



Composition and structure of the helminth community of rodents in matrix habitat areas of the Atlantic forest of southeastern Brazil

Camila dos Santos Lucio^{a,b,*}, Rosana Gentile^b, Thiago dos Santos Cardoso^{a,b,c},
Fernando de Oliveira Santos^{a,b}, Bernardo Rodrigues Teixeira^b, Arnaldo Maldonado Júnior^b,
Paulo Sergio D'Andrea^b

^a Programa de Pós-Graduação em Biodiversidade e Saúde / IOC/Fiocruz-RJ, Brazil

^b Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios- IOC/Fiocruz-RJ, Brazil

^c Fundação Oswaldo Cruz, Programa Fiocruz de Fomento à Inovação - INOVA FIOCRUZ, Av. Brasil 4365, Rio de Janeiro, CEP 21040-360, RJ, Brazil

ARTICLE INFO

Keywords:

Anthropogenic areas
Ecology
Nematoda
Parasite
Parasitism
Small mammals

ABSTRACT

The predominant landscape of the Atlantic Forest of the Brazilian state of Rio de Janeiro is made up of forest fragments surrounded by a matrix of modified habitat, which may influence the occurrence and distribution of host species and their parasites in comparison with the original continuous forest. The present study describes the structure, composition, and diversity of the helminth community found in rodents in two areas of an open matrix of different status of conservation. The abundance, intensity, and prevalence were calculated for each helminth species in rodent species. The influence of biotic and abiotic factors on the abundance and prevalence of the helminth species was also investigated. Community structure was analyzed based on the beta diversity and a bipartite network. Nine helminth species were recovered from *Akodon cursor*, *Necromys lasiurus* and *Mus musculus*, with the greatest helminth species richness being recorded in *A. cursor* (S = 8), followed by *N. lasiurus* (S = 6), and *M. musculus* (S = 3). Only three of the helminths recorded in *A. cursor* had been recorded previously in this rodent in the Atlantic Forest, where 12 different helminths have been recorded, so that the other five are new occurrences for this rodent. All the helminth species of *N. lasiurus* had been reported previously in this rodent in the Cerrado and Caatinga regions. *Mus musculus* was infected with the same helminths as the local fauna. Host species and locality were the most important factors influencing helminth abundance and prevalence. Beta-diversity was high for infracommunities indicating more substitutions of helminth species than losses among individuals. Three helminth species were shared by the three host species. The reduced beta-diversity observed in the component communities was consistent with the overlap observed in the helminth fauna of the host species.

1. Introduction

Modifications of the landscape may affect a range of ecological processes and biological parameters and, ultimately, may alter the fitness of the local species (Palmeirim et al., 2019). In Brazil, much of the original forest cover has been converted into farmland and urban infrastructure (Estavillo et al., 2013). This process has reduced the majority of Brazilian biomes to habitat mosaics, with remnants of native forest surrounded by an anthropogenic matrix. This matrix may be formed by farmland, pastures or non-native grassland at varying successional stages. The Atlantic Forest has significant levels of biodiversity and is one of the Brazilian forest formations that have been most

impacted, with only 12.4% of its original cover now remaining (FUNDAÇÃO SOS MATA ATLÂNTICA 2018), which supports the classification of this region as a hotspot of biodiversity (Mittermeier et al., 1998).

Part of these deforested areas of the Atlantic Forest is formed by a matrix of open grassland, which is not an appropriate habitat for most of the native small mammals (Umetsu et al., 2008), but may favour the presence of some generalist rodents or exotic synanthropic species (Pardini et al., 2010; Gonçalves et al., 2016). The sigmodontine rodent *Necromys lasiurus* (Lund, 1840), is typical of the open formations of the Cerrado and Caatinga biomes in Brazil and in temperate grassland in Argentina and Paraguay (Patton et al., 2015), also found in open or

* Corresponding author. Programa de Pós-Graduação em Biodiversidade e Saúde / IOC/Fiocruz-RJ, Brazil.

E-mail address: camilalucio@aluno.fiocruz.br (C.S. Lucio).

<https://doi.org/10.1016/j.ijppaw.2021.07.001>

Received 28 April 2021; Received in revised form 24 June 2021; Accepted 7 July 2021

Available online 9 July 2021

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disturbed areas of the Atlantic Forest (Oliveira-Santos et al., 2018). *Akodon cursor* (Winge, 1887) is the most abundant sigmodontine rodent of the Atlantic Forest, occurring predominantly in the coastal lands below 1,170 m in forested and disturbed areas and also in isolated mesic forests in the Caatinga (Geise, 2012). *N. lasiurus* and *A. cursor* have been reported in high abundances in anthropogenic matrix areas of the Atlantic Forest of Rio de Janeiro state (Pires et al., 2010). These two species, together with the sigmodontine rodent *Oligoryzomys nigripes* (Olfers, 1818) and the exotic house mouse, *Mus musculus* (Linnaeus, 1758), form the principal rodent community found in these areas (Oliveira-Santos et al., 2018). Furthermore, it is important to mention that *N. lasiurus*, *A. cursor*, *O. nigripes*, and *M. musculus* have all been identified as reservoirs of zoonotic agents elsewhere (Fonseca et al., 2011; Limongi et al., 2013; Oliveira et al., 2014).

The occurrence of invasive mammals, and their parasites, may have a major impact on the structure of resident mammal communities, their parasite-host relationships, and may eventually modify the transmission cycles of many etiological agents (Bush et al., 2001). In this scenario, invasive species, which are often highly competent for the transmission of certain zoonotic agents (Bruno and Bard, 2012; Herrera et al., 2008; Sales et al., 2010), may transmit them to native species, a process known as spillover. In counterpart, invasive species may also lose their natural parasites and/or acquire new parasites from native species, which may result in an increase in the abundance of these parasites and an associated increase in the probability of infection of the native species, a process known as spillback (Poulin, 2017).

Helminths are one of the principal parasite groups found in rodents (Han et al., 2016; Kersul et al., 2020). Helminths are considered to be good indicators of environmental changes (Vidal-Martínez and Wunderlich, 2017) and represent a public health problem in many parts of the world, where they are the principal agents that cause parasitic diseases in humans and other animals, both wild and domestic (Han et al., 2015). In fact, the characteristics of the environment, including seasonality and habitat, as well as the evolutionary history and functional attributes of the hosts, such as their age, size of their home range, and population density, may influence the parasitological parameters, such as abundance and prevalence of these parasites (Simões et al., 2010; Kamiya et al., 2014; Cardoso et al., 2016; Dallas et al., 2019). Given this, studies of parasite communities contribute to the understanding of the local and regional processes that affect the distribution patterns of species at different ecological scales. The infracommunity scale refers to the parasite species present in an individual host, and the component community scale refers to the parasite species in a host population (Bush et al., 1997).

Despite the impact of the fragmentation of the Atlantic Forest on the occurrence and distribution of mammal species and their parasites, no data are available on the ecological parameters of these interactions in areas of open matrix. Moreover, previous studies of the helminth fauna of *N. lasiurus* were carried out in Cerrado (Costa et al., 2019; Grossmann, 2015) and Caatinga (Quentin, 1967, 1968; Durette-Desset, 1968; Quentin et al., 1968; Simões et al., 2017), with a single report (one host with one helminth species) in an agroforestry of the Atlantic Forest (Kersul et al., 2020), and another study in the Silver River basin, Argentina (Robles, 2008). Considering the studies of *A. cursor* helminth fauna, they were conducted in forested and forest fragment areas of the Atlantic Forest (Gomes et al., 2003; Simões et al., 2011) and also in the same agroforestry cited for *N. lasiurus* (Kersul et al., 2020). Yet, there is no study of the helminth fauna of *M. musculus* in populations established in wild environments in the Atlantic Forest. In this context, the present study describes the structure, composition, and diversity of the helminth community of rodent species in two contiguous areas of open Atlantic Forest matrix with distinct land use in their surroundings. The similarities in the parasite species composition among hosts were determined and the results were compared with previous studies of the helminth fauna of these mammalian hosts. We hypothesize that: (i) the helminth fauna of *N. lasiurus* in the Atlantic Forest is similar to its helminth fauna

in Cerrado and Caatinga regions; (ii) *A. cursor* helminth fauna follows the records found in forested and forest fragment areas of the Atlantic Forest; and (iii) *Mus musculus* shows the helminths of the local hosts, as it is a generalist and exotic species found in the rodent community, which was introduced since the European colonization in Brazil. We also investigated the influence of biotic (host species, age and sex) and abiotic (locality) factors on the helminth abundance and prevalence in each rodent species. A bibliographic survey of the helminth fauna of these three rodents, as well as all records for the helminth species found, were also provided herein.

