

Ectoparasites of small-mammals: determinants of community structure in South American savannah

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SUMMARY

This study aimed to assess the contribution of hosts characteristics (rodents and marsupials) in the organization of ectoparasite communities present in woodland patches in western central Brazil. We verified the effect of host species, sex, body mass and vertical strata in addition to the role of seasonality on the ectoparasite composition, richness and abundance. The total sampling effort was 22 032 trap-nights equally distributed in 54 woodland patches. Variance partition and principal coordinate analysis were used to verify the existence of significant relationships between response variables and predictors. As expected, host species was the most important variable in ectoparasite community assembly. The composition, richness and abundance of mites and lice were highly influenced by host species, although higher for mites than for lice. Host body mass had a determining role on the richness and abundance of tick species. Vertical stratification and seasonality had weak influence, while the sex of the host had no influence on the organization of these communities. The results are closely related to the evolutionary characteristics of the species involved, as well as with local environmental characteristics of the study area.

Key words: Didelphimorphia, Rodentia, savannah, variation partitioning, mites, ticks, lice.

INTRODUCTION

Factors that determine the composition and structure of natural communities is one of the central themes of ecology (see Ricklefs and Schluter, 1993). In general, the species compositions in communities are arrangements of species grouped considering their morphological, ecological and evolutionary characteristics according to the environmental characteristics and interrelationships between species and the regional species pool (Cornwell and Ackerly, 2009). For parasite communities the same assumptions are valid; however, community assembly rules are more complex, since in addition to the parasites and environmental characteristics, host morphological, ecological and evolutionary traits also have an important role on the organization of communities (May and Anderson, 1990; Krasnov *et al.* 1998).

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In this sense, several factors have been identified as responsible for the structural organization of parasite communities (Morand and Poulin, 1998; Combes, 2001). Among them, host identity is considered a major factor (Bell and Burt, 1991; Guégan and Huguény, 1994; Poulin and Valtonen, 2002; Krasnov *et al.* 2005, 2008, 2014; Lareschi and Krasnov, 2010) since hosts are an ultimate habitat for parasites, providing a termo-stable site to live, forage and reproduce. To a lesser extent, other factors have been observed, for example, the effect of space (Krasnov *et al.* 2005, 2014; Lareschi and Krasnov, 2010), climate (Krasnov *et al.* 2005, 2008; Lareschi and Krasnov, 2010), host size (Guégan and Huguény, 1994; Muñoz and Cribb, 2005; Harrison *et al.* 2010) and host sex (Klein, 2004; Krasnov *et al.* 2011).

Most studies seeking to understand these relationships prioritize endoparasite communities, while those considering ectoparasite communities focus primarily on a single group (Krasnov *et al.* 2006, 2008, 2014) and/or cover a large geographical scale (Krasnov *et al.* 2006, 2008, 2012, 2014; Cruz *et al.*

2012; Linardi and Krasnov, 2013). Thus, regional studies evaluating the entire community of ectoparasites associated with hosts are rare (but see Lareschi and Krasnov, 2010). Another important factor to consider is the degree of importance of each factor, which may vary among different biogeographical regions, since each region has a unique set of species and environmental characteristics. In addition, each region can also have distinct levels of host–parasite specialization and evolutionary history (Marshall, 1981; Korallo *et al.* 2007; Krasnov *et al.* 2012).

Based on the above assumptions, there are some gaps to be filled, including: (i) What factors can influence ectoparasite community in a regional scale with no major environmental variation (e.g. vegetation, climate, etc.)? (ii) Are the processes that generate the assembly patterns in a wide spatial scale also translated into the community assembly structure on a smaller spatial scale? In this sense, the present study aims to assess the contribution of host traits (rodents and marsupials) in the organization of ectoparasite communities present in woodland patches in a savannah region of Brazil. Specifically we ask: what is the relative effect of host species, sex and body mass, as well as the host environment (portion of the vertical strata – on the ground or in the understory – and the season – dry or wet – in which each host was captured), on the composition, richness and abundance of ectoparasite communities? We predict that the host traits (species, sex and body mass) would have a preponderant role in the organization of ectoparasite communities, since the study was conducted on a small spatial scale and geographical/environmental variation should be barely noticeable. However, ectoparasites belonging to different taxa differ in their evolutionary history and the degree of host association. Therefore, ectoparasites that are closely associated with their hosts (e.g. mites and lice) would tend to be more influenced by host characteristics, while ectoparasites that spend most of their life cycle outside the host (e.g. ticks) would be more influenced by environmental characteristics (vertical strata and seasonality).

