

Are fluvial islands “real” islands for arboreal mammals? Uncovering the effect of patch size under the species–area relationship

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Abstract

Aim: We tested the “habitat amount hypothesis”, which predicts that the effect of patch size on number of species results from a “sample area effect” rather than an “island effect”. Specifically, we (1) compared parameters of the species–area relationship (SAR) of arboreal mammals in forested fluvial islands and continuous forest, and (2) separated the effects of island size and of landscape-scale habitat amount on species richness.

Location: Middle-Solimões River region, Central Amazon.

Methods: We surveyed arboreal mammals along line-transects on 15 fluvial floodplain islands and nine transects in continuous floodplain forest. Transect length varied according to island size. Transects of similar length were established in continuous 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 between the two SARs using ANCOVA. We used multiple regressions to separate the effects of island size and of habitat amount on the rarefied number of species across multiple spatial scales (500–6,000 m).

Results: The two species–area curves showed similar slopes, but the intercept was lower for islands. Multiple regressions showed the best fit at the 5,500 m spatial scale. At this scale, habitat amount predicted species richness, whereas island size did not.

Main conclusions: We conclude that the apparent effect of patch size on the number of species may be simply due to the sample area effect and that no island effect operates on this patchy system. Accordingly, island size *per se* does not increase the number of species at a sample site. Fluvial islands should not be treated as “real” islands from the island biogeography perspective. In sum, we found support for the habitat amount hypothesis for predicting the richness of arboreal mammals on fluvial islands.

KEYWORDS

Amazon, fluvial landscapes, habitat amount hypothesis, island biogeography, island effect, local patch, river dynamics, sample area effect, species richness, species–area curve

1 | INTRODUCTION

The species–area relationship (SAR) is considered one of the few laws in ecology. It predicts that the number of species per sample

increases with increasing sample area in a logarithmic manner, whether in a region of continuous habitat or across habitat patches (Preston, 1962). MacArthur and Wilson (1963, 1967) proposed the theory of island biogeography to explain the SAR

pattern, stating that the slope of the relationship across oceanic islands should be steeper than across samples on the mainland as the ratio between extinction and colonization on islands of a given size is higher than that on similarly sized areas in the mainland. This species deficit from enhanced extinction would increase as the size of the island and its corresponding sampled area decrease. The idea that habitat patches are comparable to oceanic islands has become popular in ecology and conservation biology since MacArthur & Wilson's publication. This theoretical background led researchers to construct species–area curves (i.e. Type IV curve *sensu* Scheiner [2003], or island species–area relationship, ISAR, *sensu* Triantis, Guilhaumon and Whittaker [2012]) for several types of habitat patches (reviewed in Watling & Donnelly, 2006; Triantis et al., 2012; Matthews, Guilhaumon, Triantis, Borregaard & Whittaker, 2015).

The steeper slope for oceanic islands became known as the “island effect” and steep slopes have been associated with high isolation and, consequently, low immigration rates (Matthews et al., 2015; Triantis et al., 2012; Watling & Donnelly, 2006). MacArthur and Wilson (1967) also predicted that SARs from oceanic archipelagos would have lower intercepts than the SAR on the mainland. This expectation was derived from the idea that isolation reduces species dispersal, thereby decreasing the number of transient species that maintain sustainable populations on islands by periodic immigration. This prediction was empirically confirmed for “true islands”, i.e. any areas of land surrounded by water (Matthews et al., 2015; Triantis et al., 2012).

But, what is the expected slope of SAR across habitat patches on the mainland? Should it be steep, as on MacArthur & Wilson's islands, or shallow, as across samples of continuous habitat? These questions were recently posed by Fahrig (2013). Although previous empirical studies showed a direct 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) challenges the notion that patch size *per se* affects species richness. She argues that this apparent patch size effect might result from a “sample area effect”. In this case, the number of species increases with increasing patch size simply because of the greater sample area allocated to larger patches. This sample area effect is the simplest explanation for the SAR pattern in habitat patches.

A more appropriate manner to verify the existence of an island effect in a given patch system is to compare the slope of the SAR from a set of differently sized habitat patches with the slope from a set of sample sites equal in size to those patches, but contained within continuous habitat (Fahrig, 2013; Figure 1). If the sample area effect alone explains SAR in habitat patches, then species richness is expected to increase at similar rates for both continuous habitat and habitat patches (Figure 1b). On the other hand, if a true island effect occurs and habitat patches are analogous to remote islands, their SAR slope would be steeper than in continuous habitat (Figure 1c).

