INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA
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A MATRIZ É O ELEMENTO DA PAISAGEM MAIS IMPORTANTE PARA A COMPOSIÇÃO DE PEQUENOS MAMÍFEROS NÃO VOADORES EM UM MOSAICO AMAZÔNICO DE FLORESTA E SAVANA

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Manaus, Amazonas
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Sinopse:

Estudou-se a relação entre a composição de espécies de pequenos mamíferos da região de Alter do Chão (Município de Santarém, Pará, Brasil) e o tamanho da mancha, a conectividade local, e a proporção de distintas matrizes ao redor das manchas de floresta amostradas. Avaliou-se qual das três variáveis da paisagem é mais importante para definir a composição de espécies e as implicações destes resultados para a conservação.

Palavras-Chave: Amazônia oriental, conectividade, tamanho da mancha, ecologia de paisagem, conservação.

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“ Por tanto amor

Por tanta emoção

A vida me fez assim

Doce ou atroz

Manso ou feroz

Eu, caçador de mim

Preso a canções

Entregue a paixões

Que nunca tiveram fim

Vou me encontrar

Longe do meu lugar

Eu, caçador de mim

Nada a temer senão o correr da luta

Nada a fazer senão esquecer o medo

Abrir o peito à força numa procura

Fugir às armadilhas da mata escura

Longe se vai

Sonhando demais

Mas onde se chega assim

Vou descobrir

O que me faz sentir

Eu, caçador de mim”

Canção “Caçador de Mim”, de Sérgio Magrão e Luiz Carlos Sá, consagrada na voz de Milton Nascimento.

Resumo

Entender a dinâmica de paisagens é necessário para embasar decisões sobre o desenho de reservas, especialmente quando é preciso conciliar sobre onde e como mitigar impactos negativos quando o distúrbio é inevitável. Os efeitos do tamanho e da conectividade/isolamento de manchas sobre os organismos têm sido extensivamente estudados. Estes efeitos são fortes em geral, mas podem ser positivos ou negativos, o que leva a conclusões confusas e potencialmente enganosas. A perspectiva tamanho-conectividade é um resultado do conceito de paisagem binário de habitat e não-habitat, originado nas Teorias de Biogeografia de Ilhas e de Metapopulações, que não considera a variação na matriz. A matriz pode influenciar na qualidade e na conectividade da mancha e estudos recentes têm demonstrado que os tipos de matriz têm efeitos diferentes sobre distintas espécies. Nós testamos os efeitos de tamanho da mancha, conectividade e matriz sobre pequenos mamíferos não voadores em um mosaico semi-natural no leste da Amazônia (Alter do Chão, Pará), uma região ameaçada com a crescente pressão das atividades de pecuária e plantação de soja. Amostramos 16 parcelas padronizadas, 14 em manchas de floresta e duas em floresta contínua. Para capturar os pequenos mamíferos, utilizamos armadilhas com isca, 30 Sherman® e 30 Tomahawk®, e uma linha de armadilha de interceptação de queda com oito baldes de plástico de 60L em cada parcela, durante quatro noites, em três expedições de campo. Com ferramentas de SIG, calculamos o tamanho das manchas, a conectividade local a partir do Índice de Proximidade, e as proporções em volta de cada mancha amostrada dos dois principais tipos de matriz na paisagem: floresta em regeneração e savana amazônica. Usamos o NMDS de uma dimensão e regressão múltipla para testar as relações entre variáveis resposta e preditoras. Capturamos 178 indivíduos de 16 espécies e a ordenação com o NMDS mostrou um padrão geral de substituição de espécies, o qual foi significativamente relacionado com o tipo de matriz. A conectividade local mostrou evidências de estar positivamente relacionada com a composição de espécies, e o tamanho da mancha não teve relação significativa. Quanto maior a conectividade local das manchas, mais parecidas eram suas assembleias às das manchas situadas em matriz de floresta em regeneração, e estas assembleias eram também as mais parecidas àquelas encontradas nas parcelas de floresta contínua, o que sugere que a matriz florestal está aumentando a conectividade local de suas manchas. Houve uma segregação de espécies ao longo do gradiente de matriz. A maioria das espécies associadas à matriz de floresta em regeneração foram em geral roedores, relativamente grandes e principalmente frugívoros, ao passo que a maioria das espécies associadas à matriz de savana eram marsupiais, menores, principalmente insetívoros. Como os distintos tipos de matriz selecionam diferentes assembleias de pequenos mamíferos, a matriz aumenta a diversidade de pequenos mamíferos na paisagem estudada e isto deve ser levado em consideração no manejo da Área de Preservação Ambiental de Alter do Chão. A maior parte das espécies de pequenos mamíferos provavelmente pode ser mantida em manchas de floresta, desde que estas estejam rodeadas pela matriz apropriada.

Abstract

Understanding of landscape dynamics is necessary to support decisions about reserve design that need to take into account compromises about where and how to mitigate negative impacts when disturbance is inevitable. Patch size and connectivity/isolation effects on organisms have been extensively investigated and are usually strong, but the effects may be positive or negative, which leads to misleading conclusions. The patch-connectivity perspective is a result of the binary landscape concept of habitat and non-habitat, originated in Island Biogeography and Metapopulation Theories, so the matrix variation is not considered in many studies. The matrix may influence patch quality and connectivity, and recent studies have shown that the types of matrix may have different effects on different species. We tested the effects of patch size, connectivity and matrix on non-volant small mammals in a semi-natural mosaic in eastern Amazonia (Alter do Chão village, Pará state), a region threatened with increasing cattle and soybean activities pressure. We sampled 16 standard plots in 14 forest patches and 2 continuous forest. To capture small mammals, we used 30 Sherman® and 30 Tomahawk® baited live traps and 8 pitfall traps made of 60L plastic buckets per plot, during 4 nights, in 3 field expeditions. Using GIS tools, we calculated the patch size, local connectivity with the Proximity Index, and proportions around sampled patches of the two main types of matrix present in the landscape: regrowth forest and amazonian savananna. We used one-dimensional NMDS and multiple regression to test the relationships among response and predictor variables. We captured 178 individuals from 16 species and the NMDS ordination showed a general pattern of species turnover that was significantly related to the type of matrix. The local connectivity showed evidence to be related to species composition and patch size showed no significant relation. The greater the patch local connectivity, the more similar their assemblages were to those located in regrowth-forest matrix, and these assemblages were also more similar to those in the continuous-forest plots, which suggests regrowth-forest matrix is enhancing local connectivity to its patches. There were a segregation of species along the gradient from patches immersed in savanna matrix to those in regrowth-forest matrix. Most species associated with the regrowth-forest matrix were rodents, which are mostly relatively large and mainly frugivorous, while most species associated with the savanna matrix were smaller, mostly insectivorous, marsupials. As different types of matrix selected for different kinds of small-mammal assemblages, the matrix enhances small-mammal diversity in the landscape studied and this should be taken into consideration in management of the Alter do Chão Environmental Protection Area. Most small-mammal species can probably be maintained in forest fragments as long as these are surrounded by the appropriate matrix.

