

Sigmodontine community and species responses to El Niño and precipitation in different levels of forest degradation

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Few studies have focused on rodent communities at the margins of an ecoregion or the limits of species' distributions, where the community may be more sensitive to extrinsic variables, both biotic and abiotic. This study evaluates sigmodontine rodent species diversity and overall abundance, and variation associated with climatic variables, in three locations with differing levels of habitat degradation. The study was conducted in northeastern Paraguay, near the western limit of the Upper Paraná Atlantic Forest and near the distributional limits of the three most abundant species in the study sites. Three mark-recapture grids were established and classified as least, moderately and most-degraded based on an analysis of several vegetation parameters. The grids were sampled for five consecutive nights, six times during two years. Shannon diversity and overall abundance were calculated for each sample. Monthly Multivariate ENSO Index and rainfall values were obtained from publicly available resources. Product-moment correlations were calculated between community and climatic parameters, including cumulative values for the climatic variables. The same correlations were calculated for the three common sigmodontine species. 1,632 captures were recorded, representing 13 sigmodontine species. Species richness in the samples (one session on one grid) varied from four to seven. *Akodon montensis*, *Hylaeamys megacephalus* and *Oligoryzomys nigripes* were the three most abundant species. In general, species diversity was negatively correlated with ENSO index, precipitation and precipitation anomaly, including cumulative one- to six-month cumulative values of each. Total sigmodontine abundance was positively correlated with the climatic variables. However, these correlations were not uniform among the three levels of habitat degradation, nor did the three abundant species show similar correlation patterns. The three most abundant species are each near their distributional limits, whereas several less abundant species have distributions that extend well beyond the study area. This somewhat counter-intuitive result bears further investigation in other sites at ecoregional margins, to determine whether it is a commonly observed pattern, or an exception. Overall sigmodontine abundances were generally reflective of *Akodon montensis* abundance, which generally correlated with precipitation (including cumulative amounts). Our analyses of these longitudinal data showed two major effects on sigmodontine species diversity and population. First, they are impacted by habitat and secondly, they are affected by climate (ENSO, precipitation). However, individual species are not impacted similarly. *Akodon montensis* abundances primarily were correlated with abiotic (climatic) variables, and the correlations were consistent across habitats (biotic factors). In contrast, *Hylaeamys megacephalus* abundance was correlated with climatic variables in two habitats, but not the moderately-degraded habitat, and *Oligoryzomys nigripes* abundance was not correlated with climate in the most-degraded habitat.

Pocos estudios se han centrado en las comunidades de roedores en los márgenes de una ecorregión o en los límites de las distribuciones de las especies, donde la comunidad puede ser más sensible a las variables extrínsecas, tanto bióticas como abióticas. Este estudio evalúa la diversidad de especies y la abundancia general de roedores sigmodontinos, y la variación asociada con las variables climáticas, en tres lugares con diferentes niveles de degradación del hábitat. Se establecieron tres parcelas de captura-marca-recaptura y se clasificaron como la menos, moderada y más degradadas basadas en un análisis de vegetación de varios parámetros. Las parcelas fueron muestreadas durante cinco noches consecutivas, seis veces durante dos años. La diversidad de Shannon y la abundancia general se calcularon para cada muestra. El índice mensual de ENOS multivariable y los valores de precipitación se obtuvieron de sitios accesibles en Internet. Las correlaciones producto-momento se calcularon entre los parámetros climáticos y de la comunidad, incluidos los valores acumulados para las variables climáticas. Se calcularon las mismas correlaciones para las tres especies comunes de sigmodontinos. Se registraron 1,632 capturas, representando 13 especies sigmodontinos. La riqueza de especies en las muestras (una sesión en una parcela) varió de cuatro a siete. *Akodon montensis*, *Hylaeamys megacephalus* y *Oligoryzomys nigripes* fueron las tres especies más abundantes. En general, la diversidad de especies se correlacionó negativamente con el índice ENOS, la precipitación y la anomalía de la precipitación, incluidos los valores acumulativos de uno a seis meses de cada uno. La abundancia total de sigmodontinos se correlacionó positivamente con las variables climáticas. Sin embargo, estas correlaciones no fueron uniformes entre los tres niveles de degradación del hábitat, ni tampoco entre las tres especies abundantes. Las tres especies más abundantes están cada una cerca de sus límites de distribución, mientras que varias especies menos abundantes tienen distribuciones que se extienden mucho más allá de este sitio. Este resultado algo contraintuitivo conlleva una mayor investigación en otros sitios en los márgenes ecorregionales, para determinar si es un patrón observado comúnmente, o una excepción. Las abundancias de sigmodontinos generalmente reflejaron la abundancia de *Akodon montensis*, que generalmente se correlacionó con la precipitación (incluidas las cantidades acumuladas). Las conclusiones destacadas de este estudio fueron: (1) diferentes niveles de degradación del hábitat se correlacionan con la variación en la diversidad de especies y la abundancia general de los sigmodontinos, y las especies individuales no muestran los mismos niveles de correlación entre los diferentes hábitats; y (2) la variabilidad climática (ENOS y precipitación) también afecta la diversidad de especies sigmodontinos y la abundancia de la población, y las especies comunes no muestran correlaciones similares entre sí. Las abundancias de *Akodon montensis* se correlacionaron principalmente con variables abióticas (climáticas), y las correlaciones fueron consistentes en todos los hábitats (factores bióticos). En contraste, la abundancia de *Hylaeamys megacephalus* se correlacionó con las variables climáticas en dos hábitats, pero no en el hábitat moderadamente degradado, y *Oligoryzomys nigripes* no se correlacionó con el clima en el hábitat más degradado.

Key words: Climatic variables; habitat quality; mark-recapture sampling; Paraguay; population abundance; species diversity; upper Paraná Atlantic Forest.