An additional sampling design to look for effects of patch size *per se* on number of species, but controlling for the sample area

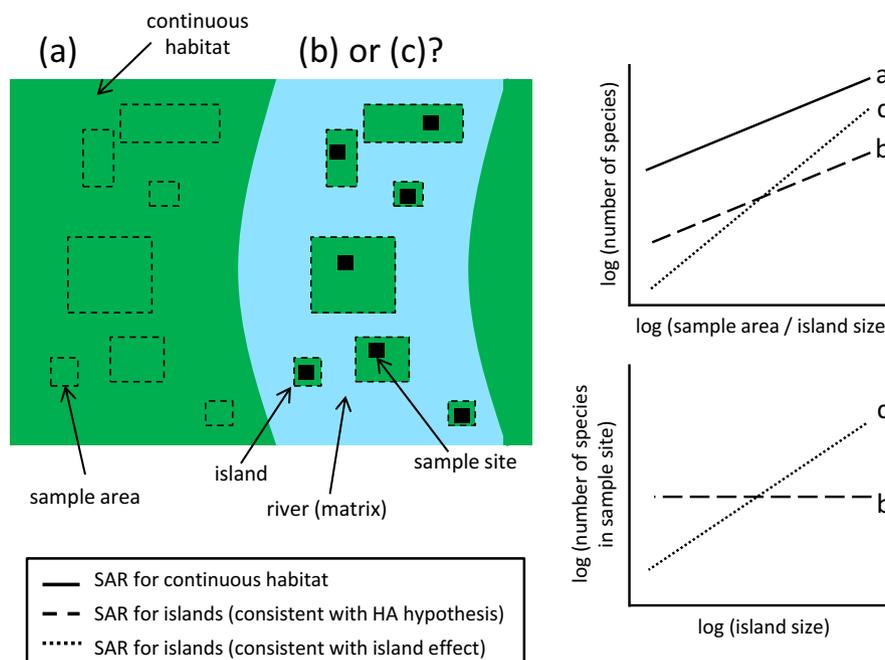


FIGURE 1 Predictions of the habitat amount (HA) hypothesis for a hypothetical fluvial landscape. The number of species increases with sample area contained in continuous forest because of the sample area effect (a). The HA hypothesis predicts that the species–area relationship (SAR) for islands has a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

effect, is to standardize sampling effort across habitat patches. 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 if no island effect operates on this patch system. This expectation is independent of increases in the size of patches where samples are embedded (Fahrig, 2013; Figure 1b, lower graph).

Indeed, Sampaio, Lima, Magnusson and Peres (2010) and Santos-Filho, Peres, Silva and Sanaiotti (2012) found no effect of patch size on the number of mid- to large-sized mammals and small mammals, respectively, when using sample sites of fixed size within differently sized Amazonian forest fragments. Despite these findings, patch area has been considered the main driver of mammal richness (e.g., Benchimol & Peres, 2013; Boyle & Smith, 2010), although most studies have not attempted to control the sample area effect on SAR (but see Benchimol & Peres, 2015; Michalski & Peres, 2007).

It was within this context that Fahrig (2013) proposed the “habitat amount (HA) hypothesis”. According to this hypothesis, the amount of habitat in the local landscape should be the main driver of the distribution of species in patchy systems. The “local landscape” is the area within a given distance from the sample site (Figure 2) and it can extend beyond the confines of a focal patch. The appropriate distance for defining the size of the local landscape is that distance from the sample site at which the landscape structure shows the strongest effect on the response of species; this distance

is called the “scale of effect” (Martin & Fahrig, 2012). The HA hypothesis predicts that the number of species in equally sized sample sites increases with increasing HA in the local landscape. Additionally, it predicts that the number of species in a sample site contained in a given patch is independent of that patch's size, unless the area of the patch affects the total HA in the local landscape.

Here we tested the HA hypothesis using forested river islands as models of habitat patches. Although they are technically “true islands” (i.e., portions of land surrounded by water), they are treated as habitat patches in our model. Our aim was to verify whether there is an island effect operating in these patches by analysing the SARs (Type IV or ISAR curves) of arboreal mammals. Specifically, we compared the SAR from sample sites within a set of forested islands with the SAR from a set of independent sample sites within continuous forest. If fluvial islands are equivalent to oceanic islands, we expect their SAR pattern to be steeper than that of continuous forest (Figure 1c). On the other hand, if an island effect does not modulate the species–area curve on fluvial islands, as the HA hypothesis predicts, we expect similar SAR slopes in both situations, due only to the sample area effect (Figure 1b).

Finally, we also asked whether and how island size and HA in the landscape affect species richness estimated with standardized sampling effort at each sample site. For this, we defined multi-scale local landscapes (i.e., areas within buffer distances from sample sites) for each island sample site (Figure 2). If a true island effect modulates SAR on these fluvial islands, we expect that species richness increases with island size even after fixing sample size. On the other hand, if the HA hypothesis is true, species richness of fixed-size samples should be independent of island size but should increase with increasing HA in the local landscape (Figure 2).

