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Helminth community structure of the white-bellied woolly mouse opossum *Marmosa constantiae* Thomas, 1904 in Central-West Brazil

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Abstract

Marmosa constantiae is a species of marsupial restricted to the central portion of South America. In Brazil, it occurs in the northwestern region including five states of the Amazon, Cerrado, and Pantanal biomes. However, there is no study of the helminth fauna or helminth community structure for this marsupial. The aims of this study were to describe the species composition and to analyse the structure of the helminthic community of *M. constantiae* in an area of the Amazon Arc in Sinop, north of the state of Mato Grosso, Brazil. Parasites were searched in 53 specimens of this marsupial, among which 44 were infected with at least one helminth species. Parasitic helminths were counted and identified. Nine species were collected: seven nematodes, one cestode, and one acanthocephalan. The most abundant species were *Gracilioxyuris agilisis*, *Travassostrongylus scheibelorum, Pterygodermatites sinopiensis*, and *Subulura eliseae.* These species were the only dominant ones in the component community. No significant differences were observed in the abundance and prevalence of helminths between male and female hosts. Host body size significantly influenced helminth abundance in males. The pattern of community structure considering the infracommunities in this locality indicated more species replacement than species loss along the environmental gradient. This is the first study to report the helminth fauna and the helminth community structure of *M. constantiae.*

Introduction

Parasites can directly interfere with host individuals, populations, and communities (Poulin 1999; Bellay *et al.* 2018), affecting several processes, such as competition, migration, speciation, reproduction, quality of life, and behaviour, and consequently affecting biodiversity (Hudson 2005). In addition, several intrinsic and extrinsic factors may influence the distribution and abundance of parasites, thus modulating parasite diversity (Morand 2015). Host attributes, such as host sex and age, have been identified as important factors influencing parasite abundance and prevalence (Costa-Neto *et al.* 2019; Boullosa *et al.* 2020; Cirino *et al.* 2020).

Helminth community studies of Neotropical marsupials are scarce. Most of them were carried out for large marsupials, such as *Didelphis marsupialis* (Jiménez *et al.* 2011; Freitas *et al.* 2022), *Didelphis aurita* (Costa-Neto *et al.* 2019), *Didelphis albiventris* (Silva & Costa 1999; Zabott *et al.* 2017; Cirino *et al.* 2022), *Metachirus myosurus* (Cirino *et al.* 2020), and *Philander opossum* (Ramírez-Cañas *et al.* 2019). Much attention has been paid to the species of the genus *Didelphis* because they can occur in high abundances in peridomicile and rural areas and are known to be reservoirs of zoonoses (Lima *et al.* 2012; Jansen *et al.* 2015; Bezerra-Santos *et al.* 2020). Nevertheless, for the genus *Marmosa*, there is only one study comparing the helminth structure of two sympatric species of this genus (*M. demerarae* and *M. murina*) in French Guiana (Byles *et al.* 2013). The scarcity of such studies concerning small marsupials highlights a large gap in knowledge about this group.

The white-bellied woolly mouse opossum *Marmosa constantiae* Thomas, 1904 (Didelphimorphia, Didelphidae) is geographically distributed in the central portion of South America and occurs in parts of Brazil, eastern Bolivia, Paraguay, and Argentina (Smith & Owen 2016). In Brazil, it occurs in the northwestern region, including the states of Acre, Amazonas, Mato Grosso, Pará, and Rondônia (Silva *et al.* 2019). This species occurs in the Amazon, Cerrado, and Pantanal

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biomes of the Neotropical region, is arboreal, is often found in the understorey of forests and occasionally at the ground level, and has an insectivorous-omnivorous diet (Faria *et al.* 2019).

There are few studies of helminth species descriptions for *M. constantiae* (Andrade-Silva *et al.* 2022a, b). However, there are no studies of its helminth fauna or helminth community structure. The aims of the present study were to describe the species composition and analyse the parasitological parameters of the helminth fauna of *M. constantiae* in the Amazonian Arc, a municipality of Sinop in the northern state of Mato Grosso, Brazil. We also analysed the helminth community structure of *M. constantiae* in this locality.

Materials and methods

Study area

This study was carried out on 16 sample transects settled in forest fragments ranging from 81.7 to 19.838 ha in the municipality of Sinop (11°49′1.71″ S, 55°24′39.05″ W) in the state of Mato Grosso, Brazil. The area is within an ecological transition landscape of the Cerrado/Amazon biomes consisting of forest patches surrounded by pastures and monoculture plantations. This area is of special interest not only because it is located between two biomes but because the region of the Amazonian Arc has been suffering strong recent anthropic action (Silva Jr. *et al.* 2021). According to the Köppen classification, the climate in the region is tropical hot and humid (Aw) with monsoon-type rainfall in transition to the superhumid equatorial climate (Am) of the Amazon (Alvares *et al.* 2013). In this region, the average annual temperatures range from 24 °C to 27 °C, with an average annual rainfall of 2,000 mm. Two well-defined seasons are noted: a rainy season from October to April and a dry season from May to September (Priante-Filho *et al.* 2004).