Introduction

The composition and dynamics of terrestrial small-mammal communities in the Neotropics are to date poorly documented (Mares 1982; Lacher and Mares 1986; Mares and Ernest 1995; Willig *et al.* 2000; Owen 2013). Accordingly, studies of terrestrial small-mammal communities are increasingly the focus of intensive studies. However, the majority of these studies are either broad-scale comparisons of faunal communities (Ojeda *et al.* 2000; Willig *et al.* 2000), or are evaluations of a community situated well within the geographic and ecologic boundaries of the ecoregion being evaluated (e. g., Ribeiro and Marinho-Filho 2005; Bernardes 2006; Becker *et al.* 2007; Magnusson *et al.* 2010). With the increasing fragmentation of ecoregions, it will be increasingly important to assess community composition and dynamics in marginal patches of a particular ecoregion (Santos 2008; Owen 2013). Faunal members of such communities are presumed to be living near the limits of their capabilities in terms of their abiotic (e. g., soils, weather, climate) and biotic environment (vegetation composition and structure, predators, competitors). Moreover, such communities are likely to be sensitive to extrinsic variables such as climate change and anthropogenic changes in land use (Willig *et al.* 2000; Carnaval and Moritz 2008; Meserve *et al.* 2011; Owen 2013; de la Sancha *et al.* 2014). Importantly, a detailed understanding of the responses of rodent communities and their more common species to both biotic and abiotic variations in their environment is necessary for developing predictive models for the emergence of rodent-borne zoonotic pathogens (Glass *et al.* 2002; Goodin *et al.* 2006; Keesing *et al.* 2010; Han *et al.* 2015; Eastwood *et al.* 2018; Morand *et al.* 2019).

Most of eastern Paraguay is within the historical distribution of the Upper Paraná Atlantic Forest (UPAF), which is a Biodiversity Hotspot and Conservation Priority Area (Myers *et al.* 2000; Willig *et al.* 2000). This ecoregion has experienced extensive land-use conversion for ranching and agriculture resulting in less than 7 % of the original footprint remaining (Klink and Moreira 2002; Klink and Machado 2005; Silva *et al.* 2006; Huang *et al.* 2007, 2009). This study evaluates the temporal dynamics and particularly the effects of the El Niño / Southern Oscillation (ENSO) and precipitation on the sigmodontine rodent communities occupying three types of habitat degradation, near the western limit of the UPAF in eastern Paraguay. We hypothesized that substantial fluctuations in rodent species diversity and sigmodontine population abundance would result from fluctuations in the abiotic variables mentioned above, and that these effects would be dissimilar in the three communities sampled, due to differing levels of habitat degradation. Moreover, we expected that some species would be more responsive to climatic (abiotic) fluctuations, whereas others might be more sensitive to habitat degradation.

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 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 Moist Broadleaf Forest in the biome map of Olson *et al.* 2001), and receives an annual average precipitation of approximately 1550 mm (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/ge/, accessed 17 March 2019).

The three sampling grids were evaluated based on an extensive series of vegetation structural characteristics, measured at each of the trap stations in each grid. Means of these vegetation measures were used as general measures for each grid. These were standardized to a mean of zero and standard deviation of one, to mitigate against effects of character size. Eigenvectors were extracted from the correlation matrix of standardized characters and evaluated using Principal Component Analysis (PCA; Sneath and Sokal 1973). Following preliminary analyses, six characters were included in the final PCA, as being important descriptors of both forest quality and rodent habitat: dead wood on ground, maximum canopy height, distance to nearest trees, percentage coverage by forbs, logs (fallen trees) in vicinity, and presence of orange trees. Degradation levels were judged to be positively associated with the first two principal components, which together represented 95% of the variance (Table 1). Thus, more degraded (poorer) forest habitat is associated with forbs, logs (fallen trees), and orange trees (*Citrus aurantium*, an introduced species which has acclimatized in disturbed forest). Less degraded forest habitat is associated with more dead wood (fallen branches, not fallen trees), higher canopy and lower distance to the nearest tree. Based on these criteria, Grid B (centered at -24.141° S, -55.366° W) was designated as “least degraded”, Grid A (-24.123° S, -55.505° W) was “moderately degraded”, and Grid G (-24.131° S, -55.537° W) was “most degraded”. Grid names and designations are consistent with other publications based on data developed in this project.

Sampling methods and protocol. Each 12 by 12 sampling grid consisted of 144 trap stations, with the traps placed 10 m apart. Sampling was conducted six times (July and November 2015, February, July and November 2016, and February 2017). July is winter, and typically dry, whereas November is the beginning of the summer and the peak of the rainy season, and February is the end of summer, with intermediate rainfall levels. In each sampling session, traps were opened for five nights on each grid. In the first sampling session two traps were placed at each station (one trap on the ground, one on a plywood platform 2 to 3 meters above the ground, in vines or branches). Thereafter (for the remaining five sampling sessions) three traps were placed at each station (two on the ground, one on a platform above ground). Thus, 432 traps were open each night for the remaining five sampling sessions resulting in 2,160 trap-nights per sampling session with the total effort for the six sampling sessions of the study being 36,720 trap-nights.

