

Helminth communities of sigmonontine rodents in cocoa agroforestry systems in Brazil

Maíra G. Kersul^a, Natália A. Costa^{b,c}, Raquel G. Boullosa^{b,d}, Adna A.S. Silva^e, Élson O. Rios^f, Alexandre D. Munhoz^g, Beatriz E. Andrade-Silva^{b,c}, Arnaldo Maldonado Júnior^b, Rosana Gentile^{b,*}, Martin R. Alvarez^f

^a Programa de Pós-Graduação em Ciência Animal, Universidade Estadual de Santa Cruz, Campus Soane Nazaré de Andrade, Rodovia Jorge Amado, Km 16, Bairro Salobrinho, 45662-900, Ilhéus, Bahia, Brazil

^b Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, RJ, Brazil

^c Programa de Pós-Graduação em Biologia Parasitária, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Avenida Brasil, 4.365, Manguinhos, 21040-360, Rio de Janeiro, RJ, Brazil

^d Programa de Pós-Graduação em Biodiversidade e Saúde, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Avenida Brasil, 4.365, Manguinhos, 21040-360, Rio de Janeiro, RJ, Brazil

^e Programa de Pós-Graduação em Zoologia, Universidade Estadual de Santa Cruz, Campus Soane Nazaré de Andrade, Rodovia Jorge Amado, Km 16, Bairro Salobrinho, 45662-900, Ilhéus, Bahia, Brazil

^f Coleção de Mamíferos “Alexandre Rodrigues Ferreira” (CMARF), Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Campus Soane Nazaré de Andrade, Rodovia Jorge Amado, Km 16, Bairro Salobrinho, 45662-900, Ilhéus, Bahia, Brazil

^g Departamento de Ciências Agrárias e Ambientais, Universidade Estadual de Santa Cruz, Campus Soane Nazaré de Andrade, Rodovia Jorge Amado, Km 16, Bairro Salobrinho, 45662-900, Ilhéus, Bahia, Brazil

ARTICLE INFO

Keywords:

Atlantic forest
Ecology
Mammals
Nematoda
Parasite
Parasitism

ABSTRACT

Agroforestry is an alternative kind of land use where the native vegetation is surrounded or intercalated by crops of economic interest. This system may maintain species richness by promoting the habitat heterogeneity or serving as ecological corridors. The aim of this study was to describe the gastrointestinal helminth fauna and to analyse the parasitological parameters of the helminth communities of six sigmodontine rodents in a cocoa agroforestry system in the municipality of Ilhéus, state of Bahia, Northeast Brazil. This is a novel study of helminth fauna in this kind of agroforestry. Rodents were captured in live-traps and euthanised for helminth recovery. Specimens were counted and identified to the species level whenever possible. Helminth abundance, intensity, and prevalence were calculated for each species and each host. The total abundance and prevalence of helminths were compared among localities and three attributes of the host: species, gender and age using generalised linear models. Considering all rodents, 52.14% of them were parasitised with at least one helminth species. Eight nematode species were identified and another seven morphospecies were identified to the genus level. The most abundant species were *Hassalstrongylus epsilon*, *Stilestrongylus eta*, *Guerrerostrongylus zetta*, and *Syphacia alata*. The opportunistic host species *Oligoryzomys nigripes* and *Akodon cursor*, besides the water rat *Nectomys squamipes*, were the most infected species for helminth parasites. *Hylaemys seuanezi* was also an important host with the highest helminth species richness. This is the first report of the helminth fauna for this host. The locality most distant from the native vegetation and closest to the city had the highest helminth prevalence and mean species richness. The species richness in the helminth communities of *Euryoryzomys rus-satus*, *N. squamipes* and *O. nigripes* in these Cabruca agroforests were within the range found in studies carried out in Atlantic Forest areas.

1. Introduction

The Atlantic Forest is one of the most devastated and fragmented

Brazilian biomes due to anthropogenic activities, with only 14.3% of its original area remaining as preserved forest (SOS Mata Atlântica, Instituto Nacional de Pesquisas Espaciais (INPE), 2019). Agriculture

* Corresponding author. Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Av. Brasil 4365, Manguinhos, 21040-360, Rio de Janeiro, RJ, Brazil.

E-mail address: rgentile@ioc.fiocruz.br (R. Gentile).

<https://doi.org/10.1016/j.ijppaw.2019.11.008>

Received 31 July 2019; Received in revised form 18 November 2019; Accepted 30 November 2019

2213-2244/ © 2019 The Authors. Published by Elsevier Ltd on behalf of Australian Society for Parasitology. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

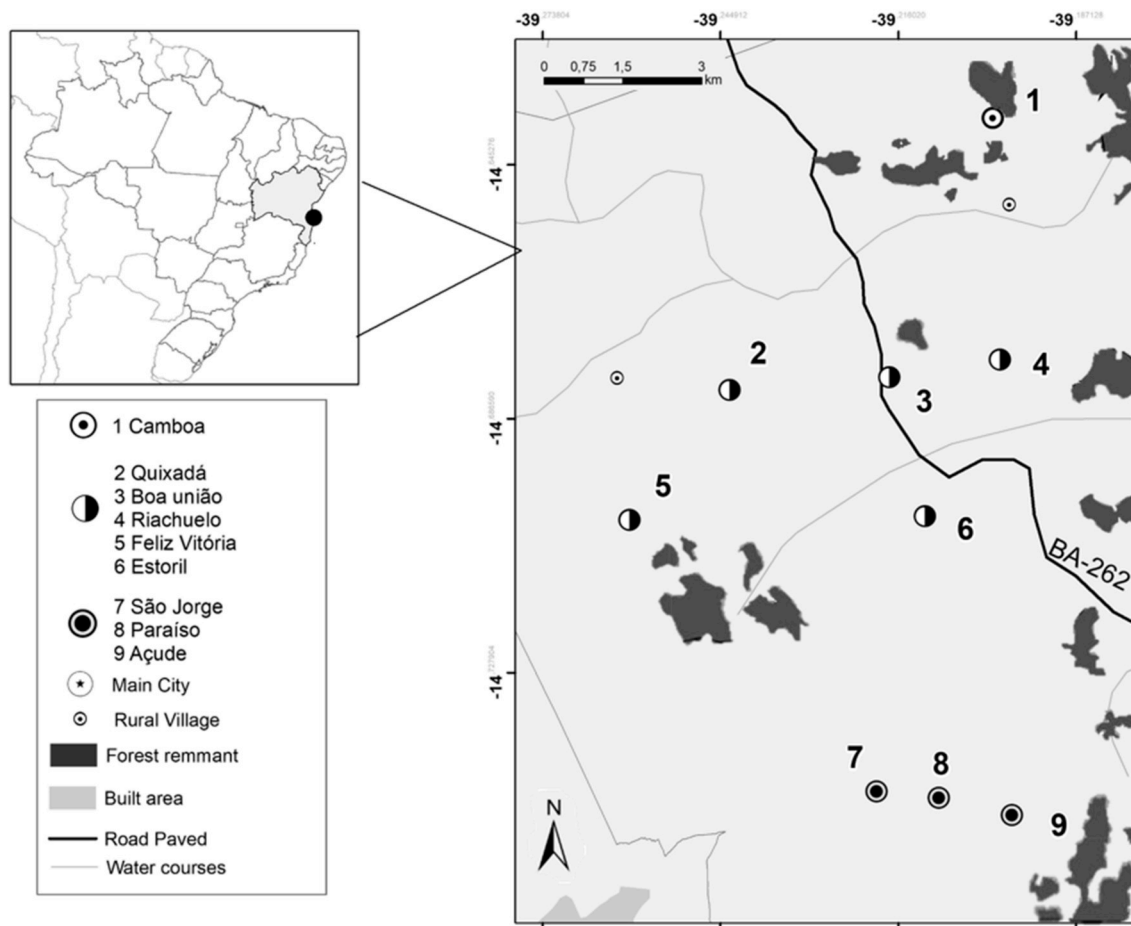


Fig. 1. Study area of the Cabruca System including nine sampling localities of agroforestry farms, where the small mammal survey was carried out, Ilhéus, state of Bahia, Brazil.

and cattle breeding are among the most important economic activities that caused environmental degradation of the natural areas in this biome. However, an alternative kind of land use for agriculture purposes is agroforestry. In agroforestry systems, native trees or shrubs are surrounded or intercalated by crops of economic interest in order to maintain species richness and preserve the ecosystem functions, among several other benefits (Setenta and Lobão, 2012). Agroforestry maintains the biodiversity by increasing the habitat heterogeneity, serving as corridors and reducing the environmental disturbance caused by usual agricultural activities (Schroth et al., 2004).

