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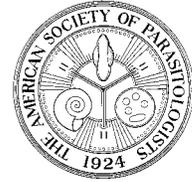
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METACOMMUNITY STRUCTURE OF HELMINTHS OF *NECROMYS LASIURUS* (RODENTIA: SIGMODONTINAE) IN DIFFERENT LAND USE AREAS IN THE BRAZILIAN CERRADO

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KEY WORDS ABSTRACT

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The ecology of host–parasite interactions can be studied in the infracommunity and component community scales, which may show different patterns in species distributions, interacting and affecting each other on a regional scale. Few studies have been carried out concerning the structure and variation of the helminth communities of wild rodents in Brazil. The rodent *Necromys lasiurus* is typical from the mammalian fauna of the Cerrado biome; however, the environmental disturbances are making this species occur in rural areas and in other biomes where it may act as host/reservoir of many diseases. This study aimed to describe the composition and structure of the helminth metacommunity in the rodent *N. lasiurus* in the Brazilian Cerrado, Uberlândia, State of Minas Gerais, using the analysis of metacommunity structure. Rodents were sampled in 3 habitat types: borders of soybean and corn plantations, pasturelands, and preserved areas of Cerrado borders. Adult helminths of 8 species were found in the gastrointestinal tract: *Protospirura numidica criceticola*, *Physaloptera* sp., *Pterygodermatites* (*Paucipectines*) *zygodontomis* (Spirurida), *Stilestrongylus freitasi* (Rhabditida), *Trichuris navonae* (Trichurida) and *Syphacia* (*Syphacia*) *alata* (Oxiurida) of the Phylum Nematoda; *Rodentolepis akodontis* (Cyclophyllidea) of the Phylum Platyhelminthes; and *Moniliformis* sp. (Moniliformida) of the Phylum Acanthocephala. Season and the kind of land use favored some helminths species in this rodent, especially in the plantation area, although diversity was not largely influenced by the land use. Plantation areas could provide an increase in the host abundance and the occurrence of other rodent species, favoring a higher rate of parasite exchange among different hosts. A checkerboard structure of metacommunity was found on the infracommunity scale, which suggests the existence of interspecific competition. A quasi-nested structure of metacommunity was observed on the component community scale showing that most species were influenced by the same environmental gradient and that the species-poor communities were subsets of species-rich communities. *Syphacia alata*, *P. zygodontomis*, *S. freitasi*, and *R. akodontis* were dominant species in all habitats and represented the core-species in the metacommunity.

Investigations on the occurrence, distribution, and community structure of parasites are fundamental to understand host–parasite interactions and the ecosystem dynamics and, consequently, to provide basic support for the knowledge of biodiversity. In this way, studies of community ecology help to describe and evaluate the patterns of species abundances, distributions, and their interactions in different environments. Moreover, the parasites in a given community must have

characteristics that allow them to survive not only in the host but also in the host's habitat (Dallas and Presley, 2014). The influence of the abiotic environment on the parasite is a determining factor for its occurrence, affecting its abundance, prevalence, intensity, and geographical distribution (Ollerenshaw and Smith, 1969; Froeschke et al., 2010). Regarding some parasites, the land use of the environment is an important factor influencing these parameters (Simões et al., 2010).

Table I. Capture sites of *Necromys lasiurus* in Uberlândia, Minas Gerais State, Brazil.

Locality	Habitat	Geographical coordinates
Eldorado Farm	Cerrado/ Pasturelands	18°59'45''S, 48°27'34''W 18°59'50''S, 48°26'72''W
Fernanda Farm	Cerrado/ Plantations	18°57'69''S, 48°04'47''W 18°57'66''S, 48°04'56''W
Glória Farm	Cerrado	18°57'04''S, 48°12'14''W
Flower Field	Cerrado	19°00'42''S, 48°19'17''W
Bálsamo Farm	Pasturelands	19°01'53''S, 48°11'85''W
Veadinho Farm	Plantations	18°57'20''S, 48°03'95''W

The ecology of host–parasite interactions are commonly studied in 2 ecological scales; the infracommunity, constituted by species within each individual host, and the component community constituted by species in a population of a host species (Bush et al., 1997). These 2 scales may show different patterns in species distributions, and local communities may interact and affect each other on a regional scale (Presley et al., 2010). The metacommunity analysis (Leibold and Mikkelsen, 2002; Leibold et al., 2004) is a more recent approach to understand how communities are structured and how organisms respond to ecological changes at different spatial scales. A metacommunity can be defined as a set of local communities linked by the dispersion of multiple species that potentially can interact (Gilpin and Hanski, 1991; Winegardner et al., 2012). The analysis of elements of metacommunity structure (EMS) evaluates the patterns of species distribution along the environmental gradient and how these species respond to ecological changes at different spatial scales (Leibold and Mikkelsen, 2002; Presley et al., 2010). Although the application of this theory is relatively new to host–parasite interactions, it is very promising for the study of parasite communities (Dallas and Presley, 2014) and in understanding the emergence of zoonotic diseases (Suzán et al., 2015).

The ecological interactions of helminths and mammals are good models for studying the parasitism in different ecosystems due to their biological characteristics (Maldonado Júnior et al., 2006; Cardoso et al., 2016; Simões et al., 2016). Among the mammalian orders, rodents are the most diversified group, especially sigmodontines (Patton et al., 2015). They may harbor a large number of parasites and may act as wild reservoirs of zoonoses (Han et al., 2015). Regarding the helminths, environmental changes may influence their biological parameters, resulting in changes in their ecological interactions with the host populations (Bush et al., 2001) and, thus, allowing their use as indicators of environmental changes (Gardner and Campbell, 1992).