MATERIALS AND METHODS

Study area and data collection

This study was carried out in 54 woodland patches in a savannah region, located in the Paraguay River basin in the border of Pantanal, central–western Brazil (Fig. 1). Data collection was carried out during the rainy seasons of February/March 2012 and November/December 2012, and the dry seasons of July/August 2012 and June/July 2013. Details on the study region and procedures to capture and identification of small mammals and their ectoparasites have been described elsewhere (Sponchiado *et al.* 2015a, b).

Data analyses

In all analyses, we consider only the first capture of each host. In addition, we analysed the host species that had at least one parasite species recorded.

The variance partitioning analysis (Borcard *et al.* 1992; Peres-Neto *et al.* 2006) was used to quantify how much each predictor explains the response variable when all predictors are analysed simultaneously. This analysis allows us to extract the portion of the variance explained by each predictor separately and in conjunction with other variables. We used as dependent variable the ectoparasite community composition considering each host captured as sample unit; the independent variables were: identity (categorical variable: host species), use of vertical stratum (categorical variable: host captured on the ground or in the understory), host body mass (quantitative variable measured in grams), host sex (categorical variable: male or female) and seasonality (categorical variable: host captured in dry or rainy season). These analyses were conducted separately for each ectoparasite order, i.e. mites, ticks or lice.

We limited variance partitioning analysis to four predictors to avoid many interaction terms arising from more than four predictors, which would generate difficulty in results interpretation. In addition, the varpart function we applied [Vegan package (Oksanen *et al.* 2011)] is also limited to a maximal of four predictors. Thus, we used only the four independent variables with the strongest relationship with the dependent variable in the variance partitioning, considering the value of R^2 . For the parasite species composition data, in this previous selection, first, we performed a principal component analysis (PCoA – dissimilarity Bray–Curtis) to summarize the community structure into orthogonal axes; we then used the first and second axes in the regressions.

We repeated the same analyses considering the total richness and abundance of the main ectoparasite orders separately as dependent variables. For composition and richness analyses, we excluded ectoparasites that were not identified to species level because they could represent more than one species (e.g. larvae of *Amblyomma* sp. and protonymphs of *Ornithonyssus* sp.). However, all ectoparasites were considered for the analysis of total abundance. For ectoparasite composition matrix, we used the Hellinger transformation to correct the asymmetry between species abundance (Legendre and Gallagher, 2001). We also logarithmized ($\log x + 1$) the total abundance data in order to reduce its dispersion.

Subsequently, we apply a PCoA to observe the general patterns of relationship between ectoparasites and the variables that had greater explanatory power in the variance partitioning analysis. In these analyses, we grouped the abundance of ectoparasite species by family (Ixodidae, Argasidae, Laelapidae,

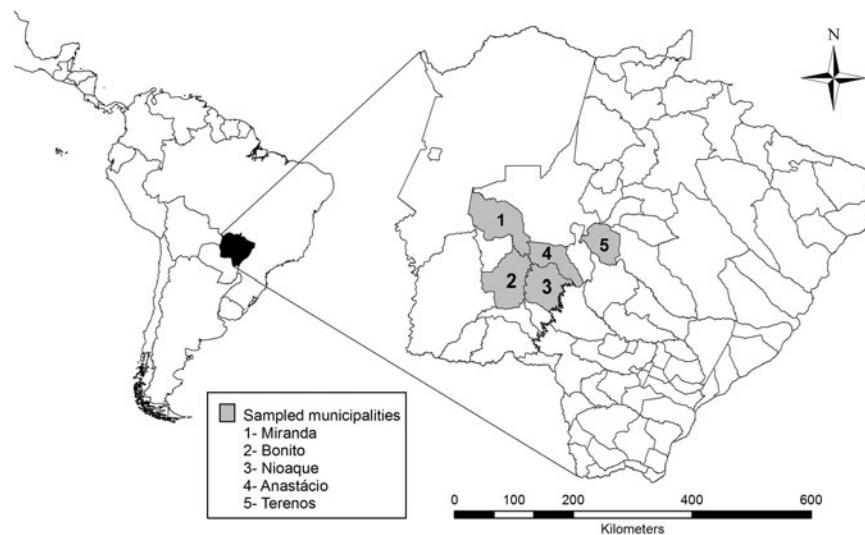


Fig. 1. Municipalities where small-mammal ectoparasites were sampled in a savannah region in Brazil.