Inserted in the Atlantic Forest in Northeast Brazil, the southern area of the state of Bahia is known as the Cocoa Region due to its agroforestry of cocoa crops, where cocoa trees grow under the shadows of the native vegetation. This kind of land use that is present in this region over 200 years is called the Cabruca system (Lobão et al., 1997). The Cocoa Region is situated between the Pardo and Contas rivers along the seacoast.

Species surveys and ecological studies are fundamental to evaluate the impacts of agroforestry systems on the local biodiversity. A recent review on the conservation status of the mammals of the state of Bahia compiled a list of 41 threatened and near threatened species, of which eight were rodents (Cassano et al., 2017). The Atlantic Forest was the biome with the highest number of species on this list (Cassano et al., 2017). Other surveys on small mammals in the state of Bahia include a check list of rodents and marsupials of Ilhéus and Pau Brazil (Geise and Pereira, 2008) and the specimens collected for the study of yellow fever between 1943 and 1945 (Vaz, 2005). In the Cocoa Region, a few studies have evaluated the impact of the Cabruca system on the conservation of mammals. Cassano et al. (2012) concluded that this system might be

favourable for the conservation of large mammals. Silva (2017) observed that the species richness of small mammals in the Cabruca was similar to that of the native areas and richer than that in other agricultural systems, although specialist species were more affected.

Sigmodontine rodents are very abundant and one of the most diversified and complex groups among Neotropical mammals, inhabiting deserts, highlands, and tropical forests (Patton et al., 2015). The subfamily Sigmodontinae (Cricetidae) includes approximately 380 species in approximately 86 genera (Patton et al., 2015). These rodents are frequently found around human dwellings, in rural areas, and in crops, where they might have close contact with humans and domestic animals. Therefore, these rodents are of high concern in the transmission dynamics of parasites of public health importance, as well as veterinary importance, since they are known to be wild reservoirs of several zoonoses. Among the diseases they can transmit are hantaviruses (Oliveira et al., 2014), rickettsiosis (Rozenal et al., 2017), Chagas disease (Jansen et al., 2015), and helminthiasis (Maldonado Jr. et al., 2006).

Among parasites, helminths are good environmental indicators (Gardner and Campbell, 1992) and excellent models for ecological studies of host-parasite interaction in natural (Simões et al., 2010) and anthropogenic habitats (Simões et al., 2011). There is so far no study on the parasitism of helminths in small mammals in the Cocoa Region, Brazil, nor in the state of Bahia. Considering the gaps in the literature on the rodent fauna and their gastrointestinal parasites in the region, the aim of this study was to describe the helminth fauna and to compare the parasitological parameters of the helminth communities of six sigmodontine rodents in a Cabruca agroforestry system in Northeast Brazil. The results were discussed comparing with other studies carried

out in the Atlantic Forest in relation to species composition and parasitological parameters.

2. Materials and methods

2.1. Study area

The study was conducted in an agroforestry system in the municipality of Ilhéus (14°42'40"S, 39°14'29.7"W), state of Bahia, Brazil (Fig. 1). The study area included nine cocoa agroforests: Camboa; Boa União, Estoril, Feliz Vitória, Quixadá, Riachuelo, Açude, Paraíso, and São Jorge (Fig. 1). In all of these farms, the Cabruca system is dominated by cocoa trees (*Theobroma cacao*), representing 82% of its area, with a few remnants of native vegetation, corresponding to 5% of the system, and also open areas, such as pastures, annual plantations, and peridomicile areas (Faria et al., 2006). The climate of the region is tropical humid (Af), according to the Köpen classification (Ayoade, 1986), with high temperatures and rainfall throughout the year. The average temperature is 25 °C and the average annual rainfall is 1200 mm (Mori et al., 1983).

2.2. Rodent sampling and helminth recovery

The sampling of rodents occurred in July 2016 and September 2016 during seven consecutive days each month, in all sampling sites. In each agroforestry, a plot of 1 ha (100 × 100 m) was set, with a minimum distance of 100 m from the border of the farm. In each plot, we placed a 60 × 100 m grid with 24 trapping stations, spaced 20 m apart. In each station, two traps were placed on the ground and at the understory, alternately (one Sherman® 30 × 9 × 8 cm and one Tomahawk® 45 × 16 × 16 cm). The traps were baited with a mixture of banana, peanut butter, sardines in soybean oil, cornmeal, and oat flakes. Additionally, six pitfall traps (60 L buckets) were installed in each plot, 10 m apart, and 30 m from the trapping grid. The total sampling effort was 1440 trap-nights in Sherman and Tomahawk traps and 120 trap-nights in pitfall traps.

The rodents were weighed, measured, had their sex and reproductive condition recorded, and euthanised for helminth recovery. All the animals were preserved by taxidermy and deposited as voucher specimens in the Mammal Collection "Alexandre Rodrigues Ferreira" of the Santa Cruz State University (CMARF-UESC) (*A. cursor* – MRA 0853; *E. russatus* – MRA 0777; *H. seanezi* – MRA 0800; *N. lasiurus* – MRA 0913; *N. squamipes* – MRA 0776; *O. nigripes* – MRA 0787).

The stomach, thoracic, and abdominal cavities, and small and large intestine were examined separately for helminths under a stereoscopic microscope. The helminths were carefully removed and washed out from the mucosa and preserved in 10% AFA (2% acetic acid, 3% formaldehyde, and 95% ethanol). The nematodes were cleared in lactophenol. The Cestodes were stained in Semichon's carmine, dehydrated in an increasing alcohol series, and mounted in Canada Balsam according to the method described by Amato et al. (1991). The specimens were counted and identified using a Zeiss Standard 20 light microscope. The species were identified according to Yamaguti (1961), Yorke and Maplestone (1969), Vicente et al. (1997), and Anderson (2000). Voucher specimens of the identified helminth species were deposited at the Helminthological Collection of Instituto Oswaldo Cruz (CHIOC numbers: *G. gomesae* – 38772; *G. zetta* – 38779; *H. epsilon* – 38778; *P. bispiculata* – 38773; *S. aculeata* – 38777; *S. eta* – 38776; *S. freitasi* – 38775; *S. alata* – 38774).

The captures and animal handling were performed according to the Ethical Committee on Animal Use of the Santa Cruz State University (license CEUA-UESC No. 003/2013, 021/2014). The capture of the animals was authorised by the Brazilian Government's Chico Mendes Institute for Biodiversity and Conservation (ICMBIO, N. 17131–4).

2.3. Data analysis

Helminths abundance, intensity, and prevalence were calculated according to Bush et al. (1997) for each species and each host separately (each component community), as follows: The mean abundance was considered as the total number of helminths of a certain species divided by the number of hosts analysed. The mean intensity was calculated as the total number of helminths of a certain species divided by the number of hosts infected by this species. The prevalence was considered as the ratio between the number of infected animals and the total number of animals analysed.

The abundance and prevalence were compared only for the most prevalent helminth species (two species) in relation to host gender. The prevalences were compared using a Chi-square contingency test. The abundances were compared using a Mann-Whitney test.

The total abundance and prevalence of helminths, considering all the hosts collected, were compared among the host species, genders, ages, and localities using generalised linear models (GLM) with a linear distribution. The best models were chosen using the corrected Akaike information criterion (models with Δ AICc less than two). The models were compared with the null model by analysis of variance (ANOVA). For this analysis, the rodents were classified as young or adults according to their dental development. The nine farms were grouped into three localities according to their proximity as follows: Locality 1, Camboa (in the north of the study area); Locality 2, Boa União, Estoril, Feliz Vitória, Quixadá, and Riachuelo (in the central area), and Locality 3, Açude, Paraíso, and São Jorge (in the south) (Fig. 1).

Helminth species richness was calculated as the number of species present in each component community (each host species). The mean species richness (MSR) was considered as the mean richness of the infracommunities (each host individual). A bipartite network analysis was carried out to illustrate the associations among the helminth species with the sigmodontine rodent hosts.

The significance level used was 5% in all of the analyses. Univariate tests were performed using the Past software, version 3:09 (Hammer et al., 2001). The GLM analyses were performed using the vegan package (Oksanen et al., 2018) in RStudio software version 1.0.136 (R Core Team, 2018).

3. Results

Sixty-nine sigmodontine rodents of six species were captured and analysed for gastrointestinal helminths. The rodent species were *Akodon cursor* (Winge, 1887), *Euryoryzomys russatus* (Wagner, 1848), *Hylaeamys seanezi* (Weksler, Geise, and Cerqueira, 1999), *Nectomys squamipes* (Brants, 1827), *Necromys lasiurus* (Lund, 1840), and *Oligoryzomys nigripes* (Olfers, 1818). The most abundant rodent was *H. seanezi*, which was captured in five farms of the three localities (Table 1). No rodent was captured in the São Jorge and Paraíso farms, both in locality 3. Except for *N. lasiurus*, which had only one individual captured, the species with the greatest fraction of individuals infected by at least one helminth species was *O. nigripes* with 83.3% of the examined animals infected by helminths, followed by *N. squamipes* with 71.4% of the animals infected, and *A. cursor* with 70% of the specimens infected (Table 1).

