characterize each species in the community. Each helminth species was classified in the community as dominant ($I \geq 1.0$), co-dominant ($0.01 \leq I \leq 1.0$) or subordinate ($I < 0.01$).

Similarities in helminth species composition and richness among localities (CFMA, Pau-da-Fome, Uricanal, Bonfim, Barragem-do-Caxambú, Pamparrão and Porteira Verde) were evaluated using the non-metric Multidimensional Scaling (nMDS) analysis. In this analysis, the species presence or absence and the Jaccard distance measure were used.

The structure of the helminth metacommunity was evaluated on a regional scale in relation to infracommunity, considering each infected host as a site, and to component community, considering each locality as a subset of hosts. These analyses were performed including all infected animals of the entire study using the EMS analysis. The structure of the metacommunity was also analysed separately on a local scale for each municipality (Rio de Janeiro – peri-urban; Petrópolis – sylvatic; Sumidouro – rural), only in relation to infracommunity in order to compare with the regional metacommunity structure. The three elements of metacommunity structure were evaluated according to Leibold and Mikkelson (2002) and Presley *et al.* (2010). In the EMS analysis, when coherence is significantly positive (number of embedded absences larger than that of the randomly generated matrix), the other parameters are also analysed. When the coherence is not significant, the distribution of the species in the environmental gradient is random. When coherence is significantly negative (number of embedded absences less than that of the randomly generated matrix), a checkerboard distribution is observed (Leibold and Mikkelson, 2002). Nested, Clementsian, Gleasonian and evenly spaced structures are based on the significance of the turnover and boundary clumping, and whether these elements are positive or negative (Leibold and Mikkelson, 2002).

Chi-square tests and nMDS analysis were performed using the statistics package *R* (R Core Team, 2017), and the GLM analysis used the *vegan* package (Oksanen *et al.*, 2017) in RStudio software version 1.0.136. The metacommunity structure analysis used MATLAB R2017B software (MathWorks Inc., Naticks, MA, USA; EMS script available at http://faculty.tarleton.edu/higgins/metacommunity-structure.html). The level of significance was 5% in all the analyses.

Results

During the study, 73 specimens of *D. aurita* were captured, 48 in the peri-urban environment, 13 in the sylvatic areas and 12 in the rural areas. The helminth richness was composed of 14 species belonging to three phyla. Nine species of the phylum Nematoda were found: *Aspidodera railliet* Travassos, 1913 (Ascaridida, Aspidoderidae), *Cruzia tentaculata* (Rudolphi, 1819) Travassos, 1922 (Ascaridida, Kathlaniidae), *Trichuris minuta* Rudolphi, 1819 (Trichocephalida, Trichuridae) and *Trichuris didelphis* Barero, 1959 (Trichocephalida, Trichuridae) in the large intestine; *Travassostrongylus orloffi* Travassos, 1935 (Rhabditida, Viannaiidae), *Viannaia hamata* Travassos, 1914 (Rhabditida, Viannaiidae) and *Globocephalus marsupialis* Freitas & Lent,

1936 (Rhabditida, Ancylostomatidae) in the small intestine; *Heterostrongylus heterostrongylus* Travassos, 1925 (Rhabditida, Angiostrongylidae) in the bronchus and pulmonary bronchioles; and *Turgida turgida* (Rudolphi, 1819) Travassos, 1919 (Spirurida, Physalopteridae) in the stomach. Four species of the phylum Platyhelminthes were identified: three trematode species, *Duboisiella proloba* Baer, 1938 (Strigeidida, Strigeidae), *Brachylaima advena* Dujardin, 1843 (Brachylaemiformes, Brachylaimidae) and *Rhopalias coronatus* (Rudolphi, 1819) Stiles; Hassall, 1898 (Plagiorchiida, Rhopaliidae) in the small intestine, and one species of Cestoda, which was not identified, also located in the small intestine. One species of the phylum Acanthocephala was found in the small intestine, *Oligacanthorhynchus microcephalus* (Rudolphi, 1819) Schmidt, 1972 (Archiacanthocephala, Oligacanthorhynchidae). The species richness was highest in the peri-urban environment (s = 5.32, total = 13 species), followed by the sylvatic environment (s = 3.92, total = 12 species) and the rural environment (s = 2.08, total = 5 species).

No host was infected with all helminth species; only 4.1% were not infected by any helminth species. A total of 145 adult helminths were recovered from *H. heterostrongylus*, 615 from *T. turgida*, 3660 from *C. tentaculata*, 1268 from *A. raillieti*, 5679 from *V. hamata*, 1065 from *T. orloffi* and 112 from *O. microcephalus*. *Viannaia hamata* and *C. tentaculata* were the most abundant species of the study. The most prevalent species were *C. tentaculata* and *T. turgida* (table 1). The seven most abundant species were highly aggregated relative to each studied habitat type (table 2).

Heterostrongylus heterostrongylus had significant differences in prevalence in relation to habitat with higher values in the sylvatic environment (tables 1 and 3). *Cruzia tentaculata* was the second most abundant species, with its abundance being significantly higher in the peri-urban habitat (tables 1 and 4). Statistically significant differences were observed in abundance and prevalence of *T. orloffi* in relation to host, habitat and season, with the abundance and prevalence being higher for males, in the peri-urban habitat and in the dry season (tables 1, 3 and 4). Prevalence of *V. hamata* was significantly higher in male hosts and in the peri-urban habitat (tables 1 and 3). In *O. microcephalus*, prevalence was significantly higher in females and in the peri-urban habitat (tables 1 and 3). For *T. turgida* and *A. raillieti*, no statistically significant differences were found in relation to the analysed parameters.

The sex ratios of *T. turgida*, *H. heterostrongylus* and *O. microcephalus* did not differ from 1 : 1. *Cruzia tentaculata*, *A. raillieti*, *V. hamata* and *T. orloffi* had significantly more females than males ($\chi^2 = 61.48$, $P < 0.0001$; $\chi^2 = 14.25$, $P = 0.0001$; $\chi^2 = 549.02$, $P = 0.0001$; $\chi^2 = 32.45$, $P = 0.0001$, respectively).

Helminth abundance correlations were analysed between *C. tentaculata* and *A. raillieti*, collected in the large intestine, and between *V. hamata* and *T. orloffi*, collected in the small intestine, all presenting direct life cycles. Only *V. hamata* and *T. orloffi* showed a co-occurrence in the hosts ($r_s = 0.50$, $P \leq 0.0001$, N = 47).

