



Importance of the matrix in determining small-mammal assemblages in an Amazonian forest-savanna mosaic

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ABSTRACT

Patch-size and connectivity effects on organisms are usually strong, but may be positive or negative, depending on the landscape context. A binary habitat/non-habitat perspective that fails to consider matrix heterogeneity often explains these inconsistent results, as matrix influences patch quality and connectivity differently for different species. Here we tested the effects of patch size, connectivity and matrix type on non-volant small-mammal assemblages in an eastern-Brazilian Amazonian forest-savanna mosaic. We sampled 14 forest-patches and 2 continuous-forest plots, using 60 baited live traps and 8 pitfall traps (60 L) per plot in 3 field expeditions. We estimated connectivity using the Proximity Index and matrix type as the proportions of savanna or regrowth forest around patches. We used one-dimensional NMDS, ANCOVA and multiple regression to test the relationships among species composition, species traits and predictor variables. We captured 178 individuals of 16 small-mammal species and an NMDS ordination showed a pattern of assemblage change that was strongly related to matrix type. Connectivity and patch size had no statistically significant effect on assemblage composition. Species associated with patches in regrowth-forest matrix were mostly rodents, relatively large and mainly frugivorous, while species associated with savanna-matrix patches were smaller, mostly insectivorous, marsupials. This may be related to how matrix is used by small mammals and affects patch quality, rather than how it limits animal movements. Composition of small-mammal assemblages in patches depended on the type of surrounding matrix, so matrix heterogeneity enhances small-mammal assemblage diversity in this landscape and should be taken into consideration in regional conservation-unit management plans.

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1. Introduction

Understanding landscape dynamics can lead to better comprehension of ecosystem functions and species persistence. Land use accentuates natural landscape dynamics, causing habitat alteration and fragmentation. Fragmentation, by reducing habitat patches and increasing patch isolation, affects species diversity and abundance. As predicted by the species–area relationship (Preston, 1962), patch size usually has strong effects on the number of species occupying a patch (Laurance et al., 2011). However, these effects are not always positive (Laurance et al., 2011; Fahrig, 2003), mostly because patches are commonly considered as closed communities and because the amount of

habitat in the area surrounding the patch is frequently ignored (Fahrig, 2013). This can lead to results that are inconsistent among studies (Debinski and Holt, 2000; Fahrig, 2003).

Habitat isolation also has strong effects, usually showing negative relationships with the number and abundance of species (Debinski and Holt, 2000; Bailey et al., 2010), and causing changes in species composition (Pardini et al., 2005; Vieira et al., 2009). Isolation can be measured in terms of connectivity, though some connectivity measures are considered more realistic than others (Kindlmann and Burel, 2008; Rayfield et al., 2011; McGarigal, 2015). The use of less-appropriate connectivity measures, such as the nearest neighbor distance, can lead to misleading conclusions (Fahrig, 2013; Bender et al., 2003) and connectivity measures that consider the area of patches located in a buffer around the focal patch are generally more appropriate to indicate effective local connectivity (Bender et al., 2003).

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The patch size–connectivity perspective is a result of the binary landscape concept of habitat and non-habitat, originated in island biogeography (MacArthur and Wilson, 1967) and metapopulation theories (Levins, 1969). This approach ignores the heterogeneity of the matrix (Ricketts, 2001; Prevedello and Vieira, 2010), which can lead to inconsistent results (Laurance, 2008). The matrix may influence patch quality and connectivity in many ways (Laurance et al., 2011). Matrix effects have received increasing attention and recent studies have shown that matrix type may have different effects on different species or taxa (Ricketts, 2001; Prevedello and Vieira, 2010; Watling et al., 2011). In the Prevedello and Vieira (2010) meta-analysis, 95% of studies showed effects of matrix type, but in 56% of those studies patch and isolation variables had greater effects than did the matrix. In the tropics, non-flying mammal-species richness and composition may be affected by matrix type (Daily et al., 2003), and matrix was important to predict species richness and persistence in Amazon forest patches (Gascon et al., 1999). Therefore, matrix effects are relevant, but may have varied intensities and their importance in relation to patch and isolation variables is still poorly understood.

The Amazon tropical forest remains one of the largest and least fragmented in the World, but it has already lost about 12% of its original extent and shall lose another 9 to 28% by 2050, especially in drier areas along its southern border (Soares-Filho et al., 2006). Threats to the Amazon are mainly from cattle and soy-bean culture, which frequently cause fragmentation of natural habitats, and highways pose a threat that usually accompanies agricultural activities (Soares-Filho et al., 2006). A large portion of the Brazilian state of Pará, situated in the eastern Amazon, is subject to impacts caused by the BR-163 Highway, which links the city of Cuiabá, in Mato Grosso state, to the township of Santarém in Pará (Fearnside, 2007). The area around Alter do Chão village, Santarém Municipality, is covered by a landscape containing forest patches surrounded by different matrix types, and was designated as an Environmental Protection Area (EPA). This landscape offers the opportunity to investigate how matrix and patch characteristics affect organisms, which could improve the efficiency of future management actions in the region.

Non-volant small mammals clearly respond to changes in the landscape caused by fragmentation and habitat loss (Gascon et al., 1999; Pardini et al., 2005; Umetsu and Pardini, 2007; Santos-Filho et al., 2012), so they are a suitable group to study these effects. Differences in small-mammal functional traits, such as diet, body size and locomotory habits, may facilitate species coexistence (Galetti et al., 2016), and some of these traits have been associated with landscape characteristics (Pardini, 2004; Holland and Bennett, 2009). They also play important ecological roles as primary and secondary consumers (Paglia et al., 2012), prey of many species (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011), and seed predators and dispersers (Vieira and Izar, 1999; Pimentel and Tabarelli, 2004), and may be keystone species in some environments (Ernest and Brown, 2001).

Here, we test the effects of patch size, connectivity and matrix type on the structure of small-mammal assemblages of forest patches in the Alter do Chão landscape. Our objective was to determine which of these landscape variables is most related to small-mammal assemblage structure. We also tested if species functional traits were associated with the variables related to species composition. We measured assemblage structure through species composition, because species complementarity among sites is recommended for selecting sites for conservation (Margules and Pressey, 2000) and because recent studies have shown that species composition responds strong and clearly to environmental changes, much more so than the frequently-used measure of species richness (Su et al., 2004; Solar et al., 2016).

2. Material and methods

2.1. Study area

Alter do Chão is a village on the right bank of the Tapajós River, located in Santarém Municipality, Pará State, in eastern Brazilian Amazonia.

The climate is humid tropical, with rainy season between December and June and dry season between July and November. Mean annual rainfall is 2192 mm, most rain falls between February and April (919 mm) and least between August and October (115 mm). Mean annual temperature is 27.5 °C and mean monthly temperature varies little throughout the year (INMET, 2009).

The village is surrounded by a mosaic composed mainly of forest patches immersed in an Amazonian-savanna matrix, the latter surrounded by continuous forest. All forests in the area are classified as semi-deciduous tropical (Cintra et al., 2013). The savanna is covered mostly by herbs and grasses with sparse trees, even though there is a gradient of tree cover (Magnusson et al., 2008). The forest has a relatively open understory and >50 tree families, but Myrtaceae, Flacourtiaceae and Leguminosae are the most common (W.E. Magnusson and I. Amaral, unpubl. data). The whole landscape was probably forested approximately 2000 years ago (Sanaiotti et al., 2002). There is no certainty about forest-patch origins, but the observations of Bates (1892) are the earliest record of forest patches in the region, so they are at least 150 years old, probably much older. The matrix transition to savanna may have been a consequence of the fires induced by paleoindian agriculture (Iriarte et al., 2012), as this region has been inhabited for millennia (Stenborg et al., 2012).

