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ILHAS FLUVIAIS SÃO ILHAS "VERDADEIRAS" PARA OS MAMÍFEROS?  
RESPOSTAS DAS ESPÉCIES ÀS MUDANÇAS NA  
ESTRUTURA ESPACIAL DA PAISAGEM

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Manaus, Amazonas

Março, 2016

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### Sinopse

Estudou-se a relação espécie-área de mamíferos arborícolas ocorrendo em ilhas fluviais e em sítios de floresta contínua. Avaliaram-se os efeitos do tamanho da ilha e da quantidade de habitat na paisagem local na riqueza de espécies. Avaliou-se também a influência da quantidade de habitat na paisagem e a resistência da matriz na composição de espécies.

**Palavras-Chave:** ecologia, distribuição, mamíferos arborícolas, várzea, artefato de amostragem.

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*"... Eu concordo com a ideia de colocar as ilhas como 'áreas não amostradas'.  
A questão das ilhas, por si só, dará um trabalho à parte. Um mestrado interessante para  
mostrar o processo de colonização das ilhas em função de seu tamanho e de sua idade.  
Era uma ideia muito interessante do Márcio [Ayres] que nunca foi realizada.  
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Trecho de e-mail de Helder Queiroz para Fernanda Paim, em 15/05/2012.

## Resumo

Desde a publicação da teoria da biogeografia de ilhas, a ideia de que manchas de habitat são comparáveis a ilhas oceânicas popularizou-se na ecologia e, mais tarde, na biologia da conservação. Mais recentemente, surge a ecologia da paisagem, a qual busca explicar a relação entre os padrões espaciais de estrutura da paisagem e os processos ecológicos. Um dos padrões espaciais mais estudados é a relação espécie-área (REA), a qual prevê que áreas maiores devem conter maior riqueza de espécies. Porém, a constatação desses efeitos pode estar enviesada se o número de espécies em uma ilha ou parcela (fragmento) de habitat aumentar *somente* em decorrência do incremento da área amostrada ao invés de ser influenciado pelo tamanho da mancha *per se*. Em decorrência desse debate, recentemente foi proposto que a quantidade de habitat na paisagem local do entorno das manchas simplifica os efeitos do seu tamanho e isolamento e, por isso, deve ser o principal fator determinante da distribuição de espécies em sistemas de manchas. Os objetivos desse trabalho foram: (i) testar se a REA de mamíferos habitando ilhas fluviais na região do médio-Solimões, Amazônia Central, ocorre devido a um efeito de ilha ou a um artefato amostral; (ii) avaliar os efeitos independentes da quantidade de habitat na paisagem e do tamanho da ilha na riqueza de espécies estimada por um esforço amostral padronizado; e (iii) analisar como a quantidade de habitat e a resistência da matriz ao fluxo biológico na paisagem estão relacionados com a composição de espécies das ilhas. Para isso, registrou-se a ocorrência de mamíferos em 15 ilhas fluviais, cujas paisagens foram caracterizadas espacialmente a partir de imagens de satélite. A REA de mamíferos nas ilhas foi explicada somente pelo efeito da área amostral e o seu padrão não se manteve quando a riqueza de espécies foi estimada em amostras de tamanho padronizado, independente do tamanho da ilha. A quantidade de habitat na paisagem local foi capaz de prever a riqueza de espécies estimada por um esforço amostral padronizado, bem como o padrão de estrutura da assembleia de mamíferos nas ilhas. Por outro lado, a resistência da matriz não apresentou relação com a composição de espécies de mamíferos nas ilhas. Embora as ilhas fluviais estudadas representem áreas de terra isoladas por uma matriz de água, elas não podem ser consideradas ilhas "verdadeiras" sob a perspectiva de equilíbrio do modelo de MacArthur-Wilson. Em suma, esse estudo suporta a hipótese de que a quantidade de habitat explica a distribuição de mamíferos nas ilhas fluviais do médio-Solimões.

## Abstract

### **Are fluvial islands "real" islands? Revealing the effects of landscape structure on mammal assemblage**

After the publication of the theory of island biogeography, the idea that habitat patches are comparable to oceanic islands have popularized in ecology, and later in conservation biology. The discipline of landscape ecology came afterward, studying the relationship between spatial patterns of landscape structure and ecological processes. One such pattern is the species-area relationship (SAR), which predicts that larger areas will contain more species. However, the patch size effects may be biased if the number of species in a given island or fragment increase *only* due the increment of the sampled area, instead of a patch size effect *per se*. Recently, it has been proposed that the amount of habitat in the local landscape simplifies both patch size and isolation effects and, consequently, it should be the main driver of species distribution in patchy systems. This study aimed to: (i) test if SAR from mammals inhabiting fluvial islands in the middle-Solimões River region, in Central Amazon, occurs due to an island effect or to a sample area effect; (ii) evaluate the independent effects of habitat amount in landscape and island size on species richness estimated by a standardized sampling effort; and (iii) analyze how habitat amount in landscape and matrix resistance are related to species composition. For this, the occurrence of mammals in fluvial islands was registered on 15 islands, and the landscapes surrounding the islands were characterized based on satellite images. The sample area effect alone explained the SAR found in the islands, and the relationship did not remain after species richness being accessed by standardized sampling effort. Habitat amount in the local landscape was able to predict the species richness estimated by standardized sample effort, and was also related to the species composition pattern. On the other hand, matrix resistance was not correlated with species composition. Even if islands are considered literally as true islands, i.e. portions of land surrounded by water, these findings suggest that these islands may not be considered as "real" islands under the equilibrium perspective of MacArthur-Wilson model. These findings support the hypothesis that habitat amount in landscape explains the distribution of mammal species in the fluvial islands of middle-Solimões region.

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## **Introdução geral**

Desde a publicação da teoria da biogeografia de ilhas (MacArthur e Wilson, 1967), a ideia de que manchas de habitat são comparáveis às ilhas oceânicas popularizou-se na ecologia e, mais tarde, na biologia da conservação. O modelo de MacArthur-Wilson constitui, entretanto, apenas uma das hipóteses propostas para explicar um dos poucos padrões genuínos da ecologia: a relação espécie-área (REA). Essa relação prevê um aumento do número de espécies à medida que aumenta a área amostrada em uma relação logarítmica, seja em uma região de habitat contínuo ou em sistemas isolados (Arrhenius, 1921; Williams, 1943; Preston, 1962). Por conta disso, os ecólogos passaram a ver o tamanho das manchas de habitat como o principal determinante da distribuição das espécies em sistemas de manchas.

No entanto, os efeitos do tamanho de manchas de habitat foram questionados recentemente por Fahrig (2013). Fahrig sugeriu que eles devem ocorrer devido ao 'efeito da área amostral'; ou seja, um fragmento de habitat maior deve conter mais espécies que um fragmento menor devido apenas à amostragem de uma área maior. Isso significa que o padrão da REA encontrado em manchas de habitat seria um artefato de amostragem ao invés de um modelo complexo de equilíbrio entre colonização e extinção de espécies em função do isolamento ('efeito de ilha'). Fahrig (2013) propôs, então, a 'hipótese da quantidade de habitat', a qual postula que a quantidade de habitat na paisagem local deve ser o principal fator determinante da distribuição das espécies em sistemas de manchas.

Nesse contexto, testo no Capítulo I se a REA de mamíferos arborícolas habitantes de ilhas fluviais na região do médio-Solimões, Amazônia Central, ocorre devido a um efeito de ilha ou ao efeito de área amostral. Também avaliei os efeitos independentes da quantidade de habitat na paisagem e do tamanho da ilha na riqueza de espécies estimada por um esforço amostral padronizado. Ainda que Fahrig (2013) tenha se limitado a tratar apenas da resposta da riqueza de espécies à quantidade de habitat, ela apontou que as espécies também devem responder à qualidade da matriz na qual as manchas estão inseridas. Desta forma, analiso no Capítulo II como a quantidade de habitat e a resistência da matriz na paisagem estão relacionadas com a composição de espécies de mamíferos habitantes de ilhas fluviais.

## **Objetivos**

### **Objetivo geral**

Avaliar a influência da estrutura da paisagem na assembleia de mamíferos em ilhas fluviais na região do médio-Solimões, Amazônia Central.

### **Objetivos específicos**

- Verificar se a relação espécie-área de mamíferos arborícolas em ilhas fluviais ocorre devido ao 'efeito de ilha' ou ao 'efeito da área amostral'.
- Separar os efeitos da quantidade de habitat na paisagem local e do tamanho da ilha na riqueza de espécies estimada por um esforço amostral padronizado.
- Analisar como a quantidade de habitat na paisagem local e a resistência da matriz estão relacionadas com a composição de espécies de mamíferos das ilhas fluviais.

## Capítulo I.

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**Are fluvial islands 'real' islands for arboreal mammals?  
Uncovering patch size effects under the species-area  
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**ORIGINAL ARTICLE****Are fluvial islands "real" islands for arboreal mammals? Uncovering patch size effects under the species-area relationship**

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**Short running head: Are fluvial islands "real" islands for arboreal mammals?**

## ABSTRACT

**Aim** We tested the 'habitat amount hypothesis' of Lenore Fahrig, which predicts that patch size effect on number of species is due to the 'sample area effect' rather than the 'island effect'. For this, we (1) analyzed parameters of the species-area relationship (SAR) of arboreal mammals in fluvial island forests and continuous forest, and (2) separated the effects of island size and of habitat amount on species richness in island forests.

**Location** Middle-Solimões River region, Central Amazon.

**Methods** We surveyed arboreal mammals' occurrence along line-transects of different lengths, determined by island size, on 15 fluvial floodplain islands and along nine line-transects, also of variable length, in continuous floodplain forest. We used power transformed (log-log) models to construct a SAR for the set of island transects and another SAR for the set of continuous forest transects. We compared slope and intercept parameters between the two SARs using ANCOVA. We used multiple regressions to separate effects of island size and of habitat amount on rarefied number of species, in a multi-scale spatial approach.

**Results** The two species-area curves, of fluvial islands and of continuous forest, had similar slopes, but intercept was lower for islands. Multiple regressions showed best fit at the spatial scale of 2000 meters, at which the habitat amount in the local landscape explained species richness of samples, whereas island size did not.

**Main conclusions** We conclude that an apparent patch size effect on the number of species is simply due to the sample area effect and that no island effect operates on this patch system. Island size *per se* does not increase the number of species at a sample site. Alternatively, habitat amount was an effective predictor of the species richness of samples. Our findings support Fahrig's habitat amount hypothesis.

## KEYWORDS

Fluvial landscapes, habitat amount hypothesis, island biogeography, island effect, local patch, patch-landscape scale, river dynamics, sample area effect, species richness, species-area curve.

## INTRODUCTION

The species-area relationship (SAR) is nowadays considered one of the few laws in ecology. It predicts that the number of species per sample increases with increasing sample size in a logarithmic manner, whether in a region of continuous habitat or across patches of habitat (Preston, 1962). MacArthur & Wilson (1963, 1967) proposed the theory of island biogeography to explain the SAR pattern, stating that the SAR for a set of islands should be different from that for a set of sample sites on the mainland. Specifically, the slope of the relationship across oceanic islands should be steeper than across samples on the mainland.

This steeper slope for oceanic islands became known as the 'island effect' and it occurs because the ratio between extinction and colonization rates on an island of a given size is higher than in the same size area on the mainland. This species deficit from enhanced extinction increases as the size of the island and its corresponding sampled area decrease (MacArthur & Wilson, 1967). The island effect was indeed confirmed for remote islands and, afterward, researchers have constructed species-area curves [i.e. Type IV curve *sensu* Scheiner (2003), or island species-area relationship, ISAR, *sensu* Triantis *et al.* (2012)] for several types of habitat patches, assuming that habitat patches are analogous to remote islands (revised in Watling & Donnelly, 2006; Triantis *et al.*, 2012; Matthews *et al.*, 2015).

MacArthur & Wilson (1967) also predicted that SARs from oceanic archipelagos would have lower intercepts because isolation would reduce species dispersal, thereby reducing the number of transient species that would maintain sustainable populations on islands by the immigration process. This prediction was also confirmed empirically for 'true islands', i.e. areas of land surrounded by water (Matthews, Guilhaumon, *et al.*, 2015; Triantis *et al.*, 2012).

But what is the expected slope of SAR across habitat patches on the mainland? Should it be steeper, as on MacArthur & Wilson's islands, or shallower, as across samples of continuous habitat? These questions were recently posed by Fahrig (2013). Though prior studies have documented an empirical relationship between patch size and species richness for several organisms, including plants, invertebrates and vertebrates (see meta-analyses of Triantis *et al.*, 2012; and Matthews *et al.*, 2015), Fahrig (2013) challenged the notion that patch size *per se* has an effect on species richness. She argued that this

apparent patch size effect might result from a 'sample area effect'. In this case, the number of species should increase with patch size simply because of the greater sample area allocated to larger patches. The sample area effect is the simplest explanation for the SAR pattern in habitat patches.

Based on MacArthur & Wilson's theory, Fahrig (2013) suggested a more appropriate manner to verify the existence of an island effect in a given patch system by comparing the slope of SAR from a set of different-sized habitat patches with the slope of SAR from a set of sample sites equal in size to those patches, but contained within continuous habitat (Fig. 1). If sample area effect alone explains SAR in habitat patches, the number of species would increase with similar rates both in continuous forest and habitat patches (Fig1b). On the other hand, if a true island effect occurs and habitat patches are analogous to remote islands, their SAR pattern would be steeper than that of continuous habitat (Fig. 1c).

Another appropriate sampling design to look for effects of patch size *per se* on number of species, but controlling for the sample area effect, is to standardize sampling effort across habitat patches. Fahrig (2013) stated that, if random samples of fixed size taken from homogeneous habitat have the same number of species on average, then random samples drawn from patches should show this same pattern – even if one increases the size of the patches within which the samples are embedded (Fig. 1, lower graph). In fact, Sampaio *et al.* (2010) and Santos-Filho *et al.* (2012) found no evidence for effects of patch size on number of mid- to large-sized mammals and small mammals, respectively, in equal-sized samples within forest fragments in Amazonia.

Several studies have suggested that patch area is the main driver of mammal response in Neotropical forest patches, predicting species occurrence (Arroyo-Rodríguez & Dias, 2010; Benchimol & Peres, 2014, 2015a), richness (Benchimol & Peres, 2013; Boyle & Smith, 2010) and composition (Benchimol & Peres, 2015b). If sample area effect is controlled and the species richness still increases with patch size, then the equilibrium model of island biogeography theory might indeed explain the SAR pattern. Otherwise sample area effect would be the only explanation. Most studies, however, have not attempted to control the sample area effect on SAR in their analyses (but see Michalski & Peres, 2007; Benchimol & Peres, 2015b).

In this context, Fahrig (2013) then proposed the 'habitat amount hypothesis', which posits that the amount of habitat in the local landscape should be the main driver of species' distribution in patchy systems. According to the habitat amount (HA) hypothesis, the number of species in equal-sized sample sites should increase with HA in the local landscape. The 'local landscape' is the area within a given distance of the sample site (Fig. 2a). The appropriate distance from the sample would be the one at which the landscape structure affects most strongly the species responses, the 'scale of effect' (Martin & Fahrig, 2012). The HA hypothesis predicts that the number of species in a sample site contained in given patch is independent of that patch's size, unless the area of the patch affects the total HA in the local landscape (see example in Fig. 2a).

