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Sympatry and habitat associations of sigmodontine rodents in a neotropical forest-savanna interface

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Abstract

Small mammal communities in the Neotropics are composed largely of sigmodontine rodents. However, many questions regarding these communities remain unanswered, especially those pertaining to fine-scale sympatry and habitat selection. To address this, we examined sigmodontine community structure and vegetation in the western margin of the Upper Paraná Atlantic Forest and the southwestern-most extent of the Cerrado (CE) (an extensive South American savanna ecoregion) of Paraguay. Vegetation classifications were derived from satellite imagery combined with maps based on extensive ground-based surveys. The three most abundant species (*Akodon montensis*, *Hylaeamys megacephalus*, and *Oligoryzomys nigripes*) were found most often in microsympatry with conspecifics, and were negatively associated with other species. *Akodon montensis* was associated with high forest (HF), and *H. megacephalus* with bamboo

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understory (BU), whereas *O. nigripes* did not exhibit a habitat preference. The first two species' distributions within the landscape were found to be driven primarily by habitat selection, and *O. nigripes* by a behavioral response (avoidance) to the presence of the other two species. Moreover, habitat influences whether or not a particular species associates with, or avoids, conspecifics or other species.

Keywords

behavioral response; Cerrado; habitat selection; Interior Atlantic Forest; Paraguay

Introduction

In the Neotropics, sigmodontine rodents often comprise rich components of the faunal communities (Emmons and Feer 1997, D'Elfa and Pardiñas 2015). However, many questions concerning habitat selection and sympatry constraints remain unanswered. Answers to these questions would enable better understanding of the composition and dynamics of rodent communities on a very local scale (i.e. the scale at which the individual rodent experiences its environment). These questions include where the animal lives within the habitat matrix, and with which individuals (conspecific or otherwise) it shares this space.

Sympatry of rodent species, including sigmodontines, is most often studied across a broad or mesoscale landscape, and often is inferred from known distributional limits of the species. When evaluated more precisely, it has often been with respect to habitat preferences (Poindexter et al. 2012a), or potential horizontal transfer of parasites (Gettinger et al. 2011, Lareschi and Galliari 2014) or pathogens (Chu et al. 2009).

Over the past two decades, numerous studies have investigated habitat associations of sigmodontine rodents throughout the Neotropics. Schnell et al. (2010) evaluated habitat preferences of *Sigmodon mascotensis* J. A. Allen 1897 in a dry coastal area of western Mexico, and Poindexter et al. (2012b) evaluated four common rodent species in the same area. Delciellos et al. (2016) reported that habitat structure was an important determinant of small mammal assemblages in fragments of Atlantic Forest in Rio de Janeiro state, Brazil. Moreover, distinct microhabitat associations have been reported for a variety of sigmodontine species in freshwater marsh (Bonaventura et al. 2003), secondary Atlantic Forest remnants (Puttker et al. 2008), a southern Atlantic Forest site (Melo et al. 2011, 2013), and the Pampas region in southern Brazil (Sponchiado et al. 2012). Owen et al. (2010) found distinct habitat associations for *Akodon montensis* Thomas 1913 in a western Atlantic Forest region. Polop et al. (2014) also reported on habitat associations for three sigmodontine species [*Oligoryzomys longicaudatus* (Bennett 1823), *Abrothrix hirta* (reported as *Abrothrix longipilis* (Waterhouse 1837)), and *Abrothrix olivacea* (Waterhouse 1837)] in a southern Andean region. Although several of these studies have investigated microhabitat associations of sigmodontine rodents in different biomes, none have evaluated both microsympatry and microhabitat associations, or have quantitatively separated these two independent characteristics of species within a sigmodontine community.

For the purposes of this study, microsympatry is defined as two or more species captured at the same trap site. Spatially, this means that they were captured within 2 m or less of each other (the amount that a trap might be displaced when rebaited, replaced after a capture, or to avoid ants). Temporally, this definition includes a species being at the same trap site within 1–10 days of the other species (sampling periods for the lines was from two to 11 nights). Our analyses also evaluated the tendency of each species to occur at sites with other individuals of the same species.

Our study was designed to answer three interrelated questions regarding sigmodontine rodent species: (1) Do any of the rodent species exhibit microsympatry with, or avoidance of, conspecifics or other species? (2) Do any of the species exhibit microhabitat selection? and (3) If microsympatry with conspecifics or with other species is detected, is it more frequent in one or more of the habitat types?

In this paper, we use the term “associate” to indicate a statistically significant frequency of occurrence (either positive or negative) between a species and a habitat, or between a species and the same or other species. We use “behavioral response” to mean a significant positive or negative response to the presence of either a conspecific or an individual of another species. We follow Mayor et al. (2009) in their definition of habitat selection as “the disproportionate use of resources or conditions by living things”. Our study evaluated habitat selection on only one scale, which we term microhabitat. Each trap site is assumed to sample a dimensionless point within the habitat matrix of the forest, although in practical terms it samples a habitat with an area of ca. 2 m in diameter. As such, each trap site was presumed to be sampling one of eight different vegetation types.

The study was conducted in a heterogeneous landscape at the interface between two extensive South American ecoregions. It is hypothesized that in such marginal areas with a more heterogeneous habitat matrix, small mammal species might be more strictly associated with the habitat(s) fulfilling their niche requirements, and thus that microsympatry and microhabitat selection might be more pronounced than in localities of more homogeneous habitat (Lozada and Guthmann 1998, Lozada et al. 2000, Bonvicino et al. 2002, Owen 2013).

Materials and methods

Study site

The study was conducted in the Reserva Natural del Bosque Mbaracayú (RNBM), a natural reserve of ca. 65,000 ha in Canindeyú Department, northeastern Paraguay (Figure 1). This site is located within the climate type Cfa (temperate, without dry season, hot summer – Peel et al. 2007). The RNBM is located near the western margin of the Interior Atlantic Forest (IAF – depicted as tropical and subtropical moist broadleaf forest in the biome map of Olson et al. 2001), and near the southwestern extent of the Cerrado (CE) (part of the tropical and subtropical grass and shrubland biome, *ibid*). Isolated patches of CE extend into the area shown as IAF, including the eastern portion of the RNBM, where a large (ca. 6000 ha) patch is located.