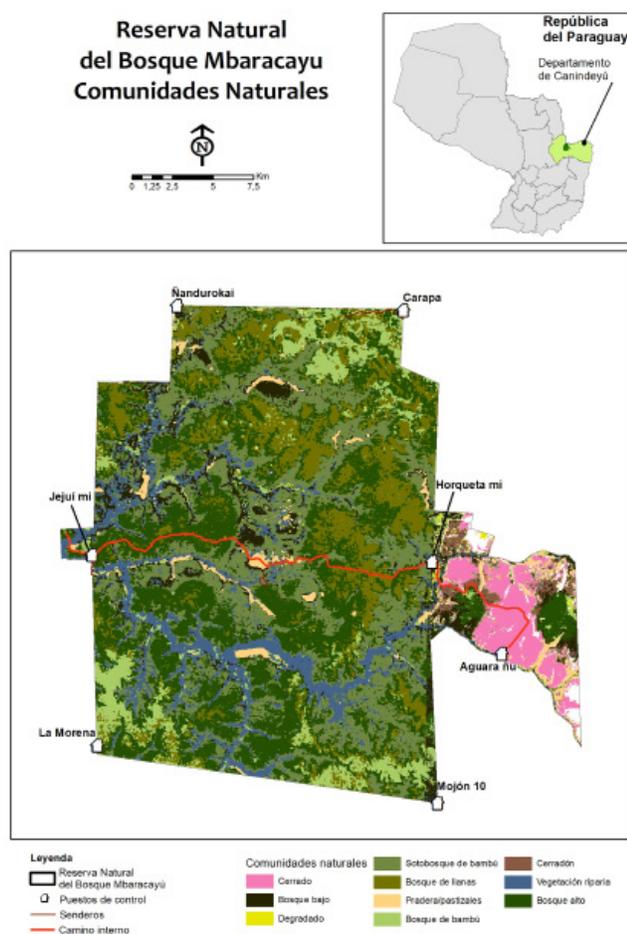


Figure 1. Map of the Reserva Natural del Bosque Mbaracayú and its location within Paraguay, and land cover based on supervised classification of satellite imagery combined with extensive ground-truthing using habitat categorization by local Ache (Indigenous) people. See text for location and description of sampling grids. Map based on Naidoo and Hill (2006) and Peña-Chocarro *et al.* (2010).

Environmental data. Monthly multivariate ENSO index (MEI) values (Wolter and Timlin 1993, 1998) were downloaded from the Physical Sciences Division of the Earth Sciences Laboratory, U.S. National Oceanic and Atmospheric Administration (<https://www.esrl.noaa.gov/psd/enso/mei/data/meiv2.data>) for the time period beginning one year before rodent sampling began, until the final sampling period. Precipitation data (Precip) were obtained for the same time period from the Climatic Research Unit of the University of East Anglia accessed via a Google Earth application (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.02/ge/). Precipitation data are presented as 0.5-degree grid aver-

Table 1. Loadings of six vegetation measures on principal components 1 and 2, and percent of variance explained by these two components.

| Vegetation | PC-1 | PC-2 |
|------------------------------|--------|--------|
| Percent coverage by forbs | 0.972 | 0.185 |
| Percent coverage by deadwood | -0.788 | 0.602 |
| Maximum canopy height | -0.816 | -0.533 |
| Minimum distance to trees | 0.245 | -0.942 |
| Presence of fallen trees | 0.947 | -0.140 |
| Presence of orange trees | 0.960 | 0.233 |
| % of variance | 62.2 | 32.8 |

ages. Because the RNBM lies approximately equally on two of the grid squares, the precipitation values for those two squares were averaged to calculate monthly precipitation values for the study site. Monthly precipitation values were also downloaded for the 30 years prior to the study (1984 to 2013) to calculate historical monthly precipitation means and standard deviations. Monthly precipitation anomaly values (Anom) were calculated by subtracting the monthly means from the recorded precipitation amounts during the study. To evaluate the effect of ENSO on precipitation at the study site, Pearson product-moment correlations were calculated between MEI and Precip (current month and monthly lagged values for from 1-6 months), and between MEI and Anom (current and lagged for from 1 to 6 months).

Correlations between rodent community measures and abiotic measures. For comparison with rodent community and population measures, MEI, precipitation and precipitation anomaly values were listed for each of the six sampling months, as well as cumulative MEI, precipitation and anomaly for the two, three, four, six, and twelve-month periods ending with each sampling month (MEI1 – MEI12, Precip1 – Precip12, Anom1 – Anom12). Total sigmodontine abundance (all species included) and species diversity (Shannon index) were calculated for each of the three grids and each of the six sampling sessions. Because abundance values may be expected to conform to a Poisson distribution, a Shapiro-Wilk test was conducted, which failed to reject the null hypothesis of normality ($W = 0.96, P = 0.602$). Thus, we did not transform the abundance values. Product-moment correlations were then calculated between each of these two rodent community measures and each of the climatic variables. We arbitrarily considered correlations with an absolute value > 0.70 to indicate potential climatic predictors (MEI, precipitation and precipitation anomaly) of fluctuations in population measures (species diversity, total abundance and species abundances), which corresponds to a 93 % confidence interval around $r = 0$. All calculations were made in Microsoft Excel™, with the exception of calculations pertaining to the principal components analyses, which were conducted using NTSYSpc ver. 2.2 (Rohlf 2005).

Results

Based on monthly precipitation data from the 30 years prior to this study (1984 to 2013), October – December (spring and early summer) is normally the peak rainy season at the study site, with another shorter period in April – May (autumn). The second period is much less consistent, having a higher standard deviation of precipitation amount than any other month of the year.

Among the abiotic variables, the multivariate ENSO index (MEI) correlated weakly with the current month for both precipitation and precipitation anomaly, with the correlation coefficients for both decreasing non-monotonically for increasing lag times, with very little association after three months. For current and all lagged periods, MEI correlated with the precipitation anomaly than with precipita-

tion, indicating that greater than normal rainfall is received during periods of higher MEI values (El Niño events). However, no value of *r* was greater than 0.29, and MEI, anomaly and precipitation were treated as independent abiotic variables, for the comparisons with species diversity and sigmodontine and species abundances.

A total of 1,632 captures (4.4 % overall trap success) was recorded in the sampling, involving 1,021 individual animals (611 recaptures). Overall, 13 species were encountered, two of which remain unidentified. Sigmodontine species richness varied from 4 to 6 on Grid B (least degraded), 4 to 7 on Grid A (moderately degraded), and 4 to 7 on Grid G (most degraded). *Akodon montensis* was by far the commonest species, with 64.6 % of the individuals, followed by *Hylaeamys megacephalus* (17.3 %) and *Oligoryzomys nigripes* (9.0 %, Table 2). Shannon species diversity varied from 0.70 to 1.11 on Grid B, 0.73 to 1.32 (Grid A), and 1.00 to 1.41 (Grid G). Total sigmodontine abundance (species combined) ranged from 17 to 88 (B), 27 to 111 (A), and 23 to 53 (G; Table 3).