Sample collection method

Samples were collected during a study of an ectoparasite network of small mammals (Mendonça *et al.* 2020). Two expeditions were carried out during eight consecutive nights: the first during the rainy season in November–December 2016 and the second during the dry season in June 2017. The marsupials were captured using Tomahawk® (Model 201, 16 in × 5 in × 5 inches, Wisconsin, USA) and Sherman (Model XLK, 3 in × 3.75 in × 12 in, Florida, USA) live traps. Traps were arranged alternately at the ground level and in the understorey (at a height of at least 1.5 m from the ground). The bait was composed of a mixture of banana, peanut butter, cornmeal, sardine, and vanilla flavouring.

Following the standards of the Federal Council of Veterinary Medicine in Resolution No. 1000 (https://www.cfmv.gov.br/) and of the Federal Council of Biology in Resolution No. 301 (https://cfbio.gov.br/), the captured animals were anaesthetized, measured, sexed, and euthanized. All individuals were submitted to taxidermy, and voucher specimens were deposited in the Zoological Collection of the Federal University of Mato Grosso, Cuiabá, state of Mato Grosso, Brazil (Supplementary Table S1).

The study was carried out under approval of the Chico Mendes Institute for Biodiversity Conservation (ICMBio, licence n° 8863-1) for the collection of small nonflying mammals and by the Ethics Committee on the Use of Animals (CEUA) of the Federal University of Mato Grosso (UFMT) (protocol n° 23108.076870/2015-41).

Helminth specimen collection, fixation, and identification

The organs and the gastrointestinal tract of each animal were removed immediately after euthanasia. The stomach, intestines, lungs, liver, and heart of the hosts were separated in Petri dishes and dissected using a stereoscopic microscope for helminth recovery. All helminths found were collected and processed according to Hoffman (1987), washed in physiological solution, and stored in 70% ethanol.

Specimens of the phylum Nematoda were cleared with 50% lactophenol, and specimens of the phylum Plathyhelminthes and the phylum Acanthocephala were stained with Carmine of Langeron (Amato *et al.* 1991). The specimens were posteriorly placed on temporary slides and examined using a Nikon Eclipse E200MVR light microscope (Nikon Corporation, Tokyo, Japan). Digital images were captured using a compound microscope (Zeiss Standard 20) with TCapture Imaging Application Software Version 5.1.1.0 (N). Specific morphological characters were used to identify the specimens, based on studies by Vicente *et al.* (1997) and Anderson *et al.* (2009), as well as on articles describing related species. The voucher specimens were deposited at the Helminthological Collection of the Oswaldo Cruz Institute (Supplementary Table S1).

Data analysis

The mean abundance, mean intensity, and prevalence of each helminth species were calculated according to Bush *et al.* (1997). We calculated the parasite species richness for each infracommunity; the mean parasite species richness (the mean number of helminth species considering all infracommunities); and the estimated parasite species richness in order to investigate whether the observed number of species was equivalent to the expected number of parasite species for the entire dataset. The estimated species richness was calculated using the nonparametric Jackknife 1 estimator (Magurram 2004).

We compared abundance and prevalence in relation to host sex for helminth species with a prevalence of more than 10%. We used the non-parametric Mann–Whitney test to compare parasite abundance and the $\chi 2$ contingency test to compare prevalence. We investigated the influence of host body size on the total abundance (all helminth species) and on species richness considering the infracommunity level using linear regression, separately for each host sex. Regressions were performed between host body size and helminth abundance or richness of each host specimen. The significance of the regression coefficient (beta) was evaluated using a t test. Because body size is related to age, we hypothesized that older hosts would be more parasitized than younger hosts. The analyses were carried out using Past software, version 3.21 (Hammer *et al.* 2001). We tested the data for normal distribution using the Shapiro–Wilk test. In all analyses, the significance level considered was 5%.

According to Thul *et al.* (1985), we calculated an importance value I for each of the helminth species. From this, each species was then classified in the community as dominant ($I \geq 1.0$), codominant ($0.01 \leq I < 1.0$), subordinate ($I < 0.01$) or an unsuccessful pioneer ($I = 0$). This analysis takes into account both total abundance and prevalence of each helminth species in relation to the others.

