Fair tests of the habitat amount hypothesis require appropriate metrics of patch isolation: An example with small mammals in the Brazilian Atlantic Forest

Marcus Vinícius Vieira[a,b,*], Mauricio Almeida-Gomes[c], Ana Cláudia Delciellos[a,b], Rui Cerqueira[a,b], Renato Crouzeilles[a,d,e]

[a] Programa de Pós Graduação em Ecologia, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-902, Brazil
[b] Laboratório de Vertebrados, Departamento de Ecologia, Universidade Federal do Rio de Janeiro, CP 68020, Ilha do Fundão, Rio de Janeiro, RJ CEP 21941-902, Brazil
[c] Departamento de Ecologia, Universidade Federal de Mato Grosso do Sul, CEP 79070-900 Campo Grande, MS, Brazil
[d] Rio Conservation and Sustainability Science Centre, Department of Geography and the Environment, Pontifícia Universidade Católica, 22453900 Rio de Janeiro, Brazil
[e] International Institute for Sustainability, 22460320 Rio de Janeiro, Brazil.

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ABSTRACT

Patch size and isolation are traditionally considered as main determinants of species richness in fragmented landscapes, grounded on Island Biogeography Theory (IBT). The Habitat Amount Hypothesis (HAH) is the more recent alternative: species richness could be predicted exclusively by the total amount of habitat surrounding sampling sites. However, tests may be biased towards HAH by the use of poor metrics of patch isolation, and because landscape variables are measured only within the scale of effect for habitat amount. Here we compare the HAH, IBT, and patch isolation as predictors of species richness of forest-dependent small mammals in an Atlantic Forest fragmented landscape using two measures of patch isolation: considering all (overall) or only the nearest three (restrict) forest remnants within the scale of effect for each variable. The model with habitat amount had more support than models with patch size and isolation (representing IBT), or patch size alone, but the model with overall patch isolation was equally plausible. Had we used only restricted patch isolation, we would have found support only for the HAH, disregarding patch isolation. The appropriate metric of patch isolation is critical for robust tests of the HAH, which should be considered in future studies to avoid biased results in favour of the HAH. Our results provide strong evidence for either HAH or overall patch isolation over IBT, and both may offer simplicity to decision-making.

1. Introduction

Changes in land use are widely acknowledged as threats to biodiversity conservation worldwide (Balmford et al., 2003; Butchart et al., 2010; Hanski et al., 2013; Newbold et al., 2015). Nonetheless, there is still an intense debate about the underlying factors that drive biodiversity loss in fragmented landscapes, the core of the 'habitat fragmentation' research program (see Fahrig, 2017). Habitat loss and fragmentation are generally associated, results of the processes involving land use and conversion of natural habitats by human activities, reducing the total amount of native vegetation cover and changing the configuration of the remaining habitat (Holland and Fahrig, 2000; Bailey et al., 2010; Smith et al., 2011; Didham et al., 2012; Flick et al.,

2012). Despite this association, the search for independent contributions of habitat loss and fragmentation to biodiversity has been the focus of many studies, recognizing a potential importance of habitat spatial configuration in landscapes, independent of habitat loss effects (Fahrig, 2003, 2013).