Sumário

Introdução

Compreender as dinâmicas de paisagem pode levar a um melhor entendimento do funcionamento dos ecossistemas e da persistência de espécies. O uso da terra incrementa a dinâmica das paisagens, criando alteração e fragmentação de habitats. Por outro lado, a fragmentação que causa redução das manchas de habitat e aumento no isolamento entre estas manchas afeta a diversidade e abundância de espécies. O tamanho da mancha normalmente apresenta efeitos fortes sobre o número de espécies (Laurance et al., 2011), conforme prediz a relação espécie-área (Preston, 1964). Entretanto, essa relação nem sempre é positiva (Laurance et al., 2011; Fahrig 2003), o que pode levar a conclusões equivocadas (Debinski & Holt, 2000; Fahrig, 2003, 2013). Os efeitos do isolamento também são fortes, apresentando em geral relações negativas com o número e a abundância de espécies (Debinski & Holt, 2000), e distintas relações com composição de espécies (Pardini et al, 2005; Vieira et al., 2009). O isolamento pode ser medido em termos de quantidade de conectividade, mas algumas medidas de conectividade são consideradas mais realistas do que outras (Kindlmann & Burel, 2008; Rayfield et al., 2011; McGarigal, 2015). O uso de medidas menos apropriadas, como a distância ao vizinho mais próximo, pode levar a conclusões errôneas (Fahrig, 2013; Bender et al., 2003) e medidas de conectividade que consideram a área das manchas localizadas a determinado raio de distância da mancha focal são geralmente mais apropriadas para indicar sua efetiva conectividade local (Bender et al., 2003).

Esta perspectiva de tamanho-conectividade é resultado do conceito de paisagem binário de habitat e não habitat, originado nas Teorias de Biogeografia de Ilhas e de Metapopulações. Dessa foram, a qualidade da matriz não tem sido considerada em muitos estudos (Ricketts, 2001; Prevedello & Vieira, 2010), o que pode levar a resultados confusos (Laurance, 2008). A matriz é um dos elementos de paisagem que podem influenciar a qualidade e a conectividade da mancha de várias formas (Laurance et al., 2011). Os efeitos da matriz têm recebido crescente atenção e estudos recentes demonstraram que os tipos de matriz podem ter efeitos diferentes em espécies ou taxa distintos (Ricketts, 2001; Prevedelo & Vieira, 2010; Watling et al., 2011). Embora Prevedello e Vieira (2010) tenham encontrado que em 95% dos estudos revisados por eles o tipo de matriz tem efeitos importantes, em 56% destes estudos as variáveis de tamanho e isolamento da mancha tiveram efeitos mais fortes que os da matriz. Assim, os efeitos da matriz podem ocorrer em várias intensidades e são ainda pouco compreendidos.

A forma de medir a estrutura da assembleia também pode ser um dos fatores que causam confusão na interpretação dos resultados. A medida mais comumente utilizada é a riqueza de espécies. No entanto, esta medida não é apropriada para as assembleias que se estruturam de forma diversa à de subconjuntos aninhados. Nestes casos, a composição de espécies pode ser uma medida mais adequada. De fato, a complementariedade de espécies entre locais é recomendada para selecionar locais para conservação (Margules & Pressey, 2000), e estudos recentes têm mostrado que a composição de espécies responde clara e fortemente a mudanças ambientais (Magnusson et al, 2013), inclusive mais fortemente que medidas de riqueza de espécies (Su et al., 2004; Vieira et al., 2009; Solar et al, 2016).

A floresta tropical amazônica permanece como uma das maiores e menos fragmentadas do mundo. Entretanto, ela já perdeu cerca de 12% de sua extensão original e projeções dizem que perderá ainda mais, de 9 a 28% até 2050, especialmente nas áreas mais secas ao longo de seus limites ao sul (Soares-Filho et al., 2006, 2013). As ameaças à Amazônia advêm principalmente das atividades de pecuária e de cultura de soja (Soares-Filho et al., 2006), que geralmente causam a fragmentação de habitat naturais. Estradas são ameaças que normalmente acompanham as atividades de agricultura (Soares-Filho et al., 2006), e uma porção grande do oeste do estado do Pará é alvo de impactos causados pela BR-163, que liga Cuiabá, no Mato Grosso, a Santarém, no Pará (Nepstad et al, 2002; Fearnside, 2007). A área ao redor da vila de Alter do Chão, município de Santarém, é coberta por uma paisagem fragmentada semi-natural, com dois tipos de matriz predominantes em extensão, e compõe parte da Área de Proteção Ambiental (APA) de Alter do Chão. Em uma das matrizes predomina uma floresta em regeneração e na outra predomina savana amazônica, ambas fisionomias muito distintas e, portanto, capazes de afetar de formas diferentes os organismos que vivem nesta paisagem. Apesar de não se tratar de uma paisagem com fragmentação tipicamente antrópica, Alter do Chão oferece uma oportunidade de investigar quais características da matriz afetam sistemas de manchas de habitat, seja um sistema natural ou perturbado (Roland et al., 2000). Dessa forma, entender como os organismos respondem à fragmentação nesta paisagem pode melhorar a eficiência de ações futuras de manejo na região.

Os pequenos mamíferos não voadores são um grupo adequado para se estudar os efeitos da paisagem, pois eles respondem claramente a mudanças causadas pela fragmentação e pela perda de habitat (Bierregaard et al 1992; Laurance 1994; Lynam et al 1999; Founier-Chambrillon et al 2000; Pardini et al., 2005; Umetsu & Pardini, 2007; Santos-Filho et al., 2012). Alguns estudos mostraram que morcegos (Bernard & Fenton, 2003, 2007) e mamíferos médios ou grandes (Sampaio et al, 2010) foram pouco afetados pelos efeitos da fragmentação próximo a Alter do Chão, principalmente devido à sua alta mobilidade. Pequenos mamíferos são presumivelmente menos móveis que os outros mamíferos, o que faria deles organismos mais sensíveis aos efeitos do isolamento e da matriz. Ainda, eles têm papeis ecológicos importantes pois são consumidores primários e secundários (Rossi & Bianconi, 2011; Oliveira & Bonvicino, 2011; Paglia et al., 2012), presas para várias espécies animais (Rossi & Bianconi, 2011; Oliveira & Bonvicino, 2011), e são predadores e dispersores de semente (Grelle and Garcia, 1999; Vieira and Izar, 1999; Pimentel and Tabarelli, 2004). Isto indica que esses animais contribuem para a regeneração de florestas (Wright & Duber, 2001; DeMattia et al 2004; DeMattia et al 2006).

Neste trabalho nós testamos os efeitos do tamanho da mancha, da conectividade local e do tipo de matriz sobre a estrutura das assembleias de pequenos mamíferos não voadores das manchas de floresta na paisagem de Alter do Chão. O objetivo foi descobrir qual dessas variáveis da paisagem está mais relacionada com a estrutura da assembleia, esta medida através da composição de espécies, uma vez que já foi verificado para os pequenos mamíferos que a composição responde melhor a mudanças ambientais do que a riqueza (Mende-Oliveira et al., 2015).

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Objetivos

Objetivo geral:

Testar a hipótese de que a variação nos tipos de matriz pode ser tão ou mais importante do que as variáveis da paisagem mais comumente testadas, conectividade e tamanho da mancha, para determinar a composição de espécies de pequenos mamíferos não voadores em uma paisagem de mosaico floresta-savana, situada no leste da Amazônia.