The pattern of the helminth community structure was analysed using the Elements of Metacommunity Structure approach (Presley *et al.* 2010). In the context of the theory of metacommunity, each host containing a community of parasites (i.e., an infracommunity) is considered a local community, and the set of infracommunities forms a metacommunity (i.e., a set of local communities linked by dispersal of multiple species (Leibold *et al.* 2004)). This analysis makes it possible to understand the distribution of parasite species along the environmental gradient and the processes that shape parasite communities. This analysis was done only at the infracommunity level, where each site (local community) in the incidence matrix was represented by a host specimen, as we assessed only one component community. We evaluated the three elements of metacommunity structure (EMS) (coherence, turnover, and boundary clumping) according to the method described by Leibold and Mikkelson (2002) and Presley *et al.* (2010). The coherence element tests whether species respond to the same environmental gradient by quantifying the number of embedded absences, represented by interruptions in the distribution of a species. This element is based on a matrix of incidence of species by sites ordered by reciprocal average. When the coherence element is significant, the other elements are also assessed. The turnover element determines whether the processes that structure the diversity lead to substitution or loss of species along the gradient and is calculated by the number of species replacements in the incidence matrix. Boundary clumping quantifies the overlap of species distribution limits in the environmental gradient, which can be clumped (when the index value is above 1), hyperdispersed (when the index is below 1), or random (when boundary clumping is not statistically significant) (Presley *et al.* 2010; Braga *et al.* 2017). EMS analysis was performed using the metacom package (Dallas 2020) in R software version 4.0.3 (R CoreTeam 2021). The level of significance was 5% in all the analyses.

Results

Helminth fauna

Fifty-three specimens of *M. constantiae* were captured and analysed – 26 males and 27 females. Among them, 20 specimens were captured during the rainy season and 33 during the dry season. Forty-four animals were parasitized with at least one helminth species. A total of 1,655 helminths were recovered. Seven nematode species were identified: *Aspidodera raillieti* Travassos, 1913 (Ascaridida: Aspidoderidae); *Gracilioxyuris agilisis* Feijó *et al.* 2008 (Oxyurida: Oxyuridae); *Travassostrongylus scheibelorum* Scheibel *et al.* 2014 (Trichostrongylida: Viannaiidae); *Viannaia skrjabini* Lent & Freitas, 1937 (Trichostrongylida: Viannaiidae); *Spirura aurangabadensis* (Ali & Lovekar, 1967) (Spirurida: Spiruridae); *Subulura eliseae* Andrade-Silva *et al.* 2022a (Strongylida: Subuluridae); and *Pterygodermatites sinopiensis* Andrade-Silva *et al.* 2022b (Spirurida: Ricticulariidae). The acantocephalan *Oligacanthorhynchus microcephalus* (Rudolphi, 1819) (Archiacanthocephala, Oligacanthorhynchidae) was also identified. Four specimens of cestode were recovered, but they were not identified at a lower taxonomic level due to the fragmented condition of the material.

The overall helminth species richness was nine, as well as the estimated species richness (Jackknife 1 = 9). The mean helminth species richness was 1.57 and ranged from 0 to 5 in each infracommunity. The highest helminth species richness was observed for a male host, which had five helminth species. We recovered a total of 693 adult helminths of *G. agilisis*, 167 of *T. scheibelorum*, 93 of *P. sinopiensis*, and 66 of *S. eliseae*, which were the most abundant species (Table 1). The nematodes *V. skrjabini*, *S. auragabadensis*, and *A. raillieti* were found only in female hosts, whereas *O. microcephalus* and the cestode were found only in male hosts (Table 1).

Table 1. Mean intensity and abundance (± SD) and prevalence rates (with 95% confidence intervals) in relation to host sex for the helminth species found in *Marmosa constantiae* in Sinop, state of Mato Grosso, Brazil

Parameters	Species								
	Aspidodera raillieti	*Gracilioxyuris agilisis*	*Pterygodermatites sinopiensis*	*Spirura aurangabadensis*	*Subulura eliseae*	*Travassostrongylus scheibelorum*	*Viannaia skrjabini*	Cestoda	*Oligacanthorhynchus microcephalus*
Abundance	0.21±1.51	13.08±23.68	1.75±4.44	0.02±0.14	1.25±3.62	3.15±9.44	0.13±0.52	0.08±0.38	0.11±0.58
Male	–	17.92±24.41	2.35±4.60	–	0.92±3.73	4.54±10.07	–	0.15±0.40	0.23±0.60
Female	0.41±1.53	8.41±22.97	1.19±4.48	0.04±0.14	1.56±3.65	1.81±9.52	0.26±0.53	–	–
Intensity	11	25.67±27.93	5.81±6.57	1	9.43±4.86	8.79±14.33	1.75±0.96	2.00±0.00	2.00±1.73
Male	–	33.29±32.94	5.55±8.47	–	8±4.65	11.80±19.49	–	2.00±0.00	2.00±1.73
Female	11	17.46±20.20	4.57±3.05	1	10.5±2.65	5.44±3.24	1.75±0.96	–	–
Prevalence	1.89(0–10)	50.94(38–66)	30.19 (18–44)	1.89 (0–10)	13.21(5–25)	35.85 (23–50)	7.55 (2–18)	3.77 (0–12)	5.66 (1–15)
Male	–	53.85(33–73)	42.31 (23–63)	–	11.54 (2–30)	38.46 (20–59)	–	7.69 (0–25)	11.54 (2–30)
Female	3.70 (0–18)	48.15 (29–68)	25.93 (11–46)	3.70 (0–18)	14.81 (4–33)	33.33 (17–54)	14.81 (4–34)	–	–

The influence of host sex on helminth abundance and prevalence was investigated for *G. agilisis*, *T. scheibelorum*, *P. sinopiensis*, and *S. eliseae.* Helminth abundance and prevalence showed no statistically significant differences between host sexes (Tables 2 and 3).

