Temporal variation in small nonvolant mammal (Cricetidae and Didelphidae) microhabitat associations in the Upper Paraná Atlantic Forest

Variación temporal en asociaciones de microhábitats de pequeños mamíferos no voladores (Cricetidae y Didelphidae) en el Bosque Atlántico del Alto Paraná

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Abstract: Many questions concerning habitat preferences of Neotropical small mammals remain unanswered. These questions include where the animal lives within and among the available habitats, and the temporal (seasonal and interannual) variation in the habitat associations. The objectives of this research were: (1) to determine the associations of non-volant small mammal species (Rodentia and Didelphimorphia) with specific microhabitat characteristics including vegetation structure in an area near the western boundary of the Upper Paraná Atlantic Forest, and (2) to evaluate seasonal and interannual variation in those associations. Three grids were sampled in three seasons (Dry, Wet, Variable) during two years (2015-2017). The four predominant small mammal species (*Gracilinanus agilis*, *Akodon montensis*, *Hylaeamys megacephalus*, and *Oligoryzomys nigripes*) were evaluated for seasonal and interannual variation in habitat preferences. Each of the four exhibited seasonal and/or interannual variation in microhabitat preferences for three to six of the 17 environmental variables analyzed. This is the first study to explicitly evaluate temporal variation in habitat associations of small mammals in the Atlantic Forest ecoregion. The temporal patterns of habitat association among these four predominant species reveal a complex spatially and temporally dynamic composition and structure in this small mammal community.

Keywords: El Niño. Environmental variables. Interannual variation. Paraguay. Seasonal variation. Vegetation structure.

Resumen: Muchas preguntas sobre las preferencias de hábitat de los pequeños mamíferos neotropicales siguen sin respuesta. Estas preguntas incluyen dónde vive el animal dentro y entre los hábitats disponibles, y la variación temporal (estacional e interanual) en las asociaciones de hábitats. Los objetivos de esta investigación fueron: (1) determinar las asociaciones de especies de mamíferos pequeños no voladores (Rodentia y Didelphimorphia) con características específicas de microhábitat, incluida la estructura de la vegetación en un área cerca del límite occidental del Bosque Atlántico del Alto Paraná, y (2) evaluar la variación estacional e interanual en estas asociaciones. Se tomaron muestras de tres parcelas en tres épocas (Seca, Húmeda, Variable) durante dos años (2015-2017). Cada uno de los cuatro pequeños mamíferos predominantes (*Gracilinanus agilis, Akodon montensis, Hylaeamys megacephalus* y *Oligoryzomys nigripes*) exhibió variación estacional y/o interanual en las preferencias de microhábitats para tres a seis de las 17 variables ambientales analizadas. Este es el primer estudio que evalúa explícitamente la variación temporal en las asociaciones de hábitat de pequeños mamíferos en la ecorregión del Bosque Atlántico. Los patrones temporales de asociación de hábitat entre estas cuatro especies predominantes revelan una estructura compleja espacial y temporalmente dinámica en esta comunidad de pequeños mamíferos.

Palabras claves: El Niño. Variables ambientales. Variación interanual. Paraguay. Variación estacional. Estructura de la vegetación.

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INTRODUCTION

In the Neotropics, sigmodontine rodents and didelphid marsupials often comprise rich components of the mammal communities (Emmons & Feer, 1997; Solari *et al*., 2001; D'Elía & Pardiñas, 2015; Owen *et al*., 2018). However, many questions concerning habitat preferences remain unanswered. These questions include where the animal lives within the habitat matrix, and the temporal (seasonal and interannual) variation in the habitat associations (Owen *et al*., 2019). Answers to these questions would enable better understanding of the composition and dynamics of marsupial and rodent communities on a local scale.

Over the past two decades, several studies have investigated habitat associations of small terrestrial mammals within the Southern Cone (primarily Brazil) of South America. Delciellos *et al*. (2016) concluded that habitat structure was an important determinant of mammal assemblages in fragments of Atlantic Forest in Rio de Janeiro state, Brazil. Distinct microhabitat associations were reported for a variety of species in southern Amazonia (Santos-Filho *et al*., 2008), secondary Atlantic Forest remnants (Püttker *et al*., 2008), a western Atlantic Forest region (Owen *et al*., 2010), a southern Atlantic Forest site (Melo *et al*., 2011, 2013), the Pampas region in southern Brazil (Sponchiado *et al*., 2012), and in the southwestern Cerrado (Smith *et al*., 2012; Carmignotto *et al*., 2014).

In this study, particular interest was focused on four small mammal species which are encountered abundantly in the *Reserva Natural del Bosque Mbaracayú* (RNBM), in the Upper Paraná Atlantic Forest (UPAF) of Paraguay, which is near the western limit of the Atlantic Forest (Eastwood *et al*., 2018; Barreto Cáceres & Owen, 2019; Owen *et al*., 2020). *Gracilinanus agilis* (Burmeister, 1854) is a marsupial distributed in forests south of the Amazon Basin, east of the Andes and as far south as central Paraguay. The RNBM is near the southern limit of its distribution. Santos-Filho *et al*. (2008) reported that *G. agilis* was found both in forest and into a pasture matrix, and it is considered a generalist species. It is primarily arboreal (Smith *et al*., 2012) and utilizes dense understory vegetation of branches and vines (Carmignotto *et al*., 2015).

The rodent *Akodon montensis* Thomas, 1913 is distributed throughout the Atlantic Forest regions of Brazil, northeastern Argentina and eastern Paraguay, and into gallery forests of the Brazilian Cerrado (Pardiñas *et al*., 2016). The RNBM is near the western limit of its distribution at this latitude. *Akodon montensis* has been characterized as terrestrial (Cademartori *et al*., 2002; Vieira & Monteiro-Filho, 2003; Naxara *et al*., 2009), although it also exhibits limited climbing behavior (Machado *et al*., 2019). It is not vulnerable to habitat fragmentation (Püttker *et al*., 2008; Jordão *et al*., 2010) and is tolerant of habitat degradation (Barreto Cáceres & Owen, 2019).