Fifty-four percent of the animals were infected with at least one helminth species (36 rodents). The highest prevalence was in locality 3 (south area), where 73.68% of the animals were infected with helminths. In locality 1 (north), only 18.18% of the animals were infected and in locality 2 (central), 51.28% were infected. In locality 1, only two individual hosts were infected with one helminth species each (Table 1). In localities 2 and 3, eleven morphospecies were registered in each (Table 2), and the MSR was 0.67 and 1.17, respectively.

Considering all the hosts, the nematodes *Syphacia alata* (Quentin, 1968) and *Syphacia* spp. were found in the cecum; *Stilestrongylus eta* (Travassos, 1937) Durette-Desset, 1971, *Stilestrongylus aculeata*

Table 1

Number of individuals analysed per host species for the helminth fauna of six sigmodontine rodents in each agroforestry farm, Ilhéus, state of Bahia, Brazil. In parenthesis are the number of infected rodents in each locality.

Group	Farm	Host species					
		<i>A. cursor</i>	<i>E. russatus</i>	<i>H. seuanezi</i>	<i>N. lasiurus</i>	<i>N. squamipes</i>	<i>O. nigripes</i>
Locality 1	Camboa	1(1)	1(0)	7(0)	1(1)		1(0)
Locality 2	Boa União	2(1)		2(0)		1(1)	2(2)
	Estoril			12(2)			3(2)
	Feliz Vitória	1(1)				4(3)	3(2)
	Quixadá		2(1)			1(0)	1(1)
	Riachuelo		3(2)	1(0)		1(1)	1(1)
Locality 3	Açude	6(4)	1(1)	10(7)			2(2)
	Paraíso	0	0	0	0	0	0
	São Jorge	0	0	0	0	0	0

Table 2

Helminth species categorised by their hosts and localities of six sigmodontine rodents in each agroforestry farm, Ilhéus, state of Bahia, Brazil. In parenthesis are the host species.

Locality	Helminth Species
1	<i>Stilestrongylus aculeata</i> (<i>Akodon cursor</i>)
	<i>Stilestrongylus freitasi</i> (<i>Necromys lasiurus</i>)
2	<i>Hassalstrongylus</i> sp. (<i>Hyleamys seuanezi</i>)
	<i>Guerrerostrongylus gomesae</i> (<i>Euryoryzomys russatus</i>)
	<i>Guerrerostrongylus zetta</i> (<i>Oligoryzomys nigripes</i> , <i>Euryoryzomys russatus</i>)
	<i>Hassalstrongylus epsilon</i> (<i>Nectomys squamipes</i>)
	<i>Physaloptera bispiculata</i> (<i>Nectomys squamipes</i>)
	<i>Stilestrongylus aculeata</i> (<i>Akodon cursor</i>)
	<i>Stilestrongylus eta</i> (<i>Oligoryzomys nigripes</i>)
	<i>Syphacia alata</i> (<i>Hyleamys seuanezi</i> , <i>Akodon cursor</i>)
	<i>Syphacia</i> sp.1, 4, 5 (<i>Akodon cursor</i> , <i>Nectomys squamipes</i> and <i>Oligoryzomys nigripes</i> respectively)
3	Cestoda (Hymenolepididae) (<i>Hyleamys seuanezi</i>)
	<i>Guerrerostrongylus zetta</i> (<i>Euryoryzomys russatus</i> , <i>Oligoryzomys nigripes</i>)
	<i>Hassalstrongylus</i> sp. (<i>Hyleamys seuanezi</i>)
	<i>Physaloptera</i> sp. (<i>Hyleamys seuanezi</i>)
	<i>Stilestrongylus aculeata</i> (<i>Akodon cursor</i>)
	<i>Stilestrongylus eta</i> (<i>Oligoryzomys nigripes</i>)
	<i>Syphacia alata</i> (<i>Hyleamys seuanezi</i>)
	<i>Syphacia</i> sp.1, 2, 3, 5 (<i>Akodon cursor</i> , <i>Euryoryzomys russatus</i> , <i>Hyleamys seuanezi</i> and <i>Oligoryzomys nigripes</i> respectively)

(Travassos, 1918), *Stilestrongylus freitasi* Durette-Desset, 1968, *Hassalstrongylus epsilon* (Travassos, 1937) Durette-Desset, 1971, *Guerrerostrongylus zetta* (Travassos, 1937) Sutton and Durette-Desset, 1991, *Guerrerostrongylus gomesae* Simões, Santos and Maldonado, 2012 and *Hassalstrongylus* sp. were found in the small intestine. *Physaloptera bispiculata* Vaz and Pereira, 1935 was found in the stomach. Two cestode specimens of the family Hymenolepididae (Soulsby, 1982) were found in the small intestine. This species could not be identified because of the absent scolex in the sample. Specimens of the genus *Syphacia* Seurat, 1916 and *Hassalstrongylus* Durette-Desset, 1971 could not be identified at species level because only females were found. *Syphacia* specimens recovered from the different hosts were grouped for the GLM analysis.

Akodon cursor, *E. russatus*, *N. squamipes*, and *O. nigripes* contained three helminth species each, whereas *H. seuanezi* had five helminth species (Tables 3–7). The single individual of *N. lasiurus* captured was infected only with *S. freitasi*. The mean species richness was highest in *O. nigripes* (MSR = 1.25), followed by *N. squamipes* (MSR = 1), *E. russatus* (MSR = 0.71), *A. cursor* (MSR = 0.70), and *H. seuanezi* (MSR = 0.47).

The most abundant helminth species was the nematode *H. epsilon*, which occurred only in *N. squamipes*, followed by *S. eta* and *G. zetta*, which occurred in *O. nigripes*, and the latter also in *E. russatus* (Tables 4, 6 and 7, respectively). Besides *G. zetta*, only *S. alata* was found in more than one host species (*H. seuanezi* and *A. cursor*). All the other helminth species showed a host-species-specific pattern in this study (Fig. 2).

In *H. seuanezi*, *Hassalstrongylus* sp. was the most prevalent species and *S. alata* the most abundant with the highest intensity (Table 5).

Table 3

Mean abundance, intensity (± SD) and prevalence (95% CI) for the helminth fauna of *Akodon cursor* in nine agroforestry farms, Ilhéus, state of Bahia, Brazil. All individuals captured of this host were adults.

Parameters/Species	<i>Syphacia alata</i>	<i>Syphacia</i> sp1.	<i>Stilestrongylus aculeata</i>
Abundance	0.50 ± 1.58	0.30 ± 0.95	1.20 ± 1.48
Male	0	0	0.75 ± 0.96
Female	0.83 ± 2.04	0.50 ± 1.22	1.50 ± 1.76
Intensity	5.00 ± 0	3.00 ± 0	2.40 ± 1.14
Male	0	0	1.50 ± 0.71
Female	5.00 ± 0	3.00 ± 0	3.00 ± 1.00
Prevalence	10.00 (9.97–10.03)	10.00 (9.98–10.02)	50.00 (49.97–50.03)
Male	0	0	50.00 (49.97–50.03)
Female	16.67 (16.61–16.72)	16.67 (16.64–16.70)	50.00 (49.95–50.05)
Aggregation Indices	5.00	3.00	1.81
Male	–	–	1.22
Female	5.00	3.00	2.07

(-) indicates absence of the parasite.

Table 4

Mean abundance, intensity (\pm SD) and prevalence (95% CI) for the helminth fauna of *Euryoryzomys russatus* in nine agroforestry farms, Ilhéus, state of Bahia, Brazil. All individuals captured of this host were adults.

Parameters/Species	<i>Guerrerostrongylus zetta</i>	<i>Guerrerostrongylus gomesae</i>	<i>Syphacia</i> sp2.
Abundance	6.43 \pm 10.42	2.57 \pm 6.80	0.43 \pm 1.13
Male	5.20 \pm 10.55	0	0.60 \pm 1.34
Female	9.50 \pm 13.44	9.00 \pm 12.73	0
Adult	7.5 \pm 10.99	0	0.50 \pm 1.22
Young	0	18	0
Intensity	15.00 \pm 11.53	18.00 \pm 0	3.00 \pm 0
Male	13.00 \pm 0	0	3.00 \pm 0
Female	19.00 \pm	18.00 \pm 0	0
Adult	15.00 \pm 11.53	0	3.00 \pm 0
Young	0	18.00	0
Prevalence	42.86 (42.61–43.10)	14.29 (14.12–14.45)	14.29 (14.26–14.31)
Male	40.00 (39.70–40.30)	0	20.00 (19.96–20.04)
Female	50.00 (49.40–50.60)	50.00 (49.44–50.56)	0
Adult	50.00 (49.72–50.28)	0	16.67 (16.64–16.70)
Young	0	100	0
Aggregation Indices	16.90	18.00	3.00
Male	21.38	–	3.00
Female	19.00	18.00	–
Adult	16.09	–	3.00
Young	–	*	–

* Only one host analysed. (-) indicates absence of the parasite. Cases without SD represent only one host analysed.