Here we tested Fahrig's hypothesis using forested river islands as models of habitat patches. Though technically 'true islands' (portions of land surrounded by water), in our model they are treated as habitat patches. Our aim was to verify if there is an island effect operating in these patches, analyzing the SAR (Type IV or ISAR curves) of arboreal mammals occurring in samples from fluvial forested islands. Specifically, we compared the SAR from sample sites contained in a set of forested islands with the SAR from a set of sample sites within continuous forest. If fluvial islands are equivalent to oceanic islands, their SAR pattern should be steeper than in continuous forest (Fig. 1c). On the other hand, if an island effect does not modulate the species-area curve on fluvial islands, as Fahrig's hypothesis predicts and as we expected, both SARs would have similar slopes, responding only to the sample area effect (Fig. 1b).

We also asked whether and how island size and HA in landscape affect the species richness, estimated with standardized sampling effort, at each sample site. For this, we adapted Fahrig's concept of local landscape (Fig. 2a), defining local landscape as the area within a given distance from the island perimeter, and not from the sample site (Fig. 2b). If island effect is modulating SAR on these islands, its effect should be apparent in the SAR pattern, using a fixed sample size. On the contrary, if the HA hypothesis is correct, species richness should be independent of the island size but increase with the proportion of habitat in the landscape (Fig. 2).

## MATERIAL AND METHODS

### Study region

Sampling was near the confluence of the Solimões and Japurá Rivers, in the Central Amazon (Fig. 3). The interfluvium at these rivers' junction is a floodplain forest ecosystem, called *várzea*. It is protected by the Mamirauá Sustainable Development Reserve (IDSM, 2010) and recognized as a Ramsar site and a natural site of the World Heritage Convention. *Várzea* forests are seasonally flooded by nutrient-rich white-water rivers (Prance, 1979). The local annual flood pulse in the study region has a vertical amplitude of up to 12 m (Ramalho *et al.*, 2009), reaching its maximum around June and its minimum level between October and November (IDSM, 2010).

### *Fluvial islands as model of habitat patches*

The geomorphologic dynamics of the river constantly modify the spatial structure of Amazonian riverscapes (Peixoto *et al.*, Nelson, & Wittmann, 2009; Puhakka, Kalliola, Rajasilta, & Salo, 1992). Erosion, transport and deposition of sediments create new sites of terrestrial habitats – the fluvial islands (Kalliola, Salo, Puhakka, & Rajasilta, 1991). Here we consider the fluvial islands within these riverscapes as our model for habitat patches. It has been shown that river dynamics affects species distribution in terrestrial environments (Salo *et al.*, 1986; Toivonen, Maki, & Kalliola, 2007), and creates conditions that facilitate dispersal and occurrence of species on fluvial islands [e.g., birds (Cintra, Sanaiotti, & Cohn-Haft, 2007; Rosenberg, 1990) and primates (Ayres & Clutton-Brock, 1992; Rabelo *et al.*, 2014)].

Some may argue that fluvial islands may be considered ephemeral patches for those species with long generation time (Shepherd & Brantley, 2005). However, we consider that these islands are an appropriate patch model to test Fahrig's hypothesis because we avoided ephemeral islands, considering only islands that last long enough to sustain two or more generations of the species of our study group (see "Sampling design" section, below). Furthermore, even if island size varies over time, the HA hypothesis posits that the amount of habitat in the landscape should be the main driver of biological responses (Fahrig, 2013).

## Study group

Because *várzea* forests are seasonally flooded but the forest canopy is permanently emergent, mammals inhabiting these forests have mainly arboreal and semi-arboreal habit. This guild includes mainly primates, but also sloths, anteaters, coatis and squirrels. Studying this group in landscape research is advantageous because, since these animals live in the forest and spend most of their time in the canopy, especially when the forest is flooded, we can be quite sure that we are correctly defining their habitat: forest (Fahrig, 2013). Another convenience of studying this group in *várzea* forests is that they usually have high densities in this ecosystem, probably because of the high forest productivity (Peres, 1997), which increases their detection rates.

## Sampling Design

We adopted a mixed patch-landscape scale sampling design. In this approach, each sample unit is represented by a landscape. The response variable is measured within a focal patch (the island), whereas the predictor variable can be measured both in the patch and/or in the local landscape around the patch, within a given distance from the focal patch (McGarigal & Cushman, 2002; exemplified in Fig. 2b). An alternative adaptation of patch-landscape design assesses the response variable not in the patches but in equal-sized sample sites, with the landscape predictors measured within a specified radius of these sample sites (Fahrig, 2013; exemplified in Fig. 2a). We used the first approach above because, otherwise, island size would affect the HA in landscape if we considered Fahrig's concept of local landscape in our study system (see Fig. 2).

We sampled 15 focal islands of varying size (151 - 3,625 ha). We conducted a multi-scale study in order to find the appropriate scale to detect the predictors' effects on our study group, the scale of effect (Martin & Fahrig, 2012). For this we used four buffer distances (500, 1000, 1500 and 2000 meters) from each island's perimeter to define its local landscape (Fig. 3). We chose the 15 focal islands based on the following criteria: (i) islands that were surrounded by water even during the low water season; (ii) minimum distance of 2 km between islands to avoid overlapping landscapes (only two landscapes overlapped at the buffer scales of 1500 and 2000 meters); and (iii) island minimum age of 30 years, determined using a historical series of Landsat Thematic Mapper satellite images, to avoid ephemeral islands for the species of our study.

Sampling of mammals was conducted along linear transects, i.e. our sample sites, on the alluvial islands and in the adjacent continuous floodplain forest. Transect length on islands (1.2-11.6 km) was directly correlated to island size (Appendix S1). The range of transect lengths within the continuous forest was the same as on the islands, as Fahrig (2013) suggested to test her hypothesis.

## **Data collection**

### *Sampling of mammals*

From 2013 to 2014, we conducted the mammal surveys along line-transects, following a standardized protocol (Peres, 1999). Surveys consisted of quiet walks on trails conducted by two trained observers, at a constant speed around 1.5 km/h. We carried out the surveys in the morning, from 06.30 h to 11.30 h, and afternoon, from 14.00 h to 17.00 h, and interrupted sampling during rainy periods. We recorded occurrence of species by sightings and vestiges, such as vocalization and feces. We also recorded the occurrence of the semi-arboreal species by footprints and signs of digging. We conducted four surveys on each line-transect, separated by intervals of at most 20 days, and only during the low-water season (September to November) of each year, in order to minimize possible effects of seasonality on species detections.

### *Island size and habitat amount*

We used a Landsat 8 Operational Land Imager scene from 24 October 2014 to extract the island and landscape cover types and their spatial configurations. For each landscape, we performed a semi-supervised classification into five land cover classes (forest, shrub, herbaceous, sand and water), using the Semi-Automatic Classification Plug-in for QGIS 2.8.1 (QGIS Development Team, 2015). Forest was defined as the habitat. All other land cover types were considered as matrix. We then used the classified raster images to calculate the area of habitat on each island and within its local landscape, for each of the four buffer scales of local landscapes. These metrics were calculated using the 'raster' 2.2-31 (Hijmans, 2014) and 'sp' (Bivand, Pebesma, & Gomez-Rubio, 2013) packages in R 3.1.3 software (R Development Core Team, 2015).

## **Data analysis**

We fitted linear regression models to estimate slope ( $z$ -value) and intercept ( $c$ -value) of two SARs, one for the set of islands and another for continuous forest. Before

conducting the analysis, we log-transformed both the number of species in each sample site and the length of the line-transect that constituted that sample, because power (log-log) models have better performance in explaining SAR (Watling & Donnelly, 2006; Matthews *et al.*, 2015). This transformation to a linear relationship was also needed because we used an analysis of covariance (ANCOVA) with interaction to compare SAR from sample sites contained on islands with SAR from samples of continuous forest. The ANCOVA compares two or more regression lines by testing the effect of a categorical factor on the response variable, while controlling for the effect of a continuous independent covariate. In this case, we considered the different-sized sample sites as the sample units, the actual number of detected species in a sample site as the response variable, the type of site in which the line-transect was contained (*i.e.*, island or continuous forest) as the categorical factor, and the length of the line-transect as the covariate. By constructing our island SAR in this fashion, the x-axis is associated with both increasing transect length and increasing island size (Appendix S1).

To evaluate the separate effects of island size and habitat amount in the landscape on the number of species in a sample site, we firstly controlled for the effect of sample area because our sample sites varied in size. We accomplished this task by using a rarefaction procedure to standardize survey effort across all sample sites. This procedure allows estimating the number of species in a random subsample of a standardized number of individuals. This is an appropriate measure when richness is examined for correlation with other factors (Hurlbert, 1971). We considered the rarefied number of species as our response variable in this analysis. Since our landscapes varied in size, we used the proportion of habitat as a proxy for HA in the local landscape. We also log-transformed island forest area, proportion of habitat and rarefied number of species before conducting this analysis. Then, we performed a Pearson's correlation analysis to evaluate the collinearity between island size and HA. Finally, we used multiple regression models, one for each spatial scale, to evaluate how species richness responds to island size and habitat amount separately. We considered that the most appropriate scale, the scale of effect, would be that showing the best fit of the global model, *i.e.* the highest  $R^2$  value (Martin & Fahrig, 2012; Fahrig, 2013). All analyses were performed using 'vegan' 2.2-1 package (Oksanen *et al.*, 2013), inside R 3.1.3 statistical software (R Development Core Team, 2015).

## RESULTS

We found 14 mammal species (Appendix S2), belonging to the orders Primates (10), Pilosa (2), Carnivora (1) and Rodentia (1). Ten species were detected on islands, while 13 were detected on continuous forest.

Linear regression models showed a strong pattern of SAR for both islands ( $F_{1, 13} = 13.19$ ;  $R^2 = 0.50$ ;  $P < 0.01$ ) and continuous forest ( $F_{1, 7} = 17.20$ ;  $R^2 = 0.71$ ;  $P < 0.01$ ). We found steep slope estimates for SAR from both islands ( $z$ -value = 0.58) and continuous forest ( $z$ -value = 0.40). The estimated intercept of SAR from islands ( $\log c$ -value = 0.51) was lower than that from continuous forest ( $\log c$ -value = 1.25), suggesting that the number of species is lower on forested islands than in continuous forest.

The ANCOVA showed that the size of sample site has a positive effect on the number of species that it harbors ( $F = 27.39$ ;  $P < 0.01$ ). This effect was similar between islands and continuous forest, since the interaction test failed to detect a significant difference between slopes ( $F = 0.93$ ;  $P = 0.34$ ; Fig. 4). However, as seen in the linear regression analysis, the number of species differed between islands and continuous forest as evidenced by their SARs' different intercepts ( $F = 11.16$ ;  $P < 0.01$ ; Fig. 4).

We found the best fit of our multiple regression models at the spatial scale of 2000 meters (global  $R^2 = 0.60$ ; Fig. 5a). At this scale, habitat amount explained the rarefied number of species, whereas island size did not (global model:  $F_{2, 12} = 8.757$ ;  $P < 0.01$ ; Fig. 5b & c; Table 1). We also found a significant global fit at the other spatial scales (Table 1). However, none of the predictors had significant partial effects on species richness at these scales, except for a marginal significance of HA at the scale of 1500 meters (global model:  $F_{2, 12} = 6.517$ ;  $R^2 = 0.52$ ;  $P < 0.05$ ; Table 1). The Pearson correlation analysis showed that island size and habitat amount were highly correlated at the first two scales of analysis ( $r = 0.91$  and  $r = 0.78$ , respectively; Appendix S3).

## DISCUSSION

### Interpretation of SAR's parameters

We estimated steep slopes in both SARs (0.58 for islands and 0.40 for continuous forest). Although Preston (1962) stated that slopes of SAR should fit inside a canonical range of 0.17-0.33, empirical studies have consistently found slope values outside this range (revised in Connor & McCoy, 1979; Triantis *et al.*, 2012; Matthews *et al.*, 2015). Steep slopes have been associated with high isolation and, consequently, low immigration rates (Watling & Donnelly, 2006). World-wide meta-analysis showed that, for true islands, there is a general pattern of increasing  $z$ -values from inland water-body to continental-shelf and then to oceanic islands (Triantis *et al.*, 2012; Matthews *et al.*, 2015).

Higher  $z$ -values were also found in data sets spanning small scales of magnitude of island area (Triantis *et al.*, 2012). This may be an explanation for the steep slopes that we found because the line-transect lengths, which represent the island size, varied only one order of magnitude (1.2-11.6 km in islands and 1.2-12.0 km in continuous forest). However, irrespective of the explanations for high  $z$ -values, it is worth noting that the steep SAR slope that we found for our fluvial islands, though as steep as the slopes from oceanic islands (Triantis *et al.*, 2012; Matthews *et al.*, 2015), was not statistically different from the slope estimated for the sample sites embedded in continuous forest. These findings suggest that caution is needed when looking for a "canonical" biological explanation for the slope parameter of SAR, especially when comparing these values among studies.

Regarding the intercepts of both SARs, we found a lower intercept for fluvial islands: 0.51 on islands and 1.25 in continuous forests. The meta-analyses of Triantis *et al.* (2012) and of Matthews *et al.* (2015) shown that  $\log c$ -values tend to decrease from inland water-bodies to continental-shelf and then to oceanic islands. They also found that the intercept tends to decrease from plants to invertebrates and to vertebrates species. Based on such patterns, the intercept value that we found would be expected for our taxonomic group, but not for fluvial islands. Our  $\log c$ -value was even lower than reported for most oceanic islands (Triantis *et al.*, 2012; Matthews *et al.*, 2015). SARs from river islands should have a higher intercept than oceanic islands due to their lower distance to potential species pool. However, if the dynamics of large fast-flowing rivers,

such as the Solimões and Japurá, increase the resistance of the matrix to animal movement, species dispersal would be expected to decrease.

Another possible explanation for the lower values of  $\log c$  in our island system is related to the local ecological conditions (MacArthur & Wilson, 1967). In this case, even if species could reach the islands, if islands do not have ecologically suitable conditions to sustain populations, compared to continuous forest, the number of species on the islands would be expected to be lower than in continuous forest. For example, ephemeral fluvial islands, even with more than 30 years age, may have less mature forest or may have had mature forest for less time. The intercept parameter is highly variable and has been largely overlooked in reported SAR research, which makes its interpretation more difficult than that of slopes (Connor & McCoy, 1979a; Triantis *et al.*, 2012; Matthews *et al.*, 2015).

With so much variation for  $z$  and  $c$  values *among* island systems and taxonomic groups, it is difficult to interpret the biological significance of these parameters *within* a particular island system and for a target group. An appropriate manner to analyze the SAR's parameters of a given patch system would be comparing them with the SAR's parameters of the adjacent continuous habitat (Fahrig, 2013), as we have done. Fahrig (2013) listed just six studies that conducted this kind of comparison. Consistent with our results, all found that the sample area effect alone explains SAR from habitat patches (Collinge, 2000; Laurance *et al.*, 2002; Middleton & Merriam, 1983; Paciencia & Prado, 2005; Shirley & Smith, 2005; Shmiegelow, Machtans, & Hannon, 1997).