Habitat imaging

A detailed digital map (Figure 1) of vegetation cover is available for the reserve, with seven of the eight vegetation types mentioned in this report being descriptive of the traditional classification system recognized by Ache indigenous people (Naidoo and Hill 2006). The other vegetation type (CE) is described in Peña-Chocarro et al. (2010). The spatial mapping was based on a Landsat 7 TM satellite image of the Mbaracayú area from 28 February 2003. Thus, the vegetation classifications used in the present study are a high-resolution product of supervised classification of satellite imagery combined with extensive ground-based surveys utilizing traditional ecological knowledge (Table 1).

Rodent sampling

In August 2014, 22 line transects, each with 50 Sherman™ traps (7.6×8.9×22.9 cm, H. B. Sherman Traps, Inc., Tallahassee, FL, USA), were placed at a variety of sites throughout the reserve with the majority in IAF habitats and several in transitional and CE habitats. Traps were spaced approximately 10 m apart along a line transect. The sites were selected based on the detailed habitat map mentioned earlier (Figure 1) with the objective of sampling as many habitat types as possible. Between 20 and 30% of the traps were placed from 1 to 3 m above ground, on branches or in vines as the habitat permitted, and the remainder were on the ground. Because this was an intensive sampling effort, logistic issues precluded all lines from being in place for an equal number of nights, or all habitats from being sampled equally or proportionally. Total sampling effort was 8650 trap-nights. Details of sampling design and schedule are provided in Eastwood et al. (2018).

Standard tissue specimens were collected from each captured rodent and frozen in liquid nitrogen, and tissue specimens not consumed in analyses will be deposited in the frozen tissue collections of the Natural Science Research Lab of The Museum, Texas Tech University. Voucher specimens were prepared as fluid-preserved with skull extracted and cleaned, are temporarily housed in the collections of RDO, and will be deposited in the Museo Nacional de Historia Natural del Paraguay. Field identifications of specimens were confirmed or corrected by examination of the skulls, and many were also confirmed from sequences of cytochrome B (*cyt B*) and/or cytochrome C oxidase I (*COI*) genes, as described in Eastwood et al. (2018) (data not shown, sequences available from CBJ on request). Sigmodontine rodent taxonomy follows D'Elía and Pardiñas (2015) and authors therein.

Coordinates were taken at each capture site with a Garmin GPS model 62stc, which was consistent within ca. 3 m under the dense canopy foliage of this forest. Using these coordinates, habitat type was determined from the base map of Figure 1 for each point where one or more captures occurred. GPS coordinates were determined independently for each capture, and thus habitat type was determined more than once for the capture sites where multiple captures occurred. Because the coordinates recorded independently for these capture points might vary by a small amount, for two of the capture sites where habitat type was determined multiple times, two different habitat types were assigned to the same capture site, indicating that the site lay on the boundary between two habitat types [bamboo understory (BU) and riverine forest (RV); high forest (HF) and liana forest (LiF)].

Statistical analyses were conducted using BIOMstat for Windows, v. 4.0 (Rohlf and Slice 2014) and R version 3.4.4 (R Core Team 2018), which includes the *cooccur* package (Griffith et al. 2016), EMT package (Menzel 2013), and G*Power package (Faul et al. 2007). Species richness was estimated over the entire study and per habitat using the nonparametric Jackknife 1 method with 1000 replicates using EstimateS software, v 9.1.0 (Colwell 2013).

Specimens reported in this article were collected under Permiso de Colecta Científica N°. 011/2014, issued by the Secretaría del Ambiente, Paraguay. Animals which were collected were euthanized following the Animal Care and Use Committee guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (Sikes et al. 2011). All animal procedures were approved (Approval No. 14024-03) by the Texas Tech University Institutional Animal Care and Use Committee (IACUC), which follows the 8th Edition of the Guide for the Care and Use of Laboratory Animals (Guide), NRC 2011. The study did not involve endangered or protected species.

Microsympatry analyses

Microsympatry was analyzed by calculating the joint probability of species co-occurring at the same trap site for all species pairs. The exact probability of observing more extreme co-occurrence frequencies (a two-tailed test) was calculated, and used to classify the observed frequency of association between two species as positive, negative, or random (“*cooccur*” package in R, Griffith et al. 2016). Thus, we tested the null hypothesis of random species co-occurrence patterns, where expected capture frequencies are based on observed captures. Our data are presence-only data, the capture sites are not spatially explicit, and habitat is the only covariate recorded; therefore, we believe this reduced model is most appropriate to apply (compared to generalized linear models).

As the analysis used capture site as the experimental unit, and multiple captures of the same species at a given trap station were possible, we created a conspecific dummy variable for each species to indicate the presence/ absence of conspecifics at a given trap station (i.e. more than one of a given species). For example, the datum for a trap station at which two *Hylaeamys megacephalus* (Fischer 1814) and three *Akodon montensis* Thomas 1913 were encountered would include the presence of each species as well as the presence of conspecific dummy variable of each species at that site, whereas a trap station at which two *A. montensis* and one *Oligoryzomys nigripes* (Olfers 1818) were captured would count the presence of each species as well as the presence of the conspecific *A. montensis* dummy variable. If more than two individuals of the same species were captured at a given trap station, the data were recorded as the presence of that species as well as the presence of a conspecific. Species associations were tested for only the three predominant species at the study sites, as explained in the results.