Stilestrongylus aculeata was the most abundant and prevalent species in the rodent *A. cursor* (Table 3), although the intensity was higher for *S. alata*. *Guerrerostrongylus zetta* showed the highest prevalence and abundance in *E. russatus*, however, the intensity was higher for *G. gomesae* in this host (Table 4). *Hassalstrongylus epsilon* had the highest prevalence, abundance, and intensity in *N. squamipes* (Table 6), whereas this was the case for *S. eta* in *O. nigripes* (Table 7).

Syphacia alata occurred only in an adult female of *A. cursor* in Boa União and in three males of *H. seuanezi* in Açude and Feliz Vitória. *Syphacia* spp., which occurred in low abundance and prevalence in all host species, except for *N. lasiurus*, was found predominantly in adult male hosts, only in Açude and Feliz Vitória. *H. epsilon* was found only in two adult male hosts and one young female of *N. squamipes* in Feliz

Vitória. *Physaloptera* sp. was found only in an adult male of *H. seuanezi* in Açude. *Physaloptera bispiculata* occurred in two females of *N. squamipes* in Riachuelo and Boa União, with low abundances. *Hassalstrongylus* sp. occurred only in adults and, predominantly, in male hosts of *H. seuanezi*. *Stilestrongylus eta* occurred only in *O. nigripes*, predominantly in male hosts, since only one female was infected with this helminth. *Stilestrongylus aculeata* occurred in low abundance only in *A. cursor* in the three localities. *Stilestrongylus freitasi* occurred only in an adult female of *N. lasiurus* in Camboa. *Guerrerostrongylus gomesae* was found only in a young female of *E. russatus* in Quixadá. *Guerrerostrongylus zetta* occurred predominantly in males of *E. russatus* and *O. nigripes*, with only one female of *E. russatus* infected. The two specimens of cestode were found in a young female and an adult male

Table 5

Mean abundance, intensity (\pm SD) and prevalence (95% CI) for the helminth fauna of *Hylaeamys seuanezi* in nine agroforestry farms, Ilhéus, state of Bahia, Brazil.

Parameters/Species	<i>Hassalstrongylus</i> sp.	<i>Syphacia alata</i>	<i>Syphacia</i> sp3.	<i>Physaloptera</i> sp.	Hymenolepididae
Abundance	1.72 \pm 4.37	2.91 \pm 15.72	0.88 \pm 4.28	0.03 \pm 0.18	0.06 \pm 0.25
Male	2.05 \pm 4.85	4.23 \pm 18.95	1.27 \pm 5.15	0.05 \pm 1.00	0.05 \pm 1.00
Female	1.00 \pm 3.16	0	0	0	0.10 \pm 0.32
Adult	2.20 \pm 4.86	3.60 \pm 17.79	1.12 \pm 4.83	0.04 \pm 0.21	0.04 \pm 0.20
Young	0	0.43 \pm 1.13	0	0	0.14 \pm 0.38
Intensity	7.85 \pm 7.06	31.00 \pm 50.24	14.00 \pm 14.14	1.00 \pm 0	1.00 \pm 0
Male	7.50 \pm 7.06	31.00 \pm 50.24	14.00 \pm 14.14	1.00 \pm 0	1.00
Female	10.00 \pm 0	0	0	0	1.00
Adult	7.86 \pm 6.52	45.00 \pm 62.23	14.14 \pm 14.14	1.00 \pm 0	1.00
Young	0	3.00 \pm 0	0	0	1.00
Prevalence	21.88 (21.83–21.92)	9.38 (9.20–9.55)	6.25 (6.20–6.30)	3.13 (3.13)	6.25 (6.25)
Male	27.27 (27.34–27.21)	13.64 (13.38–13.89)	9.09 (9.02–9.16)	4.55 (4.55)	4.55 (4.55)
Female	10.00 (9.94–10.06)	0	0	0	10.00 (9.99–10.01)
Adult	28.00 (27.94–28.06)	8.00 (7.78–8.22)	8.00 (7.94–8.06)	4.00 (4.00)	4.00 (4.00)
Young	0	14.29 (14.26–14.31)	0	0	14.29 (14.28–14.29)
Aggregation Indices	11.12	85.03	20.92	1.00	1.00
Male	11.52	84.91	20.82	1.00	1.00
Female	10.00	–	–	–	1.00
Adult	10.72	87.94	20.86	1.00	1.00
Young	–	3.00	–	–	1.00

(-) indicates absence of the parasite. Cases without SD represent only one host analysed.

Table 6Mean abundance, intensity (\pm SD) and prevalence (95% CI) for the helminth fauna of in *Nectomys squamipes* nine agroforestry farms, Ilhéus, state of Bahia, Brazil.

Parameters/Species	<i>Hassalstrongylus epsilon</i>	<i>Syphacia</i> sp4.	<i>Physaloptera bispiculata</i>
Abundance	45.43 \pm 88.83	0.86 \pm 1.57	0.71 \pm 1.50
Male	59.25 \pm 117.17	0.50 \pm 1.00	0
Female	27.00 \pm 46.77	1.33 \pm 2.00	1.67 \pm 1.89
Adult	47.40 \pm 104.88	0.40 \pm 0.89	0.80 \pm 1.79
Young	40.50 \pm 57.28	2.00 \pm 2.83	0.50 \pm 0.71
Intensity	106.00 \pm 118.49	3.00 \pm 1.41	2.50 \pm 2.12
Male	118.50 \pm 164.76	2.00 \pm 0	0
Female	81.00 \pm 0	4.00 \pm 0	2.50 \pm 2.12
Adult	118.50 \pm 164.76	2.00 \pm 0	4.00 \pm 0
Young	81.00 \pm 0	4.00 \pm 0	1.00 \pm 0
Prevalence	45.43 (40.75–44.96)	28.57 (28.53–28.61)	28.57 (28.54–28.61)
Male	50.00 (46.33–53.67)	25.00 (24.97–25.03)	0
Female	33.33(31.64–35.03)	33.33 (33.26–33.41)	66.67 (66.60–66.74)
Adult	40.00 (37.06–42.94)	20.00 (19.97–20.03)	20.00 (19.95–20.05)
Young	50.00 (47.46–52.54)	50.00 (49.87–50.13)	50.00 (49.97–50.03)
Aggregation Indices	173.69	2.89	3.13
Male	231.71	2.00	–
Female	81.00	4.00	2.60
Adult	232.04	2.00	4.00
Young	81.00	4.00	1.00

(-) indicates absence of the parasite.

of *H. seuanezi*, both in Açude.

The abundance and prevalence of *Hassalstrongylus* sp. and *S. aculeata* did not differ significantly according to host gender ($U = 92$; $p = 0.325$; $\chi^2 = 1.2$; $p = 0.273$ and $U = 9.5$; $p = 0.65$; $\chi^2 = 0$; $p = 1$, respectively). This analysis could not be performed for the other helminth species due to insufficient data for the analysis.

The GLM analysis performed for all helminths species considering all hosts indicated that helminth abundance was influenced by host species (Table 8), with highest abundances in the helminth component community of *N. squamipes*, however, the null model was also plausible. For helminth prevalence, the only plausible models included host species and locality; and host species, host gender, and locality (Table 9).

4. Discussion

This is the first report of the parasitism of helminths in small mammals in the Cabruca System of the Cocoa Region and the first study

of helminth communities of wild small mammals in the state of Bahia, Brazil. Since this kind of agroforestry is very common and one of the most important economic activities in this region, survey studies of the local fauna and their parasites are basic and imperative to evaluate the impact of this kind of land use on the biodiversity. Other reports of helminth infection in small mammals in the state of Bahia have investigated *Schistosoma mansoni* in the water rat *N. squamipes* (Silva and Andrade, 1989) and the helminth community in the exotic rat *Rattus norvegicus* in urban areas (Carvalho-Pereira et al., 2018).