The savannas around Alter do Chão burn at intervals of 1–3 years, mainly due to human activities (Magnusson et al., 2010). However, there is an area of forest-transition vegetation, which is probably an old savanna that has not burnt entirely for at least the past 30 years (A.P. Lima, unpubl. data; W.E. Magnusson pers. obs.). Some savanna patches that existed in this area around 20 years ago have had their size reduced due to reduced burning (W.E. Magnusson pers. obs.). The matrix around the forest patches in that area is mainly regrowth forest with little or no grass cover. According to the Mausel et al. (1993) classification, this matrix is a forest in advanced secondary succession (>30 years) and the forest patches and continuous forest are mature forest. Regrowth forest is drier and shorter than mature forest (10–20 and 20–30 m high, respectively), with trees much thinner and in higher density (C. Borges-Matos, pers. obs.). We considered the regrowth-forest matrix a “natural” land-cover, since it is part of a local succession process of forest reestablishment. The savanna is a natural physiognomy; in Alter do Chão its origin and expansion may be related to ancient human activities, but not to modern changes in land-cover, such as clearing for plantations or pasture. Hence, we considered the savanna matrix a “semi-natural” land-cover.

2.2. Site samples

All plots were sampled for small mammals in May/June (wet season), August/September and October/November (dry season) of 2015. We sampled 16 plots located in 14 forest patches and in 2 continuous-forest sites (Fig. 1). Patches were chosen according to facility of access and to maintain little overlap among their buffers (see Section 2.4). The standard plot consisted of four parallel 250 m straight lines that summed a total length of 1 km, separated from each other by 50 m. Four plots had either 3 or 5 lines, due to local restrictions or because patches were small and too irregular in shape, but the total length of their lines was also 1 km, so the area sampled was equal for all plots.

The savanna matrix was not sampled because we were interested only in forest-dwelling small mammals, and all species previously registered for the plots (Souza, 2002; A.P. Lima, unpubl. data) are considered forest species (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011). In addition, the savanna matrix has been surveyed intensively for small mammals during the past 29 years (Magnusson et al., 1995; Layme et al., 2004; Magnusson et al., 2010; W.E. Magnusson and A.P. Lima, unpubl. data) and the only species of small mammal regularly found was *Necromys lasiurus*, a species that has not been recorded in forest in the region. The only forest species captured during these decades of research were a few individuals of the genus *Proechimys* (species not

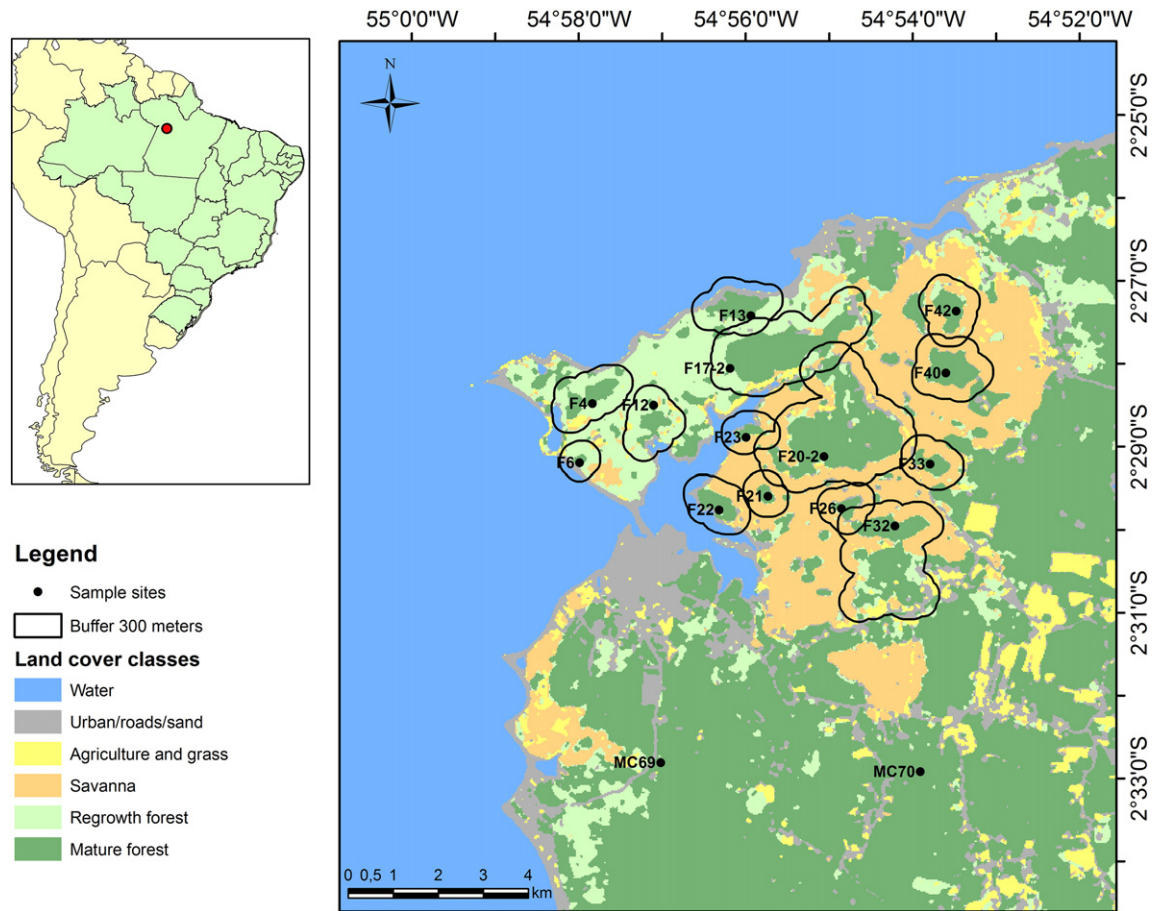


Fig. 1. Six classes of land cover in the study area. Each plot sampled is indicated by its code. The type of plot is given by the letters at the beginning of the code: F = Patch, MC = Continuous Forest.

identified) and a few juvenile *Didelphis marsupialis* (W.E. Magnusson and A.P. Lima, unpubl. data). The areas of regrowth forest were not sampled.

2.3. Small-mammal data collection

We used the same number, types and arrangement of traps in all plots, for the same number of nights. In each plot, we used 30 Sherman® ($8 \times 9 \times 20$ cm) and 30 Tomahawk® live traps ($15 \times 15 \times 35$ cm), and 8 pitfall traps made of 60 L plastic buckets. We positioned only one live trap at each 15 m interval along grid lines, completing 60 trap stations per plot. Traps were set in the following sequence: a Sherman trap on the ground in the first station, a Tomahawk trap on the ground in the second station (both on the right side of the line), a Sherman trap about 2 m above ground in the third station, a Tomahawk trap about 2 m above ground in the fourth station (both on the left side of the line). This sequence was repeated along the 1000 m lines in each plot. In plots with 5 lines, excessive division of 1000 m length excluded a few trap stations, so some of the distances between trap stations had to be reduced (minimum of 10 m) to accommodate the 60 traps, but we always sampled 1 km in total length in each plot. Traps were baited with a slice of banana, a cotton wad impregnated with cod-liver oil and a mixture of peanut butter, corn meal and soybean oil.