Hylaeamys megacephalus (G. Fischer, 1814) is a tropical lowland forest oryzomyine, distributed from Trinidad and Tobago, the Caribbean and Atlantic coast of Venezuela and the Guianas, southward across eastern Amazonia and the Cerrado to central eastern Paraguay. The RNBM is near the southern limit of its distribution. *Hylaeamys megacephalus* is a generalist species with high habitat tolerance, inhabiting primary, secondary and degraded forests (Percequillo *et al*., 2016). In the Upper Paran Atlantic Forest it was encountered in all three levels of habitat degradation (Barreto Cáceres & Owen, 2019; Owen *et al*., 2019). In the same forest, Owen *et al*. (2020) found them preferentially associated with bamboo understory.

Oligoryzomys nigripes (Olfers, 1818) is a small oryzomyine distributed from northeastern Brazil through the Atlantic Forest and Cerrado ecoregions southward through eastern Paraguay and northeastern Argentina to Uruguay (Bonvicino *et al*., 2016). The RNBM is near the western limit of its distribution at this latitude. *O. nigripes* is a habitat generalist (Martin *et al*., 2012; Garcia, 2018; Owen *et al*., 2020), generally found in forested areas (Cáceres *et al*., 2011), and not vulnerable to forest fragmentation (Püttker *et al*., 2008). Owen *et al*. (2019) found this species to consistently represent around 9% of the sigmodontine rodent community on sampling grids with three different levels of forest degradation, and it did not exhibit microhabitat selection.

This study was conducted in a heterogeneous landscape at the western limit of the Atlantic Forest, an extensive South American ecoregion. Previous studies hypothesized that in such marginal areas with a more heterogeneous forest habitat mosaic, small mammal species might be more strictly associated with the habitat(s) best fulfilling their niche requirements, and thus that microhabitat preference might be more detectable than in localities of more homogeneous habitat (Lozada & Guthmann, 1998; Lozada *et al*., 2000; Bonvicino *et al*., 2002; Owen, 2013). Moreover, the close proximity of multiple microhabitats may facilitate the movement of resident small mammal species from one habitat type to another, so that they may alter their microhabitat associations through time, responding either to seasonal or irregular environmental variation between years. Finally, the four predominant species at the study site are all near their biogeographic limits, and thus may be restricted to certain habitat types within this marginal UPAF habitat. This study evaluates habitat preference explicitly on one scale, termed microhabitat, and evaluates seasonal and interannual variation in habitat associations for each of four common small-mammal species.

MATERIALS AND METHODS

STUDY SITE

The study was conducted in the *Reserva Natural del Bosque Mbaracayú* (RNBM), a natural reserve of 64,405.7 hectares that is located in Canindeyú department, northeastern Paraguay between latitudes -24.00 and -24.25 and longitudes -55.33 and -55.53 (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 Upper Paraná Atlantic Forest (UPAF), depicted as tropical and subtropical moist broadleaf forest in the biome map of Olson *et al*. (2001). The reserve comprises a mosaic of ten different habitat types, eight of which are UPAF and two of which pertain to Cerrado (Naidoo & Hill, 2006; Peña-Chocarro *et al*., 2010). This study was conducted within the mosaic of Atlantic Forest habitat types of the Reserve.

SAMPLING DESIGN AND ENVIRONMENTAL VARIABLES

Three sampling grids were established, two of 12 x 12 stations and one of 13 x 11: the centroid of Grid A (144 stations) was -24.1239, -55.5048; Grid B (143 stations) -24.1412, -55.3664; and Grid G (144 stations) -24.1306, -55.5369. Trap stations were separated by 10 m. Each grid was sampled six times for five nights during three seasons (Dry, Wet and Variable, *sensu* Owen & Camp, in press) for two years (June 2015 – March 2017). An extreme El Niño event occurred during the first of the two sampling years, with precipitation higher than average (DINAC, 2016), although maintaining the historical seasonal pattern of dry, wet and variable seasons (Figure 2).

During the first sampling session each station had one Sherman Trap™ (7.6 x 8.9 x 22.9 cm) placed on the ground and one placed 1 to 2.5 m above ground in branches or vines. All subsequent sessions included two traps placed on the ground and one above ground. Total sampling effort for the study was 36,365 trap-nights. A mixture of oats and peanut butter was used as bait in the traps, and they were rebaited each morning when checked for captures. For ease of comparing with previous studies based on this field investigation, grid designations (A, B, G) and sampling sessions (2 to 7) correspond with those in the these publications (*e.g.*, Barreto Cáceres & Owen, 2019; Owen *et al*., 2019; Sánchez-Martínez & Owen, 2020). All animals captured in the third and sixth sampling session were collected and prepared as standard voucher specimens. A total of 1,143 vouchers were examined after preparation, and all field identifications were confirmed for the four species evaluated in this paper.