Correlations between climatic and population measures were quite variable. In general, species diversity was negatively correlated with the three sets of climatic variables (MEI, precipitation, precipitation anomaly, and their cumulative values; Figure 2). In contrast, total sigmodontine abundance was positively correlated with the three climatic variables.

Predictors of species diversity. Notwithstanding a generally negative correlation with the climatic variables, species diversity appeared to be only loosely associated with those variables which we evaluated (Table 4), with only Grids B and G (least and most degraded) showing an “important” (absolute value > 0.70) correlation with current month precipitation, and no other climatic variable. On both grids, species diversity correlated most strongly with current-month values of MEI and precipitation, generally decreasing with

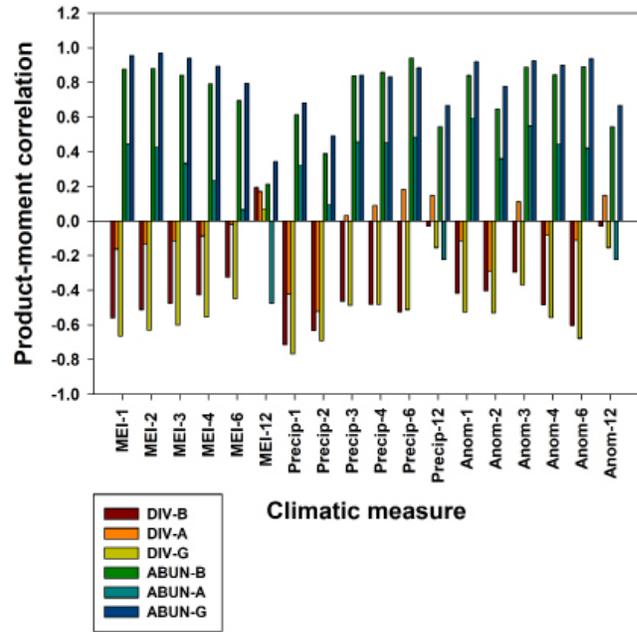


Figure 2. Correlograms showing product-moment correlations between sigmodontine species diversity and total abundance with MEI, precipitation and precipitation anomaly, shown for 1, 2, 3, 4, 6 and 12-month cumulative values. Grid B, least degraded; Grid A, moderately degraded; Grid G, most degraded.

increasing cumulative values. In contrast, species diversity on these same two grids correlated best with the six-month cumulative value for precipitation anomaly (Figure 2). On the moderately degraded grid (A), species diversity was negatively correlated with nearly all climatic variables, although strongly with none (Table 4), and the strongest correlations were with the two-month cumulative values of precipitation and precipitation anomaly (Figure 2).

Predictors of sigmodontine abundance. Sigmodontine abundance was strongly positively correlated with 11 of the 18 climatic variables on Grid B (least degraded), showing an immediate increase with higher MEI and anomaly values, as

Table 2. Summary of species encountered on each grid, for all six sampling sessions combined. Least, moderate and most refer to level of habitat degradation, as evaluated using a principal components analysis of six environmental variables, measured at each of 144 trap stations on each grid, and averaged for the grid.

| Species | Grid B (least) | | Grid A (moderate) | | Grid G (most) | | Overall | |
|----------------------------------|----------------|----------|-------------------|----------|---------------|----------|----------|----------|
| | # indiv. | Percent. | # indiv. | Percent. | # indiv. | Percent. | # indiv. | Percent. |
| <i>Akodon montensis</i> | 254 | 71.9% | 279 | 64.7% | 127 | 53.6% | 660 | 64.6% |
| <i>Calomys callosus</i> | 1 | 0.3% | 2 | 0.5% | 8 | 3.4% | 11 | 1.1% |
| <i>Eurozomys russatus</i> | 2 | 0.6% | 0 | 0.0% | 0 | 0.0% | 2 | 0.2% |
| <i>Hylaeamys megacephalus</i> | 45 | 12.7% | 75 | 17.4% | 57 | 24.0% | 177 | 17.3% |
| <i>Juliomys pictipes</i> | 2 | 0.6% | 0 | 0.0% | 0 | 0.0% | 2 | 0.2% |
| <i>Necomys lasiurus</i> | 0 | 0.0% | 3 | 0.7% | 0 | 0.0% | 3 | 0.3% |
| <i>Oecomys mamorae</i> | 0 | 0.0% | 1 | 0.2% | 0 | 0.0% | 1 | 0.1% |
| <i>Oligoryzomys mattogrossae</i> | 9 | 2.5% | 17 | 3.9% | 10 | 4.2% | 36 | 3.5% |
| <i>Oligoryzomys nigripes</i> | 31 | 8.8% | 40 | 9.3% | 21 | 8.9% | 92 | 9.0% |
| <i>Oligoryzomys</i> sp. | 5 | 1.4% | 12 | 2.8% | 6 | 2.5% | 23 | 2.3% |
| <i>Rhipidomys macrurus</i> | 1 | 0.3% | 0 | 0.0% | 2 | 0.8% | 3 | 0.3% |
| <i>Sooretamys angouya</i> | 2 | 0.6% | 2 | 0.5% | 5 | 2.1% | 9 | 0.9% |
| <i>Oryzomyine</i> sp. | 1 | 0.3% | 0 | 0.0% | 1 | 0.4% | 2 | 0.2% |
| Totals | 353 | 100.0% | 431 | 100.0% | 237 | 100.0% | 1021 | 100.0% |

Table 3. Species richness and Shannon diversity and total abundance for sigmodontine rodents on three sampling grids during six sampling sessions in the Reserva Natural del Bosque Mbaracayú. Grid B had the least degraded habitat, Grid A was moderately degraded, and Grid G the most degraded. See text for further description of grid habitats.