2. Materials and methods

2.1. Study area

The present study was conducted in the São João River Basin Environmental Protection Area (APA-BRSJ), on the border between the municipalities of Casimiro de Abreu and Silva Jardim (22°33'25.99"S, 42°12'06.01"W), and in the Poço das Antas Biological Reserve (REBIO Poço das Antas) in the municipalities of Silva Jardim and Casimiro de Abreu (22°30'11.85" S, 42°16'02.73"W), in the state of Rio de Janeiro, southeastern Brazil (Fig. 1). The mean temperature for the study period was 28.9 °C (minimum of 18 °C and maximum of 37 °C). Total rainfall was of 1217 mm from April 2017 to March 2018 (first year of the study) and 1640 mm from April 2018 to March 2019 (second year of the study). Data were obtained from the automatic meteorological station in Silva Jardim (INMET, 2020).

The REBIO Poço das Antas and the APA-BRSJ are located within a region covered originally by Atlantic Forest habitats, which included paleolagoons, swamps, mangroves, and marshes (ICMBIO, 2005). A dam was constructed between 1971 and 1975, which aimed to support the socio-economic recovery of the region of the Rio São João valley (ICMBIO, 2005). The completion of the dam, together with the establishment of a canal network, initiated an intense process of land drainage, which resulted in the modification of the region's hydrography, including the Aldeia Velha and São João rivers, which were channeled and had their natural courses altered. This drainage process led to the formation of peat bogs, which are extremely vulnerable to wildfires (ICMBio, 2005; Barros, 2007). The modification of this landscape reduced the original forest cover by 60%, with only 10% of dense forest (ICMBio, 2005). The REBIO Poço das Antas and APA-BRSJ are currently separated by the Aldeia Velha and São João canals and have distinct systems of land use and management (ICMBIO, 2005; Mello et al., 2008). This separation did not exist prior to the canal-building process.

The REBIO Poço das Antas is a strictly protected area of Atlantic Forest biodiversity, which was established in 1974 (ICMBIO, 2005), although it has a long history of human impact, such the cattle ranching and some subsistence farming. This reserve now implements regular management measures to preserve and recover its biological diversity and natural ecological processes. Since the creation of the reserve in 1974 to the present day, there has been a minimization of human impacts, in which the presence of cattle ranching and subsistence farming is no longer found within REBIO Poço das Antas. Currently, the region has areas of anthropic fields surrounded by secondary forest remnants in different successional stages: lowland forest (lowland forest/alluvial forest), hillside forest (morrote forest/submontane forest), pioneer formation with river influence, lowland capoeira (lowland capoeira/alluvial capoeira), hillside capoeira (morrote capoeira/submontane capoeira) and anthropic fields (Vieira and Pessoa, 2001). The study samplings were carried out in a region called Ilha dos Barbados. In this area, the matrix vegetation cover is homogeneous, mainly composed by grasses such as *Imperata brasiliensis*, *Panicum maximum* and *Melinis minutiflora*, and by ferns, shrubs and scattered pioneer trees (Pires et al., 2002). The APA-BRSJ is a sustainable use conservation unit which was created to protect and conserve water resources and forest remnants

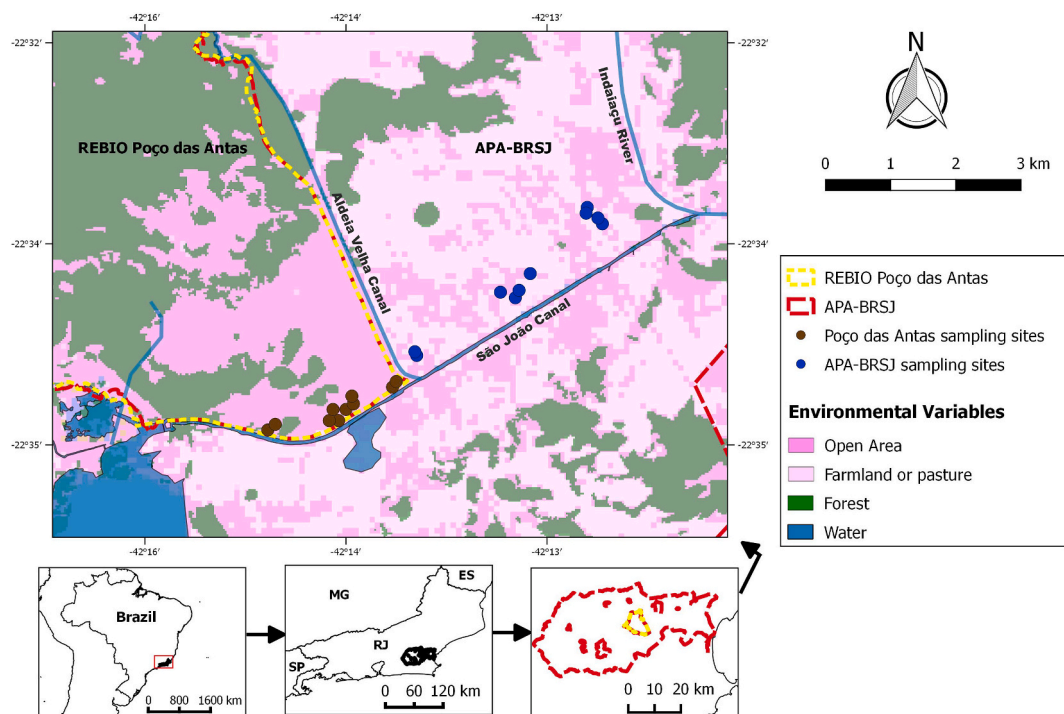


Fig. 1. Location of the sampling sites within the REBIO Poço das Antas and the APA-BRSJ in Rio de Janeiro state (RJ), southeastern Brazil, showing the distribution of the different vegetation types and the canals that separate the two reserves.

(Mello et al., 2008), with a predominance of open anthropogenic matrices due to intensive land use by subsistence farmers and their livestock. In the sampling areas, there is a predominance of grasses, as in Ilha dos Barbados, in addition to the presence of small forest fragments. However, it differs from REBIO Poço das Antas mainly because it has pastures and areas with exposed soil resulting from land use. The surrounding areas are mainly devoted to subsistence planting with the presence of human dwellings. Unlike REBIO Poço das Antas, the influence of anthropic action continues nowadays.

2.2. Collection and examination of rodents

Rodents were captured in two localities of the Atlantic Forest matrix in the REBIO Poço das Antas and APA-BRSJ, on drained land dominated by peat bog and pasture (Fig. 1). The rodents were trapped using 300 Sherman (Tallahassee, Florida; 7.62 cm × 9.53 cm × 30.48 cm) and 100 Tomahawk (Hazelhurst, Wisconsin; 40.64 cm × 12.70 cm × 12.70 cm) live-traps, which were deployed along 10 linear transects. The traps were baited with a mixture of a banana, flaked corn meal, peanut butter, and sardine or bacon. Each capture session included five consecutive nights in April 2017, September 2017, and September 2018. Standard biosafety procedures were employed during all handling of biological samples (Lemos & D'Andrea, 2014). All the animals were euthanized for the collection of tissue samples and the recovery of the helminths. The age of the animals were estimated based on a set of physical characteristics, including body mass and length, and reproductive condition, defined for each species according to the parameters defined in previous sigmodontine studies (Gentile et al., 2000). The animals were submitted to taxidermy and the voucher specimens were deposited in the mammal collection at LABPMR/IOC-Fiocruz in Rio de Janeiro. The rodent specimens were identified taxonomically based on their morphology and karyotypes—diploid and fundamental chromosome numbers (Bonvicino, 2011).

