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HELMINTH COMMUNITY STRUCTURE OF THREE SIGMODONTINE RODENTS IN THE ATLANTIC FOREST, SOUTHERN BRAZIL

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Abstract: Ecological studies of host-parasite interactions are common in rodents. However, despite the widespread occurrence of endoparasites in those animals, there is a lack of information about the community structure of these parasites. The aims of this study were to describe the species composition and the community structure of helminths of the rodents *Oligoryzomys nigripes*, *Akodon montensis* and *Euryoryzomys russatus* (Rodentia, Sigmodontinae), and to investigate the influence of host species, age and gender on the abundance and prevalence of helminths. The pattern of the metacommunity structure of the helminths of *A. montensis* was also analysed. Small mammals were captured in Serra do Tabuleiro State Park, Santo Amaro da Imperatriz, state of Santa Catarina, Brazil. Helminths were identified and counted. Each species had its abundance, intensity and prevalence estimated for each host. The influence of host species, age and gender on abundance and prevalence of helminths was tested using generalized linear models (GLM). The metacommunity was analysed by calculating the Elements of Metacommunity Structure (EEM) for infracommunities. In *O. nigripes,* the species *Guerrerostrongylus zetta* and *Stilestrongylus lanfrediae* (Nematoda, Heligmonellidae) were found. *A. montensis* harboured *G. zetta*, *Trichofreitasia lenti* (Nematoda, Heligmonellidae), *Trichuris navonae* (Nematoda, Trichuridae), *Angiostrongylus* sp. (Nematoda, Angiostrongylidae), *Litomosoides chagasfilhoi* (Nematoda, Onchocercidae) and *Rodentolepis akodontis* (Plathyhelmintes, Cestoda). In the *E. russatus* rodent, the species *G. zetta, Stilestrongylus rolandoi* (Nematoda, Heligmonellidae) and *Raillietina guaricanae* (Plathyhelmintes, Cestoda) were found. This study presented new records of the helminths *S. rolandoi* and *R. guaricanae* in *E. russatus,* and of *L. chagasfilhoi* in *A. montensis.* The helminth metacommunity structure of *A. montensis* presented a random pattern of species distribution, characterized by a non-coherent structure along the environmental gradient, indicating different environmental requirements due to the infection of this host by helminths with different life cycles.

Keywords: Cestoda; ecology; metacommunity; Nematoda; parasitism.

INTRODUCTION

Sigmodontine rodents are highly diverse among Neotropical mammals, comprising nearly 380 species (Patton *et al.* 2015). This subfamily is broadly spread, occurring from the sea level to Andes and from rainforests of the Amazon to xeric environments along the Pacific coast in South and Central America and Southern North America (Patton *et al.* 2015). Some of these rodents may also occur around human dwellings and in rural areas. They are largely related to zoonosis and parasitic outbreaks (Han *et al.* 2016), acting as hosts and/or reservoirs of several parasites. Sigmodontine rodents were found infected by several parasites, such as: protozoans (Vaz *et al.* 2007), helminths (Maldonado *et al.* 2006), bacterias (Rozental *et al.* 2017), and hantavirus (Oliveira *et al.* 2014). These findings highlight the veterinary and public health importance of these rodents in the transmission of parasites.

Rodents are commonly used as models in ecological studies of host-parasite interactions and parasite communities (Püttker *et al.* 2008, Simões *et al.* 2011, Cardoso *et al.* 2018). Among parasites, helminths are an excellent group for such studies, due to the characteristics of their transmission. However, regarding the wild rodents of the Neotropics, there is a great lack of studies considering helminth's faunas and community structures. Some of the previous studies which focused on helminth's fauna and community structure of the sigmodontines *Akodon montensis* Thomas 1913, *Oligoryzomys nigripes* Olfers, 1818 (Püttker *et al.* 2008, Simões *et al.* 2011, Panisse *et al.* 2017, Cardoso *et al.* 2018) and *Euryoryzomys russatus* Wagner, 1848 (Panisse *et al.* 2017) were carried out in the Atlantic Forest. However, only two were developed in the state of Santa Catarina, southern Brazil. Vicente *et al.* (1987) conducted a survey on the helminth fauna of small mammals in Santa Catarina Island; and Kuhnen *et al.* (2012) developed a study on the helminth communities of small rodents in the Serra do Tabuleiro State Park (STSP hereafter), in the Southeast of the state of Santa Catarina, as well as in Santa Catarina Island.

Although the STSP is the largest conservation unit with complete protection of the biodiversity in the state of Santa Catarina (IMA 2018), there is a large gap of studies concerning wildlife parasites in this area. The aim of this study was to survey the helminth fauna and analyse the community structure of three sigmodontine rodents, *O. nigripes*, *A. montensis* and *E. russatus*, in the STSP, a preserved area of the Atlantic Forest in the state of Santa Catarina, southern Brazil. We investigated the influence of the host species, age and gender on abundance and prevalence of the helminths. We also analysed the pattern of the metacommunity structure of the helminths in *A. montensis*, the most abundant host species in this study.