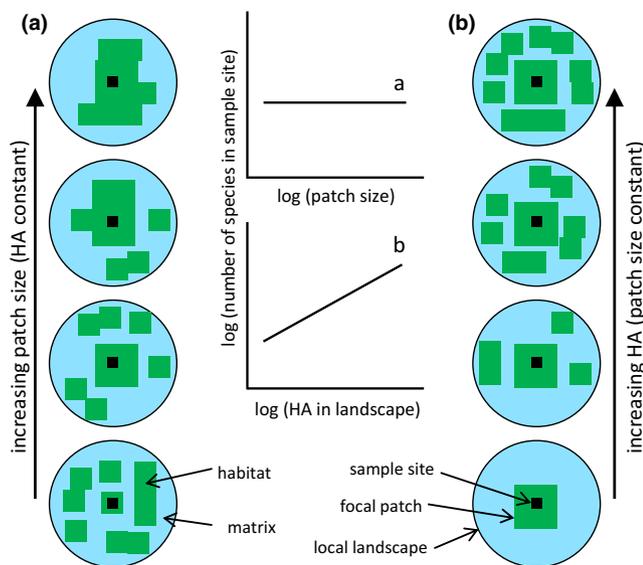


FIGURE 2 Predictions of the independent effects of habitat amount (HA) in the local landscape and of island size on species richness. The “local landscape” is the area within a given distance (or one of multiple distances) from the sample site within a focal patch. The HA hypothesis predicts that species richness in a sample site within a given patch is independent of that patch's size, when HA in the local landscape remains constant (scenario [a]; upper graph). Also, species richness in sample site increases with HA in the local landscape, even if the size of local patch is constant (scenario [b]; lower graph). Adapted from Fahrig (2013)

2 | MATERIALS AND METHODS

2.1 | Study region

Sampling was near the confluence of the Solimões and Japurá rivers in Central Amazon (Figure 3). The interfluvium at these rivers' junction is a floodplain forested ecosystem, called *várzea*, which is protected by the Mamirauá Sustainable Development Reserve (IDSMD, 2010). *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 (IDSMD, 2010).

2.1.1 | Fluvial islands as model of habitat patches

The spatial structure of Amazonian riverscapes are often highly dynamic (Peixoto, Nelson & Wittmann, 2009; Puhakka, Kalliola, Rajasilta & Salo, 1992). Erosion, transport and deposition of sediments create new sites of terrestrial habitat: the fluvial islands (Kalliola,