All field procedures followed the standards of capture, handling, and care recommended by the Ethics Committee on the Use of Animals of the Oswaldo Cruz Foundation (license CEUA LW-39/14) and a federal

license for the capture of wild mammals (58374-2 MMA/ICMBio/SISBIO).

2.3. Collection and identification of helminths

The thoracic and abdominal cavities of the rodent specimens, including the stomach, and small and large intestine, were examined under a stereoscopic microscope for the identification of helminths. All the helminths were washed twice in saline to remove tissue debris and preserved in 70% ethanol for later identification and counting. The nematodes were cleared with lactophenol, and the cestodes and acanthocephalans were stained with Langeron's carmine, differentiated by 0.5% hydrochloric acid, dehydrated in an alcohol series, diaphanized in methyl salicylate, and mounted in Canada balsam on microscopic slides (Amato et al., 1991, modified). In some trichostrongylid species, cross sections of the specimens were obtained for the examination of the synlophe using a stereoscopic microscope. All the specimens were analyzed by light microscopy, and the morphometry was analyzed using digital images taken with a Zeiss AxioCam HRC (Göttingen, Germany) using the AxioVision Rel. 4.7 software (Zeiss, Göttingen, Germany). The taxonomic identification of the helminths were based on Travassos (1937), Yamaguti (1961), Khalil et al. (1994), Vicente et al. (1997), Anderson et al. (2009), and Amin (2013). The specimens were deposited in the scientific collection of helminths at the Laboratory of the Biology and Parasitology of Wild Mammal Reservoirs- IOC/Fiocruz-RJ.

2.4. Data analysis

Population parameters (abundance, prevalence and intensity) were calculated for each species of helminth according to Bush et al. (1997), considering the variables: host sex (male or female), age (juvenile or adult), and species (*Akodon cursor*, *N. lasiurus* or *M. musculus*), and locality (APA-BRSJ or REBIO Poço das Antas). The overall helminth species richness was determined as the number of species found in all the hosts examined. The mean species richness of the helminths was determined by the sum of the number of species found in each

infracommunity divided by the total number of infracommunities analyzed. The mean abundance was given by the total number of helminths of a given species divided by the number of hosts analyzed. The mean intensity was considered as the total number of helminths of a given species divided by the number of hosts infected by this species. The prevalence was the ratio between the number of infected hosts and the total number of hosts analyzed.

Species accumulation curves were constructed in order to evaluate the adequacy of the sampling effort. The curves were built using the collector method, considering a descending order from the highest to the lowest value of the total helminth richness for each infracommunity. This analysis was run for the infracommunities of each host species separately.

The abundance and prevalence of the helminth species, which occurred in more than one host species, were compared among host species, sex, and age, and locality, which reflects the different types of land use, using generalized linear models (GLMs). Models containing all possible combinations of the variables were tested (global model: Host species + Host sex + Host age + Locality). The best models were chosen using the corrected Akaike Information Criterion (AICc), in which the plausible models were identified when $\Delta AICc \leq 2$.

Parasite importance indices were calculated in order to understand the role of a given helminth species in the helminth community.

Dominant parasites has mostly higher abundance and prevalence in relation to the other parasite species in a certain community. The indices were calculated following Thul et al. (1985) for each host component community. Helminth species in the community were classified as dominant (species that mostly contribute to the community) ($I \geq 1.0$), co-dominant (contribute significantly to the community, although to a lesser degree than the dominant species) ($0.01 \leq I < 1.0$) or subordinate (occur infrequently and contribute less than other species to the community) ($0 < I < 0.01$).

A bipartite network analysis was carried out between the rodent and helminth species to represent 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 rodent.

Beta-diversity, which represents a change in species composition and abundance in a community between distinct sites (Whittaker 1960), were evaluated by calculating the multiple-site dissimilarity for both the infra- and component communities considering both areas together. Beta-diversity was decomposed into spatial turnover and nestedness to investigate whether diversity was driven by the replacement or loss of helminth species, respectively, as proposed by Baselga (2010). This analysis was based on a dissimilarity matrix of the Sorensen index.

The GLM analyses and the species accumulation curves were run in the *vegan* package (Oksanen et al., 2017), the bipartite network analysis

Table 1

Mean (\pm SD) abundance, mean (\pm SD) intensity, prevalence (95% confidence intervals), and site of infection of the helminth species recorded in *Akodon cursor* (Rodentia, Cricetidae) in relation to the age and sex of the host, and the type of matrix surveyed in the REBIO Poço das Antas, municipality of Silva Jardim, state of Rio de Janeiro, Brazil. A dash (–) indicates the absence of the species in the respective category.

Species						
Parameter	<i>P. numidica criceticola</i>	<i>P. (Pauciceptines) zygodontomis</i>	<i>M. necromysi</i>	<i>S. aculeata</i>	<i>S.eta</i>	<i>S. freitasi</i>
Infection site	Stomach	Small intestine	Small intestine	Small intestine	Small intestine	Small intestine
Life Cycle	Indirect	Indirect	Indirect	Direct	Direct	Direct
Abundance	0,29 \pm 0,98	0,01 \pm 0,11	0,01 \pm 0,11	0,15 \pm 1,30	0,10 \pm 0,82	0,43 \pm 2,67
Male (n = 43)	0,40 \pm 1,22	0,02 \pm 0,15	0,02 \pm 0,15	0	0	0,72 \pm 3,45
Female (n = 29)	0,14 \pm 0,44	0	0	0,38 \pm 2,04	0,24 \pm 1,29	0
Juvenile (n = 29)	0,17 \pm 0,66	0	0	0	0	1,07 \pm 4,17
Adult (n = 43)	0,37 \pm 2,61	0,02 \pm 0,21	0,02 \pm 0,21	0,26 \pm 1,68	0,16 \pm 1,07	0
REBIO Poço das Antas (n = 71)	0,30 \pm 0, 99	0,01 \pm 0,12	0,01 \pm 0,12	0,16 \pm 1,31	0,10 \pm 0,83	0,44 \pm 2,69
Intensity	2,10 \pm 1,89	1,00 \pm 0	1,00 \pm 0	11,00 \pm 0	7,00 \pm 0	15,50 \pm 6,36
Male (n = 43)	2,43 \pm 2,15	1,00 \pm 0	1,00 \pm 0	0	0	15,50 \pm 6,36
Female (n = 29)	1,33 \pm 0,58	0	0	11,00 \pm 0	7,00 \pm 0	0
Juvenile (n = 29)	2,50 \pm 0,71	0	0	0	0	15,50 \pm 6,36
Adult (n = 43)	2,00 \pm 2,07	1,00 \pm 0	1,00 \pm 0	11,00 \pm 0	7,00 \pm 0	0
REBIO Poço das Antas (n = 71)	2,10 \pm 1,89	1,00 \pm 0	1,00 \pm 0	11,00 \pm 0	7,00 \pm 0	15,50 \pm 6,36
Prevalence	12,50 (11,78–13,23)	1,39 (1,30–1,48)	1,39 (1,30–1,48)	1,39 (0,43–2,35)	1,39 (0,78–1,99)	2,78 (0,80–4,75)
Male (n = 43)	16,28 (15,12–17,44)	2,33 (2,18–2,47)	2,33 (2,18–2,47)	0	0	4,65 (1,36–7,95)
Female (n = 29)	10,35 (9,83–10,86)	0	0	3,45 (1,07–5,83)	3,45 (1,94–4,96)	0
Juvenile (n = 29)	6,90 (6,13–7,66)	0	0	0	0	6,90 (2,04–11,76)
Adult (n = 43)	18,61 (16,10–21,10)	2,33 (2,12–2,52)	2,33 (2,12–2,52)	2,33 (0,72–3,93)	2,33 (1,31–3,35)	0
REBIO Poço das Antas (n = 71)	14,09 (13,35–14,82)	1,41 (1,32–1,50)	1,41 (1,32–1,50)	1,41 (0,44–2,38)	1,41 (0,79–2,03)	2,82 (0,81–4,82)
<i>T. navonae</i>						<i>S. (Syphacia) alata</i>
Large intestine						Large intestine
Direct						Direct
0,29 \pm 0,85						0,03 \pm 0,24
0,42 \pm 0,98						0,05 \pm 0,30
0,10 \pm 0,56						0
0,21 \pm 0,62						0,07 \pm 0,37
0,35 \pm 0,97						0
0,30 \pm 0,85						0,03 \pm 0,24
2,10 \pm 1,20						2,00 \pm 0
2,00 \pm 1,23						2,00 \pm 0
3,00 \pm 0						0
1,50 \pm 1,00						2,00 \pm 0
2,50 \pm 1,23						0
2,10 \pm 1,20						2,00 \pm 0
13,89 (13,26–14,51)						1,39 (1,21–1,56)
20,93 (19,92–21,87)						2,33 (2,04–2,62)
3,45 (2,80–4,10)						0
13,79 (13,07–14,52)						3,44 (3,02–3,88)
13,95 (13,02–14,88)						0
14,09 (13,45–14,72)						1,41 (1,23–1,59)