Pitfall traps were disposed in a single line, 10 m distant from each other and connected by a 60 cm-high fence of black plastic sheet, stapled to 1 m-high stakes of wood. The pitfall-trap line was located parallel to and equidistant from the two central grid lines of the plot. When this was not possible because of soil conditions or the plot had 3 or 5 lines, the pitfall-trap line was located between lines 1 and 2 or 3 and 4. Pitfall traps were not baited.

We visited all 16 plots in every field expedition, except for plots F13 (not sampled in the third expedition) and MC69 (sampled for only one night in the third expedition) due to problems with landowner permission. Sampling lasted 5 days; we installed the traps on the first day and effective sampling occurred over the following 4 nights. During sampling, every plot was visited daily and bait was changed when necessary. A few specimens of each species were collected to compose a reference collection and to guarantee their correct identification. Voucher specimens are housed in the mammal collection of the Instituto Nacional de Pesquisas da Amazônia (INPA) (voucher numbers INPA-M 7150 to 7727). All other individuals were marked with numbered tags (Monel Small Animal Ear Tag, size 1, LOG Materiais®) and released. Animal manipulation and marking were in accordance with the Guidelines of the American Society of Mammologists (Sikes et al., 2011). All procedures were carried out under Instituto Chico Mendes de Biodiversidade (ICMBio) license number 47376-1 and INPA Ethical Committee authorization (protocol 004/2015).

2.4. Landscape-variable metrics

We generated a land-cover map of the Alter do Chão region. All Geographic Information System procedures were undertaken using QGIS software version 2.12.3 (QGIS, 2016). We used a Landsat 8 (LS8) image of 30 October 2014 available from the U.S. Geological Survey website (<http://earthexplorer.usgs.gov/>), datum WGS 84, UTM 21S. We adjusted the image for surface reflectance and made atmospheric correction, then snipped the area of interest and generated a multiband raster file (bands 2–7 of LS8). With this file, we carried out a semi-automatic supervised classification with 11 to 32 training areas for each cover type, depending on its extension and need for accuracy, using

the Semi-Automatic Classification Plugin (SCP) (Congedo et al., 2013) available in QGIS. We calculated the classification total accuracy in 97.5% with the SCP tool Accuracy. We recognized six principal land-cover classes in our landscape (Fig. 1).

Patch sizes (PS) were calculated in QGIS using Field Calculator and Identify Features tools. The matrix was described using two largely complementary variables: savanna and regrowth forest. They were the largest components of the matrix and where savanna predominated there was little regrowth forest and vice-versa. We calculated a 300 m wide buffer around each sampled patch (Fig. 1), using the QGIS tool Buffer, and then calculated the percentage of savanna (SM) and regrowth forest (RM) in matrix in the whole area contained within each buffer using QGIS and Excel. We chose the buffer distance of 300 m because it corresponded to the largest buffer size that avoided high overlap among buffers of different patches and because it resulted in a mean total area of 2.35 km², which is likely to enclose the home ranges of all species recorded in the area. *Didelphis marsupialis* is the species registered with the largest home range, a maximum of 1.65 km² (Sunquist et al., 1987). We used the proportion rather than the amount of either savanna or regrowth forest to avoid correlation with patch size.

Connectivity (Co) was calculated using the Proximity Index as in McGarigal (2015) in the software Fragstats (McGarigal et al., 2012). This index measures the sum of areas (m²) of all patches that at least touch a pre-established buffer around the focal patch, divided by the nearest edge-to-edge distance squared (m²) from those patches to the focal patch. We used the same 300 m buffer as for the types of matrix. Connectivity values are relative, and here they were divided by 100,000 for ease of presentation.

2.5. Data analysis

We used non-metric multidimensional scaling (NMDS) to reduce the dimensionality of the species composition, based on the dissimilarity version of the Bray–Curtis index. This was done after site standardizing data (dividing the number of individuals registered for each species in a given site by the total number of individuals of all species registered for that site). We compared the proportion of variance in original dissimilarity matrix explained by ordinations in one, two and three dimensions. The data from continuous-forest plots were used in the NMDS calculations, but were not included in the statistical analyses with predictor variables.

We used multiple regressions to test if the landscape predictor variables were associated with the assemblage pattern detected in the NMDS ordination. All landscape variables were tested for the Variation Inflation Factor (VIF), in order to check if their effects were confounded in the multiple regression because of multicollinearity. Proportion of savanna in matrix (SM) and proportion of regrowth forest in matrix (RM) were largely, but not completely, complementary. They were also highly negatively correlated (Pearson's $r = -0.873$, $p < 0.001$), so they could not be included in the same regression and were analyzed separately.

To test the relationships between functional traits and assemblage pattern we used Analysis of Covariance (ANCOVA). We calculated the NMDS value for each species, a weighted average based on the patch NMDS value and the standardized number of individuals of each species, and tested these values with mean body mass, order, diet and locomotory habits for each species. The categorical variables were confounded and could not be included together in the analysis, so each was analyzed separately with body mass. All analyses were performed using the R software (R Development Core Team, 2015).

3. Results

We captured 178 individuals from 16 non-volant small-mammal species in the 14 forest patches and 2 continuous-forest plots at Alter do Chão, including 7 species of rodents (2 cricetid and 5 echimyid) and 9 didelphid marsupials (Table 1). Our effort per plot was of 720 trap-

nights for live traps and of 96 trap-nights for pitfalls, except for F13 and MC69, with 480 and 540 trap-nights for live traps, and 64 and 72 trap-nights for pitfalls, respectively. Taxonomy of small mammals in Amazonia is challenging, mostly because many congener species have very similar morphologies and their taxonomic and geographic distributional limits are not yet well known. Molecular based methodologies, such as DNA sequencing, is currently clarifying interspecific taxonomic limits. We have examined the external morphology of all collected specimens and we are in the process of generating barcoding sequences in order to support these taxonomic identifications. Therefore, we conservatively used cf. in the species name of some individuals when doubts remained based solely on morphological criteria. The expression *aff* for marsupials of the genus *Monodelphis* expresses our opinion that these individuals may belong to a new species that have affinities with *M. adusta* (see Pavan et al., 2014), due to their external resemblance. This does not affect our conclusions about assemblage differences, because future changes in taxonomy of the species registered are unlikely to affect the number of species recorded or their functional traits.

The NMDS ordination in one dimension captured 72% of the variance in the original Bray–Curtis distances among plots. NMDS ordinations in two and three dimensions only captured an additional 19% and 22% of the variance, respectively. We tested two-dimensional NMDS for our predictor variables. Correlations between the axes was low (Pearson = 0.026, Spearman = 0.007), so we tested each axis in a separate multiple regression. The first axis was related to matrix type only (Savanna Multiple Regression: $P = 0.075$, $R^2 = 0.328$, % savanna: $p = 0.011$; Regrowth Forest Multiple Regression $P = 0.056$, $R^2 = 0.369$, % regrowth forest: $p = 0.007$). There were no statistically significant relationships with the second axis (Savanna Multiple Regression: $P = 0.305$, $R^2 = 0.081$; Regrowth Forest Multiple Regression: $P = 0.158$, $R^2 = 0.209$). The prediction power of multiple regressions decreased when two-dimensional NMDS was used, probably due to the loss of degrees of freedom. Considering this and that results with one or two NMDS axes were qualitatively similar, subsequent analyses were done only on the one-dimensional configuration.