The view that spatial configuration of habitat fragments matters is supported by Island Biogeography Theory, hereafter IBT (MacArthur and Wilson, 1963, 1967), but also by the role of matrix and isolation between fragments (reviewed in Prevedello and Vieira, 2010). Following IBT, both patch size and isolation are primary determinants of species richness. However, some species are able of moving between habitat patches due to their tolerance to matrix areas (i.e. less or unsuitable habitat areas) (Ricketts, 2001; Crouzeilles et al., 2013, 2014;
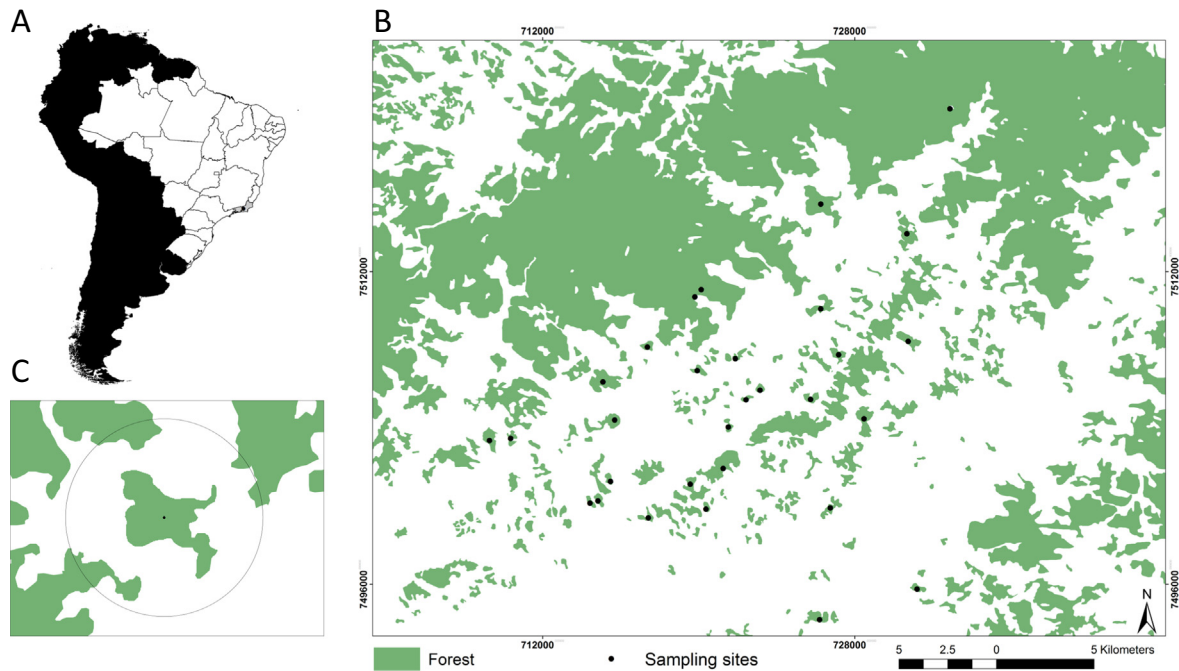

Fig. 1. Study area in (a) the state of Rio de Janeiro, Brazil, showing (b) the 30 sampling sites in forest fragments and within the continuous area in the Guapi-Macacu river basin, and (c) the buffer size of 2000 m around one sampling site in detail.

Pardini et al., 2010; Prevedello and Vieira, 2010). Species ability to move through the matrix indicates that individuals may not be restricted to habitat patches, which highlights the role of the matrix in biodiversity conservation, and the importance of isolation/connectivity between fragments (Spiegel and Nathan, 2007; Roe et al., 2009; Prevedello and Vieira, 2010; Püttker et al., 2011; Schultz et al., 2012).

Alternatively, a hypothesis proposed by Fahrig (2013), the 'habitat amount hypothesis' (hereafter HAH), challenges the notion that patches are the natural unit of measurement for species richness. It suggests that species richness could be predicted exclusively by the total amount of habitat surrounding sampling sites, even though patch size and isolation contribute to total amount of habitat. The amount of habitat - rather than either patch size or isolation - would be the most important predictor of species persistence in fragmented landscapes, i.e. the higher the amount of habitat in a landscape, the greater should be the species richness in a sampling site. The effects of either patch size or isolation on species richness would provide no additional explanation over the amount of habitat (Fahrig, 2013).