Comparing the helminth prevalence among localities, we observed the largest proportion of infected animals in locality 3 (south area), where more than 70% of the captured animals were infected with helminths, corroborating the GLM analysis of helminth prevalence, in which the variable “locality” was present in both selected models. This locality also had the highest helminth MSR considering all hosts. Moreover, *H. seuanezi*, *O. nigripes*, *A. cursor*, and *E. russatus* were found in the three localities, and except for *A. cursor*, they were found to be

Table 7Mean abundance, intensity (\pm SD) and prevalence (95% CI) for the helminth fauna of *Oligoryzomys nigripes* in nine agroforestry farms, Ilhéus, state of Bahia, Brazil. All individuals captured of this host were adults.

Parameters/Species	<i>Guerrerostrongylus zetta</i>	<i>Syphacia</i> sp5.	<i>Stilestrongylus eta</i>
Abundance	5.25 \pm 8.28	0.83 \pm 2.59	15.67 \pm 22.43
Male	5.73 \pm 8.51	0.91 \pm 2.70	17.00 \pm 23.02
Female	0	0	1.00
Intensity	10.50 \pm 9.20	5.00 \pm 2.70	26.86 \pm 23.91
Male	10.50 \pm 9.20	5.00 \pm 5.66	31.17 \pm 23.09
Female	0	0	1.00
Prevalence	50.00 (49.85–50.15)	16.67 (16.62–16.71)	58.33 (57.93–58.74)
Male	54.55 (54.38–54.71)	18.18 (18.13–18.23)	54.55 (54.11–54.98)
Female	0	0	1.00
Aggregation Indices	13.06	2.59	32.10
Male	12.64	8.02	31.16
Female	–	–	*

* Only one host analysed. (-) indicates absence of the parasite. Cases without SD represent only one host analysed.

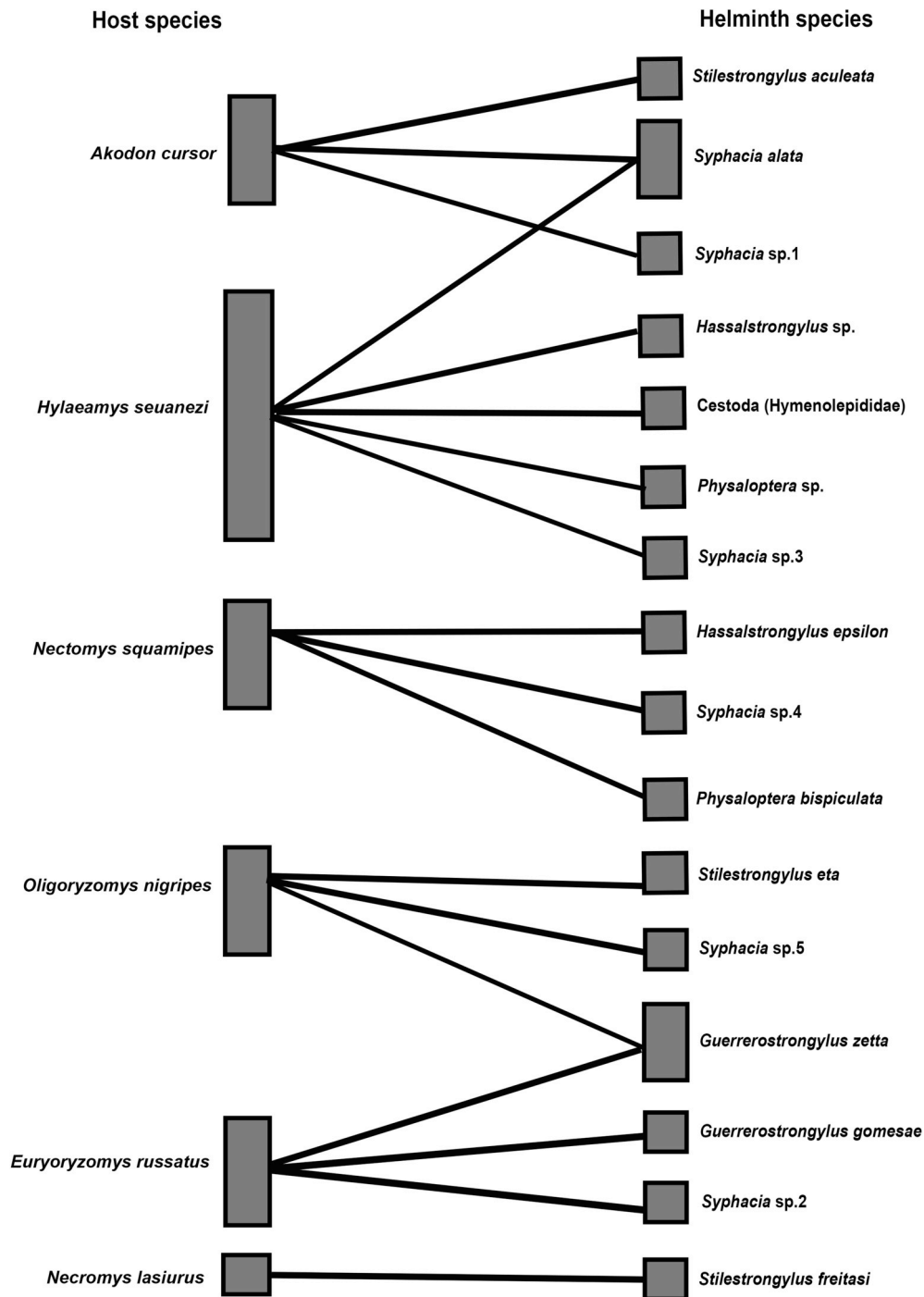


Fig. 2. A bipartite network analysis indicating the sigmodontine rodents – helminths associations in nine agroforestry farms, Ilhéus, state of Bahia, Brazil.

Table 8

Generalised linear models (GLMs) of the effects of host species, host gender, host age and locality on the helminth abundance of six sigmodontine rodents in nine agroforestry farms, Ilhéus, state of Bahia, Brazil. Only the models with $\Delta AICc < 10$ are presented. Plausible models ($\Delta AICc < 2$) are in bold.

Model	AICc	$\Delta AICc$	wAICc
Null	685.879	0	0.351
Host	686.073	0.194	0.319
Host + Sex	687.956	2.077	0.124
Host + Age	688.478	2.599	0.095
Host + Locality	689.663	3.784	0.053

infected only in localities 2 and 3. The farms of locality 3 are more distant from the native vegetation remnants and also closer to the city of Itabuna, which is an urban area. Paraíso and São Jorge farms have the smallest density of trees, and, therefore, were more affected by the land use and forest degradation than the others, as a consequence of the anthropic effect observed (Silva, 2017). Moreover, Açude farm is very heterogeneous, with the presence of rubber trees and regenerating shrubs, besides cocoa trees. This kind of heterogeneity in this farm might have resulted in a higher abundance and species richness of these parasites in relation to the north and central areas. These results highlight that more attention should be paid to that area in further investigations.

Although *H. seanezi* had the highest helminth species richness, the

Table 9

Generalised linear models (GLMs) of the effects of host species, host gender, host age and locality on the helminth prevalence of six sigmodontine rodents in nine agroforestry farms, Ilhéus, state of Bahia, Brazil. Only the models with Δ AICc < 10 are presented. Plausible models (Δ AICc < 2) are in bold.

Model	AICc	Δ AICc	wAICc
Host + Locality	90.236	0	0.596
Host + Sex + Locality	91.921	1.685	0.256
Host + Sex + Age Locality	93.358	3.122	0.125
Host	98.457	8.221	0.009
Locality	99.435	9.199	0.006
Host + Sex	99.657	9.421	0.005
Null	104.21	13.974	0.0005

MSR was lowest in this host and only *O. nigripes* had an MSR higher than one. This might indicate that the infracommunities were not species saturated, with very few infracommunities showing more than two species. Indeed, only three rodents of *H. seuanzei* had three helminth species, which was the highest infracommunity richness observed.

The host species influenced the helminth prevalence, since this variable was present in the two selected models of the GLM analysis and in the helminth abundance analysis. Among the three most parasitised species, *O. nigripes* and *A. cursor* are habitat generalist species, occurring in several kinds of habitats, including areas around human dwellings (D'Andrea et al., 2007) and preserved and disturbed forests (Cronemberger et al., 2019). Nevertheless, *N. squamipes*, which is a water rat, occurs near watercourses and streams (D'Andrea et al., 2007), and was present only in four farms in locality 2. This restricted habitat preference (Gentile and Fernandez, 1999) and the aggregated distribution of this rodent in the environment might have resulted in a higher abundance of helminths among the infracommunities of this species than the other hosts, corroborating the GLM analysis of the helminth abundance, in which the only plausible model included only the host species as a variable. However, the high abundance of *H. epsilon* in one individual host and the fact that the null model was also plausible in this analysis should also be considered.