The nMDS analysis indicated that, except for the rural locality Porteira Verde in the municipality of Sumidouro, localities with more anthropogenic impact were grouped in the centre of the plot. Those localities set in the margins of the plot represented environments with lower levels of disturbance, such as Barragem-do-Caxambú and Uricanal in PARNASO (fig. 1).

The nematodes *T. turgida*, *C. tentaculata* and *A. raillieti* were dominant in all habitats, while the other helminths were either co-dominant or subordinate (Table 5). *Heterostrongylus heterostrongylus* was dominant only in the sylvatic habitat; *V. hamata*

was dominant in the sylvatic and peri-urban environments; *T. orloffi* was dominant only in the peri-urban environment; *O. microcephalus* was dominant only in the rural environment; and *R. coronatus* was dominant only in the sylvatic habitat (table 5).

The metacommunity analysis indicated that the helminth species showed a coherent structure on the regional scale (table 6). Considering all infracommunities, we observed a quasi-nested structure with stochastic species loss (species turnover and boundary clumping were not significant) (table 6, fig. 2a). Considering all component communities, the observed structure was nested with stochastic species loss (significant negative species turnover and non-significant boundary clumping) (table 6, fig. 2b). On both analyses, species-poor sites had subsets of species-rich sites (fig. 2a, b). Considering each municipality separately, the structure of the metacommunities at the infracommunity level was random in Rio de Janeiro and Sumidouro (urban and rural areas) (non-significant coherence) and revealed a checkerboard structure in Petrópolis (sylvatic area) (significant negative coherence) (table 6).

Discussion

This is the first study of the helminth community structure of *D. aurita*. One previous study reported the structure of helminth communities for another species of the genus *Didelphis*; it was carried out in French Guiana on the component community level (Jiménez *et al.*, 2011). The present study represents a pioneering investigation of the metacommunity structure of the helminths of a Neotropical marsupial.

The most abundant species in the present study (*V. hamata*, *C. tentaculata*, *A. raillieti* and *T. orloffi*) have also been found in other studies of helminth fauna of the genus *Didelphis*. Antunes (2005) found *C. tentaculata* to be the most abundant and prevalent species in *Didelphis albiventris* in Rio Grande do Sul, followed by *A. raillieti*, *T. turgida* and *V. hamata*. *Cruzia tentaculata* was also the most abundant species in *D. aurita* in the state of Rio de Janeiro, followed by *A. raillieti*, *V. hamata* and *T. turgida* in a study by Gomes *et al.* (2003). Silva and Costa (1999) found *C. tentaculata*, *A. raillieti*, *V. hamata*, *T. orloffi*, *T. turgida*, *T. didelphis* and *R. coronatus* in *D. albiventris* in Belo Horizonte. Jiménez *et al.* (2011) found *A. raillieti* and *C. tentaculata* to be the most abundant species of *Didelphis marsupialis* in French Guiana.

Didelphis aurita is a new host for the nematodes *G. marsupialis* and *T. didelphis*. This study provides the first record of the species *G. marsupialis*, *H. heterostrongylus*, *T. orloffi*, *T. minuta*, *T. didelphis* and *D. proloba* in Rio de Janeiro, the first record of *A. raillieti*, *C. tentaculata*, *H. heterostrongylus*, *T. orloffi*, *T. minuta*, *T. didelphis*, *T. turgida*, *V. hamata* and *O. microcephalus* in Petrópolis, and the first record of *H. heterostrongylus* and *O. microcephalus* in Sumidouro.

The greater abundance of females observed in *C. tentaculata*, *A. raillieti*, *V. hamata* and *T. orloffi* suggests an ecological strategy to their reproduction. Increased egg production could contribute to the host infection (Oliveira-Menezes *et al.*, 2011). In polygamous mating systems, sex ratios favouring females may increase the chances of mating (Poulin, 2007).

All the helminth species analysed in this study showed high aggregation rates. Heterogeneity among hosts in relation to parasite exposure is considered to be one of the main factors associated with parasite aggregation (Poulin, 2013).

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Table 1. Intensity, abundance (± SD) and prevalence (95% confidence interval) of the helminth species of *Didelphis aurita* in the state of Rio de Janeiro, Brazil, in relation to habitat, host gender and season.