Macronyssidae, Rhopansyllidae) or order (Phthiraptera). The later was grouped by order because of the low number of captured lice representing different families. In these analyses, we consider only the parasitized hosts. The abundance data for families/order were logarithmized ($\log x + 1$) to reduce dispersion.

All analyses were performed using the Vegan package (Oksanen *et al.* 2011) in the R environment (Development Core Team, 2012).

RESULTS

We captured 1040 small mammals belonging to 20 species, eight marsupials and 12 rodents. Among these, 563 specimens (of four marsupial and 11 rodent species) were parasitized. *Calomys tener* (Winge, 1887), *Cryptonomus cf. agricolai* (Moojen, 1943), *Marmosa constantiae* (Thomas, 1904), *Marmosa murina* (Linnaeus, 1758) and *Philander opossum* (Linnaeus, 1758) were captured in small numbers and did not have ectoparasites. We identified 40 ectoparasite species of four orders (Mesostigmata, Ixodida, Phthiraptera and Siphonaptera) and ten families (Laelapidae, Macronyssidae, Ixodidae, Argasidae, Hoplopleuridae, Polyplacidae, Trimenoponidae, Gyropidae, Haematopinidae and Rhopansyllidae), totalling 16 398 ectoparasites (Table 1, online Supplementary S1).

The host sex predictor showed the weakest relationship with composition, richness and abundance for mites and ticks (online Supplementary S2). Thus, this variable was excluded from the variance partitioning analysis for these groups. Seasonality showed the weakest relationship with composition, richness and abundance of lice; therefore, it was excluded from further analysis for this dependent variable (online Supplementary S2).

For mites (Mesostigmata), host species was determinant as a pure factor (composition – Adj. $R^2 = 0.68$; richness – Adj. $R^2 = 0.73$ and abundance – Adj. $R^2 = 0.75$) with a small influence of seasonality (online Supplementary S3). The vertical stratification and host mass, when considered as single factors, were not significant (online Supplementary S3). When we analysed the factors together, the relationship between host species and vertical stratification showed a secondary contribution to community assembly (Fig. 2, online Supplementary S3).

The factors analysed did not have great influence on the composition of ticks (Ixodida); only host species (Adj. $R^2 = 0.09$) and host body mass (Adj. $R^2 = 0.01$) were significant, but explained little of the variation in the data. On the other hand, host species factor alone (Adj. $R^2 = 0.13$), host species plus host body mass (Adj. $R^2 = 0.44$) and these two factors together with vertical stratification (Adj. $R^2 = 0.44$) were important to determine tick richness. Considering the species abundance, the factors that had more influence alone were host species (Adj. $R^2 = 0.13$) and host body mass (Adj. $R^2 = 0.10$). Together, these two factors explained 17% of variation in the data, and 10% when considered together with vertical stratification (Fig. 3, online Supplementary S4).

Similarly to mites, lice (Phthiraptera) also had host species a key factor in the group organization (composition – Adj. $R^2 = 0.43$; richness – Adj. $R^2 = 0.49$ and abundance – Adj. $R^2 = 0.46$, pure factor); however, this effect was not as high as it was for mites. The other factors were not significant when analysed separately. All together, the most important factors for community assemblage were: host species, host body mass, and vertical stratification, although this relationship was weak (Fig. 4, online Supplementary S5).