Microsympatry associations (random, positive, or negative) of these rodents may be evaluated as a null hypothesis (H_0) and a series of alternate hypotheses (H_1 to H_6). Each alternate hypothesis may be characterized as a behavioral response to the presence of another individual (either conspecific or of another species) and/or as an expression of habitat selection. The null hypothesis (H_0) is that individuals of a species are captured at

randomly expected frequencies with conspecifics and with other species. We evaluated microsympatry occurrences with respect to the null hypothesis and the following six alternate hypotheses.

If individuals of a species are captured less frequently than expected with conspecifics, then:

H₁: it is a territorial species (a behavioral response).

If individuals of a species are captured more frequently than expected with conspecifics, then:

H₂: it is a social (albeit perhaps temporarily, e.g. during courtship and mating) and/or non-territorial species (behavioral response);

H₃: they are actively selecting a particular microhabitat (habitat selection);

Note: both H₂ and H₃ might be valid.

If individuals of a species are captured less frequently than expected at the same sites as one or more other species, then:

H₄: they are actively avoiding encountering the other species (behavioral response);

H₅: they are selecting different microhabitats (habitat selection); Note: both H₄ and H₅ might be valid.

Finally, if individuals of a species are encountered at the same sites as another species more often than expected, then:

H₆: the two species are actively selecting the same microhabitat (habitat selection).

These six alternative hypotheses, and their characterizations as behavioral responses or habitat selection by the species, are summarized in Table 2.

Habitat selection analyses

As no metadata were recorded from empty traps, our data are “presence-only” data where the vegetation classification is the single categorical covariate. Statistical methods to determine species distribution based on presence-only data are well-documented, and typically involve generating random “pseudo-absence” data points (e.g. Busby 1991, Engler et al. 2004, Elith et al. 2006). We used the vegetation classification system mentioned earlier to calculate percent land cover for each habitat in RNBM (Naidoo and Hill 2006, Pefia-Chocarro et al. 2010), and used these values to test a null hypothesis of random species distribution at RNBM. To test whether a given species showed a pattern of microhabitat association different from random based on habitat availability, a multinomial exact test was utilized (R package EMT, using 100,000 Monte Carlo simulations to estimate the probabilities and Pearson’s residuals to calculate differences from expected). If the null hypothesis was rejected for the goodness-of-fit of a given species distribution, a *post hoc* exact binomial test was used to test whether the observed frequency at a given habitat against all other habitats differed from random. p-Values were adjusted using the Bonferroni method (Dunn 1961). This method, using percent land cover to calculate expected values, is fundamentally the same as generating pseudo-absence data points, with the exception that

we employ an exact test. By adjusting for multiple comparisons, our inferences are more conservative than other approaches, which is advisable given the study design.

Microsympatry in microhabitats

To test whether species co-occurrence patterns are consistent across habitats, the pairwise probabilistic joint species co-occurrence analysis was performed as described earlier, per habitat. In these analyses, we tested only the three most abundant species captured in four habitats. Species pairs were tested as described earlier, where the trap station was considered the experimental unit.

Results

Estimation of species richness and sampling effort

Sigmodontine rodents of 11 species were captured and collected over 20 nights from the line transects. The 417 captures were recorded from 294 capture sites, and the number of captures at a trap site varied from one to six rodents. Eight (<2%) of the captures were in traps placed above the ground, and these included only *Akodon montensis* and *Hylaeamys megacephalus*, both of which were captured in abundance in ground-level traps. Thus, vertical stratification was not considered to be a confounding factor in our analyses.

The captures were associated with eight habitat types (Table 3). The estimated species richness curve [Jackknife 1 \pm standard deviation (SD) = 14.8 \pm 1.7] suggested that further sampling would likely reveal more species (Figure 2). The species accumulation curves per habitat (not shown) and the species richness estimators (Table 3) suggest that, although sampling was not exhaustive, sampling was representative in that the Jackknife 1 species richness estimates closely matched the observed species richness in seven of the eight habitats (within one species of observed).

Microsympatry (species co-occurrences)

Seventy-seven of the 294 capture sites had two to six captures of eight of the 11 species [*Akodon montensis*, *Calomys calossus* (Rengger 1830), *Hylaeamys megacephalus*, *Nectomys squamipes*, *Oligoryzomys mattogrossae* (J. A. Allen 1916), *Oligoryzomys nigripes*, *Scapteromys aquaticus* (Fischer 1814), and *S. angouya* (Thomas 1920)], and these are the cases that we used to analyze microsympatry. These captures occurred in six of the eight habitats sampled [2/14 sites in bamboo forest (BF), 26/90 in BU, 24/103 in HF, 17/41 in LiF, 2/6 in meadow/grassland (MG), and 6/33 in RV]. Due to low observed frequencies of eight of the 11 species (which together made up 4.3% of total captures) (Figure 3A; Table 3), we considered species co-occurrence for only the three most abundant species (*A. montensis*, *H. megacephalus*, and *O. nigripes*), which represented 95.7% of the total captures. We found negative associations between each of the three different-species pairings: *A. montensis* and *H. megacephalus*, *A. montensis* and *O. nigripes*, and *H. megacephalus* and *O. nigripes* (Figure 3B). That is, these three species pairs were found to occur less frequently at the same capture site than expected based on the joint probability of co-occurrence. We also analyzed conspecific co-occurrence of these three species and found that each is positively associated with its conspecifics (Figure 3A). As discussed in Griffith

et al. (2016), the large number of capture sites allowed high statistical power to support these significant species pair associations ($1-\beta > 0.99$).

Microhabitat selection

The number of captures in a vegetation type varied from four (CE) to 134 (HF). The number of captures of a species varied from one [*Cerradomys maracajuensis* (Langguth and Bonvicino 2002), *Delomys dorsalis* (Hensel 1873), *Scapteromys aquaticus*] to 299 (*Akodon montensis*). Table 3 lists the species encountered and the habitats where they were captured.