### **Fluvial islands and river dynamics**

We used the rarefied number of species as the response variable in order to standardize sampling effort and found no evidence of patch size (island size) affecting arboreal mammal richness for fluvial islands. However, Benchimol & Peres (2015b) used a similar resampling approach and found a strong positive relationship between patch size and number of vertebrate species on true inland islands, in Central Amazon. Their island system consisted of an archipelago of land-bridge islands isolated by filling a reservoir behind the Balbina hydro dam in 1986. Both islands system, Balbina land-bridge and our river islands, are surrounded by an inhospitable aquatic matrix.

However, these two island systems differ from one another in terms of their present stability and their formation processes.

While Balbina land-bridge islands were created and maintained by the formation of the reservoir, river islands may be created and modified by a variety of processes. Some fluvial islands may emerge by deposition of sediments in the river channel, which creates sand bars that are followed by primary succession (Kalliola *et al.*, 1991; Puhakka *et al.*, 1992). In this case, islands are empty new sites, and species will only occur in the island after dispersal and colonization. Other islands may be generated by river meanders pinching off a peninsula of continuous floodplain forest (Puhakka *et al.*, 1992; Peixoto *et al.*, 2009). In this type of formation, species already inhabit the island when it is isolated from the shore (Ayres & Clutton-Brock, 1992; Rabelo *et al.*, 2014), in a process similar to that of the land-bridge islands of Balbina.

In this context, some may argue that SAR pattern depends on how islands originated. The SAR pattern implicitly assumes that all sites share the same potential species pool and are similar in their historical and environmental features (Cutler, 1994; MacArthur & Wilson, 1967). Because the spatial structure of these riverscapes are in constant change and islands may be created and modified by a combination of processes (Puhakka *et al.*, 1992), we controlled the islands age by choosing focal islands with at least 30 years of existence, although some islands have changed in size and shape over time. However, we agree that this control of the ephemeral character of the islands may have not been effective, as the islands may have different histories beyond 30 years ago. This dynamic nature of these Amazonian riverscapes could have contributed to the absence of an effect of island size on the SAR pattern, after controlling for the sample area effect.

### **Habitat amount effect**

At this point, we may conclude that if the size of an island varies over time, the influence of its present size may be small, so that some other factor will be a stronger predictor of the species richness in sample sites. Fahrig (2013) suggested that HA would be the prime factor predicting the number of species in sample sites because it combines both effects of patch size and isolation in a single measure. The proportion of habitat in the landscape, independent of forested island area, was able to predict species richness for our fluvial island sample sites, and this was best observed at the spatial scale of 2000 meters.

Because we adopt a patch-landscape sampling design, in which landscapes varied in size, HA in landscape were highly correlated with island area at the two smaller scales (Appendix S3), despite being measured by the proportion of habitat in the landscape. This is probably the reason why our overall regression model was significant, but the coefficients of the two collinear predictors were not significant, at the smaller spatial scales. Collinearity is a common statistical problem in multiple regression analyses because variable effects cannot be separated. Since it is a problem that cannot be solved, the best way to deal with collinear independent variables is to avoid them by a well-designed sampling strategy (Dormann *et al.*, 2013). However, collinearity is widespread in landscape ecology research (Eigenbrod, Hecnar, & Fahrig, 2011), which implies that the predictors that are commonly investigated, e.g. patch size and isolation, are inevitably correlated with HA (Fahrig, 2013). A prior analysis of the relationship between variables in an existing patch system would help to avoid collinearity and detect appropriately the effects of predictors in any spatial scale. It is worth noting that collinearity was not a problem in the third and fourth scales in our analysis (1500 m and 2000 m), at which we successfully separated the effects of HA and island size.

## CONCLUSIONS

So, are fluvial islands 'real' islands for arboreal mammals? We found no island effect operating on these fluvial islands. The rate of increase in number of species with the size of sample was similar for islands and for continuous forest. This means that, different from most previous studies, patch size *per se* does not increase the species richness of a sample site. Of course, bigger islands contain more species than smaller ones, but this occurs only due to the sample area effect. If fluvial islands are not analogous to oceanic islands, the equilibrium model of island biogeography may not be appropriate for explaining the species richness pattern of these inland islands. Other hypothesis, such as the 'habitat diversity hypothesis' (Báldi, 2008; Williams, 1943) or even the null model 'passive sampling hypothesis' (Arrhenius, 1921; Connor & McCoy, 1979), should be further explored as potential explanations for SAR on these river islands. Habitat amount stood out as a better predictor of the species richness of the sample sites, and its strongest effect was detected at the scale of 2000 meters. As far as we know, this is the first published test of the HA hypothesis. Our findings support the

hypothesis of Lenore Fahrig, at least in fluvial landscapes. We highlight the significance of these understudied river islands as a topic of study for understanding species distribution across these landscapes.

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## **SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Correlation between island size and transect length.

**Appendix S2** Species detected in the sample sites.

**Appendix S3** Collinearity between HA and island size.

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## **BIOSKETCH**

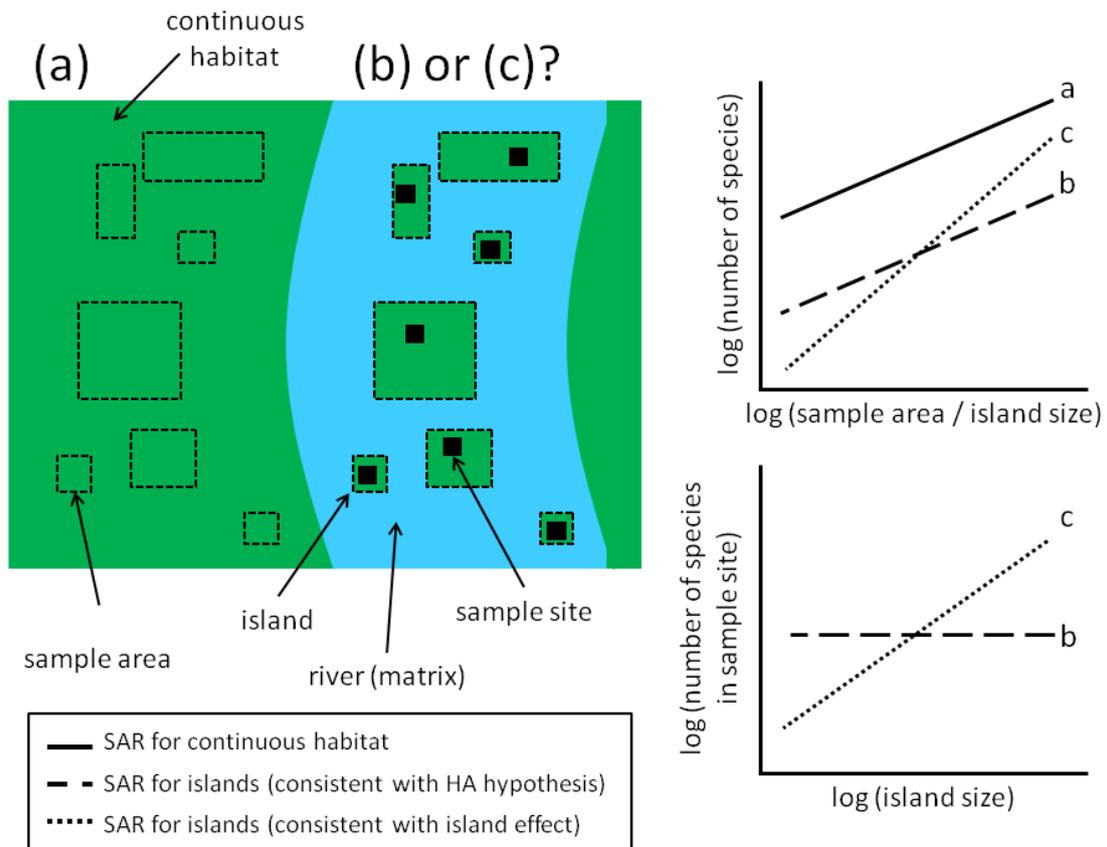
**Rafael Rabelo** is interested in understanding the distribution patterns of species and assemblages among environmental gradients. His recent work has focused on species' responses to changes in landscape structure. This article is a product of Rabelo's MSc thesis, conducted at the Ecology Graduate Program of Brazil's National Institute for Amazon Research (INPA).

Author contributions: R.M.R. conceived and designed the study, with input from all other authors; R.M.R. collected and analyzed the data; all authors contributed to the interpretation; and R.M.R. led the writing, with input from all other authors.

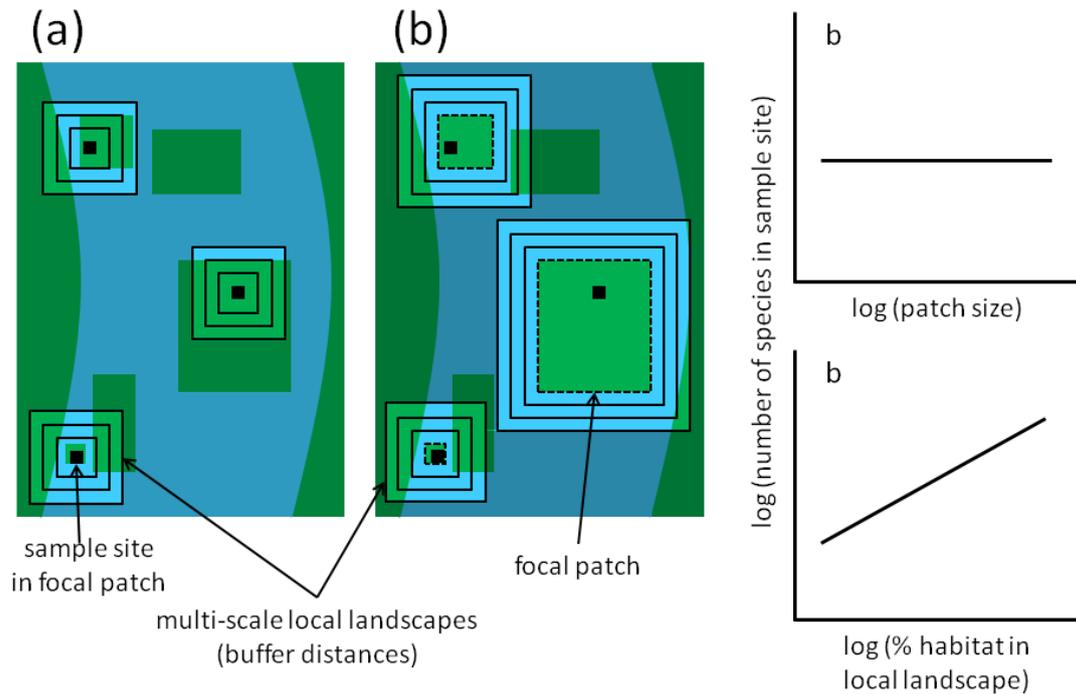
**Table 1.** Summary of multiple regression analyses of the separate effects of habitat amount and island size on the richness of mammals at four landscape spatial scales.

Landscape spatial scale (m)	Partial regressions	<i>t</i>	<i>P</i>
500	Species richness*		
	Habitat amount	1.160	0.27
1000	Island size	0.176	0.86
	Species richness*		
1500	Habitat amount	0.703	0.49
	Island size	1.211	0.258
2000	Species richness*		
	Habitat amount	1.987	0.07
2000	Island size	1.057	0.31
	Species richness**		
	Habitat amount	2.663	<b>0.02</b>
	Island size	1.378	0.19

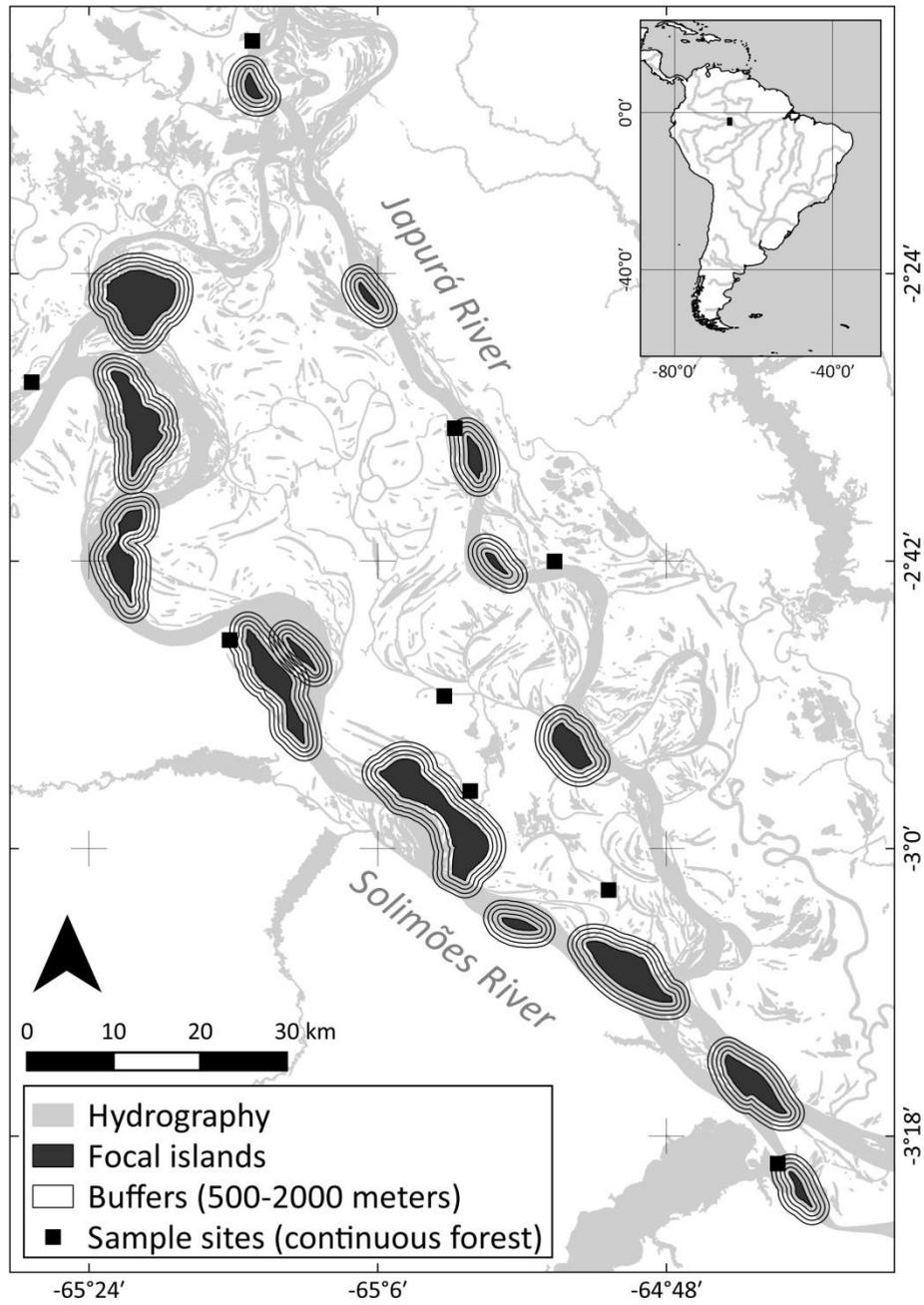
Species richness is the response variable in each regression model and represents the estimated number of species based on the rarefaction procedure. Asterisks (\*  $P < 0.05$ ; \*\*  $P < 0.01$ ) indicate statistically significant global models. Bold values indicate significant effects of partial predictors (significance set at  $P < 0.05$ ).