MATERIAL AND METHODS

Studied site

The STSP (27°43'25.79"S, 48°48'52.39"W, *datum* WGS84) is a natural reserve of Atlantic Forest with an area of 84,130 ha. The Park is located in the municipalities of Florianópolis, Palhoça, Águas Mornas, São Bonifácio, São Martinho, Imaruí, Paulo Lopes and Santo Amaro da Imperatriz (Figure 1). The current study was conducted in Santo Amaro da Imperatriz, which encompasses 61.5 % of the territory of the reserve (Brüggemann 2014).

The STSP is composed by forests in different stages of ecological succession, including Restingas and Dunes, Mangroves, Dense and Mixed Ombrophilous Forest and Highland Fields, with records of invasive and exotic species (IMA 2018). The study was conducted in areas of Dense Ombrophylous vegetation with continuous canopy cover ranging from eight to 15 meters, semi-open understory, predominance of medium-sized trees, and presence of watercourses. The climate of the region is subtropical (Cfa) according to Kopen's classification, characterized by cold winter and hot summer, without a marked rainfall season (Ayoade 1986).

Sampling and examination of rodents

Rodents were collected in Tomahawk (40.64 cm × 12.70 cm × 12.70 cm) and Sherman (7.62 cm × 9.53 cm × 30.48 cm) traps, baited with a mixture of peanut butter, banana, oats and bacon. Traps were placed on the ground in six transects of 15 trapping points spaced 20 m apart. Six additional traps were placed in the understorey, three of each type intercalated. Pitfall traps (65 litres buckets spaced 10 m apart) were additionally placed in four transects. Trappings were carried out during ten consecutive days in September/2014 and May/2015.

Rodents were euthanized for recovery of helminths and their bionomic data (gender, reproductive condition, body mass and external measures) was recorded. Rodent species were identified by external and cranial morphology, and cytogenetic and molecular analyses, when necessary. The rodents were taxidermized and deposited in the mammal collection of the Paraíba Federal University (UFPB) (voucher numbers: 9502, 9414 and 9641).

Helminths specimens were collected and fixed in 65° AFA solution (93 parts 70 % ethanol, 5 parts 4 % formalin and 2 parts 100 % acetic acid) according to Amato *et al.* (1991). Some specimens were stored in 70 % ethanol for further molecular analysis. Specimens were counted using a stereoscopic microscope and analysed with a Zeiss Standard 20 light microscope. The species were identified according to Yamaguti (1961), Khalil *et al.* (1994) and Vicente *et al.* (1997). Helminth specimens were deposited at the Helminthological Collection of the Oswaldo Cruz Institute (CHIOC numbers: 38566, 38596, 38597, 38598 and 38599).