The host gender also seemed to influence the helminth occurrence, based on the GLM analysis, indicating that most of the infected animals were males. This is a common pattern observed in endoparasites of small mammals (Zuk and McKean, 1996), and can be attributed to a more exploratory behaviour of males, what has already been observed in sigmodontine rodents, such as *O. nigripes* and *A. cursor* (Püttker et al., 2006; Owen et al., 2010).

The present study was the first to characterise the helminth fauna of the sigmodontine rodent *Hylaeamys seuanzei*. This host had the highest species richness in the present study, considering the component community of this host, with five morphospecies, among which four were nematodes and one, a cestode.

Considering the helminth fauna observed for *A. cursor*, this is the first record of *S. alata* in this host. Three other species of this genus have been reported for *A. cursor*, *Syphacia carlitosi*, *Syphacia kinsellai* (Simões et al., 2011), and *Syphacia obvelata* (Gomes et al., 2003). Other helminths reported in this host are *Hassalstrongylus epsilon*, *Guerrerostrongylus zetta* (Gomes et al., 2003), *Stilestrongylus lanfrediae*, *Stilestrongylus eta*, *Gerrerostrongylus zetta*, *Angiostrongylus sp.*, *Litomosoides silvai*, *Canaania obesa*, *Rodentolepis akodontis* (Simões et al., 2011), and *Listomosoides chagasfilhoi* (Moraes-Neto et al., 1997). In studies which evaluated the helminth community of this rodent in Atlantic Forest fragments in southeastern Brazil, Gomes et al. (2003) found four species and Simões et al. (2011) registered nine helminth species. Thus, both reported higher helminth species richness than our study. However, it must be considered that both reports were regional studies encompassing several localities. Yet, the mean intensity for *S. aculeata*, the only species in common among studies, were higher in those studies

when compared to the present results, whereas prevalences were lower (Gomes et al., 2003: I = 24, P = 4; Simões et al., 2011: I = 13, P = 24).

This is the first report of *G. gomesae* in the rodent *E. russatus*. *Guerrerostrongylus zetta* has been previously found in *E. russatus* (Gomes et al., 2003 host reported as the synonymy *Oryzomys intermedius*; Boullosa et al., in press). Gomes et al. (2003) found *G. zetta* with higher prevalence (54.5%) and intensity (45.7) than our study. Boullosa et al. (in press) found higher intensity (65) and lower prevalence (3.6%) for this species in a preserved area of Atlantic Forest in southern Brazil. Other helminth species firstly reported for this host include *Hassalstrongylus luquei*, described by Costa et al. (2014); *Stilestrongylus rolandoi*, described by Boullosa et al. (2019); and *Stilestrongylus kaaguyporai*, described by Panisse and Digiani (2018). Other reports for this host are of *Gerrerostrongylus ulysi*, *Stilestrongylus lanfrediae*, *Syphacia evaginata*, *Tapironema coronatum*, *Trichuris sp.* (Panisse et al., 2017), *Hassalstrongylus sp.*, *Hymenolepis sp.*, *Strongyloides sp.*, *Syphacia sp.* (Kuhnen et al., 2012), *Angiostrongylus costaricensis* (Graeff-Teixeira et al., 1990) (host reported as the synonymy *Oryzomys russatus*), and *Raillietina guaricanae* (César and Luz, 1993) (host reported as the synonymy *Oryzomys intermedius*). Specimens of the families Nippostrongylinae and Ancylostominae were also found in *E. russatus* (Kuhnen et al., 2012; Panisse et al., 2017). Helminth species richness observed for this host was similar to the results of Boullosa et al. (in press), which found three species, however, Kuhnen et al. (2012) reported six morphospecies, both in a preserved area of the Atlantic Forest in southern Brazil. Gomes et al. (2003) found only one species in this host. In a regional study carried out in Atlantic Forest areas in Misiones, Argentina, Panisse et al. (2017) recorded seven helminth species.

All the helminths found in *N. squamipes* have been previously reported to occur in this host. *H. epsilon* was previously reported with lower intensity and prevalence than our study by Gomes et al. (2003) (I = 15, P = 28%) and Maldonado Jr. et al. (2006) (I = 52, P = 6.3%), whereas the same studies reported higher values for *P. bispiculata* when compared to our results (Gomes et al., 2003: I = 14, P = 76%; Maldonado Jr. et al., 2006: I = 10.8, P = 40.5%). Panisse et al. (2017) also registered *H. epsilon* in this host in a regional study in Atlantic Forest areas of Argentina with high intensity and prevalence (I = 285, P = 100%). Studies on the helminths of the water rat *N. squamipes* also reported the occurrence of the nematodes *Hassalstrongylus sp.* (Kuhnen et al., 2012), *Litomosoides chagasfilhoi* (Moraes-Neto et al., 1997; Maldonado Jr. et al., 2006), *Syphacia venteli* (Gomes and Vicente, 1984; Gomes et al., 2003; Maldonado Jr. et al., 2006; Robles and Navone, 2010), *Litomosoides navonae* and *Trichuris travassosi* (Panisse et al., 2017). Maldonado Jr. (2006) also reported the presence of the trematodes *Echinostoma paraensei* and *Schistosoma mansoni* and the cestode *Raillietina sp.* in the water rat. When comparing with the helminth communities for this host in the Atlantic Forest, Gomes et al. (2003) found similar species richness than the present study (three species), while Kuhnen et al. (2012) found only one species, Panisse et al. (2017) reported four species, and Maldonado Jr. et al. (2006) found seven helminth species in this host in a disturbed rural area of the Atlantic Forest domain.

Since only one specimen of the rodent *N. lasiurus* was captured, its helminth fauna could not be analysed. However, the only helminth found, *S. freitasi*, has already been reported in this rodent in Cerrado and Caatinga biomes (Simões et al., 2017; Costa et al., 2019). The only study on the helminth fauna of *N. lasiurus* in the Atlantic forest was carried out in open matrix areas and reported six species: *Protospirura numidica criceticola*, *S. freitasi*, *Pterygodermatites zygodontomis*, *Syphacia alata*, *Trichuris navonae* and *Rodentolepis akodontis*, and all were dominants, except for *R. akodontis* (Lucio, 2019). Other helminths reported for this rodent include, *Stilestrongylus stilesi*, *Syphacia criceti* and *Hymenolepis sp.* (Costa et al., 2019).

For the rodent *O. nigripes*, all the helminth species found had been reported in previous studies. *Guerrerostrongylus zetta* was also found

with higher intensity than the present study by Simões et al. (2011) (I = 30, P = 21.4%), Panisse et al. (2017) (I = 47.7, P = 96.3), Gomes et al. (2003) (I = 17.6, P = 28%), Cardoso et al. (2016) (I = 20.9, P = 20.9%), Boullosa et al. (in press) (I = 11.4, P = 76%) and Werk et al. (2016) (I = 5.63, P = 78). *Stilestrongylus eta* was found with lower intensity and prevalence than ours by Simões et al. (2011) (I = 18.3, P = 5.3%) and by Gomes et al. (2003) (I = 11.1, P = 50%). *Syphacia* infection in this host was previously reported to be *S. kinsellai* (Simões et al., 2011; Panisse et al., 2017), described for this host by Robles and Navone (2007). Several other helminth species have been reported in studies of helminth communities of this rodent, including nematodes, trematodes, and cestodes (Simões et al., 2011; Cardoso et al., 2016; Panisse et al., 2017). Helminth species richness reported for this host in the Atlantic Forest were similar to the present results in most of the studies, which showed two helminth species (Gomes et al., 2003; Kuhnen et al., 2012; Cardoso et al., 2018; Boullosa et al., in press), except for the regional studies of Simões et al. (2012) and Panisse et al. (2017), which registered 12 and six species, respectively.

5. Conclusions

This is a novel study of the helminth fauna of sigmodontine rodents in the Brazilian Cabruca agroforestry system. The results indicated that the south of the study area was the most prone to helminth infection of those rodents, and that the opportunistic species, such as *O. nigripes* and *A. cursor*, besides the water rat *N. squamipes*, were the most infected species for helminth parasites in this study. The rodent *H. seuanesi* was also an important host in the community since it had the highest helminth species richness, although it had low helminth prevalence. The study indicated a high host-specificity for most of the helminth species. Considering the helminth communities of small rodents in these Cabruca agroforests, the observed helminth species richness were within the range found in previous studies carried out in Atlantic Forest areas for most of the hosts captured with available data in literature. In relation to species composition, this is the first report on the helminth fauna of *H. seuanesi*, and the first records of *G. gomesae* in *E. russatus* and *S. alata* in *A. cursor*.