was generated using the *bipartite* package (Dormann et al., 2008), and the beta diversity analyses were run in the *betapart* package (Baselga et al., 2018) of the R software, version 4.0.3 (R Core Team, 2020).

3. Results

3.1. Composition and structure of the helminth community

A total of 412 rodent specimens were collected and analyzed in the present study, including 208 *N. lasiurus*, 71 *A. cursor*, and 47 *M. musculus* captured in the REBIO Poço das Antas, and 75 *N. lasiurus*, 10 *M. musculus*, and one *A. cursor* in the APA-BRSJ. Overall, 58% (n = 239) of these rodents were infected with at least one species of helminth, and a total of 3342 helminth specimens were recovered.

Nine helminth species were identified in the present study (Tables 1–3): seven nematodes –*Protospirura numidica criceticola* (Quentin et al., 1968), *Stilestrongylus freitasi* (Durette-Desset, 1968), *Stilestrongylus aculeata* (Travassos, 1918), *Stilestrongylus eta* (Travassos,

1937), *Pterigodermitis (Paucipectines) zygodontomis* (Quentin, 1967), *Syphacia (syphacia) alata* (Quentin, 1968), and *Trichuris navonae* (Robles, 2011), the cestode *Rodentolepis akodontis* (Rêgo, 1967), and the acanthocephalan *Moniliformis necromysi* (Gomes et al., 2020).

A higher total helminth species richness was recorded for *A. cursor* in comparison with *N. lasiurus* and *M. musculus* (Table 4). Despite this, the highest mean richness was recorded in *N. lasiurus* in comparison with the other two species. (Table 4). The species accumulation curves indicated that sampling effort was sufficient to determine the helminth species richness of the three rodent species (Fig. 2). All nine helminth species were registered in REBIO Poço das Antas, however, only five of them were found in APA-BRSJ (Tables 1–3).

The bipartite network analysis showed a high level of overlap in the helminth species among the hosts (Fig. 3). All the helminths recorded in *M. musculus* were shared with the other two species, and five of the eight helminth species found in *A. cursor* were also present in *N. lasiurus*.

Four species including, *P. (Paucipectines) zygodontomis*, *M. necromysi*, and *S. (Syphacia) alata*, recorded in *A. cursor*, and *R. akodontis*

Table 2

Mean (±SD) abundance, mean (±SD) intensity, prevalence (95% confidence intervals), and site of infection of the helminth species recorded in *Necromys lasiurus* (Rodentia, Cricetidae) in relation to the age and sex of the host, and the type of matrix surveyed in the APA-BRSJ, municipality of Casimiro de Abreu, and in the REBIO Poço das Antas, municipality of Silva Jardim, state of Rio de Janeiro, Brazil. A dash (–) indicates the absence of the species in the respective category.

Parameter	Species			
	<i>P. numidica criceticola</i>	<i>P. (Paucipectines) zygodontomis</i>	<i>S. freitasi</i>	<i>S. (Syphacia) alata</i>
Infection site	Stomach	Small intestine	Small intestine	Large intestine
Life Cycle	Indirect	Indirect	Direct	Direct
Abundance	4,34 ± 0,21	0,90 ± 2,54	1,97 ± 8,42	3,23 ± 13,66
Male (n = 137)	4,38 ± 12,24	0,80 ± 2,33	1,34 ± 6,98	3,02 ± 10,79
Female (n = 146)	4,33 ± 11,12	1,00 ± 2,73	2,41 ± 9,44	3,46 ± 15,97
Juvenile (n = 153)	4,30 ± 9,99	0,79 ± 2,22	3,14 ± 11,03	3,41 ± 12,74
Adult (n = 130)	4,39 ± 13,35	1,03 ± 2,87	0,58 ± 3,00	3,02 ± 14,75
APA-BRSJ (n = 75)	10,52 ± 19,85	1,37 ± 3,38	3,85 ± 11,69	9,04 ± 24,20
REBIO Poço das Antas (n = 208)	2,12 ± 4,98	0,73 ± 2,14	1,19 ± 6,79	1,14 ± 5,29
Intensity	8,91 ± 14,40	4,64 ± 3,99	19,89 ± 19,27	22,88 ± 29,79
Male (n = 137)	9,10 ± 16,43	4,23 ± 3,81	18,30 ± 19,76	17,21 ± 20,82
Female (n = 146)	9,10 ± 14,76	5,00 ± 4,19	20,59 ± 20,10	31,38 ± 38,92
Juvenile (n = 153)	8,89 ± 12,91	4,32 ± 3,49	22,90 ± 21,08	20,08 ± 25,15
Adult (n = 130)	9,21 ± 18,22	5,15 ± 4,51	10,86 ± 7,99	28,07 ± 37,44
APA-BRSJ (n = 75)	17,15 ± 23,06	5,42 ± 4,88	26,27 ± 19,04	27,12 ± 36,00
REBIO Poço das Antas (n = 208)	4,69 ± 6,63	4,22 ± 3,45	15,77 ± 18,82	15,80 ± 12,86
Prevalence	48,76 (48,68–48,85)	19,44 (18,37–20,50)	9,90 (6,36–13,42)	14,13 (8,41–19,86)
Male (n = 137)	48,18 (41,62–54,73)	18,98 (17,73–20,23)	7,23 (3,73–11,04)	17,52 (11,74–23,30)
Female (n = 146)	47,59 (41,80–53,78)	20,00 (18,58–21,21)	11,72 (6,80–16,38)	11,03 (2,72–19,35)
Juvenile (n = 153)	48,37 (43,30–53,43)	18,30 (17,18–19,43)	13,73 (8,13–19,32)	17,00 (10,54–23,45)
Adult (n = 130)	47,69 (40,35–55,04)	20,00 (18,42–21,58)	5,38 (3,73–7,04)	10,77 (2,66–18,88)
APA-BRSJ (n = 75)	61,33 (46,96–75,71)	25,33 (22,89–27,78)	14,67 (6,21–23,13)	33,33 (15,80–50,86)
REBIO Poço das Antas (n = 208)	43,27 (41,10–45,43)	17,31 (16,38–18,24)	8,17 (5,22–11,12)	7,21 (4,91–9,51)
<i>T. navonae</i>				<i>Rodentolepis akodontis</i>
Large intestine				Small intestine
Direct				Indirect
0,65 ± 1,91				0,12 ± 0,33
0,60 ± 1,73				0,10 ± 0,30
0,71 ± 2,07				0,14 ± 0,35
0,62 ± 1,66				0,12 ± 0,32
0,69 ± 1,76				0,12 ± 0,32
0,50 ± 1,25				0
0,68 ± 2,08				0,16 ± 0,37
3,70 ± 3,07				1,00 ± 0
3,73 ± 2,68				1,00 ± 0
3,68 ± 3,39				1,00 ± 0
3,96 ± 3,67				1,00 ± 0
3,46 ± 2,43				1,00 ± 0
2,53 ± 1,68				0
4,30 ± 3,45				1,00 ± 0
17,67 (16,87–18,47)				12,01 (11,88–12,15)
16,06 (15,13–16,99)				10,21 (10,05–10,38)
19,31 (18,23–20,39)				13,79 (13,61–13,97)
15,68 (14,85–16,53)				12,41 (12,25–12,58)
20,00 (19,03–20,96)				11,54 (11,36–11,71)
20,00 (19,09–20,90)				0
15,87 (14,96–16,68)				16,34 (16,19–16,51)

Table 3

Mean (\pm SD) abundance, mean (\pm SD) intensity, prevalence (95% confidence intervals), and site of infection of the helminth species recorded in *Mus musculus* (Rodentia, Cricetidae) in relation to the age and sex of the host, and the type of matrix surveyed in the APA-BRSJ, municipality of Casimiro de Abreu, and in the REBIO Poço das Antas, municipality of Silva Jardim, state of Rio de Janeiro, Brazil. A dash (–) indicates the absence of the species in the respective category.

