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Habitat amount hypothesis and passive sampling explain mammal species composition in Amazonian river islands

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Abstract

Nested structures of species assemblages have been frequently associated with patch size and isolation, leading to the conclusion that colonization–extinction dynamics drives nestedness. The 'passive sampling' model states that the regional abundance of species randomly determines their occurrence in patches. The 'habitat amount hypothesis' also challenges patch size and isolation effects, arguing that they occur because of a 'sample area effect'. Here, we (a) ask whether the structure of the mammal assemblages of fluvial islands shows a nested pattern, (b) test whether species' regional abundance predicts species' occurrence on islands, and (c) ask whether habitat amount in the landscape and matrix resistance to biological flow predict the islands' species composition. We quantified nestedness and tested its significance using null models. We used a regression model to analyze whether a species' relative regional abundance predicts its incidence on islands. We accessed islands' species composition by an NMDS ordination and used multiple regression to evaluate how species composition responds to habitat amount and matrix resistance. The degree of nestedness did not differ from that expected by the passive sampling hypothesis. Likewise, species' regional abundance predicted its occurrence on islands. Habitat amount successfully predicted the species composition on islands, whereas matrix resistance did not. We suggest the application of habitat amount hypothesis for predicting species composition in other patchy systems. Although the island biogeography perspective has dominated the literature, we suggest that the passive sampling perspective is more appropriate for explaining the assemblages' structure in this and other non-equilibrium patch systems.

Abstract in Portuguese is available with online material.

KEYWORDS

community assembly, habitat patch, island biogeography, matrix resistance, nestedness, non-equilibrium, riverscapes, sample area effect

1 | INTRODUCTION

Ecologists have historically identified several patterns in the distribution of assemblages across sites (Leibold & Mikkelson, 2002). A 'nested pattern' is frequently observed in species assemblages occurring in patchy systems, in which the species composition of a depauperated assemblage usually comprises a subset of the species composition of a richer assemblage (Patterson & Atmar, 1986). A matrix recording species occurrences across sites, ordered by column and row totals, may reveal a nested structure (Figure 1A).

After Patterson and Atmar (1986), ecologists have discussed the roles of extinction and colonization on creating nestedness (Wright, Patterson, Mikkelson, Cutler, & Atmar, 1998). Following the equilibrium perspective (MacArthur & Wilson, 1967),

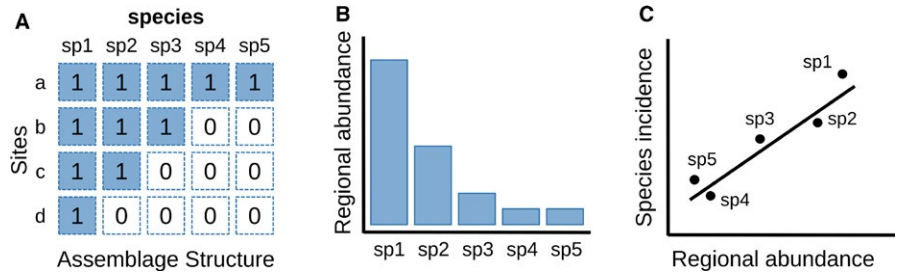

FIGURE 1 Nestedness in assemblage structure. (A) The pattern of nested subsets in a species-site matrix displaying the occurrence of species across sites—the species composition of poorer sites represents a subset of the species composition of richer sites. (B) Hypothetical representation of the natural variation of the regional abundance of species. (C) The passive sampling model predicts that the regional abundances of species drive their occupancy (i.e., species' incidence across sites), thereby influencing the structuring of assemblages [Colour figure can be viewed at wileyonlinelibrary.com]