To test the HAH one essential first step is to identify the 'scale of landscape effect' (Holland et al., 2004), i.e. the landscape size that shows the highest predictive power to predict species richness. Fahrig (2013) proposed ad hoc determination of the scale of landscape of effect by testing a wide range of radii around the sampling sites based on information on the species movement abilities. Two critical issues are involved: (i) the scale of effect should be determined for isolation and habitat amount independently (Boscolo and Metzger, 2009), and (ii) the effectiveness of this metric used to actually represent patch isolation. By considering a scale of effect only for the amount of habitat, disregarding a potential scale of effect for patch isolation, the results can be biased, as the "appropriate" scale of effect for habitat amount implies a previous adjustment in the relationship between the amount of habitat and species richness. Two common types of patch isolation metrics are the mean distance from the sampling site to the three nearest habitat patches (but sometimes only one distance to the nearest habitat patch) (Weigelt and Kreft, 2013; Lindgren and Cousins, 2017), and the mean distance from the sampling site to all habitat patches within a pre-determined scale of landscape effect (e.g. Boscolo and Metzger, 2009, 2011; Crouzeilles et al., 2014). The choice of the

distance to the closest habitat patch as a metric of isolation increases variation between sampling units due to sampling error, reducing the power of statistical inference. More importantly, habitat amount is measured considering the whole amount of habitat cover within a scale of effect, but if isolation is measured considering a (small) sample of distances to neighbouring habitat patches, the explanatory power of patch isolation is likely to be limited simply because of the larger sampling errors involved. In this regard, the mean distance to all habitat patches within an appropriate scale of effect is a more accurate measure of patch isolation, less affected by sampling error.

Here we test the HAH for forest-dependent small mammal species in an Atlantic Forest fragmented landscape, contrasting it with IBT and patch isolation as alternative hypotheses. Our main methodological novelty was to include two metrics of patch isolation, measured at their scale of effect, to evaluate how the choice of isolation metrics can impact tests of the HAH: (i) the mean distance of the sampling site to the three nearest habitat patches within the scale of landscape effect, hereafter 'restricted patch isolation', and (ii) the mean distance of the sampling site to all habitat patches within the scale of landscape effect, thereafter 'overall patch isolation'.

2. Material and methods

2.1. Study area

The study was carried out in the Guapi-Macacu River basin, located in the municipalities of Guapimirim (22°20′S and 42°59′W), Cachoeiras de Macacu (22°28′S and 42°39′W), and Itaboraí (22°44′S and 42°51′W), in the state of Rio de Janeiro, southeastern coast of the Brazilian Atlantic Forest (Fig. 1). The Guapi-Macacu river basin has on average 45% of forest cover (Fidalgo et al., 2008), with a gradient of increasing forest cover towards the northern portion of the basin, where the Serra dos Órgãos National Park and Três Picos State Park are located. Most of the fragments, however, are small (< 50 ha) and isolated by a matrix of pastures, plantations, paved roads, and urban areas (Cabral and Fiszon, 2004; Pedreira et al., 2009; Vieira et al., 2009; Delciellos et al., 2016). The climate is mild humid-mesothermic (Nimer, 1989), and the forest vegetation is classified as dense evergreen forest (IBGE, 2012). The

vegetation of continuous forest sites varies from disturbed forests in early stages of succession to relatively undisturbed forests in more inaccessible areas (Almeida-Gomes and Rocha, 2014). The vegetation of the fragments is disturbed to various degrees, with a relatively open understory containing a high number of palms (e.g. *Astrocaryum aculeatissimum*), *Cecropia* spp., and lianas (Finotti et al., 2012; Delciellos et al., 2016).

2.2. Field methods

Non-volant small mammals were sampled once in 30 sites (27 forest fragments and 3 within continuous forests), each during five consecutive days between 1999 and 2009 (11 in fragments and 2 in continuous forest from 1999 to 2001, and 14 in fragments and 1 in continuous forest from 2005 to 2009) (Fig. 1). We chose sampling sites surrounded by varying degrees of forest cover, fragments of different sizes and mean distances to other fragments (see 'Landscape variables' for details on fragment sizes and distances between them). In each site four transects were established from the edge to the interior of forest, each transect with 16 trap stations, 20 m apart. Each trap station had two live traps on the ground, one Tomahawk® (model 201, $40.6 \times 12.7 \times 12.7$ cm, Tomahawk Live Trap Co., Tomahawk, Wisconsin) and one Sherman® (model XLK, $7.6 \times 9.5 \times 30.5$ cm, H. B. Sherman Trap Co., Tallahassee, Florida). Six live traps (Tomahawk and Sherman alternated) of each transect were set 1 to 2 m above the ground. The live traps above the ground were set in places with connection between tree canopies to capture mammals with arboreal and scansorial habits. Total sampling effort was 640 trap-nights per site.