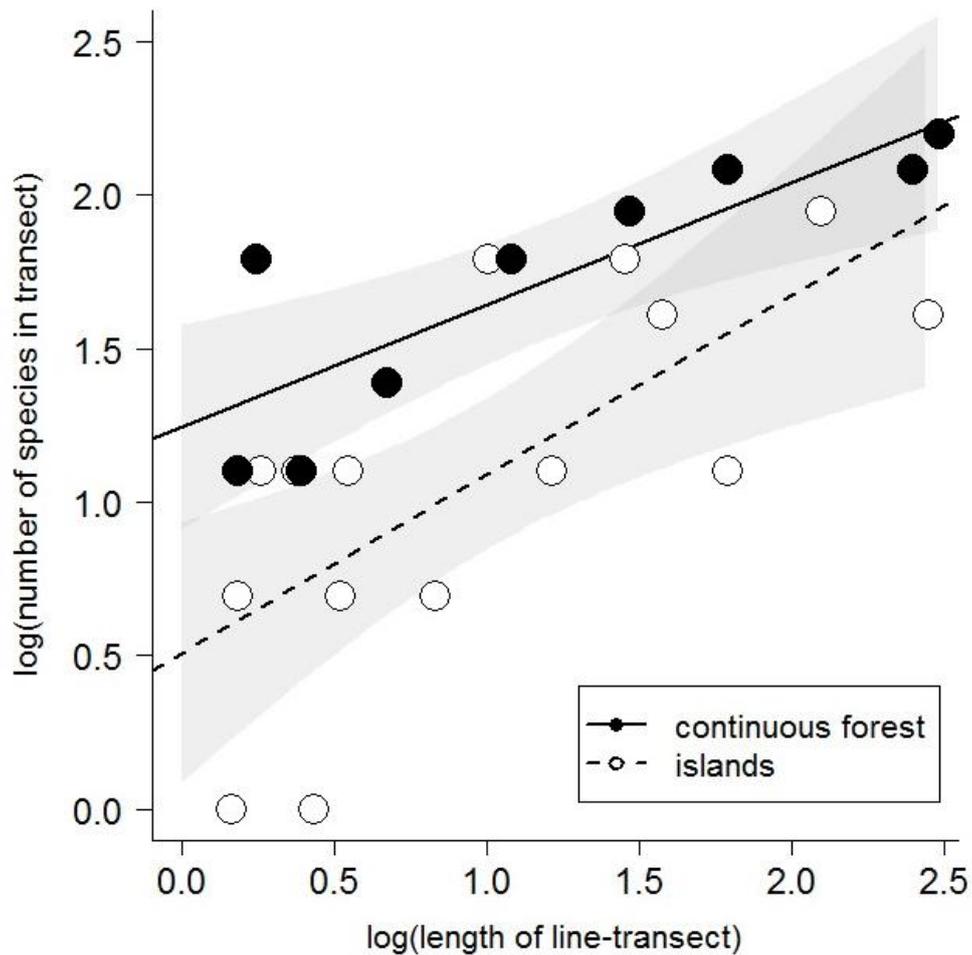
**Figure 1.** Predictions of habitat amount (HA) hypothesis for a hypothetical fluvial landscape. The number of species increases with sample area contained in continuous forest because of the sample area effect (a). The HA hypothesis predicts that species-area relationship (SAR) for islands should have a slope similar to the SAR for continuous forest [shown in (b); upper graph]. Consequently, if the number of species is measured in equal-sized sample sites (black squares), it should be constant with increasing island size [(b), lower graph]. Even so, we would expect a lower intercept than that of continuous forest in this case, because islands are isolated by an inhospitable aquatic matrix for mammals. In contrast, the island effect predicts that the slope of SAR for islands is steeper than that of continuous forest but also with lower intercept [(c), upper graph]. In this case, even if the number of species is assessed in equal-sized sample sites, it should increase with island size (lower graph).



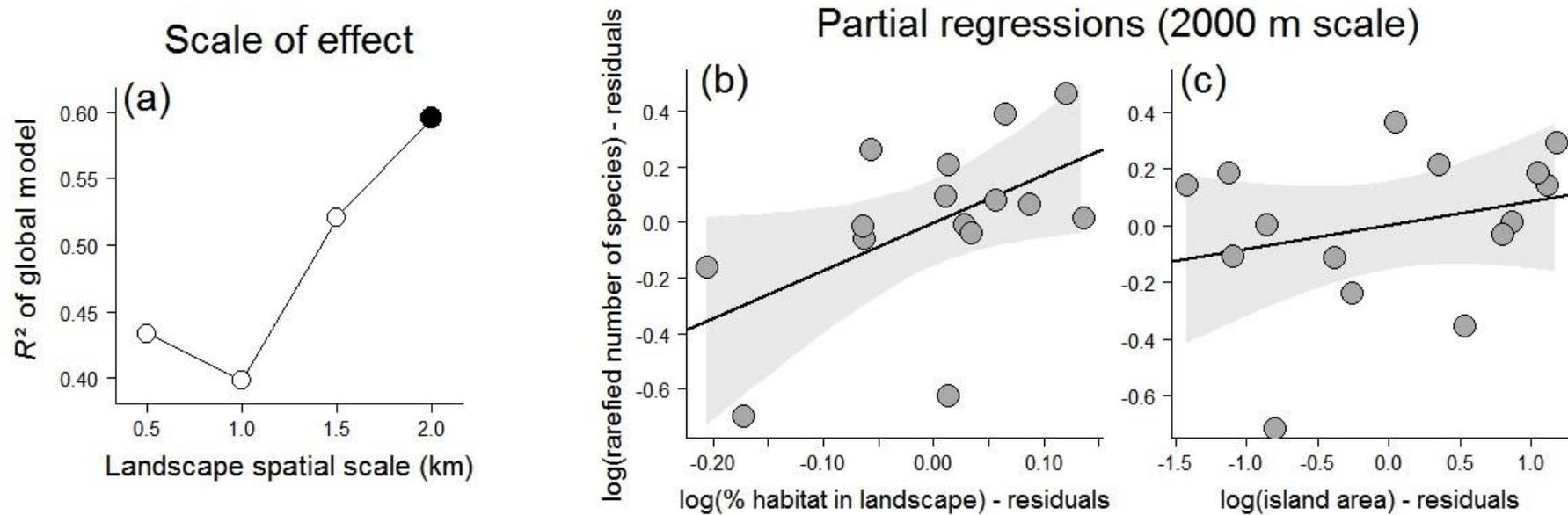
**Figure 2.** Examples of patch-landscape scale sampling designs. The 'local landscape' is the area within a given distance (or one of multiple distances) measured from the sample site within a patch (a), or measured from the focal patch perimeter (b). Although the habitat amount (HA) hypothesis uses the concept of local landscape exemplified in (a), we adopted the concept shown in (b) because, otherwise, island size would affect the HA in the landscape and we could not separate the two effects. The HA hypothesis predicts that the number of species in a sample site contained in given patch is independent of that patch's size (upper graph), but increases with the HA in the landscape (lower graph). Because landscape size increases with island size in (b), HA is measured by the proportion of habitat in the landscape, in this case.



**Figura 3.** Distribution of sample sites in the Middle-Solimões region, Central Amazon, Brazil.



**Figure 4.** Species-area relationships (SAR) for arboreal mammals inhabiting islands and continuous forest. White circles represent line-transects contained in focal islands, whereas black circles represent line-transects contained in adjacent continuous forest. Dashed and solid lines represent fitted power (log-log) models of SAR for islands and continuous forest, respectively, with their 95% confidence interval (shaded gray). The number of species in a sample site increases as the size of sample site (i.e. length of line-transect) increases, both for islands and continuous forest and at similar rates, i.e. similar slopes. However, the number of species in islands is lower than in continuous forest, i.e. the intercept of SAR for islands is lower than that for continuous forest.



**Figure 5.** Effects of habitat amount (HA) and island size on the estimated richness of arboreal mammal species, as predicted by a multiple regression analysis. (a) Association between the landscape spatial scale ( $x$ -axis) and the strength of the relationship ( $R^2$ ;  $y$ -axis) between the predictors and the estimated species richness. The black circle indicates the scale at which any of the partial predictors (in this case, HA) had a significant effect on the response variable. The strongest fit was at the fourth spatial scale, in which HA, independently of island area, had a significant positive effect on estimated species richness (b), whereas island area, independently of HA, did not (c). Shaded gray represents the 95% confidence interval.

## Capítulo II.

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Rabelo, R.M; Aragón, S; Bicca-Marques, J.C; Nelson, B.W.  
**Nestedness of mammal assemblage on fluvial islands:  
the influence of habitat amount in landscape.** Manuscrito  
em preparação – *Ecography*.

**ORIGINAL RESEARCH****Nestedness of mammal assemblage on fluvial islands: the influence of habitat amount in landscape**

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## **ABSTRACT**

Nested structure of species assemblages have been frequently associated with patch size and isolation, leading ecologists to conclude that nestedness is driven by colonization-extinction dynamics. The habitat amount (HA) hypothesis challenge the notion that patch size and isolation have distinct effects on species richness, arguing that both effects occur due to the 'sample area effect' and are components of the habitat amount in the local landscape. Additionally, it predicts that matrix may also influence species richness. It has been shown that HA, and not island size, predicts mammal species richness occurring in fluvial islands of Solimões and Japurá Rivers, Central Amazon. Here we tested if habitat amount and matrix resistance in landscapes may predict the species composition of mammal assemblage in these fluvial forested islands. We surveyed mammals' occurrence in 15 fluvial islands and performed a NMDS ordination to reduce the dimensionality of data and access the assemblage structure. We measured the habitat amount and matrix resistance at four spatial extents on each landscape. We then used multiple regression models to verify the independent effects of HA and matrix resistance on species composition. In all spatial scales, habitat amount, and not matrix resistance, was capable to predict the species composition on islands, but the strongest relationship occurred at the spatial scale of 1000 m. These findings suggest that nestedness in these river islands may be a result of passive sampling, the null model, which predicts that larger islands contain more species, only due to a sampling artifact. Habitat amount proved to be an effective measure of landscape spatial structure, and it should be further explored to understand the relationship between habitat and species distribution. Our findings show that HA hypothesis may also be applied for predicting species composition, rather than only species richness, in patch systems.

## **INTRODUCTION**

Understanding how species assemblages are distributed, and which factors influence their distributions, is one central question in ecology. Historically, ecologists have identified several distinct patterns in the distributions of assemblages among sites (Leibold and Mikkelson 2002). One prominent pattern that is frequently observed in species assemblages occurring in patchy systems is the nested subsets pattern, in which

species composition from a depauperate assemblage usually constitutes a subset of the species composition in a richer assemblage (Patterson and Atmar 1986).

The nested structure can be visualized in a matrix of species versus sites, recording the occurrence of each species in each site. Assuming that there would be only one environmental or ecological gradient structuring an assemblage, if we sort a species-site matrix by this supposed gradient, species would be progressively lost, forming the nested structure of the assemblage (Fig. 6). Originally, analyses searched for nested structure in assemblages simply by ordering the sites in relation to their species richness, but to infer about any possible causes of the nested pattern, it has been suggested that these analyses must be combined with an appropriate gradient analysis (Leibold and Mikkelson 2002, Ulrich et al. 2009).

Several mechanisms have been proposed to be the cause of the nested pattern (Ulrich et al. 2009). After Patterson and Atmar (1986), ecologists raised a discussion on whether nestedness would be predominantly dominated by extinction or colonization processes (Wright et al. 1998). In the MacArthur-Wilson (1967) equilibrium model, island size would determine the extinction rates, whereas island isolation would influence immigration rates. Based on this equilibrium model, studies have commonly used patch size and isolation as variables to sort species-site matrices (Patterson 1990, Cook and Quinn 1995, Lomolino 1996, Wright et al. 1998, Bruun and Moen 2003). Basically, when an area-sorted matrix generate a nested pattern, the conclusion is that nestedness may be derived from differential extinction process, while if nestedness appear in a isolation-sorted matrix, differential immigration should be the explanation for the nested structure (Wright et al. 1998).

Recently, Fahrig (2013) questioned patch size and isolation as separate effects on species richness, arguing that both effects are driven by the underlying process of 'sample area effect'. This means that number of species varies with patch size only because of the sample area represented by the patch. Similarly, since the habitat in a landscape surrounding a focal patch is the primary source of colonists, the focal patch will be more isolated from its pool of species as amount of habitat in the landscape reduces. Thus, number of species in a focal patch depends on the sample area represented by the surrounding habitat, which affects its immigration rate (Fig. 6a). She then proposed the

'habitat amount hypothesis', which posits that habitat amount (HA) in the local landscape should be the main driver of species' distribution in patch systems.

In this context, the 'local landscape' would be defined by the area within an appropriate distance from a sample site contained in a focal patch (Fahrig 2013). This appropriate spatial extent is based on the fact that landscape structure affects more strongly some species than others, in different spatial scales (Martin and Fahrig 2012). Since knowing the scale at which species would respond to the independent variables – the 'scale of effect' – is frequently impossible a priori, multi-scale designs should be necessary for investigating the habitat amount effects on species.

According to Fahrig (2013), the HA hypothesis would substitute two predictors, patch size and isolation, for a single predictor variable, habitat amount. However, she noted that HA should not be the only driver of species richness, based on the wide evidence that matrix can also affects species richness (Prevedello and Vieira 2010). Matrix type contributes to effective isolation of a patch, once matrix permeability corresponds to its capacity of facilitate biological flow and depends on the distance to a source area and its resistance to organism movement (Metzger and Décamps 1997). Fahrig limited herself in discussing mainly the responses of species richness, but since nestedness necessarily implies that species richness varies across patches, we propose that HA and matrix resistance may also predict species composition in a nested-structured assemblage (Fig. 6b).

Here we tested Fahrig's hypothesis using river islands as a model for habitat patches, and mammal species composition as the response variable. It has been already shown that HA, and not island size, predicts the mammals richness in these islands, supporting the HA hypothesis on this patch system (R. Rabelo et al., in prep.). Our aim was to evaluate how mammal assemblage structure responds independently to HA and to matrix resistance, in multiple spatial scales of local landscapes. If assemblage structure does not respond to HA nor to matrix resistance, then HA hypothesis may not be applied for predicting species composition. On the other hand, if the assemblage structure is associated with amount of habitat and with matrix resistance, as we expected (Fig. 6), HA hypothesis may also be applied to predict species composition, and these variables should be better explored in further studies about causes of assemblage structure.

## MATERIAL AND METHODS

### Study area and group

Sampling was concentrated in the middle-Solimões and Japurá Rivers, close to their confluence, in Central Amazon (Fig. 7). This interfluvium constitutes a floodplain forest ecosystem, called *várzea*, which is protected by the Mamirauá Sustainable Development Reserve (IDSMS 2010). *Várzea* forests are seasonally flooded by nutrient-rich white-water rivers (Prance 1979), where the annual range of water level reaches up to 12 meters in average (Ramalho et al. 2009), with its maximum level occurring around June and its minimum level between October and November in the study region (IDSMS 2010).