Species			
Parameter	<i>P. numidica criceticola</i>	<i>P. (Paucipetines) zygodontomis</i>	<i>S. freitasi</i>
Indection site	Stomach	Small intestine	Small intestine
Life Cycle	Indirect	Indirect	Direct
Abundance	0,68 \pm 4,65	0,35 \pm 1,89	0,16 \pm 1,19
Male (n = 38)	0,92 \pm 5,68	0,5 \pm 2,30	0,23 \pm 1,44
Female (n = 19)	0,42 \pm 1,12	0,05 \pm 0,23	0
Juvenile (n = 17)	2,29 \pm 8,46	1,18 \pm 3,38	0
Adult (n = 40)	0	0	0,36 \pm 1,76
APA-BRSJ (n = 10)	3,9 \pm 10,97	2,40 \pm 4,27	0,90 \pm 2,85
REBIO Poço das Antas (n = 47)	0	0	0
Intensity	19,5 \pm 22,63	6,67 \pm 6,03	9,00 \pm 0
Male (n = 38)	35,00 \pm 0,00	9,50 \pm 4,95	9,00 \pm 0
Female (n = 19)	4,00 \pm 1,53	1,00 \pm 0,00	–
Juvenile (n = 17)	13,00 \pm 15,58	6,67 \pm 6,03	–
Adult (n = 40)	0	0	9,00 \pm 0
APA-BRSJ (n = 10)	13,00 \pm 19,08	6,00 \pm 5,10	9,00 \pm 0
REBIO Poço das Antas (n = 47)	0	0	0
Prevalence	3,51 (–0,349–7,37)	5,26 (3,70–6,83)	2,00 (2,00–3,00)
Male (n = 38)	2,63 (–3,14–8,41)	5,26 (2,92–7,60)	2,56 (–0,29–5,42)
Female (n = 19)	10,53 (8,91–12,14)	5,26 (4,93–5,59)	0
Juvenile (n = 17)	17,65 (4,78–30,52)	17,65 (12,51–22,78)	0
Adult (n = 40)	0	0	4,00 (2,53–5,46)
APA-BRSJ (n = 10)	30,00 (8,25–51,75)	40,00 (31,53–48,48)	10 (4,36–15,64)
REBIO Poço das Antas (n = 47)	0	0	0

Table 4

Total and mean helminth species richness recorded in each rodent host in the APA-BRSJ, municipality of Casimiro de Abreu, and in the REBIO Poço das Antas, municipality of Silva Jardim, state of Rio de Janeiro, Brazil.

Host species	Overall helminth species richness	Mean helminth species richness
<i>Akodon cursor</i>	8	0.38 \pm 0.70
<i>Necomys lasiurus</i>	6	1.22 \pm 1.18
<i>Mus musculus</i>	3	0.14 \pm 0.48

found in *N. lasiurus* were co-dominant in the present study. All the other species were dominant (Table 5).

The beta-diversity among helminth infracommunities was 0.98, with much larger turnover (0.97) than nestedness (0.01). For the component community scale, beta diversity was 0.43, with low values of both turnover (0.11) and nestedness (0.32).

3.2. Parasitological parameters

The nematodes *Protophysa n. criceticola* and *P. (Paucipetines) zygodontomis*, which were found infecting the three host species, presented the highest intensity in *M. musculus* (Tables 1–3). In the GLM analysis, plausible explanatory models for *P. n. criceticola* included host species and locality for abundance (Table 6), and host species, locality,

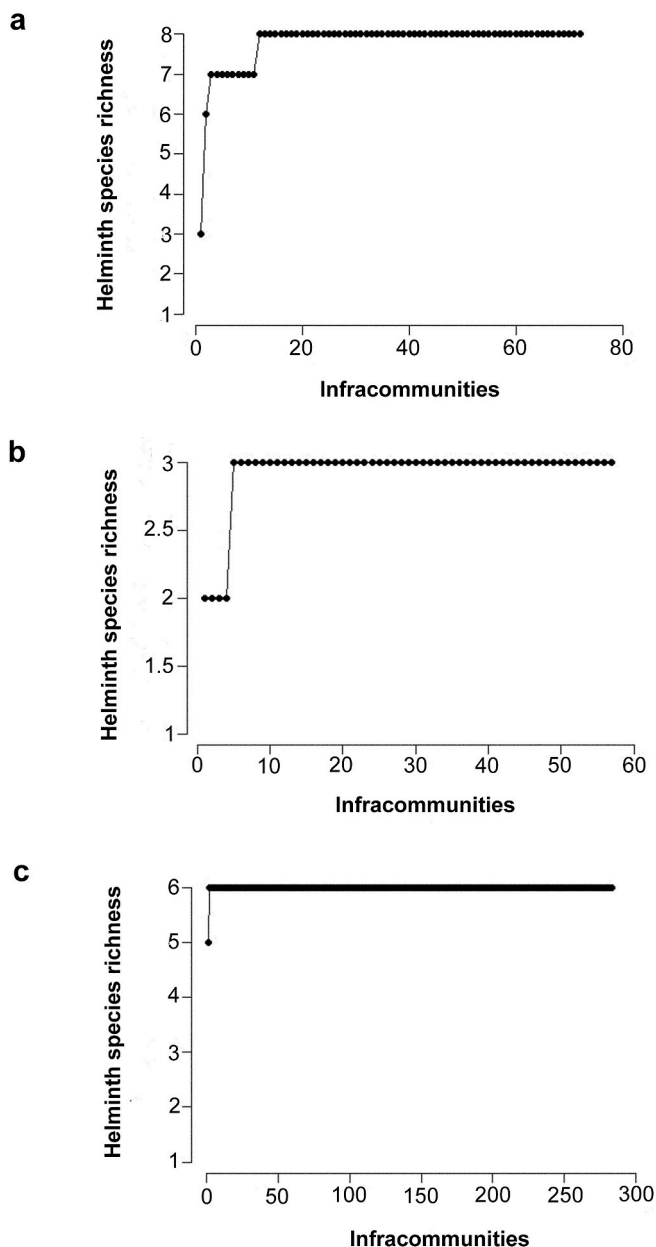


Fig. 2. Species accumulation curve of the helminths recorded in each mammalian host: a. *Akodon cursor* b. *Mus musculus* c. *Necomys lasiurus*.

and host age for prevalence (Table 7). For *P. (Paucipetines) zygodontomis*, plausible models included host species, locality and host age for both abundance and prevalence (Tables 6 and 7). The highest abundance and prevalence of these parasites were observed in the *N. lasiurus* specimens collected in the APA-BRSJ (Tables 1–3). The age of the hosts also influenced these parameters, with a greater prevalence of *Protophysa n. criceticola* and *P. (Paucipetines) zygodontomis* in juvenile hosts, while the latter helminth was more abundant in adult hosts (Tables 1–3).

Stilestrongylus freitasi, which was also recorded in the three rodent species, was most abundant and prevalent in the juvenile female specimens collected in the APA-BRSJ (Tables 1–3). This helminth was most prevalent in *N. lasiurus*. In the GLM analyses, host age, host sex and locality were present in the plausible models for abundance and prevalence (Tables 6 and 7). For prevalence, host sex was also included in the selected models (Table 7). The greatest mean intensity of this parasite was recorded in *N. lasiurus*, followed by *A. cursor* (Tables 1–3).