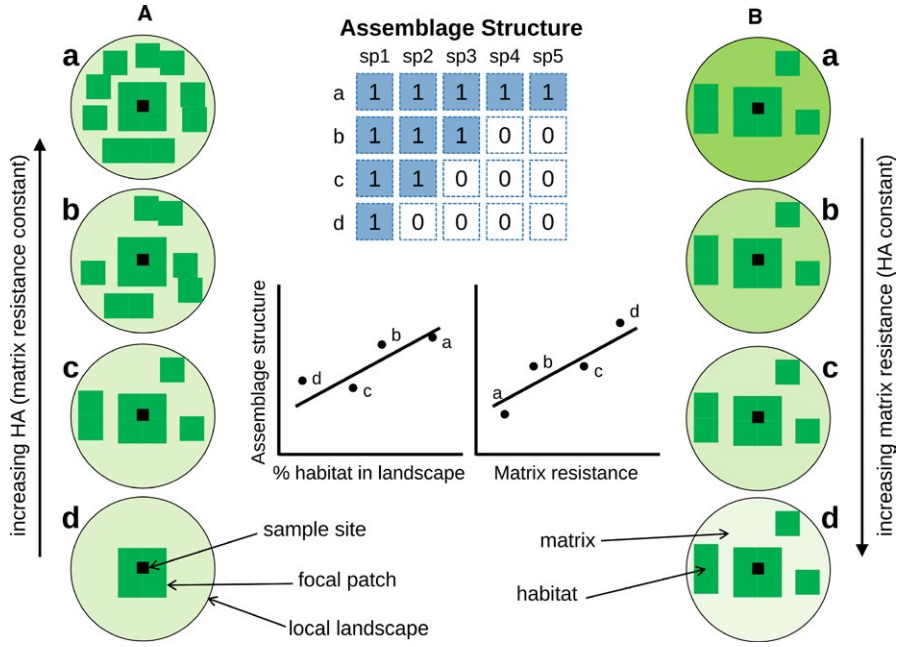

FIGURE 2 Predictions of the effects of habitat amount (HA) in the surrounding landscape and matrix resistance on assemblage structure. A hypothetical gradient of favorability decreases from landscapes 'a' to 'd'. More favorable landscapes are expected to contain more species. Favorability in (A) is represented by HA in the landscape. The HA hypothesis predicts that the number of species in a sample site increases with increasing HA in the landscape, even if the size of the patch where the sample site is embedded remains unchanged. We hypothesize that HA also allows to predict an assemblage's species composition because a nested pattern implies changes in species richness. Matrix resistance increases from 'a' to 'd' in (B). We predict that species richness is inversely related to matrix resistance to biological flow within the landscape if HA is held constant. Therefore, a low-resistance matrix allows the movement of a larger array of species in the landscape, while only stronger dispersers are capable of colonizing a patch surrounded by a highly resistant matrix [Colour figure can be viewed at wileyonlinelibrary.com]

researchers have used patch size and isolation as variables to sort species-site matrices to infer the causes of nestedness (Bruun & Moen, 2003; Cook & Quinn, 1995; Lomolino, 1996; Patterson, 1990; Wright et al., 1998). In this perspective, selective extinction would be the likely cause of nestedness if an area-sorted matrix generates a nested pattern. On the other hand, if a nested pattern arises in an isolation-sorted matrix, differential immigration would be a better explanation for the nested structure (Wright et al., 1998).

However, a simpler and predominant explanation for a nested pattern is based on the 'passive sampling' perspective (Connor & McCoy, 1979; Ulrich, Almeida-Neto, & Gotelli, 2009). In this perspective, habitat patches are analogous to 'passive targets' that randomly accumulate (or retain) individuals. Larger targets (or larger patches) accumulate more species from the regional pool than do smaller ones simply by chance. Similarly, more abundant species in the regional pool are more likely to occur in any patch than are rare species, also by chance only (Figure 1). Therefore, the passive sampling is an appropriate null perspective for explaining nestedness, especially in systems that cannot meet the assumptions of an equilibrium model (Cutler, 1994; MacArthur & Wilson, 1967). This is the case of dynamics or non-equilibrium patch systems (Shepherd & Brantley, 2005).

Recently, Fahrig (2013) challenged the notion that patch size and isolation *per se* affect species distribution in patch systems, proposing that a 'sample area effect' drives their apparent effects. First, larger patches contain more species than smaller ones simply because they constitute a larger sample area in the landscape. Second, since the habitat amount (HA) within a landscape surrounding a focal patch is the primary source of colonists, the focal patch will be more isolated from its source of species as the HA in the landscape decreases. Therefore, the number of species in a focal patch depends on the sampled area represented by the surrounding habitat, which affects its immigration rate (Figure 2A), that is, a larger HA in the landscape will sample a larger portion of the regional species pool. The 'HA hypothesis' posits that HA in a local landscape is the main driver of species distribution in patchy systems because it combines the effects of both patch size and isolation into a single predictor. This hypothesis has raised a current debate in landscape ecology for explaining patterns of species richness in patch systems (Haddad et al., 2017; Hanski, 2015; Melo, Sponchiado, Cáceres, & Fahrig, 2017; Rabelo, Bicca-Marques, Aragón, & Nelson, 2017).

Matrix type can also affect species richness in habitat patches (Prevedello & Vieira, 2010), although the HA hypothesis posits that it has a secondary role compared to the HA effect (Fahrig, 2013). Matrix type contributes to effective patch isolation because its permeability/resistance may facilitate/compromise biological flow (Metzger & Décamps, 1997). Although the HA hypothesis deals primarily with species richness as the response variable, we propose that HA, together with matrix resistance, can also predict species composition of a nested-structured assemblage (Figure 2B). We base our hypothesis on the fact that nestedness necessarily implies that species richness varies across patches.