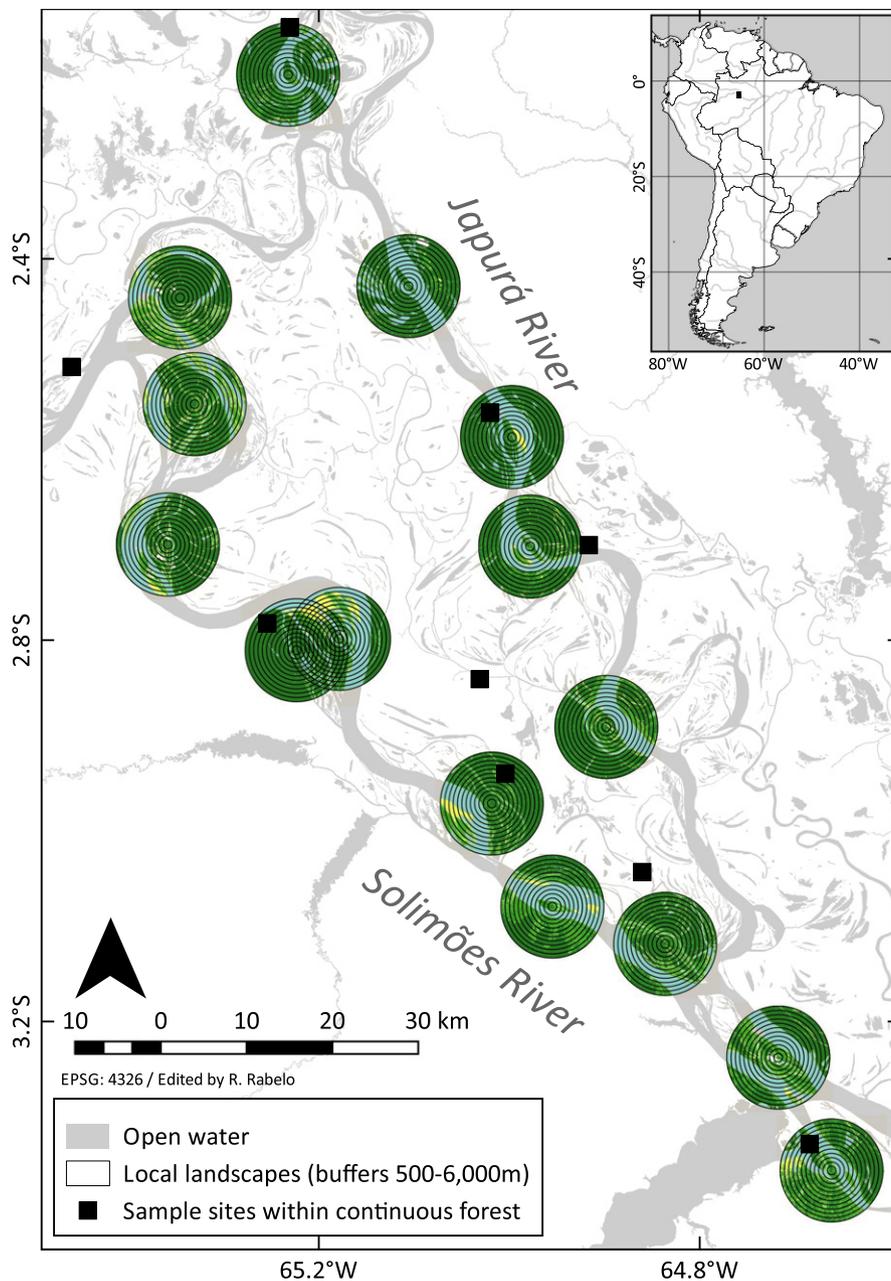


FIGURE 3 Distribution of local landscapes and sample sites in the Middle-Solimões region, Central Amazon, Brazil

Salo, Puhakka & Rajasilta, 1991). Here, we use fluvial islands within these riverscapes as our model of habitat patches. River dynamics affects species distribution in terrestrial environments (Salo et al., 1986; Toivonen, Maki & Kalliola, 2007) by facilitating dispersal and influencing species' occurrence on fluvial islands (e.g., birds: Cintra, Sanaiotti & Cohn-Haft, 2007; Rosenberg, 1990 primates: Ayres & Clutton-Brock, 1992; Rabelo et al., 2014). Although fluvial islands may represent ephemeral patches for species with long generation times (Shepherd & Brantley, 2005), we consider them appropriate patch models for testing the HA hypothesis. We restricted our sample to islands that have lasted long enough to sustain two or more generations of our study species to avoid the influence of ephemeral islands on the results (see "Sampling design" section, below).

2.2 | Study group

Mammals inhabiting *várzea* forests are mostly arboreal (primates and sloths) because the canopy of these seasonally flooded forest is permanently emerged. Scansorial (anteaters and squirrels) or terrestrial (coatis) species can also be found. Most of these mammals rarely descend to the ground but they occasionally move through shrub and herbaceous vegetation, walk on sandy substrates or even swim in rivers and lakes. Therefore, only a structured forest environment fulfils all requirements that characterize "habitat" for our assemblage (Fahrig, 2013). Another convenience of studying these mammals in *várzea* forests is their usually high population densities (Peres, 1997). Dense populations enhance detection rate, reducing the risk of false negatives in surveys.

2.3 | Sampling design

We adopted a mixed patch-landscape scale sampling design. In this approach, a landscape represents each sample unit. The response variable is measured within a focal patch (the island), whereas the predicting variables can be measured both at the patch and/or at the surrounding local landscape within a given distance from the focal patch (McGarigal & Cushman, 2002). An alternative adaptation of the patch-landscape design assesses the response variable in equally sized sample sites with landscape predictors measured within a specified radius from them instead of at the patches (Fahrig, 2013; Figure 2).

We sampled 15 focal islands of varying size (151–3,625 ha) and adopted a multi-scale approach to find the appropriate scale to detect the predictors' effects on our study group, the scale of effect (Martin & Fahrig, 2012). We used 12 buffer distances (500–6,000 m at 500-m intervals) from each sample site within islands to define their local landscapes (Figure 3). We chose focal islands based on the following criteria: (i) islands permanently surrounded by water (i.e., even during the low water season); (ii) minimum distance of 2 km between islands' edges to avoid overlapping landscapes (only two out of 15 landscapes overlapped at the buffer scales of 3,000–6,000 m); and (iii) minimum island age of 30 years (determined using a historical series of Landsat Thematic Mapper satellite images) to avoid ephemeral islands for our study species.

Mammal surveys were conducted along linear transects (our sample sites) on the alluvial islands and in nine independent sample sites distributed in the adjacent continuous floodplain forest (black squares in Figure 3). Transect length on islands (1.2–11.6 km) was directly correlated with island size (see Fig. S1.1). The range of transect lengths within the continuous forest sample sites was the same as those on the islands, as suggested by Fahrig (2013) to test her hypothesis.

2.4 | Data collection

2.4.1 | Mammal survey

From 2013 to 2014, we conducted the surveys along line-transects, following a standardized protocol (Peres, 1999). Two trained observers conducted the surveys by quietly walking trails at constant speed of *c.* 1.5 km/hr. We carried out surveys in the morning (06.30–11.30 hr) and afternoon (14.00–17.00 hr). Sampling was interrupted during rains. We recorded the occurrence of species via sightings or vestiges, such as vocalizations, faeces, footprints and signs of digging in the case of semi-arboreal species, to improve detection.

We conducted four surveys separated by intervals of a maximum of 20 days on each line-transect during two low-water seasons (September to November) of 2013 and 2014. We limited surveys to the low-water seasons to minimize potential seasonal effects on species' detection, but we were unable to visit all islands during a single low-water season due to logistical constraints.

2.4.2 | 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. We performed a semi-supervised classification of landscapes into five 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 cover was our habitat class, whereas all other classes were considered matrix. We calculated the area of forest habitat on each island and within their 12 buffer scales of local landscape. 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).