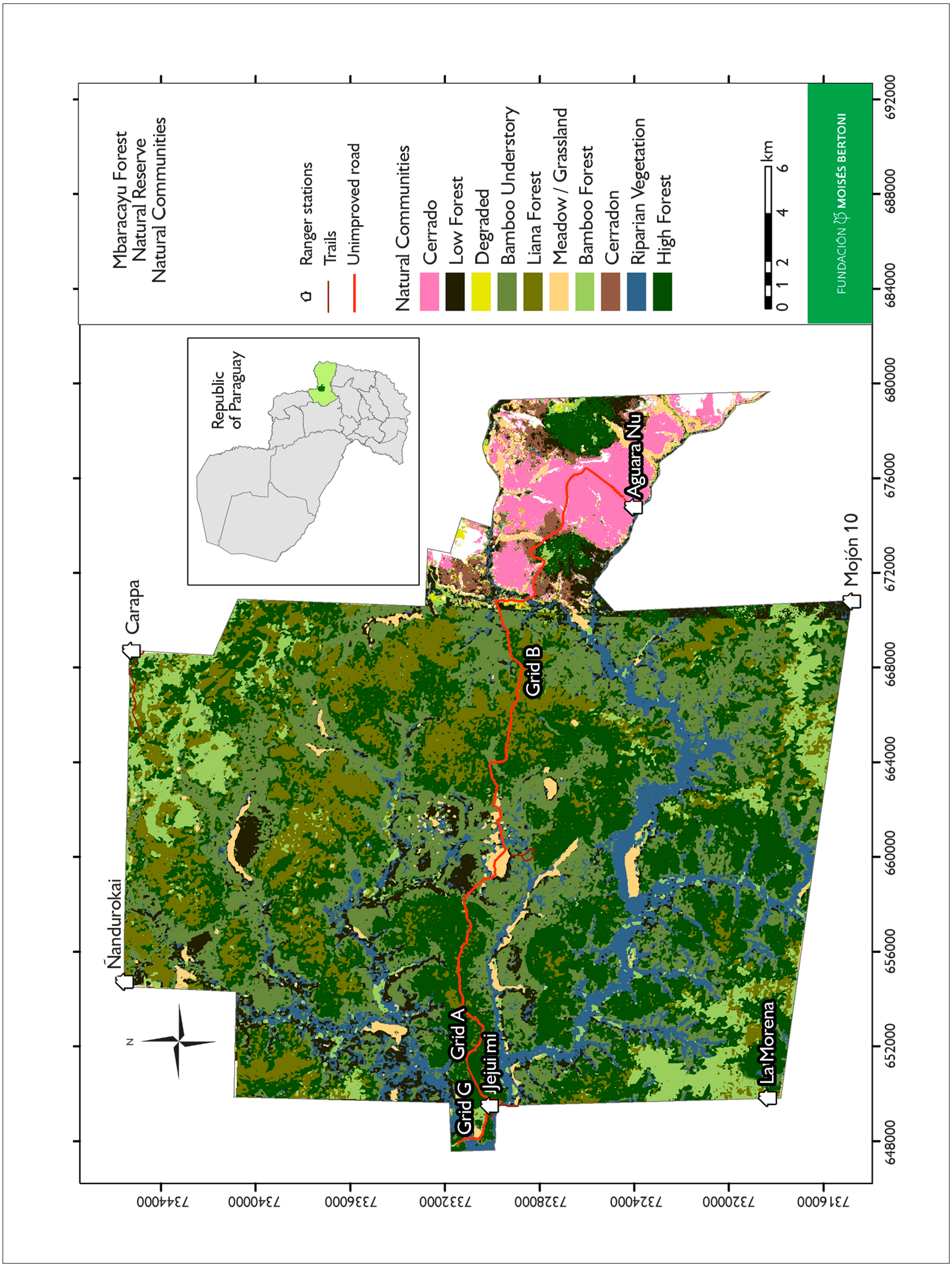

Figure 1. *Reserva Natural del Bosque Mbaracayú* (RNBM) within Canindeyú Department, Paraguay, showing complex mosaic of habitat types. See text for geographical location of the RNBM, and for precise coordinates of the three sampling grids. Map: L. Rodríguez.

In this study microhabitat is defined as the habitat immediately surrounding each trap station within the habitat matrix of the forest. In practical terms it is measured as 17 environmental variables within an area of ca. 2 m in diameter centered on each trap station (Schnell *et al*., 2010; Poindexter *et al*., 2012). Measures were recorded at each of the 431 trap stations included in the three sampling grids, during the first mammal sampling session and repeated during the second session, to ensure that seasonal variation of environmental variables could be detected. No important differences (≥ 10 % in ≥ 10 of the cases) were found between the samples taken in different seasons. Thus, data from the two seasons were averaged for each station, and the mean values were used for the analyses reported here. Three of the 17 variables were nominal, one meristic, seven were percentages and six were direct-measure continuous variables (Table 1). Sampling methods for the environmental variables are described in Schnell *et al*. (2010) and Poindexter *et al*. (2012).

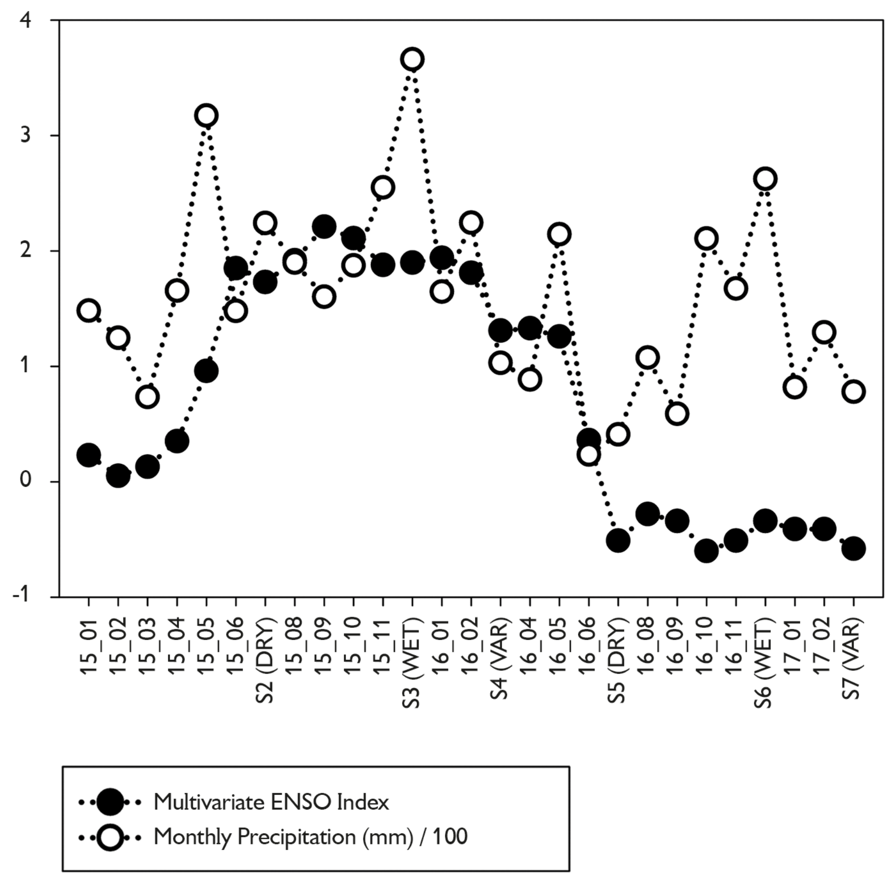

Figure 2. Multivariate ENSO Index (MEI) values and precipitation from January 2015 (approximately 6 months before first sample) through March 2017 (final sample). Abscissa is time (YR-MO), with sampling sessions 2-7 indicated in the month they occurred. MEI value shown for each month is the mean of that month and the previous month, *i.e.*, 15_01 is the mean of December 2014 and January 2015. Ordinate is MEI values (solid circles) and precipitation (open circles, in mm, divided by 100). Precipitation data from Climatic Research Unit (n. d.). MEI data from Multivariate ENSO Index (MEI) (n. d.).

Table 1. List of classification variables used to identify each capture, and the 17 environmental variables measured to characterize the microhabitat. Sampling methods for the environmental variables as described in Schnell *et al*. (2010) and Poindexter *et al*. (2012).