Here, we analyze the pattern and potential drivers of mammal assemblage composition on river islands in central Amazon. These fluvial islands originate from a complex river dynamics that constantly modifies the spatial structure of riverscapes (Peixoto, Nelson, & Wittmann, 2009), which makes them a non-equilibrium patch system (Shepherd & Brantley, 2005). We have previously tested the HA hypothesis in this system and shown that island size only affects the number of species because of the sample area effect (Rabelo et al., 2017). Here, we investigate whether island assemblages show a nested pattern and test whether species' regional abundances predict their occurrence on islands. We expect that a species' relative abundance in the regional pool determines its local island occurrence (Figure 1), suggesting that the passive sampling null model is a parsimonious explanation for the structure of the species assemblages found on these islands.

We also test the HA hypothesis using species composition, not richness, as the response variable. Our aim here was to evaluate whether and how assemblage structure responds to HA and to matrix resistance at multiple spatial scales of local landscapes. If these landscape variables are associated with assemblage structure as expected (Figure 2), the HA in the landscape is also a good predictor of species composition on this patch system.

2 | MATERIAL AND METHODS

2.1 | Study area and study species

We sampled islands and the continuous forest near the confluence of the Solimões and Japurá rivers in central Amazon (Figure 3). The interfluvium at these rivers' junction is a floodplain forest ecosystem,

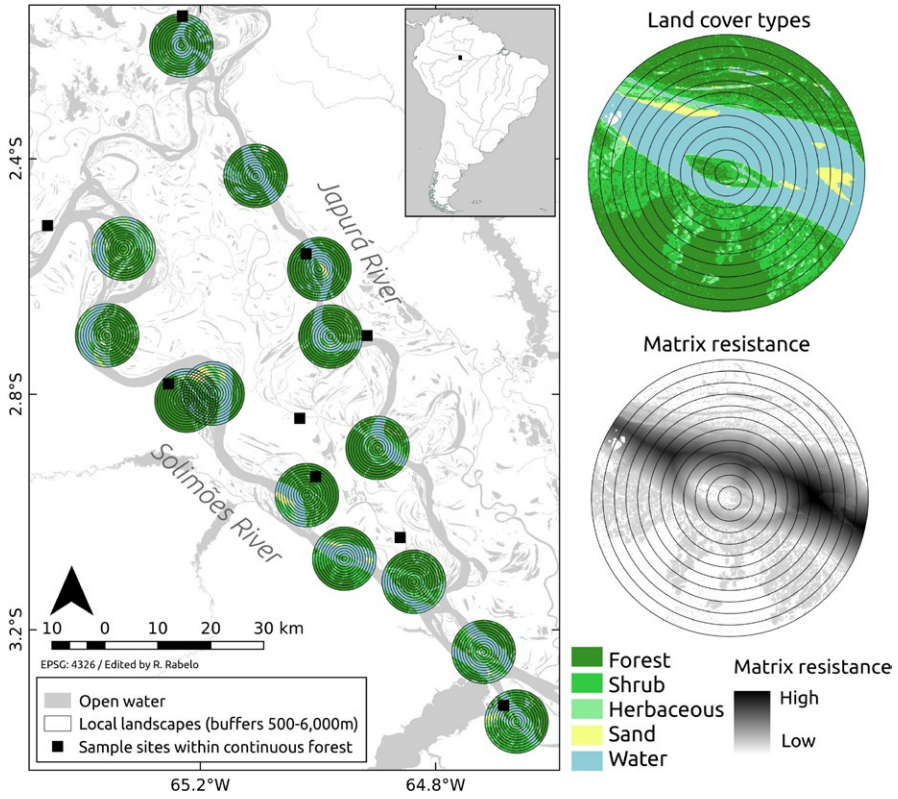

FIGURE 3 Distribution of local landscapes and continuous forest sample sites in the Middle-Solimões region, central Amazon. An example of a multi-scale local landscape and its matrix resistance surface is shown on the right [Colour figure can be viewed at wileyonlinelibrary.com]

called *várzea*, which is protected by the Mamirauá Sustainable Development Reserve (IDSM 2010). *Várzea* forests are seasonally flooded by nutrient-rich white-water rivers (Prance, 1979). The average annual range of the water level is 12 m (Ramalho et al., 2009), reaching its maximum level around June and its minimum between October and November (IDSM 2010).