Table 1. Richness (R) and abundance (A) of small-mammal ectoparasite collected on woodland patches in a savanna region of Brazil. Number of host parasitized/non-parasitized in parentheses

	Mesostigmata		Ixodida		Phthiraptera		Siphonaptera		Total	
	R	A	R	A	R	A	R	A	R	A
Host identity (563/467)	24	11 380	8	3230	7	1784	1	4	40	16 398
Didelphimorphia (221/439)	3	103	8	3128	1	2	–	–	12	3233
<i>Didelphis albiventris</i> (108/20)	1	1	7	2457	–	–	–	–	8	2458
<i>Gracilinanus agilis</i> (70/329)	1	26	2	420	–	–	–	–	3	446
<i>Monodelphis domestica</i> (5/3)	1	75	1	1	1	2	–	–	3	78
<i>Thylamys macrurus</i> (38/87)	1	1	2	250	–	–	–	–	3	251
Rodentia (342/28)	21	11 277	5	102	6	1782	1	4	32	13 165
<i>Calomys callosus</i> (19/4)	4	739	1	2	1	7	–	–	6	748
<i>Cerradomys maracajuensis</i> (4/1)	3	139	–	–	–	–	–	–	3	139
<i>Cerradomys scotti</i> (13/0)	2	309	1	1	1	26	–	–	4	336
<i>Hylaeamys megapcephalus</i> (28/0)	3	2107	1	33	–	–	1	4	4	2144
<i>Nectomys rattus</i> (2/0)	3	14	1	2	1	15	–	–	5	31
<i>Oecomys cleberi</i> (5/2)	2	49	–	–	–	–	–	–	2	49
<i>Oecomys mamorae</i> (25/0)	4	793	–	–	1	18	–	–	5	811
<i>Oecomys roberti</i> (2/1)	2	5	–	–	–	–	–	–	2	5
<i>Oligoryzomys nigripes</i> (2/0)	2	14	–	–	–	–	–	–	2	14
<i>Rhipidomys macrurus</i> (156/19)	4	2793	3	17	1	42	–	–	8	2852
<i>Thrichomys fosteri</i> (86/1)	4	4315	4	47	2	1674	–	–	10	6036
Vertical stratum (563/467)	24	11 380	8	3230	7	1784	1	4	40	16 398
Ground (297/86)	21	7955	8	2673	6	1690	1	4	36	12 322
Understory (266/381)	17	3425	4	557	5	94	–	–	26	4076
Host body mass (563/467)	24	11 380	8	3230	7	1784	1	4	40	16 398
<100 g (370/451)	23	6947	5	756	7	145	1	4	36	7852
100–400 g (120/11)	13	3812	5	651	2	1343	–	–	20	5806
401–750 g (73/5)	4	621	7	1823	2	296	–	–	13	2740
Seasonality (563/467)	24	11 380	8	3230	7	1784	1	4	40	16 398
Dry season (264/258)	19	5906	7	2146	4	578	–	–	30	8630
Wet season (299/209)	20	5474	5	1084	7	1206	1	4	33	7768
Host sex (563/467)	24	11 380	8	3230	7	1784	1	4	40	16 398
Male (289/249)	21	5687	7	2028	7	418	1	3	36	8136
Female (274/218)	22	5693	7	1202	5	1366	1	1	35	8262

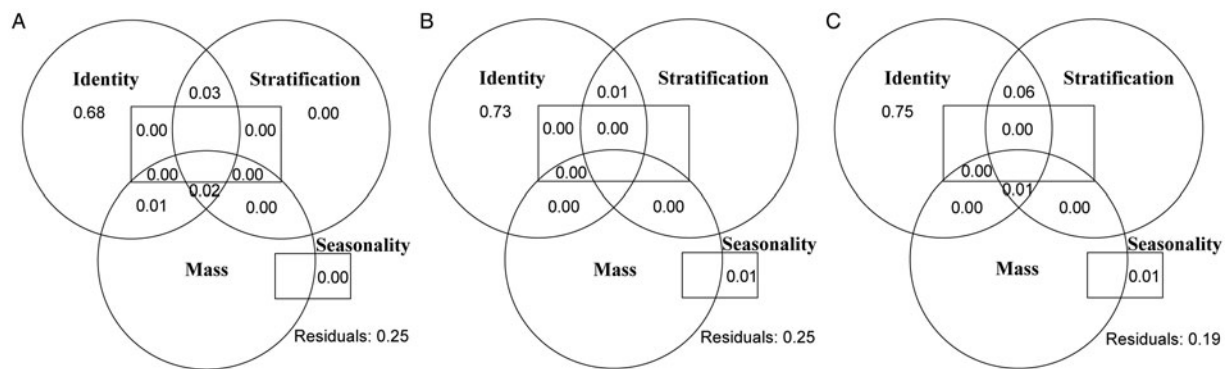


Fig. 2. Venn diagram representing the percentage of variation partitioned of mites (Mesostigmata) associated with small mammals in woodland patches of a savannah region in Brazil. Each circle or rectangle represents the percentage of variance explained by each predictor as a pure factor and as shared effects between factors. (A) Composition; (B) richness and (C) abundance. Values <0 were not showed.