Syphacia (Syphacia) alata was more abundant in the juvenile

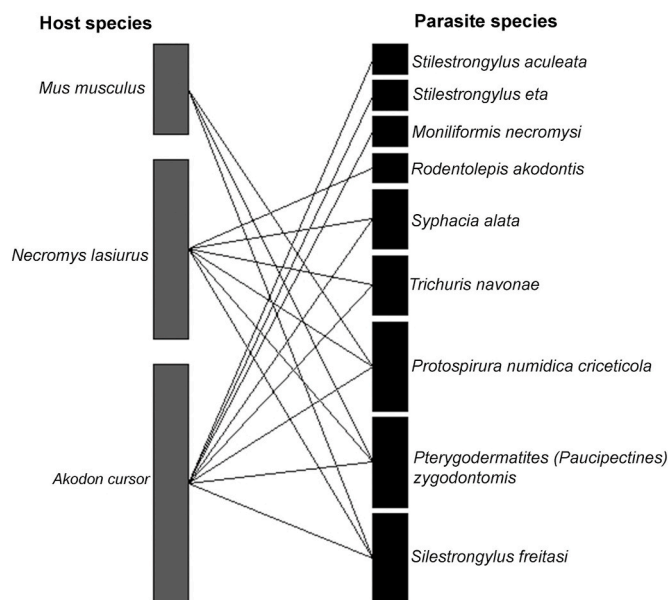


Fig. 3. Bipartite plot of the interactions between the mammal hosts and the helminth parasites identified in the present study.

Table 5

Importance indices for the helminth communities recorded in *Akodon cursor*, *Necromys lasiurus*, and *Mus musculus* in the APA-BRSJ, municipality of Casimiro de Abreu, and in the REBIO Poço das Antas, municipality of Silva Jardim, state of Rio de Janeiro, Brazil.

Host species	Helminth species	Index of importance	Category	
<i>A. cursor</i>	<i>P. numidica criceticola</i>	41.67	Dominant	
	<i>P. (Paucipectines) zygodontomis</i>	0.20	Co-Dominant	
	<i>M. necromysi</i>	0.20	Co-Dominant	
	<i>S. aculeata</i>	2.18	Dominant	
	<i>S. eta</i>	1.39	Dominant	
	<i>S. freitasi</i>	12.30	Dominant	
	<i>T. navonae</i>	41.67	Dominant	
	<i>S. (Syphacia) alata</i>	0.40	Co-Dominant	
	<i>N. lasiurus</i>	<i>P. numidica criceticola</i>	68.88	Dominant
		<i>P. (Paucipectines) zygodontomis</i>	5.70	Dominant
<i>S. freitasi</i>		6.33	Dominant	
<i>R. akodontis</i>		0.47	Co-Dominant	
<i>T. navonae</i>		3.76	Dominant	
<i>S. (Syphacia) alata</i>		14.86	Dominant	
<i>M. musculus</i>	<i>P. numidica criceticola</i>	49.06	Dominant	
	<i>P. (Paucipectines) zygodontomis</i>	45.28	Dominant	
	<i>S. freitasi</i>	5.66	Dominant	

N. lasiurus collected in the APA-BRSJ and was most prevalent in the juvenile males of this rodent, also in the APA-BRSJ (Tables 1 and 2). Selected models of the GLM analyses included host species, locality and host age for abundance and prevalence, and also host sex for prevalence analysis (Tables 6 and 7).

Trichuris navonae was most abundant and prevalent in the adult *N. lasiurus* collected in the APA-BRSJ (Tables 1 and 2). However, the null model was also plausible in the GLM analysis of this species (Tables 6 and 7). The highest mean intensity of this parasite was also recorded in *N. lasiurus* (Tables 1–3).

Table 6

Generalized Linear Models (GLMs) of the abundance of the most prevalent helminth species recovered from *Akodon cursor*, *Necromys lasiurus*, and *Mus musculus* according to the sex and age of the host, and locality in the APA-BRSJ, municipality of Casimiro de Abreu, and in the REBIO Poço das Antas, municipality of Silva Jardim, state of Rio de Janeiro, Brazil. $\Delta AICc$ = difference between the model with the smallest AICc (corrected Akaike Information Criterion) and the respective model; Weight = Akaike weight, K = the number of parameters included in the model. Except for the null model, only models with $\Delta AICc \leq 2$ are shown here.

Helminth species	Model	AICc	$\Delta AICc$	Weight	K
<i>Protospirura .numidica criceticola</i>	Host species + Locality	3033.3	0.00	0.520	5
	Null	3067.0	33.76	0.000	2
<i>Pterygodermatite. (Paucipectines) zygodontomis</i>	Host species + Locality	1827.0	0.00	0.387	5
	Host species + Locality	1828.3	1.31	0.201	3
	Host species + Host Age + Locality	1828.9	1.87	0.152	6
<i>Stilestrongylus freitasi</i>	Null	1839.8	12.81	12.81	2
	Host Age + Locality + Host Sex	2778.3	0.00	0.344	6
	Locality + Host Sex	2778.9	0.68	0.245	5
<i>Syphacia (syphacia) alata</i>	Null	2790.6	12..29	0.001	2
	Locality	2767.4	0.00	0.411	3
	Host species + Locality	2769.9	1.51	0.193	4
	Host Age + Locality	2769.2	1.81	0.166	4
	Null	2789.8	22.56	0.000	2
<i>Trichuris. navonae</i>	Host species	923.9	0.00	0.250	3
	Host species + Host age	924.7	1.06	0.147	4
	Null	924.9	1.21	0.137	2
	Host species + Locality	925.3	1.52	0.117	4

4. Discussion

The present study is the first to analyse the helminth fauna and community structure of the helminths that infect rodents found in the anthropogenic open matrix of the Atlantic Forest. Overall, the helminth community overlapped considerably among the host species, and presented a low beta-diversity at the component community level. This probably reflected the homogenization for exposure to the parasites and their development among the different host species. At an infra-community level, however, the high beta-diversity and the greater number of substitutions than losses of helminth species indicates that the intraspecific variation among the host characteristics, such as age, sex, and the immune response to infection, act as environmental filters, which influence the occurrence, abundance, and distribution of parasites at this scale (Combes, 2001; Thomas et al., 2005).

The helminth community found in *M. musculus* (three species) was shared entirely with the other two rodents, *A. cursor* and *N. lasiurus*, while the latter species shared five of its six helminth species with *A. cursor*. The opportunistic and terrestrial habits of these rodents (Witmer and Jójola, 2006; Paglia et al., 2012; Cardoso et al., 2016; Costa et al., 2019), together with the overlap in their diets (M. Rodrigues, unpublished data) likely contributed to the high degree of overlap in the parasite fauna of these hosts. The abundance and/or population density of these hosts may also be considered to be an important predictor of parasite species richness (Kamiya et al., 2014; Dallas et al., 2019), given that hosts with a high population density will tend to increase local transmission through the growth in the rates of contact among individuals (May and Anderson, 1979; Püttker et al., 2008). In this case, the large number of *N. lasiurus* specimens captured in both localities during the present study, which suggests a high population density when

Table 7

Generalized Linear Models (GLMs) of the prevalence of the most prevalent helminth species recovered from *Akodon cursor*, *Necomys lasiurus*, and *Mus musculus* according to the sex and age of the host, and the locality in the APA-BRSJ, municipality of Casimiro de Abreu, and in the REBIO Poço das Antas, municipality of Silva Jardim, state of Rio de Janeiro, Brazil. $\Delta AICc$ = difference between the model with the smallest AICc (corrected Akaike Information Criterion) and the respective model; Weight = Akaike weight, K = the number of parameters included in the model. Except for the null model, only models with $\Delta AICc \leq 2$ are shown here.