Objetivos específicos:

1 – Identificar as espécies de pequenos mamíferos que ocorrem atualmente nas manchas de floresta do mosaico;

2 – Verificar se há um padrão na composição das espécies das manchas amostradas;

3 – Descrever as variáveis da paisagem tamanho da mancha, conectividade local e proporções ao redor das manchas dos dois principais tipos de matriz existentes;

4 – Testar qual é a relação entre o padrão da composição de espécies de pequenos mamíferos e as três variáveis da paisagem.

Capítulo I.

Borges-Matos, C.; Aragón, S. C.; da Silva, M. N. F.; Fortin, M. J. & Magnusson, W. E. **The matrix is what matters the most to small mammals in an Amazonian forest-savanna mosaic.** Manuscrito em preparação para *Biological Conservation*.

The matrix is what matters the most to small mammal in an Amazonian forest-savanna mosaic.

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THE MATRIX IS WHAT MATTERS THE MOST TO SMALL MAMMALS IN AN AMAZONIAN FOREST-SAVANNA MOSAIC

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Keywords: Eastern Amazon, connectivity, patch size, landscape ecology, conservation.

Abstract

Patch size and connectivity/isolation effects on organisms and are usually strong, but may be positive or negative, which leads to confounding results. This binary habitat/non-habitat perspective fails to consider matrix heterogeneity. The matrix influences patch quality and connectivity differently for different species. We tested the effects of patch size, connectivity and matrix type on non-volant small-mammal assemblages in a semi-natural mosaic in eastern Brazilian Amazonia. We sampled 14 forest-patch and 2 continuous-forest plots, using 60 baited live traps and 8 pitfall traps (60L) per plot in 3 field expeditions. We calculated the local connectivity with the Proximity Index and the matrix type as the proportions of savanna or regrowth forest around forest patches. We used one-dimensional NMDS and multiple regression to test the relationships among response and predictor variables. We captured 178 individuals of 16 small-mammal species and the one-dimensional NMDS ordination showed a pattern of species turnover that was strongly related to matrix type. There was evidence of an effect of local connectivity on assemblage composition, but not for patch size. Regrowth forest in the matrix appears to enhance local connectivity among patches. Species associated with regrowth-forest matrix were mostly rodents that were relatively large and mainly frugivorous, while species associated with savanna matrix were smaller, mostly insectivorous, marsupials. Each matrix type was associated with distinct small-mammal assemblages, so matrix variation enhances small-mammal diversity in the landscape studied. This should be taken into consideration in regional conservation-unit management plans.

1. Introduction

Understanding landscape dynamics can lead to better understanding of ecosystem functions and species persistence. Land-use accentuates landscape dynamics creating habitat alteration and fragmentation. In turn, fragmentation by reducing habitat patches and increase the isolation among habitat patches affect species diversity and abundance. Indeed patch size usually has strong effects on species number (Laurance et al., 2011), as predicted by the species-area relationship (Preston, 1964). However, this relationship is not always positive (Laurance et al., 2011; Fahrig 2003), which leads to equivocal conclusions (Debinski and Holt, 2000; Fahrig, 2003, 2013). Habitat isolation has also strong effects, usually showing negative relationships with the number and the abundance of species (Debinski and Holt, 2000), and different relationships with species composition (Pardini et al., 2005; Vieira et al., 2009). Habitat isolation can be measured in terms of the amount of the 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).

The patch-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; Hanski, 1998). This approach ignores the quality of the matrix (Ricketts, 2001; Prevedelo and Vieira, 2010), which can lead to confounding results (Laurance, 2008). The matrix is in fact one of the landscape elements that 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 a meta-analysis performed by Prevedello and Vieira (2010), 95% of the studies they reviewed showed effects of the type of matrix, but in 56% of these studies patch and isolation variables had greater effects than did the matrix. Therefore, matrix effects may have varied intensities and are still poorly understood.

The way to measure assemblage structure also can be one of the factors that cause confusion in results interpretation. The most commonly used measure is species richness, but it is not appropriate to the assemblages that has a structure other than nested subsets. In these cases, species composition can be a more adequate measure. Indeed, species complementarity among site is recommended for selecting sites for conservation (Margules and Pressey, 2000) and recent studies have shown that species composition responds strong and clearly to environmental changes (Magnusson et al, 2013), and much more so than species richness measures (Su et al., 2004; Vieira et al., 2009; Solar et al, 2016).

The Amazon tropical forest remains one of the largest and least fragmented landscapes in the World, but it has already lost about 12% of its original extent and projections say it will lose another 9 to 28% by 2050, especially in drier areas along its southern border (Soares-Filho et al., 2006, 2013). Threats to the Amazon are mainly from cattle and soy-bean culture (Soares-Filho et al., 2006), activities that most commonly cause fragmentation of natural habitats. Highways are a threat that usually accompanies agricultural activities (Soares-Filho et al., 2006), and a large portion of western Pará state is subject to impacts caused by the BR-163 Highway, that links Cuiabá in Mato Grosso to Santarém in Pará (Nepstad et al., 2002; Fearnside, 2007). The area around Alter do Chão village, Santarém Municipality, is covered by a semi-natural fragmented landscape with different matrix types, and forms part of an Environmental Protection Area (EPA). Even though it is not a typical human-fragmented landscape, it offers the opportunity to investigate which characteristics of the matrix affect a system of habitat patches, whether they are natural or disturbed (Roland et al., 2000). Therefore, understanding how organisms respond to fragmentation in this landscape can improve the efficiency of future management actions in the region.

Non-volant small mammals are a suitable group to study landscape effects, as they clearly respond to changes in the landscape caused by fragmentation and habitat loss (Bierregaard et al., 1992; Laurance 1994; Lynam, 1997; Founier-Chambrillon et al., 2000; Pardini et al., 2005; Umetsu and Pardini, 2007; Santos-Filho et al., 2012). Some studies have shown that bats (Bernard and Fenton, 2003, 2007) and medium and large mammals (Sampaio et al., 2010) were little affected by fragmentation effects near Alter do Chão, mostly due to their high mobility. Small mammals are presumably less mobile than the other mammals, which possibly makes them more sensitive to isolation and matrix effects. In addition, they play important ecological roles as primary and secondary consumers (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011; Paglia et al., 2012), prey of many species (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011), and seed predators and dispersers (Grelle and Garcia, 1999; Vieira and Izar, 1999; Pimentel and Tabarelli, 2004). The latter indicates that small mammals contribute to forest regeneration (Wright and Duber, 2001; DeMattia et al., 2004; DeMattia et al., 2006).

Here we tested the effects of patch size, local connectivity and matrix type on the structure of non-volant small-mammal assemblages of forest patches in the Alter do Chão landscape, Pará State. The objective was to find out which, if any, of these landscape variables is more related to small-mammal assemblage structure, which was measured through species composition, as it was verified for small mammals that composition responds more strongly to environmental changes than richness (Mendes-Oliveira et al., 2015).

2. Material and Methods

2.1. Study Area

Alter do Chão is a village in Santarém Municipality, Pará State, on the right bank of Tapajós River. The climate is humid tropical, with rainy season between December and June - 75% of the annual precipitation - and March as the rainiest month (331 mm), and dry season between July and November, with September as the driest month (30 mm). The coldest month is July (mean temperature of 25°C) and the hottest is October (mean temperature of 26°C) (INMET, 2009).