Given the diversity of species that this group of parasites shows, helminth parasite communities of wild animals are still poorly understood (Hugot et al., 2001; Poulin, 2007). In Brazil, few studies have been done concerning the structure and variations in the helminth communities in wild rodents (Maldonado Júnior et al., 2006; Simões et al., 2010, 2011). However, some of them evaluated the influence of biotic and abiotic factors on parasite parameters such as abundance, intensity, and prevalence; the studies indicated that the kind of habitat, season, and host characteristic might affect some parasite species (Püttker et al., 2008; Simões et al., 2010; Cardoso et al., 2016). There is only one

report so far on the patterns of metacommunity structure for helminths of Neotropical rodents (Cardoso et al., 2018) and another one for a Neotropical marsupial (Costa-Neto et al., 2018).

The rodent *Necromys lasiurus* (Lund, 1840) has terrestrial habits and thrives in several biomes including Cerrado, Caatinga, Pantanal, and open areas of the Atlantic Forest and is considered to be an invasive species in the latter biome (Reis et al., 2011). This rodent may act as an opportunistic species, occurring in several disturbed environments including forest fragments, peridomestic, and rural areas (Gentile and Fernandez, 1999; Olifiers et al., 2005). In these areas, this species can reproduce greatly, a behavior modification that has been directly associated with zoonotic diseases (Suzuki et al., 2004; Limongi et al., 2013; Oliveira et al., 2014). Furthermore, this rodent is known to be an important reservoir of Hantavirus (Limongi et al., 2013; Oliveira et al., 2014) and arenavirus (Fernandes et al., 2015; Sabino-Santos et al., 2016), and it can act as a reservoir/host of *Trypanosoma cruzi* (Orozco et al., 2014).

There has been only one study published on the helminth fauna of *N. lasiurus* so far (Grossmann, 2015), carried out in the Brazilian Cerrado, which is the most important biome where this rodent occurs (Bonvicino et al., 2008). In addition, Cerrado is the Brazilian biome that is currently suffering the highest degree of environmental degradation. A few other studies reported the occurrence of helminth species in this rodent in the Caatinga biome (Quentin, 1967, 1968; Quentin et al., 1968; Durette-Desset, 1968). The present study aims to describe the gastrointestinal helminth fauna of the rodent *N. lasiurus* and analyze the community structure of the helminths in different areas of the Cerrado biome in Uberlândia, State of Minas Gerais, Brazil. Herein, we test 3 hypotheses concerning the helminth fauna in this rodent: (1) The helminths' prevalence and abundance are influenced by the habitat type where the host occurs, season, and/or host gender; (2) the helminth diversity of *N. lasiurus* is affected by the different land uses within the Cerrado biome; and (3) in the helminth metacommunity analyzed, species occur in a non-random pattern in both infracommunity and component community scales.

MATERIALS AND METHODS

Study area

The present study was carried out in rural areas within the Cerrado biome in the municipality of Uberlândia, State of Minas Gerais, Brazil. The municipality is about 850 m high. The climate is seasonal tropical, with a dry winter between May and September and a rainy summer between October and April. The annual average temperature is 22 C and the total annual rainfall is 1,650 mm (INMET, 2015). The study was conducted in 6 farms (Table I) in which 3 general habitat types were sampled: (1) 'Cerrado' representing border areas of preserved Cerrado vegetation, forming small fragments characterized by several deciduous plant species, low and tortuous trees with irregular and twisted branches, evidence of burnings, watercourses, and arid soil full of organic matter; (2) 'Pasturelands' in rural areas, used for raising cattle, covered with grass of the genus *Brachiaria* in dry soil, with isolated shrubs and an absence of rocky outcrops; and (3) 'Plantations' situated on the borders of soy and corn monocultures in rural areas with very flat topography, with dry

soil, no livestock, and the presence of rocky outcrops and human dwellings.

Rodent sampling

Four rodent samplings were carried out over a year, one in each season, in December 2011 (summer), March 2012 (autumn), August 2012 (winter), and November 2012 (spring). Only the August sampling was considered a dry-season sampling according to meteorological data on the region (INMET, 2015). Animals were live-captured using Sherman® (Tallahassee, Florida) ($7.62 \times 9.53 \times 30.48$ cm) and Tomahawk® (Hazelhurst, Wisconsin) ($40.64 \times 12.70 \times 12.70$ cm) live-traps baited with a mixture of banana, peanut butter, bacon, and oats.

Animals were euthanized for helminth recovery and tissue collection. Only adult animals were considered for the analysis in order to avoid bias. Adult animals were determined by a set of characteristics, including body mass, body length, and reproductive condition, separately for each gender according to other sigmodontine studies (Gentile et al., 2000). All animals were submitted to taxidermy processes and deposited as voucher specimens in the zoological collection of the National Museum in Rio de Janeiro. Identification of the rodent specimens was done by the external morphology and confirmed via karyotype analysis (diploid number account).

The animals were collected in collaboration with the Municipality of Uberlândia during a Hantavirus survey, with authorization from the Chico Mendes Institute for Biodiversity and Conservation (ICMBio license 13373-1). All field procedures followed both the standards of capture, handling, and care recommended by the Ethics Committee on Animal Use at the Oswaldo Cruz Foundation (in accordance with protocols L-049/08 and 066/08) as well as biosafety recommendations (Lemos and D'Andrea, 2014).

Helminths recovery and identification

Helminths were collected from the rodents' thoracic and abdominal cavities and organs using a stereoscopic microscope to detect them. All helminths were counted and identified. Nematodes were diaphanized with lactophenol. Cestodes and acanthocephalans were stained with Langeron carmine, differentiated by 0.5% hydrochloric acid, dehydrated in an alcohol series, diaphanized in methyl salicylate, and fixed in Canada balsam (Amato et al., 1991, modified). For some specimens, cross-sections of the helminths were performed in order to study the synlophe using a stereoscopic microscope. All specimens were analyzed using a light microscope, and the structures were measured using digital images taken with a Zeiss AxioCam HRC (Zeiss, Göttingen, Germany) using the accessory software AxioVision Rel. 4.7 (Zeiss, Göttingen, Germany). Taxonomic identification of these parasites was carried out based on Travassos (1937), Yamaguti (1961), Khalil et al. (1994), Vicente et al. (1997), Anderson et al. (2009), and other specific literature. Voucher specimens of the helminths were deposited in the Helminthological Collection of the Oswaldo Cruz Institute.