| Year | Month | Session | RICH-B | RICH-A | RICH-G | DIV-B | DIV-A | DIV-G | ABUN-B | ABUN-A | ABUN-G |
|------|-------|---------|--------|--------|--------|-------|-------|-------|--------|--------|--------|
| 2015 | Jul | 2 | 4 | 7 | 6 | 0.94 | 1.01 | 1.22 | 82 | 111 | 53 |
| 2015 | Nov | 3 | 5 | 6 | 4 | 0.70 | 0.73 | 1.00 | 71 | 79 | 47 |
| 2016 | Feb | 4 | 5 | 6 | 7 | 0.97 | 1.32 | 1.30 | 88 | 63 | 52 |
| 2016 | Jul | 5 | 6 | 5 | 6 | 1.11 | 1.18 | 1.41 | 40 | 50 | 32 |
| 2016 | Nov | 6 | 5 | 4 | 5 | 1.00 | 0.87 | 1.31 | 17 | 27 | 23 |
| 2017 | Feb | 7 | 6 | 6 | 5 | 0.89 | 1.20 | 1.28 | 55 | 101 | 30 |

well as with three, four and six-month cumulative precipitation. No strong correlations were found between abundance and twelve-month cumulative values (Table 4). Similarly, abundance on Grid G (most degraded) showed strong correlations with 13 of the 18 climatic variables, and no strong correlations with twelve-month cumulative values. In contrast, Grid A (moderately degraded) exhibited no strong correlation of sigmodontine abundance with any climatic variable.

Abundant species, species diversity and total abundance. The three most abundant species in this study were *Akodon montensis*, *Hylaeamys megacephalus* and *Oligoryzomys nigripes*, with 64.6 %, 17.3 % and 9.0 % of all individuals, respectively (Table 2). Because *A. montensis* represents nearly two-thirds of the overall population, abundance levels of this species generally correlate strongly and positively with total sigmodontine abundance (Figure 3). Moreover, an increased proportion of *A. montensis* corresponds on each grid with a decrease in species diversity, as measured by the Shannon Index (Figure 4).

The three most abundant species exhibited differing correlation patterns with total sigmodontine abundance, in the different levels of habitat degradation. *Akodon montensis* was consistently strongly correlated with total abundance, across the three grids. In contrast, *H. megacephalus* was strongly correlated with total abundance on Grids B and G (least and most degraded), and essentially uncorrelated on Grid A (moderately degraded), and *O. nigripes* most strongly correlated on Grids B and A, and uncorrelated on Grid G (most degraded; Figure 5).

As mentioned, on Grid A (moderately degraded), *H. megacephalus* showed only a low correlation with total abundance, although it showed a strong positive correlation with species diversity. On grids A and G, *A. montensis* and *H. megacephalus* showed strongly contrasting responses in the sampling session of February 2016 (the end of the strong El Niño event of late 2015), with *Akodon* decreasing and *Hylaeamys* increasing, after which percentages returned to earlier levels. In contrast, neither of these two species were affected by the El Niño event on Grid B (least degraded; Figure 6).

Discussion

The Sigmodontine community composition and relative abundances of the three most abundant species in this study were similar to those from other studies in the Atlantic Forest habitat of the RNBM (Owen et al. 2010; Eastwood

et al. 2018). However, there are considerable differences between this community and others in Atlantic Forest (e. g., Cademartori et al. 2004; Carmignotto and Aires 2011; Melo et al. 2011; Galiano et al. 2013; Maestri and Marinho 2014; Barros et al. 2015; Machado et al. 2019). One noteworthy difference was that while *Hylaeamys megacephalus* was abundant on all sites in our study, it is absent in more southerly latitudes, reflecting its tropical distribution from the north coast of Venezuela southward across Amazonia and terminating in east-central Paraguay. *Akodon montensis* reaches the western limit of its more subtropical distribution in eastern Paraguay and northern Argentina, as does *Oligoryzomys nigripes*, which is distributed from northeastern Brazil southward to Uruguay (D'Elia and Pardiñas 2015). Thus, although each is widely distributed, the three most abundant species in this study are all near the limits of their distributions.

Higher overall sigmodontine abundance was generally associated with lower species diversity in this study, indicat-

Table 4. Climatic variables arranged in order from highest to lowest correlation coefficient with each community measure (sigmodontine species diversity (Shannon Index) and total sigmodontine abundance), for each grid (B, least degraded; A, moderately degraded; G, most degraded). Climatic measures with negative correlation coefficients are shown in parentheses. Measures with absolute value of correlation coefficient > 0.70 are shown in bold face.

| Species diversity | | | Total abundance | | |
|-------------------|------------|-------------------|-----------------|-------------|-----------------|
| Grid B | Grid A | Grid G | Grid B | Grid A | Grid G |
| MEI-12 | Precip-6 | MEI-12 | Precip-6 | Anom-1 | MEI-2 |
| (Anom-12) | MEI-12 | (Anom-12) | Anom-6 | Anom-3 | MEI-1 |
| (Precip-12) | Anom-12 | (Precip-12) | Anom-3 | Precip-6 | MEI-3 |
| (Anom-3) | Precip-12 | (Anom-3) | MEI-2 | Precip-3 | Anom-6 |
| (MEI-6) | Anom-3 | (MEI-6) | MEI-1 | Precip-4 | Anom-3 |
| (Anom-2) | Precip-4 | (Precip-4) | Precip-4 | MEI-1 | Anom-1 |
| (Anom-1) | Precip-3 | (Precip-3) | Anom-4 | Anom-4 | Anom-4 |
| (MEI-4) | (MEI-6) | (Precip-6) | MEI-3 | MEI-2 | MEI-4 |
| (Precip-3) | (Anom-4) | (Anom-1) | Anom-1 | Anom-6 | Precip-6 |
| (MEI-3) | (MEI-4) | (Anom-2) | Precip-3 | Anom-2 | Precip-3 |
| (Precip-4) | (Anom-6) | (MEI-4) | MEI-4 | MEI-3 | Precip-4 |
| (Anom-4) | (Anom-1) | (Anom-4) | MEI-6 | Precip-1 | MEI-6 |
| (MEI-2) | (MEI-3) | (MEI-3) | Anom-2 | MEI-4 | Anom-2 |
| (Precip-6) | (MEI-2) | (MEI-2) | Precip-1 | Precip-2 | Precip-1 |
| (MEI-1) | (MEI-1) | (MEI-1) | Precip-12 | MEI-6 | Precip-12 |
| (Anom-6) | (Anom-2) | (Anom-6) | Anom-12 | (Precip-12) | Anom-12 |
| (Precip-2) | (Precip-1) | (Precip-2) | Precip-2 | (Anom-12) | Precip-2 |
| (Precip-1) | (Precip-2) | (Precip-1) | MEI-12 | (MEI-12) | MEI-12 |