2.5 | 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 the samples of continuous forest. We log-transformed the number of species and the length of the line-transect of each sample site before conducting the analysis because power (log-log) models perform better in explaining SAR (Matthews et al., 2015; Watling & Donnelly, 2006). This transformation into a linear relationship was also necessary because we used an analysis of covariance (ANCOVA) with interaction between independent variables to compare island and continuous forest SARs. 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 differently sized sample sites as sample units, the actual number of detected species in a sample site as the response variable, the type of site (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 (see Fig. S1.1).

To evaluate the separate effects of island size and HA in the local landscape on the number of species in a sample site, we first controlled for the effect of sample area because our island sample sites varied in size. We accomplished this task by using a rarefaction procedure to standardize sampling effort across sites. This procedure allows estimating the number of species in samples of equal completeness. We used a rarefaction based on sampling completeness, rather than sample size, because standardizing samples by size (Hurlbert, 1971) usually underestimates species richness of richer assemblages (Chao & Jost, 2012). We considered in this analysis the rarefied number of species as our response variable and forested area within islands and within local landscapes as our predictors. We also log-transformed island forest area, HA and the 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 HA separately. We also rerun the regression models without considering overlapping landscapes (see Appendix S2 for further details). We considered that the scale of effect would be that showing the best fit of the global model, i.e. the highest R^2 value (Fahrig, 2013; Martin & Fahrig, 2012). We also used the AIC selection approach in addition to the multiple regressions to verify the consistency of our results, given that multiple regression may not effectively separate the effects of collinear predictors (see “AIC Selection” section on Appendix S2 for further details). All analyses were performed using “vegan” 2.2-1 (Oksanen et al., 2013) and “INEXT” (Hsieh, Ma & Chao, 2016) packages, within R 3.1.3 statistical software (R Development Core Team, 2015).

3 | RESULTS

We found 14 mammal species (see Table S3.3) belonging to the orders Primates (10), Pilosa (2), Carnivora (1) and Rodentia (1). We detected 10 species on islands and 13 in continuous forest.

We found a strong SAR pattern with steep slope estimates for both islands ($F_{1,13} = 13.19$; $R^2 = .50$; $p < .01$; z -value = 0.58) and continuous forest ($F_{1,7} = 17.20$; $R^2 = .71$; $p < .01$; z -value = 0.40). The number of species appears to be lower on islands than in continuous forest as the estimated intercept of SAR from islands ($\log c$ -value = 0.51) was lower than that from continuous forest ($\log c$ -value = 1.25).

We also found that the size of the sample site (transect length) has a positive effect on the number of species that it harbours (ANCOVA: $F = 27.39$; $p < .01$). This effect was similar between islands and continuous forest, since the interaction test failed to detect a significant difference between slopes ($F = 0.93$; $p = .34$; Figure 4). However, the number of species differed between islands and continuous forest as seen in the simple regression models and evidenced by their different SARs' intercepts ($F = 11.16$; $p < .01$; Figure 4).

The Pearson correlation analysis showed that island size and HA were highly correlated at the first six scales of analysis (500–3,000 m), but were not collinear at the last three scales (5,000–6,000 m; see Fig. S1.2). We found the best fit of our multiple regression models at the spatial scale of 5,500 m (global $R^2 = .57$; Figure 5a). HA explained the rarefied number of species at this scale, whereas island size did not (global model: $F_{2,12} = 7.934$; $p < .01$; Figure 5b & c; Table 1). The exclusion of overlapping landscapes from the analysis did not change this result (see Table S2.1). We also found a significant global fit at other spatial scales (Table 1), but significant partial effects on species richness were restricted to the last four scales (4,500–6,000 m; Table 1, see Fig. S2.3). The AIC selection procedure showed similar results. Models at wider scales (4,000–5,500 m) showed the best fit to our data, while models including island size tended to rank among the lowest (see Table S2.2). We indicated a set of six best models ($\Delta AIC < 2$) instead of a single best model because of selection uncertainty in the AIC approach. Although two of the six best models included both island size and

HA as predictors, the effect of the latter was more important (see slope coefficients in Table S2.2).

4 | DISCUSSION

4.1 | “Island effect” or “sample area effect”?

We did not find evidence of an island effect operating in our patch system. Although the SAR slope of fluvial islands (0.58) was as steep as those reported for oceanic islands (Matthews et al., 2015; Triantis et al., 2012), it did not differ from that of our continuous forest sites (0.40). Alike other empirical studies (reviewed in Connor & McCoy, 1979; Matthews et al., 2015; Triantis et al., 2012), our values are outside the theoretically expected canonical range of 0.17–0.33 (Preston, 1962). Higher z -values were also found in data sets spanning a small range of island sizes (Triantis et al., 2012). This trend may explain the steep slopes that we found because the length of our line-transects (directly related to island size) varied by only one order of magnitude (1.2–11.6 km). Therefore, a “canonical” biological explanation for SAR slope may be inappropriate for inter-study comparisons.