The village is surrounded by a mosaic composed mainly of patches of forest immersed in an Amazonian-savanna matrix, the latter surrounded by continuous forest, all forests are considered semi-deciduous tropical forest (Cintra et al., 2013). The Tapajós River borders the western and northern portions of the area (Figure 1). The savanna is covered mostly by herbs and grasses with some sparse trees, even though there is a gradient of greater and lesser tree cover (Magnusson et al., 2008). The forest has a relatively open understory, with tree species common in the region (Sanaiotti et al., 2002). 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 these patches are at least 150 years old, and probably much older. The matrix transition to a savanna may have been a consequence of the fires induced by paleoindian agriculture (Serena, 1984), as this region has been inhabited for millennia (Neves, 2006).

The savannas around Alter do Chão burn at intervals of 1-3 years, mainly due to human activities (Magnusson et al., 2010). There is an area of forest-transition vegetation on the northern portion of the region, which is probably an old savanna that has not burnt 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 Mausel et al. (1993), this matrix can be considered a forest in advanced secondary succession (>30 years), and forests of the patches and continuous forest can be considered as mature forest. The patches have undergone different degrees of exploitation, such as rubber extraction in the past (about 30 years ago) and hunting until nowadays (C. Borges-Matos, pers. obs.).

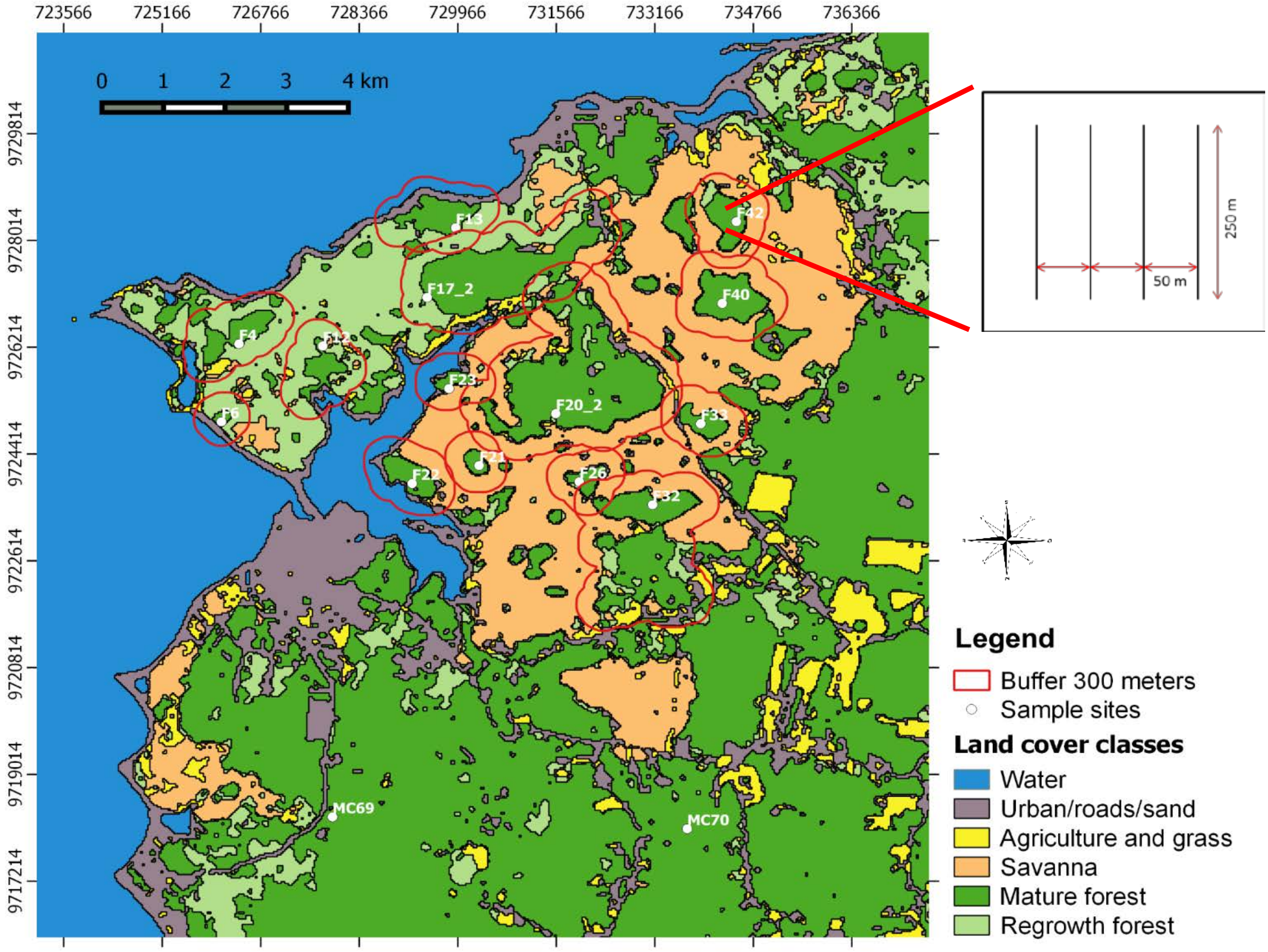

Figure 1: Six distinct classes of land cover in the study area. Each plot sampled has their respective code. F=Patch, MC=Continuous Forest. The arrangement of sampling lines within each plot is shown in the top right. Alter do Chão village is located in the larger gray area in the mapa.

2.2. Site Samples

All plots were sampled for small mammals in May/June (wet season), August/September (dry season) and October/November (dry season) of 2015. We sampled 16 plots: 14 in forest patches and 2 in continuous forest (Figure 1).

Patches were chosen according to facility of access and to maintain little overlap among their buffers (see section 2.4). Each patch or continuous forest point had only one plot. The standard plot consisted of four parallel 250 m straight lines separated from each other by 50 m (Figure 1). Four of the patches that were too small for the standard plot lines had either 3 or 5 lines, but the total length of the lines was 1 km, so the area sampled was approximately equal for all plots.

The matrix was not sampled because we were interested only in forest-dwelling small mammals, and all species already registered for the plots (Souza, 2002; A.P. Lima, unpubl. data) are considered forest species (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011). However, the savanna matrix has been surveyed intensively for small mammals during the past 29 years (Magnusson et al., 1995; Layme et al., 2004; Ghizoni et al., 2005; Magnusson et al., 2010; W.E. Magnusson and A.P. Lima, unpubl. data) and the only species of small mammal regularly found in the savanna was *Necromys lasiurus*, a species that has not been recorded in forest in the region. The only forest species captured during these three decades of research were a few individuals of the genus *Proechimys* (species not identified), captured in small clumps of bushes adjacent to forest, and a few juvenile *Didelphis marsupialis* (W.E. Magnusson and A.P. Lima, unpubl. data). *Didelphis marsupialis* has been seen in the middle of the savanna at night, but no other species of small mammal has been recorded more than 50 m from forest.

2.3. Small-mammal data collection

We used the same number, type and arrangement of traps in all plots, for the same number of nights. In each plot we used 30 Sherman® (8 x 9 x 20 cm) and 30 Tomahawk® live traps (15 x 15 x 35 cm), and 8 pitfall traps made of 60L plastic buckets. We positioned the live traps at 15 m intervals along the grid lines. Traps were set in the following sequence: a Sherman trap on the ground, a Tomahawk trap on the ground on one side of the line, a Sherman trap 2 m above ground, a Tomahawk trap 2 m above ground on the other side of the line. The sequence was repeated along the 1000 m of trap line in each plot. In the four plots that had 3 or 5 lines, some of the distances between traps had to be reduced (minimum distance of 10 m) to accommodate the 60 traps. Traps were baited with a mixture of peanut butter, corn meal and kitchen oil, a slice of banana and a cotton wad impregnated with a cod-liver oil.