Data analysis

Parasitological parameters were calculated for each species of helminth according to Bush et al. (1997) considering these

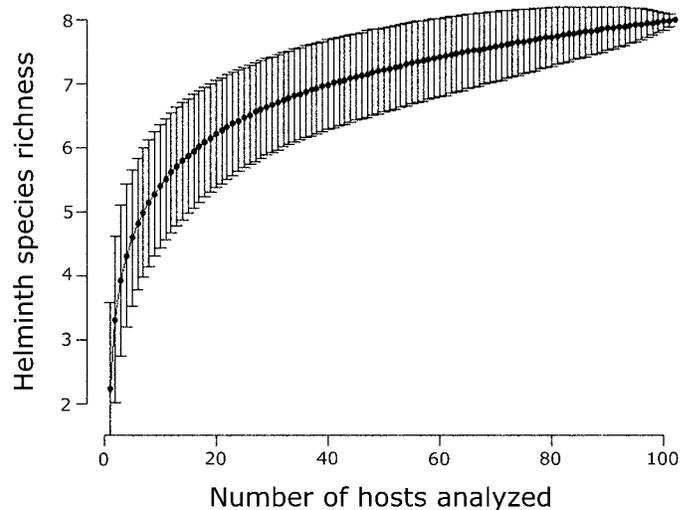


Figure 1. Rarefaction curve for helminth species richness of *Necromys lasiurus* in Uberlândia, Minas Gerais State, Brazil. Vertical bars indicate the confidence interval of 95%.

variables: host gender (males and females), season of the year (dry or rainy), and habitat (Cerrado, pastureland, or plantation). Mean abundance was considered as the total number of helminths of a species divided by the number of hosts analyzed. The mean intensity was considered as the total number of helminths of a species divided by the number of animals infected by this species. The prevalence was the ratio between the number of infected animals and the total number of animals analyzed. The aggregation index of each helminth species whose prevalence was ≥ 10 was determined using the variance-to-mean ratio of the parasite abundance, considering the infected hosts of each species. Helminth sex ratios of dioecious species were analyzed using the chi-square test.

Abundances and prevalences were compared in relation to host gender, season of the year, and habitat type only for the 4 most abundant species, considering each species separately. Helminths abundances were compared using generalized linear models (GLM) (global model: Host Gender + Season + Habitat). The best models were chosen using the corrected Akaike information criterion (AICc), so the models with $\Delta AICc \leq 2$ were considered plausible. Only models whose effects were significant were considered. When sufficient data were not available to perform a GLM, abundances were compared using the Mann-Whitney and Kruskal-Wallis tests. Prevalence rates were compared using the chi-square contingency test. Data were tested for normal distribution using the Shapiro-Wilk test.

Total species richness was measured as the number of helminth species found while mean richness was measured as the sum of the species found in each individual host divided by the number of hosts analyzed. Expected richness was estimated using the Jackknife 2 estimator, which is non-parametric and based on presence/absence of each species (Magurran, 2004). Beta-diversity indices were also estimated using the Whittaker index (Whittaker, 1960) between each habitat and overall. A species rarefaction curve was performed in order to assess sample size adequacy. We assumed that for a given helminth species, hosts were infected in the habitat of the localities where they were

Table II. Abundance and intensity (\pm SD), prevalence (95% confidence intervals), and aggregation indices (variance to mean ratio) in relation to host gender, season, and habitat type for each helminth species of *Necromys lasiurus* in Uberlândia, Minas Gerais State, Brazil. The dash (—) indicates absence of the species.

Parameters	Species			
	<i>Syphacia alata</i>	<i>Pterygodermatites zygodontomis</i>	<i>Stilestrongylus. freitasi</i>	<i>Protospirura numidica criceticola</i>
Abundance	13.33 \pm 49.41	2.97 \pm 4.75	58.42 \pm 97.21	0.23 \pm 1.02
Male	4.26 \pm 14.52	2.97 \pm 4.68	49.16 \pm 89.90	0.37 \pm 1.43
Female	19.95 \pm 63.19	2.71 \pm 4.81	65.17 \pm 103.10	0.12 \pm 0.56
Rainy season	0.69 \pm 1.95	2.14 \pm 2.92	11.25 \pm 31.30	0.64 \pm 1.66
Dry season	20.23 \pm 60.46	3.42 \pm 5.46	84.15 \pm 111.23	—
Cerrado	11.12 \pm 34.37	1.88 \pm 1.96	44.88 \pm 69.17	0.59 \pm 2.18
Pasturelands	18.67 \pm 66.24	2.95 \pm 4.15	90.26 \pm 130.92	0.19 \pm 0.70
Plantations	8.98 \pm 32.07	3.39 \pm 6.04	32.07 \pm 46.73	0.12 \pm 0.40
Intensity	46.90 \pm 84.71	5.05 \pm 5.28	83.93 \pm 107.59	2.30 \pm 2.54
Male	18.30 \pm 27.44	5.05 \pm 4.94	78.3 \pm 103.38	2.67 \pm 3.14
Female	61.95 \pm 100.65	4.71 \pm 5.57	87.39 \pm 111.13	1.75 \pm 1.50
Rainy season	4.17 \pm 3.27	3.85 \pm 2.96	28.93 \pm 45.67	2.30 \pm 2.54
Dry season	58.04 \pm 94.13	5.65 \pm 6.07	97.44 \pm 114.21	—
Cerrado	27.00 \pm 51.47	2.67 \pm 1.83	76.30 \pm 76.44	5.00 \pm 5.66
Pasturelands	80.30 \pm 122.38	5.52 \pm 4.25	121.28 \pm 139.06	2.00 \pm 1.41
Plantations	30.67 \pm 54.90	5.79 \pm 6.99	45.34 \pm 49.46	1.25 \pm 0.50
Prevalence	28.43 (28.12–28.74)	58.82 (58.79–58.85)	69.61 (69.00–70.21)	9.80 (9.79–9.81)
Male	23.26 (23.12–23.39)	60.47 (60.42–60.51)	62.79 (61.93–63.95)	13.95 (13.94–13.97)
Female	32.20 (31.69–32.72)	57.63 (57.67–57.59)	74.58 (73.73–75.42)	6.78 (6.78)
Rainy season	16.67 (16.65–16.69)	55.56 (55.53–55.59)	38.89 (38.56–39.22)	27.80 (27.76–27.80)
Dry season	34.85 (34.38–35.32)	60.61 (60.56–60.65)	86.36 (85.51–87.22)	—
Cerrado	41.18 (40.65–41.70)	70.59 (70.56–70.62)	58.82 (57.77–59.88)	11.76 (11.73–11.80)
Pasturelands	23.26 (22.62–23.89)	53.49 (53.45–53.53)	74.42 (73.17–75.67)	9.30 (9.30–9.31)
Plantations	29.27 (28.95–29.58)	58.54 (58.48–58.60)	70.73 (70.27–71.19)	9.76 (9.75–9.76)
Aggregation Indices	183.11	7.58	163.09	—
Male	49.52	6.6	164.39	—
Female	200.17	8.55	163.1	—
Rainy season	5.5	3.98	87.06	—
Dry season	180.69	8.71	147.03	—
Cerrado	106.24	2.05	106.6	—
Pasturelands	234.96	5.84	189.9	—
Plantations	114.59	10.75	68.08	—