Live traps were checked early in the morning and the bait replaced if necessary, which was a mixture of peanut butter, banana, oats, and bacon. From 1999 to 2001, captures were part of the small mammal surveys of the Project of Conservation and Use of Brazilian Biological Diversity (PROBIO; Ministério do Meio Ambiente/The Global Environment Facility). Captured individuals were removed from the study area, euthanized, and deposited in the Museu Nacional/Universidade Federal do Rio de Janeiro (MN/UFRJ). From 2005 to 2009, captured individuals were housed in individual plastic cages, fed *ad libitum*, and released at their original capture site at the end of the trapping session. Only unidentified animals were euthanized and deposited in MN/UFRJ. Body mass, head-body and tail lengths, sex, and reproductive condition of all individuals were recorded. This study was approved by the IBAMA/MMA (Authorization numbers 87/05-RJ, 099/06-RJ, 13861-1, 13861-2, 16703). Trapping and handling conformed to guidelines sanctioned by the American Society of Mammalogists (Sikes et al., 2011). We assumed that there was no difference in species composition between seasons, wet and dry, as already tested in Vieira et al. (2009) and Delciellos et al. (2016).

2.3. Selection of forest species

Non-volant small mammals can exhibit distinct (Pardini et al., 2005; Vieira et al., 2009), but also quick responses to landscape changes (Metzger et al., 2009). They also affect ecosystem dynamics through predation, herbivory and seed dispersal (e.g. Vieira et al., 2003; Brum et al., 2010). We selected species of small mammals that live exclusively within the forest and with similar movement abilities to determine effects of habitat amount on estimated species richness. Therefore, the open habitat dweller mouse, *Akodon cursor*, was excluded, as well as exotic species occasionally captured in the matrix or at the edge of forests (*Rattus rattus* and *Mus musculus*). Additionally, we excluded the marsupial *Didelphis aurita* due to its large size (580–1610 g in our study area), much larger than all other small mammals of the Atlantic Forest, generally weighting < 500 g (Paglia et al., 2012). Traditionally, species of *Didelphis* have been included as "small mammals" simply because their individuals are captured in the same traps, but their relatively large body size, large movements and inter-patch crossing ability imply

that they are differently affected by landscape structure (Vieira and Cunha, 2008; Forero-Medina and Vieira, 2009; Crouzeilles et al., 2010).

2.4. Landscape variables

The scale of effect for each landscape variable was determined combining the ad hoc approach proposed by Fahrig (2013), comparing a range of scales of varying in radius, but also based on results of Jackson and Fahrig (2012). They found that dispersal distance has a strong and positive influence on scale of landscape effect, which will vary between four and nine times the mean dispersal distance of the studied species. Mean dispersal distance was estimated for the smallest (*Oligoryzomys nigripes*) and largest (*Philander frenatus*) body size species captured by us using the empirical models of Whitmee and Orme (2013), which predict mammal species dispersal distance based on ecological and life history traits. The estimated mean dispersal distances multiplied by four and nine (based on Jackson and Fahrig, 2012) resulted in landscape sizes of 300 and 6700 m radius, lower and upper limits respectively. Finally, we defined 10 hierarchical scales of landscape sizes around each sampling site with radius of 300, 450, 700, 1200, 1700, 2000, 3000, 4000, 5000, and 6700 m.