The plots ordinated along the NMDS axis were segregated non-randomly and this segregation was in accordance with the type of matrix that predominated around them. Plots surrounded mostly by savanna were clustered to the left, with negative values on the NMDS axis, while plots surrounded mostly by regrowth forest were on the right of the ordination, where the NMDS values were positive (Fig. 2).

Most species showed clear segregation along the axis, in a general pattern of species substitution (Fig. 2). Species in patches in regrowth-forest matrix were mostly rodents, heavier and predominately frugivorous, while those in savanna-matrix patches were mostly marsupials, lighter and predominately insectivorous. Two marsupial species, *Marmosa demerarae* and *Marmosops pinheiroi*, were present in almost all plots. There was no strong pattern associated with locomotory mode. The ANCOVA results showed taxonomic order ($F_{2, 13} = 4.35$, $P = 0.036$) and diet ($F_{2, 13} = 3.84$, $P = 0.049$) were significantly related to NMDS values, but locomotory habits were not ($F_{3, 12} = 2.81$, $P = 0.085$). Mass contributed significantly to most analyses ($F_{2, 13} = 4.35$, $p = 0.020$; $F_{2, 13} = 3.84$, $p = 0.086$; $F_{3, 12} = 2.81$, $p = 0.037$, respectively). The lack of statistical significance of mass in the analysis with diet is likely because there was a tendency for mass to differ among feeding habits (ANOVA: $F_{1, 14} = 3.95$, $P = 0.067$).

The multiple regression of the NMDS axis against the landscape variables using percentage of savanna to describe the matrix (Fig. 3; Appendix A) indicated that the proportion of savanna in the matrix (SM) contributed significantly to the multiple regression, but patch size (PS) did not. The probability that there was no effect of connectivity (Co) on composition was low ($p = 0.073$), but not statistically significant at $p = 0.05$. The partial regressions indicated a strong negative effect of SM (Fig. 3C) and a weaker positive effect of Co (Fig. 3B) on the values of the NMDS ordination, indicating these variables selected for different assemblages. Effects of patch size (Fig. 3A) were weak. The VIF for SM,

Table 1

Species of non-volant small mammals registered in this study and their mass, locomotory and dietary characteristics. All species are considered to be forest specialists (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011).

Family	Species	Weight ^a (g)	Locomotion ^b	Diet ^b
Didelphidae	<i>Caluromys philander</i>	57–270	Arboreal	Frugivore/omnivore
Didelphidae	<i>Didelphis marsupialis</i>	310–508	Scansorial	Frugivore/omnivore
Didelphidae	<i>Gracilinanus emiliae</i>	14	Arboreal	Insectivore/omnivore
Didelphidae	<i>Marmosa demerarae</i>	30–162	Arboreal	Insectivore/omnivore
Didelphidae	<i>Marmosa murina</i>	20–69	Scansorial	Insectivore/omnivore
Didelphidae	<i>Marmosops pinheiroi</i>	7–45	Scansorial	Insectivore/omnivore
Didelphidae	<i>Metachirus nudicaudatus</i>	190	Terrestrial	Insectivore/omnivore
Didelphidae	<i>Monodelphis cf. glirina</i>	63	Terrestrial	Insectivore/omnivore
Didelphidae	<i>Monodelphis aff. adusta</i>	17–29	Terrestrial	Insectivore/omnivore
Cricetidae	<i>Oecomys cf. bicolor</i>	15	Arboreal	Frugivore/seed predator
Cricetidae	<i>Oecomys cf. rutilus</i>	20	Arboreal	Frugivore/seed predator
Echimyidae	<i>Lonchothrix emiliae</i>	70–230	Arboreal	Frugivore/omnivore
Echimyidae	<i>Mesomys cf. stimulax</i>	125	Arboreal	Frugivore/omnivore
Echimyidae	<i>Proechimys roberti</i>	70–305	Terrestrial	Frugivore/granivore
Echimyidae	<i>Proechimys cf. gardneri</i>	163–185	Terrestrial	Frugivore/granivore
Echimyidae	<i>Proechimys cf. goeldii</i>	140–285	Terrestrial	Frugivore/granivore

^a Minimum and maximum weights (in grams) for each species considering all individuals caught that were weighed (including juveniles).

^b Paglia et al., 2012.

Co and PS were 1.03, 1.64 and 1.61, respectively, indicating that there was little multicollinearity among the predictor variables. Similar results were obtained for the multiple regression using the percentage of regrowth forest to describe the matrix (Fig. 4; Appendix A). The partial regressions indicated a strong positive effect of RM (Fig. 4C) and a weaker but also positive effect of Co (Fig. 4B) on the NMDS values. This indicates that these variables selected for the same assemblages. The VIF for RM, Co and PS were 1.01, 1.61 and 1.60, respectively.

A greater proportion of savanna in the matrix was associated with negative NMDS values, which represent assemblages in which marsupials predominate. Connectivity and proportion of regrowth forest in the matrix showed an opposite effect; they were associated with positive NMDS values, which represent assemblages dominated by rodents.

Even though patch size was not statistically significantly related to small-mammal composition, the probabilities associated with the null

hypothesis of no effect were relatively low (<0.15) in both multiple regression models. This, coupled with the trend for a negative effect of patch size on NMDS values, indicates that a larger sample size might be able to detect a statistically significant effect of patch size.

One plot (F20-2) was distant from the others (Figs. 3 and 4) and had high leverage. We ran the multiple-regression analyses excluding plot F20-2. The results are provided as supplementary material in Appendix B. They showed that the proportion of the variance explained by the regression models increased by about 20% and all variables became statistically significant. However, even without F20-2, the percentage of matrix type remained the most important variable, with the lowest *p*-value and the highest *r*² of the partial regression. Therefore, we consider that results with or without the high leverage plot were in general qualitatively the same and we did not exclude the plot in order to avoid information loss.