Exact binomial tests with adjusted two-tailed p-values were performed to determine positive/negative associations of a given species with habitat under the null hypothesis of random distribution based on habitat availability (Table 4). *Akodon montensis* was found to occur more frequently than expected in LiF habitat [$p(\text{LiF}) = 0.211$, $p_{\text{adj}} = 0.009$], and less frequently than expected in BF [$p(\text{BF}) = 0.040$, $p_{\text{adj}} = 0.037$], low forest (LF) [$p(\text{LF}) = 0.017$, $p_{\text{adj}} < 0.001$], and CE habitats [$p(\text{CE}) = 0.000$, $p_{\text{adj}} < 0.001$] (Table 4). All other species-habitat associations were not different than expected under the null hypothesis of random distribution based on percent land cover. However, at least three habitat associations were significantly different from expected prior to p-value adjustment: inspection of 95% confidence intervals indicates that more *Hylaeamys megacephalus* were encountered in BU habitat and fewer in BF habitat than expected, and more *Oligoryzomys nigripes* were encountered in RV habitat than expected (Table 4). Thus, our estimates of species habitat associations are very conservative. Post-hoc analysis of achieved power indicated that the sample size of *A. montensis* enabled a high power to detect associations with specific habitats ($1-\beta > 0.98$), and the smaller sample size of *H. megacephalus* ($n = 61$) reduced the power of the significant association observed in BU habitat ($1-\beta = 0.65$).

Microsympatry site associations with habitat selection

Six allospecific species co-occurrences were observed, distributed among six habitat types (Figure 3). To determine if species co-occurrence patterns were similar across habitat types, we analyzed pairwise species co-occurrence between the three most abundant species at the four habitats (BU, HF, LiF, and RV) in which all three species were present. These results are compared to the analysis of species associations earlier, where the habitat variable was not included (Figure 3A). Negative associations between *Akodon montensis* and *Hylaeamys megacephalus* were noted in BU, HF, and LiF habitats, but the association was classified as random in RV (Figure 3B). In addition, a negative association between *A. montensis* and *Oligoryzomys nigripes* was found in HF and RV, and between *H. megacephalus* and *O. nigripes* in BU (Figure 3B). The negative association between *A. montensis* and *H. megacephalus* was the strongest association across three habitats (especially BU and HF), and the negative associations between the less abundant *O. nigripes* and other species were weak (based on effect sizes, data not shown). In general, the RV had overall weak associations, compared to the HF habitat, with only a negative association between *A. montensis* and *O. nigripes* detected.

Discussion

Each of the three most abundant species exhibited positive associations with conspecifics and was negatively associated with the other two species. Thus, these results do not support H_0 (random association), H_1 (avoidance of conspecifics), or H_6 (positive association with other species) (Table 5). Typically, probabilistic tests of species associations analyze the presence/absence of a species on a larger scale (e.g. per habitat), and have not evaluated fine-scale associations of individuals with conspecifics. We tested these hypotheses specifically by analyzing species pair associations per capture site, which allowed us to detect significant associations between individuals.

Akodon montensis, *Hylaeamys megacephalus*, and *Oligoryzomys nigripes* were each positively associated with conspecifics, thus supporting either H_2 or H_3 , and negatively associated with each of the other two species (support for H_4 or H_5). In the microhabitat analyses, *A. montensis*, *H. megacephalus*, and *O. nigripes* were positively associated (prior to the Bonferroni adjustment of p values) with three different habitats (LiF, BU, and RV, respectively). Taken together, these two analyses strongly suggest that the lack of co-occurrence among these three species is due to differing habitat selection.

The final question we addressed was whether the instances of microsympatry for each of the three species occurred more or less often in particular habitats. In other words, broad habitat associations may be correlated with species co-occurrence on a finer scale, and may provide insight into whether interspecific behavioral responses are associated with particular habitats in this community. In general, we found that microhabitat does affect the tendencies of each species to co-occur. For example, we detected negative interspecific co-occurrences with *Akodon montensis* in all four habitats, which may suggest that *A. montensis* is a behaviorally dominant species. However, *Hylaeamys megacephalus* was the only species which was positively associated with BU, and the other two species tended to avoid *H. megacephalus* in this habitat. Similarly, *Oligoryzomys nigripes* was the only species positively associated with RV, and we detected a negative co-occurrence pattern between *O. nigripes* and *A. montensis* in this habitat. Thus, if *A. montensis* is a behaviorally dominant species, then perhaps *H. megacephalus* and *O. nigripes* were able to overcome the social dominance of *A. montensis* in BU and RV habitats, respectively.

Interestingly, no species showed statistical over- or underabundance in the HF, yet on a fine scale *Akodon montensis* was negatively associated with *Hylaeamys megacephalus* and *Oligoryzomys nigripes* in this habitat. Therefore, perhaps niche partitioning facilitated species co-existence in the HF habitat in contrast to other habitats. Collectively, the data suggest that if a species exhibits a positive association with a habitat, then there is a greater likelihood of observing negative co-occurrence with other species in that habitat. In other words, there is evidence that interspecific behavioral responses are important determinants of species habitat selection in this community.

We limited our analysis to habitats in which the three predominant species co-occurred, although we note that the CE, BF, and LF habitats may be interesting habitats in which to test this hypothesis, as *Akodon montensis* was negatively associated with these habitats and

at least one of the other two species was not captured there. Calhoun (1963) described the importance of behavioral responses, including both intra- and interspecific dominance hierarchies, in small mammals. Future studies should investigate the interspecific social dominance in sigmodontine communities, and our data suggest that habitat would be an important covariate in interpreting these interactions.

A limited number of studies have evaluated microsympatry in sigmodontine rodents (e.g. Oliveira et al. 2014), or the ramifications of it (e.g. in zoonosis maintenance – Allen et al. 2009, Chu et al. 2009, Olival et al. 2017). Studies of small-scale or microhabitat associations in these rodents are numerous (Lozada and Guthmann 1998, Lozada et al. 2000, Lacher and Alho 2001, Dalmagro and Vieira 2005, Goodin et al. 2009, Owen et al. 2010, Melo et al. 2011, 2013, Delciellos et al. 2016). However, to the best of our knowledge, no study has been reported previously which investigates these two very important components of sigmodontine community structure together, or reports that microhabitat differences significantly affect microsympatry probabilities.