River dynamics constantly modifies the spatial structure of these riverscapes (Puhakka et al. 1992, Peixoto et al. 2009), and creates fluvial islands by the erosion, transport and deposition of sediments (Kalliola et al. 1991). Here we consider the fluvial islands as our model of habitat patch. River dynamics indeed affects species distribution in terrestrial environments (Salo et al. 1986, Toivonen et al. 2007), and may create conditions that facilitate dispersal and occurrence of species in fluvial islands [e.g., birds (Rosenberg 1990, Cintra et al. 2007) and primates (Ayres and Clutton-Brock 1992, Rabelo et al. 2014)].

Some may argue that fluvial islands may be considered ephemeral patches to species with long generation time (Shepherd and Brantley 2005). However, we consider that these fluvial islands are an appropriate patch model to test HA hypothesis because we avoided sampling in ephemeral islands, considering only islands that last long enough to sustain two or more generations of the species of our study group (see "Sampling design" section, below). Furthermore, even if island size varies over time, HA hypothesis posits that amount of habitat in landscape is the main driver of biological responses (Fahrig 2013).

Because *várzea* forests are seasonally flooded, mammals inhabiting these forests have mainly arboreal and semi-arboreal habit. This guild includes mainly primates, but also sloths, anteaters, coatis and squirrels. Furthermore, long-term studies within Mamirauá Reserve have shown that jaguars (*Panthera onca*) also reside in these flooded forests, even in the high water season (E. E. Ramalho, unpublished data). Studying mammals in

these landscapes is advantageous because, since these animals live in the forest and spend most of their time in the canopy, especially when the forest is flooded, we can be quite sure that we are correctly defining their habitat a prerequisite to test HA hypothesis (Fahrig 2013). Besides, another convenience of studying this group in *várzea* forests is that they usually have high densities in this ecosystem, probably because of the high forest productivity (Peres 1997), which increases their detection rates.

### **Sampling Design**

We adopted a mixed patch-landscape scale sampling design. In this approach, each sample unit is represented by a landscape. The response variable is measured within a focal patch (the island), whereas the predictor variable can be measured both in the patch and/or in the local landscape around the patch, within a given distance from the focal patch (McGarigal and Cushman 2002).

We sampled 15 focal islands with varying size (151.11 - 3624.66 ha) and used four buffer distances (500, 1000, 1500 and 2000 meters) from the island perimeter to define their local landscapes (Fig. 7). We conducted a multi-scale study in order to find the appropriate scale to detect the effects of predictors in our study group, the 'scale of effect' (Martin and Fahrig 2012). We chose the focal islands based on the following criteria: (i) islands that were still surrounded by water during the low water season; (ii) minimum distance of 2 km between islands to avoid overlapping landscapes (only two landscapes were overlapped in the scales of 1500 and 2000 meters); and (iii) island minimum age of 30 years confirmed in the historical series of Landsat TM satellite images, to avoid ephemeral islands for the species of our study.

### **Data collection**

Sampling of mammals were conducted along linear transects contained in the focal islands. Transect length varied from 1.2 to 11.6 km and were directly correlated to island size (Pearson correlation:  $r = 0.94$ ,  $p < 0.001$ ). From 2013 to 2014, we conducted mammal surveys, following a standardized protocol (Peres 1999). Surveys consisted of quiet walks on trails conducted by two trained observers, at constant speed around 1.5 km/h. We carried out the surveys in the morning, from 06:30 h to 11:30 h, and afternoon, from 14:00 h to 17:00 h, and interrupted sampling during rainy periods. We recorded occurrence of species by sightings and vestiges, such as vocalization and feces. We also recorded the occurrence of jaguars and semi-arboreal species by footprints and

signs of digging. We conducted four surveys on each line-transect, separated by intervals of at most 20 days, and only during the low-water season (September to November) of each year, in order to minimize possible effects of seasonality in species' detection.

We used a Landsat 8 Operational Land Imager scene from 24 October 2014 (low water season) to extract the island and landscape cover types and their spatial configurations. During the low water season, as the water level drops, areas of sand, herbaceous and shrub vegetation emerge, narrowing the width of rivers and adding heterogeneity to the matrix around the islands. For each landscape, we performed a semi-supervised classification into five land cover classes (forest, shrub, herbaceous, sand and water), using the Semi-Automatic Classification Plug-in for QGIS 2.8.1 (QGIS Development Team 2015). Forest was defined as the habitat and all other land cover types were considered as matrix. We then used the classified raster images to calculate the area of habitat within local landscapes, i.e. habitat amount metric.

Our index of matrix resistance constituted a metric that considered both distance and resistance of each matrix type to animal movement (Metzger and Décamps 1997). We calculated the matrix resistance metric based on the following equation:

$$MR = \frac{\sum_{i=1}^{AM} IE_i}{AM}$$

- in which  $IE_i = I_i \times R_i$  and represents the effective isolation of pixel "i";
- $I_i$  is the linear distance of the pixel "i" to the nearest pixel of habitat;
- $R_i$  is the resistance of the matrix type present in the pixel "i" to biological flow;
- $AM$  is the number of matrix pixels within the landscape.

Because studies on animal movement are scarce on the literature, resistance coefficients ( $R_i$ ) are typically used to fill this gap (Zeller et al. 2012). Since we found no empirical data available to base the resistance values, we used expert's opinion. For this, we sent closed format questionnaires (Supplementary material Appendix 1) to 50 experts, asking them to assign a resistance weight to each matrix type for each species individually and for the overall group of species. We asked them to assign a value of resistance weight from 0 to 10, considering that '0' would be an environment without any resistance, similar to the forested habitat, and '10' would be a matrix type highly resistant to biological flow, comparable to an absolute barrier to animal movement.

Because the distributions of their responses were not symmetric (see Supplementary material Appendix 1, Fig. A3), we used the median of their opinions for the overall group as the resistance coefficients ( $R_i$ ) of matrix types.

Both habitat amount and matrix resistance metrics were obtained for each of the four spatial scales of local landscapes. These metrics were calculated using the raster 2.2-31 (Hijmans 2014) and sp (Bivand et al. 2013) packages in R 3.1.3 software (R Development Core Team 2015).

### **Data analysis**

Firstly, we construct a species-site abundance matrix: a table of species (columns) versus site (rows) recording the abundance of each species in each island. Before performing the analysis, we had to exclude two islands from the species-site abundance matrix because no species were recorded in those islands. We also excluded one island because it probably was created by a formation process which is different from all other islands (see "Discussion" section, below, see also Rabelo et al. 2014). We decided to exclude this island from the analysis because, otherwise, it would break the assumption of nested pattern, which presumes that there are no overriding historical or environmental differences between sites (Cutler 1994). We then standardized species abundances applying standardization to equal totals (SAT) to the sample sites (rows). This standardization of sample sites was done in order to control the sample area effect, since this procedure reduces the differences between sizes of sample sites. Then we also standardized species abundances applying SAT to species (columns). This second standardization was performed in order to control the effect of abundance variation, reducing the difference between abundant and rare species. We choose the SAT method because it has been pointed as a robust standardization method for ordinations of ecological communities (Faith et al. 1987). Afterwards, we performed a non-metric multidimensional scaling (NMDS) ordination of the species-site abundance matrix, with the aim to reduce the dimensionality of the assemblage structure. We performed the NMDS ordination based on the Bray-Curtis pairwise dissimilarities between sample sites, and reduced the assemblage structure pattern in one dimension. The resulting axis from this procedure was used to represent the mammal assemblage composition (McCune and Grace 2002).

Since our landscapes varied in size according to island size and, therefore, amount of habitat within landscape is correlated with landscape size, we used the proportion of habitat within the landscape as a proxy for HA in the local landscape. Then, we used multiple regression models, one for each spatial scale, to verify how species composition responds to habitat amount and matrix resistance independently. To deal with the variability of expert's responses about resistance values, we repeated the multiple regression modeling using, not only the median value of their responses, but also the first and the third quartiles. This was done with the purpose of verify the sensitivity of the matrix resistance index to the expert opinions. Finally, we considered that the most appropriate scale, the scale of effect, would be the one at which the global multiple regression model had the best fit, i.e. the highest  $R^2$  value (Martin and Fahrig 2012, Fahrig 2013). All analyses were performed using vegan 2.2-1 package (Oksanen et al. 2013), inside R 3.1.3 statistical software (R Development Core Team 2015).

## RESULTS

We found seven mammal species (Supplementary material Appendix 2), belonging to the orders Primates (2), Pilosa (2), Carnivora (2) and Rodentia (1). The NMDS ordination captured the structure of species assemblage considering their relative abundance (Fig. 8), and the MDS 1, i.e., the axis derived from the ordination procedure, explained 52% of the variance of species composition.

We received responses from 29 of the 50 questionnaires that we send to specialists. There was a general tendency of increasing resistance weight from shrub to herbaceous vegetation, then to sand and finally to water, based on expert's opinion (Supplementary material Appendix 1, Fig. A3).

We found a significant global fit at all four spatial scales of analysis. In all scales, only HA in landscape explained the structure of mammals assemblage (Table 1), but the strongest fit of multiple regression models occurred at the spatial scale of 1000 meters (global model:  $F_{2,9} = 12.55$ ;  $R^2 = 0.74$ ;  $p < 0.01$ ; Fig. 9; Table 1). These patterns did not changed when we considered the first (global model:  $F_{2,9} = 12.61$ ;  $p < 0.01$ ) nor the third quartiles (global model:  $F_{2,9} = 12.52$ ;  $p < 0.01$ ; Supplementary material Appendix

A3, Table A3), instead of median, as the resistance coefficients attributed by the expert's opinion.

## **DISCUSSION**

### **The assemblage structure pattern**

A perfect nested pattern would arrange species and sites on a triangular shape, with no unexpected presences or absences, but perfect nestedness is rarely seen on nature (Patterson and Atmar 1986, Wright et al. 1998, Fischer and Lindenmayer 2005, Matthews et al. 2015). A number of methods have been proposed to measure the statistic significance of nested patterns (see syntheses of Wright et al. 1998, and Ulrich et al. 2009), and they are frequently based on presence-absence matrices, assuming that a "zero" indicates that a given species does not occur in a given site. Nevertheless, because field ecologists are commonly not capable to detect every species occurring in a site, nested pattern may be an artifact, given that the detection of the pattern depends on the absences (Cam et al. 2000).

We opted for a different approach to uncover the strongest pattern of assemblage structure, using a NMDS ordination of the species-site abundance matrix. This procedure showed a very clear, though not perfect, nested pattern in the assemblage structure (Fig. 8). The NMDS ordination, used with the Bray-Curtis dissimilarity coefficient, has been point out as the most robust and effective indirect ordination method for the analysis of community data, especially when the aim is to recover the compositional dimensions associated with underlying environmental gradients (Minchin 1987).

### **The equilibrium perspective of nestedness**

Selective extinction has been proposed to be the most frequent mechanism in explaining nested pattern (Patterson and Atmar 1986), and Leibold and Mikkelsen (2002) exemplified how this process should occur: 1) a set of patches/islands that have been recently isolated start with the same species composition, 2) immigration is interrupted, 3) extinction occurs in the same order in each patch, but 4) species go extinct more rapidly in smaller patches than in larger ones.

In this context, selective extinction would occur in land-bridge systems: systems in which patches are originally part of the same continuum and then undergo subsequent isolation. In this case, biota already inhabits the patch prior to its isolation. The association of nested pattern with patch size has been widely documented for land-bridge systems, which led researchers to conclude that selective extinction may be the driver of nestedness in these systems (see meta-analyses of Wright et al. 1998, Watling and Donnelly 2006, Matthews et al. 2015).

Nonetheless, selective immigration may also explain nested subsets, deterministically adding species to assemblages. This should occur by differential dispersal abilities of species according to island isolation, in a way that stronger dispersers could colonize a greater set of islands than weaker dispersers, so colonization process would generate and maintain the nested structure (Patterson 1990, Cook and Quinn 1995). Differently from extinction-dominated systems, nested pattern caused by immigration should occur in systems in which patches are isolated since its initial creation. In this case, an assemblage will only inhabit a patch if species are capable to disperse and colonize it. Thus, patch isolation should play an important role in structuring nested assemblages in this type of system, and studies have indeed found such association (Patterson 1990, Cook and Quinn 1995, Lomolino 1996; but see Wright et al. 1998, Bruun and Moen 2003).

The association of nested pattern with patch size or isolation does not necessarily mean that nestedness is caused by differential extinction or immigration, respectively. Wright and Reeves (1992) point out that the nested pattern in land-bridge systems may be a result of the fact that, since colonization has been "shut off", selective extinction is free to generate a nested pattern without the confounding effects of immigration. On the other hand, nestedness in immigration-dominated systems will tend to be less evident because some level of local extinction of populations is expected. Furthermore, if we assume that extinction and immigration depend only on area and isolation, respectively, we neglect other processes that may also affect species richness and composition on islands' biota, such as the rescue effect and the target area effect (Brown and Kodric-brown 1977, Lomolino 1990, 1996). Therefore, there is no a priori reason to expect extinction to be more deterministic or dominant than immigration.

At this point, it seems that knowing the geomorphologic processes that create the fluvial islands would be the prime information to base the question of which mechanisms are driving nestedness on this system. Islands of white-water rivers, such as Solimões and Japurá, tend to be formed by the deposition of sediments in the river channel, creating sand bars, which are followed by primary succession (Kalliola et al. 1991, Puhakka et al. 1992). These types of islands are then empty new sites, which will only contain biota by dispersal process.

However, fluvial islands may also be formed by avulsion process, in which erosion in river's meanders "cut off" an area of land, creating an island and changing the channel position (Puhakka et al. 1992, Peixoto et al. 2009). In this type of formation, when the island is isolated from the shore, it carries together its belonging biota (Ayres and Clutton-Brock 1992, Rabelo et al. 2014). Both processes may have created the islands of our study region, but we cannot be sure of which processes formed which islands based only on the spatial structure of the landscapes. Geomorphologic analyses could clarify this issue and it probably would help to understand how mammal assemblage became structured in the islands.

### **The 'passive sampling' perspective**

The notion that species richness and composition are determined by island size and isolation, and consequently dominated by the balance between extinction and colonization, is an equilibrium perspective (MacArthur and Wilson 1967, Brown and Kodric-brown 1977, Lomolino 1990). A much simpler explanation for species-area relationship and nested patterns is based on the 'passive sampling' model (Connor and McCoy 1979). In this model, patches are analogous to "passive targets" that accumulate individuals randomly.

In this perspective, larger targets would accumulate more individuals than smaller ones, only by chance. Similarly, based on the differences in abundance among species, abundant species are more likely to occur in a given patch than rare species, also only by chance. Originally, the passive sampling model did not considered isolation effects explicitly, but it is perfectly possible to think about the distance to the source of species, instead of area of the patch, and construct analogous predictions. The passive sampling has also been proposed to be a mechanism that originate nested pattern in assemblages (Haila et al. 1993, Andrén 1994a, b, Cutler 1994, Fischer and Lindenmayer 2002).