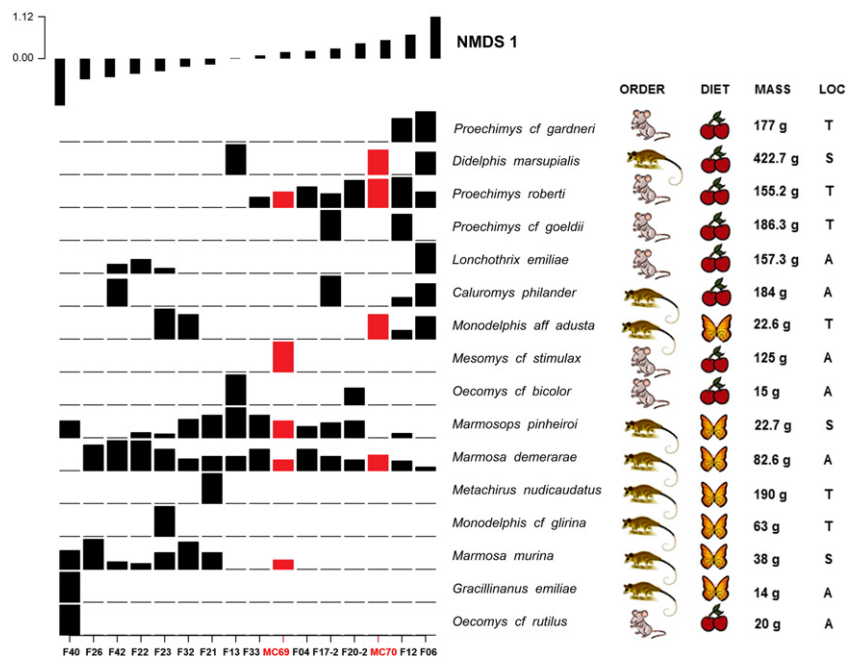


Fig. 2. Ordination of plots along the one-dimensional NMDS. The plots are indicated by their codes in the bottom of the ordination graph (from F40 to F06). The two continuous-forest plots are highlighted in red (grey in the printed version of this article). The height of bars represents the abundance relative to the total number of individuals for the species. The taxonomic order (rodent or marsupial), predominant diet (insectivore or frugivore), the mean body mass for each species in grams (g), considering all specimens captured in the field and weighed, and locomotory habits (T = Terrestrial, A = Arboreal, S = Scansorial) are given on the right of each species name. Order, diet and locomotion are according to Paglia et al. (2012).

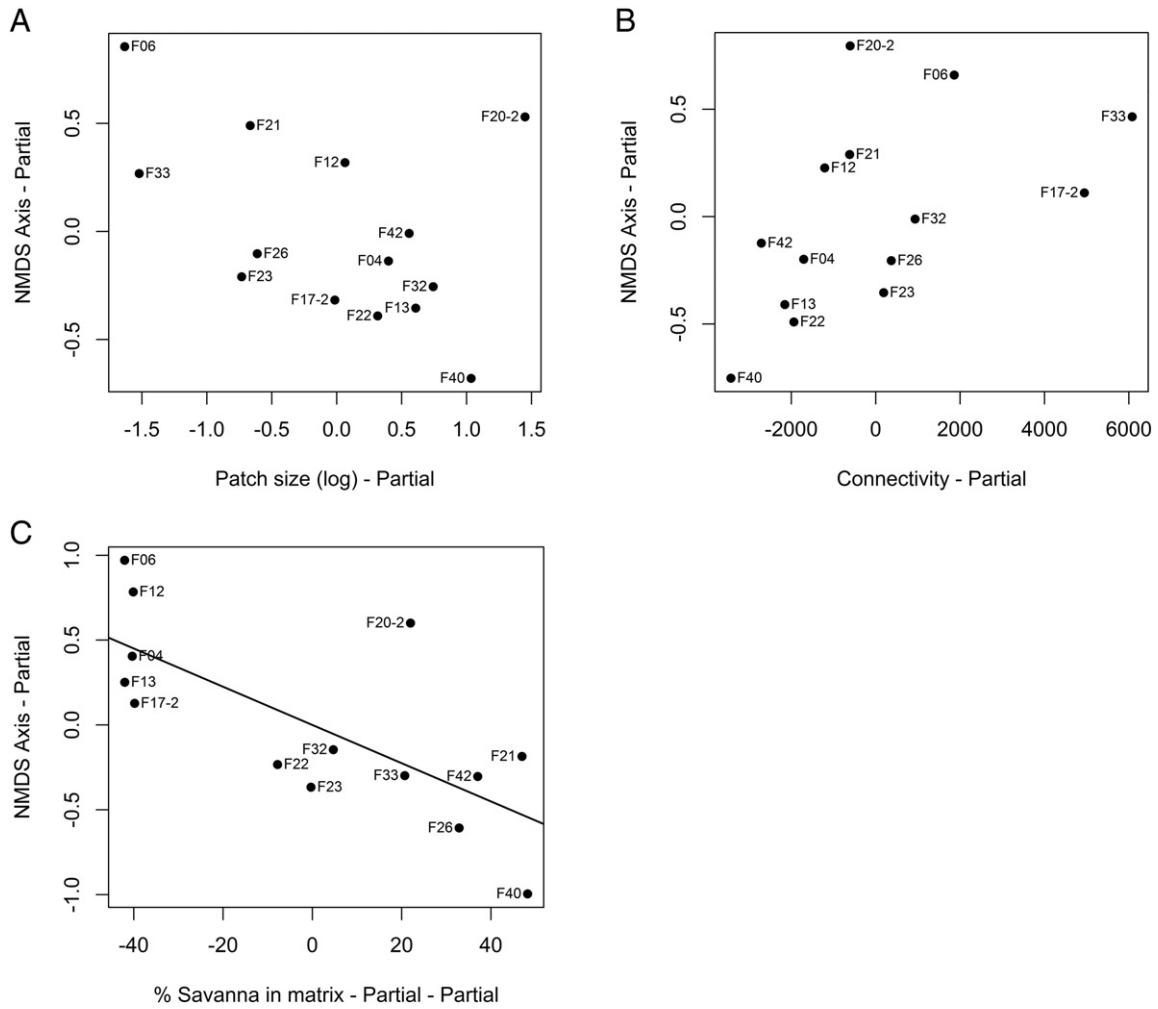


Fig. 3. Partial regressions derived from the multiple regression ($NMDS = 3.126 - 0.01126 \times SM + 8.726 \times Co - 0.2192 \times PS$; adjusted $R^2 = 0.45$, $F_{3,10} = 4.487$, P -value = 0.031) of the NMDS axis against the landscape variables patch size ($p = 0.124$, $r^2 = 0.16$ of partial regression), connectivity ($p = 0.073$, $r^2 = 0.23$ of partial regression) and percentage of savanna in matrix ($p = 0.008$, $r^2 = 0.49$ of partial regression).

4. Discussion

Even though most landscape studies have found that patch size and isolation effects on organisms are stronger than matrix effects (reviewed in [Prevedello and Vieira, 2010](#)), we found the opposite result in this study. The non-volant small-mammal assemblage composition at Alter do Chão was not statistically significantly related to patch size or connectivity, but had a strong and statistically significant relationship with matrix type. The partial regressions indicated that connectivity captured around 20% of the composition-data variance not associated with the other variables, but proportion of savanna or regrowth forest in the matrix captured more (49% and 55%, respectively). Therefore, the matrix seems to be the most important landscape variable in determining small-mammal composition in this landscape.

Similar results were found by [Santos-Filho et al. \(2012\)](#) and [Umetsu and Pardini \(2007\)](#) in fragmented landscapes in Amazonia and Atlantic Forest, respectively. Both studies found that matrix quality was strongly related to the small-mammal composition and, in the Amazonian study, matrix was the landscape element most strongly related with composition and other assemblage measures. In the [Santos-Filho et al. \(2012\)](#) study, the matrix was composed mainly of pasture, while we investigated matrices with more natural elements, which could suggest that matrix heterogeneity is important to small-mammal composition in Amazonia regardless of either anthropogenic or natural origins. In contrast, [Vieira et al. \(2009\)](#) found little influence of matrix types on the

small-mammal composition of Atlantic Forest patches. There, patch size and isolation were the most important landscape elements. Such differences could be because in the area studied by [Vieira et al. \(2009\)](#) pasture occupied the largest part of the matrix and other matrix elements covered only small areas.