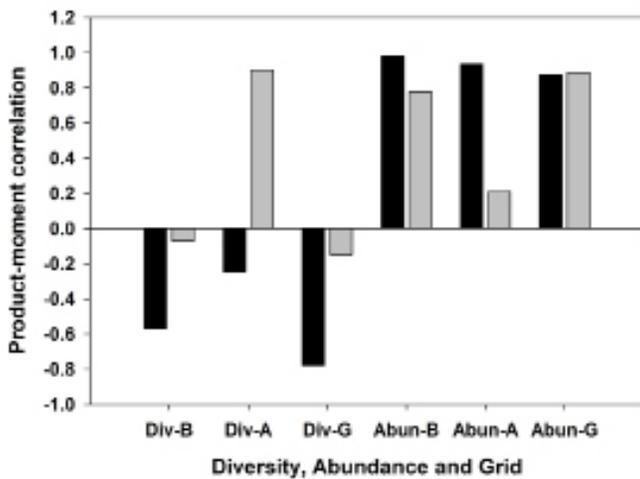


Figure 3. Correlogram showing product-moment correlations between *Akodon montensis* and *Hylaeamys megacephalus* population abundances, with species diversity and total sigmodontine abundance on three sampling grids. Grid B, least degraded; Grid A, moderately degraded; Grid G, most degraded. Black bars, *Akodon montensis*; gray bars, *Hylaeamys megacephalus*.

ing that the diversity index was driven primarily by evenness, rather than species richness. In fact, species richness varied little throughout the study, whereas abundances varied substantially. This finding contrasts with those reported in other studies in which species diversity and abundance were both highest in the same habitat or in the same season (e. g., Gastal 1997; Alho 2005; Asfora et al. 2009).

Hannibal and Neves-Godoi (2015) found *Hylaeamys megacephalus* to be more abundant and more broadly distributed among habitats than *Akodon montensis* in a study in Mato Grosso do Sul, Brazil. Similarly, Santos (2008) found *H. megacephalus* to be more abundant than an unidentified *Akodon* species in an Amazon-Cerrado interface area. In our study, increased overall abundance was due primarily to increased abundance of *Akodon montensis*. However, on Grids A and G (moderately and most degraded) in one sampling session (February 2016) an increase in overall abundance resulted from an increase in *Hylaeamys megacephalus*, while the proportion of *A. montensis* in the population decreased. This sampling session coincided with the end of an “exceptionally intense” El Niño event (Dirección Nacional de Aeronautica Civil 2016). This inverse relationship between the two most abundant species, apparently in response to the El Niño event, was negligible on Grid B (least degraded). To our knowledge, this complex interaction of population response by these two abundant species has not been reported elsewhere, and certainly bears further study and confirmation.

Effects of habitat degradation. Several important studies have documented differences in sigmodontine species diversity and abundance in response to different habitat quality or degradation (e. g., Gastal 1997; Cerqueira et al. 2003; Alho 2005; Melo et al. 2011; Sponchiado et al. 2012; Galiano et al. 2013; de la Sancha et al. 2014). Results of the present study also document such differences associated with differing levels of habitat degradation.

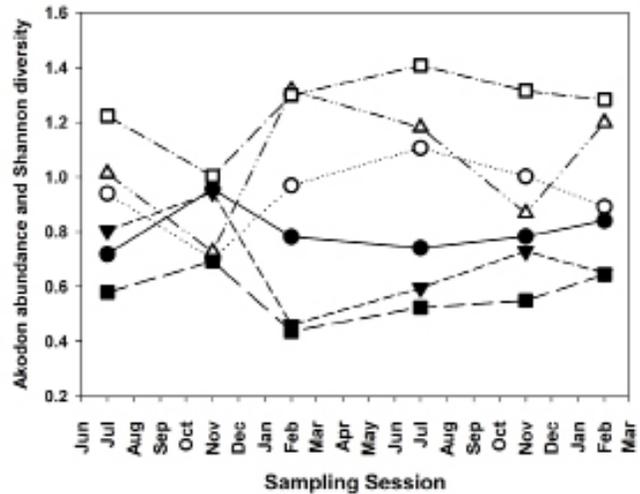


Figure 4. *Akodon montensis* population abundances (expressed as percentage of total sigmodontine abundance) and Shannon species diversity. Closed figures, *A. montensis* abundances; open figures, Shannon diversity. Circles, Grid B; triangles, Grid A; squares, Grid G.

Habitat degradation affects species diversity. Species diversity increased with increased habitat degradation. Diversity was highest in the most degraded habitat (Grid G; Shannon Index $H = 1.25 \pm 0.135$ across six sampling sessions), lowest in the least degraded habitat (Grid B, $H = 0.94 \pm 0.135$), and intermediate in the moderately degraded habitat (Grid A, $H = 1.05 \pm 0.223$). However, the effect of habitat degradation was less consistent in the moderately degraded habitat, as indicated by the higher standard deviation of species diversity levels across sampling sessions.