### **Habitat amount**

The HA hypothesis has some similarities with the passive sampling explanation for nestedness. Both explanations posit that patch size and isolation are driven by the sample area effect: larger areas will sample more species than smaller ones (Connor and McCoy 1979, Fahrig 2013). The passive sampling model goes beyond in predicting also species composition, once abundant species have higher probabilities to occur in any given patch.

Combining the two explanations, landscapes with higher proportions of habitat will sample inevitably more species than those with less proportion of habitat. Another study in these same fluvial islands has shown that the increasing number of species with increasing size of the island is only an artifact of sampling (R. Rabelo et al., in prep).

When the number of species is measured in equal-sized sample sites, irrespective of the island size, HA in the landscape, and not island size, predicts the species richness.

Based on this conclusion, we could have anticipated our findings that HA in the landscape would also be capable to predict species composition, especially if the assemblage has a nested structure.

It is worth noting that, under the passive sampling viewpoint, the relationship between area and species richness or composition is solely as a sampling phenomenon, rather than a result of biological processes such as extinction or immigration, and this is why passive sampling should be considered the as null hypothesis (Connor and McCoy 1979). On the other hand, when proposed the HA hypothesis, Fahrig (2013) did not deny that extinction and colonization would drive the species richness. The point of HA hypothesis is that there is nothing special about patches that would require immigration-extinction dynamics to be measured in the scale of the individual patch. In addition, the hypothesis implies that is patch size and isolation effects are redundant, since both are components of HA in the landscape, and affect species richness mainly through the sample area effect.

### **Matrix resistance**

We consider that assessing matrix resistance coefficients by the opinion of specialists was an efficient alternative, since empirical data on habitat use by the species were not available. Additionally, even taking into account the variation of their opinions, we still

have the same pattern of results, and did not find any association between species composition and matrix resistance, at any spatial scale.

Matrix type may indeed affect species richness within a patch, although its effects are generally weaker compared with habitat amount (Prevedello and Vieira 2010, Fahrig 2013). However, if the resistance of a matrix type to animal movement is species-specific (Prevedello and Vieira 2010), a whole assemblage may not respond to matrix effects if species have different vagilities. Analyzing the effects of matrix on each species individually may be more appropriate in this case.

## **CONCLUSIONS**

Mammal assemblage occurring in fluvial islands showed a nested structure pattern. Habitat amount in the landscape was capable to predict the mammal assemblage structure, and it was better observed in the scale of 1000 meters. Irrespectively if nestedness is generated by extinction or colonization processes, habitat amount proved to be an effective measure of landscape spatial structure that is capable to predict species composition, and it should be further explored to understand the relationship between habitat and species distribution.

We may not discard the possibility that nestedness of mammal assemblage in these islands may be a result of the passive sampling model, the null model, which predicts that larger islands contain more species, as well as common species are more likely to occur in any given patch than rare species, only by chance. To infer about the influence of colonization-extinction dynamics on the assemblage structure, geomorphologic studies of island formation process may be necessary. Our findings show that HA hypothesis may also be applied for predicting species composition, rather than only species richness, in patch systems.

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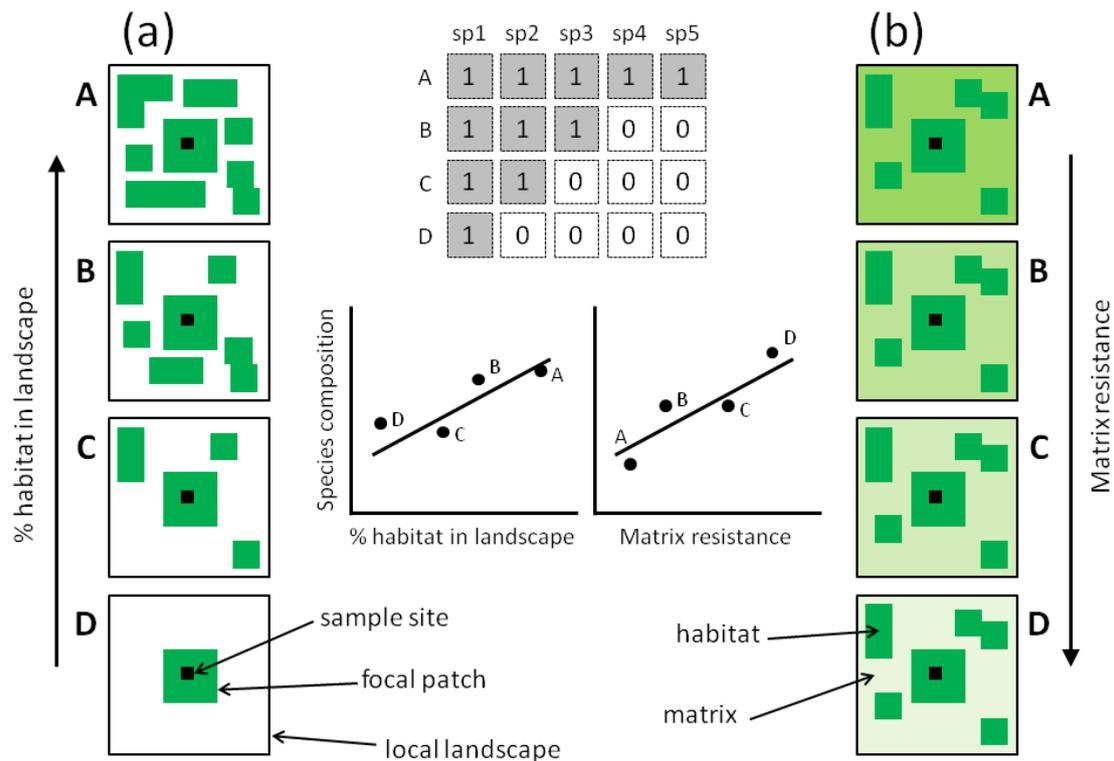
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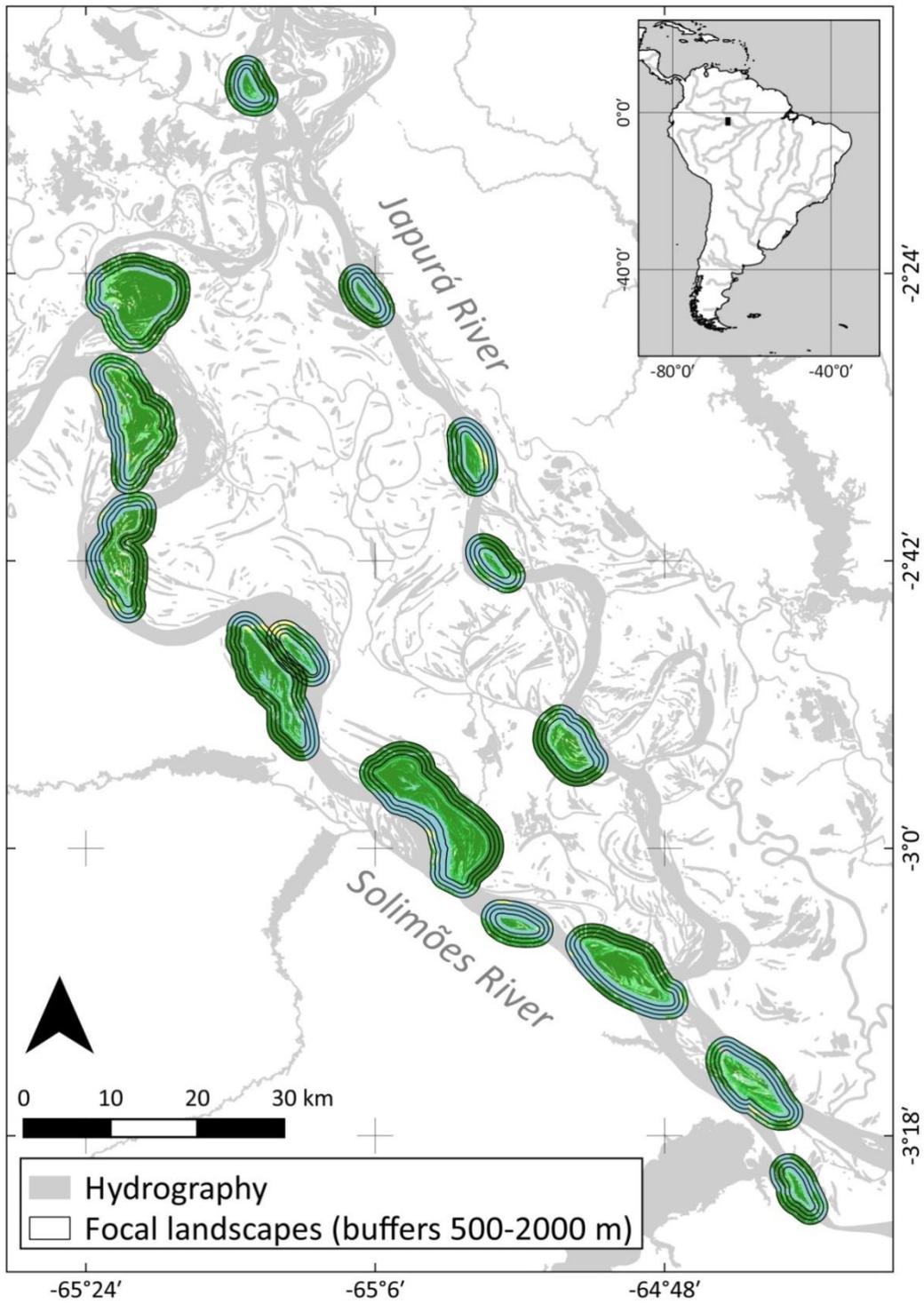
**Table 1.** Summary of multiple regression analyses of independent effects of habitat amount and matrix resistance on mammal composition.

Landscape spatial scale (m)	Partial regressions	F(2,9)	global R <sup>2</sup>	t	p
500	MDS 1**	10.42	0.70		
	habitat amount			4.146	<b>0.002</b>
	matrix resistance			1.187	0.263
1000	MDS 1**	12.55	0.74		
	habitat amount			4.899	<b>0.001</b>
	matrix resistance			0.587	0.570
1500	MDS 1**	8.51	0.65		
	habitat amount			4.285	<b>0.002</b>
	matrix resistance			-0.404	0.695
2000	MDS 1*	4.939	0.52		
	habitat amount			3.137	<b>0.011</b>
	matrix resistance			0.308	0.765

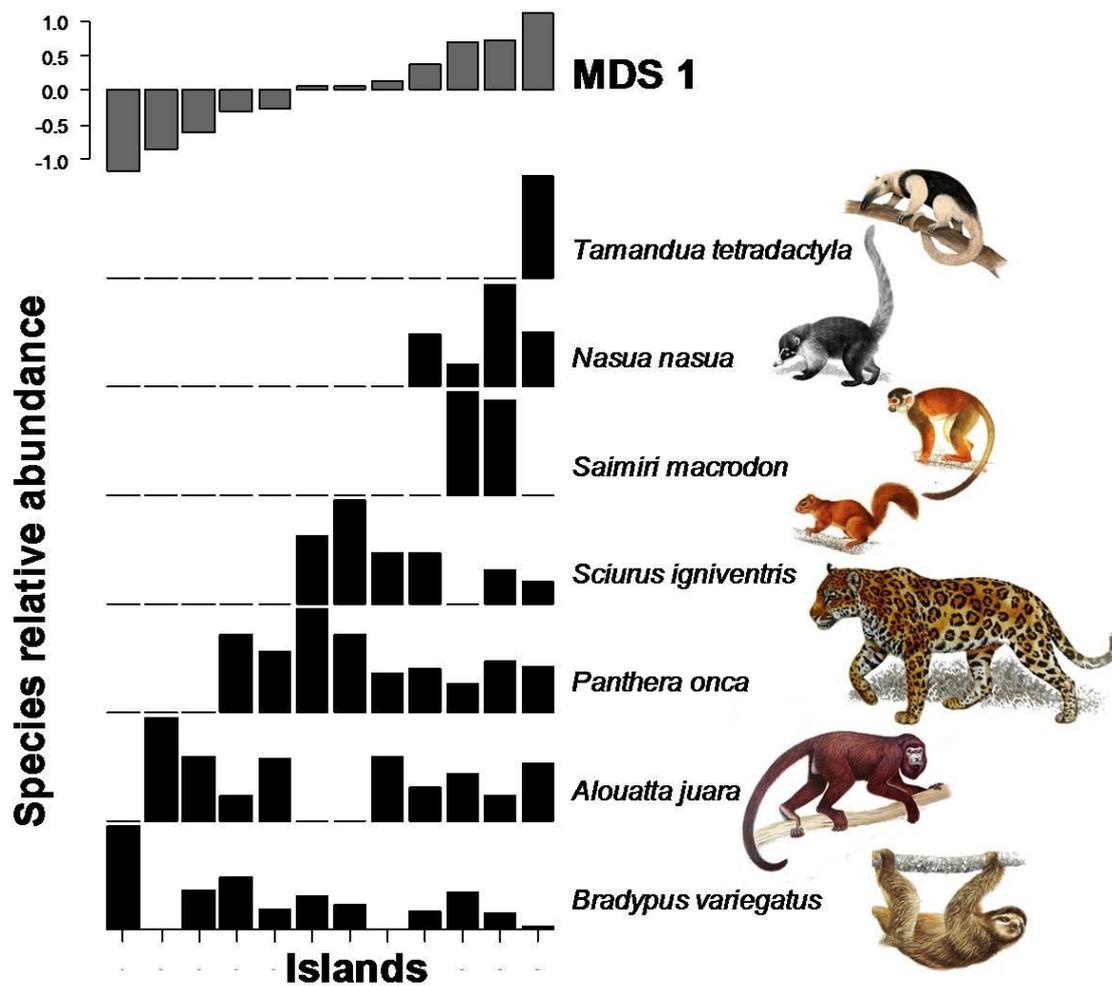
MDS 1 is the response variable in each regression model and represents the species composition of mammal assemblage based on the NMDS ordination. Asterisks indicate statistically significant global models (\*p < 0.05; \*\*p < 0.01). Bold values indicate significant effect of partial predictors.