Many of the habitat preferences reported herein corroborate or complement those of previous studies, summarized by Pardiñas et al. (2015), Percequillo (2015), and Weksler and Bonvicino (2015). For example, our results show that *Akodon montensis*, *Hylaeamys megacephalus*, and *Oligoryzomys nigripes* exhibit negative microsympatric associations with each other. Moreover, their microhabitat associations (*A. montensis* with HF, *H. megacephalus* with BU) and avoidances (*A. montensis* with RV and “other” habitats) do not indicate responses to any of the same habitats. Nevertheless, the co-occurrence both of *A. montensis* with *H. megacephalus*, and of *A. montensis* with *O. nigripes*, at the same capture sites was noted in four different habitats, more than that was found for any other species pair. This highlights the importance of the report by Chu et al. (2009) of microsympatry of *A. montensis* with *O. nigripes*. Each of these species harbors a distinct strain of orthohantavirus and hence their sympatry can lead to spillover and reassortment. Understanding patterns of microsympatry and microhabitat selection among rodent species carrying known zoonotic virus, such as *A. montensis* and species of *Oligoryzomys*, can help improve modeling efforts to predict potential outbreaks in rodents and the potential for spillover and disease in human populations (Allen et al. 2012, Olival et al. 2017).

It is important to note that the eight habitat designations in this study are based primarily on traditional ecological knowledge, a fundamental difference from previous studies of small mammal habitat associations. Thus, our habitat categories correspond only partially with those based on measurements of vegetation structure, and some of our results may appear to contradict earlier reports. For example, Goodin et al. (2009) examined microhabitat associations of *Akodon montensis* using a suite of 24 vegetation and environmental variables, of which 10 were included in their final logistic model of microhabitat associations. They reported that *A. montensis* was positively associated with the small bamboo *Merostachys clausenii*, whereas we found no significant association of *A. montensis* with BU habitat, which is dominated by this bamboo species. We are hesitant to state that one of these approaches is superior to the other, or that one result is more valid or informative than the other. We instead note that these different sources of habitat information enable us to ask different questions, although the differences may be subtle. In much the

same way that multi-scale approaches to small mammal community composition provide complementary insights (Hannibal et al. 2018), utilization of Traditional Ecological Knowledge combined with more “modern” methods can provide useful insight into mammalian ecology (Zuercher et al. 2003). Thus, our results should be viewed as complementary, rather than contradictory to reports by other authors. Given that we are fundamentally attempting to understand the environment as closely as possible to the way the small mammals are experiencing it, it would be difficult to conclude that quantitative vegetation structure data would be more appropriate than traditional ecological knowledge, or *vice versa*.

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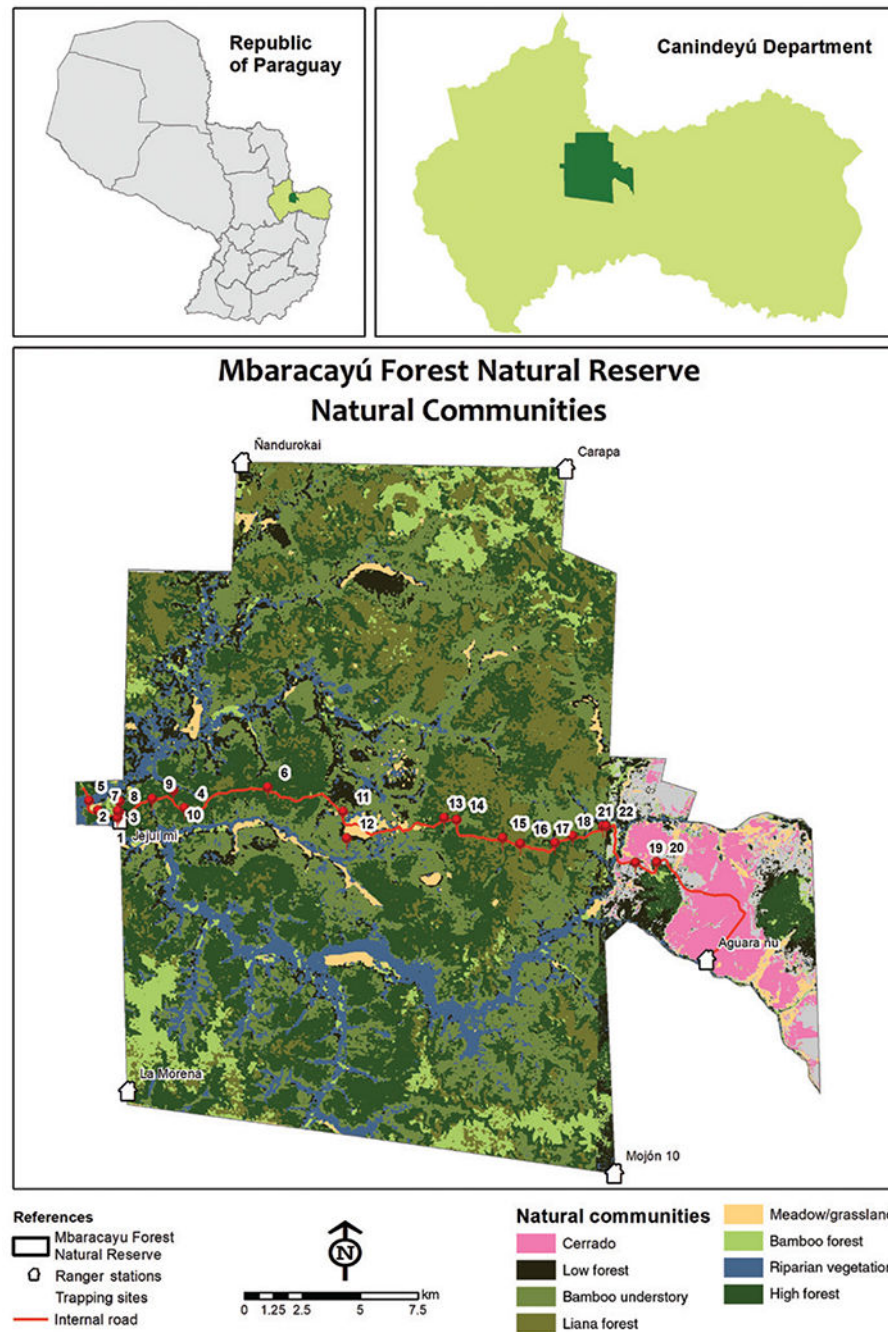