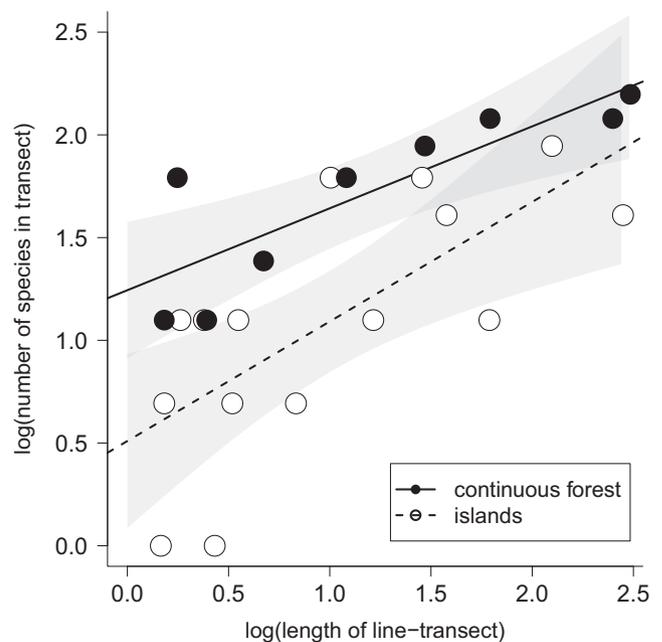


FIGURE 4 Species–area relationships (SAR) for arboreal mammals inhabiting islands and continuous forest in Middle-Solimões region, Central Amazon. White circles represent line-transects on focal islands and black circles represent line-transects in adjacent continuous forest. Dashed and solid lines represent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

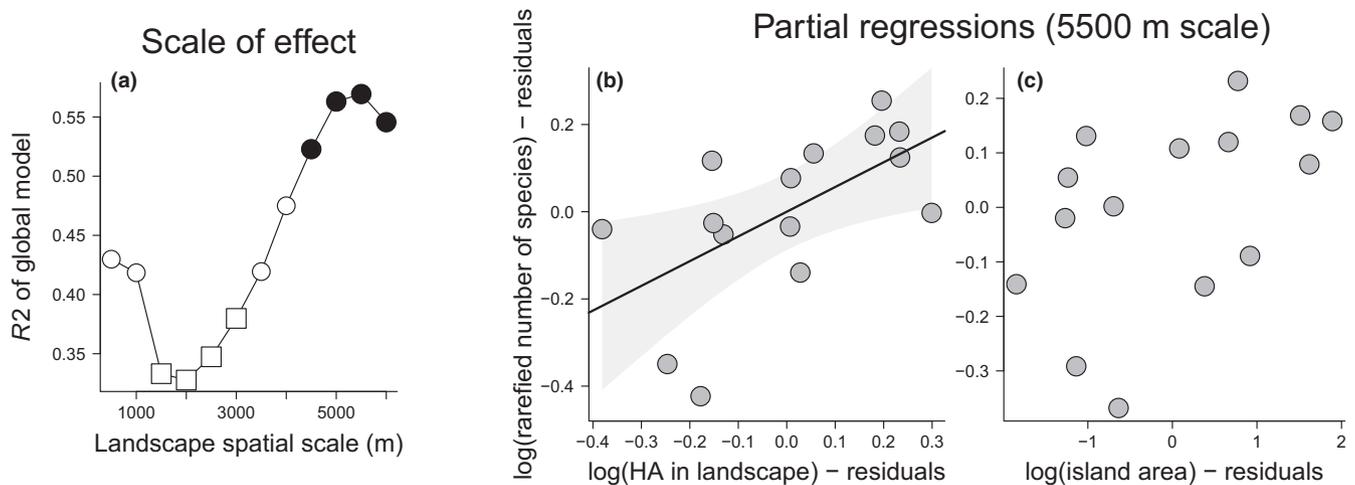


FIGURE 5 Effect of habitat amount (HA) and of island size on the estimated richness of arboreal mammal species in Middle-Solimões region, Central Amazon. (a) Association between the landscape spatial scale (x-axis) and the strength of the relationship (global R^2 ; y-axis) between the predictors and the estimated species richness. Open squares indicate the scales at which the global model fit was not significant; open circles indicate the scales at which the global model fit was significant, but significant partial effects were not detected; and black circles indicate the scales at which the global model was significant and the partial effect of at least one predictor was significant (see Table 1 for statistical results). The strongest fit was found at the scale of 5,500 m, where HA had a significant (positive) partial effect on species richness (b), island area had no partial effect (c), and both predictors were not correlated (see Appendix S1). Shaded grey represents the 95% confidence intervals

The lower SAR intercept of our fluvial islands compared with that of continuous forest sites is expected for vertebrates inhabiting islands (Matthews et al., 2015; Triantis et al., 2012). However, our fluvial islands' logc value was even lower than those often reported for oceanic islands (Matthews et al., 2015; Triantis et al., 2012), despite their higher proximity to the potential species pool of the continuous forest. We believe that the low intercept in our islands reflects the naturally low mammal richness on the continuous forest of the study region (13 species).