Declaration of competing interest

All authors declare no conflicts of interest.

Acknowledgments

We thank the owners of cacao farms for authorizing the field study and the Caipora and Rhipi fraternities for field assistance. This work was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq – PPBio) Rede Bio.M.A [457524/2012–0], Universidade Estadual de Santa Cruz (UESC) [00220.1100.1264; 00220.1100.1645 and 00220.1100.1536] and Instituto Oswaldo Cruz. NAC, BAS and RGB received grants from Coordenação de Aperfeiçoamento de Nível Superior (CAPES) – Brasil - finance code 001; RGB received grants from Fundação Oswaldo Cruz (FIOCRUZ); MGK received grants from CNPq and from Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB). RG received researcher grants from CNPq.

References

Amato, J.F.R., Walter, A.B., Amato, S.B., 1991. Protocolo para Laboratório: Coleta e Processamento de Parasitas do Pescado. Imprensa Universitária, Universidade Federal Rural do Rio de Janeiro, Seropédica, Brasil.

Anderson, R.C., 2000. Nematode Parasites of Vertebrates: Their Development and Transmission, second ed. (Wallingford, Oxon, UK).

Ayoade, J., 1986. Introdução a Climatologia Dos Trópicos. Difel, São Paulo, Brasil.

Boullosa, R.G., Simões, R.O., Andrade-Silva, B.E., Gentile, R., Maldonado Jr., A., 2019. A new heligmonellid (Nematoda) species of the genus *Stilestrongylus* in *Euryoryzomys*

russatus (Rodentia: Sigmodontinae) in the Atlantic forest, southern Brazil. J. Helminthol. 93, 352–355. <https://doi.org/10.1017/S0022149X18000251>.

Boullosa, R.G., Cardoso, T.S., Costa-Neto, S.F., Teixeira, B.R., Freitas, T.P.T., Maldonado Jr., A., Gentile, R., (in press). Helminth community structure of three sigmodontine rodents in the Atlantic Forest, southern Brazil. *Oecologia Australis*.

Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *J. Parasitol.* 83, 575–583. <https://doi.org/10.2307/3284227>.

Cardoso, T.S., Simões, R.O., Luque Jr., J.L.F., M, A., Gentile, R., 2016. The influence of habitat fragmentation on helminth communities in rodent populations from a Brazilian Mountain Atlantic Forest. *J. Helminthol.* 90, 460–468. <https://doi.org/10.1017/S0022149X15000589>.

Cardoso, T.S., Macabu, C.E., Braga, C.A.C., Simões, R., Costa-Neto, Socrates, F., Maldonado Jr., Arnaldo, Gentile, R., Luque, J.L.F.A., 2018. Helminth metacommunity structure of wild rodents in a preserved area of the Atlantic Forest, southeast Brazil. *Rev. Bras. Parasitol. Vet.* 27, 495–504. <https://doi.org/10.1590/S1984-296120180066.495-504>.

Carvalho-Pereira, T., Souza, F.N., Santos, L., Walker, R., Pertile, A.C., de Oliveira, D.S., Costa, F., 2018. The helminth community of a population of *Rattus norvegicus* from an urban Brazilian slum and the threat of zoonotic diseases. *Parasitology* 145, 797–806. <https://doi.org/10.1017/S0031182017001755>.

Cassano, C.R., Barlow, J., Pardini, R., 2012. Large mammals in an agroforestry mosaic in the Brazilian Atlantic forest. *Biotropica* 44, 818–825. <https://doi.org/10.1111/j.1744-7429.2012.00870.x>.

Cassano, C.R., Rocha, J.M.A., R, A.M., Bernardo, C.S.S., Biancon, G.V., Campiolo, S., 2017. Primeira avaliação do status de conservação dos mamíferos do Estado da Bahia, Brasil. *Oecologia Aust* 21, 156–170. <https://doi.org/10.4257/oeco.2017.2102.06>.

César, T.C.P., Luz, E., 1993. *Raillietina* (Raillietina) *guaricana* n. sp. (Cestoda-Davaineidae), parasite of wild rats from the environmental protection area of Guaricana, Paraná, Brazil. *Mem. Inst. Oswaldo Cruz* 88, 85–88. <https://doi.org/10.1590/S0074-02761993000100013>.

Costa, M.A.R., Maldonado J, A., Bóia, M.N., Lucio, C.S., Simões, R.O., 2014. A new species of *Hassalstrongylus* (Nematoda: Heligmonellidae) from *Euryoryzomys russatus* (Rodentia: Sigmodontinae) in the Atlantic forest, Brazil. *Neotrop. Helminthol.* 8, 235–242. <https://www.arca.fiocruz.br/handle/icict/10088> ISSN: 1995-1043.

Costa, N.A., Cardoso, T.S., Costa Neto, S.F., Maldonado Junior, A., Gentile, R., 2019. Metacommunity structure of helminths of *Necomys lasiurus* (Rodentia: Sigmodontinae) in different land use areas in the Brazilian Cerrado. *J. Parasitol.* 105, 271–282. <https://doi.org/10.1645/17-199>.

Cronemberger, C., Delciellos, A.C., Barros, C.S., Gentile, R., Weksler, M., Braz, A.G., Teixeira, B.R., Loretto, D., Vilar, E.M., Pereira, F.A., Santos, J.R.C., Geise, L., Pereira, L.G., Aguiar, M., Vieira, M.V., Estrela, P.C., Junger, R.B., Honorato, R.S., Moratelli, R., Vilela, R.V., Guimarães, R.R., Cerqueira, R., Costa-Neto, S.F., Cardoso, T.S., Nascimento, J.L., 2019. Mamíferos do Parque Nacional da Serra dos Órgãos: atualização da lista de espécies e implicações para a conservação. *Oecologia Aust* 23, 191–214. <https://doi.org/10.4257/oeco.2019.2302.02>.

D'Andrea, P., Gentile, R., Maroja, L., Fernandes, F., Coura, R., Cerqueira, R., 2007. Small mammal populations of an agroecosystem in the Atlantic forest domain, southeastern Brazil. *Braz. J. Biol.* 67, 179–186. <https://doi.org/10.1590/S1519-69842007000100025>.

Faria, D., Laps, R.R., Baumgarten, J., Cetra, M., 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic forest of southern Bahia, Brazil. *Biodivers. Conserv.* 15, 587–612. <https://doi.org/10.1007/s10531-005-2089-1>.

Gardner, S., Campbell, M., 1992. Parasites as probes for biodiversity. *J. Parasitol.* 78, 596–600. <https://doi.org/10.2307/3283534>.

Geise, L., Pereira, L.G., 2008. Rodents (Rodentia) and marsupials (Didelphimorphia) in the municipalities of Ilhéus and Pau Brasil, state of Bahia, Brazil. Check list J. Species list. *Distribution* 4, 174–177. <https://doi.org/10.15560/4.2.174>.

Gentile, R., Fernandez, F.A.S., 1999. Influence of habitat structure on a streamside small mammal community in a Brazilian rural area. *Mammalia* 63, 29–40. <https://doi.org/10.1515/mamm.1999.63.1.29>.

Gomes, D.C., Cruz, R.P., Vicente, J.J., Pinto, R.M., 2003. Nematode parasites of marsupials and small rodents from Brazilian Atlantic Forest in the state of Rio de Janeiro, Brazil. *Rev. Bras. Zool.* 20, 699–707. <https://doi.org/10.1590/S0101-81752003000400024>.

Gomes, D.C., Vicente, J., 1984. Helminthos parasitos de *Necomys squamipes* (Brants) do Município de Sumidouro, RJ. *Mem. Inst. Oswaldo Cruz* 79, 67–73.

Graeff-Teixeira, C., Avila-Pires, F.D., Machado, R.C.C., Camillo-Coura, L., Lenzi, H.L., 1990. Identificação de roedores silvestres como hospedeiros do *Angiostrongylus costaricensis* no sul do Brasil. *Rev. Inst. Med. trop. S. Paulo* 32, 147–150. <https://doi.org/10.1590/S0036-46651990000300001>.

Hammer, Ø., Harper, D., Ryan, P., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaentol. Electron.* 4, 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Jansen, A., Xavier, S., Roque, A., 2015. The multiple and complex and changeable scenarios of the *Trypanosoma cruzi* transmission cycle in the sylvatic environment. *Acta Trop.* 151, 1–15. <https://doi.org/10.1016/j.actatropica.2015.07.018>.

Kuhnen, V.V., Graipel, M.E., Pinto, C.J.C., 2012. Differences in richness and composition of gastrointestinal parasites of small rodents (Cricetidae, Rodentia) in a continental and insular area of the Atlantic Forest in Santa Catarina state, Brazil. *Braz. J. Biol.* 72, 563–567. <https://doi.org/10.1590/S1519-69842012000300019>.