The animals were captured under the authorization of the Brazilian Government's

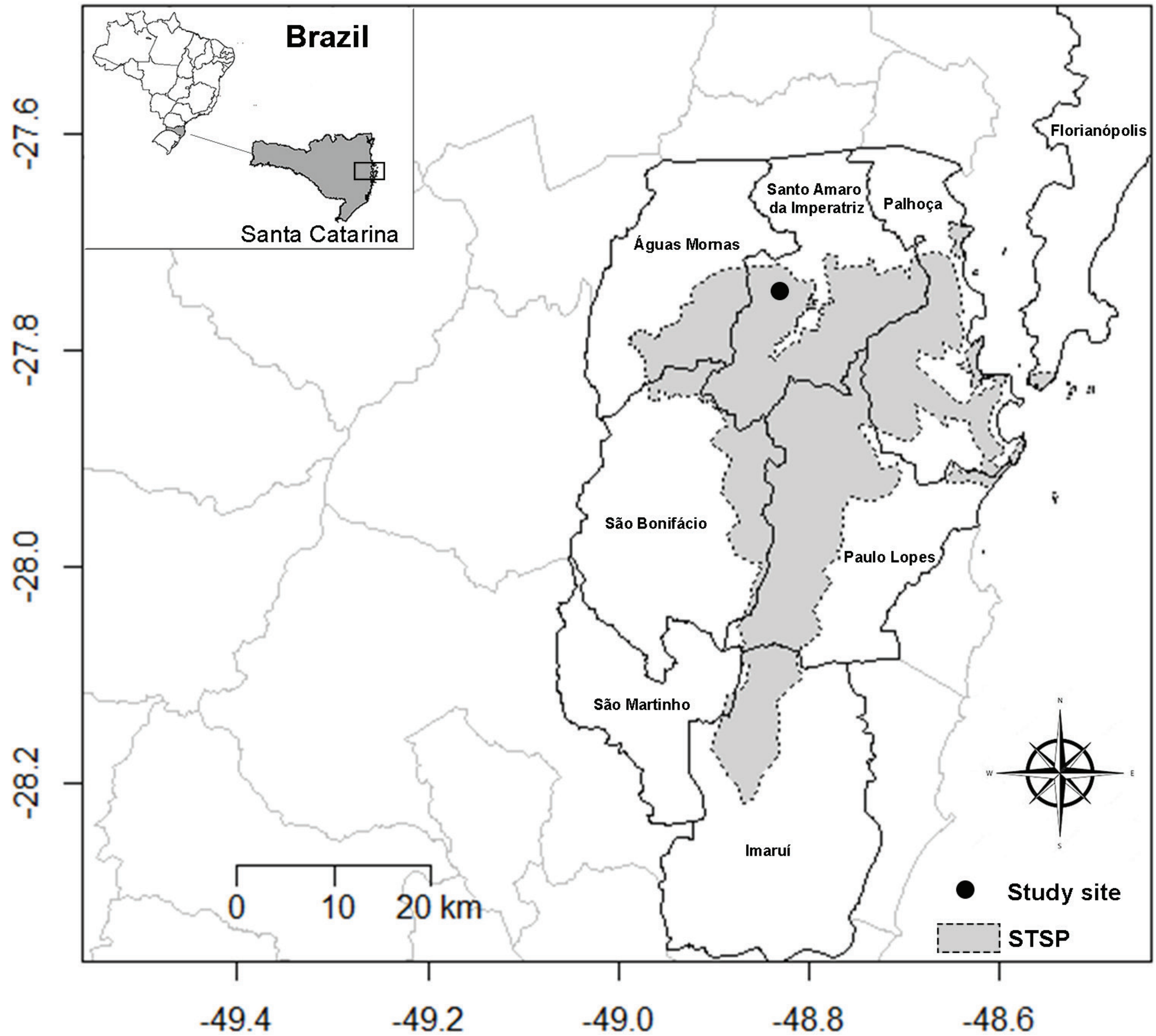

Figure 1. Map of the study site in the Serra do Tabuleiro State Park (STSP), Southeast of the state of Santa Catarina, Brazil.

Chico Mendes Institute for Biodiversity and Conservation (ICMBIO license 26934-1) and by the Environmental Institute of the state of Santa Catarina (IMA license 043/2014 GERUC/ DEC). All procedures followed the guidelines for capture, handling and care of animals from the Ethical Committee on Animal Use of the Oswaldo Cruz Foundation (LW- 39/14), and the standards of biosafety.

Data analysis

The parasitological parameters were calculated according to Bush *et al.* (1997) for each helminth species for the infracommunity (within an individual host) and the component community (the host population) levels. Mean abundance was considered as the total number of helminths of a species divided by the number of hosts analysed. Mean intensity was the total number of helminths of a species divided by the number of animals infected by the species. Prevalence was the ratio between the number of infected animals and the total number of animals analysed. The spatial aggregation level was calculated using the variance to mean ratio of the number of helminths per host. The total helminth species richness was considered as the number of helminth species present in each host species. The mean helminth species richness was considered as the sum of the richness of each host individual divided by the number of hosts analysed for each host species.

The influence of host species, age and gender on abundance and prevalence of helminths was tested using generalized linear models (GLM) with Gaussian and Binomial distributions, respectively. This analysis was performed only for the helminth species shared between rodent species, which showed sufficient data for these comparisons. The best models were chosen using the corrected Akaike information criterion (AICc). The ages of the animals were estimated based on body mass (g) and reproductive condition, dividing the individuals in two classes: young (≤ 14 g to males and ≤ 12 g to females in *O. nigripes*, ≤ 25 g to males and ≤ 22 g to females in *A. montensis* and ≤ 38 g to males and ≤ 43 g to females in *E. russatus*) and adults (≥ 15 g to males and ≥ 13 g to females in *O. nigripes*, ≥ 26 g to males and ≥ 23 g to females in *A. montensis* and ≥ 39 g to males e ≥ 44 g to females in *E. russatus*). The helminth community structure was characterized using an importance index (I) of each helminth species according to Thul *et al.* (1985) for adult helminths. When I ≥ 1.0, the species was considered to be a dominant species; 0.01 ≤ I < 1.0, co-dominant species and 0 < I < 0.01, subordinate species.

The metacommunity structure of the helminths was investigated only in *A. montensis,* which had sufficient data. This analysis was carried out at the level of infracommunity, using the elements of metacommunity structure (EMS) (coherence, turnover and boundary clumping), according to Leibold & Mikkelson (2002). The coherence element tests if the species respond to the same environmental gradient. The turnover element determines whether the processes that structure the diversity lead to substitution or loss of species along the gradient. Boundary clumping quantifies the overlap of species distribution limits in the environmental gradient (Leibold & Mikkelson 2002). The GLM analyses were performed using the vegan package (Oksanen *et al.* 2018) in R software version 3.4.2 (R Core Team 2018). The EMS analysis was performed in Matlab R2018a software (MathWorks) using the EMS Script (Higgins 2008). The significance level used was 5 % in all the analyses.