Concerning the influence of host body size on total helminth abundance or on species richness in each infracommunity, a direct relationship was observed between male host body size and total helminth abundance (beta = 0.416, t = 2.240, p = 0.035). This relationship was not observed in female hosts (beta = 0.077, t = -0.032, p = 0.975). Concerning species richness, no significant relationship was observed for males (beta = 0.141, t = 0.697, p = 0.493) or females (beta = -0.066, t = 0.288, p = 0.776).

The helminth species *G. agilisis*, *T. scheibelorum*, *P. sinopiensis*, and *S. eliseae* were dominant in the component community of *M. constantiae*, whereas *A. raillieti*, *V. skrjabini*, and *O. microcephalus* were codominant, and *S. aurangabadens* and Cestoda were subordinate (Table 4).

Table 2. Chi-square and probability values of helminth prevalence in relation to host sex for the most abundant helminth species found in *Marmosa constantiae* in Sinop, state of Mato Grosso, Brazil

Species	χ^2	*p*
Gracilioxyuris agilisis	0.056	0.813
Pterygodermatites sinopiensis	0.782	0.376
Subulura eliseae	0.095	0.758
Travassostrongylus scheibelorum	0.072	0.790

Table 3. Mann-Whitney U and probability values of helminth abundance in relation to host sex for the most abundant helminth species found in *Marmosa constantiae* in Sinop, state of Mato Grosso, Brazil

Species	U	p
Gracilioxyuris agilisis	300.5	0.343
Pterygodermatites sinopiensis	322.5	0.539
Subulura eliseae	338.5	0.716
Travassostrongylus scheibelorum	331.5	0.693

Table 4. Importance indices for each helminth species found in *Marmosa constantiae* in Sinop, state of Mato Grosso, Brazil

Helminths species	Importance indices	Classification
Gracilioxyuris agilisis	78.299	Dominant
Pterygodermatites sinopiensis	6.236	Dominant
Subulura eliseae	1.933	Dominant
Travassostrongylus scheibelorum	13.276	Dominant
Aspidodera raillieti	0.046	Codominant
Viannaia skrjabini	0.117	Codominant
Oligacanthorhynchus microcephalus	0.075	Codominant
Spirura aurangabadensis	0.004	Subordinate
Cestoda	0.003	Subordinate

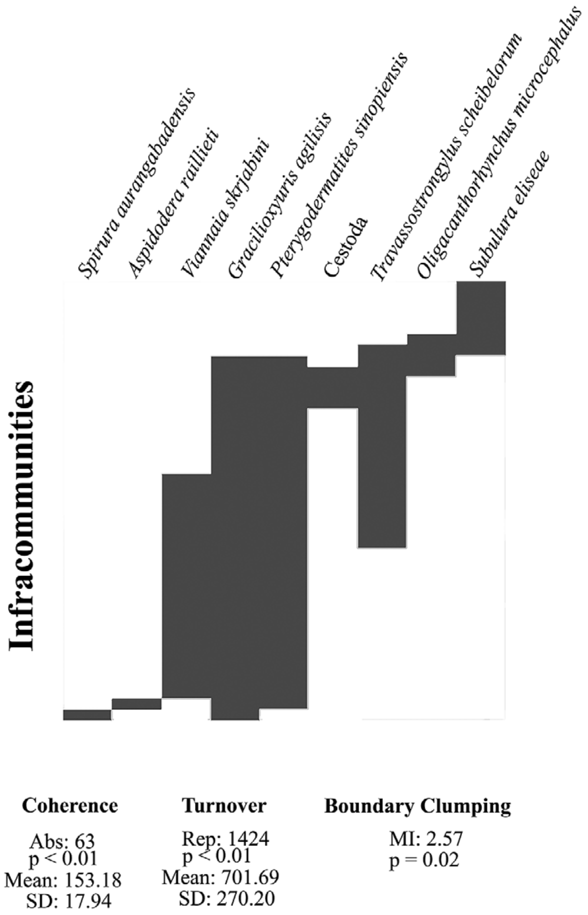

Figure. 1 Ordinated matrix, using elements of metacommunity structure (coherence, turnover, and boundary clumping), for the helminth metacommunity of *Marmosa constantiae* (Didelphimorphia, Didelphidae) in the ecotone area of the biomes Cerrado/Amazonia in Mato Grosso state, Brazil. Abs = embedded absences; p = p-valor (α = 0.05); Mean = mean values of the randomized matrices; SD = standard deviation of the randomized matrices; Rep = number of replacements; MI = Morisita index.

The patterns of the helminth metacommunity structure were coherent with more species replacements than species loss, showing a Clementsian pattern (Figure 1). This pattern indicates that species distribution along the environmental gradient was more clumped than expected by chance and that their distribution boundaries were coincident.