Lobão, D.E., Pinho, L.M., Carvalho, D.L., Setenta, W.C., 1997. Cacao-Cabruca: um modelo sustentável de agricultura tropical. *Indícios Veementes, FNDPF, São Paulo. Ano III.* pp. 10–24.

- Lucio, C.S., 2019. Composição e estrutura da helmintofauna gastrointestinal de uma comunidade de roedores em área de matriz aberta de Mata Atlântica do estado do Rio de Janeiro. [Master Dissertation]. Fundação Oswaldo Cruz, Rio de Janeiro, Brasil.
- Maldonado Jr., A., Gentile, R., Fernandes-Moraes, C.C., D'Andrea, P.S., Lanfredi, R.M., Rey, L., 2006. Helminth communities of *Nectomys squamipes* naturally infected by the exotic trematode *Schistosoma mansoni* in southeastern Brazil. *J. Helminthol.* 80, 369–375. <https://doi.org/10.1017/JOH2006366>.
- Moraes-Neto, A.H.A., Lanfredi, R.M., Souza, W., 1997. *Litomosoides chagasfilhoi* sp.nov. (Nematoda: Filarioidea) parasitizing the abdominal cavity of *Akodon cursor* (Winge, 1987) (Rodentia; Muridae) from Brazil. *Parasitol. Res.* 83, 137–143. <https://doi.org/10.1007/s004360050223>.
- Mori, S.A., Boom, B.M., Carvalho, A.M., Santos, T.S., 1983. Southern Bahia moist forest. *Bot. Rev.* 49, 155–232. <https://doi.org/10.1007/BF02861011>.
- Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P., O'hara, R., Simpson, G., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., 2018. Vegan: community ecology Package. Available in. <https://cran.r-project.org/web/packages/vegan/index.html> 2.21.19.
- Oliveira, R.C., Guterres, A., Fernandes, J., D'Andrea, P.S., Bonvicino, C.R., Lemos, E.R., 2014. Hantavirus reservoirs: current status with an emphasis on data from Brazil. *Viruses* 6, 1929–1973. <https://doi.org/10.3390/v6051929>.
- Owen, R., Goodin, D., Koch, D., Chu, Y., Jonsson, C., 2010. Spacial temporal variation in *Akodon montensis* (Cricetidae: Sigmodontinae) and hantaviral seroprevalence in subtropical forest ecosystem. *J. Mammology* 91, 467–481. <https://doi.org/10.1644/09-MAMM-A-152.1>.
- Panisse, G., Digiani, M.C., 2018. A new species of *Stilestrongylus* (Nematoda, Heligmonellidae) from the Atlantic forest of misiones, Argentina, parasitic in *Euryoryzomys russatus* (Cricetidae, Sigmodontinae). *Parasitol. Res.* 117, 1205–1210. <https://doi.org/10.1007/s00436-018-5801-2>.
- Panisse, G., Digiani, M.C., Notarnicola, J., Galliari, C., Navone, G., 2017. Description of the helminth communities of sympatric rodents (Muroidea: Cricetidae) from the Atlantic Forest in northeastern Argentina. *Zootaxa* 4337, 243–262. <https://doi.org/10.11646/zootaxa.4337.2.4>.
- Patton, J.L., Pardiñas, U.F., D'Elfa, G., 2015. Rodents. In: *Mammals of South America*, vol. 2 University of Chicago Press, Chicago, USA.
- Püttker, T., Meyer-Lucht, Y., Sommer, S., 2006. Movement distances of five rodent and two marsupial species in forest fragments of the coastal Atlantic rainforest, Brazil. *Ecotropica* 12, 131–139.
- R Core Team, 2018. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>, Accessed date: 21 February 2019.
- Robles, M.R., Navone, G., 2007. A new species of *Syphacia* (Nematoda: Oxyuridae) from *Oligoryzomys nigripes* (Rodentia: Cricetidae) in Argentina. *Parasitol. Res.* 101, 1069–1075. <https://doi.org/10.1007/s00436-007-0595-7>.
- Robles, M.R., Navone, G., 2010. Redescription of *Syphacia venteli* travassos 1937 (Nematoda: Oxyuridae) from *Nectomys squamipes* in Argentina and Brazil and description of a new species of *Syphacia* from *Melanomys caliginosus* in Colombia. *Parasitol. Res.* 106, 1117–1126. <https://doi.org/10.1007/s00436-010-1772-7>.
- Rozental, T., Ferreira, M.S., Guterres, A., Mares-Guia, M., Teixeira, B.R., Gonçalves, J., Bonvicino, C.R., D'Andrea, P.S., Lemos, E.R.S., 2017. Zoonotic pathogens in Atlantic forest wild rodents in Brazil: bartonella and coxiella infections. *Acta Trop.* 168, 64–73. <https://doi.org/10.1016/j.actatropica.2017.01.003>.
- Schroth, G., Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, H.L., Izac, A.-M.N., 2004. *Agroforestry and Biodiversity Conservation in Tropical Landscapes*. Island Press, Washington DC, USA.
- Setenta, W., Lobão, D.E., 2012. *Conservação Produtiva: cacau por mais 250 anos*. Câmara Brasileira do Livro, São Paulo, Brasil.
- Silva, T.M., Andrade, Z.A., 1989. Infecção natural de roedores silvestres pelo *Schistosoma mansoni*. *Mem. Inst. Oswaldo Cruz* 84, 227–235. <https://doi.org/10.1590/S0074-02761989000200011>.
- Silva, A.A.S., 2017. *Diversidade de pequenos mamíferos não voadores e a intensificação do manejo em agroflorestas no sul da Bahia, Ilhéus - Bahia*. [Master Dissertation]. Universidade Estadual de Santa Cruz, Ilhéus, Brasil.
- Simões, R.O., Gentile, R., Rademaker, V., D'Andrea, P.S., Herrera, H., Freitas, T., Lanfredi, R., Maldonado Jr., A., 2010. Variation in the helminth community structure of *Thrichomys pachyurus* (Rodentia, Echimyidae) in two sub-regions of the Brazilian Pantanal: the effects of land use and seasonality. *J. Helminthol.* 84, 266–275. <https://doi.org/10.1017/S0022149X09990629>.
- Simões, R.O., Souza, J.G.R., Maldonado Jr., A., Luque, J.L., 2011. Variation in the helminth community structure of three sympatric sigmodontine rodents from the coastal Atlantic Forest of Rio de Janeiro, Brazil. *J. Helminthol.* 85, 171–178. <https://doi.org/10.1017/S0022149X10000398>.
- Simões, R.O., Garcia, J.S., Costa-Neto, S.F., Santos, M.M., Faro, M.J., 2017. Survey of helminths in small mammals along the aqueduct of the São Francisco river in the Caatinga biome. *Oecologia Aust* 21, 88–92. <https://doi.org/10.4257/oeco.2017.2101.10>.
- SOS Mata Atlântica, Instituto Nacional de Pesquisas Espaciais (INPE), 2019. <https://www.sosma.org.br>, Accessed date: 22 January 2019.
- Vaz, S., 2005. *Mamíferos colecionados pelo serviço de estudos e pesquisas sobre a febre amarela nos municípios de Ilhéus e Buerarema, estado da Bahia, Brasil*. *Arq. Mus. Nac.* 63, 21–28 ISSN 0365-4508.
- Vicente, J.J., Rodrigues, H., Gomes, D.C., Pinto, R.M., 1997. Nematoides do Brasil. Parte V: Nematoides de Mamíferos. *Rev. Bras. Zool.* 14, 1–452. <https://doi.org/10.1590/S0101-81751997000500001>.
- Werk, D., Gallas, M., Silveira, E., Périco, E., 2016. New locality records for *Guerrerostrongylus zetta* (travassos, 1937) Sutton & Durette-Desset, 1991 (Nematoda: Heligmonellidae) parasitizing *Oligoryzomys nigripes* (Olfers, 1818) (Rodentia: Sigmodontinae) from southern Brazil. *Check List.* 12, 1861. <https://doi.org/10.15560/12.2.1861>.
- Yamaguti, F., 1961. *Sistema helminthum*. In: *The Nematodes of Vertebrates*. Interscience Publishing, Inc, New York, USA.
- Yorke, W., Maplestone, P., 1969. *The Nematode Parasites of Vertebrates*. Hafner Publishing Co., London, UK.
- Zuk, M., McKean, K.A., 1996. Sex differences in parasite infections: patterns and processes. *Int. J. Parasitol.* 26, 1009–1023. [https://doi.org/10.1016/S0020-7519\(96\)80001-4](https://doi.org/10.1016/S0020-7519(96)80001-4).