collected, as *N. lasiurus* presents short movements and small home-range sizes (Pires et al., 2010).

Community indices of the importance of each species were calculated according to Thul et al. (1985) considering the whole study. Species were classified as dominant ($I \geq 1.0$); co-dominant, contributing significantly to the community, although to a lesser extent than the dominant species ($0.01 \leq I < 1.0$); and subordinate, which occur infrequently and, although they may develop and reproduce, do not contribute significantly to the community ($0 < I < 0.01$).

The structure of the helminth metacommunity was investigated using the elements of metacommunity structure (EMS) framework (Leibold and Mikkelsen, 2002) at 2 levels: the infracommunity scale (local scale), considering each infected host as a site; and the component community scale (regional scale), considering each farm as a site. Farms in which no helminth species were recorded were excluded from the matrix before ordering. The pattern of the metacommunity structure obtained at each level

was analyzed according to the 3 elements of each EMS. (1) Coherence is a measure that tests whether species respond to the same environmental gradient, i.e., the degree to which a pattern can be grouped into a single dimension. This element evaluates the number of absences in the species incidence matrix (embedded absences). (2) Species turnover represents the number of species replacements in this dimension. (3) Boundary clumping represents how the limits of distribution for each species are distributed between the sites along the environmental gradient. It can be clumped, over-dispersed, or randomly distributed (Leibold and Mikkelsen, 2002). The null model used permutes species across sites but considers the observed species richness for each site in all randomizations performed.

Diversity analysis, importance indices, and metacommunity structure analysis were performed considering only adult gastrointestinal helminths, of which *N. lasiurus* is the definitive host. EMS was analyzed using MATLAB R2017b functions written by C. L. Higgins (MathWorks, 2017). The chi-square tests, the

Table II. Extended.

<i>Physaloptera</i> sp.	Species			
	<i>Trichuris navonae</i>	<i>Rodentolepis akodontis</i>	<i>Moniliformis</i> sp.	<i>Cysticercus fasciolaris</i>
0.01 ± 0.10	0.01 ± 0.10	1.71 ± 4.16	0.71 ± 3.36	0.03 ± 0.22
—	—	1.63 ± 3.48	1.23 ± 4.73	0.07 ± 0.34
0.02 ± 0.13	0.02 ± 0.13	1.76 ± 4.63	0.32 ± 1.78	—
—	—	1.97 ± 4.14	2.00 ± 5.48	0.03 ± 0.17
0.02 ± 0.12	0.02 ± 0.12	1.56 ± 4.20	—	0.03 ± 0.25
—	—	2.53 ± 4.27	3.24 ± 7.01	—
—	0.02 ± 0.15	2.12 ± 5.36	—	—
0.02 ± 0.16	—	0.98 ± 2.27	0.37 ± 2.34	0.07 ± 0.35
1.00	1.00	3.63 ± 5.49	10.29 ± 8.69	1.50 ± 0.77
—	—	4.12 ± 4.57	13.25 ± 10.05	1.50 ± 0.77
1.00	1.00	3.35 ± 5.99	6.33 ± 5.86	—
—	—	4.44 ± 5.32	4.50 ± 5.32	1.00
1.00	1.00	3.22 ± 5.62	—	2.00
—	—	3.91 ± 4.83	11.00 ± 9.49	—
—	1.00	3.96 ± 6.88	—	—
1.00	—	2.86 ± 3.18	15.00	1.50
0.98 (0.98)	0.98 (0.98)	47.06 (47.03–47.08)	6.86 (6.84–6.88)	1.96 (1.96–1.97)
—	—	39.53 (39.50–39.57)	9.30 (9.26–9.35)	4.65 (4.65)
1.69 (1.69)	1.69 (1.69)	52.54 (52.50–52.58)	5.08 (5.07–5.10)	—
—	—	44.44 (44.40–44.49)	19.44 (19.39–19.50)	2.78 (2.78)
1.52 (1.52)	1.52 (1.52)	48.48 (48.45–48.52)	—	1.52 (1.51–1.52)
—	—	64.71 (64.64–64.77)	29.41 (29.31–29.52)	—
—	2.33 (2.33)	53.49 (53.44–53.54)	—	—
2.33 (2.33)	—	34.15 (34.12–34.17)	2.44 (2.42–2.46)	4.88 (4.87–4.88)
—	—	10.16	16.03	—
—	—	7.47	18.15	—
—	—	12.15	9.79	—
—	—	8.68	15.00	—
—	—	11.32	—	—
—	—	7.22	15.20	—
—	—	13.6	—	—
—	—	5.30	15.00	—

univariate tests, and the diversity and richness estimates were performed using the Past software, version 3:09 (Hammer et al., 2001). The rarefaction curve and the GLM analyses were performed using the vegan package (Oksanen et al., 2017) in RStudio software, version 1.0.136 (R Core Team, 2017). A significance level of 5% was used in all analyses.