Figure 1: Map of Reserva Natural del Bosque Mbaracayú, showing location within Paraguay, and vegetation cover based on supervised classification of satellite imagery combined with extensive ground sampling using habitat categorizations of local Ache (indigenous) people. Numbered points indicate locations of the 22 trap lines of 50 trap stations each. See Materials and methods for more detailed information regarding the trap lines. Vegetation cover categories based on data from Naidoo and Hill (2006) and Peña-Chocarro et al. (2010).

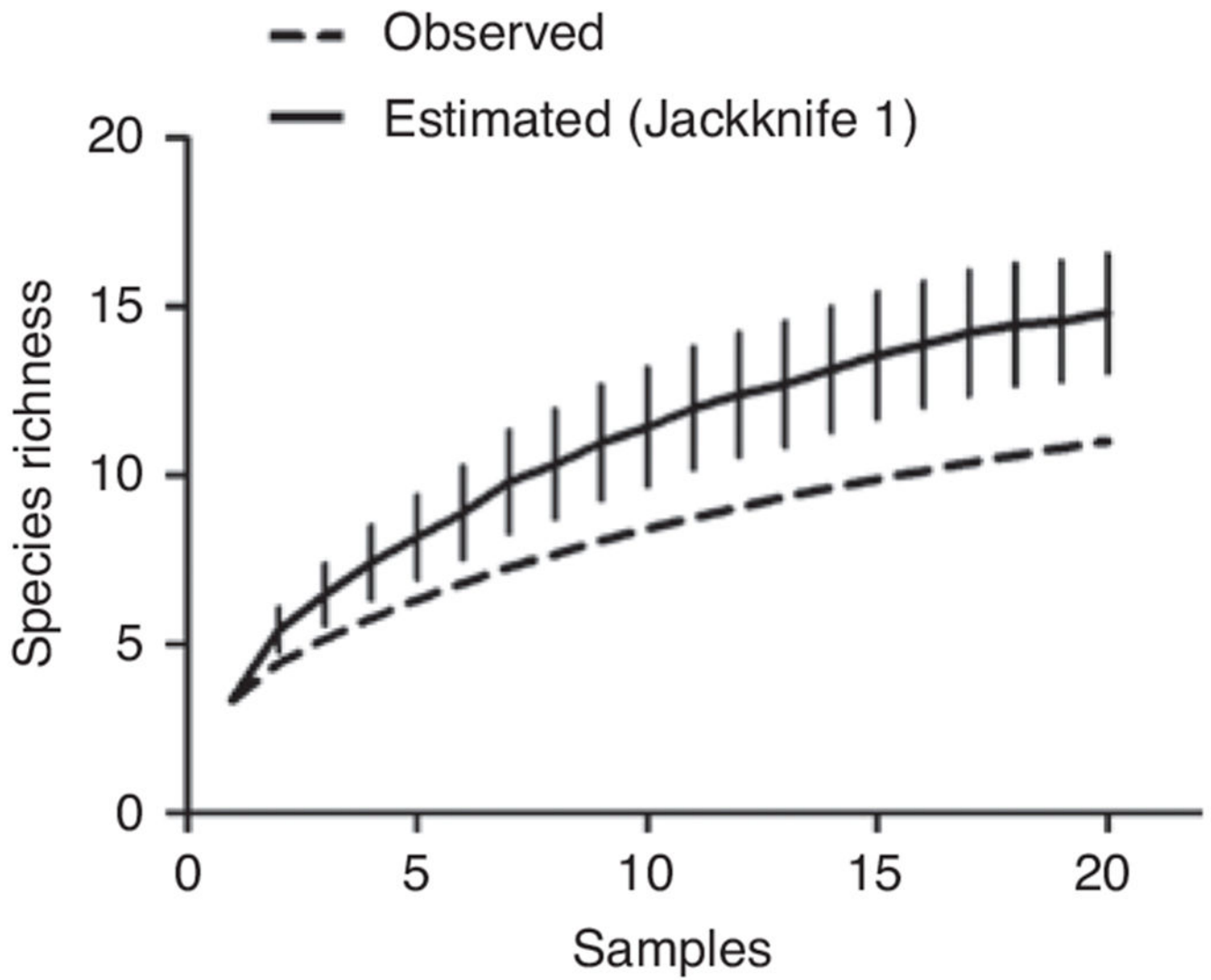


Figure 2: Observed species accumulation curve and estimated species richness (Jackknife 1 with standard deviation) of sigmodontine rodents captured over 20 nights in various habitats at Reserva Natural del Bosque Mbaracayú, Paraguay.