Plots associated with greater connectivity were generally located in the regrowth-forest patches at Alter do Chão, and the assemblages of the regrowth-forest patches were similar to those found in continuous forest. This is probably an indication that the more forest-like habitat there is in the matrix, the more similar small-mammal assemblages become to continuous-forest assemblages. Apparently, matrix composed of regrowth forest enabled a higher degree of connectivity among older-forest patches. That is in accordance with the findings of [Baum et al. \(2004\)](#) and [Watling et al. \(2011\)](#) that matrix can enhance connectivity and improve the prediction power of connectivity measures. Another possible and non-exclusive process is that small mammals are using regrowth-forest matrix as secondary habitat. The results of [Gascon et al. \(1999\)](#) suggest that forest-species from central Amazonia, including small mammals, use matrix not only for movement, but also for reproduction. In this sense, the patches in regrowth forest could be nearly functioning as a single patch of continuous forest, even though composed of different-age forest patches.

If regrowth-forest matrix is enhancing connectivity among forest patches and may be used as habitat by small-mammal species, this type of matrix has high permeability to small mammals. Forest

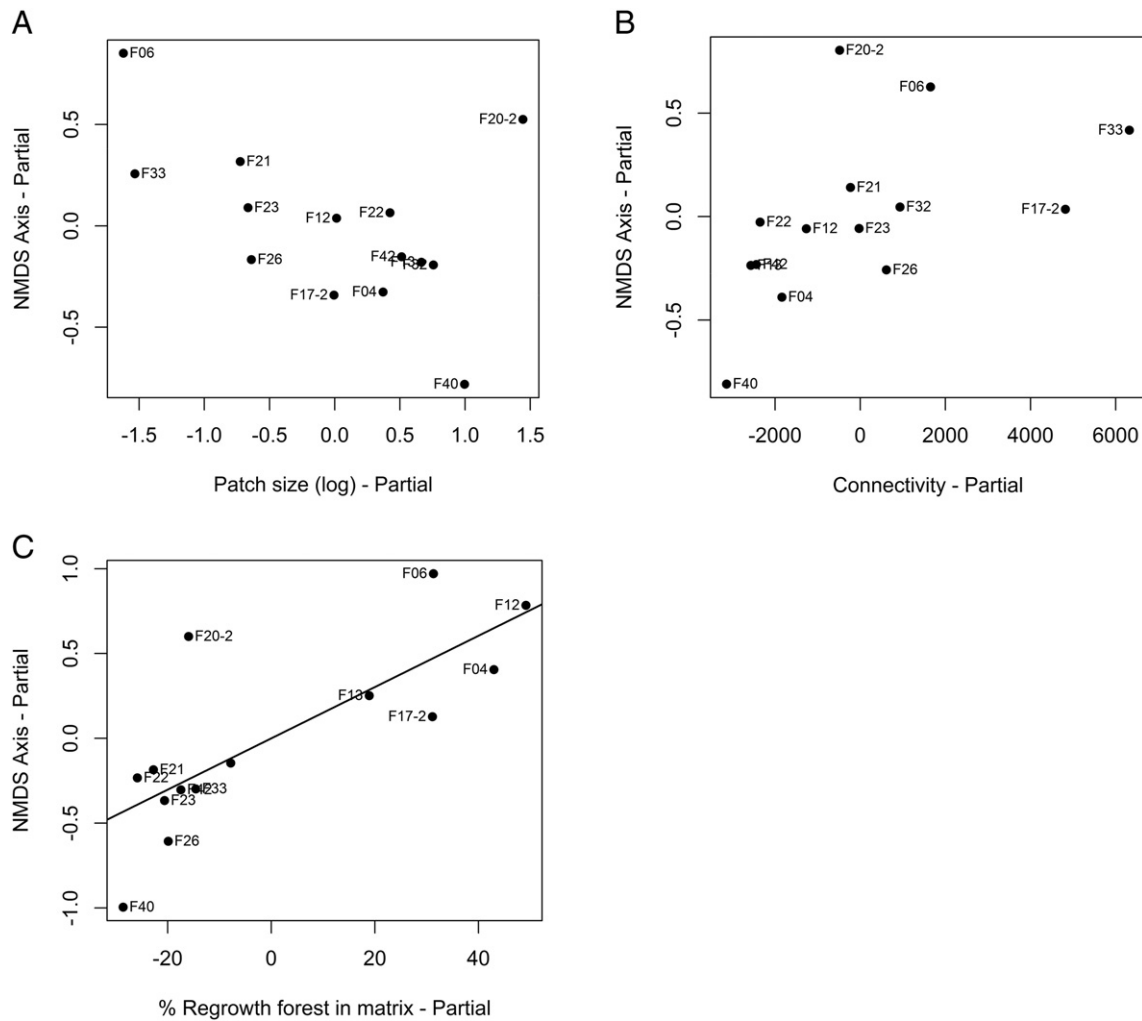


Fig. 4. Partial regressions derived from the multiple regression ($NMDS = 2.207 + 0.01512 \times RM + 7.844 \times Co - 0.2188 \times PS$; adjusted $R^2 = 0.52$, $F_{3,10} = 5.786$, P -value = 0.015) of the NMSD axis against the landscape variables: patch size ($p = 0.100$, $r^2 = 0.16$ of partial regression), connectivity ($p = 0.078$, $r^2 = 0.22$ of partial regression) and percentage of regrowth forest in matrix ($p = 0.003$, $r^2 = 0.56$ of partial regression).

regrowth is usually more permeable to forest specialists than non-forest matrices (Umetsu and Pardini, 2007; Laurance et al., 2011). Conversely, the savanna matrix may be less permeable to small mammals, since it is very different from the forest (Prevedello and Vieira, 2010). As species that occur in continuous forest also occur in forest patches completely isolated by the savanna, they must be able to disperse through the whole matrix, even though they do not establish in the savanna (W.E. Magnusson and A.P. Lima, unpubl. data). This suggests that even the least permeable matrix in this forest-savanna landscape is not an absolute barrier to the small mammals. Indeed, studies at Alter do Chão with bats, ants, large mammals and birds (Bernard and Fenton, 2007; Vasconcelos et al., 2006; Sampaio et al., 2010; Cintra et al., 2013, respectively) indicated that isolation has little effect on species richness or composition. Perhaps the way matrix is affecting small-mammal composition in forest patches is more related to how species are able to use the matrix than to permeability to movement, even though this is the most commonly recognized matrix effect on animals (Fahrig, 2007; Eycott et al., 2012). Moreover, the way matrix affects patch quality (e.g. edge effects) (Laurance et al., 2011) may be another driving process. The difference in forest structure between patches located in regrowth-forest or savanna matrix, including a notably higher occurrence of palm trees in savanna-matrix patches (C. Borges-Matos, pers. obs.), may be evidence that matrix is affecting patch quality.

Despite the trend seen in patch-size analysis and that it showed an effect when plot F20-2 was excluded, there was generally no strong

effect of patch size. The Alter do Chão matrix as a whole does not seem to be an absolute barrier to small-mammal species. If the matrix is permeable and small mammals are able to use part of it as habitat, patch size may have little influence on species composition. However, given the extensive literature, it is likely that patch size has an effect, even if we could not detect it statistically. This effect would be similar to savanna effects, because larger patches are associated with small-mammal assemblages similar to those present in savanna-matrix patches. This is counter intuitive, as larger patches are usually related to higher amount of habitat in their surroundings (Fahrig, 2003, 2013) i.e. higher connectivity, and higher connectivity was associated with the assemblages in regrowth-matrix patches. Larger forest areas are leading to assemblages dominated by rodents, while our results on patch size indicate that larger patches are dominated by marsupials. We do not have an explanation for this, but it could be that pure patch size effects are being altered by other landscape variables. Perhaps matrix type is causing cascade effects on small-mammal assemblages, affecting not only patch quality but also ecological relationships, in a way that interpretation of patch size effects depends on the patch landscape context (Fahrig, 2003).