River dynamics constantly modifies the spatial structure of these riverscapes (Peixoto et al., 2009; Puhakka, Kalliola, Rajasilta, & Salo, 1992), creating fluvial islands by the erosion, transport, and deposition of sediments (Kalliola, Salo, Puhakka, & Rajasilta, 1991). Here, we consider the fluvial islands within these riverscapes as our model of habitat patches. River dynamics affects species distribution in terrestrial environments (Toivonen, Maki, & Kalliola, 2007) and can facilitate dispersal and influence species' occurrence on fluvial islands (e.g., birds: Cintra, Sanaiotti, & Cohn-Haft, 2007; and primates: Rabelo et al., 2014). Although fluvial islands can be considered ephemeral patches for species with long generation times (Shepherd & Brantley, 2005), we consider them appropriate patch models to test the HA hypothesis. We restricted our sample to islands that have lasted long enough to sustain two or more generations of the species of our study group to minimize the influence of ephemeral islands on the results (see 'Sampling design' section, below).

The mammals inhabiting *várzea* forests are mostly arboreal (primates and sloths). However, scansorial (anteaters and squirrels) and terrestrial (coatis and jaguars) species can also be present. Long-term studies within the Mamirauá Reserve have shown that even jaguars reside and remain in the flooded forest during the high-water season (E. E. Ramalho, unpublished data). The arboreal mammals rarely descend to the ground, but can occasionally move through shrubby and herbaceous vegetation, walk on sandy substrates, or even swim in rivers and lakes. The terrestrial species also spend most of their time in the canopy, especially during flooding. Therefore, we only consider those environments that fulfill all requirements to constitute 'habitat' for our mammal assemblage as structured forests (Fahrig, 2013). *Várzea* forest mammals are good study models because they often reach high population densities (Peres, 1997), thereby increasing survey detection rate and reducing the risk of false negatives.

2.2 | Sampling design

We adopted a mixed patch-landscape scale sampling design. In this approach, each landscape represents a sample unit. The response variable is measured within a focal patch (the island), whereas the predictor variable can be measured both at the patch and 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 not in the patches, but in equal-sized sample sites with landscape-scale predictors measured within a specific radius from them (Fahrig, 2013; Figure 2).

We sampled 14 focal islands (Supporting information Table S1) and adopted a multi-scale approach to find the appropriate scale to detect the predictor's 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 the sample sites of each island to define that sample's local landscape for each scale (Figure 3). We chose the islands based on the following criteria: (a) surrounded by water, even during the low-water season; (b) minimum distance between islands' edges of 2 km to avoid overlapping landscapes (only 2 out of 14 landscapes overlapped at the buffer scales of 3,000–6,000 m); and (c) minimum age of 30 years (determined using a historical series of Landsat Thematic Mapper satellite images) to avoid islands that are too ephemeral for our study group (e.g., jaguar generation time ~7 years, de la Torre, González-Maya, Zarza, Ceballos, & Medellín, 2018). We removed newly formed islands younger than 30 years because this period is insufficient for the development of a forest with an adequate structure to harbor arboreal mammals. Islands under this age are dominated by pioneer vegetation and rarely hold late-succession forest patches (Peixoto et al., 2009; Wittmann, Junk, & Piedade, 2004).

2.3 | Data collection

Mammal sampling was conducted along a single linear transect on each island (Figure 3). Transect length varied from 1.2 to 11.6 km and it was directly correlated to island size (Pearson correlation: $r = 0.94$, $p < 0.001$), making patch size an intrinsic characteristic of each sample. We also surveyed mammals at nine independent sample sites distributed in the adjacent continuous floodplain forest (black squares in Figure 3) to estimate the relative regional abundance of species in the source pool. Surveys consisted of quiet walks on trails by two trained observers at *ca.* 1.5 km/hr following a standardized protocol (Peres, 1999). We carried out the surveys in the morning (06:30–11:30 hr) and afternoon (14:00–17:00 hr), interrupting them during rains. We recorded species via sighting and vestiges, such as calls and feces. We also recorded the occurrence of jaguars and semi-arboreal species via footprints and fresh signs of digging. We conducted four surveys per transect, separated by no more than 4 days, during the low-water season (September to November) of either 2013 or 2014. We limited surveys to the low-water season to minimize potential seasonal effects on species detection. We were unable to visit all islands during a single low-water season due to logistical constraints.

We used a Landsat 8 Operational Land Imager (OLI) scene from 24 October 2014 (low-water season) to extract the landscape cover types and their spatial configurations. As the water level drops, areas of sand, and herbaceous and shrub vegetation emerge, narrowing the width of rivers and adding heterogeneity to the matrix surrounding islands. All GIS processing was undertaken using QGIS software version 2.8.1 (QGIS Development Team 2015). We used three of the OLI spectral bands (near infrared, red, and green) at a 30-m spatial resolution to perform a semi-supervised classification using the Semi-Automatic Classification Plugin available in QGIS. We

obtained 8 to 15 training areas for each of five pre-defined cover classes (forest, shrub, herbaceous, sand, and water) via visual interpretation of a false-color composite of the same three bands. We found an accuracy between 94.8% and 97.1% in the validation of our classifications. Forest was defined as habitat, whereas the other four classes were treated as matrix types. We used the classified raster image to calculate the area of habitat within each local landscape at each buffer scale, that is, the habitat amount (HA) metric.