Parameters	*Heterostrongylus heterostrongylus*	*Turgida turgida*	*Cruzia tentaculata*	*Aspidodera raillieti*	*Viannaia hamata*	*Travassostrongylus orloffi*	*Oligacanthorhynchus microcephalus*
Intensity	6.12 ± 4.96	11.25 ± 11.89	71.09 ± 108.38	29.93 ± 32.17	141.98 ± 252.38	28.03 ± 30.25	4.15 ± 5.17
Male	4.94 ± 3.30	9.98 ± 7.80	82.66 ± 120.66	31.13 ± 33.52	146.87 ± 276.69	29.52 ± 32.76	1.60 ± 5.86
Female	9.67 ± 11.41	16.36 ± 20.52	36.35 ± 51.38	27.15 ± 27.89	122.37 ± 128.91	15.25 ± 13.44	3.14 ± 2.27
Peri-urban	5.31 ± 3.21	10.17 ± 8.26	95 ± 128.04	33.86 ± 36.48	144.46 ± 306.18	28.62 ± 35.15	4.66 ± 6.31
Rural	2	14.87 ± 24.47	8 ± 7.08	16.4 ± 15.60			2.4 ± 1.77
Sylvatic	8.57 ± 9.74	13.29 ± 8.43	20.72 ± 11.73	24.77 ± 26.42	132 ± 137.52	6	2
Dry	3.88 ± 2.10	8.12 ± 6.04	70.16 ± 94.97	31.38 ± 31.45	233.25 ± 356.41	34.19 ± 40.55	2.5 ± 1.74
Rainy	7.25 ± 6.33	13.87 ± 14.82	71.78 ± 118.94	28.88 ± 33.10	81.12 ± 94.72	20.41 ± 14.71	5.93 ± 7.06
Abundance	2.01 ± 4.93	8.48 ± 11.89	54.53 ± 108.38	17.63 ± 32.16	77.79 ± 245.99	14.58 ± 29.45	1.53 ± 5.10
Male	1.58 ± 2.98	7.83 ± 7.80	62 ± 119.86	16.67 ± 33.52	83.92 ± 274.40	17.93 ± 32.35	1.61 ± 5.72
Female	3.41 ± 8.72	10.58 ± 22.10	29.94 ± 55.29	20.76 ± 27.89	57.59 ± 113.54	3.59 ± 11.83	1.29 ± 2.14
Peri-urban	1.77 ± 3.19	8.47 ± 8.25	77.18 ± 128.04	20.45 ± 36.48	96.31 ± 294.33	22.06 ± 34.09	2.04 ± 6.19
Rural	0.16 ± 0.57	9.91 ± 23.54	4 ± 6.67	6.83 ± 13.93			1 ± 1.59
Sylvatic	4.61 ± 9.74	7.15 ± 8.35	17.53 ± 11.73	17.15 ± 25.81	81.23 ± 127.78	0.46 ± 1.66	0.15 ± 0.55
Dry	0.96 ± 1.94	6.34 ± 6.03	52.62 ± 94.97	17.65 ± 31.45	116.62 ± 356.41	22.43 ± 40.55	1.09 ± 1.74
Rainy	2.83 ± 6.27	10.14 ± 14.82	56.02 ± 118.94	17.60 ± 33.10	47.48 ± 91.24	8.46 ± 14.12	1.87 ± 6.64
Prevalence	32.87 (32.84–32.91)	75.34 (75.26–75.43)	76.71 (75.92–77.51)	58.90 (58.66–59.14)	54.79 (52.98–56.59)	52.05 (51.83–52.27)	36.99 (36.94–37.02)
Male	32.14 (32.11–32.16)	78.57 (78.50–78.63)	75 (73.99–76.00)	53.57 (53.29–53.85)	57.14 (54.84–59.44)	60.71 (60.44–60.98)	35.71 (35.66–35.76)
Female	35.29 (35.16–35.42)	64.70 (64.36–65.04)	82.35 (81.51–83.19)	76.47 (76.04–76.89)	47.05 (45.33–48.78)	23.53 (23.34–23.70)	41.17 (41.14–41.20)
Peri-urban	33.33 (33.30–33.36)	83.33 (83.25–83.40)	81.25 (80.09–82.40)	60.41 (60.08–60.74)	66.66 (64.00–69.33)	77.08 (76.77–77.39)	43.75 (43.69–43.80)
Rural	8.33 (8.32–8.34)	66.66 (66.24–67.09)	50 (49.87–50.12)	41.66 (41.41–41.91)			41.66 (41.66–41.69)
Sylvatic	53.84 (53.67–54.01)	53.84 (53.70–53.99)	84.61 (84.41–84.81)	69.23 (68.02–70.43)	61.53 (59.31–63.76)	7.69 (7.66–7.72)	7.69 (7.68–7.70)
Dry	25 (24.97–25.01)	78.12 (78.05–78.19)	75 (73.94–76.05)	56.25 (55.90–56.59)	50 (46.04–53.95)	65.62 (65.17–66.07)	43.75 (43.73–43.76)
Rainy	39.02 (38.96–39.08)	73.17 (73.02–73.31)	78.05 (76.88–79.21)	60.97 (60.65–61.29)	58.53 (57.64–59.43)	41.46 (41.32–41.60)	31.70 (31.64–31.77)

	Duboisiella proloba	*Brachylaima advena*	*Trichuris minuta*	*Globocephalus marsupialis*	*Rhopalias coronatus*	Cestoda	*Trichuris didelphis*
Intensity	16.45 ± 25.45	17.83 ± 16.69	10.16 ± 8.32	8.75 ± 3.13	23.25 ± 13.97	4 ± 1	2.5 ± 0.59
Male	3.23 ± 13.03	3.62 ± 16.21	2.17 ± 8.09	0.51 ± 0.69		0.07 ± 0.54	0.01 ± 0.13
Female		11		6 ± 1.6	13.28 ± 20.95		4 ± 1.06
Periurban	16.45 ± 13.94	17.83 ± 17.36	11 ± 8.65	9.66 ± 0.74	2 ± 0.29		0.14 ± 0.02
Rural							
Sylvatic			1	6 ± 2	30.33 ± 25.98	4	4 ± 1.33
Dry	18.22 ± 16.66	18 ± 19.02	9.16 ± 4.58	1 ± 0.17			1 ± 0.17
Rainy	2.66 ± 0.41	8.99 ± 1.65	8.99 ± 1.63	1.28 ± 0.82	13.18 ± 2.26	0.66 ± 0.09	0.66 ± 0.09
Abundance	2.47 ± 11.18	2.93 ± 14.01	1.67 ± 7.0	0.47 ± 2.84	1.27 ± 9.34	0.05 ± 0.47	0.06 ± 0.48
Male	3.23 ± 12.81	3.62 ± 15.92	2.17 ± 7.95	0.51 ± 3.16		0.07 ± 0.53	0.01 ± 0.13
Female		0.64 ± 2.75		0.35 ± 1.5	5.47 ± 19.63		0.23 ± 1
Periurban	3.85 ± 13.80	4.55 ± 17.19	2.57 ± 8.56	0.61 ± 3.41	0.04 ± 0.29		0.02 ± 0.14
Rural							
Sylvatic			0.07	0.43 ± 1.17	7 ± 22.62	0.30 ± 1.15	0.30 ± 1.15
Dry	5.12 ± 16.66	4.5 ± 19.02	1.71 ± 4.58	0.03 ± 0.17			0.03 ± 0.17
Rainy	2.53 ± 4.87	8.66 ± 7.31	8.54 ± 14.63	3.79 ± 7.31	12.51 ± 9.75	0.63 ± 2.43	0.63 ± 2.43
Prevalence	15.06 (15.15–14.98)	16.43 (16.54–16.33)	16.43 (16.48–16.38)	5.47 (5.50–5.45)	5.47 (5.54–5.41)	1.36 (1.37–1.36)	2.73 (2.74–2.73)
Male	19.64 (19.75–19.53)	19.64 (19.77–19.50)	21.42 (21.49–21.36)	5.35 (5.38–5.33)		1.78 (1.79–1.78)	1.78 (1.78–1.78)
Female		5.88 (5.92–5.84)		5.88 (5.90–5.85)	41.17 (41.47–40.87)		5.88 (5.89–5.86)
Periurban	23.40 (24.53–23.27)	25.53 (25.68–25.37)	23.40 (23.48–23.32)	6.38 (6.41–6.35)	2.12 (2.13–2.12)		2.12 (2.12–2.12)
Rural							
Sylvatic				7.69 (7.72–7.66)	23.07 (23.47–22.68)	7.69 (7.71–7.67)	7.69 (7.71–7.67)
Dry	28.12 (28.30–27.94)	25 (25.21–24.78)	18.75 (18.80–18.69)	3.12 (3.12–3.12)			3.12 (3.12–3.12)
Rainy	4.87 (4.90–4.85)	7.31 (7.40–7.23)	14.63 (14.71–14.55)	7.31 (7.35–7.27)	9.75 (9.87–9.63)	2.43 (2.44–2.43)	2.43 (2.44–2.43)