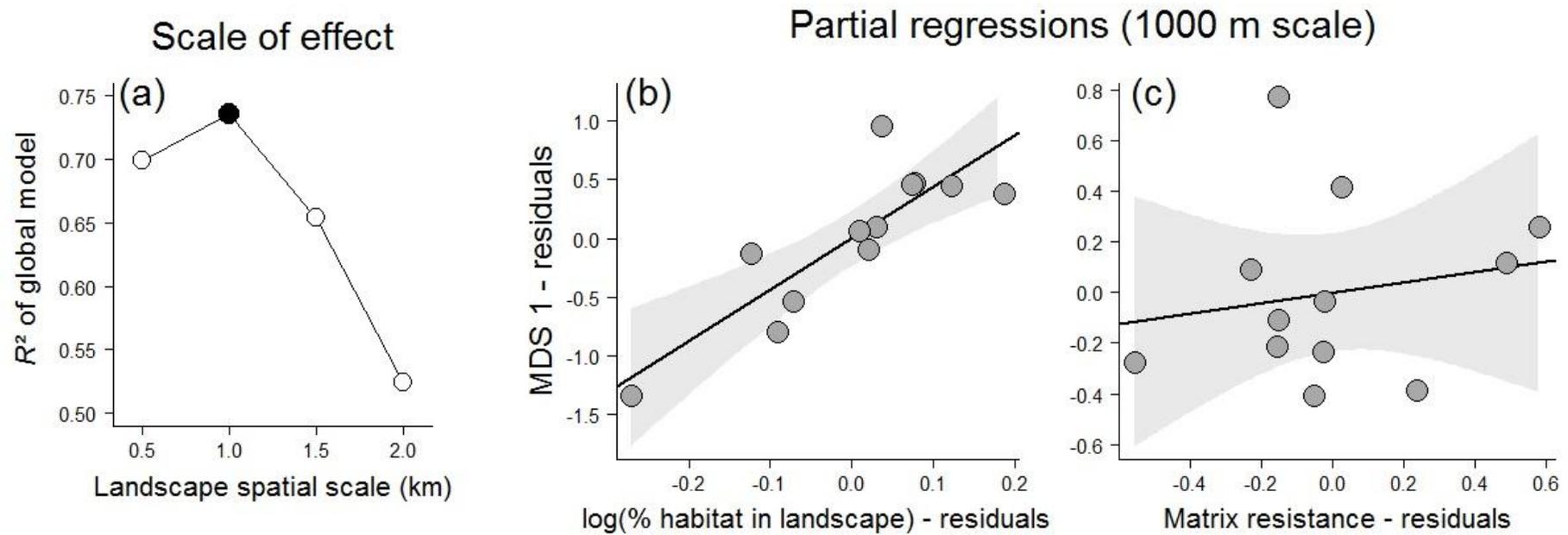
**Figure 6.** Predictions for the effects of habitat amount (HA) in landscape and matrix resistance on assemblage structure. The assemblage structure presents a nested pattern which can be visualized in a species-site matrix of species occurrence. The gradient of favorability decreases from A to D, and consequently sites more favorable contain more species. On (a), favorability is represented by HA in landscape. The HA hypothesis predicts that number of species in a sample site should increase with HA in landscape, even if the size of the patch where the sample site is contained does not vary. Because nested pattern necessarily implies changes in species richness, we predict that HA will also be able to predict the species composition of the assemblage. On (b), matrix resistance increases from A to D. We predict that as more resistant is the matrix to biological flow in the landscape, less species should occur in a sample site within a given patch, even with HA being constant. In this case, more species would be able to move through the landscape with low matrix resistance, whereas only stronger dispersers would be able to colonize or persist in a given patch surrounded by a highly resistant matrix.



**Figure 7.** Distribution of landscapes in the Middle-Solimões region, Central Amazon.



**Figure 8.** Structure of mammal assemblage in islands. Islands are sorted by MDS 1 axis, which was derived from NMDS ordination. The assemblage show a nested subset pattern, in which islands with lower scores of MDS 1 contain a subset of species from that islands with higher scores.



**Figure 9.** Effects of habitat amount and matrix resistance on species composition (MDS 1), as predicted by multiple regression analysis. (a) Association between the landscape spatial scale ( $x$ -axis) and the strength of the relationship ( $R^2$ ;  $y$ -axis) between the predictors and the species composition. The black circle indicates the scale with the strongest fit, in which partial regressions are presented in graphs (b) and (c). At this scale, habitat amount in landscape, independently of matrix resistance, had a strong association with species composition (b), whereas matrix resistance did not (c).

## Síntese

Ao longo das últimas décadas, ecólogos e conservacionistas têm comparado as manchas de habitat às ilhas oceânicas de MacArthur & Wilson (1967). Tais comparações têm visado o entendimento dos padrões de distribuição das espécies sob uma perspectiva de equilíbrio entre extinção e colonização.

Mostrei nesse trabalho que essa perspectiva pode não ser apropriada para ilhas fluviais como modelo de manchas de habitat e tendo os mamíferos arborícolas como grupo de estudo. Embora as ilhas fluviais sejam áreas de terra isoladas por uma matriz de água, não encontrei evidências de que a relação espécie-área seja modulada pela dinâmica entre colonização e extinção. Isso foi comprovado (i) pela ausência de efeito de ilha, ou seja, o incremento do número de espécies com a área amostrada é o mesmo em ilhas e na floresta contínua, e (ii) a relação espécie-área não se manteve após a riqueza de espécies ser estimada em amostras de tamanho padronizado, independente do tamanho da ilha. Portanto, as ilhas fluviais como manchas de habitat para mamíferos não representam ilhas “verdadeiras” conforme a teoria da biogeografia de ilhas.

A quantidade de habitat na paisagem local foi capaz de prever a riqueza de espécies estimada por um esforço amostral padronizado, bem como o padrão de estrutura da assembleia de mamíferos das ilhas. Além disso, a resistência da matriz não apresentou relação com a composição de espécies das ilhas. Se a quantidade de habitat na paisagem for o principal determinante da distribuição de espécies em sistemas de manchas, isso significa que considerar manchas de habitat como unidades de estudo pode ser incorreto, uma vez que as populações e comunidades bióticas podem não ser entidades delimitadas espacialmente por uma mancha de habitat (Ricklefs, 2008; Fahrig, 2013). Portanto, medir as respostas biológicas ao nível do sítio amostral, ao invés do nível da mancha, pode ser mais apropriado para entender a distribuição das espécies em sistemas de manchas.

O modelo de equilíbrio de MacArthur-Wilson como uma hipótese explicativa da relação espécie-área tem dominado a literatura. No entanto, hipóteses alternativas enfatizando outros processos que podem causar a relação entre riqueza de espécies e área (e.g., 'diversidade de habitat', Williams, 1943; 'amostragem passiva', Connor & McCoy, 1979) têm sido propostos para explicar esse padrão. O presente estudo suporta a hipótese da quantidade de habitat (Fahrig, 2013) para explicar a distribuição de mamíferos arborícolas nas ilhas fluviais do médio-Solimões.

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**APÊNDICE A - MATERIAL SUPLEMENTAR DO MANUSCRITO  
SUBMETIDO PARA *Journal of Biogeography* (Capítulo I)**

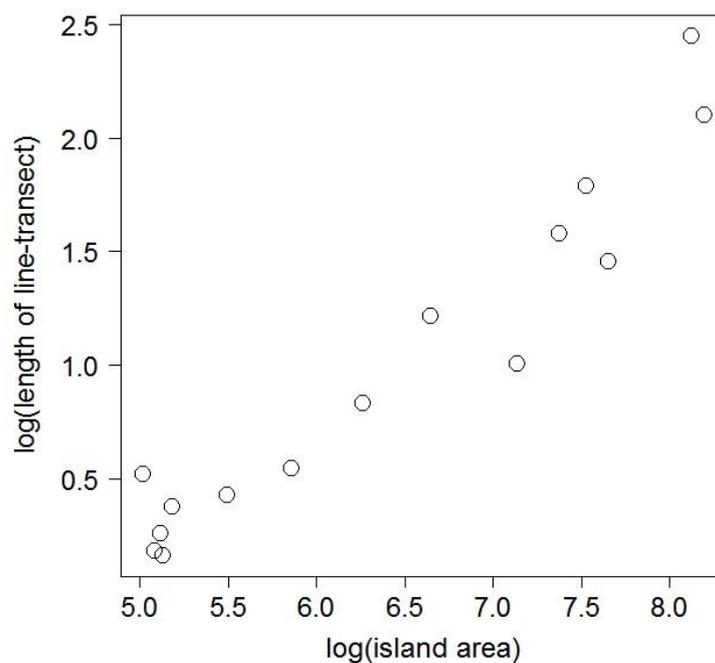
*Journal of Biogeography*

**SUPPORTING INFORMATION**

**Are fluvial islands 'true' islands for arboreal mammals? Uncovering patch size effects behind the species-area relationship pattern**

Rafael M. Rabelo, Susan Aragón, Júlio César Bicca-Marques, Bruce W. Nelson

**Appendix S1** Correlation between island size and transect length.



**Figure S1.1.** Correlation between island area and length of line-transect measured by the Pearson correlation. There was a strong positive correlation between island area and length of line-transect contained in the island ( $r = 0.96$ ,  $P < 0.001$ ).

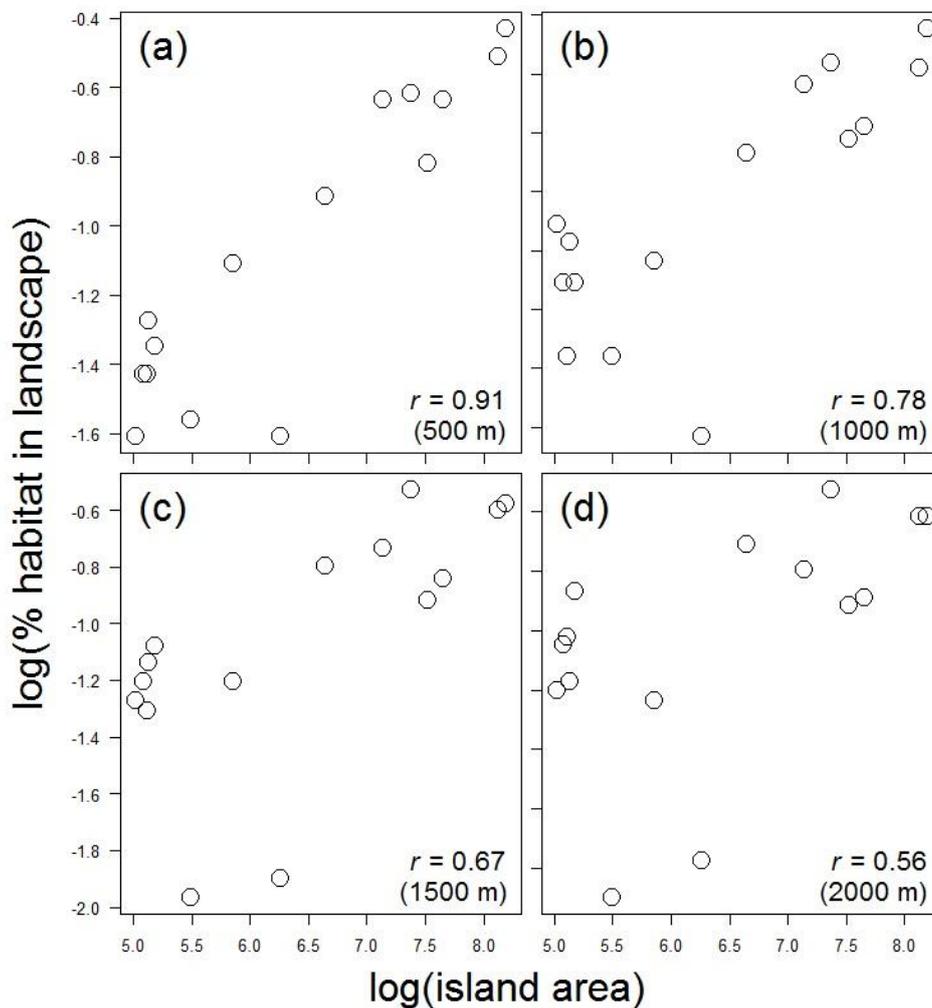
**Appendix S2** Species detected in the sample sites.

Table S2.1. List of species registered in sample sites within islands (N = 15) and continuous forest (N = 9).

Species	Common name	# records		% occupied sites	
		Islands	Cont. forest	Islands	Cont. forest
<b>PRIMATES</b>					
<i>Alouatta juara</i>	Juruá Red Howler Monkey	61	61	0.67	0.78
<i>Ateles chamek</i>	Black-faced Black Spider Monkey	1	4	0.07	0.11
<i>Cacajao calvus</i>	Bald Uakari	4	9	0.07	0.44
<i>Callicebus</i> sp.	Titi monkey	0	2	0.00	0.11
<i>Cebuella pygmaea</i>	Pygmy Marmoset	0	1	0.00	0.11
<i>Pithecia cazuzai</i>	Cazuza's Saki	2	0	0.07	0.00
<i>Saimiri cassiquiarensis</i>	Humboldt's Squirrel Monkey	0	5	0.00	0.22
<i>Saimiri macrodon</i>	Ecuadorian Squirrel Monkey	11	17	0.20	0.44
<i>Saimiri vanzolinii</i>	Vanzolini's Squirrel Monkey	0	97	0.00	0.33
<i>Sapajus macrocephalus</i>	Large-headed Capuchin	4	63	0.07	0.78
<b>PILOSA</b>					
<i>Bradypus variegatus</i>	Brown-throated Sloth	26	6	0.60	0.33
<i>Tamandua tetradactyla</i>	Southern Tamandua	1	1	0.07	0.11
<b>CARNIVORA</b>					
<i>Nasua nasua</i>	South American Coati	12	8	0.27	0.67
<b>RODENTIA</b>					
<i>Urosciurus igniventris</i>	Northern Amazon Red Squirrel	19	19	0.40	0.56

### Appendix S3 Colinearity between HA and island size.

We observed the colinearity between the predictors using a simple Pearson correlation in each scale of analysis (500, 1000, 1500, 2000 meters). We found a significant positive correlation between the variables in all scales, but the strength of the correlation decreased as the spatial scale increased (Fig.S3.2). The fourth scale (2000 m) had the weakest correlation between the predictors, and it was the only scale in which we found significant effects (considering  $P < 0.05$  as limit of significance) of HA on species richness (see main text).



**Figure S3.2.** Correlation between island area and habitat amount (HA) measured by the Pearson correlations at the four spatial scales.

## APÊNDICE B - MATERIAL SUPLEMENTAR DO MANUSCRITO EM PREPARAÇÃO PARA *Ecography* (Capítulo II)

### SUPPLEMENTARY MATERIAL

Rabelo R. M., Aragón S., Bicca-Marques J. C. and Nelson B. W. 2016. Nestedness of mammal assemblage on fluvial islands: the influence of habitat amount in landscape. - *Ecography* 000: 000-000.

**Appendix 1.** Accessing the resistance coefficients by experts' opinion.

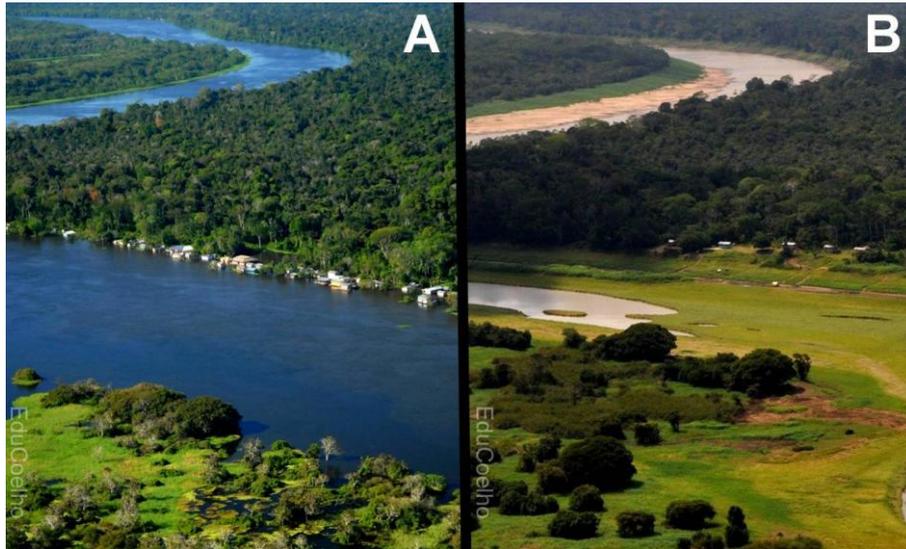
We send the bellow closed format questionnaire to 50 specialists, explaining our study, characterizing our landscapes carefully, and asking them to assign a resistance weight to each type of matrix in the fluvial landscapes. Questionnaires were prepared in the Google Forms© and send to experts by e-mail.