RESULTS

Helminth species

In total, 102 specimens of *N. lasiurus* were collected and analyzed for the helminth fauna, distributed in 66 rodents during the rainy season and 36 during the dry season. In total, 7,896 helminths were recovered and 92.16% (n = 94) of the hosts were infected with one or more helminth species. Among male hosts, 88.37% were infected with helminths (n = 38/43) and among females, 94.91% were infected (n = 56/59). The rarefaction curve

for helminth species richness stabilized after 93 infracommunities sampled, indicating sample size adequacy (Fig. 1).

Eight species of adult helminths were identified (Table II). Six species were nematodes: *Protospirura numidica criceticola* Quentin, Karimi & Rodriguez de Almeida, 1968 and *Physaloptera* sp. Rudolphi, 1819 in the stomach; *Pterygodermatites (Paucipectines) zygodontomis* (Quentin, 1967); *Stilestrongylus freitasi* Durette-Desset, 1968 and *Trichuris navonae* Robles, 2011 in the small intestine; and *Syphacia (Syphacia) alata* Quentin, 1968 in the large intestine. One species from the phylum Platyhelminthes was found in the small intestine, the cestode *Rodentolepis akodontis* Rêgo, 1967. The Acanthocephalan *Moniliformis* sp. Travassos, 1915 was identified in the small intestine. The cestode *Cysticercus fasciolaris* (larval form of *Taenia taeniaeformis* Batsch, 1786 of which rodents are the intermediate hosts) was also observed encysted in the liver. This species was not included in the community analyses.

Table III. Generalized linear models (GLM) for *Syphacia alata* and *Stilestrongylus freitasi* abundances of *Necromys lasiurus* in Uberlândia, Minas Gerais state, Brazil. Models in bold are considered plausible. Models not significant or with $\Delta AICc > 10$ are not presented.

Parameter	Model		
	AICc	$\Delta AICc$	WAICc
<i>Syphacia alata</i>			
Season	1086.594	0	0.69
Null	1088.214	1.744	0.31
<i>Stilestrongylus freitasi</i>			
Habitat + Season	1209.067	0	0.72
Habitat + Season + Host gender	1211.334	2.267	0.23
Season	1215.178	6.111	0.03
Season + Host gender	1217.335	8.268	0.01
<i>Pterygodermatites zygodontomis</i>			
Null	610.266	0	1

Helminth population parameters

The species with the highest total prevalence values were *St. freitasi*, *Pt. zygodontomis*, *R. akodontis*, and *Sy. alata* (Table II). The prevalence was compared in relation to host gender, habitat, and season only for these 4 species. No significant difference was found in helminth prevalence in any species regarding host gender or habitat ($P > 0.05$). In relation to season, *St. freitasi* showed a significantly higher prevalence during the dry season ($\chi^2 = 4.94$, $P = 0.02$).

Seasonality may have influenced the occurrence of *Moniliformis* sp. and *Pr. n. criceticola* because they were found only during the rainy season (Table II). The only host infected with *T. navonae* was found in pastureland, and the only host with *Physaloptera* sp. was found in plantation area. *Moniliformis* sp. was observed only in Cerrado and plantation areas, and *C. fasciolaris* was found only in plantation areas (Table II).

The most abundant parasites, with the highest intensity and prevalence rates, were the nematodes *Sy. alata*, *St. freitasi*, and *Pt. zygodontomis* (Table II). The cestode *R. akodontis* was not very abundant but showed high prevalence indices. *Stilestrongylus freitasi*, which was the most abundant species with the highest intensity, showed differences in abundances under habitat and season criteria (first model of Table III). The highest values of abundance were observed in animals captured in pasturelands and during the dry season (Table II). The GLM analysis performed for *Sy. alata* showed that seasonality might have influenced the abundance of this species, which was higher during the dry season; however, the null model was also plausible (Table III). *Pterygodermatites zygodontomis* abundance did not present significant differences among the categories analyzed, as the only plausible model was the null model (Table III). *Rodentolepis akodontis* showed significantly higher abundance only in Cerrado hosts (Habitat: $Hc = 6.27$, $P = 0.043$, station: $U = 1,166$, $P = 0.86$, sex: $U = 1,177.5$, $P = 0.504$).

All species analyzed for aggregation presented a highly clumped distribution either across hosts, considering all the hosts, or for each category analyzed (Table II). *Syphacia alata*, *Pt. zygodontomis*, *St. freitasi*, and *Pr. n. criceticola* had significantly more

Table IV. Importance indices for the helminths of *Necromys lasiurus* in Uberlândia, Minas Gerais State, Brazil.

Species	Importance indices	Classification
<i>Stilestrongylus freitasi</i>	86.38	Dominant
<i>Syphacia alata</i>	78.05	Dominant
<i>Pterygodermatites zygodontomis</i>	3.71	Dominant
<i>Rodentolepis akodontis</i>	1.70	Dominant
<i>Moniliformis</i> sp.	0.10	Co-dominant
<i>Protospirura numidica criceticola</i>	0.04	Co-dominant
<i>Physaloptera</i> sp.	0.0006	Subordinate
<i>Trichuris navonae</i>	0.00020	Subordinate

females than males ($\chi^2 = 270.06$, $P = 0$; $\chi^2 = 122.97$, $P = 0$; $\chi^2 = 228.02$, $P = 0$, $\chi^2 = 3.91$, $P = 0.047$, respectively).