RESULTS

One hundred and ninety-nine rodents were captured: 146 (44 infected specimens) *A. montensis*, 28 *E. russatus* (19 infected specimens) and 25 *O. nigripes* (19 infected specimens). Nine helminth species were collected in these three hosts studied, totalling 691 adult helminth specimens. The helminth fauna of *A. montensis* was composed by the nematodes *Angiostrongylus* sp., *Guerrerostrongylus zetta* (Travassos, 1937) Sutton & Durette-Desset, 1991, *Litomosoides chagasfilhoi* Moraes Neto, Lanfredi & Souza, 1997, *Trichofreitasia lenti* Sutton & Durette-Desset, 1991, *Trichuris navonae* Robles, 2011, and the cestode *Rodentolepis akodontis* Rêgo, 1967 (Table 1). The specimens of the genus *Angiostrongylus* Kamensky, 1905 could not be identified because only female specimens were found. Three helminth species were found in *E. russatus*: the nematodes *G. zetta* and *Stilestrongylus rolandoi* Boullosa, Simões, Andrade-Silva,

Table 1. Mean abundance and mean intensity of the helminths followed by standard deviation, minimum and maximum, helminth prevalence (%) with 95 % confidence limits, and indices of aggregation of *Akodon montensis* in relation to host gender (females: N = 66; males: N = 80), host age (young: N = 26; adults: N = 120) and overall (N = 146) in the Serra do Tabuleiro State Park, state of Santa Catarina, Brazil. Cases without SD indicates one specimen infected. Life cycles classifications were based on Taylor *et al.* (2017).

Categories	*Angiostrongylus* sp.	*Guerrerostrongylus zetta*	*Litomosoides chagasfilhoi*	*Trichofreitasia lenti*	*Trichuris navonae*	*Rodentolepis akodontis*
Mean Abundance	0.01 ± 0.16 (0-2)	0.12 ± 0.70 (0-5)	0.02 ± 0.24 (0-3)	0.60 ± 2.29 (0-15)	0.12 ± 0.75 (0-8)	0.26 ± 0.83 (0-8)
Female	0.03 ± 0.24	0.18 ± 0.83	0.04 ± 0.36	0.56 ± 2.30	0.01 ± 0.12	0.30 ± 1.06
Male	0	0.07 ± 0.56	0	0.65 ± 2.30	0.21 ± 0.99	0.22 ± 0.59
Young	0	0.23 ± 0.99	0	0.23 ± 0.99	0	0.19 ± 0.49
Adult	0.01 ± 0.18	0.10 ± 0.62	0.02 ± 0.27	0.69 ± 2.48	6.66 ± 0.82	0.27 ± 0.89
Mean Intensity	2.00	3.60 ± 1.51 (1-5)	3.00	5.56 ± 4.64 (1-15)	2.27 ± 2.50 (1-8)	1.65 ± 1.49 (1-8)
Female	2.00	4.00 ± 0	3.00	6.16 ± 5.26	1.00	1.81 ± 2.08
Male	0	3.00 ± 2.82	0	5.20 ± 4.49	2.83 ± 2.63	1.50 ± 0.67
Young	0	3.00 ± 2.82	0	3.00 ± 2.82	0	1.25 ± 0.50
Adult	2.00	4.00 ± 0	3.00	5.92 ± 4.81	2.57 ± 2.50	1.73 ± 1.62
Prevalence	1.36 (0 – 1.361)	3.424 (3.421 - 3.427)	0.680 (0.679 - 0.681)	10.95 (10.94 - 10.96)	4.79 (4.791 - 4.797)	15.75 (15.749 - 15.757)
Female	1.515 (1.514 - 1.516)	4.545 (4.539 - 4.551)	1.515 (1.513 - 1.517)	9.09 (9.08 - 9.10)	1.51 (0 – 1.511)	16.660 (16.658 - 16.674)
Male	0	2.50 (2.496 - 2.504)	0	12.50 (12.49 - 12.51)	7.50 (0 – 7.510)	15.00 (14.996 - 15.004)
Young	0	7.69 (7.68 - 7-.70)	0	7.69 (7.68 - 7.70)	0	15.38 (15.378 - 15.390)
Adult	0.833 (0.832 - 0.834)	2.50 (2.497 - 2.503)	0.833 (0.832 - 0.834)	11.66 (11.65 - 11.67)	5.83 (5.829 - 5.837)	15.83 (15.828 - 15.838)
Aggregation indice	2.00	4.01	3.00	8.65	4.57	2.70
Site of Infection	Pulmonary artery	Small intestine	Abdominal cavity	Small intestine	Large intestine	Small intestine
Life cycle	Indirect	Direct	Indirect	Direct	Direct	Indirect

Gentile & Maldonado, 2018 and the cestode *Raillietina guaricanae* César & Luz, 1993 (Table 2). In *O. nigripes,* we observed two species: the nematodes *G. zetta* and *Stilestrongylus lanfrediae* Souza, Digiani, Simões, Luque, Rodrigues-Silva & Maldonado, 2009 (Table 3). *Oligoryzomys nigripes* also presented higher mean helminth species richness (0.92) in relation to the other hosts (0.39 and 0.36 for *E. russatus* and *A. montensis*, respectively). Despite this difference, the helminth species richness of each infracommunity varied from 0 up to 2 in all host species. All helminth species were highly aggregated in the host populations (Tables 1, 2 and 3).

Guerrerostrongylus zetta was the only helminth species shared by the three host species, although presented higher values of mean abundance and prevalence in *O. nigripes* and higher mean intensity in *E. russatus* (Tables 2 and 3). In this latter host, *S. rolandoi* had the highest abundance and prevalence values (Table 2). In *A. montensis*, *T. lenti* had the highest mean abundance and mean intensity, and *R. akodontis,* the highest prevalence rate (Table 1). In *O. nigripes*, *G. zetta* was the most abundant and prevalent species (Table 3).