Pitfall traps were disposed in a single line, 10 meters distant from each other and connected by a 60cm-high plastic fence. The pitfall-trap line was always 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 plot F13 (not sampled in the third expedition) and plot MC69 (sampled for only one night during the third expedition) due to problems with landowner permission. Sampling lasted 5 days in all plots. We installed the traps on the first day and effective sampling occurred over the following 4 nights. We sampled 2 or 3 plots simultaneously, depending on logistical limitations. During the four sampling days, 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. All other individuals were marked with numbered tags (Monel Small Animal Ear Tag, size 1, LOG Materiais®) and released. Recapture data were not included in our analysis. All procedures were carried out under Instituto Chico Mendes de Biodiverisdade (ICMBio) license number 47376-1 and INPA Ethical Committee authorization (protocol 004/2015).

2.4. Landscape-variable metrics

We generated a map of the Alter do Chão region to calculate values of the predictor landscape variables. 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/), in the website's original datum WGS 84, UTM 21N. After correcting the image by adjusting for surface reflectance and making atmospheric correction, we 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 training areas, using the Semi-Automatic Classification Plugin (SCP) (Congedo et al., 2013) available in QGIS. We calculated the classification accuracy with the SCP tool Accuracy and the total accuracy was 97.5%.

We recognized six principal land cover classes in our landscape, which we refer to as follows: “water”, “urban/road/sand”, “agriculture and grass”, “savanna”, “mature forest” and “regrowth forest”. Urban, roads, and sand (mostly beaches) were classed together because they have similar spectral responses and ecological restriction for the small mammals. Grass in “agriculture and grass” can correspond either to pasture or to small patches of natural grasslands without trees. “Regrowth forest” corresponds to the savanna in transition to forest, the forest in advanced secondary succession (Mausel et al., 1993), which dominated the matrix in the northwest of the study area.

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. We calculated the percentages of savanna (SM) and of regrowth forests in the matrix (RM) in a buffer around each patch. We calculated a 300 m wide buffer around each sampled patch (Figure 1) using the QGIS geoprocessing tool Buffer and then calculated the percentage of each type of matrix in each buffer area using QGIS and Excel. We chose the radius of 300 m because it was the largest size that avoided high overlap among buffers of different patches. The proportion of the buffer with each matrix component was used rather than the amount of each component to avoid correlation with patch size. Local connectivity (LC) 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 of all patches that at least touch a pre-established buffer around focal patch (m^2) divided by the nearest edge-to-edge distance squared from the same patches to the focal patch (m^2). We used the same 300 m buffer as for the components of the matrix. LC is adimensional, so LC values are relative, and here they were divided by 100000 for ease of presentation.

2.5. Data analysis

We used non-metric multidimensional scaling (NMDS) to reduce the dimensionality of the species composition to one axis, based on the dissimilarity version of the Bray-Curtis index after site standardization by division by the total. We compared the proportion of the variance in the 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 of relationships 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. All analyses were performed using the R software (R Development Core Team, 2015).

The two measures of matrix composition, proportion of savanna in matrix (SM) and proportion of regrowth forest in matrix (RM) were largely, but not completely, complementary because they were the largest components of the matrix. They were also highly negatively correlated (Pearson's r = -0.873), so they cannot be included in the same regression. We decided a priori to use SM, but the results for RM, which were qualitatively similar, are provided as supplementary material in the Appendix A.

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 2 cricetid rodents, 5 echymid rodents and 9 didelphid marsupials (Table 1). The identity of some species cannot be determined with certainty based on morphology, which is why some species identities are given as *cf*.

Table 1: Taxonomy of non-volant small-mammal species 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	*Caluromys philander*	57-270	Arboreal	Frugivore/omnivore
Didelphidae	*Didelphis marsupialis*	310-508	Scansorial	Frugivore/omnivore
Didelphidae	*Gracilinanus emiliae*	14	Arboreal	Insectvore/omnivore
Didelphidae	*Marmosa demerarae*	30-162	Arboreal	Insectvore/omnivore
Didelphidae	*Marmosa murina*	20-69	Scansorial	Insectvore/omnivore
Didelphidae	*Marmosops pinheiroi*	7-45	Scansorial	Insectvore/omnivore
Didelphidae	*Metachirus nudicaudatus*	190	Terrestrial	Insectvore/omnivore
Didelphidae	*Monodelphis* cf. *glirina*	63	Terrestrial	Insectvore/omnivore
Didelphidae	*Monodelphis* aff. *adusta*	17-29	Terrestrial	Insectvore/omnivore
Cricetidae	*Oecomys* cf. *bicolor*	15	Arboreal	Frugivore/seed predator
Cricetidae	*Oecomys* cf. *rutilus*	20	Arboreal	Frugivore/seed predator
Echimyidae	*Lonchothrix emiliae*	70-230	Arboreal	Frugivore/omnivore
Echimyidae	*Mesomys* cf. *stimulax*	125	Arboreal	Frugivore/omnivore
Echimyidae	*Proechimys roberti*	70-305	Terrestrial	Frugivore/granivore
Echimyidae	*Proechimys* cf. *gardneri*	163-185	Terrestrial	Frugivore/granivore
Echimyidae	*Proechimys* cf. *goeldii*	140-285	Terrestrial	Frugivore/granivore

[a] Minimum and maximum weights considering all individuals caught (including juveniles) and weighed for each species.
[b] Paglia et al., 2012.

An NMDS ordination in one dimension captured 72% of the variance in the original Bray-Curtis distances among plots. Most species showed clear segregation along the axis and tended to be clustered to the left, distributed across all sites, or to the right of the ordination (Figure 2). The general pattern was of turnover, rather than nestedness or spatial-guild structure. Species aggregated to the right of the ordination were mostly rodents and those on the left were mostly marsupials. Two marsupial species, *Marmosa demerarae* and *Marmosops pinheiroi*, were present in almost all plots. There was segregation of body weights and diets along the NMDS axis: heavier and mostly frugivorous species were clustered to right and lighter mostly insectivorous species were clustered to the left or distributed across all sites. Locomotion habits did not seem to influence in species segregation along NMDS axis.