When the abundance of ectoparasite species of each host were grouped by family (except lice, which were grouped in order) and ordered through a principal coordinate analysis, the first axis explained 59.52%, while the second axis explained 15.05% of data variation. The first axis showed a separation between hosts parasitized mainly by ticks

(Ixodidae and Argasidae) and those infested by mites (Laelapidae, Macronyssidae), lice (Phthiraptera) and fleas (Rhopanopsyllidae). In the second axis, there was a separation of hosts parasitized by Ixodidae, Macronyssidae and Phthiraptera from those parasitized by Argasidae. When we considered host family (Didelphidae, Cricetidae and

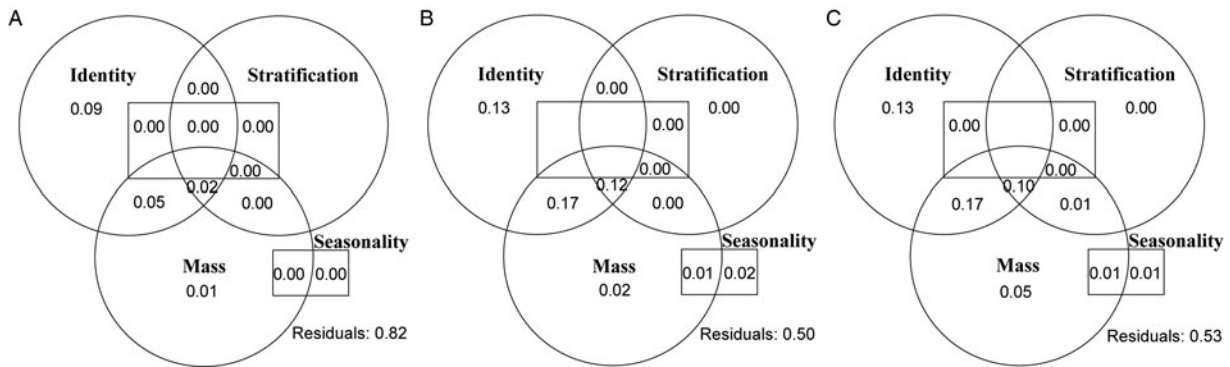


Fig. 3. Venn diagram representing the percentage of variation partitioned of ticks (Ixodida) associated with small mammals in woodland patches of a savannah region in Brazil. Each circle or rectangle represents the percentage of variance explained by each predictor as a pure factor and as shared effects between factors. (A) Composition; (B) richness and (C) abundance. Values <0 were not showed.

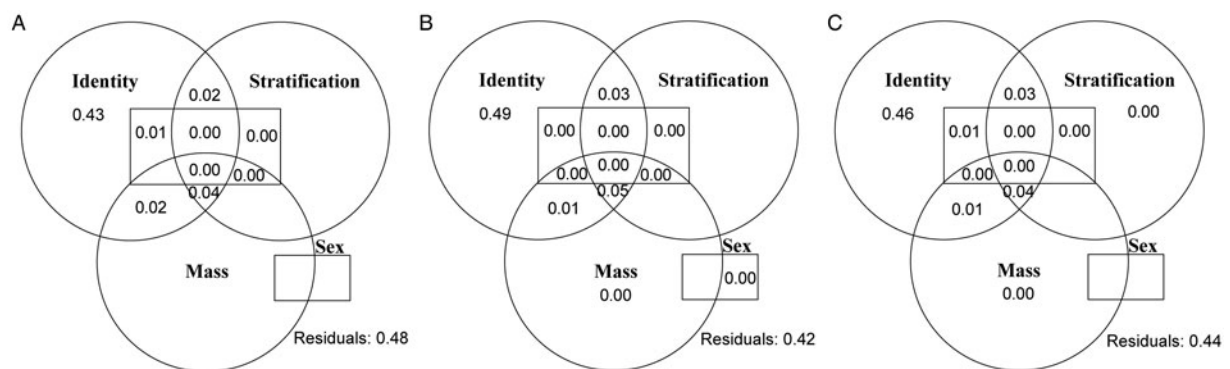


Fig. 4. Venn diagram representing the percentage of variation partitioned of lice (Phthiraptera) associated with small mammals in woodland patches of a savannah region in Brazil. Each circle or rectangle represents the percentage of variance explained by each predictor as a pure factor and as shared effects between factors. (A) Composition; (B) Richness and (C) abundance. Values <0 were not showed.