Boscolo and Metzger (2009) found that multi-scale models can result in better predictions than single scale models, thus, we measured three landscape variables within these 10 landscape sizes to identify the scale of effect for each one: (i) habitat amount, (ii) 'restricted patch isolation', i.e. the mean distance of the sampling site to the nearest three other habitat patches, and (iii) ´overall patch isolation', i.e. the mean distance of the sampling site to all habitat patches within a specific scale. Patch size is the fourth variable, but it is not affected by the scale of landscape effect. Forest cover was used as a proxy for habitat amount. Despite variation in vegetation composition and structure between sampling sites (Finotti et al., 2012; Delciellos et al., 2016), much of this variation is associated with edge effects, more common in small and isolated fragments. Habitat availability decreases faster than forest cover, but it should be proportional to the amount of forest remaining (Almeida-Gomes et al., 2016). Habitat amount around sampling sites ranged from 24 to 100%, and from 7 to 77% for the landscape sizes of 300 and 6700 m radii, respectively, comprising most of the gradient of habitat amount. Habitat amount should be the best predictor of habitat availability when the whole gradient is considered, from 0 to 100% of habitat amount (Villard and Metzger, 2014), hence our local landscapes cover this gradient.

The maximum value of isolation was the radius of the local landscape size when there were no neighbouring habitat patches within the local landscape. A sampling sites was considered fully connected to other areas of habitat when the patch it was located extended beyond that radius, hence received '0' (zero) for isolation. These criteria were applied to both measures of patch isolation, restricted and overall. Restricted patch isolation ranged from 0 to 300 m, and from 0 to 2347 m for the landscape sizes of 300 and 6700 m radii, respectively. Overall patch isolation ranged from 0 to 300 m, and from 0 to 5013 m for the landscape sizes of 300- and 6700-m radii, respectively. Patch size was measured as the size of the forest fragment (ranging from 12 to 194 ha), or 400 ha for continuous forest sites, about twice the size of the largest fragment (194 ha) within a sampling site. Pearson correlation between predictor landscape variables was also considered after their best scale of effect was determined. The minimum, mean and maximum distances among the sampling sites were 419.4 m, 10,500 m, and 29,071 m, respectively. Landscape variables were obtained from the map produced by SOS Mata Atlântica and INPE (2005) (Fig. 1). All variables were measured using R 3.1.1 (R Development Core Team, 2014).

2.5. Data analysis

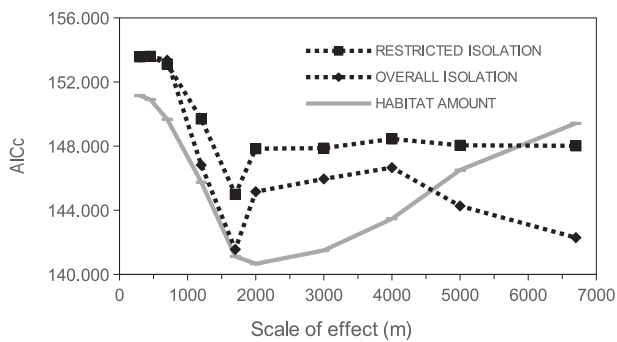Variation in the number of individuals captured results not only

Fig. 2. Support (AICc) for models differing only in scale of effect (radius of local landscape), for the three variables measured within the local landscape. The model with the lowest AICc loses relatively less information, defined as the best supported.

from differences in abundance but also from varying capture probabilities in time and space (e.g. Pacheco et al., 2013). Therefore, notwithstanding the fixed sampling design and effort, we used as response variable the Chao 1 estimator of asymptotic minimum species richness for each sampling site (Chao, 1984; Colwell and Coddington, 1994). When the number of doubletons was zero, the bias-corrected form of Chao 1 was used (Chao et al., 2005). Spatial correlation in the response variable, estimated species richness, was evaluated by Mantel correlation r (Mantel, 1967) between Euclidean distances and differences in species richness between sites (Legendre and Legendre, 2012), using the packages vegan (Oksanen et al., 2013) and ade4 (Dray and Dufour, 2007) in R 3.1.1 (R Development Core Team, 2014).

The relationship between estimated species richness and area of habitat should follow a power law function according to the species-area relationship (Dengler, 2009). Habitat amount also represents area of available habitat, measured as a proportion of the landscape area, hence both patch size and habitat amount should follow a power law with estimated species richness. This power law relationship was incorporated by treating species estimates in sampled forest sites as a typical Poisson process, using a canonical log link function in Generalized Linear Models (Bolker et al., 2009), and using the logarithm of patch size or habitat amount.