The small-mammal species showed nonrandom clustering. Most species associated with the regrowth-forest matrix are rodents, which are mostly relatively large and mainly frugivorous, while most species associated with the savanna matrix are smaller, mostly insectivorous, marsupials. Galetti et al. (2016) found a similar pattern of diet

partitioning for rodents and marsupials of the Atlantic Forest. Nevertheless, those authors concluded that divergence in trophic niche was related to locomotor habits, not to body size, which is opposite to our findings. The authors suggested that the food resources available vary along the forest-strata gradient in the Atlantic Forest, which may not be true for the Amazonian forest plots we studied. In any case, it is not obvious why there should be species segregation at Alter do Chão. Regrowth forests often have high fruit availability (DeWalt et al., 2003), but they are also considered to have high arthropod biomass (Malcolm, 1997), providing resources for both frugivorous and insectivorous species. Hence, both groups could be expected to establish in regrowth-forest patches, but frugivorous species largely predominated. Among other possibilities are influences of patch characteristics, competition and predation. Understanding what causes the strong structure in small-mammal assemblages at Alter do Chão will require more autecological studies.

In any case, matrix type was the landscape variable most related to species composition. Connectivity was possibly related, but matrix had the largest effect, so it is the key element to enhance assemblage diversity in the Alter do Chão landscape. Results also bring knowledge about the poorly studied Amazonian-savanna systems and demonstrate their conservation value in fragmented areas. This information may be important to management of the Alter do Chão Environmental Protection Area, as further fragmentation of the forest is undergoing in the region. If it is not possible through conservation or restoration measures to have forests large enough to hold all small-mammal species, they could persist in a landscape with complementary assemblages distributed in patches surrounded by different matrices. Therefore, the maintenance of large proportions of different matrix type around patches might be key to small-mammal conservation in this and similar landscapes.

5. Conclusions

Our results indicated that patch size had no detectable effect on small-mammal species composition, and there was evidence of a slight effect of connectivity, but it was not statistically significant. However, forest-type matrix seemed to favor connectivity and may be used as secondary habitat by small mammals. This could explain that assemblages from patches in regrowth-forest matrix are more similar to those of continuous forest. Surprisingly, the matrix types surrounding forest patches were clearly and strongly related to small-mammal assemblages of patches and species showed a non-random association with matrix types. The reasons for this segregation are not clear, but may be related to the way matrix is used by small mammals and affects patch quality, rather than how it limits animal movements. Nonetheless, the types of matrix selected for different assemblages, so the matrix was the most important landscape variable to define small-mammal composition. The maintenance of both savanna and regrowth forest in the matrix could be key to small-mammal conservation in Alter do Chão and similar landscapes.

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Supplementary data (Appendices A and B)

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References

- Bailey, D., Schmidt-Entling, M.H., Eberhart, P., Herrmann, J.D., Hofer, G., Kormann, U., Herzog, F., 2010. Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *J. Appl. Ecol.* 47, 1003–1013.
- Bates, H.W., 1892. *A Naturalist on the River Amazon*. Murray, London.
- Baum, K.A., Haynes, K.J., Dilleuth, F.P., Cronin, J.T., 2004. The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85 (10), 2671–2676.
- Bender, D.J., Tischendorf, L., Fahrig, L., 2003. Using patch isolation metrics to predict animal movement in binary landscapes. *Landsc. Ecol.* 18, 17–39.
- Bernard, E., Fenton, M.B., 2007. Bats in a fragmented landscape: species composition, diversity and habitat interactions in savannas of Santarém, Central Amazonia, Brazil. *Biol. Conserv.* 134, 332–343.
- Cintra, R., Magnusson, W.E., Albernaz, A., 2013. Spatial and temporal changes in bird assemblages in forest fragments in an eastern Amazonian savannah. *Ecol. Evol.* 3 (10), 3249–3262.
- Congedo, L., Munafó, M., Macchi, S., 2013. Investigating the relationship between land cover and vulnerability to climate change in Dar Es Salaam. Working Paper. Sapienza University, Rome (Available at: http://www.planning4adaptation.eu/Docs/papers/08_NWP-DoM_for_LCC_in_Dar_using_Landsat_imagery.pdf).
- Daily, G.C., Ceballos, G., Pacheco, J., Suzán, G., Sánchez-Azofeifa, A., 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conserv. Biol.* 17 (6), 1814–1826.
- Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* 14 (2), 342–355.
- Development Core Team, R., 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria (URL <http://www.R-project.org>).
- DeWalt, S.J., Maliakal, S.K., Denslow, J.S., 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *For. Ecol. Manag.* 182, 139–151.
- Ernest, S.K.M., Brown, J.H., 2001. Delayed compensation for missing keystone species by colonization. *Science* 292, 101–104.
- Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., Pullin, A.S., 2012. A meta-analysis on the impact of different matrix structures on species movement rates. *Landsc. Ecol.* 27 (9), 1263–1278.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515.
- Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21, 1003–1015.
- Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *J. Biogeogr.* 40, 1649–1663.
- Fearnside, P.F., 2007. Brazil's Cuiabá-Santarém (BR-163) highway: the environmental cost of paving a soybean corridor through the Amazon. *Environ. Manag.* 39, 601–614.
- Galetti, M., Rodarte, R.R., Neves, C.L., Moreira, M., Costa-Pereira, R., 2016. Trophic niche differentiation in rodents and marsupials by stable isotopes. *PLoS One* 11 (4), e0152494. <http://dx.doi.org/10.1371/journal.pone.0152494>.
- Gascon, C., Lovejoy, T.E., Bierregaard Jr., R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species richness in tropical forest remnants. *Biol. Conserv.* 91, 223–229.
- Holland, G.J., Bennett, A.F., 2009. Differing responses to landscape change: Implications for small mammal assemblages in forest fragments. *Biodivers. Conserv.* 18, 2997–3016.
- INMET, 2009. Instituto Nacional de Meteorologia. Available in: <http://www.inmet.gov.br/portal/> (Accessed in 01.05.2016).
- Iriarte, J., Power, M.J., Rostain, S., Mayle, F.E., Jones, H., Watling, J., Whitney, B.S., McKey, D.B., 2012. Fire-free land use in pre-1492 Amazonian savannas. *Proc. Natl. Acad. Sci.* 109, 6473–6478.
- Kindlmann, P., Burel, F., 2008. Connectivity measures: a review. *Landsc. Ecol.* 23, 879–890.
- Laurance, W.F., 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biol. Conserv.* 141, 1731–1744.
- Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Williamson, G.B., Benítez-Malvido, J., Vasconcelos, H.L., Van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: a 32-year investigation. *Biol. Conserv.* 144, 56–67.
- Layne, V.M.G., Lima, A.P., Magnusson, W.E., 2004. Effects of fire, food availability and vegetation on the distribution of the rodent *Bolomys lasiurus* in an Amazonian savanna. *J. Trop. Ecol.* 20, 183–187.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15, 237–240.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton, NJ.