Variables	Description
Classification	
ID	Specific identification
Year	1 = 2015-16, 2 = 2016-17
Season	Dry (June-July), Wet (November-December), Variable (February-March)
Environmental variables	
Nominal	
Orange	1 or 0, presence or absence of *Citrus aurantium* L., 1753 (invasive species) within 10 m
Log	1 or 0, presence or absence of log (fallen tree) within 10 m
Height	1 = captured on ground, 2 = captured above ground
Meristic	
Bushes	Number of bushes within 1 m
Continuous	
Direct	
Slope	Slope of ground measured in degrees
Treedist	Distance to nearest tree
Canopy1	Height of 1st canopy
Canopy2	Height of 2nd canopy
Canopy3	Height of 3rd canopy
Maxcan	Maximum canopy height
Percentages	
Percan	Percentage closure of canopy
Woody	Percentage of 2 x 2 m quadrat covered by woody plants
Forbs	Percentage of 2 x 2 m quadrat covered by forbs
Grasses	Percentage of 2 x 2 m quadrat covered by grasses
Litter	Percentage of 2 x 2 m quadrat covered by vegetative litter
Deadwood	Percentage of 2 x 2 m quadrat covered by dead wood
Bare	Percentage of 2 x 2 m quadrat with no cover (bare ground)

SMALL MAMMAL SAMPLING

Field identification of animals and subsequent identification of prepared specimens followed keys provided in Voss & Jansa (2009) and D'Elía & Pardiñas (2015). Identifications of prepared specimens confirmed field identifications. All standard data of each captured individual were recorded: specific identification, weight, sex, reproductive status and age (adults, sub-adults or juveniles, based on external characteristics of reproductive status, juvenile or adult pelage and weight). Each animal was marked with a Passive Integrated Transponder (PIT) tag (Biomark, Inc.). Every capture was included in the analyses, as each capture was considered to be an independent expression of microhabitat preference by the species, as measured by the 17 environmental variables recorded for each station. Adults and subadults were included in the dataset but juveniles were not, as their capture location was presumed to be at least partially a function of their natal nest-site location (*i.e.*, not selected by the juvenile individual).

Animal sampling and collection were carried out under Scientific Collection Permits No. 011/2014, 132/2015 and 269/2016 (Secretary of the Environment, currently the Ministry of Environment and Sustainable Development, Paraguay), and the guidelines of the Animal Care and Use Committee of the American Society of Mammalogists (Sikes *et al*., 2011, 2016). Animal handling protocols were approved by the Institutional Animal Care and Use Committee of Texas Tech University (IACUC Approval No. 14024-03). Specimens[1] are temporarily deposited in the author's research collection, which is an accredited research collection under Approval 004/2015 by the Secretary of the Environment, Paraguay. Following research use of the specimens, they will be deposited in an accredited Paraguayan collection. Tissue which were harvested from the specimens (including blood samples from the released specimens) are deposited in the Genetic Resources Collections of the Museum of Texas Tech University (TTU).

ANALYTIC METHODS

Using environmental variables from all sites with one or more captures, Spearman correlations were calculated among all pairs of environmental variables, in order to visualize overall correlation patterns of species-environmental associations. This provides a context within which to interpret correlations among variables for which one or more species have significant seasonal or interannual variation in preferences. These correlations analyses were conducted only on the environmental variables, disregarding the species which were captured at those trap stations.

Using all capture records during all sessions for the four species being evaluated, a series of Mann-Whitney Rank Sum pairwise comparisons was used to identify significant seasonal and interannual variation. Pairwise correlations were calculated between each of the species-variable associations showing significant temporal variation. This was done separately for the suites of seasonal and interannual associations. For those species-variable pairs showing seasonal variation, Spearman Rank correlations were used to identify non-significant subsets among seasons. To visualize both the seasonal and interannual patterns of response of the four species to environmental variables, the data for each species were plotted for each variable for which the species showed significant temporal variation. A value of $P \leq 0.05$ was considered significant for all tests. All statistical tests were done using SigmaPlot™ 12.3 (Systat Software, Inc.).

RESULTS

A total of 1,614 captures (4.4% trap success) were recorded during the study, including 947 individuals and 667 recaptures. The captures included two orders (Didelphimorphia and Rodentia), two families (Didelphidae and Cricetidae) and 17 species (Table 2 and complementary material). Of the 1,614 captures, 1,554 (96.3%) were of subadult or adult animals and thus were included for the correlation analyses among environmental variables. Based on all environmental measures from all capture records, of the 136 pairwise comparisons among the 17 environmental variables, Spearman correlations were significantly positive for 38, negative for 53, and non-significant for 45 (Figure 3). The number of positive correlations ranged from zero (Capture height) to seven (Canopy2); negative correlations from one (Capture height) to seven (Canopy2); and non-significant correlations from two (Slope, Litter) to 15 (Capture height). This indicates that in general (*i.e.*, considering all species together), capture height of small mammals was independent of other environmental variables, whereas Canopy2 (height of second canopy) was either positively or negatively correlated with 14 of the 16 other environmental variables.

[1] See complementary material to this article, in a table available at link: http://editora.museu-goeldi.br/bn/artigos/cnv15n3_2020/Owen_tableS1.pdf