We obtained a metric of matrix resistance (MR) for each surrounding landscape at each buffer scale. This metric considered the distance to habitat, the resistance of each matrix type to animal movement, and the matrix area in the local landscape (Metzger & Décamps, 1997), as follows:

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

where $IE_i = I_i * R_i$ represents the effective isolation of pixel '*i*'; I_i is the linear distance from pixel '*i*' to the nearest pixel of habitat; R_i is the resistance coefficient to biological flow of the matrix type present in pixel '*i*'; and AM is the number of matrix pixels within the landscape.

Resistance coefficients (R_i) are necessary because of the scarcity of studies on animal movement (Zeller, McGarigal, & Whiteley, 2012). In the absence of data to estimate resistance values, we consulted expert researchers. We sent a closed format questionnaire (Appendix S1) to 50 mammal specialists, asking them to assign a resistance weight from 0 to 10 to each matrix type for each species individually and for the overall group of species. A '0' resistance indicates a fully permeable environment similar to the forested habitat, whereas a '10' value qualifies a matrix type as highly resistant to biological flow comparable to an impermeable barrier to animal movement. We received responses from 29 experts (=58% response rate). Specialists tended to assign an increasing resistance from shrub to herbaceous vegetation, then to sand and, finally, water (Supporting information Figure S3). We took the median of all scores of each matrix type as its resistance coefficient (R_i) because the response distribution was asymmetric. We estimated habitat amount and matrix resistance for each spatial scale of the 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).

2.4 | Data analysis

We constructed a matrix of species abundance by site: a table of species (columns) versus sites (rows) containing the raw counts of each species on each island. We excluded two islands from the matrix because they harbored no mammal. We estimated the degree of nestedness of mammal assemblages across the remaining 12 islands using metrics based on overlap and decreasing fill with both presence–absence (NODF) and abundance data (WNODF; Almeida-Neto & Ulrich, 2011). We determined the significance of nestedness using a null model that changes matrix structure while maintaining column and row marginal totals (i.e., the fixed-fixed [FF] algorithm) to simulate 1,000 random matrices, following the recommended approuach of Ulrich et al. (2009). We performed this analysis using the NODF Program (Almeida-Neto & Ulrich, 2011). We also separated the nestedness component from the turnover component to evaluate their independent contributions to the total variation of species composition in the assemblage (i.e., beta-diversity) as proposed by Baselga (2010). This analysis was performed using the 'betapart' R package (Baselga, Orme, Villeger, Bortoli, & Leprieur, 2018).

We also assessed the change in species composition across the study islands via a non-metric multidimensional scaling (NMDS) ordination of the species-site matrix. Prior to performing the matrix ordination, we controlled for the sample area effect as our islands had different sampling efforts according to island size. We accomplished this task by dividing the abundance of species in each matrix cell by the total abundance in the matrix row (site). We performed this standardization of samples to equal totals (SAT) to reduce the discrepancy between sites with different sampling efforts (i.e., the sample area effect). We also applied SAT to matrix columns (species) to minimize the difference between abundant and rare species. Standardization of the species-site matrices prior to ordination procedures helps to identify the strongest intrinsic pattern of assemblage structure, and SAT has been recognized as a robust standardization method for ecological ordinations (Faith, Minchin, & Belbin, 1987). We then performed a two-axis NMDS ordination based on the Bray–Curtis pairwise dissimilarities between sample sites, reducing the assemblage structure pattern to two axes (McCune & Grace, 2002).

We fitted a simple regression model to test whether the relative regional abundance of a species's predicts its respective occurrence on islands. We used the species scores derived from the NMDS ordination as the response variable to fit this model. These species' scores correspond to the order of species in the ordered species-site matrix, that is, they represent the species relative incidence on islands according to the NMDS ordination. We also constructed a species-site matrix with the continuous forest sample sites, then applied the same standardization procedure with the SAT method, and used the sum of the relative abundances of species in all sample sites to represent the relative regional abundance of each species.