Community structure

Helminth species richness ranged from 0 to 6 among the infracommunities, with mean richness at 2.27, indicating that none was saturated with species. The overall estimated richness was 8.35 ± 1.97 , similar to the observed ($n = 8$). Cerrado had 6 species, and pastureland and plantation had 7 species each. The estimated richness was 6.09 ± 1.14 for Cerrado, 6.10 ± 1.48 for pasturelands, and 7.43 ± 1.98 for plantations. The overall beta-diversity among habitats was 0.2 and among infracommunities was 2.22. Beta-diversity between Cerrado and pasturelands was 0.23, between Cerrado and plantations was 0.08, and between pasturelands and plantations was 0.14.

The helminth community contained 4 dominant species: the nematodes *Sy. alata*, *Pt. zygodontomis*, *St. freitasi*, and the cestode *R. akodontis* (Table IV). *Moniliformis* sp. and *Pr. n. criceticola* were considered co-dominant and the other helminths were subordinate (Table IV).

The helminth metacommunity structure presented distinct patterns for the 2 scales investigated. On the infracommunity

Table V. Elements of the helminths metacommunity structure for infracommunity and component community of *Necromys lasiurus* in Uberlândia, Minas Gerais State, Brazil. Abbreviations: Abs = embedded absences; P = probability; SD = standard deviation; Rep = observed replacements; Mean = average of randomly generated matrices; MI = Morisita's Index; (—) = not applicable.

EMS/scales	Infracommunity	Component community
Coherence		
Abs	331	0
P	0.002	0.04
Mean	203.80	3.30
SD	41.80	1.61
Turnover		
Rep	—	7
P	—	0.72
Mean	—	8.07
SD	—	4.09
Clumping		
MI	—	0
P	—	0.42

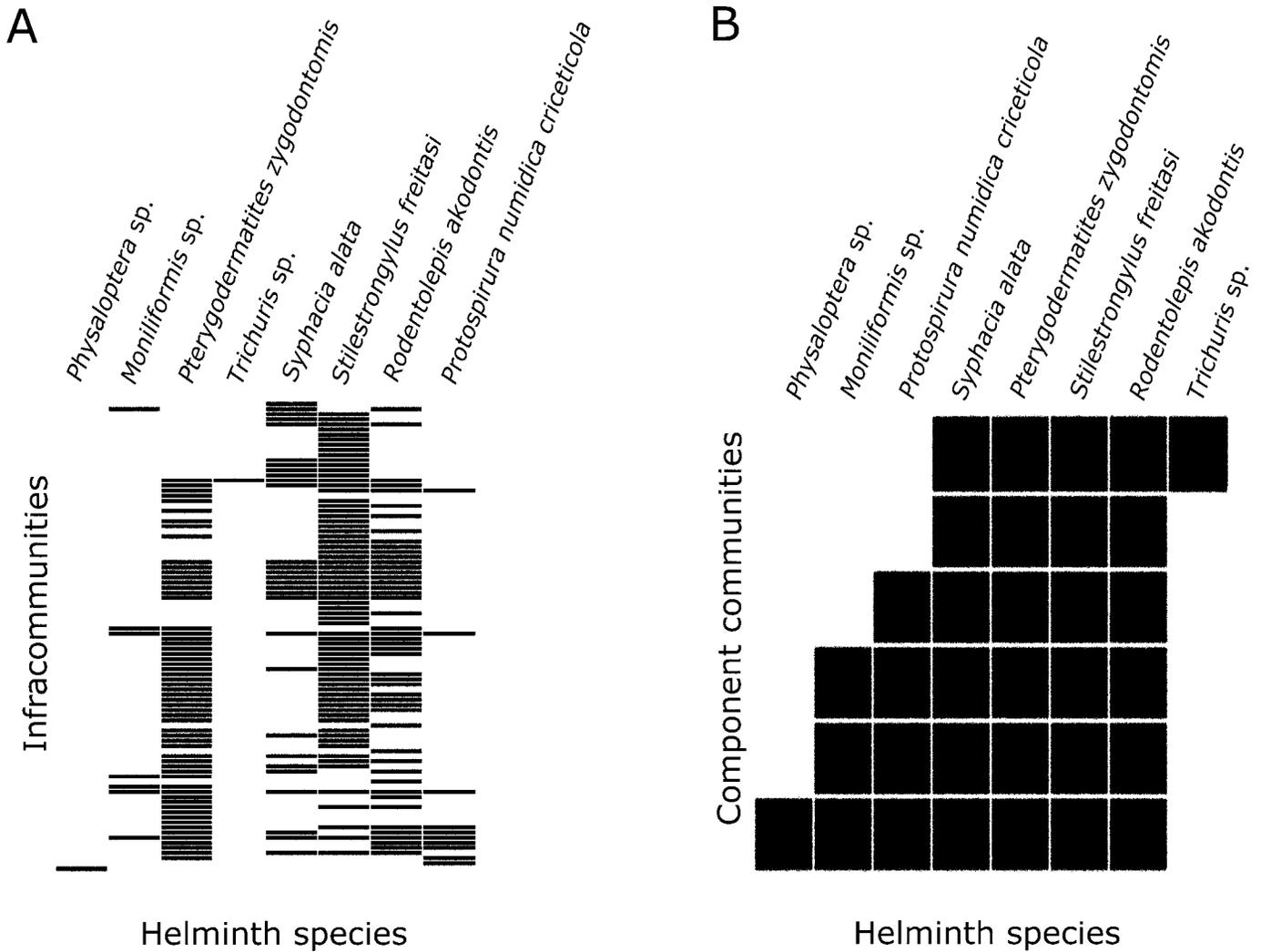


Figure 2. Ordinated matrix for the helminth metacommunity of *Necromys lasiurus* in Uberlândia, Minas Gerais State, Brazil. (A) Infracommunities, corresponding to each infected host. (B) Component communities, corresponding to each farm where the animals were captured. Embedded absences were not filled.

scale, a checkerboard structure was observed (Fig. 2A; Table V) with significant negative coherence (greater number of embedded absences among infracommunities than expected at random). On the component community scale, the structure was quasi-nested with stochastic species loss (positive coherence, negative but non-significant species turnover, and non-significant boundary clumping) (Fig. 2B; Table V). In this scale, species-poor sites were characterized by the occurrence of the dominant species *Sy. alata*, *Pt. zygodontomis*, *St. freitasi*, and *R. akodontis* and were subsets of richer sites, mostly in plantation habitat.