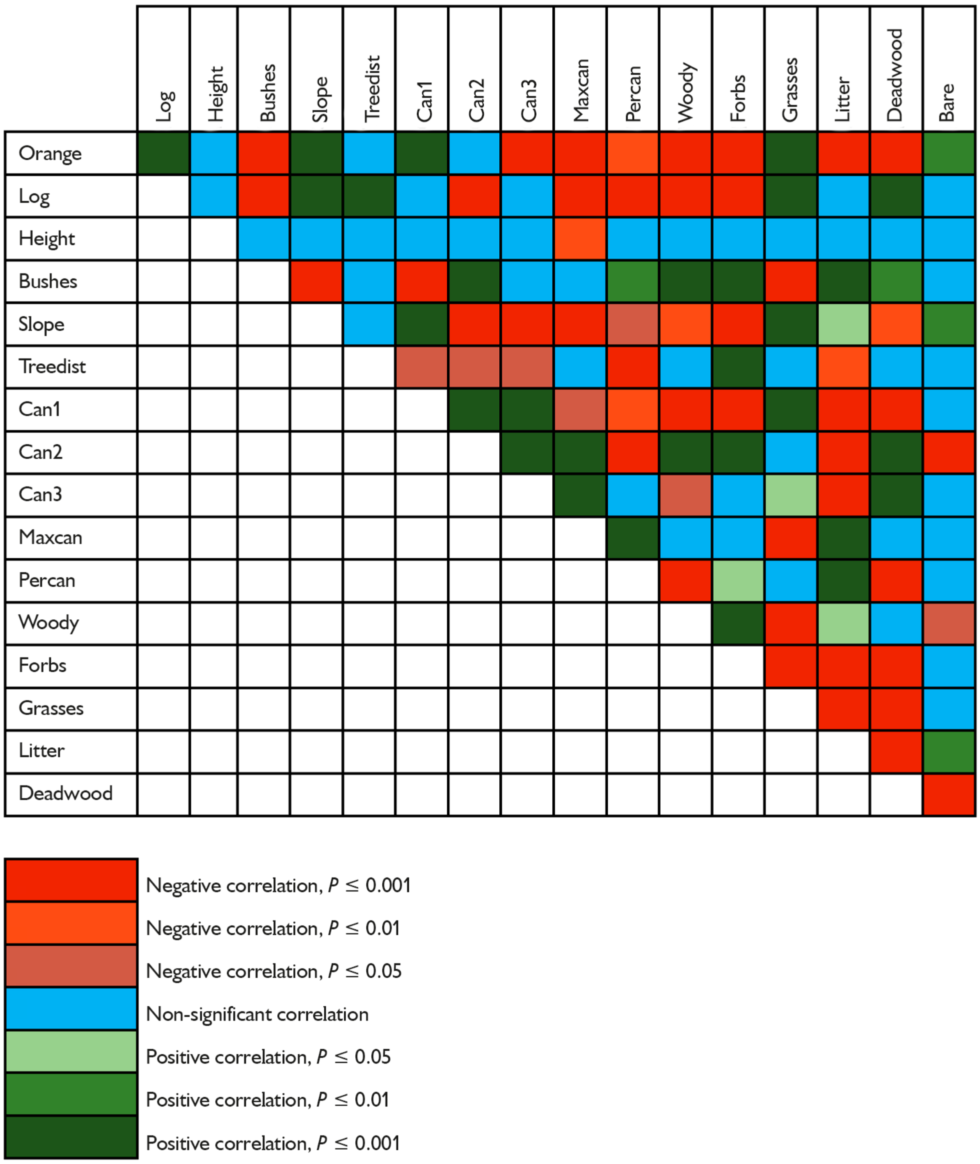

Figure 3. Heatmap indicating significance levels of Spearman correlations for all pairwise comparisons of environmental variables evaluated in this study, based on all 1,554 captures of 17 small mammal species.

Only the species that were captured in all six sampling sessions (*Gracilinanus agilis*, *Akodon montensis*, *Hylaeamys megacephalus*, and *Oligoryzomys nigripes*) were included in the analyses of temporal variation in habitat preference (Table 2). Seasonal variation was found for six environmental variables, in one or two species, and seven variables were significant for interannual variation in one or two species (Table 3).

Gracilinanus agilis was more likely to be captured near Orange trees and Woody understory plants in the variable season, in an area with more Grasses in the wet season, and with more ground Litter in the dry season. *Akodon montensis* shared those seasonal preferences of Woody plants and Grasses, was captured near more ground Litter in the variable season, and with a higher Canopy1 in the dry season. *Hylaeamys megacephalus* did not exhibit seasonal variation in its association with any environmental variable. *Oligoryzomys nigripes* was found associated with more Bare ground during the variable season (Table 4).

Table 2. Number of captures of adult and subadult individuals of small mammal species during the six sampling sessions evaluated in this study. Sampling sessions were: 2 = June – July 2015 (Dry season); 3 = November – December 2015 (Wet); 4 = February – March 2016 (Variable); 5 = June – July 2016 (Dry); 6 = November – December 2016 (Wet); 7 = February – March 2017 (Variable). Sampling session designations (2 to 7) correspond to designations used in other studies based on this field sampling (see Material and Methods).

Species	Captures per sampling session						
	2	3	4	5	6	7	Total
Didelphimorphia							
Didelphidae							
Cryptonanus chacoensis (Tate, 1931)	0	1	0	0	0	0	1
Gracilinanus agilis (Burmeister, 1854)	16	2	2	12	5	9	46
Marmosa paraguayana (Tate, 1931)	1	0	2	0	0	2	5
Monodelphis dimidiata (Wagner, 1847)	0	0	0	0	2	0	2
Monodelphis kunsi Pine, 1975	0	0	0	0	0	1	1
Rodentia							
Cricetidae							
Akodon montensis Thomas, 1913	288	325	106	129	93	119	1060
Calomys callosus (Rengger, 1830)	7	10	2	0	0	0	19
Euryoryzomys russatus (Wagner, 1848)	0	1	0	0	0	0	1
Hylaeamys megacephalus (G. Fischer, 1814)	60	26	50	34	15	22	207
Juliomys pictipes (Osgood, 1933)	0	0	0	1	0	1	2
Necromys lasiurus (Lund, 1840)	2	3	0	0	0	0	5
Oecomys mamorae (Thomas, 1906)	0	0	0	0	1	0	1
Oligoryzomys mattogrossae (Allen, 1916)	11	1	8	17	0	12	49
Oligoryzomys nigripes (Olfers, 1818)	26	21	16	22	12	20	117
Oligoryzomys sp.	1	0	10	9	2	2	24
Rhipidomys macrurus (Gervais, 1855)	0	0	0	2	0	2	4
Sooretamys angouya (Fischer, 1814)	0	1	1	1	5	2	10
Total	412	391	197	227	135	192	1554

Table 3. Environmental variables for the four abundant species that exhibited significant (α ≤ 0.05, by Mann-Whitney Rank Sum test) seasonal (Season) and/or interannual (Year) variation in their association (X). For description of variables see Table 1. Also included non significant (-) variables in the table for comparison with significant ones.