Echimyidae), Didelphidae were shown to be parasitized mainly by ticks, while rodents (Cricetidae and Echimyidae) were parasitized mainly by mites, lice and fleas (Fig. 5A). On the other hand, when we categorized hosts based on their vertical stratification (ground or understory), the ordination showed a separation mainly in axis 2, with hosts captured on the ground parasitized by Ixodidae, Macronyssidae and Phthiraptera, while hosts captured in the understory were parasitized by Argasidae (Fig. 5B). Likewise, when we considered the host body mass, the separation was also given by the second axis, with host of larger mass more related with Ixodidae, Macronyssidae and Phthiraptera (Fig. 5C). We also categorized the data based on seasonality (captures in the dry or rainy season) and sex of host, but the ordination did not show any clear pattern, as also found in the partition analysis.

DISCUSSION

Our data showed that the organization of ectoparasite communities related to small mammals is determined mainly by host species, being this factor

important (mainly for mites and lice rather than ticks) to explain the ectoparasite composition, richness and abundance. The community structure, in general, remained constant between individuals of a particular host species, but differed between host species. This pattern was consistent even without the influence of other analysed factors. This result was expected because numerous studies have found a similar pattern for different groups of ectoparasites (Krasnov *et al.* 2005, 2008, 2014; Lareschi and Krasnov, 2010). In the study area, we found a strong specificity among ectoparasite/host relationship. Almost every ectoparasite species had its specific host and therefore, each host had a particular parasitic fauna (Sponchiado *et al.* 2015b). This is mainly attributed to the coevolution process or coadaptation of parasites and hosts, which contributes to a given ectoparasite species to become adapted to one or more characteristics of a particular host species (Ward, 1992; Poulin, 1998; Combes, 2001). However, an ectoparasite community of a particular host is not only composed by specialist species, but also by generalist ones, such as ticks (Sponchiado *et al.* 2015a, b). For this reason, when