We used each site's score on the first NMDS axis to represent its mammal assemblage composition. To evaluate how species composition responds to habitat amount and matrix resistance, we initially found the scale at which each predictor best predicts the response variable, namely the scale of effect (Martin & Fahrig, 2012). Therefore, we used an AIC model selection approach to choose the best scale of effect for each predictor variable (habitat amount and matrix resistance), as predictors may have different scales of effect (see Appendix S3). After having found the scale of effect for each landscape predictor, we used another model selection procedure to evaluate how landscape predictors affect species composition, according to four candidate models with the following predictors: null, HA only, MR only, and HA + MR. We also included island size as a predictor in candidate models to evaluate whether it affects species composition (see Appendix S3). We performed these analyses using

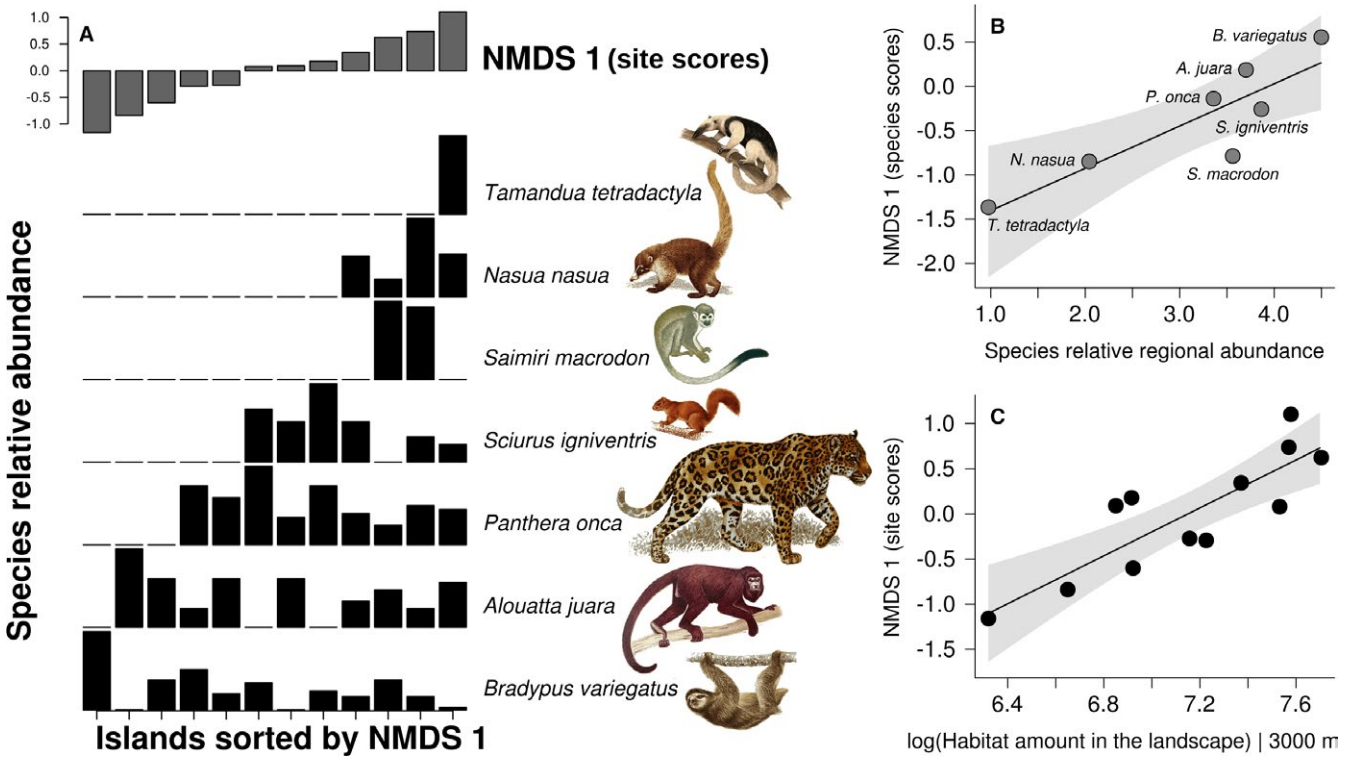

FIGURE 4 Structure of the mammal assemblage of central Amazon River islands. (A) Islands sorted by the NMDS 1 axis according to the NMDS ordination. Islands with negative NMDS 1 scores contain fewer species that are true subsets of species composition found in islands with positive scores. (B) Relationship between the species' relative regional abundances and their occurrence in islands. The NMDS 1 (species scores) corresponds to the order of species in graph (A), that is, the species incidence, and species with negative scores are those that occur in fewer islands. The graph shows that the higher the relative abundance of species in the regional pool, the higher the number of islands inhabited by it. (C) Effects of habitat amount on species composition (NMDS 1—site scores). Habitat amount in the landscape at the 3,000-m spatial scale showed a strong association with the assemblage pattern of species composition presented in (A). Illustrations from INBio (anteater), Stephen Nash (howler and squirrel monkey), and John Oriszo (all others) [Colour figure can be viewed at wileyonlinelibrary.com]

the vegan 2.2-1 (Oksanen et al., 2013) package, inside R 3.1.3 statistical software (R Development Core Team 2015).