	Gracilinanus agilis		*Akodon montensis*		*Hylaeamys megacephalus*		*Oligoryzomys nigripes*	
Variables	Season	Year	Season	Year	Season	Year	Season	Year
Orange	X	-	-	X	-	-	-	-
Log	-	-	-	-	-	X	-	-
Height	-	-	-	X	-	-	-	X
Bushes	-	-	-	-	-	-	-	-
Slope	-	-	-	-	-	X	-	-
Treedist	-	-	-	-	-	-	-	-
Canopy1	-	-	X	-	-	-	-	-
Canopy2	-	-	-	-	-	-	-	X
Canopy3	-	-	-	-	-	-	-	-
Maxcan	-	-	-	-	-	-	-	-
Percan	-	-	-	-	-	-	-	-
Woody	X	-	X	-	-	-	-	-
Forbs	-	-	-	-	-	-	-	-
Grasses	X	-	X	X	-	X	-	-
Litter	X	-	X	X	-	-	-	-
Deadwood	-	-	-	-	-	-	-	-
Bare	-	-	-	-	-	-	X	-

Table 4. Subsets of non-significantly different seasonal means (indicated by shared letters A or B, α ≤ 0.05, by Spearman rank correlations) of the variables for which small nonvolant mammal species showed seasonal variation. For descriptions of environmental variables see Table 1. Seasons: W = wet, D = Dry, V = Variable.

(Continue)

Gracilinanus agilis				*Akodon montensis*				*Oligoryzomys nigripes*			
Orange				Canopy1				Bare			
Season	Mean			Season	Mean			Season	Mean		
W	0.00	A	B	V	1.22	A		D	0.10	A	
D	0.04	A		W	1.28		B	W	0.23	A	B
V	0.27	A	B	D	1.29		B	V	0.76		B
Woody				Woody							
Season	Mean			Season	Mean						
W	5.71	A		W	7.49	A					
D	7.79	A		D	8.30	A	B				
V	14.32		B	V	8.48		B				

Table 4. (Conclusion)

Gracilinanus agilis				*Akodon montensis*				*Oligoryzomys nigripes*
Grasses				Grasses				
Season	Mean			Season	Mean			
V	2.27	A		V	11.69	A		
D	7.79	A		D	14.72	A		
W	25.00		B	W	16.45		B	
Litter				Litter				
Season	Mean			Season	Mean			
W	37.86	A		D	45.16	A		
V	55.68		B	W	46.00	A		
D	56.54		B	V	49.18		B	

CORRELATIONS AMONG SPECIES-VARIABLE ASSOCIATIONS

Among significant seasonal species-variable associations, those of *G. agilis* to Orange trees and *A. montensis* to Litter were positively correlated (*i.e*. a concordant temporal pattern was observed in the data), as were those of *A. montensis* to both Canopy1 and Grasses. The temporal pattern of *G. agilis* with regard to Woody plants was negatively correlated with the same species' seasonal association with Grasses, as were those of *G. agilis* to Woody plants and *A. montensis* to Canopy1. Of 36 possible pair-wise correlations among species-variable associations, 32 were non-significant (Figure 4A).

Among the 36 possible correlations of significant interannual species-variable associations, five were found to be positively correlated and three negatively correlated (Figure 4B). The interannual pattern exhibited by *A. montensis* with regard to Orange trees and Height of capture was concordant with the response of the same species to Grasses and Litter, respectively. The response of *A. montensis* to Orange trees and Grasses was concordant in both cases with those of *H. megacephalus* to Grasses, and the response of *O. nigripes* to Canopy2. The response of *O. nigripes* to capture Height was negatively correlated to the response to Grasses by both *A. montensis* and *H. megacephalus*, and the response of *O. nigripes* to Canopy2 was negatively correlated to the same species' response to Height. Twenty-eight of the 36 possible correlations were non-significant.

Significant seasonal and interannual responses of the four species to environmental variables are graphed in Figure 5. These graphs show the temporal association of the species with the variables, and indicate whether the significantly correlated response is seasonal, interannual or both.

SEASONAL VARIATION

Six of the 17 environmental variables (Orange tree, Canopy1, Woody plants, Grasses, Litter, Bare ground) had seasonally variable responses from one or two of the four species examined. Three of the four abundant species exhibited seasonal variation in their associations with from one to four environmental variables. Both *G. agilis* and *A. montensis* exhibited temporal variation in associations with four variables, three of which (Woody plants, Grasses and Litter) were the same. *Oligoryzomys nigripes* showed seasonal variation in its association with Bare ground, being most strongly associated with this variable in the Variable season. *Hylaeamys megacephalus* was not found to have seasonal variation in association with any environmental variable.

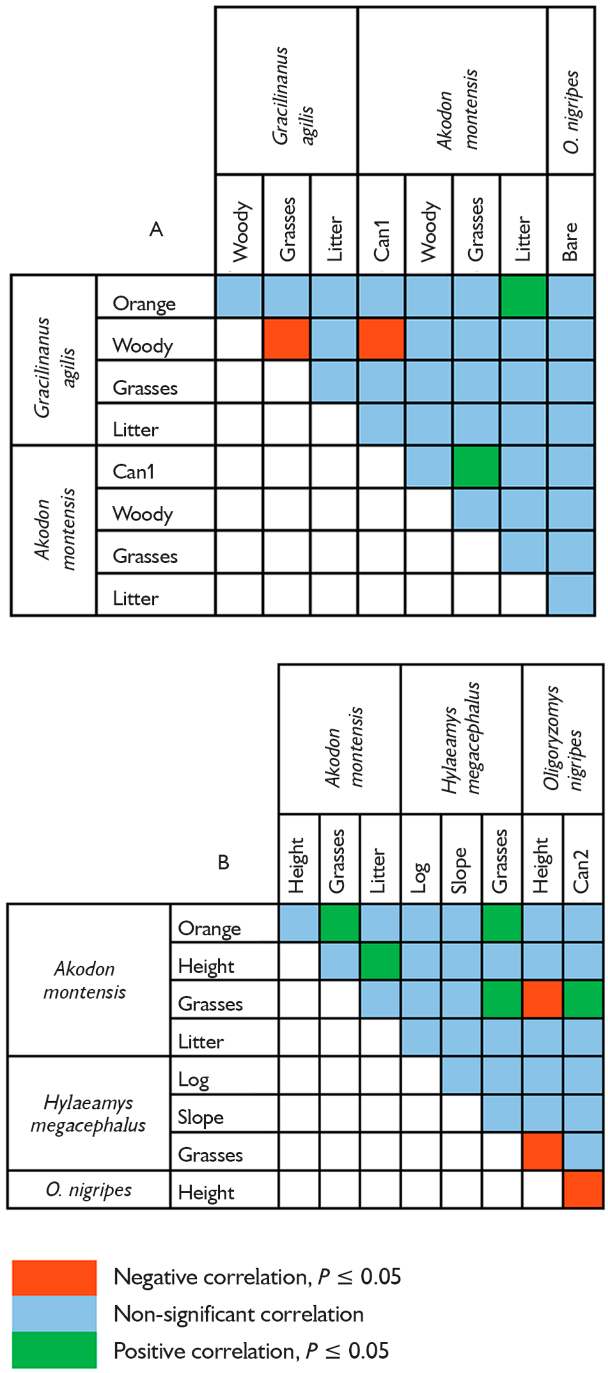

Figure 4. Heatmaps indicating significance levels of Spearman correlations for all pairwise comparisons of environmental variables for which a small mammals species exhibited significant seasonal (A) or interannual (B) variation in association with the variable.