Table 2. Aggregation indices of each helminth species of *Didelphis aurita* for each habitat in the state of Rio de Janeiro, Brazil.

Species	Aggregation index		
	Rio de Janeiro (Peri-urban)	Petropólis (Sylvatic)	Sumidouro (Rural)
Heterostrongylus heterostrongylus	12.26	20.57	15.21
Turgida turgida	16.76	9.76	21.34
Duboisiella proloba	50.45	-	-
Brachylaima advena	66.04	-	-
Trichuris minuta	28.95	-	-
Cruzia tentaculata	214.40	7.85	54.41
Globocephalus masupialis	16.63	6	-
Aspidodera raillieti	59.57	38.86	57.88
Rhopalias coronatus	67.66	67.67	-
Cestoda	-	4	-
Viannaia hamata	776.90	975.03	-
Travassostrongylus orloffi	59.28	58.45	-
Trichuris didelphis	3.38	4	-
Oligacanthorhynchus microcephalus	16.95	2	23.42

Table 3. Generalized linear models for the helminth prevalences in relation to habitat, host gender and season for helminth species of *Didelphis aurita* in the state of Rio de Janeiro, Brazil. AICc, Akaike information criterion corrected for small sample size; ΔAICc, difference between the AICc of a model and the model of lowest AICc; W, Akaike weight; K, number of parameters; *P*, significance level of the model.

Species	Models	AICc	ΔAICc	W	K	*P*
Heterostrongylus heterostrongylus	Habitat	92.3	0	0.387	3	0.03
	Null	94.5	2.24	0.127	1	-
Travassostrongylus orloffi	Host gender + Habitat	62.9	0	0.382	4	<0.01
	Season + Habitat + Host gender	63.4	0.48	0.301	5	<0.01
	Season + Habitat	64.3	1.40	0.190	4	<0.01
	Null	103.1	40.26	0	1	-
Viannaia hamata	Habitat	84.8	0	0.535	3	<0.01
	Host gender + Habitat	86.6	1.78	0.220	4	<0.01
	Null	102.6	17.81	0	1	-
Oligacanthorhynchus microcephalus	Habitat	95.5	0	0.363	3	0.02
	Host gender + Habitat	96.4	0.93	0.228	4	0.03
	Null	98.3	2.76	0.091	1	-

Table 4. Generalized linear models for the helminth abundances in relation to habitat, host gender and season for helminth species of *Didelphis aurita* in the state of Rio de Janeiro, Brazil. AICc, Akaike information criterion corrected for small sample size; ΔAICc, difference between the AICc of a model and the model of lowest AICc; W, Akaike weight; K, number of parameters; *P*, significance level of the model.

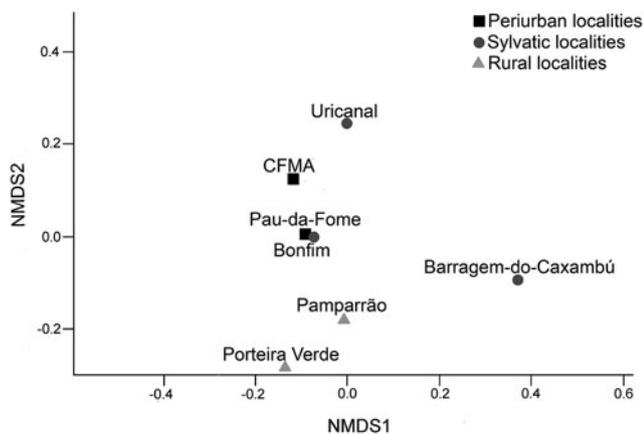| Species	Models	AICc	ΔAICc	W	K	*P*
Cruzia tentaculata	Habitat	892.3	0	0.553	4	0.042
	Null	894.4	2.18	0.128	2	-
Travassostrongylus orloffi	Season + Habitat	697.9	0	0.367	5	0.005
	Habitat	698.9	1	0.222	4	0.009
	Habitat + Host gender	699.6	1.76	0.152	5	0.012
	Season + Habitat + Host gender	699.7	1.81	0.148	6	0.011
	Null	704.2	6.36	0.015	2	-

Fig. 1. Similarity in species composition among localities for helminths of *Didelphis aurita* in the state of Rio de Janeiro, Brazil, using non-metric multidimensional scaling (nMDS).

The nested and quasi-nested results obtained for the metacommunity structure considering component communities and infracommunities, respectively, indicate that areas with a lower species richness form subsets of areas with high species richness. In species-poor sites, hosts share fewer parasites among themselves, and in species-rich sites, there is a sharing of a greater diversity of parasites. The quasi-nested structure indicates a weaker structuring pattern than the nested one, but with the same characteristics. A predictable pattern of species loss among sites characterizes a nested structure, in this case, when a species is absent from a particular site, it is predicted to be absent from all sites with fewer species (Presley *et al.*, 2010). The nested pattern is commonly observed in parasite communities (van der Mescht *et al.*, 2016) and indicates that hosts accumulate parasite species gradually and predictably (Poulin, 2007).