Helminth species	Model	AICc	$\Delta AICc$	weight	k
<i>Protospirura .numidica criceticola</i>	Host species + Locality	442.5	0.00	0.497	4
	Host species + Locality + Host Age	444.0	1.56	0.228	5
	Null	535.3	92.79	0.000	1
<i>Pterigodermatite. (Paucipectines) zygodontomis</i>	Host species + Locality	321.1	0.00	0.510	4
	Host species + Locality + Host Age	323.1	1.97	0.190	5
	Null	339.7	18.56	0.000	5
<i>Stilestrongylus freitasi</i>	Host species + Host Sex	215.9	0.00	0.204	5
	Host species + Locality + Host Sex	216.8	0.85	0.133	6
	Host species	217.1	1.13	0.116	3
	Host species + Locality	217.3	1.39	0.102	4
	Host species + Host Sex + Host Age	217.6	1.64	0.090	6
	Null	222.0	6.06	0.010	1
	Host species + Locality	225.2	0.00	0.318	3
<i>Syphacia (syphacia) alata</i>	Host species + Locality + Host Sex	225.9	0.70	0.224	5
	Host species + Locality + Host Sex + Host Age	226.9	1.64	0.140	6
	Host species + Host Age + Locality	226.9	1.65	0.140	4
	Null	256.1	30.85	0.000	1
	Null	334.0	0.91	111	1
<i>Trichuris naonae</i>	Null	334.0	0.91	111	1

compared to the other species, may have contributed to the niche overlap among the rodent species or even increased inter and intra-specific contact, contributing to the sharing of parasites observed among the different rodent species and among individuals within species.

The higher mean parasite species richness recorded in *N. lasiurus* in relation to the other hosts suggests that its infracommunities are more susceptible to infection and reflects the co-infection of the helminth species observed in this host.

On the other hand, the greater total helminth species richness was found in *A. cursor* in comparison with the other two rodent species. This result is consistent with the findings of Simões et al. (2011) in the Serra dos Órgãos National Park and neighbouring forest fragments in the state of Rio de Janeiro, which found nine helminth species for this host; and with other studies for its congener *A. montensis* (Simões et al., 2011 S = 12; Boullosa et al., 2020, S = 6; Cardoso et al., 2020, S = 6; Kuhnen et al., 2012, S = 6). Except for the study of Simões et al. (2011), only Kersul et al. (2020) reported the helminth community of *A. cursor* within a locality. They observed two helminth species in agroforestry mosaics in the Atlantic Forest of Ilhéus, in Bahia state (Supplementary Material). The other studies were reports of species occurrence (Supplementary Material). Overall, only three (*S. eta*, *S. aculeata* and *S. (syphacia) alata*) of the 12 helminths species known to infect *A. cursor* in the forests and fragments of the Atlantic Forest were recorded in the present study (Supplementary Material). Thus, *A. cursor* is a new host for the nematodes *P. n. criceticola*, *P. (Paucipectines) zygodontomis*, *S. freitasi*, *T. navonae* and for the acanthocephalan *M. necromysi*.

Helminths of the genus *Moniliformis* are common in *R. rattus* (Simões

et al., 2016). The infection of this genus in wild hosts was previously related to the habitat sharing between wild and synanthropic rodents in anthropogenic areas (Costa et al., 2019). It is important to note that the present study is the first report of the infection of *A. cursor* by the helminths *P. (Paucipectines) zygodontomis*, *Moniliformis necromysi*, and *S. freitasi*, so this study not only amplifies the distribution of these helminths, but also confirms a new host for those parasites (Supplementary Material). Two other helminths, *P. numidica criceticola* and *T. navonae*, observed in *A. cursor* in the present study, have previously been recorded parasitizing the congener, *Akodon montensis*, in fragments of Atlantic Forest (Boullosa et al., 2020; Cardoso et al., 2019).

Costa et al. (2019) recently evaluated the helminth fauna of *N. lasiurus* in the Cerrado savanna of Uberlândia, in different types of habitat, and recorded a total of nine helminth species. Also in the Cerrado, in the Águas Emendadas Ecological Station in the municipality of Planaltina, in the Brazilian Federal District, Grossmann (2015) recorded eight helminth species in *N. lasiurus* (Supplementary Material). Robles (2008) found two helminth species in *N. lasiurus* (reported as *N. benefactus*) in several provinces of Argentina (supplementary Material). In an agroforestry mosaic in the Atlantic Forest of Ilhéus, however, Kersul et al. (2020) recorded only a single helminth in this rodent. In addition, in the Caatinga dry forest areas, six helminth species have been reported parasitizing *N. lasiurus* (Quentin, 1967, 1968; Durette-Desset, 1968; Quentin et al., 1968; Simões et al., 2017) (Supplementary Material). The helminth fauna of *N. lasiurus* reported in the literature has a total of 13 helminth species (Supplementary Material). The six helminth species recorded in the present study, in open habitat areas within the Atlantic Forest, are clearly a subset of the helminthfauna already described for this host. Thus, the helminth fauna observed in the open matrix of the REBIO Poço das Antas and APA-BRSJ, which are dominated by grasses, are in accordance with the *N. lasiurus* helminth fauna observed in the Cerrado and Caatinga. Therefore, as the geographic range of *N. lasiurus* is increasing in the deforested areas of the Atlantic Forest in Rio de Janeiro state by dispersal (Oliveira-Santos et al., 2018), we suggest herein that some of these helminth species, such as *P. (Paucipectines) zygodontomis*, which was recorded only in this rodent species before this study, might have been dispersed to the Atlantic Forest by this rodent. However, this hypothesis needs to be confirmed with further studies.

The present study is the first to record the helminth fauna of *M. musculus* in populations established in wild environments within the Atlantic Forest. In addition, none of the helminth species found in this rodent (*P. n. criceticola*, *P. (Paucipectines) zygodontomis* and *S. freitasi*) were registered in the literature for *M. musculus* (Supplementary Material). The helminth fauna of this rodent in natural environments is poorly-known, given that this species is rare in non-domestic environments (Choquenot and Ruscoe 2000; Reis et al., 2011; Panti-May et al., 2020). In fact, most of the available studies describe helminth infection under laboratory conditions (Singleton and Krebs 2007). Field studies have mostly focused on domestic or peri-domestic environments, in Africa, Europe, Central America, Oceania, and Asia, where other helminth species have been recorded, presumably reflecting the influence of the local native fauna (Tattersall et al., 1994; Kataranovski et al., 2008; Diagnen et al., 2016; Hancke and Suarez 2018; Moradpour et al., 2018; Hernandez et al., 2020). In Brazil, only two studies have focused on the helminth fauna of *M. musculus*. One study was done in the urban environment of Aracaju, Sergipe state, where Guimarães et al. (2014) recorded three species (Supplementary Material). Another study was conducted in the natural environment of the Cerrado of Planaltina, in central Brazil, where Grossman (2015) recorded four helminth species (Supplementary Material), two of which were shared with *N. lasiurus* and one with *Calomys expulsus*. In the present study, all three helminth species observed in *M. musculus* were also part of the helminth fauna of *N. lasiurus* and *A. cursor*, confirming the overlap of the helminth fauna in these open areas of the Atlantic Forest.

The majority of the helminth species recorded in the present study

were dominant in their component communities. In both *A. cursor* and *N. lasiurus*, the co-dominant species were the least abundant or prevalent in their communities, with no subordinate species in either case. In addition, parasites may be more abundant in infracommunities with relatively few helminth species, in comparison with species-rich infracommunities (Poulin, 2007), which is consistent with the small number of co-dominant species recorded in both *A. cursor* and *N. lasiurus*, and the presence of only dominant species in *M. musculus*. The cestode *R. akodontis*, found parasitizing *N. lasiurus*, and the acanthocephalan *M. necromysi*, found in *A. cursor*, were characterized by reduced prevalence, intensity, and abundance in their respective hosts, and were thus considered co-dominant species in this study.

The abundance and prevalence of parasites in host populations are influenced by several factors, especially related to the host attributes (Cardoso et al., 2020). These factors may have different effects among the species of a given community. Among the analyzed factors, host species was the most important explanatory variable for both, helminth abundance and prevalence, as it was present in a larger number of plausible models. For prevalence, it was present in all plausible models. These results indicate that some helminth species may have differences in their compatibility among the host species. It is known that functional traits shape host-parasite interactions for helminths and mammals (Cardoso et al., 2021). Thus, other host traits, especially physiological and immunological, which are related to the host-parasite compatibility filters (Combes, 2001; Poulin, 2007), could also be important for their vulnerability to parasites resulting in the discrepant values on the parameters among the rodent species for many of these helminths.