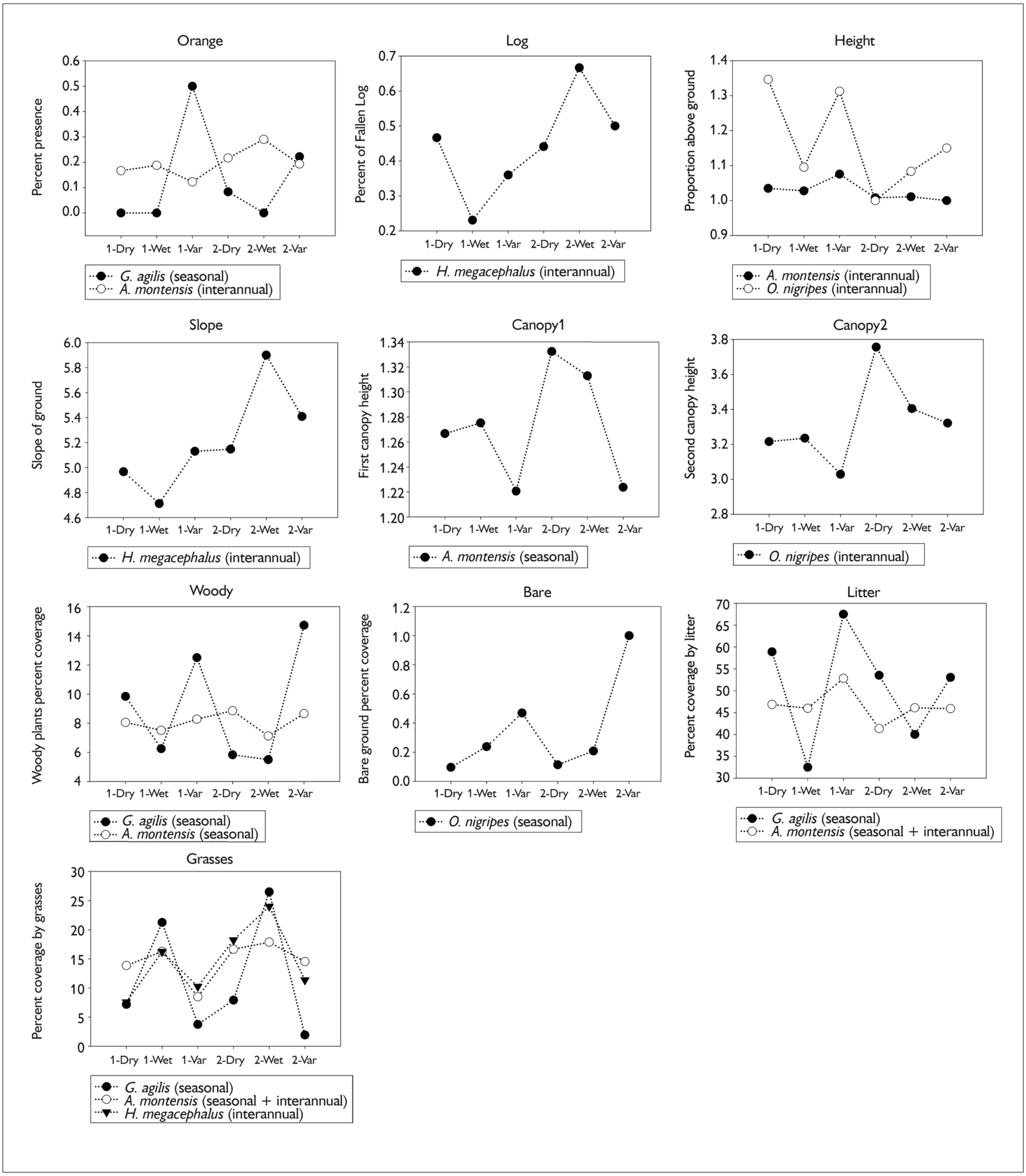

Figure 5. Environmental variables for which one or more species exhibited significant seasonal or interannual variation. Six samples were conducted, with samples in the Dry, Wet and Variable seasons of each of two years. Abscissa indicates sampling year (1 or 2) and season (Dry, Wet, Variable). Legend below each graph indicates the species exhibiting significant variation, and whether the variation was seasonal, interannual or both.

INTERANNUAL VARIATION

Seven of the 17 environmental variables showed interannual variation in microhabitat preference by one or more of the four abundant species. The marsupial *Gracilinanus agilis* did not exhibit interannual variation in association with any environmental variable, whereas the three rodent species showed significant interannual differences in their associations with from two to four environmental variables. *Akodon montensis* associated more strongly in the first (El Niño) year with Litter and was captured more frequently above the ground, and in the following (normal) year associated more strongly with Orange trees and Grasses. *Hylaeamys megacephalus* associated more strongly in the normal year with fallen Logs, steeper Slope and more Grasses. *Oligoryzomys nigripes* exhibited higher average capture Height in the El Niño year, and was associated with a higher Canopy2 in the normal year.