The nMDS analysis indicated that closer localities in the plot represent greater similarities in species composition, suggesting that the clustered localities may have common ecological characteristics that favour the presence of the helminth species. The analysis revealed a central grouping of localities with urban–sylvatic interface environments. Moreover, the nMDS also indicated lower diversity of species among environments. Thus, according to both analyses, nMDS and EMS, the component community of the rural area represented a subset of the component communities of the peri-urban and sylvatic areas. This pattern was also reflected in the infracommunities. The occurrence of dominant species with higher abundance and prevalence, such as *C. tentaculata*, *T. turgida* and *A. raillieti*, in the localities with lower richness indicates that these parasites belong to the core of the component communities. Species such as *G. marsupialis*, *R. coronatus*, *T. didelphis* and *O. microcephalus* occurred in some of the communities and were usually subordinate or co-dominant, forming an intermediate group in the nested pattern. A third group of species, including *D. proloba*, *B. advena* and *T. minuta*, which occurred in only one component community and mostly at a lower abundance and prevalence, can be considered satellite species, contributing to the nested structuring pattern and confirming our hypothesis.

Turgida turgida and *A. raillieti*, which occurred in most of the infracommunities, regardless of the habitat, host gender or season, are widely distributed in Brazil, occurring in all the Brazilian biomes (Santos *et al.*, 1990; Vicente *et al.*, 1997; Silva and

Table 5. Importance indices of each helminth species of *Didelphis aurita* for each habitat in the state of Rio de Janeiro, Brazil.

	Heterostrongylus heterostrongylus	Turgida turgida	Cruzia tentaculata	Aspidodera raillieti	Viannaia hamata	Travassostrongylus orloffi	Oligacanthorhynchus microcephalus
Rio de Janeiro (Peri-urban)	0.356472	4.327052	35.42599452	7.496376228	39.7101	10.5178	0.5524239
	Co-dominant	Dominant	Dominant	Dominant	Dominant	Dominant	Co-dominant
Sumidouro (Rural)	0.121729	57.94279	14.24223981	24.04139	-	-	3.65185636
	Co-dominant	Dominant	Dominant	Dominant	Unsuccessful	Unsuccessful	Dominant
Petrópolis (Sylvatic)	2.932142	4.54482	17.50908	14.01145	58.97794	0.006981	0.00698129
	Dominant	Dominant	Dominant	Dominant	Dominant	Subordinate	Subordinate

	Duboisiella proloba	Brachylaima advena	Trichuris minuta	Globocephalus marsupialis	Rhopalias coronatus	Cestoda	Trichuris didelphis
Rio de Janeiro (Peri-urban)	0.534439255	0.689321952	0.357277	0.023353	0.000536855	-	0.000268
	Co-dominant	Co-dominant	Co-dominant	Co-dominant	Subordinate	Unsuccessful	Subordinate
Sumidouro (Rural)	-	-	-	-	-	-	-
	Unsuccessful	Unsuccessful	Unsuccessful	Unsuccessful	Unsuccessful	Unsuccessful	Unsuccessful
Petrópolis (Sylvatic)	-	-	0.006981	0.041888	1.905892209	0.027925161	0.027925
	Unsuccessful	Unsuccessful	Subordinate	Co-dominant	Dominant	Co-dominant	Co-dominant

Table 6. Results of the analysis of the elements of metacommunity structure for the helminth metacommunity recovered from *Didelphis aurita* in Rio de Janeiro, Petrópolis and Sumidouro municipalities, state of Rio de Janeiro, Brazil. Abs, embedded absences; SD, standard deviation; Rep, replacements; IM, Morisita's index.

Areas	Scales	Coherence				Range turnover				Boundary clumping		Metacommunity structure
		Abs	P	Mean	SD	Rep	P	Mean	SD	IM	P	
Overall	Component communities	12.0	<0.01	30.1	4.69	52.0	<0.01	181.3	45.0	1.14	0.26	Nested random species loss
	Infracommunities	292.0	0.01	374.3	33.86	2799.0	0.34	4201.1	1473.0	1.61	0.14	Quasi-nested random species loss
Rio de Janeiro	Infracommunities	185.0	0.33	205.3	20.90	-	-	-	-	-	-	Random
Petrópolis	Infracommunities	50.0	<0.01	31.97	6.82	-	-	-	-	-	-	Checkerboard
Sumidouro	Infracommunities	8.0	0.10	12.34	2.64	-	-	-	-	-	-	Random

Costa, 1999). They mostly occur in species of the genus *Didelphis*, but have also been recorded in other marsupials (Pinto and Gomes, 1980; Vicente *et al.*, 1982, 1997; Noronha *et al.*, 2002; Gomes *et al.*, 2003). These helminths, together with *C. tentaculata*, formed the main core species of the helminth communities of *D. aurita*. Although there is a great lack of information concerning the ecology of helminths of wild animals, we suggest that these species have wider tolerance limits and niches in relation to their host, as well as to the external environment, when compared to the other helminths found in the present study. These characteristics may result in a larger distribution and abundances throughout the infracommunities and component communities.

Heterostrongylus heterostrongylus also acts as a core species in the present study, however, showing more specific requirements than the previous species, as they were more present in the preserved habitat. This species belongs to the family Angiostrongylidae, most of whose species have heteroxenous life cycles, with molluscs as intermediate hosts, presenting low specificity to infection (Anderson, 2000). Accordingly, preserved environments could provide a greater diversity of resources for the intermediate hosts, contributing to the transmission of this parasite.

Viannaia hamata and *T. orloffi* also belonged to the core of the helminth communities analysed; however, we suggest they may act as local opportunistic species, as they occurred in high abundance and prevalence, but mostly in the peri-urban environment, in males, and the latter in the dry season. The positive correlation between *T. orloffi* and *V. hamata* may be related to similarities in the host acquisition of these parasites, favouring the occurrence of both species in the small intestine. Both species are presumed to have direct life cycles, based on other species of the same superfamily Thrichostrongyloidea and are parasites of Neotropical marsupials (Durette-Desset, 1968; Gomes *et al.*, 2003). In those cases, the host usually becomes infected while feeding on items contaminated with helminth larvae, but the infection can also occur percutaneously (Anderson, 2000). The peri-urban environment provides more food resources for the opossums, where they show higher population densities than in preserved areas (Cáceres and Monteiro-Filho, 1998; Gentile *et al.*, 2000; Kajin *et al.*, 2008). Increases in host density may enhance the parasite transmission, especially in directly transmitted parasites (Bordes *et al.*, 2009). In addition, male opossums have larger movements and home ranges than females (Cáceres and Monteiro-Filho, 2001), which can increase their chances of coming into contact with parasites. Moreover, the higher abundance and prevalence of *T. orloffi* observed during dry periods may indicate that rains could carry away the eggs in the soil, reducing its availability to infect hosts.