- Magnusson, W.E., Francisco, A.L., Sanaïotti, T.M., 1995. Home-range size and territoriality in *Bolomys lasiurus* (Rodentia: Muridae) in an Amazonian savanna. *J. Trop. Ecol.* 11, 179–188.
- Magnusson, W.E., Lima, A.P., Albernaz, A.L.K.M., Sanaïotti, T.M., Guillaumet, J.L., 2008. Composição florística e cobertura vegetal das savanas na região de Alter de Chão, Santarém – PA. *Rev. Bras. Bot.* 31, 165–177.
- Magnusson, W.E., Layme, V.M.G., Lima, A.P., 2010. Complex effects of climate change: population fluctuations in a tropical rodent are associated with the southern oscillation index and regional fire extent, but not directly with the local rainfall. *Glob. Chang. Biol.* 16, 2401–2406.
- Malcolm, J.R., 1997. Insect biomass in Amazonian forest fragments. In: Stork, N.E., Adis, J., Didham, R.K. (Eds.), *Canopy Arthropods*. Chapman & Hall, London, pp. 510–533.
- Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Mausel, P., Wu, Y., Li, Y., Moran, E.S., Brondizio, E.S., 1993. Spectral identification of successional stages following deforestation in the Amazon. *Geocarto Int.* 8 (4), 61–71.
- McGarigal, K., 2015. FRAGSTATS HELP v4.2: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst (Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/documents/fragstats.help.4.2.pdf>).
- McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer Software Program Produced by the Authors at the University of Massachusetts, Amherst (Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>).
- Oliveira, J.A., Bonvicino, C.R., 2011. Ordem Rodentia, pp. 358–414. In: Reis, N.R., Peracchi, A.L., Pedro, W.A., Lima, I.P. (Eds.), *Mamíferos Do Brasil*, 2ª ed. Universidade Estadual de Londrina, Londrina, PR.
- Paglia, A.P., Fonseca, G.A.B.d., Rylands, A.B., Herrmann, G., Aguiar, L.M.S., Chiarello, A.G., Leite, Y.L.R., Costa, L.P., Siciliano, S., Kierulff, M.C.M., Mendes, S.L., Tavares, V.d.C., Mittermeier, R.A., Patton, J.L., 2012. Lista anotada dos mamíferos do Brasil/Annotated checklist of Brazilian mammals. second ed. Occasional Papers in Conservation Biology No. 6. Conservation International, Arlington, VA (76 pp.).
- Pardini, R., 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. *Biodivers. Conserv.* 13, 2567–2586.
- Pardini, R., de Souza, S.M., Braga-Neto, R., Metzger, J.P., 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biol. Conserv.* 124, 253–266.
- Pavan, S.E., Jansa, S.A., Voss, R.S., 2014. Molecular phylogeny of short-tailed opossums (Didelphidae: Monodelphis): taxonomic implications and tests of evolutionary hypotheses. *Mol. Phylogenet. Evol.* 79, 199–214.
- Pimentel, D.S., Tabarelli, M., 2004. Seed dispersal of the palm *Attalea oleifera* in a remnant of the Brazilian Atlantic forest. *Biotropica* 36 (1), 74–84.
- Preston, F.W., 1962. The canonical distribution of commonness and rarity: part I. *Ecology* 43 (2), 185–215.
- Prevedello, J.A., Vieira, M.V., 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodivers. Conserv.* 19 (5), 1205–1223.
- QGIS Development Team, 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project (<http://qgis.osgeo.org>).
- Rayfield, B., Fortin, M.J., Fall, A., 2011. Connectivity for conservation: a framework to classify network measures. *Ecology* 92 (4), 847–858.
- Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158, 87–99.
- Rossi, R.V., Bianconi, G.V., 2011. Ordem Didelphimorphia pp. 31–69. In: Reis, N.R., Peracchi, A.L., Pedro, W.A., Lima, I.P. (Eds.), *Mamíferos Do Brasil*, 2ª ed. Universidade Estadual de Londrina, Londrina, PR (2011).
- Sampaio, R., Lima, A.P., Magnusson, W.E., Peres, C.A., 2010. Long-term persistence of mid-sized to large-bodied mammals in Amazonian landscapes under varying contexts of forest cover. *Biodivers. Conserv.* 19 (8), 2421–2439.
- Sanaïotti, T.M., Martinelli, L.A., Victoria, R.L., Trumbore, S.E., Camargo, P.B., 2002. Past vegetation changes in Amazon savannas determined using carbon isotopes of soil organic matter. *Biotropica* 34 (1), 2–16.
- Santos-Filho, M., Peres, C.A., Silva, D.J., Sanaïotti, T.M., 2012. Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. *Biodivers. Conserv.* 21, 1127–1147.
- Sikes, R.S., Gannon, W.L., Animal Care and Use Committee of the American Society of Mammalogists, 2011. Guidelines of the American Society of Mammalogists for the use of the wild mammals in research. *J. Mammal.* 92 (1), 235–253.
- Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Cerqueira, G.C., Garcia, R.A., Ramos, C.A., Voll, E., McDonald, A., Lefebvre, P., Schlesinger, P., 2006. Modelling conservation in the Amazon basin. *Nature* 440, 520–523.
- Solar, R.R.C., Barlow, J., Andersen, A.N., Schoederer, J.H., Berenguer, E., Ferreira, J.N., Gardner, T.A., 2016. Biodiversity consequences of land-use change and forest disturbance in the Amazon: a multi-scale assessment using ant communities. *Biol. Conserv.* 197, 98–107.
- Souza, C.M., 2002. Ocorrência e Distribuição de Pequenos mamíferos em Fragmentos Florestais Naturais Inseridos em uma Matriz de Savana Amazônica. 77 páginas. (Dissertação de Mestrado em Ciências Biológicas—Ecologia). Instituto Nacional de Pesquisas da Amazônia, Manaus (2002).
- Stenborg, P., Schaen, D.P., Amaral-Lima, M., 2012. Precolumbian land use and settlement pattern in the Santarém region, Lower Amazon. *Amazônica* 4, 222–250.
- Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conserv. Biol.* 18, 167–173.
- Sunquist, M.E., Austad, S.N., Sunquist, F., 1987. Movement patterns and home range in the common opossum (*Didelphis marsupialis*). *J. Mammal.* 68 (1), 173–176.
- Umetsu, F., Pardini, R., 2007. Small mammals in a mosaic of forest remnants and anthropogenic habitats—evaluating matrix quality in an Atlantic forest landscape. *Landsc. Ecol.* 22, 517–530.
- Vasconcelos, H.L., Vilhena, J.M.S., Magnusson, W.E., Albernaz, A.L.K.M., 2006. Long-term effects of forest fragmentation on Amazonian ant communities. *J. Biogeogr.* 33, 1348–1356.
- Vieira, E.M., Izar, P., 1999. Interactions between aroids and arboreal mammals in the Brazilian Atlantic Forest. *Plant Ecol.* 145, 75–82.
- Vieira, M.V., Olifiers, N., Delciellos, A.C., Antunes, V.Z., Bernardo, L.R., Grelle, C.E.V., Cerqueira, R., 2009. Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. *Biol. Conserv.* 142, 1191–1200.
- Watling, J.I., Nowakiwski, A.J., Donnelly, M.A., Orrock, J.L., 2011. Meta-analysis reveals the importance of matrix for animals in fragmented habitat. *Glob. Ecol. Biogeogr.* 20, 209–217.