Trichuris navonae, *L. chagasfilhoi*, *Angiostrongylus* sp., *R. guaricanae* and *S. lanfrediae* only occurred in adult hosts (Tables 1, 2 and 3). In addition, *L. chagasfilhoi* and *Angiostrongylus* sp. only occurred in female hosts (Tables 1, 2 and 3). *Raillietina guaricanae* occurred in only one male and two female hosts of *E. russatus* (Table 2), *T. navonae* occurred in only one female and six males of *A. montensis* (Table 1) and *S. lanfrediae* in only one male and three female hosts of *O. nigripes* (Table 3). None of the helminth species exclusively occurred in young or male hosts.

The GLM analysis carried out to investigate the influence of host species, age and gender in the abundance and prevalence of *G. zetta* showed plausible models in relation to the three factors analysed (Table 4). This helminth had higher abundance and prevalence in adult female hosts

Table 2. Mean abundance and mean intensity of the helminths followed by standard deviation, minimum and maximum, helminth prevalence (%) with 95% confidence limits, and indices of aggregation of *Euryoryzomys russatus* in relation to host gender (females: N = 12; males: N = 16), host age (young: N = 10; adults: N = 1) and overall (N = 28) in the Serra do Tabuleiro State Park, state of Santa Catarina, Brazil. Cases without SD indicates one specimen infected. Life cycles classifications were based on Taylor *et al.* (2017).

Categories	*Guerrerostrongylus zetta*	*Stilestrongylus rolandoi*	*Raillietina guaricanae*
Mean Abundance	2.32 ± 12.28 (0-65)	6.39 ± 13.83 (0-57)	0.67 ± 2.72 (0-14)
Female	5.41 ± 18.76	6.83 ± 11.51	1.25 ± 4.02
Male	0	6.06 ± 15.71	0.25 ± 1.00
Young	0	6.60 ± 17.90	0
Adult	3.61 ± 15.32	6.27 ± 11.55	1.05 ± 3.36
Mean Intensity	65.00	25.50 ± 16.98 (8-57)	6.33 ± 6.80 (1-14)
Female	65.00	20.40 ± 10.60	7.50± 9.19
Male	0	32.30 ± 24.02	2.5 ± 0.88
Young	0	33.00 ± 33.94	0
Adult	65.00	22.60 ± 10.31	6.33 ± 6.80
Prevalence	3.57 (3.43 - 3.71)	25 (24.84 – 25.16)	10.71 (10.68 - 10.74)
Female	8.33 (8.00 - 8.66)	33.30 (33.10 - 33.50)	16.66 (16.59 - 16.73)
Male	0	18.75 (18.51 - 18.99)	6.25 (6.24 - 6.26)
Young	0	20.00 (19.65 - 20.35)	0
Adult	5.55 (5.33 - 5.77)	27.77 (27.60 - 27.94)	16.66 (16.61 - 16.70)
Aggregation indice	65.00	29.92	10.92
Site of Infection	Small intestine	Small intestine	Small intestine
Life cycle	Direct	Direct	Indirect

Table 3. Mean abundance and mean intensity of the helminths followed by standard deviation, minimum and maximum, helminth prevalence (%) with 95% confidence limits, and indices of aggregation of *Oligoryzomys nigripes* in relation to host gender (females: N = 12; males: N = 13), host age (young: N = 15; adults: N = 10) and overall (N = 25) in the Serra do Tabuleiro State Park, state of Santa Catarina, Brazil. Cases without SD indicates one specimen infected. Life cycles classifications were based on Taylor *et al.* (2017).

Categories	*Guerrerostrongylus zetta*	*Stilestrongylus lanfrediae*
Mean Abundance	8.68 ± 11.25 (0-76)	1.72 ± 6.00 (0-29)
Female	13.66 ± 14.21	1.16 ± 2.72
Male	4.07 ± 4.49	2.23 ± 8.04
Young	3.93 ± 7.60	0
Adult	15.08 ± 12.40	4.30 ± 9.15
Mean Intensity	11.42 ± 11.65 (1-76)	10.75 ± 12.60 (1-29)
Female	16.40 ± 14.04	4.66 ± 4.04
Male	5.88 ± 4.49	29
Young	6.55 ± 9.04	0
Adult	15.80 ± 12.40	10.75 ± 12.60
Prevalence	76 (75.86 - 76.14)	16 (15.93 - 16.07)
Female	83.33 (83.08 - 83.58)	25.00 (24.96 - 25.04)
Male	69.23 (69.16 - 69.30)	7.69 (7.56 - 7.82)
Young	60 (59.88 - 60.12)	0
Adult	153.95 (153.71 - 154.19)	83.78 (83.60 - 83.96)
Aggregation indice	14.59	20.95
Site of Infection	Small intestine	Small intestine
Life Cycle	Direct	Direct

of *O. nigripes* (Tables 1, 2 and 3).

In relation to the community structures, *G. zetta* and *S. lanfrediae* were both dominant species in *O. nigripes* component community (Table 5). In *A. montensis*, *G. zetta*, *T. lenti*, *T. navonae* and *R. akodontis* were dominant species, whereas *L. chagasfilhoi* and *Angiostrongylu*s sp. were codominant (Table 5). In *E. russatus*, all three helminth species, *G. zetta*, *S. rolandoi* and *R. guaricanae* were considered dominants (Table 5).