Habitat degradation affects overall sigmodontine abundance. The moderately degraded habitat had the highest sigmodontine abundance. Abundance was not associated monotonically with degradation extent. Grid A (moderately degraded) had the highest average abundance (72 ± 31.6), as well as being the least consistent (highest standard deviation). The most degraded habitat (Grid G) consistently had the lowest abundance (40 ± 12.8), and the least degraded habitat (Grid B) was intermediate in both mean and standard deviation (59 ± 27.0).

Habitat degradation affects different species differently. Of the three most abundant species, *Akodon montensis* abundance generally correlated highly with overall sigmodontine abundance on all three grids. Nevertheless, it showed a strong reduction in relative abundance (percentage of overall population) on Grids B and G in the February 2016 sample, at the end of a strong El Niño event. *Hylaeamys megacephalus* generally correlated strongly with overall abundance on Grids B and G (least and most degraded), but not on Grid A (moderately degraded). However, on both Grids G and A, *H. megacephalus* strongly increased in relative abundance in the February 2016 sample, benefitting apparently from either the reduction in *A. montensis*, or the heavy rains of the preceding several months, or both. *Oligoryzomys nigripes* abundance correlated with overall abundance on B and A (least and moderately degraded), but did

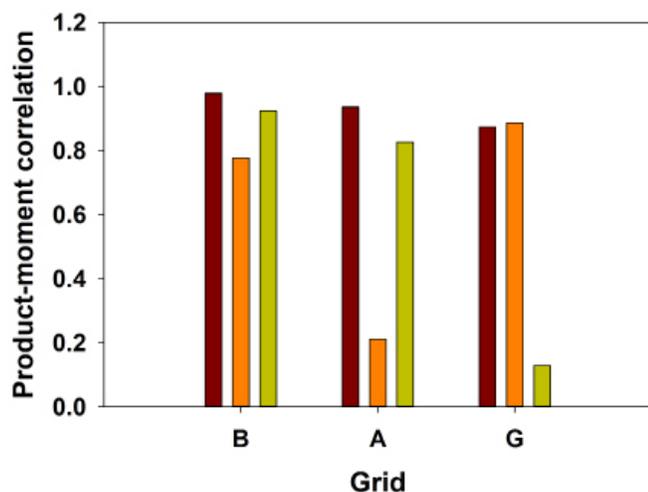


Figure 5. Correlations of population abundances of *Akodon montensis* (brown bar), *Hylaeamys megacephalus* (orange bar), *Oligoryzomys nigripes* (lemon bar), with abundances of all sigmodontine species combined.

not coincide with the overall abundance variations on Grid G (most degraded), apparently not benefiting from conditions that produced increases in the other two species.

Effects of climatic fluctuations. Numerous studies have also demonstrated effects of climatic variability (particularly precipitation) on sigmodontine community diversity, abundance and composition (e. g., [D'Andrea et al. 1999](#); [Melo et al. 2011](#); [Lacher 2012](#); [Sponchiado et al. 2012](#); [Galiano et al. 2013](#)). The present study supports the importance of climatic variability for sigmodontine community parameters, as well as for abundances of common species.

Climate variability affects species diversity. The Multivariate ENSO Index (MEI) of the current month was moderately negatively correlated with species diversity on Grids B and G (least and most degraded) with decreasing strength of correlation with increasing cumulative lengths of MEI scores. On Grid A (moderately degraded), MEI showed only very weak correlations with diversity. Current-month precipitation was also negatively correlated with species diversity on Grids B and G, with two-month cumulative precipitation slightly less strongly correlated. On Grid A, the two-month cumulative precipitation showed the strongest correlation with diversity, and present-month precipitation at a slightly lower correlation strength. In contrast to MEI and precipitation, species diversity was most strongly correlated (negatively) with four- and six-month cumulative anomaly values on Grids B and G. Again, Grid A did not follow the response pattern of the other grids, showing only low correlation values with precipitation anomaly.

Climate variability affects overall sigmodontine abundance. MEI was strongly positively correlated with overall sigmodontine abundance for Grids B and G, for current month and cumulative MEI values of up to six months, decreasing to low correlation values at 12 months. Overall abundance on Grid A was much less strongly correlated (also positively) with MEI current and cumulative values.

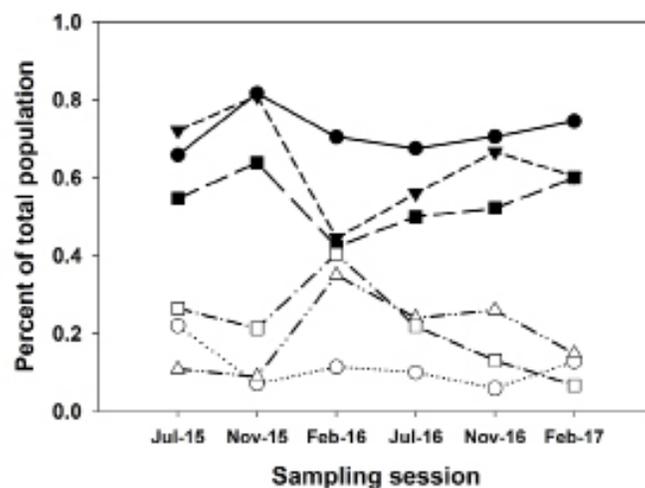


Figure 6. Chart showing relationships of population abundances of *Akodon montensis* and *Hylaeamys megacephalus*, shown as percentages of total sigmodontine abundance for each sampling session on each grid. Solid symbols, *Akodon montensis*; open symbols, *Hylaeamys megacephalus*. Circles, Grid B (least degraded); triangles, Grid A (moderately degraded); squares, Grid G (most degraded). Note the strongly contrasting changes in *A. montensis* and *H. megacephalus* in February 2016, at the end of the strong El Niño event, on Grids A and G. However, the populations on Grid B (least degraded) were not affected by the El Niño event.