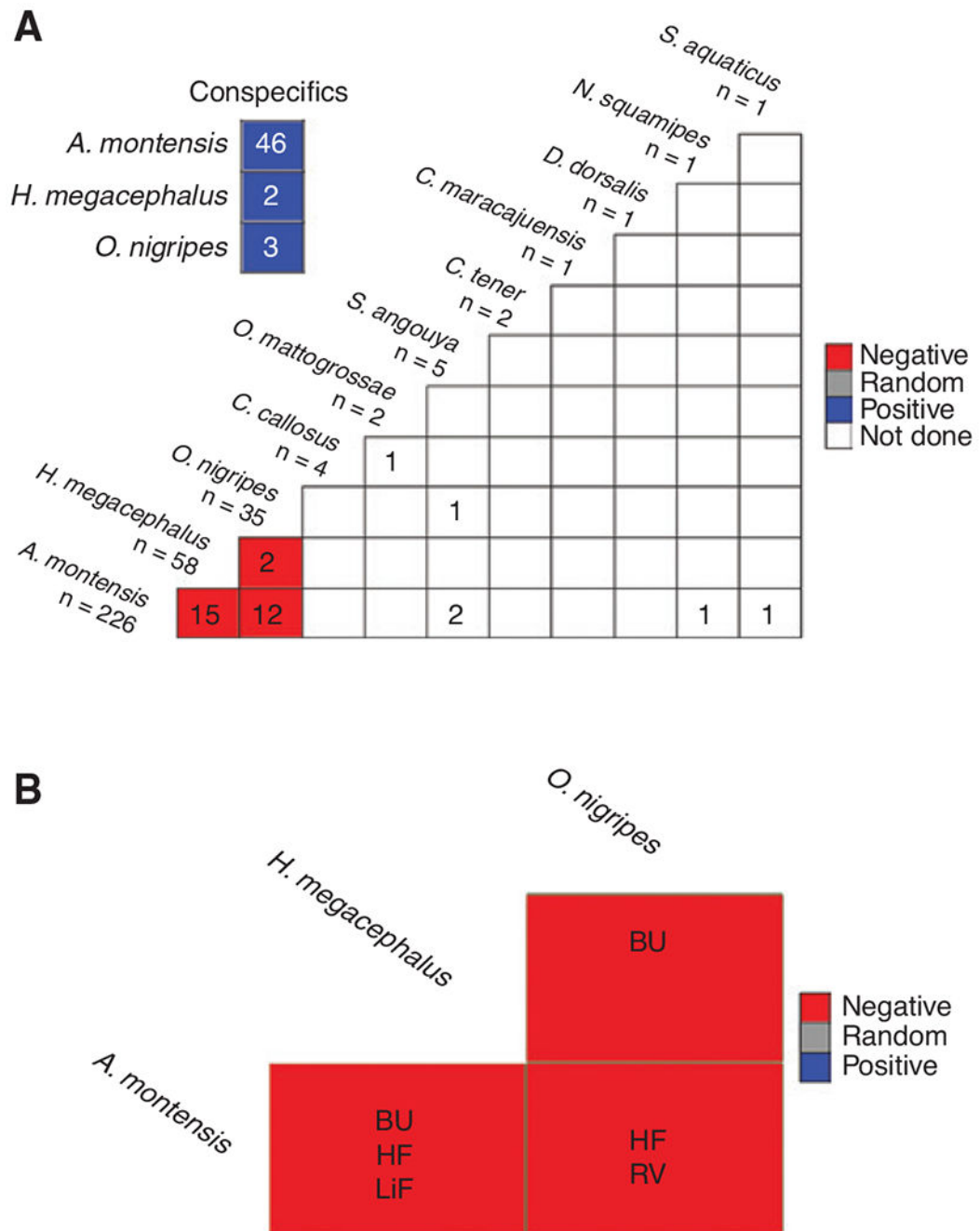


Figure 3: Species co-occurrence matrix based on probabilistic species co-occurrence (Griffith et al. 2016). Squares are colored to indicate that species were observed to co-occur more frequently than expected (“positive” association = blue), less frequently than expected (“negative” association = red), or were observed to co-occur randomly (gray). (A) Co-occurrence of all species pairs including low abundance species for which the co-occurrence analysis was not done (white squares). The number of trap sites where species occurred is given below species name. The number of observed co-occurrence trap sites is given in

squares (blank squares = no observed co-occurrence). Figure inset displays conspecific co-occurrence for the three most abundant species. (B) Species co-occurrence of the three most abundant species. Species co-occurrence at three habitats was analyzed separately. Species pairs had a negative association in habitats listed in squares (“BU” = bamboo understory forest, “HF” = high forest, “LiF” = liana forest, “RV” = riverine forest) and otherwise had a random association in those habitats.

Table 1:

Eight vegetation (= habitat) types evaluated in this study, and percentage of total area of the reserve represented by each vegetation type.

| Symbol | Name | Percent | Description |
|--------|----------------------------------|---------|---|
| BF | Big bamboo forest | 8.4 | Few trees and a predominance of <i>Guadua angustifolia</i> bamboo that can reach 10–15 m in height |
| BU | Bamboo understory forest | 23.5 | Canopy trees 15–25 m in height, and with a thick undergrowth of <i>Merosyachys clausenii</i> bamboo, which grows 1–3 m in height |
| CE | Cerrado (<i>sensu stricto</i>) | 3.8 | Wide range of open woodland, open scrub, and grassland forms, with grasses, palms, and legumes |
| HF | High forest | 31.0 | Dominated by trees reaching heights of 25 m or greater; ground cover is sparse, and composed of ferns, heliconias, and bromeliads |
| LF | Low forest | 14.2 | Most trees less than 15 m high, and less than 10 cm in diameter at breast height, with ground cover dominated by bromeliads |
| LIF | Liana (vine) forest | 7.2 | Medium to high forests with an abundance of lianas in the understory |
| MG | Meadow (grassland) | 2.5 | Few trees and a predominance of grassy vegetation; usually wet for at least part of the year |
| RV | Riverine forest | 9.4 | Locational, reflects proximity to a geographical feature, rather than a unique vegetation community |

Description of Cerrado vegetation from Peña-Chocarro et al. (2010), and others from Naidoo and Hill (2006).