3 | RESULTS

We found seven mammal species (Supporting information Table S2) belonging to the orders Primates (2), Pilosa (2), Carnivora (2), and Rodentia (1). The first NMDS axis explained 50% of the variation in species composition among sample sites (Figure 4A).

The nestedness of both the occurrence and the abundance-based matrices did not differ significantly from null assemblages ($NODF_{OBS} = 74.39$; $NODF_{EXP} = 71.83$; $p = 0.42$; and $WNODF_{OBS} = 53.27$; $WNODF_{EXP} = 48.94$; $p = 0.30$). Accordingly, the relative regional abundance of a species predicted its incidence on islands ($F_{1,5} = 16.29$; $R^2 = 0.77$; $p < 0.01$, Figure 4B). The higher the regional abundance of a species, the higher its frequency of island occupancy (Figure 4B). We found that both turnover and nestedness components contributed similarly to the overall beta-diversity ($\beta_{OVERALL}$) of the islands' mammal assemblages ($\beta_{TURNOVER} = 0.38$; $\beta_{NESTEDNESS} = 0.34$; $\beta_{OVERALL} = 0.72$).

Habitat amount in the landscape and matrix resistance affected species composition at different scales of effect (HA at 3,000 m: slope = 1.32, $p < 0.001$; MR at 500 m: slope = −0.25, $p = 0.02$; supporting information Figure S4). However, the best explanatory model only included HA, which successfully predicted the mammal species composition of our study fluvial islands ($F_{1,10} = 26.11$; $R^2 = 0.72$; $p < 0.001$; Figure 4C; Table 1). Island size and matrix resistance had significant effects on species composition only when analyzed alone, that is, they did not affect species composition after controlling for the effect of HA in the landscape (Supporting information Table S7).

4 | DISCUSSION

4.1 | 'Equilibrium' versus 'Passive sampling' perspectives

We did not detect a significant nested pattern in the assemblage structure. The observed NODF and WNODF values, which did not differ from expected null model values, imply a random structure of mammal assemblage in these fluvial islands. Additionally, the

TABLE 1 Ranking of explanatory models of the mammal species composition of Amazonian fluvial islands. NMDS 1 is the site scores from an NMDS ordination and represents the species composition of each island. The models evaluate how the species composition responds to habitat amount (HA) and to matrix resistance (MR) at their scales of effect (3,000 m for HA and 500 m for MR). Bold coefficients are significant at $p < 0.05$

Model	Intercept	Slope		*df*	AICc	ΔAIC	AIC_{weight}
		HA	MR				
NMDS 1 ~ HA (3,000 m)	**−9.48**	**1.33**	–	3	16.86	0.00	0.90
NMDS 1 ~ HA (3,000 m) + MR (500 m)	**−9.45**	**1.32**	0.00	4	21.57	4.71	0.09
NMDS 1 ~ MR (500 m)	**0.84**	–	**−0.26**	3	25.85	8.99	0.01
NMDS 1 ~ 1 (Null model)	0.00	–	–	2	28.60	11.74	0.00

species' relative incidence on islands was directly associated with the species' regional abundance. Therefore, the species' abundance in the regional pool best explains the structuring of our study island assemblages via the underlying process of passive sampling. Our results are compatible with meta-analyses showing that, when conservative null models are used, significant nestedness is considerably less common than previously reported (Matthews, Cottee-Jones, & Whittaker, 2015; Ulrich et al., 2009).

We found that the overall beta-diversity pattern of our mammal assemblage in Amazonian fluvial islands may be similarly partitioned into turnover and nestedness components. This means that two processes can equally generate the assemblages' beta-diversity: species replacement from the turnover component, and species loss from the nestedness component (Baselga, 2010). This finding corroborates the nestedness analysis performed with NODF and WNODF metrics in which we did not find a significant nested structure as expected by chance. However, as stated by Baselga (2010), we highlight that nestedness and *dissimilarity due to nestedness* are related but different concepts. The $\beta_{NESTEDNESS}$ index is a metric rooted in the framework of beta-diversity analyses, and it is not a measure of nestedness in absolute terms unlike the NODF and WNODF metrics. Instead, $\beta_{NESTEDNESS}$ is an index of dissimilarity used to account for the patterns of beta-diversity caused by nestedness.

Under the equilibrium perspective, extinction–colonization dynamics manly drives species richness and composition in habitat patches (MacArthur & Wilson, 1967). Selective extinction occurs at a rate inversely proportional to patch size especially in land-bridge systems where a species occupies habitat patches prior to their isolation (Leibold & Mikkelson, 2002). On the other hand, nested patterns caused by differential immigration resulting from dispersal limitation are expected to occur in systems composed by previously vacant patches at the time of their creation (Cook & Quinn, 1995).