DISCUSSION

Helminths species and new records

Among the 8 helminth species found in the present study, only 4 had been previously reported to be parasites of *N. lasiurus* in the Cerrado and in the Caatinga biome: *Sy. alata*, *St. freitasi*, *Pt. zygodontomis*, and *Pr. numidica criceticola* (Quentin, 1967, 1968;

Durette-Desset, 1968; Quentin et al., 1968; Grossmann, 2015). The only other study of the helminth fauna of *N. lasiurus* in the Cerrado biome, carried out in Planaltina, Federal District, Brazil (Grossmann, 2015) also reported 8 species (*St. freitasi*, *Sy. alata*, *Pr. criceticola*, *Pt. zygodontomis*, *Stilestrongylus stilesi*, *Syphacia criceti*, *Pterygodermatites* n. sp., and *Hymenolepis* sp.). However, only the first 4 aforementioned species were found in the present study.

Syphacia alata has already been reported in *Oligoryzomys nigripes* (Quentin, 1968), *Calomys callosus* (Quentin, 1971), and *N. lasiurus* (Simões et al., 2017), all in the Caatinga biome. This species has also been reported in *Sigmodontomys alfari* in Colombia (Quentin, 1969) and in *Necromys temchuki*, *Necromys benefactus*, and *Thaptomys nigrita* in Argentina (Robles, 2008).

Stilestrongylus freitasi also presented a high prevalence in *N. lasiurus* in the study by Grossmann (2015), but intensity and prevalence were lower. Simões et al. (2017) reported *St. freitasi* in the Caatinga biome infecting *N. lasiurus* and *Thrichomys*

laurentius in the State of Paraíba. *Stilestrongylus freitasi* has also been reported in *Akodon simulator* (Suriano and Navone, 1992), *Euryoryzomys lamia*, and *Cerradomys subflavus* (Vicente, 1997). Quentin (1969) reported this helminth in *Thrichomys apereoides* in the State of Pernambuco, Brazil. Our results corroborate *N. lasiurus* as the main host for *St. freitasi*, as suggested by the index of importance.

For *Pt. zygodontomis*, Grossmann (2015) reported higher prevalence, abundance, and intensity in *N. lasiurus* than in the present study. This species was reported in *Rhipidomys mastacalis*, also in Uberlândia (Cardoso, 2016; Costa et al., 2017). Quentin (1967) reported this species in *N. lasiurus* and in *Ca. callosus* (Quentin, 1971).

The cestode *R. akodontis* was previously reported in *Akodon cursor*, *Akodon montensis*, and *O. nigripes* in the Atlantic Forest biome (Rêgo, 1967; Simões et al., 2010) and in *Oxymycterus rufus* in Argentina (Guerreiro Martins et al., 2014). *Protospirura numidica criceticola* was already reported in *Ca. callosus* and *N. lasiurus* in the Caatinga biome (Quentin, 1971), in *Akodon azarae* in Argentina (Miño, 2008), and in *Oxymycterus paramensis* in Colombia (Jiménez-Ruiz and Gardner, 2003). *Moniliformis moniliformis* has been frequently reported infecting *Rattus norvegicus* (Simões et al., 2016) and eventually humans (Gonçalves et al., 2011), which suggests habitat sharing among *N. lasiurus* and synanthropic rodents. *Trichuris navonae* was previously described infecting *A. montensis* in Argentina (Robles, 2011).

The present study reported the first case of parasitism by a species of the phylum Acanthocephala (*Moniliformis* sp.) in the rodent *N. lasiurus*. In addition, the hosts' spectrum of *Physaloptera* sp., and *T. navonae* were enlarged with the inclusion of this host as well as the geographical distribution of the species *Pt. zygodontomis*, since this species was previously found only in the State of Pernambuco and Federal District, Brazil.

The aggregated distribution observed in all helminths analyzed is a frequent pattern of parasite distribution (Bush et al., 2001; Poulin, 2001), in which most parasites occur in only a portion of the host population. This pattern influences the structuring of communities and may favor higher species richness in the component community when different species occur in different infracommunities, reducing species saturation in the infracommunity level. In this case, more aggregation may result in 2 parasite species co-existing by living in different parts of the host population (Roberts et al., 2001).

Influence of biotic and abiotic factors on helminth populations

Corroborating our first hypothesis, helminths' prevalence and abundances were influenced by habitat and by season, but not by host gender, mostly for *Sy. alata* and *St. freitasi*. *Syphacia alata*, which is presumed to have a monoxenous life cycle as the other congeners (Taffs, 1976), and was one of the most dominant species in the helminth community, presented higher prevalence, abundance, and intensity than those found by Grossmann (2015). The dry winter season may favor an increase in the transmission of *Sy. alata* and *St. freitasi*, possibly due to its transmission mode, which includes contact with eggs in the perianal region of hosts (Chan, 1952). Other studies observed an increase in the population sizes of *N. lasiurus* during the dry

winter season in Cerrado (Alho and Pereira, 1985; Becker et al., 2007) and in the Atlantic Forest (Feliciano et al., 2002), corroborating the present study, which presented more captures of this rodent during the winter. This creates greater contact among individuals, facilitating the transmission of this parasite. Thus, the dry season seems to promote an increase in prevalence, intensity, and abundance of these 2 helminths in rodents. Suriano and Navone (1992) also observed higher prevalence of *Sy. alata* during the dry season in *A. simulator* in Argentina; however, the intensity and abundance were higher during the rainy season.