#### Questionnaire

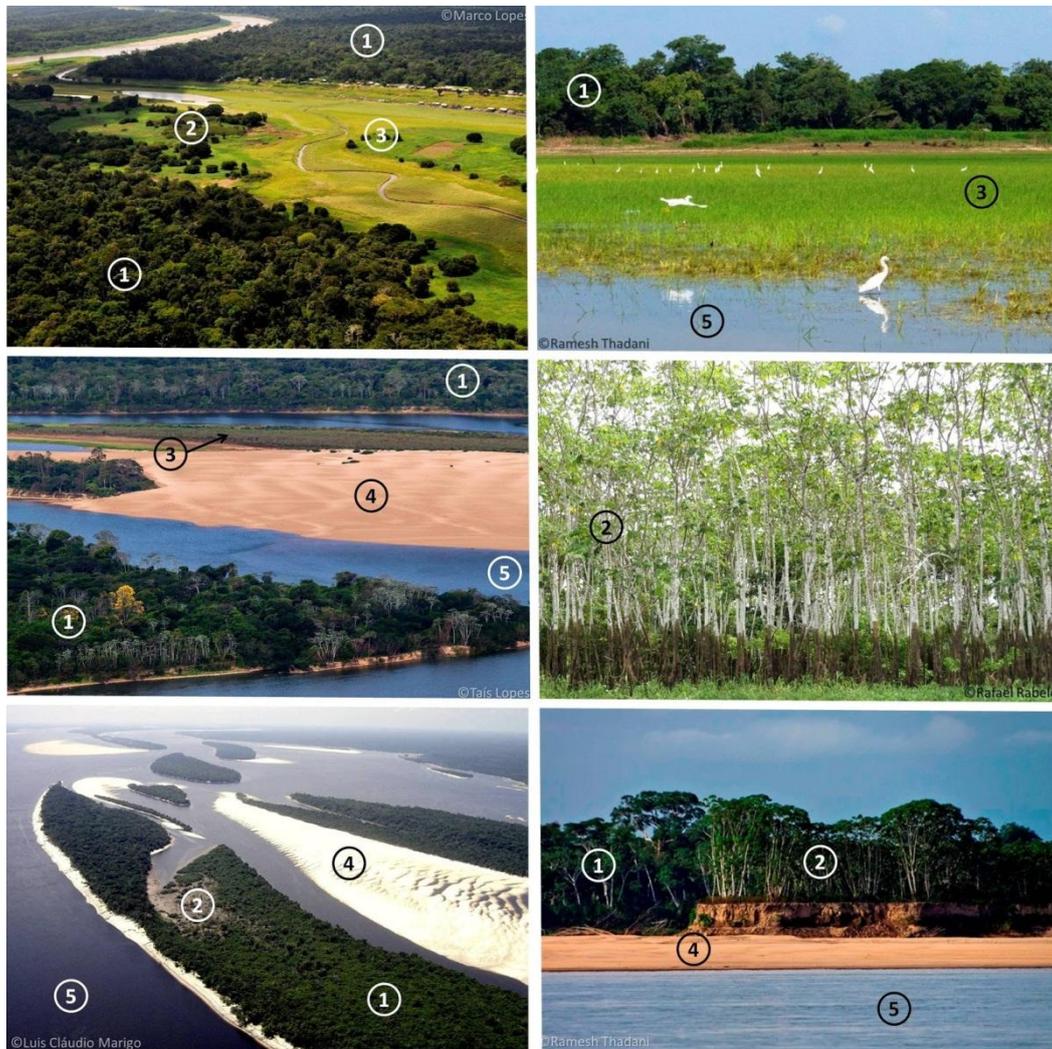
##### **Expert consultation about matrix resistance for mammals**

Thank you for your collaboration! First, a brief explanation of my work. In this study, I am evaluating how island size and matrix resistance affect the occurrence of mammals on fluvial islands. The study area is located on the Middle-Solimões River, close to its confluence with the Japurá River. This area is inserted within a floodplain várzea ecosystem. The várzea forests are seasonally flooded by nutrient-rich muddy-water rivers. The annual water level fluctuation results in aquatic and terrestrial phases. In the study area, the normal annual range of flooding can reach to 12 meters. I am using satellite imagery from the dry season to obtain the landscape attributes. In this period, as the water level drops, seasonally unflooded systems appear, including sand banks areas and low-lying areas covered with herbaceous and shrub vegetation (Fig. S1). The satellite images were classified into five classes of land cover. One of these is the “habitat” class (forest) and the other four types are non-habitat matrix with different degrees of resistance to being traversed by each mammal species. Below is a brief explanation of each land cover type and some images (Fig. S2) to exemplify:

- **Forest** (habitat): late-successional stages of várzea forest. It can be classified in three major types of forest: chavascal, low várzea and high várzea.
- **Shrub**: early-successional stages of várzea forest, areas covered with shrub communities, sparse trees and/or monospecific vegetation of *Cecropia* sp.
- **Herbaceous**: Systems predominantly covered with herbaceous plants, with areas mostly covered by annual and perennial grasses and herbs visible at low water.
- **Sand**: areas with or without sparse vegetation, comprised of banks of sand and mud exposed at low water.
- **Water**: rivers, channels and lakes.



**Figure A10.** Aerial photograph showing the high water season (A) and the low water season (B) in the Mamirauá Reserve.



**Figure A11.** Examples of the five land cover types considered in the study. (1) Forest, (2) shrub, (3) herbaceous, (4) sand and (5) water.

Due to their habit, forest is obviously the major habitat for arboreal and semi-arboreal mammals. The four types of matrix are assumed to have different resistance levels to biological flow. The matrix resistance is related to the degree of dissimilarity of its type in relation to the habitat, i.e. forest. As the difference between matrix and habitat increases, so does the matrix resistance. Therefore, a given type of matrix with low resistance should be a more permeable environment to animal movement. On the other hand, a high-resistance matrix should be an obstacle to animal movement.

To calculate the matrix resistance, I am going to use one isolation metric that is based on the matrix resistance to animal movement. And it is on this point that I would appreciate your expert contribution. As the literature about matrix resistance for this group of mammals is scarce, the resistance coefficients of each type of matrix will be based on expert opinions. Thus, the aim of this questionnaire is to assign a resistance coefficient to each type of matrix based on your knowledge.

In the next pages I am going to ask for your opinion about the degree of resistance of each type of matrix to some genera that I am studying and, finally, to the whole target-group of the research<sup>1</sup>. You can answer only for those genera that you feel you have enough affinity or knowledge.

### **Degree of matrix resistance to arboreal and semi-arboreal mammals.**

Consider the four types of matrix: shrub, herbaceous, sand and water. In a 30 x 30 meters area and on a scale from 0 to 10, which resistance weight would you assign to each type of matrix for mammals? Remember: a matrix of weight "0" should be an environment without resistance, very similar to the forested habitat. On the other hand, a matrix type of weight "10" should be very resistant to biological flow and near to an absolute barrier to animal movement.

#### **Shrub**

Without Resistance	0	1	2	3	4	5	6	7	8	9	10	Maximum Resistance
	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	

#### **Herbaceous**

Without Resistance	0	1	2	3	4	5	6	7	8	9	10	Maximum Resistance
	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	

#### **Sand**

Without Resistance	0	1	2	3	4	5	6	7	8	9	10	Maximum Resistance
	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	

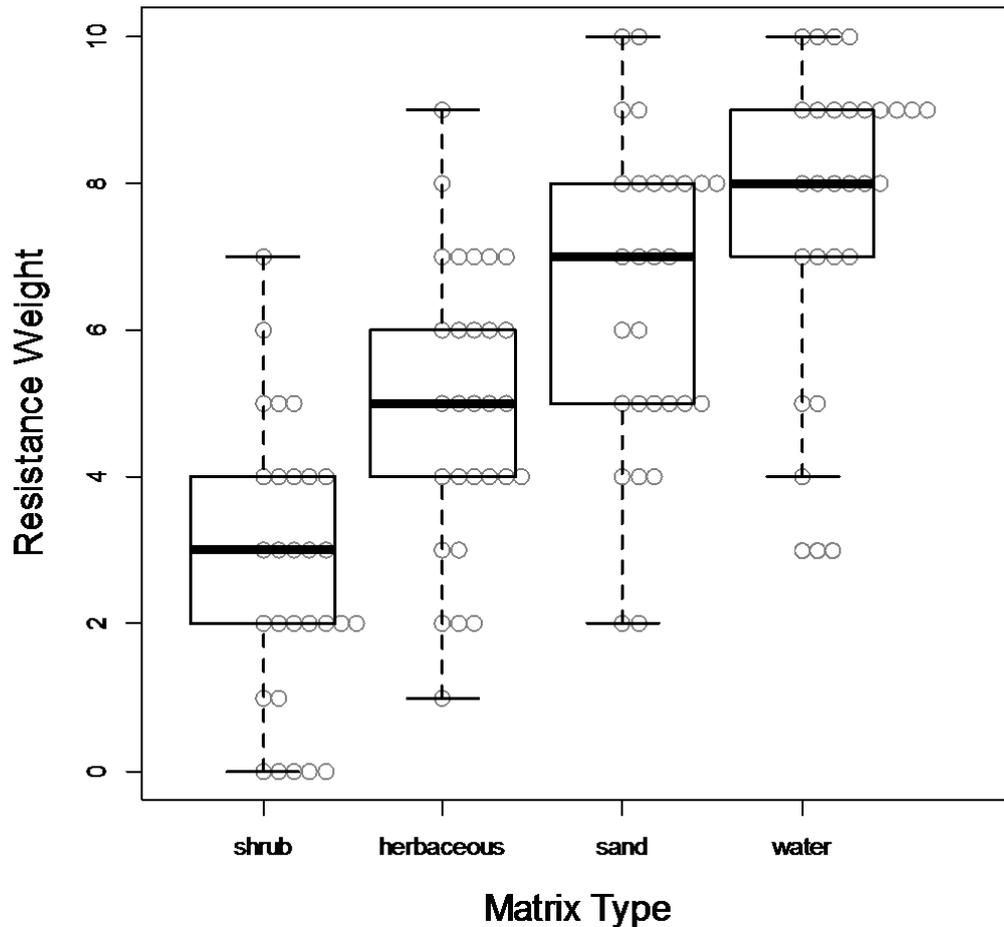
#### **Water**

Without Resistance	0	1	2	3	4	5	6	7	8	9	10	Maximum Resistance
	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	( )	

<sup>1</sup> Here we show only the last question, regarding the resistance coefficient for the overall group (mammals) to simplify the information. The questions about resistance weight for each genera were exactly the same as presented above.

### Resistance coefficient based on experts' opinion

We used the expert's opinions about resistance weight attributed for the overall taxonomic group as the resistance coefficient. Since the distribution of expert's opinion was not symmetric (Fig. S3), we considered the median of their opinions as the resistance coefficient. To verify the sensitivity of matrix resistance index to expert's opinions, we also performed the analysis using the first and third quartiles.



**Figure A12.** Variation in expert's opinion about resistance weight for each matrix type (n= 29). The box plots display the median (thick black line), the first and third quartiles (thin black box). The whiskers extend from the min to the maximum values assigned by experts. Outliers are indicated by solid circles.

**Appendix 2.** Species detected in islands.**Table A1.** List of species detected in islands (N = 12).

Species	Common name	# records	% occupied sites
PRIMATES			
<i>Alouatta juara</i>	Juruá Red Howler Monkey	55	0.75
<i>Saimiri macrodon</i>	Ecuadorian Squirrel Monkey	2	0.17
PILOSA			
<i>Bradypus variegatus</i>	Brown-throated Sloth	27	0.83
<i>Tamandua tetradactyla</i>	Southern Tamandua	1	0.08
CARNIVORA			
<i>Nasua nasua</i>	South American Coati	12	0.33
<i>Panthera onca</i>	Jaguar	19	0.75
RODENTIA			
<i>Urosciurus igniventris</i>	Northern Amazon Red Squirrel	19	0.50

**Table A2.** Species counts across islands. Species counts were standardized to equal totals firstly by columns (sites) and secondly by rows (species), to control sample area effect and abundance effect, respectively. Species-site matrix was sorted according to NMDS ordination based on Bray-Curtis dissimilarity.

	ice	mis	pir	pre	jac	jur	mic	col	cau	mar	ceu	env
<i>Tamandua tetradactyla</i>	0	0	0	0	0	0	0	0	0	0	0	1
<i>Nasua nasua</i>	0	0	0	0	0	0	0	0	3	1	5	3
<i>Saimiri macrodon</i>	0	0	0	0	0	0	0	0	0	1	1	0
<i>Urosciurus igniventris</i>	0	0	0	0	0	1	2	2	7	0	4	3
<i>Panthera onca</i>	0	0	0	1	1	1	1	1	4	2	4	4
<i>Alouatta juara</i>	0	1	5	1	3	0	0	5	9	10	6	15
<i>Bradypus variegatus</i>	1	0	3	2	1	1	1	0	5	8	4	1

**Appendix 3.** Multiple regression analyses considering the variation of expert's opinion about matrix resistance.

**Table A3.** Summary of multiple regression analyses of independent effects of habitat amount and matrix resistance on mammal assemblage, considering the first and third quartiles in the matrix resistance index.

Matrix coefficient	Landscape spatial scale (m)	Partial regressions	global R <sup>2</sup>	t	p
1 <sup>st</sup> quartile	500	MDS 1*	0.70		
		habitat amount		<b>4.224</b>	<b>0.002</b>
		matrix resistance		1.238	0.244
	1000	MDS 1*	0.74		
		habitat amount		<b>4.920</b>	<b>0.001</b>
		matrix resistance		0.619	0.550
	1500	MDS 1*	0.66		
		habitat amount		<b>4.297</b>	<b>0.002</b>
		matrix resistance		-0.450	0.663
	2000	MDS 1*	0.52		
		habitat amount		<b>3.142</b>	<b>0.011</b>
		matrix resistance		0.239	0.816
3 <sup>rd</sup> quartile	500	MDS 1*	0.70		
		habitat amount		<b>4.142</b>	<b>0.002</b>
		matrix resistance		1.189	0.262
	1000	MDS 1*	0.74		
		habitat amount		<b>4.889</b>	<b>0.001</b>
		matrix resistance		0.577	0.577
	1500	MDS 1*	0.65		
		habitat amount		<b>4.281</b>	<b>0.002</b>
		matrix resistance		-0.379	0.713
	2000	MDS 1*	0.52		
		habitat amount		<b>3.160</b>	<b>0.010</b>
		matrix resistance		0.338	0.742

MDS 1 is the response variable in each regression model and represents the species composition of mammal assemblage based on the NMDS ordination. Asterisks indicate statistically significant global models ( $p < 0.01$ ). Bold values indicate significant effect of partial predictors.