Models were compared using statistics derived from the corrected Akaike Information Criterion for small samples (AICc), especially the Akaike weights, w_i, a measure that a model is the best model in the set (Burnham and Anderson, 2002). Estimated species richness was the response variable in all models. Model selection was structured in two steps, the first to identify the best supported scale of effect for each landscape variable (Section 2.4), defined as the top-ranked model following Fahrig (2013) and Melo et al. (2017).

In the second step we compared seven models, with variables measured at their best scale of effect, representing the *a priori* set of hypotheses: (1) HAH - only habitat amount as predictor; (2, 3) IBT - patch size and overall isolation, but also patch size and restricted isolation; (4, 5) isolation – only overall or restricted isolation as explanatory variables, (6) patch size – to determine the relative importance of patch size alone; and (7) a statistical null model containing only the intercept and error as parameters. In this second step models were considered equally plausible if $\Delta_i \leq 2$. Akaike weights, w_i, were calculated considering the whole set of seven models tested. We used the generalized R^2 of Nagelkerke (1991) as a coefficient of determination to represent the goodness-of-fit of the models, varying between 0 and 1. Pearson correlations between predictor variables were also considered in the comparison of relative model support, but only IBT models had more than one predictor variables. These analyses were carried out in R 3.1.1 (R Development Core Team, 2014).

3. Results

We recorded a total of 507 individuals of 16 forest dependent small mammal species, seven belonging to the order Didelphimorphia, and nine to the order Rodentia (details of species captured in Appendix, Table A1). Estimated species richness varied from 1 to 10 within all 30 sampling sites. For more details on capture records see Vieira et al. (2009) and Delciellos et al. (2016).

The best scale of effect was almost the same for habitat amount and isolation metrics (Fig. 2, Table A2). For habitat amount the radius was 2000 m ($w_i = 0.340$; $R^2 = 0.353$), whereas for overall patch isolation and restrict patch isolation it was 1700 m ($w_i = 0.400$, $R^2 = 0.333$, and $w_i = 0.439$, $R^2 = 0.251$, respectively) (Fig. 2). For habitat amount and overall patch isolation, other landscape sizes were equally plausible ($\Delta_i \leq 2$, Table A2), but we used the best model supported by the data (lowest AICc and highest generalized R^2) as the more appropriate to test the HAH (as defined in section 2.5). The two landscapes sizes defined by these two radii had a wide range of variation in habitat amount, from 7 to 81% at 2000 m, and from 7 to 77% at 1700 m. The mean overlap between local landscapes of 2000-m radii was 26.4%, with a maximum of 86.5%. However, differences in species richness between sites were not spatially correlated (Mantel $r = -0.051$, $p = 0.667$).

Two models were equally plausible to explain forest dependent species richness of small mammals: habitat amount and overall patch isolation ($\Delta_i \leq 0.898$) (Table 1). Richness of forest-dependent small mammals increased with habitat amount, or decreased with overall patch isolation, inferred by the positive and negative model coefficients, respectively (Table 1). There was a relatively high correlation between log habitat amount and overall patch isolation (-0.599), the two top-ranked models, which could explain their similar support.

Table 1

Model selection to predict species richness of forest-dependent small mammals based on the Habitat Amount Hypothesis (HAH), Island Biogeography Theory (IBT), and patch isolation or size alone. HAH = amount of forest cover within the best scale of effect (2000-m radius); Overall patch isolation = mean distance of the sampling site to all habitat patches within the best scale of effect (1700-m radius); Restricted patch isolation = mean distance of the sampling site to the nearest three other habitat patches within the best scale of effect (1700-m radius); k = Number of parameters in the model; $logLik = -2\log$ likelihood; w_i = Akaike weights; R^2 = generalized R^2 of Nagelkerke (1991).