The helminth metacommunity structure of *A. montensis* was random (Embedded absences = 13, p = 0.35, mean = 45.32, standard deviation = 35.20), according to the EMS analysis. This pattern

Table 4. Generalized Linear Models (GLM) for the abundance and prevalence of *Guerrerostrongylus zetta* in relation to host species, sex and age in the Serra do Tabuleiro State Park, sate of Santa Catarina, Brazil. ΔAICc = difference between the model with smallest AICc (corrected version of Akaike information criterion) and each model; wAICc = Akaike weights, K = number of parameters of the model. Except for the null model, only models with ΔAICc ≤ 2 are shown.

	Model	ΔAICc	wAICc	K
Abundance				
G. zetta	Host Sex + Host Age +Host Species	0	0.809	6
	Null	44.15	0	2
Prevalence				
G. zetta	Host Species	0	0.393	3
	Host Species + Host Age	0.59	0.292	4
	Host Species + Host Sex	1.5	0.186	4
	Null	66.59	0	1

Table 5. Importance indices of each helminth species for the three hosts analysed, in Serra do Tabuleiro State Park, state of Santa Catarina, Brazil.

Host species	Helminth species	Importance indices	Classification
Akodon montensis	*Angiostrongylus* sp.	0.07	Co-Dominant
	Guerrerostrongylus zetta	3.57	Dominant
	Litomosoides chagasfilhoi	0.11	Co-Dominant
	Trichofreitasia lenti	56.50	Dominant
	Trichuris navonae	5.00	Dominant
	Rodentolephis akodontis	34.69	Dominant
Euryzoryzomys russatus	*Guerrerostrongylus zetta*	4.72	Dominant
	Stilestrongylus rolandoi	91.10	Dominant
	Raillietina guaricanae	4.14	Dominant
Oligoryzomys nigripes	*Guerrerostrongylus zetta*	95.99	Dominant
	Stilestrongylus lanfrediae	4	Dominant

is not characterized by any significant coherence, indicating independent responses of each species to the environmental gradient (Figure 2).

DISCUSSION

The present study reports new records of *R. guaricanae* in the rodent *E. russatus*, and *L. chagasfilhoi* in the rodent *A. montensis*, thus increasing the host range of these helminths. Moreover, host specificity was found in most of the helminth species, except for the nematode *G. zetta,* which occurred in the three hosts. The helminth species found in this study had previously been reported in sigmodontine rodents by Gomes *et al.* (2003), Simões *et al.* (2011), Kuhnen *et al.* (2012), Panisse *et al.* (2017) and Cardoso *et al.* (2018), except for *S. rolandoi*. This species, found in the rodent *E. russatus*, was previously described in Boullosa *et al.* (2019).

Helminth species richness and species composition differed among the three rodents collected in the study area. Comparing the results with the single study carried out in STSP, which did not identify the parasite species, Kuhnen *et al.* (2012) found six morphotypes of helminth eggs in *E. russatus,* five morphotypes in *A. montensis* and two morphotypes in *O. nigripes*. Cardoso *et al.* (2018) also found a higher total of helminth species richness in *A. montensis* (six) in comparison with other sigmodontine rodents in a preserved area of the Atlantic Forest in the state of Rio de Janeiro, where *O. nigripes* had also only two helminth species. Püttker *et al.* (2008) also showed higher helminth richness in *A. montensis* when compared to *O. nigripes*, although in disturbed areas of the Atlantic Forest in the state of São Paulo. Gomes *et al.* (2003) observed five helminth species in *Akodon cursor* (Winge, 1887), two species in *O. nigripes* (reported as *Oligoryzomys eliurus*) and only one species in *E. russatus* (reported as *Oryzomys intermedius*). Despite these findings, Simões *et al.* (2011) registered 12 helminth species in both *A. montensis* and *O. nigripes* in Teresópolis, state of Rio de Janeiro; however, their study area encompassed 13 localities, including preserved areas and Atlantic Forest fragments. Panisse *et al.* (2017) registered the occurrence of eight helminth species parasitizing *A. montensis*, seven species in *E. russatus* and six species in *O. nigripes* in the Atlantic Forest of Missiones, Argentina.

The host feeding behaviour and its microhabitat may be determinant factors for the acquisition of helminth parasites (Cardoso *et al.* 2016). This may explain the differences in the helminth fauna among host species. In our study, *A. montensis*, which is strictly terrestrial, has an insectivorous/omnivorous diet, *E. russatus*, also strictly terrestrial, has a frugivorous/granivorous diet, while *O. nigripes,* although also frugivorous/granivorous, exhibits scansorial behaviour (Paglia *et al.* 2012). We suggest that *A. montensis* had a larger species richness when compared to the other hosts due to its ecological characteristics. The terrestrial locomotion may favour the acquisition of helminths with direct life cycle, due to their close contact with the soil (Callinan & Westcott 1986). Another study showed that the arboreal habit of a Malaysian rodent, *Niviventer cremoriventer* (Miller, 1900) (Rodentia, Muridae), might have contributed to its lower infection by having directly transmitted helminths (Wells *et al.* 2007). The insectivorous/omnivorous diet can make animals more susceptible to a wider range of helminth species, including parasites that use arthropods as invertebrate hosts, and species whose eggs are set in plants.