The helminths *G. marsupialis*, *T. didelphis*, *R. coronatus* and *O. microcephalus* formed another subset of species on the metacommunity gradient, according to the nestedness. As these helminths occurred in only two kinds of habitats or in lower values than the core species, they are expected to be more specialized than the core ones. *Trichuris didelphis* was previously recorded only for *Didelphis virginiana* (Babero, 1960) and *D. albiventris* (Silva and Costa, 1999; Antunes, 2005). *Globocephalus marsupialis* was previously reported only in *Philander frenatus* (Freitas and Lent, 1936), as well as the helminth *R. coronatus* (Gomes and Vicente, 1972). The latter was also reported in *D. aurita* (Gomes, 1977). Among this subset of helminths, *O. microcephalus* is the only species that needs an intermediate host, generally invertebrate. Although occurring in all habitats, its prevalence
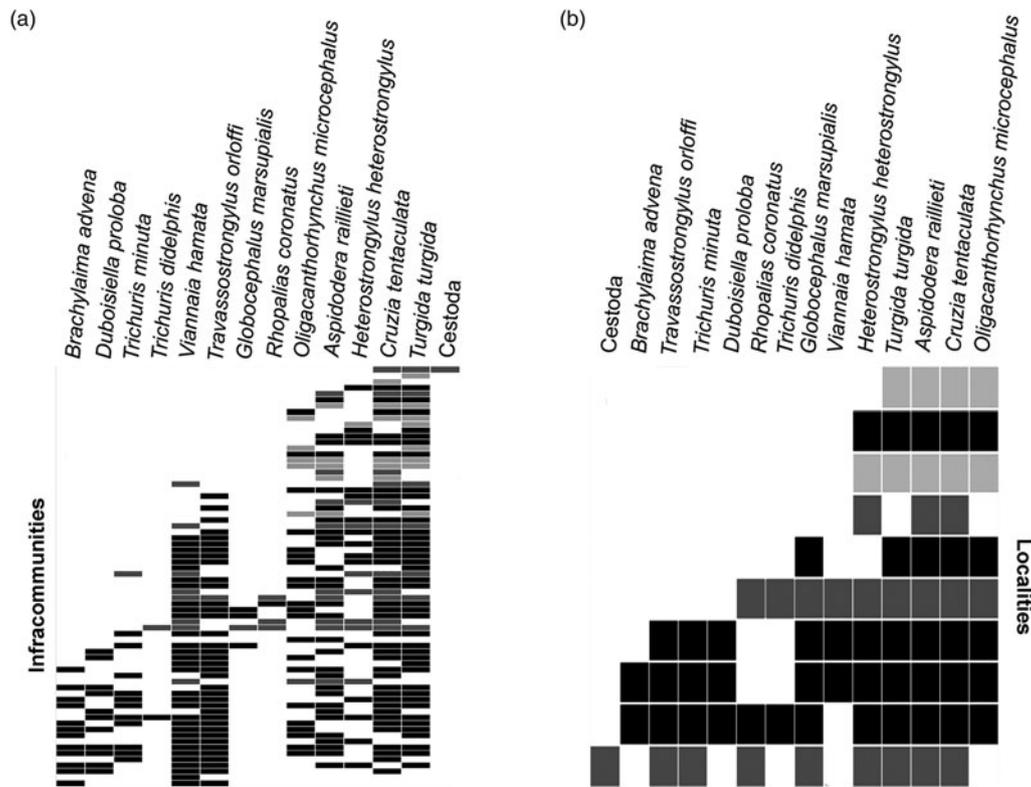
Fig. 2. Ordinated matrices for helminth metacommunities, on the infracommunity and component community levels, of *Didelphis aurita* in Rio de Janeiro, Petrópolis and Sumidouro municipalities. (a) Infracommunity level; the lines correspond to the host specimens, and columns correspond to the helminth species. (b) Component community level; the lines correspond to the localities, and columns correspond to the helminth species. Rio de Janeiro–RJ (black: CFMA includes component communities in three areas and PBSP in two areas) Petrópolis–RJ (dark grey) and Sumidouro–RJ (light grey). Embedded absences were not filled.

was higher in the peri-urban habitat, like most of the core species, but in female opossums. Invertebrates are common components of the opossum's diet (Santori *et al.*, 2012), which suggests that, in this case, infection may be more related to the diet than to the environmental exposure of the host.

The rare species, such as *D. proloba*, *B. advena* and *T. minuta*, which formed a satellite subset, probably have more specific requirements and narrower niches compared to the other species, as they were present in few infracommunities and in low numbers. *Duboisiella proloba* has been reported only twice in *D. aurita* (Travassos *et al.*, 1969; Gomes, 1977); *B. advena* has been reported in *D. aurita*, but more frequently in *P. frenatus* (Travassos *et al.*, 1969); whereas *T. minuta* was reported once in *Chironectes minimus*, *D. albiventris*, *D. marsupialis*, *Marmosa (Marmosa) murina* and in *D. aurita* (Noronha *et al.*, 2002; Antunes, 2005).

Stochastic species loss occurs when species distribution limits are determined by species-specific environmental tolerances (Presley *et al.*, 2010), i.e. when each species responds to variations of the environment in a different way. These responses are easier to observe on a larger spatial scale. When analysed separately for each municipality at the infracommunity level, the communities of urban and rural environments presented random patterns, suggesting host–parasite relationships that were specific to each environment. In those cases, the species did not respond to a single gradient, and their occurrences were scattered among the infracommunities. The non-random nested structure in the parasite community of this host became clear only when viewed on the regional scale because *D. aurita* has a large geographical range, large home ranges and is a generalist, opportunistic species.

These characteristics may promote homogenization among individual hosts in terms of their exposure to parasites within a local scale, resulting in a random structure. The checkerboard pattern found for the infracommunities in the sylvatic area, Petrópolis, suggests the possible existence of interspecific competition among the helminths as a metacommunity structuring mechanism (Presley *et al.*, 2010). A checkerboard structure may also be attributed to the occurrence of rare species in the communities (Schmera *et al.*, 2018), which mostly occurred in the sylvatic area.