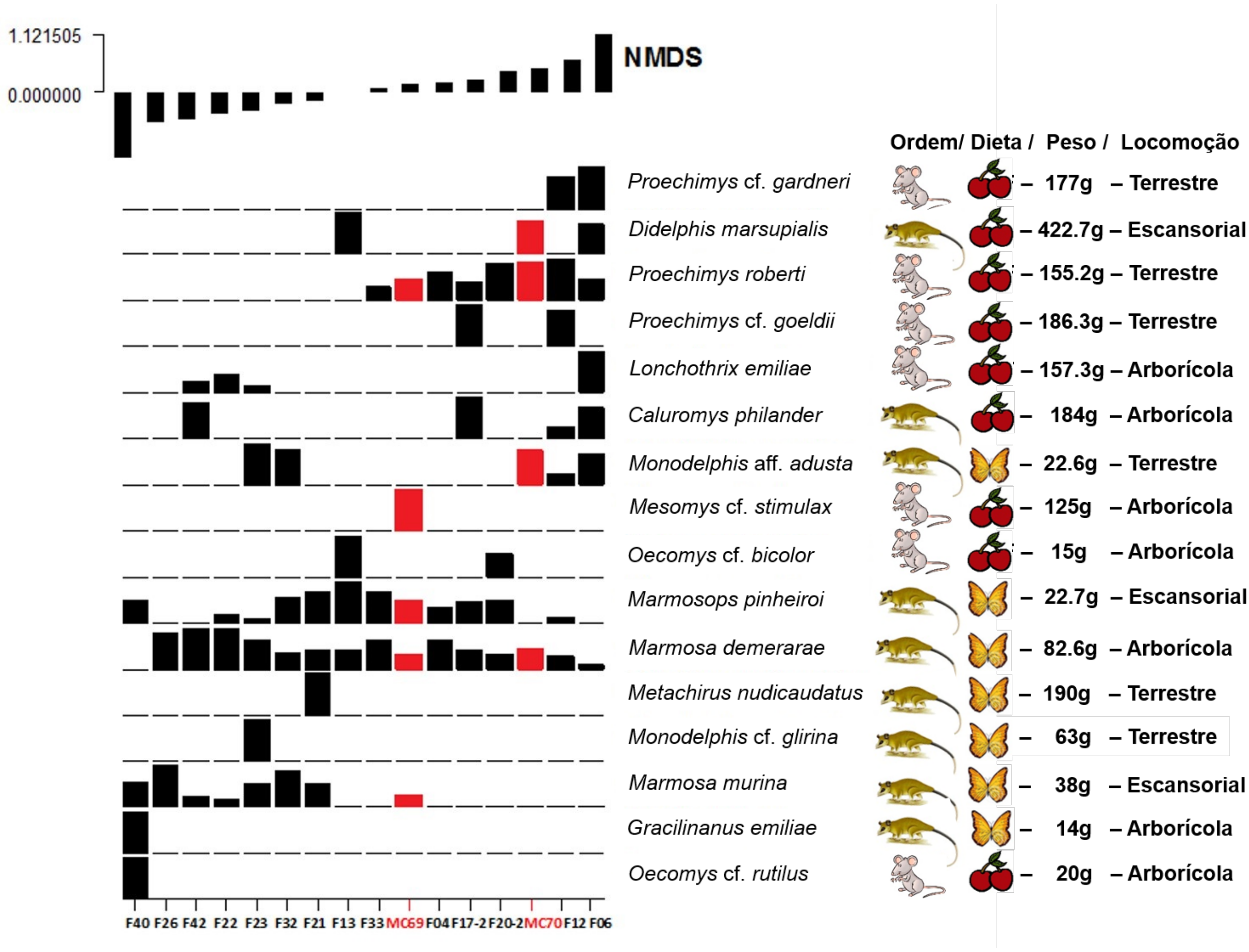

Figure 2: Ordination of plots along the one-dimensional NMDS. The two continuous-forest plots are highlighted in red. The height of bars represents the abundance relative to the total for the species. On the right of each species there are information about their order (rodent or marsupial), diet (insectivore or frugivore), the mean weight for each species in grams (g), considering all specimens captured and weighed, and locomotion habits.

The multiple regression of the NMDS axis against the landscape variables using percentage of savanna to describe the matrix (NMDS = 3.126 - 0.01126 *SM + 8.726*LC - 0.2192*PS, adjusted R^2=0.45, $F_{3,10}$= 4.487, p=0.031) showed that proportion of savanna in matrix (SM) (p=0.008) contributed significantly to the multiple regression, but patch size (PS) did not (p=0.124). Local connectivity (LC) showed evidence of having some effect on composition (p=0.073), even though its p-value was above 0.05. The partial regressions indicated a strong (r^2=0.49 for the partial regression) negative effect of SM (Figure 3C) and a weaker (r^2=0.23 for the partial regression) positive effect of LC (Figure 3B) on the values of the NMDS ordination. Effects of patch size (Figure 3A) were low (r^2=0.16 for the partial regression). The VIF for SM, LC and PS were 1.03, 1.64, 1.61, respectively, indicating that there was little multicollinearity among the predictor variables.

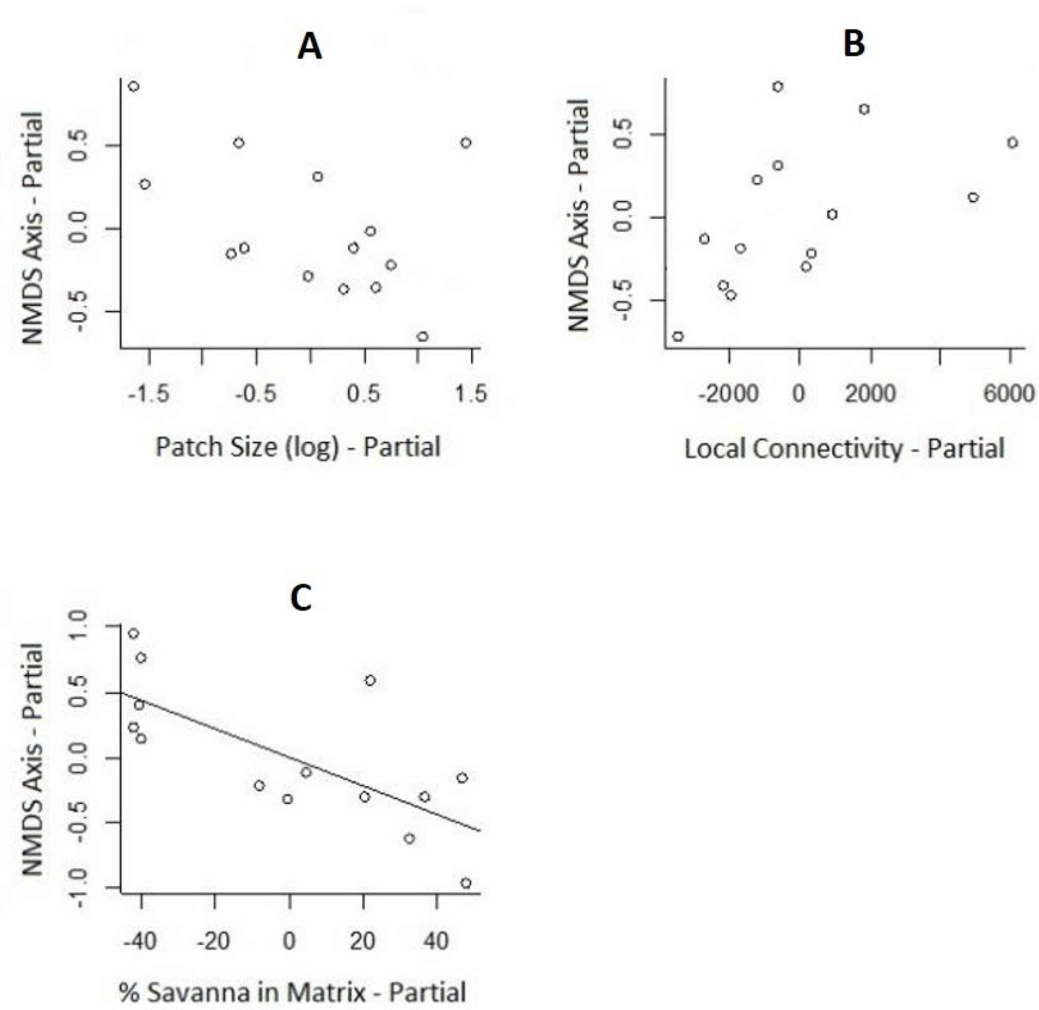

Figure 3: Partial regressions derived from the multiple regression of the NMDS axis against the landscape variables patch size, local connectivity and percentage of savanna in matrix.