Table 2:

Six alternative hypotheses for evaluating results of tests for association.

| With | Frequency of co-occurrence | |
|---------------|----------------------------|--------------------|
| | Less | More |
| Conspecifics | H ₁ (B) | H ₂ (B) |
| | | H ₃ (H) |
| Other species | H ₄ (B) | |
| | H ₅ (H) | H ₆ (H) |

Each hypothesis is defined in the text, and is characterized in the table as pertaining primarily to behavioral response (B) or habitat selection (H) by the species.

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Sigmodontine species encountered, with numbers captured per habitat type (BF, bamboo forest; BU, bamboo forest; CE, Cerrado; HF, high forest; LF, low forest; LiF, liana understory forest; MG, meadow/grassland; RV, riverine forest).

Table 3:

| Species | Habitat | | | | | | | | | | Total |
|----------------------------------|---------------|---------------|-----|---------------|---------------|-----|-----|---------------|--|--|----------------|
| | BF | BU | CE | HF | LF | LiF | MG | RV | | | |
| <i>Akodon montensis</i> | 12 | 78 | 0 | 107 | 5 | 63 | 5 | 29 | | | 299 |
| <i>Calomys callosus</i> | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | | | 4 |
| <i>Calomys tener</i> | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | | | 2 |
| <i>Cerradomys maracajuensis</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | | | 1 |
| <i>Delomys dorsalis</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | | | 1 |
| <i>Hylaeamys megalcephalus</i> | 0 | 23 | 0 | 16 | 2 | 12 | 3 | 5 | | | 61 |
| <i>Nectomys squamipes</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | | | 2 |
| <i>Oligoryzomys maitogrossae</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | | | 2 |
| <i>Oligoryzomys nigripes</i> | 3 | 13 | 0 | 12 | 0 | 2 | 0 | 9 | | | 39 |
| <i>Scapteromys aquaticus</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | | | 1 |
| <i>Sooretamys angouya</i> | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | | | 5 |
| Total | 16 | 121 | 4 | 136 | 8 | 77 | 8 | 47 | | | 417 |
| S_{obs} | 3 | 6 | 4 | 4 | 3 | 3 | 2 | 6 | | | 11 |
| S_{est} (Jackknife 1 \pm SD) | 3.9 ± 0.9 | 7.9 ± 1.3 | 7.0 | 4.9 ± 0.9 | 4.7 ± 1.0 | 3.0 | 2.0 | 8.8 ± 2.0 | | | 14.8 ± 1.7 |

Capture incidences were used to compute observed species richness (S_{obs}) and the nonparametric Jackknife 1 \pm standard deviation (SD) was used to estimate total species richness (S_{est}) (SD could not be calculated at CE, LiF, and MG habitats due to small sample sizes).

Table 4:

Observed frequency of species captured within microhabitats in the sampling grids.

| Habitat | Land cover | <i>A. montensis</i> | <i>H. megacephalus</i> | <i>O. nigripes</i> |
|---------|--------------|--|-----------------------------|-----------------------------|
| BF | 0.084 | 0.040 (0.021–0.069) [–] | 0.000 (0.000, 0.059) | 0.077 (0.016, 0.209) |
| BU | 0.235 | 0.261 (0.212, 0.315) | 0.377 (0.256, 0.510) | 0.333 (0.191, 0.502) |
| CE | 0.038 | 0.000 (0.000, 0.012) [–] | 0.000 (0.000, 0.059) | 0.000 (0.000, 0.090) |
| HF | 0.310 | 0.358 (0.304, 0.415) | 0.262 (0.158, 0.391) | 0.308 (0.170, 0.476) |
| LiF | 0.142 | 0.211 (0.166, 0.261) ^{+/#} | 0.197 (0.106, 0.318) | 0.051 (0.006, 0.173) |
| LF | 0.072 | 0.017 (0.005, 0.039) [–] | 0.033 (0.004, 0.113) | 0.000 (0.000, 0.090) |
| MG | 0.025 | 0.017 (0.005, 0.039) | 0.049 (0.010, 0.137) | 0.000 (0.000, 0.090) |
| RV | 0.094 | 0.097 (0.066, 0.136) | 0.082 (0.027, 0.181) | 0.231 (0.111, 0.393) |

Habitats are bamboo forest (BF), bamboo understory (BU), Cerrado (CE), high forest (HF), liana forest (LiF), low forest (LF), meadow/grassland (MG), and riverine forest (RV). Observed probabilities in bold face indicate observed habitat associations are different than expected occurrence based on percent land cover (95% confidence intervals calculated from quantiles of the beta distribution in parentheses). Superscripted “plus” or “minus” signs indicate significant (– or +, Padj 0.05; # or –# or ––, Padj 0.01; +++ or –––, Padj 0.001) positive or negative associations, respectively, by exact binomial tests with p-values adjusted by the Bonferroni method.

Potentially applicable hypotheses explaining associations among three most abundant species.

Table 5:

| Species 1 | Species 2 | Hypotheses to explain microsympatry of species pairs | | | | | | |
|------------------------|----------------------------|--|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|
| | | H ₁ (B) | H ₂ (B) | H ₃ (B) | H ₃ (H) | H ₄ (B) | H ₅ (H) | H ₆ (H) |
| <i>A. montensis</i> | <i>A. montensis</i> (+) | X | | X | | | | |
| | <i>H. megacephalus</i> (-) | | | X | | X | | |
| | <i>O. nigripes</i> (-) | | | X | | X | | |
| <i>H. megacephalus</i> | <i>H. megacephalus</i> (+) | X | | X | | | | |
| | <i>O. nigripes</i> (-) | | | | | X | | |
| <i>O. nigripes</i> | <i>O. nigripes</i> (+) | X | | X | | | | |

For each of the six species pairs, associations with the other species are indicated, and whether the associations are positive or negative. The applicable hypotheses are indicated for each species pair, and each of these is designated as either a behavioral response (B) or habitat selection (H) affecting the species' distribution in the sampling area. See text and Table 3 for description of each hypothesis.