Discussion

Helminth fauna

Here, we provide the first study of the helminth community structure of *M. constantiae.* This marsupial is a new host of six species of parasites – namely, *A. raillieti, G. agilisis, T. scheibelorum, V. skrjabini, S. aurangabadensis*, and *O. microcephalus.* Previous studies based on taxonomic descriptions reported *M. constantiae* as a type of host for the helminths *S. eliseae* and *P. sinopiensis* (Andrade-Silva *et al.* 2022a, b). The similarity between the observed and the expected helminth species richness indicated that probably no helminth species would be incorporated into the *M. constantiae* component community with an increase in the number of hosts sampled. The helminth fauna was composed of four helminth species with expected direct life cycles (*A. raillieti, G. agilisis, T. scheibelorum,* and *V. skrjabini*) and five species with indirect life cycles (*S. aurangabadensis, S. eliseae, P. sinopiensis, O. microcephalus*, and Cestoda).

Among the helminth species registered as parasitizing other hosts of the genus *Marmosa*, Byles *et al.* (2013) reported 12 species for *M. demerarae* and 14 for *M. murina.* Among them, only *A. raillieti* and *O. microcephalus* were also found parasitizing *M. constantiae.* However, we observed that five genera were shared among these hosts: *Travassostrongylus*, *Viannaia*, *Spirura*, *Subulura* and *Pterygodermatites.*

The study of the helminth fauna of *D. marsupialis*, which was carried out in the same locality as the present study, reported the same helminth species richness observed for *M. constantiae* (nine species). However, *D. marsupialis* and *M. constantiae* shared only two species, *A. raillieti* and *O. microcephalus,* which have been registered in several didelphids (Varella *et al.* 2022; Freitas *et al.* 2022). Jiménez *et al.* (2011) reported 10 helminth species for the marsupial *Philander opossum* in French Guiana and 12 in Mexico, among which *A. raillieti* and *O. microcephalus* were the only species in common with the present study. These results corroborate the generalist characteristics of these two helminth species.

This study provides the first record of the species *T. scheibelorum* in Brazil and expands its geographic distribution, which has thus far been described only in French Guiana parasitizing *M. demerarae* and *M. murina* (Scheibel *et al.* 2014). The genus *Travassostrongylus* has a wide geographical distribution and infects several marsupial species (Vicente *et al.* 1997).

Gracilioxyuris agilisis has already been described as parasitizing other didelphids in the Pantanal and Cerrado biomes (Feijó *et al.* 2008; Santos-Rondon *et al.* 2012). This study is the first report of this helminth in the state of Mato Grosso. The record of this parasite in *M. constantiae* reinforces the theory that pinworms and didelphids share a close evolutionary history, which corroborates Santos-Rondon *et al.* (2012), including the high prevalence found in both studies (51% and 70%, respectively).

Viannaia skrjabini was reported only in large didelphids, *D. aurita* and *Philander quica* (Temminck, 1824) in the state of Rio de Janeiro Brazil by Lent and Freitas (1937). The present study expanded the geographical distribution to an ecotone area in the state of Mato Grosso.

Spirura aurangabadensis, in turn, also had its geographic distribution expanded, since it was recorded only in India, parasitizing bats; in Malaysia, parasitizing tree shrews and primates; in Australia, parasitizing bats and marsupials; and in the state of Minas Gerais, Brazil, also parasitizing bats (Ali & Lovekar 1966; Quentin & Krishnasamy 1975; Spratt 1985, 2007).

Concerning the influence of host sex on parasitological parameters, most studies of mammalian parasites have shown higher rates of infection in male hosts than in females (Zuk & McKean 1996; Poulin 2007). However, no significant differences were observed in the abundance and prevalence of helminths between male and female hosts in our study. Regarding host body size, male host body size was an important variable for the abundance of helminth species. In studies carried out with didelphids, this relationship between host body size and helminth abundance has already been demonstrated, postulating that larger and older hosts have more parasites than young hosts (Cirino *et al.* 2020; Freitas *et al.* 2022) because they may acquire parasites during their lifetime.

Helminth community structure

Most helminth species were considered dominant or codominant in the study. Only *S. aurangabadensis* and the cestode species were considered subordinate, which indicates that these species occur infrequently and do not contribute significantly to the community (Thul *et al.* 1985). Indeed, as previously mentioned, *S. aurangabadensis* may be associated with bat fauna and may represent an occasional record of *M. constantiae* infection. The cestode, in turn, had low prevalence and the lowest abundance in the study.

The Clementsian pattern of metacommunity structure recorded for infracommunities indicates that the distribution of the helminths in *M. constantiae* is more clustered than expected by chance, forming compartments of species that replace each other along the environmental gradient – in this case, among infracommunities. Each compartment tends to be formed by species that present ecological or biological similarities or by species with interdependent phylogenetic relationships, indicating that clusters between infracommunities were formed by parasite species that co-occurred in the same infracommunity, according to the metacommunity theory (Leibold & Mikkelson 2002). Each host–parasite interaction is a result of coevolutionary processes related to the encounter–compatibility filters (Combes 2001) between parasites and hosts. Furthermore, among the dominant species, only *G. agilisis* and *P. sinopiensis* were widely dispersed across the hosts, suggesting that they are core species of the helminth fauna of *M. constantiae.* These species showed high prevalence in the metacommunity.