Precipitation correlated most strongly with sigmodontine abundance on Grids B and G in the three-, four- and six-month accumulations, again with Grid A less strongly correlated. Precipitation anomaly reflected this same pattern, as well as strong correlations with current-month anomaly for Grids B and G, with Grid A again less strongly correlated.

Climate variability affects common species differently. On Grid B (least degraded), *Akodon montensis* and *Hylaeamys megacephalus* population percentages varied very little across the six sampling sessions. Although the overall populations varied considerably, the percentages of these two species remained relatively constant. On Grids A and G, pronounced variation was seen, with *Akodon* increasing and *Hylaeamys* decreasing in the first part of the El Niño event of late 2015 ([Dirección Nacional de Aeronautica Civil 2016](#)), and then reversing those trends toward the end of that event, with *Akodon* and *Hylaeamys* of nearly equal proportions in February 2016, after which both populations returned to pre-El Niño percentages, and *Hylaeamys* decreasing nearly to zero on Grid G (most degraded) by February 2017.

In this two-year study, substantial fluctuations in rodent species diversity and sigmodontine population abundance were noted, and these were often correlated with fluctuations in the abiotic variables examined. We also found that these effects were dissimilar in the three habitats sampled, representing differing levels of habitat degradation. However, this dissimilarity was expressed as an unexpected pattern. In fact, a particularly interesting result of this investigation was that species diversity and overall sigmodontine abundance were both only poorly correlated with abiotic variables on the moderately degraded habitat (Grid A), and also were more highly variable on that grid, than in the least

and most-degraded habitats. As a result, populations on the least- and most-degraded grids could be substantially predicted by the abiotic variables, whereas populations on the moderately degraded grid were highly variable, and apparently responding to biotic or abiotic factors which were not included in our study.

Another noteworthy result was that, although several community and species population measures which were correlated with climatic variables, none showed important correlations with 12-month cumulative values of these variables. In other words, the community and its populations were not responsive to cumulative precipitation of the entire preceding year, but were responsive to the preceding half-year's events. We did not test for cumulative values between 6 and 12 months, and further investigation is needed to determine the duration of cumulative climatic events which are important to the sigmodontine populations. Additionally, the deviation of the community and population responses in the moderately habitat (Grid A) require better understanding, and may be particularly important in the context of complex interactions of populations of common species such as *Akodon montensis* and *Oligoryzomys nigripes*, which hosts to Jabora and Jucituba hantaviruses, respectively (Eastwood *et al.* 2018).

Finally, we found that some species were more responsive to climatic (abiotic) fluctuations, whereas others were more sensitive to habitat degradation. *Akodon montensis* closely followed overall abundance (which correlated positively with climatic variation) on all three grids, whereas *Hylaeamys megacephalus* did so only in the least- and most-degraded habitats, and *Oligoryzomys nigripes* only in the least- and moderately-degraded habitats.

Akodon montensis is primarily terrestrial, although it may also ascend lianas or low branches of bushes (Machado *et al.* 2019). It is primarily an Atlantic Forest species, also occurring in gallery forest of the Cerrado, whose distribution extends from Minas Gerais state to southern Brazil, and westward in Paraguay only to about where the RNBM (our study site) is located (Cáceres *et al.* 2008; Carmignotto and Aires 2011; D'Elía and Pardiñas 2015). Although our study site is near the distributional limit of this species, it was by far the most abundant encountered in the study. It was well represented in most sessions on all grids, the exceptions being Grids B and G (most- and least-degraded habitats) in February 2016, suggesting that although it is unaffected by habitat degradation *per se*, it can be affected by an interaction between biotic and abiotic factors, and in the presence of adverse climatic conditions can best maintain its high abundance levels in moderately degraded habitat (Grid A). This is an important finding, in the context of this species as the primary reservoir for Jabora Virus, a pathogenic hantavirus species.

In contrast to *A. montensis*, *Hylaeamys megacephalus* did not generally follow overall sigmodontine population trends on Grid A, but did so (responding to climatic variables) on Grids B and G. This species is a widespread, terres-

trial, primarily tropical mouse of moderate size, reaching its southern limit in the region of the RNBM (D'Elía and Pardiñas 2015). On both Grids A and G (moderately and most-degraded habitats), this species increased its representation in February 2016 (when *A. montensis* declined on those two grids), but did not do so in the least-degraded habitat (Grid B). Thus it appears to be affected by variation in the abiotic factors in habitats that are moderately or more degraded, but not in the least-degraded habitat.

Finally, *Oligoryzomys nigripes* is a scansorial forest species (encountered both on the ground and in bushes or vines above the ground), with primarily an Atlantic Forest distribution, also extending into Cerrado gallery forests (Carmignotto and Aires 2011; D'Elía and Pardiñas 2015). In our study it generally followed overall population trends (*i. e.*, responded to the climatic variables) in the least- and moderately-degraded habitats, but not in the most-degraded habitat, where it was consistently in low numbers, and did not respond to these abiotic variables affecting the other two species in those habitats.

Conclusions

Herein, we evaluated the potential value of three climatic variables for prediction of two sigmodontine community parameters—species diversity and overall abundance—in different levels of habitat degradation. In addition, we examined correlations of these abiotic variables with abundances of the three most common species. To our knowledge, this is the first study to evaluate the influences of both biotic and abiotic factors on a sigmodontine community, and to document temporal variation in abundances of common species in response to both abiotic and biotic variables. The importance of establishing predictive capability for these parameters in these communities under different levels of habitat degradation lies, among other reasons, in the potential for recognizing and predicting conditions portending outbreaks of zoonotic diseases such as hantavirus cardiopulmonary syndrome (Vadell *et al.* 2016).

This report provides an ecological baseline which will be used as context in which to evaluate the effects of resource augmentation and predator exclusion, two characteristics of peridomestic habitats, where increased transmission risk of these and other viral pathogens to humans might be expected. Additional results from this research will report on the effects of these experimental manipulations on the sigmodontine communities and species, as well as various aspects of the zoonotic viral populations associated with these rodents.

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