Local ecological conditions may also explain the lower logc values in our island system (MacArthur & Wilson, 1967). If ecological conditions of a colonized island are unsuitable for sustaining viable populations in the long-term, its species richness is expected to be lower than that of continuous forest. For example, even ephemeral fluvial islands older than 30 years may have less mature forest or may have had mature forest for less time compared with the adjacent continuous forest. The intercept parameter is highly variable and has been largely overlooked in SAR research, making its interpretation more difficult than the slope parameter (Connor & McCoy, 1979; Matthews et al., 2015; Triantis et al., 2012).

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 assemblage. An appropriate manner to analyse SAR parameters of a patch system is to compare them with those of adjacent continuous habitat (Fahrig, 2013), as we have done. We found that the sample area effect alone explains SAR from habitat patches. These findings are consistent with previous studies that conducted this kind of comparison (Collinge, 2000; Laurance et al., 2002; Middleton & Merriam, 1983; Paciencia & Prado, 2005; Shirley & Smith, 2005; Shmigelow, Machtans & Hannon, 1997).

4.2 | Is there a patch size effect?

We did not find evidence of patch size (island size) effect on the richness of arboreal mammals on fluvial islands when using the rarefied number of species as the response variable. Using a similar approach, Benchimol and Peres (2015) found a strong positive relationship between patch size and richness of vertebrate species on Central Amazon islands. Their island system consisted of an archipelago of land-bridge islands isolated in 1986 by the filling of the Balbina hydro dam reservoir. An inhospitable aquatic matrix surrounds both Balbina land-bridge islands and our river islands, but these systems differ in their stability and formation processes.

The filling of the reservoir created and maintained Balbina islands, whereas a range of processes may create and modify river islands. Fluvial islands may emerge by the deposition of sediments as sand bars in the river channel that are followed by primary succession (Kalliola et al., 1991; Puhakka et al., 1992). In this case, islands are empty new sites that depend on individual dispersal and the existence of suitable conditions to allow successful colonization and establishment of species. River meanders pinching off a peninsula of continuous floodplain forest create other type of fluvial islands (Peixoto et al., 2009; Puhakka et al., 1992). In this case, islands are already inhabited upon their isolation from the shore (Ayres & Clutton-Brock, 1992; Rabelo et al., 2014), a process similar to that of land-bridge islands.

In this context, it is possible to argue that SAR pattern depends on the origin of islands, particularly because it implicitly assumes that all sites share the same potential species pool, history and environmental features (Cutler, 1994; MacArthur & Wilson, 1967). Although we attempted to design a homogenous sample by choosing islands 30+ years-old, fluvial islands change in size and shape over time

TABLE 1 Summary of multiple regression analyses of the separate effects of habitat amount and island size on the richness of mammals at 12 landscape spatial scales in Central Amazon. Species richness is the response variable in each regression model and represents the estimated number of species based on the rarefaction procedure. Asterisks (* $p < .05$; ** $p < .01$) indicate statistically significant global models. Bold values indicate significant partial effects (significance set at $p < .05$)

Landscape spatial scale (m)	Partial regressions	t	P
500 ^a	Species richness*		
	Habitat amount	1.55	.14
	Island size	1.19	.25
1000 ^a	Species richness*		
	Habitat amount	1.45	.17
	Island size	0.05	.96
1500 ^a	Species richness		
	Habitat amount	0.42	.68
	Island size	0.86	.40
2000 ^a	Species richness		
	Habitat amount	0.27	.79
	Island size	1.12	.28
2500 ^a	Species richness		
	Habitat amount	0.68	.51
	Island size	1.04	.32
3000 ^a	Species richness		
	Habitat amount	1.08	.30
	Island size	1.03	.32
3500	Species richness*		
	Habitat amount	1.46	.17
	Island size	0.95	.36
4000	Species richness*		
	Habitat amount	1.93	.08
	Island size	0.94	.36
4500	Species richness*		
	Habitat amount	2.33	.04
	Island size	1.07	.31
5000	Species richness**		
	Habitat amount	2.67	.02
	Island size	1.43	.18
5500	Species richness**		
	Habitat amount	2.72	.02
	Island size	2.06	.06
6000	Species richness**		
	Habitat amount	2.51	.03
	Island size	2.48	.03

^aModels with highly correlated predictors (Pearson's $r > .7$).

owing to the dynamic nature of Amazonian riverscapes (Puhakka et al., 1992). Consequently, we cannot rule out the possibility that our islands experienced distinct longer term abiotic and biotic events

that contributed to the absence of a patch size effect on mammal richness despite our control of the sample area effect.