The greater abundance, intensity, and prevalence of *St. freitasi* in pasturelands can be explained by the host characteristics of habitat use, locomotion, and population dynamics. *Necromys lasiurus* is terrestrial and occurs mostly in open areas (Bonvicino et al., 2008), such as the pasturelands, which are characterized by more-homogeneous vegetation relative to other studied areas. In this way, this host seems to have a key role in establishing and maintaining the life cycle of this helminth.

The higher abundance of *R. akodontis* in the Cerrado may be attributed to the environmental heterogeneity of this habitat in relation to the other studied areas, which could be related to the variability and abundance of intermediate hosts necessary for the development of the life cycle of this species (Mares et al., 1986).

Helminth diversity and land use

Regarding our second hypothesis, species richness and diversity did not vary largely among habitats, as beta-diversity was low, especially among habitats and, consequently, were less influenced by the kind of land use than by species composition as previously discussed. Thus, the differences observed indicate that disturbed and anthropized areas may be conducive to the presence of less-dominant or less-abundant species such as *Moniliformis* sp., *Physaloptera* sp., *T. navonae*, and also *C. fasciolaris* but not to the number of species in each area.

As cited above, *Sy. alata*, *St. freitasi*, *Pt. zygodontomis*, and *R. akodontis*, which were the most abundant and dominant species, were reported in the literature infecting several host species, indicating a low host specificity. Among their host spectrum, only the rodents *O. nigripes* (host of *Sy. alata* and *R. akodontis*) and *Ce. subflavus* (host of *St. freitasi*) were captured in the study area in low abundances, the former only in the Cerrado habitat and the latter in all 3 habitats (Limongi et al., 2013). Two other rodent species of the genus *Calomys* (host of *Pt. zygodontomis*), *Calomys tener* and *Calomys expulsus*, were also captured in the study area, mostly in plantations (Limongi et al., 2013). This may indicate that these helminth species may be circulating throughout the habitats and in other hosts, resulting in their dominant pattern in the community.

The rodents *Ce. subflavus* (host of *Physaloptera galvaoi* [São Luis et al., 2015]), *O. nigripes* (host of *Trichuris travassosi* [Vicente et al., 1997]), and the synanthropic rodent *Ra. rattus* (host of *M. moniliformis* [Amin et al., 2016]), together with *N. lasiurus*, may be sharing these co-dominant and subordinate parasite species. Thus, these hosts may be contributing to the maintenance of these helminth species, whose presence would be favored in disturbed areas. Other studies on the helminth community structure of mammals have also shown higher species richness

in disturbed, fragmented, or agricultural areas (Gillespie and Chapman, 2008; Chaisiri et al., 2010).

Metacommunity structure

The third hypothesis of our study was accepted, as in both scales (infracommunities and component communities) the patterns of metacommunity structures were non-random, although the patterns were different. The checkerboard pattern of species distribution found for the metacommunity structure of gastrointestinal helminths of *N. lasiurus* on the infracommunity scale suggests the existence of interspecific competition as a structuring mechanism, resulting in mutual competitive exclusion (Presley et al., 2010). The checkerboard pattern may also occur when there are many rare species in the community (Schmera et al., 2018). Competition between intrapopulations can occur by nutrients, space, and in response to the modulation of the host immune system by the presence of a parasite (Maizels et al., 2004). We observed that when one of the dominant species was very abundant, few or no other species occurred in that infracommunity. These results, coupled with the absence of species saturation in the infracommunities, the fact that the total richness observed was much greater than the mean richness, and the microhabitat specialization by all helminth species, corroborate the possible existence of interspecific competition, mainly among the dominant species such as *St. freitasi* and *Sy. alata*, which present direct life cycles. Competition among helminth species has already been reported in nature in other mammal hosts (Haukisalmi and Henttonen, 1993; Lello et al., 2004).

The quasi-nested pattern found in the metacommunity structure on the component community scale indicates that the strength of community structuring mechanisms is weaker than that of a nested pattern, but with the same characteristics except that species turnover is random. The nested pattern means that communities with fewer species are subsets of communities with higher species richness; it indicates that hosts accumulate parasite species gradually and predictably, and this is the most expected pattern in parasite communities of wild hosts in natural environments (Poulin, 2007). Non-significant species turnover indicates that the number of times 1 species replaces another between 2 sites occurs at random, unlike other structuring patterns (Leibold and Mikkelsen, 2002). The random species loss indicates that boundary clumping is determined by species-specific environmental tolerances (Presley et al., 2010).

The host infection of a particular helminth may be due to the host–parasite encounter rate and to the potential of helminth infectivity according to the species range in the environment (Combes, 2001). The most abundant species would be the most likely to be the first ones to infect the host because species enter the community in a predictable order, with high abundance species that are more common probably being the only species present in species-poor communities (Poulin, 2001, 2007; Roberts et al., 2001). Furthermore, their establishment and abundance are based on the life-history traits of the different species (Roberts et al., 2001). In the present study, the species that will thereafter infect this host may be influenced by the presence of the first species, making it difficult for new infections or preventing them to have high abundances due to competition or modulation of the immune system, as suggested in the checkerboard pattern of the infracommunities structure. The

occurrence of the dominant helminths *Sy. alata*, *Pt. zygodontomys*, *St. freitasi*, and *R. akodontis* in species-poor sites on both scales reinforces the role of these parasites in the structuring of communities.

The present study was the first to analyze the community structure of the helminths in *N. lasiurus*. To conclude, the results indicate that the season and the kind of land use favored the occurrence of some helminths species in this rodent, especially in the plantation area, although diversity was not largely influenced by the land use. On the component community scale, *Sy. alata*, *Pt. zygodontomys*, *St. freitasi*, and *R. akodontis* were the core species of the quasi-nested pattern of the metacommunity structure observed. Plantation areas could present a larger food supply for rodents (Gheler-Costa et al., 2012), leading to an increase in the abundance of hosts and favoring the occurrence of other rodent species, where there would be a higher rate of parasite exchange among different hosts.

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