Fluvial islands contain particular habitat conditions that affect the occurrence of species. They originate from (a) the deposition of sediments as sandbars in the river channel that are followed by primary succession (Kalliola et al., 1991; Puhakka et al., 1992) or (b) the erosion of river meanders, pinching off a peninsula of continuous floodplain forest (Peixoto et al., 2009; Puhakka et al., 1992). Given that both processes can play a role in the emergence of our study islands, we cannot rule out the possibility that these islands have different long-term abiotic and biotic histories, beyond the 30-year time window available from satellite images. Therefore, we cannot reject the potential effects of these historical processes in creating the observed non-significant nested structure of our study mammal assemblages under the equilibrium perspective.

4.2 | Habitat amount hypothesis

HA in the landscape predicted the mammal assemblage structure of our study islands particularly at the 3,000-m scale. Both the HA hypothesis and the passive sampling explanation for nestedness argue that the sample area effect explains the patch size effect: Larger habitat patches 'sample' more species from the regional pool than do smaller habitat patches (Connor & McCoy, 1979; Fahrig, 2013). The passive sampling model further predicts the species composition by considering that the abundance of a species in the regional pool affects its probability of occurrence in a given patch.

We have previously shown that the size of these fluvial islands has a direct influence on their species richness simply as a consequence of the sample area effect (Rabelo et al., 2017); that is, HA in the surrounding landscape, instead of island size, explains the number of species sighted in transects of equal length. Here, we show that island size also does not affect species composition at sample sites after controlling for the effect of HA in the landscape (Supporting information Table S7). Therefore, we combined sample area effect and the perspective of passive sampling to show that HA in the landscape also drives the structuring of the mammal assemblage of these islands. That is, landscapes containing higher amounts of habitat sample more species than those with less habitat, and more abundant species are more likely to be 'sampled'.

The relationship between area and species richness or composition under the passive sampling viewpoint is solely a sampling phenomenon, rather than the outcome of biological processes, such as extinction or immigration (Connor & McCoy, 1979). This is the reason why the passive sampling is a null hypothesis. However, we argue that this simplification requires caution because a species' commonness or rarity in a given region likely relates to its biology and ecology. Therefore, the role of ecological traits, such as species abundance, should also be acknowledged. On the other hand, the HA hypothesis does not deny that extinction and colonization can drive species richness in habitat patches (Fahrig, 2013). Instead, it states that there is

nothing special about patches that require an assessment of their immigration–extinction dynamics. The latter hypothesis further implies that the effects of patch size and isolation are redundant because they are components of HA in the landscape, whose influence on species richness takes place mainly via the sample area effect.

4.3 | Matrix resistance

We only found a significant response of species composition to matrix resistance at the 500-m spatial scale when the model only included this predictor, although this model was not chosen as a plausible explanatory one in the selection procedure (Table 1). The lack of association between matrix resistance and assemblage structure can result from the fact that we measured the former during the low-water season of 2014. As the water level can vary up to 12 m (Ramalho et al., 2009) between the low- and high-water seasons, matrix resistance also varies from higher values during the high-water season to lower values in the dry season. This seasonal pattern means that mammals can colonize islands more easily in October than in June. Additionally, the ability to move through the matrix is species-specific (Prevedello & Vieira, 2010). That is, assemblage components do not respond uniformly to matrix resistance if their vagilities differ. Therefore, when matrix type affects a patch's species richness, its effects are often weaker than those of HA. Consequently, analyzing the effects of matrix on individual species is a stronger approach.

5 | CONCLUSIONS

Passive sampling explains the structuring of the mammal assemblages of central Amazon River islands: (a) Larger islands contain more species simply because they are larger 'targets' and, consequently, sample more species from the regional pool; and (b) the species composition of islands reflects the species' abundances in the regional pool because common species are more likely to occur in any given island than rare ones. Despite the discussion on whether extinction or colonization generates nestedness, habitat amount in the surrounding landscape stood out as an effective and straightforward predictor of species composition of fluvial islands. The identification of single and easy-to-measure variables is critical in the current context of pressing conservation challenges (Fahrig, 2013). We suggest that habitat amount can also be useful for predicting species composition and species richness in other patchy systems. Finally, we conclude that the passive sampling hypothesis is more appropriate than an island biogeography perspective for explaining the patterns of mammal assemblage structure in our study fluvial islands.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.p05t5d0. (Rabelo, Aragón, Bicca-Marques, & Nelson, 2018), and the Knowledge Network for Biocomplexity (KNB) Repository https://doi.org/10.5063/F1V12310.

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