4.3 | Habitat amount effect

We found that HA in the landscape was a better predictor of species richness than was island size and this effect was best observed at the 5,500 m spatial scale. Fahrig (2013) suggests that HA is the prime predictor of species richness in sample sites because it combines the effects of both patch size and isolation into a single measure. The theory behind the HA hypothesis was criticized (Hanski, 2015), and as far as we know, only a couple of studies have actually tested the hypothesis against empirical data (Haddad et al., 2017; Melo, Sponchiado, Cáceres & Fahrig, 2017). While Haddad et al. (2017) provided the first direct refutation of the HA hypothesis in their controlled and well-replicated experiments with plants and micro-arthropods, Melo et al. (2017) did find support for the hypothesis using a large dataset of small mammals in natural landscapes. Here, we also tested the exact predictions of the HA hypothesis with a number of natural landscape replicates. We found that HA may be a better predictor of the richness of arboreal mammals and that patch size effects may be biased by the sample area effect.

The correlation between HA in landscape and island area at the first six scales may explain why we found a significant fit of global models at these spatial scales without finding significant partial effects of the predictors. Collinearity is a common unsolvable statistical problem in multiple regression analyses because variable effects cannot be separated. While the best alternative is to avoid collinear independent variables (Dormann et al., 2013), this is difficult in landscape ecology, because the predictors of interest are commonly correlated (Eigenbrod, Hecnar & Fahrig, 2011; Fahrig, 2013). For that reason, researchers have used several statistical approaches to deal with correlated predictors. However, standard multiple regression analyses still perform as well or better than all other methods that account for collinearity (Smith, Koper, Francis & Fahrig, 2009). In their simulation experiment, Smith et al. (2009) found that standardized partial regression coefficients are useful measures of effect strength, even for highly correlated predictors. Therefore, we believe that the coefficients estimated by the multiple regressions at the first spatial scales may be reliable, despite the correlation between HA and island size at the smaller scales. Additionally, we found consistency in our results when using the AIC selection approach, which indicated the best models as those including HA at larger spatial scales.

On the other hand, the lack of collinearity between predictors at the larger (5,000–6,000 m) scales allowed us to successfully separate the effects of HA and island size. Both HA in the landscape and island size had positive effects on species richness at the widest scale (6,000 m), at which the effect of HA was stronger and the global fit of the model decreased (Table 1; Figure 5a). The HA in the landscape tends to become constant at wider spatial scales in the pristine forests of the Middle-Solimões river region, potentially explaining the emergence of the island size effect at these scales.

The finding of a scale of effect (5,500 m) that is wider than the spatial scales used in previous studies with mammals in the Amazon (e.g., Benchimol & Peres, 2013, 2015) suggests that these species may respond more strongly to landscape structure at larger scales. We do not believe that this stronger response at larger scales is related to the collinearity problem because the estimated scale of effect usually tends to be “pulled” close to the scales at which predictors are correlated (Miguet, Jackson, Jackson, Martin & Fahrig, 2016). Instead, we believe that this large scale of effect is related to the type of our biological response. The scale of effect is expected to be larger for biological responses that are influenced by forces acting over longer time-scales than those influenced by forces acting over shorter time-scales (Miguet et al., 2016). Assemblage richness combines information on the species occurrences, which are controlled by extinction and colonization events and generally depend on longer time spans and large spatial scales.

5 | CONCLUSIONS

So, are fluvial islands “real” islands for arboreal mammals? We contend that the answer is no and that these islands are not analogous to the oceanic islands of MacArthur & Wilson because we found no island effect operating on this system. The rate of increase in the number of species with increasing sample size was similar for islands and continuous forest. This finding means that, unlike most previous studies, patch size *per se* did not increase species richness of a sample site. It is expected that bigger islands contain more species than smaller ones, but this pattern occurs only due to the sample area effect. Therefore, the equilibrium model of island biogeography may not be appropriate for explaining the pattern of species richness of fluvial islands if they are not analogous to oceanic islands. Our conclusion asks for alternative hypotheses, such as the “habitat diversity hypothesis” (Báldi, 2008; Williams, 1943) or the “passive sampling hypothesis” (Arrhenius, 1921; Connor & McCoy, 1979), to explain SAR on these river islands. We also reveal the suitability of studying these river islands as patch models in the landscape ecology. Finally, HA was the best predictor of species richness in sample sites, and its strongest effect occurred at the 5,500-m scale. The HA hypothesis (Fahrig, 2013) raised great interest and launched a current debate in landscape ecology (Fahrig, 2015; Hanski, 2015; Haddad et al., 2017; Melo et al., 2017). We call for additional empirical tests of the hypothesis to evaluate whether it discloses a universal rule or is only applicable to particular landscape scenarios and taxonomic groups.

DATA ACCESSIBILITY

Data on species richness and its predictor variables can be downloaded directly from the link: <https://ppbiodata.inpa.gov.br/metacatui/#view/PPBioAmOc.106.3>.

AUTHOR CONTRIBUTIONS

R.M.R. conceived and designed the study, with input from all other authors; R.M.R. collected and analysed the data; all authors

contributed to the interpretation; and R.M.R. led the writing, with input from all other authors.

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BIOSKETCH

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