Considering the host age, we observed the influence of this factor in different directions depending on the helminth species. The marked prevalence and abundance of *P. numidica criceticola*, *S. (Syphacia) alata* and *S. freitasi* in juvenile *N. lasiurus* may be related to the probable precocious infection of these hosts for these helminths. Cardoso et al. (2019) also observed higher abundance and prevalence of *S. aculeata* and *S. eta* for young congener *Akodon montensis* when compared to adult individuals, and Simões et al. (2016) observed higher helminth diversity in young *Rattus norvegicus*. On the other hand, the greater abundance and prevalence of *P. (Paucipetines) zygodontomis* in adult hosts, may indicate a gradual and progressive increase in the infection of the host over its lifetime, there by increasing the abundance of parasites in the adult hosts.

Regarding host sex, a greater prevalence of *S. (syphacia) alata* was observed in male specimens of *N. lasiurus*, while *S. freitasi* was more abundant and prevalent in female specimens of this host. The higher infection rates of *S. freitasi* in female hosts contradicts the typical pattern of helminth infection in mammals, in which males normally present the highest infection rates (Zuk and McKean 1996; Poulin 2007). However, some studies have also recorded higher helminth infection rates in female hosts, in other rodent species (Simões et al., 2014; Boullosa et al., 2019; Cardoso et al., 2019; Kersul et al. 2020). Similarly, *S. aculeata* and *S. eta*, which are congeners of *S. freitasi*, were recorded only in adult female *A. cursor* collected in the REBIO Poço das Antas, which may indicate that the female hosts may be either more susceptible or exposed to these parasites.

andscape modifications may affect a number of different ecological processes and biological parameters of the local fauna, influencing the biological cycle of some parasite species, while favouring the occurrence of others (Cardoso et al., 2016). While the areas surveyed in the present study both represented the open anthropogenic matrix, differences in environmental quality, related to both the current and past types of land use, may have influenced the parasitism of the small mammals analyzed in the present study. According to the GLM analyses, locality was the second most important explanatory variable, after host species, either for helminth abundance or for prevalence, as it was present in most of the plausible models. In general, although the greatest total richness of helminth species has been observed in REBIO Poço das antas, the highest prevalence, intensity, and abundance of helminths were recorded in the

APA-BRSJ, especially for *P. (Paucipetines) zygodontomis*, *P. numidica criceticola*, *S. (Syphacia) alata* and *S. freitasi*. Moreover, a larger helminth species richness was observed in REBIO Poço das Anta in relation to the other locality. APA-BRSJ presented much higher levels of anthropogenic impact and farming activities in the surrounding of the sampling areas in comparison with the REBIO Poço das Antas, which is currently a strictly protected area.

Even so, impacted environments and human activities may have negative effects on species richness, provoking local extinction in some wild species (Joly et al., 2011), including parasites (Rózsa and Vas, 2015). The human activities may also favour the occurrence of generalist rodents (Verberk, 2012), such as the occurrence of *N. lasiurus* in the present study due to deforestation (Santos et al., 2018), and facilitate the establishment of their parasites (Bordes et al., 2015). These processes may have contributed to the occurrence of only three (*S. alata*, *S. aculeata* and *S. eta*) of the 12 helminth species known to occur in *A. cursor* in the Atlantic Forest. Moreover, considering the rodent community analyzed, the number of helminth species found in these rodents was higher in REBIO Poço das Antas ($S = 9$) than in APA-BRSJ ($S = 5$). Four (*S. aculeata*, *S. eta*, *R. akodontis*, and *M. necromysi*) of the nine helminth species recorded in the present study were recorded only in rodents from the REBIO Poço das Antas. Although the habitat of the two localities in which the rodents were sampled were not too different in their vegetation constitution, the land use and the human presence in the surroundings were very distinct and might have an influence in the species occurrence in the open matrix areas. Thus, we suggest that these differences in the land use of the areas may explain the very low abundance of the rodent *A. cursor* in APA-BRSJ, the fact that *M. musculus* was found infected with helminths only in this area, and the higher values of the parameters observed for some helminth species, as mentioned in the previous paragraph. A complementary study on the mammal helminth fauna of the forest fragments linked by the matrix and near human dwellings would give more support for this hypothesis. Anthropogenic disturbances may affect the life cycles of some parasite species (Lafferty and Kuris, 1999). Cardoso et al. (2016) observed that fragmentation could limit the occurrence of some helminth species, which were found only in less-fragmented areas, thus affecting some host-parasite interactions. The stronger environmental disturbances in APA-BRSJ in relation to REBIO Poço das Antas may be affecting the transmission of some helminths, influencing their occurrence in the region and, consequently, the host-parasite interactions. However, while this may reflect the effects of the less extensive anthropogenic impacts in this area, it may also have been related to the larger number of animals captured in the REBIO Poço das Antas, in comparison with the APA-BRSJ and to the fact that only a single host of *A. cursor* was captured in the latter locality.

5. Conclusions

The results of the present study confirmed the hypothesis that *N. lasiurus* had a helminth fauna similar to that recorded previously in the Cerrado and Caatinga areas. Even so, the majority of the helminth species found in this species are also common in Atlantic forest rodents, with the exception of *P. (Paucipetines) zygodontomis*, which has only been reported in *N. lasiurus* up to now (Supplementary Material) although, in the present study, it was also recorded in the other two host species. In the case of *A. cursor*, while all the helminths species have already been recorded in other Atlantic Forest rodent species, five of the eight species were recorded in *A. cursor* for the first time, thus expanding its known helminth fauna. While few studies are available on the helminth fauna of *Mus musculus* in natural environments, the results of the present study are consistent with the available data and with our hypothesis, which indicate that this exotic, cosmopolitan species is highly plastic, incorporating the parasites of the local mammalian fauna. Host species and locality were the most important factors influencing helminth abundance and prevalence in these rodents. Comparing between

localities, most of the helminth species had higher abundance and prevalence in the most disturbed locality (APA-BRSJ), while the less disturbed locality (REBIO Poço das Antas) had higher helminth species richness. Beta-diversity among infracommunities was high and turnover was the most important component indicating species substitution among host individuals. In counterpart, for the component community scale, beta-diversity was low, indicating partially helminth species share among the three rodents.

Author contributions

PSD and CSL did the conceptualization; CSL, FOS and BRT conducted the fieldwork; BRT did the taxonomic identification of the rodent hosts; CSL and AMJ did the taxonomic identification of the helminths; CSL, RG and TSC did the Data analysis; All authors discussed the results of data analysis, wrote and approved the manuscript.

Funding

This research was funded by the Oswaldo Cruz Institute IOC/Fiocruz, the Graduate Program in Biodiversity and Health of the Oswaldo Cruz Institute (PGBS/IOC/Fiocruz), Conselho Nacional de Desenvolvimento Científico e Tecnológico/CNPq, grant number: [439208/2018-1] and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro/FAPERJ, grant number: [E-26/010.101044/2018] and E-26/010.001597/2019.

Acknowledgments

We thank the Oswaldo Cruz Institute (IOC/Fiocruz) and the graduate program in Biodiversity and Health of the Oswaldo Cruz Institute (PGBS/IOC/Fiocruz) for supporting this study and the staff of LABPMR-IOC/FIOCRUZ who helped in the fieldwork. ICMBio authorized fieldwork at REBIO Poço das Antas and APA- Bacia do Rio São João and provided infrastructure at this sites, where we were supported by Gustavo Peixoto and Rafael Puglia. We also thank to Prof. Stephen Francis Ferrari for improving and reviewing the English text. This project was financially supported by MCTIC/CNPq N° 28/2018 project number: 439208/2018-1 and FAPERJ N° 11/2018 project number: E-26/010.101044/2018 and E-26/010.001597/2019. RG received researcher grants from CNPq (304355/2018-6).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ijppaw.2021.07.001>.

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