DISCUSSION

MICROHABITAT PREFERENCES OF PREDOMINANT SPECIES

Gracilinanus agilis

This small opossum is highly arboreal (Smith *et al*., 2012), and 45 of 46 (97.8%) of captures in this study were above the ground. In the forested areas of the Cerrado and the Atlantic Forest, it is found in Cerradão and gallery forest (Alho, 2005), in semi-deciduous transitional forest (Smith *et al*., 2012) and in forests with dense understory vegetation (Carmignotto *et al*., 2015). Barreto Cáceres & Owen (2019) reported higher population levels in areas of greater forest degradation in an Interior Atlantic Forest site, although it was present in all degradation levels sampled. Although Alho (2005) reported seasonal populational variation, no previous study has examined temporal variation in microhabitat preference by this species. In the present study *G. agilis* did not exhibit interannual variation in microhabitat preference, but did show seasonal variation with respect to four environmental variables. Three of these four variables (Woody plants, Litter, Grasses) pertain to ground cover. These results suggest that this didelphid species is more responsive to ground-level habitat variables than previously understood, and conversely may be less influenced by other structural variables (*e.g*., distance to nearest tree and canopy heights) than would be expected for a primarily arboreal species.

Akodon montensis

This species is primarily terrestrial (1,031 of 1,060 [97.3%] of captures were on the ground). Naxara *et al*. (2009) found *A. montensis* in approximately equal abundance and site occupancy in the cool-dry and the warm-wet seasons in an old-growth forest in São Paulo State. Although they did not explicitly evaluate temporal variation in habitat preference, Owen *et al*. (2010) noted that population densities of *A. montensis* exhibited different temporal patterns in three different habitats, suggesting that the different habitats were differentially favorable to this species through seasonal and/or annual cycles. A 23-month mark-recapture study of small mammals in a Cerrado locality in eastern Paraguay found that *A. montensis* was encountered during sampling sessions from May – September (dry season), and not at other times (Owen, 2013). In the present study, *A. montensis* showed significant seasonal variation for two environmental variables, interannual variation with two variables, and both seasonal and interannual variation with two other variables. Of these, three are ground-cover variables (Woody plants—seasonal, Litter—seasonal and interannual, Grasses—seasonal and interannual), which concurs with reports of the importance to *A. montensis* of dense understory vegetation, bamboo abundance, ferns and shrubs (Dalmagro & Vieira, 2005; Goodin *et al*., 2009; de Lima *et al*., 2010; Melo *et al*., 2011, 2013). This species showed weaker preference for Grasses and stronger preference for Litter during the El Niño year. It also was captured above ground more often in the El Niño year.

Hylaeamys megacephalus

This species exhibits population fluctuations associated with seasonal cycles. In the central Cerrado, it was captured most frequently in the wet season (Carmignotto *et al*., 2014), but in the western Interior Atlantic Forest it was more abundant in the dry season (Barreto Cáceres & Owen, 2019). However no previous study has been made of temporal variation in habitat preference of *H. megacephalus*. This study found no seasonal variation in habitat associations of this species. Nevertheless, interannual differences were exhibited for three environmental variables (fallen Logs, ground Slope and Grasses). In the El Niño year, it had low preference for fallen Logs in the wet season, whereas in the wet season of the following year it showed high preference for Logs. The same pattern was found for ground Slope, perhaps having to do with the rate of rainfall runoff. *Hylaeamys megacephalus* showed a higher preference for Grasses in the wet season in both years, but the preference was weaker during the El Niño year.

Oligoryzomys nigripes

Although considered scansorial (using both the ground and bushes or vines), 97 of 117 (82.9%) of captures of *Oligoryzomys nigripes* in this study were on the ground. This species is considered tolerant of a wide range of habitats, having been reported as occupying both flooded and unflooded grassland and forest in the Brazilian pampas (Sponchiado *et al*., 2012), and not preferentially associated with any of the vegetation variables in a study in Argentina (Gómez-Villafañe *et al*., 2012). Other reports have found an association with fallen logs, ground litter, vegetation density at 1 m and a high density of scrubs (Dalmagro & Vieira, 2005; de Lima *et al*., 2010; Barreto Cáceres & Owen, 2019). Temporal population variation has been reported for this species. Barreto Cáceres & Owen (2019) found higher population levels in an El Niño year than in the following year. Few previous studies are available of temporal variation in habitat preference by *Oligoryzomys nigripes*. Bonvicino *et al*. (2016) state that it prefers more open areas in the dry season, but this statement is unreferenced. In an isolated Cerrado patch in an Atlantic Forest matrix, Owen (2013) reported *O. nigripes* was encountered in small numbers during May, August and September, but not in other months. In the present study the species was found to exhibit both seasonal and interannual responses to some environmental variables. In the El Niño year, it was captured above the ground more often, but in areas with a lower second canopy. It was found in areas of bare ground least often in the dry season, in contrast to the description by Bonvicino *et al*. (2016).

INTERANNUAL VARIATION IN COMMUNITY STRUCTURE

This study found 16 significant seasonal and/or interannual associations between four species and ten environmental variables, strongly indicating that small-mammal community structure and composition are temporally dynamic, and that the species respond in complex and specifically distinct ways to a variety of environmental variables. Three of the four predominant species exhibited an interannual response to two or more environmental variables. Although the study did not include replicates of the interannual variation, it is likely that the El Niño event, with concordant increased precipitation (Figure 2), was an important driver of interannual variation. As noted, the didelphid *Gracilinanus agilis* did not exhibit an interannual response to any environmental variable, whereas each of the sigmodontine rodents did. This is strong evidence that an El Niño event could affect small mammal community structure in important ways, via the changing microhabitat associations of the more abundant species in this marginal Atlantic Forest region. As noted, this study was conducted near the distributional limits of each of the four predominant small mammal species encountered in the study. Further research should focus on whether the potential 'El Niño' effect is characteristic of these species throughout their distributions, or only near their distributional limits.

CONCLUSIONS

This is the first study to explicitly evaluate temporal variation in habitat associations of small mammals in the Atlantic Forest ecoregion. Each of four species exhibited seasonal and/or interannual variation in several of the habitat variables analyzed. Some of these species-variable associations were found to be concordant (correlated positively) or opposed (correlated negatively). Interannual variation might be attributable to the extreme El Niño event during the first year of the study, with *Akodon montensis*, *Hylaeamys megacephalus*, and *Oligoryzomys nigripes* showing significant interannual differences in their associations with four, three and two environmental variables respectively, while *Gracilinanus agilis* showed no interannual variation for any variable. Considered together, the differing temporal patterns of habitat association among these four predominant small mammals reveal a complex spatially and temporally dynamic composition and structure in this Atlantic Forest community. Further explicitly experimental studies would be required to discern specific physiologic or behavioral characteristics of the four species that result in the patterns observed in this study.

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