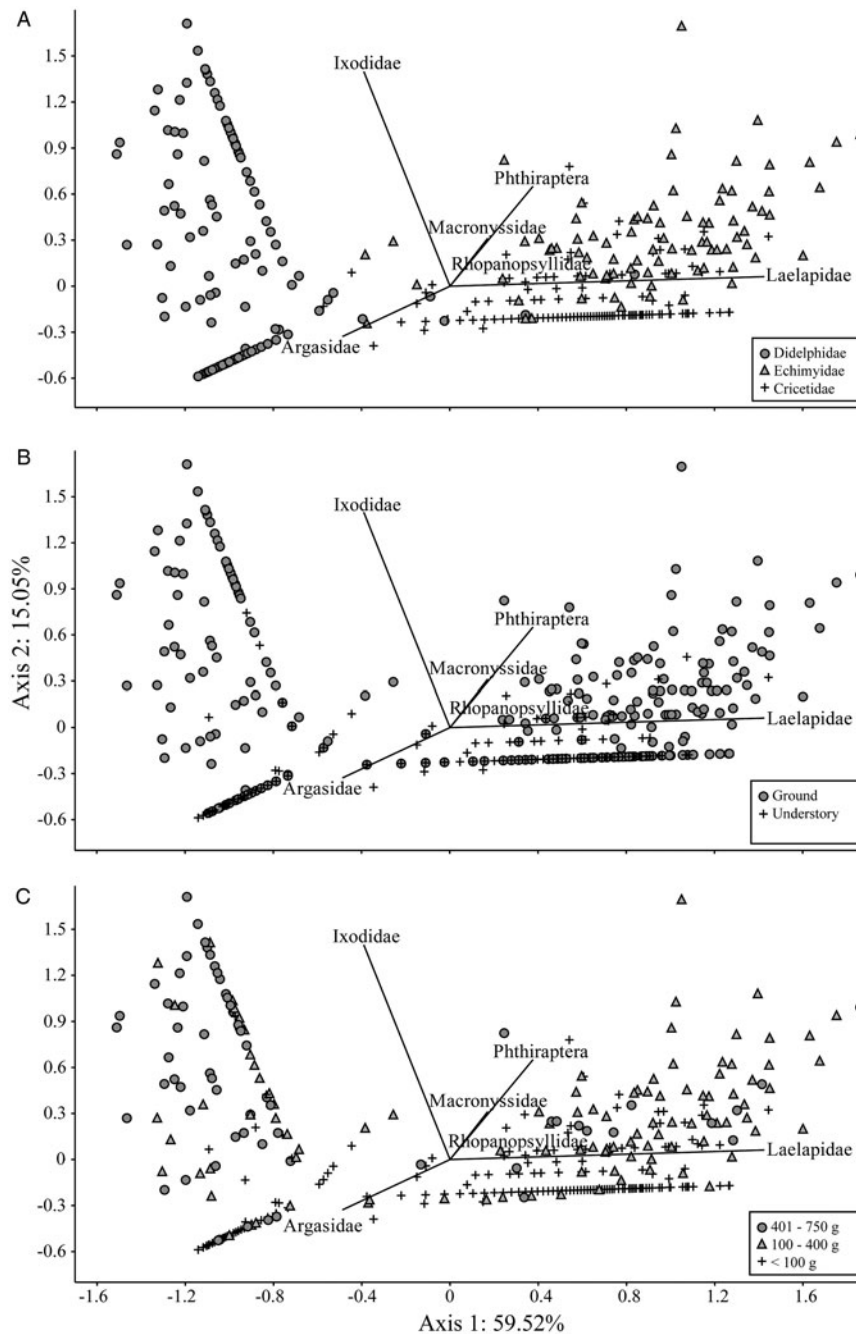


Fig. 5. Relationship between ectoparasites and the variables that had greater explanatory power in variance partition analysis. (A) host species; (B) vertical stratification and (C) host mass. The biplots comprise an ordination diagram (PCoA) of the ectoparasites community composition grouped by families/order present in each host.

we considered ticks, the strengthness of the host-parasite specificity became weak, or virtually null. Furthermore, ticks parasitized mainly marsupials, while lice and mites (Laelapidae and Macronyssidae) parasitized mainly rodents. These results emphasize the evolutionary character of the ectoparasite community assembly.

Another hypothesis is that the larger the hosts, the greater is the richness and abundance of ectoparasites (e.g. Guégan and Huguény, 1994; Muñoz and Cribb, 2005; Harrison *et al.* 2010). In part, this pattern is attributed to the fact that the larger the

host, the greater the body surface, and therefore, the dimension and amount of available niches (Korallo *et al.* 2007). Moreover, larger hosts generally have higher-energy requirements. In this sense, they need to travel longer distances searching for food resources (McNab, 1963; Mace and Harvey, 1983). Since many ectoparasite species show life stages outside the host (Bush *et al.* 2001), higher host mobility increases the chance of infestation by different ectoparasites, either by the availability in the environment or the exchange with other hosts (Nunn *et al.* 2003). Despite of this, we did not

observe any pattern related to host body mass, except when combined with other variables. In fact, to have such a strong effect of host body mass, it is necessary to have a marked intra- and inter-specific variation in body size of the host community and/or a low specificity in host–parasite relationship. In our data, the interspecific body mass variation was not high and the analysed ectoparasite communities had generally high specificity, thus justifying the low effect of host body mass on the ectoparasite composition, richness and abundance.

In turn, as ticks have low host/parasite specificity, this feature increases the importance of the body mass factor in the community organization. During the early stages of development, larvae and nymphs of ticks [stages that often parasitize small mammals (Szabó *et al.* 2013)] spend much of their time in the environment. These arthropods mainly use an ambush strategy (Needham and Teel, 1991), remaining on vegetation waiting for a potential host. The height the ticks are positioned on vegetation is directly correlated with the height of their preferred host (Szabó *et al.* 2009). Thus, the larger the host and/or the longer the distance travelled by it, the greater the chances of receiving new ticks. Corroborating these results, the PCoA plot shows that ticks (Ixodidae), as well as lice and mites (Macronyssidae), are more related with larger hosts.