Despite the higher helminth species richness in *A. montensis*, *O. nigripes* presented higher mean species richness of helminths in relation to the other hosts. This result indicates that most of the infracommunities of this rodent presented co-infection of their two helminth species, *G. zetta* and *S. lanfrediae*, which were both dominants. Only *A. montensis*, which had the highest overall helminth species richness and lowest mean species richness, presented co-dominant species, indicating a larger difference in species composition among infracommunities for this host in relation to the others.

The nematode *G. zetta,* the only common species to all three hosts, had high abundance and prevalence in *O. nigripes*. This rodent may be acting as the main host of this helminth in the study area, when compared to *A. montensis* and *E. russatus*. Simões *et al.* (2011) reported *G. zetta* infecting *O. nigripes* in the Serra dos Órgãos National Park in Teresópolis, with higher values of abundance in this rodent. *Guerrerostrongylus zetta* was previously reported not only in *O. nigripes* (Pinto *et al.* 1982, Gomes *et al.* 2003, Panisse *et al.* 2017, Cardoso *et al.* 2018), but also in other mammals, including *Cerradomys subflavus* Wagner, 1842, *Galea spixii* Wagler, 1831 and *Nectomys rattus* Brants, 1827 in the state of Goiás and Bahia (Pinto *et al.* 1982).

The highest abundance and prevalence of *G. zetta* in female individuals in the rodent *O. nigripes* contradicts the most common pattern observed in mammalian helminth studies, where male hosts are more frequently infected (Zuk & McKean 1996). Simões *et al.* (2014) have also reported higher rates of helminth infection in female hosts for other rodent species.

The species *S. lanfrediae* was recorded in the

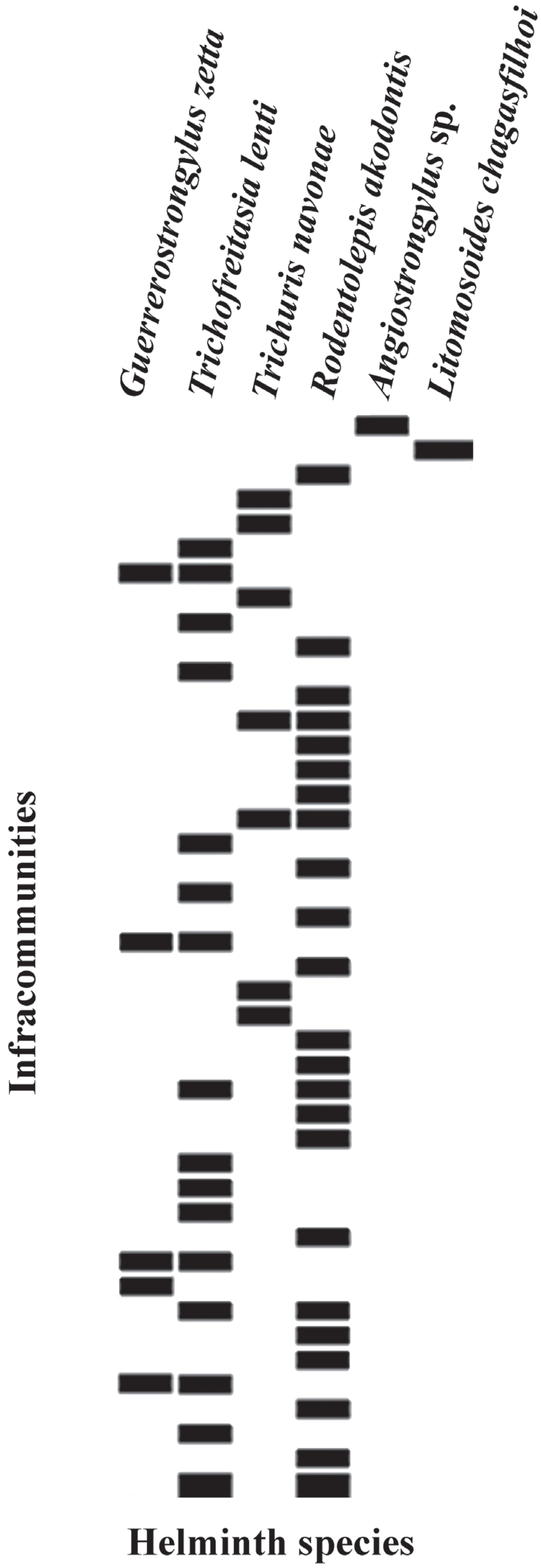

Figure 2. Ordinated matrix for the helminth metacomunity structure of *Akodon montensis* at the infracommunity scale in the Serra do Tabuleiro State Park, state of Santa Catarina, Brazil. Embedded absences were not filled.

present study infecting only *O. nigripes* with mid-term prevalence. Simões *et al.* (2011) and Cardoso *et al.* (2018) reported high prevalence values (> 40 %) of *S. lanfrediae* in this rodent in preserved and fragmented areas. The genus *Stilestrongylus* usually presents high prevalence, abundance and dominance in helminth communities of rodents (Simões *et al.* 2011, Boullosa *et al.* 2019), as observed in the present study. Simões *et al.* (2011) described the first records of *S. lanfrediae* in the rodents *A. montensis* and *A. cursor* in the state of Rio de Janeiro. Cardoso *et al.* (2018) reported this helminth species in *O. nigripes* and *Oligoryzomys flavescens* Waterhouse, 1837 also in the state of Rio de Janeiro. Panisse *et al.* (2017) reported this helminth in *O. nigripes, E. russatus* and *Soretamys angouya* Fischer, 1814 in Argentina.