Greater proportion of savanna in the matrix was associated with negative NMDS values, which are on the left side of the ordination graph (Figure 2). Local connectivity and RM (Appendix A) showed an opposite effect. They are associated with positive NMDS values, which are on the right side of the ordination graph (Figure 2).

Even though patch size was not statistically significantly related to small-mammal composition, it presented *p*-values < 0.15 in both models. Thus, there was a trend for a negative effect of patch size on NMDS values, which might indicate a type II error.

4. Discussion

Even though most landscape studies have found that patch size and isolation effects on organisms are stronger than matrix quality effects, as seen in Prevedello and Vieira (2010) review, we found an opposite result in this study. The non-volant small-mammal assemblage composition at Alter do Chão was little related to patch size, but was related to local connectivity and the composition of the matrix. The partial regressions indicated that local connectivity captured around 20% of the composition-data variance not associated with the other variables, but the proportion of savanna in the matrix or the proportion of 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 the matrix quality was strongly related to the small-mammal composition and, in the Amazonian study, matrix was the landscape element most strongly related to composition and other assemblage measures. 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 different results could be because in Vieira et al. (2009) study pasture occupied the largest part of the matrix and the other elements of the matrix covered only small areas.

Assemblages 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. Thus, the matrix composed of regrowth forest apparently enabled a higher degree of connectivity among older-forest patches, and they could be functioning as a single patch of continuous forest, even though composed of different-age forest patches. That is in accordance with the findings of Baum et al. (2004) that the matrix can enhance the effectiveness of both stepping-stones and corridors, and with the conclusion of Watling et al. (2011) that connectivity measures that incorporate matrix characteristics are better predictors of wildlife abundance and occupancy.

If regrowth forest matrix is enhancing connectivity among forest patches, this type of matrix has high permeability to small-mammal species. Forest regrowth is usually more permeable to forest specialists than non-forest matrices (Pardini, 2005; Umetsu and Pardini, 2007; Predevello and Vieira, 2010; Laurance et al., 2011). Conversely, the savanna matrix may be less permeable to small mammals, since it is very different from the forest, which usually decreases permeability (Predevello and Vieria, 2010). As species that occur in the continuous forest also occur in forest patches across the savanna matrix, they must be able to disperse through the whole matrix, even though they do not establish in the savanna, as few forest species were captured there in many years of savanna rodent monitoring (W.E. Magnusson and A.P. Lima, unpubl. data). This suggests that even the more hostile matrix in this savanna landscape is not an absolute barrier to the small mammals. Indeed, studies at Alter do Chão with other species groups, such as bats, ants, large mammals and birds (Bernard and Fenton, 2003, 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, which could mean that most animal species are able to cross the savanna and the regrowth forest matrices. Perhaps the way the matrix is affecting small-mammal composition in the forest patches is more related to how matrix affects patch quality (e.g. edge effects) (Laurance et al., 2011), than to permeability to movement, even though this is the most commonly recognized matrix effect on animals (Fahrig, 2007; Vieira et al., 2009; Eycott et al., 2012).

Despite the apparent effect of local connectivity and the regrowth-forest matrix possibly contributing to effective patch size, there was no statistically significant effect of patch size per se. In many landscapes, patch size effects on organisms are mostly because of habitat loss effects (Fahrig, 2003). In Alter do Chão habitat loss among forest patches happened at least 150 years ago, so patches are more stable than recently isolated ones, as organisms responses to changes in landscape can occur continuously throughout the years (Laurance et al., 2008). In addition, the Alter do Chão matrix as a whole does not seem to be an absolute barrier to small mammal species, they can move and are not isolated in their patches. If habitat loss effects have been stabilized and matrix is permeable to small mammals, maybe patch size does not influence so much in small-mammal species composition, thus it was not significant. If patch size has an effect, it is similar to savanna effects and contrary to the effects of connectivity, which is counter intuitive. We do not have an explanation for this, but it may be that connectivity effectively made some of the smaller patches in regrowth forest matrix larger than the larger patches surrounded by savanna.

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) results partially support this segregation, as they showed rodents and marsupials of the Atlantic Forest indeed have different trophic niches: marsupials occupy a narrower niche, mostly insectivorous, and rodents occupy a much wider niche, using diversified food resources. Nevertheless, the authors found that divergence in trophic niche was related to locomotor habits, not to body size, which is opposite to our findings. The authors suggest that the food resources available varies along the strata gradient in the Atlantic Forest, which may not be true for the Amazonian forest patches we studied. Another possibility is that size gained importance because our small-mammal species presented higher discrepancy in weight; in Galetti et al. (2016) study, most species were relatively light, only four (3 marsupials and 1 rodent) weighted 200g or more (see Paglia et al., 2012). It is possible yet that the difference in size we detected is simply a reflection of taxonomic differences: rodents and marsupials have distinct trophic niches, and the Amazonian rodents were in general larger than the Atlantic Forest rodents. In any case, it is not obvious why there should be this 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 niches to both frugivorous and insectivorous. Hence, both groups could establish in regrowth-forest patches, but this does not happen. Among other possibilities are influences of physical and vegetation characteristics of the patches, competition and predation. Understanding of what causes the strong structure in small-mammal assemblages at Alter do Chão will require more autecological studies and investigation of species interactions.

Even though the causes of small-mammal structure remain unknown, local connectivity and matrix types were the landscape variables most related to species composition. The matrix had the largest effect and, consequently, it is also the key element to enhance the group diversity in the Alter do Chão landscape. This suggests that maintenance of both savanna and regrowth-forest matrix are important to maintain small-mammal species diversity in Alter do Chão forest patches, since they result in different kinds of assemblages in the forest patches. This may be important to management of the Alter do Chão Environmental Protection Area, as further fragmentation of the forest in the region is undergoing. If it is not possible to have forests large enough to hold all small mammal species, they could survive in patches surrounded by different matrices. Therefore, the maintenance of large proportions of each matrix type around patches might be key to small mammal conservation in this landscape and in landscapes alike.

5. Conclusions

Our results indicated that patch size did not affect and local connectivity showed evidence to have an effect small-mammal species composition. Despite the lack of statistical significance, forest-type matrix seemed to favor connectivity, so the existence of regrowth forests should be encouraged, in order to obtain assemblages more similar to those of continuous forest. Surprisingly, the matrix types were clear and strongly related to small-mammal composition and the species showed a non-random association to matrix types. The reasons for this aggregation are not clear, but it is possible that they are related to the way matrix affects patch quality, rather than how it limits animal movements. In any case, we saw the types of matrix selected for different assemblages, thus the matrix was the most important landscape variable to small-mammal composition in this landscape. Therefore, the maintenance of both savanna and regrowth forest in the matrix would be key in small-mammal conservation in Alter do Chão and in landscapes alike. This might contribute to future managements in the region, as it is threatened with increasing human activities that may cause fragmentation.