The Clementsian pattern has been observed in other studies of helminth metacommunity structure. Dallas and Presley (2014) reported this pattern in the helminth metacommunity of rodents in New Mexico, which was associated with a high parasite specificity. Costa *et al.* (2022) recorded a quasi-Clementsian pattern – analogous to the Clementsian pattern – for helminths of sigmodontine rodents in an agroforestry mosaic in the Brazilian Atlantic Forest. For Brazilian marsupials, there are only two studies of helminth metacommunity structure, and both are for the genus *Didelphis* (Cirino *et al.* 2022; Costa-Neto *et al.* 2019). Cirino *et al.* (2022) recorded a Gleasonian pattern for helminths of *Didelphis albiventris* in two extremes of the Atlantic Forest. Although Gleasonian and Clementsian patterns present distinct characteristics regarding the processes that promote such distributions, both are characterized by a greater species replacement than species loss along an environmental gradient. In contrast, Costa-Neto *et al.* (2019) observed a quasi-nested structure with more species loss than species replacement for *D. aurita* in peri-urban, sylvatic, and rural environments in southeastern Brazil.

Our results indicate that host sex was not related to abundance or prevalence. However, male host body size influenced both parameters. The pattern of the community structure considering the infracommunities in this locality indicates more species replacement than species loss along the environmental gradient. This is an unprecedented study of the helminths of *M. constantiae* in an ecotone area between Cerrado and Amazonia that contributes to filling gaps in the knowledge of the helminth fauna of neotropical marsupials and to understanding the patterns of parasite community structure.

Supplementary material. The supplementary material for this article can be found at http://doi.org/10.1017/S0022149X2300038X.

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References

Ali SM and Lovekar CD (1996) On a new spirurid *Taphozoia aurangabadensis* n. g., n. sp. from a micro-bat *Taphozous kacchensis*. *Indian Journal of Helminthology* **18**, 68–73.

Alvares CL, Stape JL, Sentelhas PC, Gonçalves JLM, and Spavorek G (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* **22** (**6**), 711–728.

Amato JF, Walter AB, and Amato SB (1991) *Protocolo para laboratório: Coleta e processamento de parasitas do pescado*. Rio de Janeiro: Imprensa Universitária.

Anderson RC, Chaubaud AG, and Willmott S (2009) *Keys to the nematode parasites of vertebrates: Archival volume*. Wallingford, UK: CABI Publishing.

Andrade-Silva BE, Vilela RV, Freitas LC, Pacheco RC, Mendonça RFB, Rossi RV, and Maldonado AJ (2022a) *Subulura eliseae* sp. n. (Ascaridida: Subuluroidea), a parasite of *Marmosa* spp. from Amazon rain forest Brazil. *Journal of Helminthology* **96**, E60.

Andrade-Silva BE, Costa NA, Pacheco RC, Rossi RV, and Maldonado AJ (2022b) A new species of *Pterygodermatites* (Spirurida: Rictulariidae) in *Marmosa constantiae* Thomas, 1904 from an ecotone area of the biomes Cerrado/Amazon in the Mato Grosso state, Brazil. *Frontiers in Veterinary Science* **9**, 955453.

Bellay S, Oda FH, Campião KM, Yamada FH, and Takemoto OEF (2018) Host–parasite networks: An integrative overview with tropical examples. pp 127–140 in Dáttilo W and Rico-Gray V (Eds), *Ecological networks in the tropics: An integrative overview of species interactions from some of the most species-rich habitats on Earth*, 1st ed. Springer Publisher, New York.

Bezerra-Santos MA, Fontes CS, Nogueira BCF, Yamatogi RS, Ramos RAN, Galhardo JA, Furtado LFV, Rabelo EML, Araújo JV, and Campos AK (2020) Gastrointestinal parasites in the opossum *Didelphis aurita*: Are they a potential threat to human health? *Journal of Parasitic Diseases* **44**, 355–363. doi: 10.1007/s12639-020-01205-9.

Boullosa R, Cardoso T, Costa-Neto S, Teixeira B, Freitas T, Júnior A, and Gentile R (2020) Helminth community structure of three sigmodontine rodents in the Atlantic forest, southern Brazil. *Oecologia Australis* **24**(**3**), 577–589.

Braga C, Oliveira JA, and Cerqueira R (2017) Metacomunidades: Uma introdução aos termos e conceitos. *Oecologia Austalis* **21**(**2**), 108–118.

Bush AO, Lafferty KD, Lotz JM, and Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* **83** (**4**), 575–583.