The establishment of each parasite in its host can be attributed to heterogeneity among individual hosts in terms of exposure to parasites (Wilson *et al.*, 2001; Poulin, 2013). In addition, extrinsic factors, such as temperature and humidity, can determine the distribution of these parasites, also influencing the survival of some parasite life stages, especially the species whose eggs remain in the soil (Jiménez *et al.*, 2011, Simões *et al.*, 2016). In this way, studies carried out on regional scales, or in a set of ecological communities, may show general ecological patterns such as the structure of a metacommunity (Leibold *et al.*, 2004). In the present study we accepted our hypothesis that the helminth community has a coherent structure on a regional scale, indicating that in this parasite–host relationship the helminth species respond to the environmental gradient non-randomly but gradually and predictably on a wider spatial scale than can be observed at the local level.

References

Amato JFR, Walter AB and Amato SB (1991) *Protocolo para laboratório: coleta e processamento de parasitas do pescado*, 1st Edn. Rio de Janeiro: Imprensa Universitária da Universidade Federal Rural do Rio de Janeiro.

Anderson RC (2000) *Nematode Parasites of Vertebrates: Their Development and Transmission*, 2nd Edn. Farnham Royal: CAB International.

Anderson RC, Chaubaud AG and Willmott S (2009) *Keys to the Nematode Parasites of Vertebrates. Archival Volume*. Wallingford: CABI Publishing.

Antunes GM (2005) *Diversidade e potencial zoonótico de parasitos de* Didelphis albivrentris *Lund, 1841 (Marsupialia: Didelphidae)* (Doctoral thesis). Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Ciências Veterinárias, Porto Alegre, Brazil.

Babero BB (1960) Further studies on helminths of the opossum, *Didelphis virginiana*, with a description of a new species from this host. *Journal of Parasitology* **46**, 455–463.

Bordes F et al. (2009) Home range and parasite diversity in mammals. *American Naturalist* **173**, 467–474.

Brianti E et al. (2012) *Troglostrongylus brevior* and *Troglostrongylus subcrenatus* (Strongylida: Crenosomatidae) as agents of broncho-pulmonary infestation in domestic cats. *Parasites & Vectors* **5**, 1–12.

Bush AO et al. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *The Journal of Parasitology* **83**, 575–583.

Byles B et al. (2013) Gastrointestinal helminths of two species of mouse opossums (*Marmosa demerarae* and *Marmosa murina*) from French Guiana. *Comparative Parasitology* **80**, 210–216.

Cáceres NC and Monteiro-Filho ELA (1998) Population dynamics of the common opossum, *Didelphis marsupialis* (Mammalia, Marsupialia), in southern Brazil. *Zeitschrift fur Saugetierkunde* **63**, 169–172.

Cáceres NC and Monteiro-Filho E (2001) Food habits, home range and activity of *Didelphis aurita* (Mammalia, Marsupialia) in a forest fragment of Southern Brazil. *Studies on Neotropical Fauna and Environment* **36**, 85–92.

Caramaschi U et al. (2000) Anfíbios. In Bergallo HG, Rocha CFD, Alves MAS and Van Sluys M (Eds), *A fauna ameaçada de extinção do Estado do Rio de Janeiro*. Rio de Janeiro: Editora da UERJ, pp. 75–78.

Chagas-Moutinho VA et al. (2014) New Aspidoderidae species parasite of *Didelphis aurita* (Mammalia: Didelphidae): a light and scanning electron microscopy approach. *Acta Tropica* **130**, 162–166.

Durette-Desset MC (1968) Helmintes de marsupiaux américains, Trichostrongyloidea. *Bulletin de la Societé Zoologique de France* **93**, 581–594.

Fonseca GAB and Robinson JG (1990) Forest size and structure: competitive and predatory effects on small mammal communities. *Biological Conservation* **53**, 265–294.

Freitas JFT and Lent H (1936) Estudo sobre o gênero *Globocephalus* Molin, 1861 (Nematoda: Strongyloidea). *Memórias do Instituto Oswaldo Cruz* **31**, 69–79.

Gentile R et al. (2000) Population dynamics and reproduction of marsupials and rodents in a Brazilian rural area: a five-year study. *Studies on Neotropical Fauna and Environment* **35**, 1–9.

Gentile R et al. (2006) An ecological field study of the water rat *Nectomys squamipes* as a wild reservoir indicator of *Schistosoma mansoni* transmission in an endemic area. *Memórias do Instituto Oswaldo Cruz* **101**, 111–117.

Gibson DI, Jones A and Bray RA (2002) *Keys to the Trematoda, Volume 1.* London: CABI Publishing and the Natural History Museum.

Gilpin ME and Hanski I (1991) *Metapopulation Dynamics: Empirical and Theoretical Investigations*, 1st Edn. London: Academic Press.

Gomes DC (1977) *Contribuição ao conhecimento dos helmintos parasitos de marsupiais no Brasil, da Coleção Helmintológica do Instituto Oswaldo Cruz* (Doctoral thesis). Instituto de Biologia da Universidade Federal Rural do Rio de Janeiro, Brazil.

Gomes DC and Vicente JJ (1972) Estudo do gênero *Rhopalias* Stiles & Hassall, 1898 (Trematoda, Rhopaliasidae). *Memórias do Instituto Oswaldo Cruz* **70**, 115–133.

Gomes DC et al. (2003) Nematode parasites of marsupials and small rodents from the Brazilian Atlantic Forest in the State of Rio de Janeiro, Brazil. *Revista Brasileira de Zoologia* **20**, 699–707.

Jiménez FA, Catzeflis F and Gardner SL (2011) Structure of parasite component communities of didelphid marsupials: insights from a comparative study. *Journal of Parasitology* **97**, 779–787.

Jones A, Bray RA and Gilbson DI (2005) *Keys to the Trematoda, Volume 2.* London: CAB International.

Kajin M et al. (2008) Nine year demography of the black-eared opossum *Didelphis aurita* (Didelphimorphia: Didelphidae) using life tables. *Revista Brasileira de Zoologia* **25**, 206–213.

Khalil LF, Jones AB and Bray RA (1994) *Keys to the Cestode Parasites of Vertebrates*. Wallingford: CAB International.

Laurance WF (1999) Reflections on the tropical deforestation crisis. *Biological Conservation* **91**, 109–117.

Leibold MA and Mikkelson GM (2002) Coherence, species turnover, and boundary clumping: elements of meta-community structure. *Oikos* **97**, 237–250.