The infection by *T. lenti* in *A. montensis* corroborated the results of Simões *et al.* (2011), Cardoso *et al.* (2018) and Panisse *et al.* (2017), from which the two formers reported infection by this helminth species in this host in the state of Rio de Janeiro and the later in Argentina. Simões *et al.* (2011) also registered this helminth in *O. nigripes.* The present study is a new geographical distribution for this species and the first report of *T. lenti* in *A. montensis* in the state of Santa Catarina. The occurrence of this helminth has been previously related with preserved areas with large vegetation cover (Cardoso *et al.* 2016), as in the current study.

The species of the genus *Trichuris* Roederer, 1761 are of public health and veterinary interest, as they parasitize a large number of mammals, such as rodents, marsupials, ruminants and primates, including humans (Robles *et al.* 2014). Infected animals defecate in the soil, releasing the eggs in the faeces. Animals are infected by ingesting contaminated food with the helminth eggs containing the infective larvae. The acquisition of *T. navonae* by *A. montensis* can be related to its strictly terrestrial behaviour and its high abundance in the studied localities favouring the encounter with the eggs of this helminth species in the environment. This helminth species has been reported to infect *A. montensis* in Argentina (Panisse *et al.* 2017). Kuhnen *et al.* (2012) reported the occurrence of helminth eggs of the Trichuridae family in both *A. montensis* and *E. russatus* in the STSP.

The cestode species *R. guaricanae,* here reported in *E. russatus* for the first time, was described by César & Luz (1993) infecting *Sooretamys angouya* (reported as *Oryzomys ratticeps*) in the state of Paraná. *Raillietina* sp. has been reported to infect *O. nigripes* (Simões *et al.* 2011).

In Brazil, three species of the genus *Angiostrongylus* have been reported to infect rodents. *Angiostrongylus costaricensis* Morera & Cespedes, 1971 was described as a parasite of the mesenteric arteries of *O. nigripes* (Graeff-Teixeira *et al.* 1990), *Angiostrongylus cantonensis* Chen, 1935 has been found to parasite the pulmonary artery of synantropic rodents (Simões *et al.* 2014), and *Angiostrongylus lenzii* Souza, Simões, Thiengo, Lima, Mota, Rodrigues-Silva, Lanfredi & Maldonado, 2009 was described infecting *A. montensis* in Teresópolis, state of Rio de Janeiro (Souza *et al.* 2009). The specimens of *Angiostrongylus* sp. were posteriorly sequenced according to the methodology described in Gomes *et al.* (2015), and deposited in the GenBank (number MK841610). The sequence indicated that those specimens are neither *A. costaricensis, A. cantonensis,* nor *A. vasorum* (Baillet, 1866), when compared with the sequences available in the GenBank.

Rodentolepis akodontis, the highest prevalent helminth in *A. montensis,* was firstly described in *Akodon cursor* (reported as *Akodon arviculoides*) in the state of Espírito Santo (Rêgo 1967). Simões *et al.* (2011) also found this helminth in *A. montensis* and *O. nigripes* in the state of Rio de Janeiro, Cardoso *et al.* (2018) found this helminth in *A. montensis* and *Delomys dorsalis* (Hensel, 1872), and Guerreiro Martins *et al.* (2014) reported *R. akodontis* in Argentina in *Oxymycterus rufus.*

The present study is the first report of *L. chagasfilhoi* infection in *A. montensis.* Maldonado *et al.* (2006) found *L. chagasfilhoi* infecting the abdominal cavity of the rodent *Nectomys squamipes* in the state of Rio de Janeiro, and Moraes *et al.* (1997) found this helminth species in *A. cursor* in Rio de Janeiro.

The random pattern of the helminth metacommunity structure observed in *A. montensis* indicated that species distributions were associated with different environmental gradients, which could be attributed to host intraspecific variations and / or habitat differences. This rodent species can be considered opportunistic in relation to habitat use (Cardoso *et al.* 2016), which can favour the exploration of different environmental conditions in a heterogeneous environment. However, we must take into account the fact that the present study was carried out in a local scale and with only two samplings. The random pattern observed suggests that communities were formed by helminth species occurring independently of each other, and opportunistic host species might constitute a heterogeneous environment for the establishment of parasites with different environmental requirements. The variation in richness and composition of helminth species among host species, as well as the high host specificity, except for *G. zetta*, suggests the influence of local characteristics and biotic factors on the helminth occurrence in this area.

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