Byles B, Catzeflis F, Scheibel RP, and Jiménez FA (2013) Gastrointestinal helminths of two species of mouse opossums (*Marmosa demerarae* and *Marmosa murina*) from French Guiana. *Comparative Parasitology* **80**, 210–216.

Cirino BS, Costa-Neto SF, Maldonado Jr A, and Gentile R (2020) First study on the helminth community structure of the neotropical marsupial *Metachirus myosuros* (Didelphimorphia, Didelphidae). *Brazilian Journal of Veterinary Parasitology* **29**(**3**), e005420.

Cirino BS, Costa-Neto SF, Cardoso TS, Estrela PC, Maldonado Jr A, and Gentile R (2022) Gleasonian structure in the helminth metacommunity of the opossum *Didelphis albiventris* in two extremes of the Atlantic Forest. *Journal of Helminthology* **96**(**e7**), 1–11.

Combes C (2001) *Parasitism: The ecology and evolution of intimate interactions*. Chicago: University of Chicago Press. 728 pp.

Costa-Neto SF, Cardoso TS, Boullosa RG, Maldonado Jr A, and Gentile R (2019) Metacommunity structure of the helminths of the black-eared opossum *Didelphis aurita* in peri-urban, sylvatic and rural environments in southeastern Brazil. *Journal of Helminthology* **93**(**6**), 720–731.

Costa NA, Cardoso TS, Costa-Neto SF, Alvarez MR, Maldonado Jr A, and Gentile R (2022) Helminths of sigmodontine rodents in an agroforestry mosaic in the Brazilian Atlantic Forest: Patterns and processes of the metacommunity structure. *International Journal for Parasitology: Parasites and Wildlife* **18**, 82–91.

Dallas T and Presley SJ (2014) Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities. *Oikos* **123**(**7**), 866–874.

Dallas T (2020) Metacom: Analysis of the 'Elements of Metacommunity Structure'. *Ecography*. Available from: https://cran.r-project.org/package=metacom (accessed 26 December 2022).

Faria MB, Lanes RO, and Bonvicino CR (2019) *Guia dos marsupiais do Brasil: Guia de identificação com base em caracteres morfológicos externos e cranianos*. 1st ed. Amélie Editorial, São Caetano do Sul. 84 pp.

Feijó IA, Torres EJ, Maldonado Jr A, and Lanfredi RM (2008) A new oxyurid genus and species from *Gracilinanus agilis* (Marsupialia: Didelphidae) in Brazil. *Journal of Parasitology* **94**(**4**), 847–851.

Freitas LC, Maldonado Jr A, Mendonça RFB, Ramos DGS, Rossi RV, Pacheco RC et al. (2022) Helminth community structure of *Didelphis marsupialis* (Didelphimorphia, Didelphidae) in a transition area between the Brazilian Amazon and the Cerrado. *Brazilian Journal of Veterinary Parasitology* **31**(**2**), e002922.

Hammer O, Harper DA, and Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**(**1**), 1–9.

Hoffman RP (1987) *Diagnóstico de parasitismo veterinário*. Porto Alegre: Sulina. 156 pp.

Hudson P (2005) Parasites, diversity, and the ecosystem. pp. 1–12 in Thomas F, Renaud F, and Guégan JF (Eds), *Parasitism and Ecosystems*. Nova York: Oxford University Press.

Jansen AM, Xavier SCC, and Roque ALR (2015) The multiple and complex and changeable scenarios of the *Trypanosoma cruzi* transmission cycle in the sylvatic environment. *Acta Tropica* 15, 1–**15**. doi: 10.1016/j.actatropica.2015.07.018.

Jiménez FA, Catzeflis F, and Gardner SL (2011) Structure of parasite component communities of *Didelphid marsupials*: Insights from a comparative study. *Journal of Parasitology* **97**(**5**), 779–787.

Lent H and Freitas JFT (1937) Sur une nouvelle espéce du geme *Viannaia* Travassos, **1914**. *Papers on Helminthology*, Skrjabin's Jubilee Volume, 319–321.

Leibold MA and Mikkelson GM (2002) Coherence, species turnover, and boundary clumping: Elements of meta-community structure. *Oikos* **97**(**2**), 237–250. Available from: http://doi.wiley.com/10.1034/j.1600-0706.2002.970210.x (accessed 16 November 2022).

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF et al. (2004) The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* **7**(**7**), 601–613.

Lima MM, Sarquis O, Oliveira TG, Gomes TF, Coutinho C, Teixeira NFD et al. (2012) Investigation of Chagas disease in four periurban areas in northeastern Brazil: Epidemiologic survey in man, vectors, non-human hosts and reservoirs. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 106,143–149. doi: 10.1016/j.trstmh.2011.10.013.

Magurram AE (2004) *Measuring biological diversity*. Oxford, UK: Blackwell Publishing.

Mendonça RFB, **Colle AC**, **Freitas LC**, **Martins TF**, **Horta MC**, **Oliveira GMB** et al. (2020) Ectoparasites of small mammals in a fragmented area of the southern Amazonia: Interaction networks and correlations with seasonality and host sex. *Experimental and Applied Acarology* **81**(**1**), 117–134.