Leibold MA et al. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**, 601–613.

Moura MC, Vieira MV and Cerqueira R (2009) Occasional intraguild predation structuring small mammal assemblages: the marsupial *Didelphis aurita* in the Atlantic Forest of Brazil. *Austral Ecology* **34**, 481–489.

Noronha D, Vicente JJ and Pinto RM (2002) A survey of new host records for nematodes from mammals deposited in the helminthological collection of the Oswaldo Cruz Institute (CHIOC). *Revista Brasileira de Zoologia* **19**, 945–949.

Oksanen J et al. (2017) Vegan: community ecology package. R package version 2.4-2. Accessed on 10 February, 2017 from http://CRAN.R-project.org/package=vegan

Oliveira-Menezes A, Lanfredi-Rangel A and Lanfredi RM (2011) The first description of eggs in the male reproductive system of *Physaloptera bispiculata* (Nematoda: Spiruroidaea). *Journal of Helminthology* **85**, 142–145.

Pinto RM and Gomes DC (1980) Contribuição ao conhecimento da fauna helmintológica da Região Amazônica, Nematódeos. *Atas da Sociedade de Biologia do Rio de Janeiro* **21**, 65–74.

Poulin R (2007) *Evolutionary Ecology of Parasites*, 2nd Edn. Princeton, NJ: Princeton University Press.

Poulin R (2013) Explaining variability in parasite aggregation levels among host samples. *Parasitology* **140**, 541–546.

Poulin R and Dick AT (2007) Spatial variation in population density across the geographical range in helminth parasites of yellow perch *Perca flavescens*. *Ecography* **30**, 629–636.

Presley SJ, Higgins CL and Willig MRA (2010) Comprehensive framework for the evaluation of metacommunity structure. *Oikos* **119**, 908–917.

Prestwood AK, Nettles VF and Farrell RL (1977) Pathologic manifestations of experimentally and naturally acquired lungworm infections in opossums. *American Journal of Veterinary Research* **38**, 529–532.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. Vienna, The R Project for Statistical Computing. Accessed on 10 June, 2017 from http://www.r-project.org

Richgels KLD, Hoverman JT and Johnson PTJ (2013) Evaluating the role of regional and local processes in structuring a larval trematode metacommunity of *Helisoma trivolvis*. *Ecography* **36**, 854–863.

Rocha CFD *et al.* (2003) *A biodiversidade nos grandes remanescentes florestais do Estado do Rio de Janeiro e nas restingas dos corredores da Mata Atlântica*, 1st Edn. São Carlos: Rima Editora.

Santori RT, Lessa LG and Astúa D (2012) Alimentação, nutrição e adaptações alimentares de marsupiais brasileiros. In Cáceres NC (ed.), *Os marsupiais do Brasil: Biologia, ecologia e conservação*. Campo Grande: Editora UFMS, pp. 385–406.

Santos CP, Lent H and Gomes DC (1990) The genus *Aspidodera* Railliet & Henry, 1912 (Nematoda: Heterakoidea): revision, new synonyms and key for species. *Revista Brasileira de Biologia* **50**, 1017–1031.

Schmera D *et al.* (2018) On the reliability of the elements of metacommunity structure framework for separating idealized metacommunity patterns. *Ecological Indicators* **85**, 853–860.

Scott DM *et al.* (2006) The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. *Biological Conservation* **127**, 72–87.

Silva MGQ and Costa HMA (1999) Helminths of white-bellied opossum from Brazil. *Journal of Wildlife Diseases* **35**, 371–374.

Simões RO *et al.* (2011) Variation in the helminth community structure of the sympatric sigmodontine rodents from the coastal Atlantic forest of Rio de Janeiro, Brazil. *Journal of Helminthology* **85**, 171–178.

Simões RO *et al.* (2014) A longitudinal study of *Angiostrongylus cantonensis* in an urban population of *Rattus norvegicus* in Brazil: the influences of seasonality and host features on the pattern of infection. *Parasites & Vectors* **7**, 1–8.

Simões RO *et al.* (2016) Biotic and abiotic effects on the intestinal helminth community of the brown rat *Rattus norvegicus* from Rio de Janeiro, Brazil. *Journal of Helminthology* **90**, 21–27.

Suzán G *et al.* (2015) Metacommunity and phylogenetic structure determine wildlife and zoonotic infectious disease patterns in time and space. *Ecology and Evolution* **5**, 865–873.

Thatcher VE (2006) Endoparasitos dos marsupiais brasileiros. In Cáceres N and Monteiro Filho E (Eds), *Os marsupiais do brasil: biologia, ecologia e evolução*. Campo Grande: Editora UFMS, pp. 53–68.

Thul E *et al.* (1985) Ecology of parasitic helminths of wood ducks, *Aix sponsa*, in the Atlantic Flyway. *The Helminthological Society of Washington* **52**, 297–310.

Travassos LP (1937) *Revisão da família Trichostrongylidae Leiper, 1912*. Rio de Janeiro: Monografias do Instituto Oswaldo Cruz.

Travassos LP, Freitas JFT and Kohn A (1969) Trematódeos do Brasil. *Memórias do Instituto Oswaldo Cruz* **67**, 1–886.

Turner IM (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* **33**, 200–209.

van der Mescht L *et al.* (2016) The influence of life history characteristics on flea (Siphonaptera) species distribution models. *Parasites & Vectors* **9**, 1–10.

Vicente JJ, Gomes DC and Araujo-Filho NA (1982) Alguns helmintos de marsupiais e roedores da Ilha Grande, Estado do Rio de Janeiro. *Atas da Sociedade de Biologia do Rio de Janeiro* **26**, 3–4.

Vicente JJ *et al.* (1997) Nematoides do Brasil. Parte V: nematoides de mamíferos. *Revista Brasileira de Zoologia* **14**, 1–452.

Wilson K *et al.* (2001) Heterogeneities in macroparasite infections: patterns and processes. In Hudson PJ *et al.* (Eds), *The Ecology of Wildlife Diseases*. Oxford: Oxford University Press, pp. 6–44.

Winegardner AK *et al.* (2012) The terminology of metacommunity ecology. *Trends in Ecology and Evolution* **27**, 253–254.

Yamaguti S (1961) *Systema helminthum. Vol. III. The nematodes of vertebrates, pt. I & II*. New York, NY: Interscience Publishers Inc.