On the other hand, we observed that seasonality significantly influenced the richness and abundance of mites and ticks; however, these relationships were weak. The reproductive cycle of small mammals is generally determined by the availability of food resources, which is mainly governed by variations in temperature and precipitation throughout the year (Bergallo and Magnusson, 1999; Mendel *et al.* 2008). Thus, the birth of pups occurs mostly during periods of greater availability of food resources during the rainy season (Pinheiro *et al.* 2002). Some ectoparasites synchronize their reproduction with their hosts (Marshall, 1981; Blanco and Frías, 2001) increasing their reproduction rates. As a result, there may be an increase in parasites dispersion rates during breeding periods, in which hosts show higher population density and are more gregarious, either during copulation (horizontal transmission) or during birth and parental care of offspring (vertical transmission) (Clayton and Tompkins, 1994). Conversely, certain climatic conditions may promote the breeding and development of some ectoparasite groups. For example, some species of ticks synchronize the incubation period of eggs during the rainy season (in this case, during the spring and summer). Higher humidity and higher temperatures shorten the incubation period and increase the egg hatchability (Labruna *et al.* 2009). Thus, seasonal changes can cause an increase or decrease in reproductive rates of ectoparasites. Even if it is not valid for all species or

taxonomic groups, these changes can have a significant effect that interferes at some extent with the general pattern of community structure.

Many studies showed the importance of environment and space in the ectoparasite community assembly (e.g. Krasnov *et al.* 2005, 2006; Lareschi and Krasnov, 2010). However, most of them evaluated the species distribution along a horizontal gradient covering a large geographical range. Since the sampled patches are relatively homogeneous in vegetation structure, geographically close among each other, and biogeographically have a similar small-mammal fauna, we chose to check how the vertical stratification of host species influenced ectoparasite assembly. Regardless of where each host species was sampled (on the ground or in the understory) the parasitic fauna remained constant. Although the PCoA analysis indicated that Argasidae ticks were sampled mainly on hosts captured in the understory, and Ixodidae ticks, lice and mites were sampled mainly on hosts captured on the ground, the former was more specific to marsupials and the later more specific to rodents, emphasizing the greater interaction between taxonomy and vertical stratification in such analyses. For example, the marsupials *Gracilinanus agilis*, *Didelphis albiventris* and *Thylamys macrurus* and the rodent *Rhipidomys macrurus* have similar spatial niches, i.e. they use the understory in similar frequencies and hollow trees as shelters (Vieira and Camargo, 2012). However, while Argasidae often parasitized the three species of marsupials, only three rodent individuals were found parasitized by Argasidae. Although these species coexist in the same microhabitat, another factor besides vertical stratification (the host species as an example) is contributing to marsupials having largely different ectoparasites assemblies, even occupying similar niche of rodents.

Like the vertical stratification, the sex of host showed little or no influence on ectoparasite community assembly. We included this variable in our analysis because other studies have shown that male small mammals have higher infestation rate than females (e.g. Khokhlova *et al.* 2011; Krasnov *et al.* 2011; Kiffner *et al.* 2014; Kowalski *et al.* 2015). Males generally have larger home ranges and move more than females, resulting in more frequent contact with other individuals (Moore and Wilson, 2002) and increasing the chances of getting parasites. Moreover, androgen hormones, such as testosterone, increase their susceptibility to parasitism by causing immunosuppression (e.g. Roberts *et al.* 2004). Our results indicate that this is not a general pattern applied to all species, as also found elsewhere (e.g. Kiffner *et al.* 2013; Sponchiado *et al.* 2015a, b).

In summary, our results showed that each ectoparasite order responded differently to the analysed predictors. Host species play an important role in ectoparasite community assembly of small

mammals in the Cerrado. Then the composition, richness and abundance of mites and lice are highly influenced by the host identity, although the former in a higher extent than the later. Host body mass had an important role in the richness and abundance of tick species. The vertical stratification and seasonality had little influence, while the sex of host had no influence on the community organization. However, it is necessary to take into account that these results are closely related to the evolutionary history of the species involved and the local environmental characteristics. Thus, it is possible that the degree of importance of each predictor could change depending on the geographic region and/or the taxonomic group.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182016001906>.

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