Morand S (2015) (macro-) Evolutionary ecology of parasite diversity: From determinants of parasite species richness to host diversification. *International Journal for Parasitology: Parasites and Wildlife* **4**, 80–87.

Poulin R (1999) Body size vs abundance among parasites species: Positive relationships? *Ecography* **22**, 246–250.

Poulin R (2007) *Evolutionary ecology of parasites*. Princeton, USA: Princeton University Press.

Presley SJ, **Higgins CL, and Willig MRA** (2010) Comprehensive framework for the evaluation of metacommunity structure. *Oikos* **119**(**6**), 908–917.

Priante-Filho N, **Vourlitis GL**, **Hayashi MMS**, **Nogueira JDS**, **Campelo Jr JH**, **Nunes PC** et al. (2004) Comparison of the mass and energy exchange of a pasture and a mature transitional tropical forest of the southern Amazon basin during a seasonal transition. *Global Change Biology* **10**(**5**), 863–876.

Quentin JC and Krishnasamy M (1975) Nématodes *Spirura* parasites des Tupaia et Du Nycticèbe em Malaisie. *Annales de Parasitologie Humaine et Comparée* **50**, 795–812.

Ramírez-Cañas SA, **George-Nascimento M**, **García-Prieto L, and Mata-López R** (2019) Helminth community structure of the gray four-eyed opossum *Philander opossum* (Mammalia: Didelphidae) in the Neotropical portion of Mexico. *Journal of Parasitology* **105**(**4**), 624–629.

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. (accessed 10 November 2022).

Santos-Rondon MVS et al. (2012) *Marmosa paraguayana* (Marsupialia: Didelphidae) as a new host for *Graciloxyurus agilisis* (Nematoda: Oxyuridae) in Brazil. *Journal of Parasitology* **98**, 170–174.

Scheibel RP, **Catzeflis F**, **and Jiméñez FA** (2014) The relationships of marsupial-dwelling Viannaiidae and description of *Travassostrongylus scheibelorum* sp. n. (Trichostrongylina: Heligmosomoidea) from mouse opossums (Didelphidae) from French Guiana. *Folia Parasitologica* **61**(**3**), 242–254.

Silva Jr CHL, **Pessôa ACM**, **Carvalho NS**, **Reis JBC**, **Anderson LO**, **and Aragão LEOC** (2021) The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nature Ecology & Evolution* **5**(**2**), 144–145.

Silva MGQ and Costa HMA (1999) Helminths of white-bellied opossum from Brazil. *Journal of Wildlife Diseases* **35**(**2**), 371–374.

Silva LGDL, **Ferreira DC, and Rossi RV** (2019) Species diversity of *Marmosa* subgenus *Micoureus* (Didelphimorphia, Didelphidae) and taxonomic evaluation of the white-bellied woolly mouse opossum, *Marmosa constantiae*. *Zoological Journal of the Linnean Society* **187**, 240–277.

Smith P and Owen RD (2016) *Marmosa constantiae* (Didelphimorphia: Didelphidae). *Mammalian Species* **48**, 123–129.

Spratt DM (1985) *Spirura aurangabadensis* (Ali e Lovekar) (Nematoda: Spiruridae) from small Dasyuridae (Marsupialia). *Transactions of the Royal Society of South Australia* **109**, 25–29.

Spratt DM (2007) Asian origins for some spirurid nematode parasites found in Australian Mammals. *Transactions of the Royal Society of South Australia* **131**(**1**), 83–92.

Thul JE, **Forrester DJ**, **and Abercrombie CL** (1985) Ecology of parasitic helminths of wood ducks, Aix sponsa, in *the Atlantic flyway*. Proceedings of the Helminthological Society of Washington **52**(**2**), 297–310.

Varella K, **Vilela RV**, **Gentile R**, **Cardoso TDS**, **Costa-Neto SF**, **and Maldonado Jr A** (2022) Population genetic structure and phenotypic diversity of *Aspidodera raillieti* (Nematoda: Heterakoidea), a parasite of Didelphini marsupials in Brazil's South and Southeast Atlantic Forest. *Parasite Vectors* **15**(**1**), 1–19.

Vicente JJ, **Rodrigues HO**, **Gomes DC, and Pinto RM** (1997) Nematóides do Brasil. Parte V: Nematóides de mamíferos. *Revista Brasileira de Zoologia* **14** (**1**), 1–452.

Zabott MV, **Pinto SB**, **Viott AM**, **Gruchouskei L, and Bittencourt LHF** (2017) Helmintofauna de *Didelphis albiventris* (Lund, 1841) no município de Palotina, Paraná, Brasil. *Arquivos de Ciências Veterinárias e Zoologia da UNIPAR* **20**(**1**), 19–22.

Zuk M and McKean KA (1996) Sex differences in parasite infections: Patterns and processes. *International Journal of Parasitology* **26**(**10**), 1009–1023.