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Appendix A

The NMDS ordination summarizing the small-mammal composition of patches was related to the percentage of regrowth forest (RM), local connectivity (LC) and patch size (PS): NMDS = 2.207 + 0.01512*RM + 7.844*LC -0.2188*PS, adjusted R^2=0.52, $F_{3,10}$= 5.786, p=0.015. RM (p=0.003) contributed significantly to the multiple regression, but PS did not (p=0.100). LC showed a low probability of having no effect on composition (p=0.078). The partial regressions indicated a strong (r^2=0.56 of the partial regression) positive effect of RM (Figure A1C) and a weaker (r^2=0.22 of the partial regression) positive effect of LC (Figure A1B) on the NMDS values. This indicates these variables selected for the same assemblages. The VIF for RM, LC and PS were 1.01, 1.61, 1.60, respectively, indicating that there was little multicollinearity among the predictor variables.

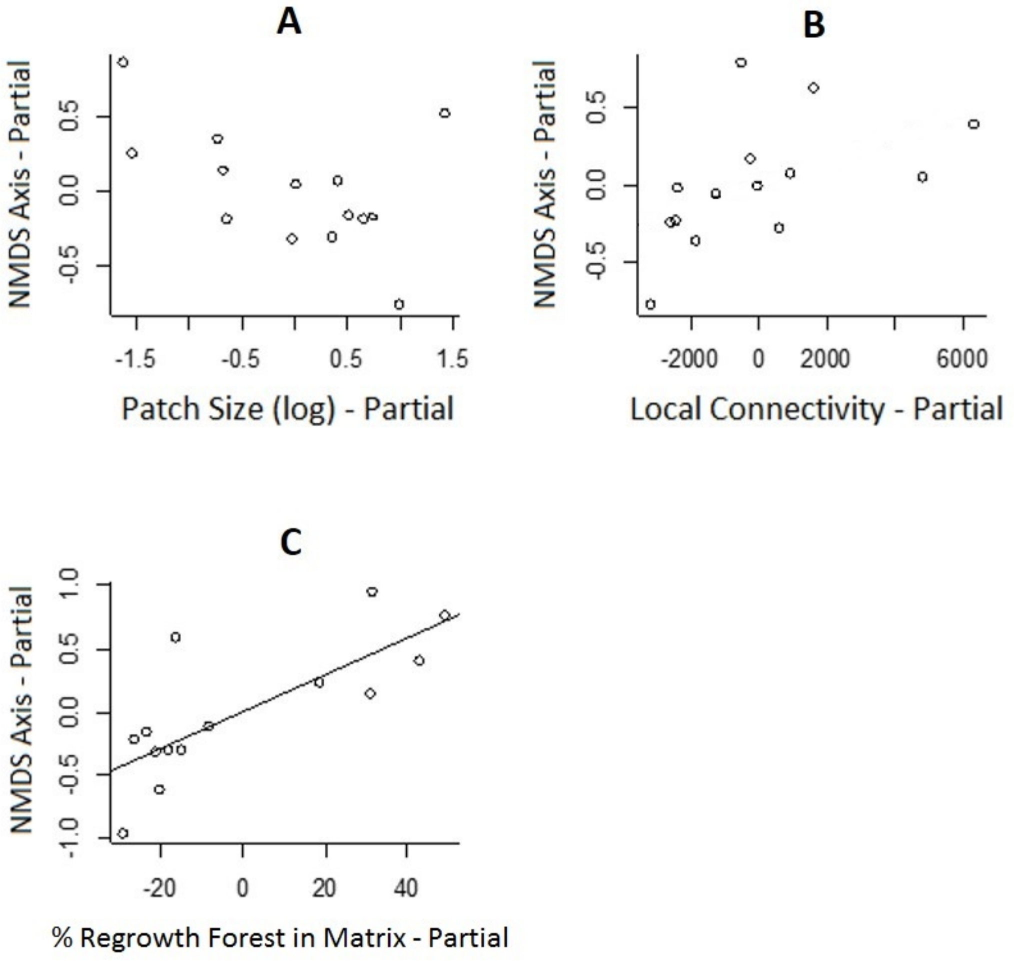

Figure A1: Partial regressions derived from the multiple regression of the NMDS axis against the landscape variables: patch size, local connectivity and percentage of regrowth forest in matrix.

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Conclusões

A composição da assembleia de pequenos mamíferos não voadores em Alter do Chão mostrou evidências de estar relacionada com a conectividade local, pouca relacionada com o tamanho da mancha e forte relação com a composição da matriz. As regressões parciais indicaram que a conectividade local captou cerca de 20% da variação nos dados de composição não associada com outras variáveis, mas as proporções de savana e de floresta em regeneração na matriz captaram uma variação maior (49% e 55%, respectivamente). Dessa maneira, a matriz parece ser o elemento da paisagem mais importante para determinar a composição de pequenos mamíferos nesta paisagem.

As manchas em matriz de floresta em regeneração apresentaram em geral maior conectividade local e suas assembleias foram similares àquelas encontradas na floresta contínua. Isto provavelmente indica que uma matriz composta de floresta em regeneração aumenta a conectividade entre suas manchas. Isto está de acordo com as constatações de Baum et al. (2004) de que a matriz pode aumentar a efetividade de corredores e de *stepping-stones*, e com as conclusões de Watling et al. (2011) que medidas de conectividade que incorporam características da matriz predizem melhor a abundância e ocupação de espécies silvestres. É possível que o mosaico de distintas florestas em Alter do Chão funcione como uma espécie de porção de floresta contínua, ainda que composta por manchas de diferentes idades.

Florestas em regeneração são normalmente mais permeáveis para especialistas florestais do que um habitat não florestal (Pardini, 2005; Umetsu & Pardini, 2007; Predevello & Vieira, 2010; Laurance et al., 2011). Por outro lado, a matriz de savana deveria ser menos permeável aos pequenos mamíferos, já que é uma vegetação muito diferente da floresta e matrizes muito diferentes do habitat original são menos permeáveis para as espécies deste habitat (Predevello & Vieria, 2010). Como espécies que ocorrem na floresta contínua também ocorrem em manchas do outro lado da matriz de savana, é possível que elas sejam capazes de se dispersar por toda a matriz. Isto sugere que até a matriz menos permeável desta paisagem, a savana, não é uma barreira absoluta para os pequenos mamíferos. Talvez a forma como a matriz afeta a composição de pequenos mamíferos das manchas florestais esteja mais relacionada a como a matriz influencia na qualidade da mancha (i.e. efeito de borda) (Laurance et al., 2011), do que com sua permeabilidade ao movimento.

As espécies de pequenos mamíferos mostraram agrupamentos não aleatórios: roedores em geral maiores e frugívoros associados à matriz de floresta em regeneração e marsupiais em geral menores e insetívoros associados à matriz de savana. Embora as causas desta segregação não sejam óbvias, a conectividade local e a matriz foram as variáveis da paisagem mais relacionadas ao padrão de composição de espécies encontrados, sendo a matriz mais fortemente relacionada. Assim, a matriz é um elemento chave para aumentar a diversidade do grupo na paisagem de Alter do Chão, o que sugere que ambos os tipos de matriz devem ser mantidos. Isto pode ser importante para o manejo da Área de Preservação Ambiental de Alter do Chão, já que é provável que haja aumento da fragmentação da floresta nesta região. Se não é possível ter uma floresta grande o bastante para conservar todas as espécies de pequenos mamíferos, elas poderiam ser mantidas em manchas rodeadas pela matriz apropriada.