Models	Intercept	Coefficient (β)				k	$logLik$	$AICc$	Δ_i	ω_i	R^2
		Log habitat amount	Overall patch isolation ($\times 10^{-3}$)	Restricted patch isolation ($\times 10^{-3}$)	Log patch size						
HAH	0.289	0.447				3	−68.108	140.661	0.000	0.484	0.350
Patch isolation (overall)	2.262		−0.625			3	−68.558	141.559	0.898	0.309	0.331
IBT (overall)	2.058		−0.567		0.038	4	−68.457	143.836	3.175	0.099	0.335
Patch isolation (restricted)	2.066			−0.586		3	−70.277	144.998	4.337	0.055	0.249
IBT (restricted)	1.585			−0.481	0.104	4	−69.312	145.547	4.886	0.042	0.296
Patch size	1.022				0.161	3	−72.201	148.847	8.186	0.008	0.147
Null	1.655					2	−74.579	151.301	10.640	0.002	0.000

Restricted patch isolation had clearly no support compared to either habitat amount or overall patch isolation, inferred by the low w_i (Table 1) (in spite of a –0.481 correlation with habitat amount, and 0.735 with overall patch isolation). Models with patch size and isolation, representing IBT, had no support ($w_i < 0.099$) compared to either habitat amount or the models with restricted and overall isolation only. Pearson correlations between the logarithm of patch size and isolation metrics (predictor variables in IBT models) were generally low: -0.386 with overall patch isolation, -0.166 with restricted patch isolation. The null model was lowest in rank, with almost no support to explain estimated species richness ($w_i = 0.002$).

4. Discussion

The HAH posits that both patch size and isolation effects on species richness are driven mainly by a simple underlying process, the sample area effect, and that species richness should increase with total habitat amount in the local landscape (Fahrig, 2013). Accordingly, models with habitat amount in local landscapes should be more supported than models with either patch size or isolation, variables of IBT (Fahrig, 2013). Indeed, our results support HAH over IBT to explain richness of forest dependent small mammals in the study region. Similar results, favouring HAH over IBT, were observed for small mammals in the Cerrado (Melo et al., 2017), arboreal mammals in Amazonian fluvial islands (Rabelo et al., 2017), and experimentally with saproxylic beetles in southeastern Germany (Seibold et al., 2017).

However, the relative importance of patch isolation as a third, alternative hypothesis to either HAH and IBT, may not have been evaluated properly in these studies because of the use of a poor metric (distance to the three nearest neighbours patches in Melo et al., 2017), or by comparing slopes and intercepts of species-area curves (Rabelo et al., 2017; Seibold et al., 2017). When a more appropriate metric was used, overall isolation, HAH and patch isolation had the same support. The correlation between habitat amount and overall patch isolation ($r = -0.599$) could be seen as the reason for the equal support received by the two models, but correlations among variables in other models were similar or even higher, and still these models had clearly less support ($\Delta_i > 3$, Table 1). Therefore, patch isolation cannot be disregarded as an alternative hypothesis to HAH.

The weak support to IBT compared to HAH or overall patch isolation demonstrates the limitations of fragments as a metaphor for oceanic islands, and the matrix as the ocean (Haila, 2002; Didham et al., 2012). Most species must be crossing the matrix between habitat patches to some degree, which would explain why habitat amount or patch isolation are better predictors of richness of forest dependent species than patch size and isolation combined. However, patch size may do better as a predictor of species richness considering larger, continental scales, comparing patch sizes of possibly two or more orders of magnitude (comparing areas of 10, 100, and 1000 ha for example).

The choice of the appropriate scale and metric of patch isolation was critical for an unbiased test of the HAH. Had we measured isolation at the same scale determined for habitat amount, our analyses would be biased, favouring support only for habitat amount, not patch isolation. Had we used only the restricted patch isolation, a poor metric of isolation, we would also have found support for habitat amount only. The use of poor metrics of patch isolation, such as restricted patch isolation, and its measure at the scale of effect for habitat amount casts doubts on studies favouring HAH suffering from these pitfalls. As Fahrig (2013) proposes that the best scale of effect should be obtained by the better fit between the amount of habitat and species richness, disregarding a scale of effect for habitat isolation could hamper a fair test of the HAH.

Our result for overall patch isolation is also in agreement with studies that support patch isolation as the determinant of population persistence, habitat availability, and species richness in landscapes (Bailey et al., 2010; Pardini et al., 2010; Boscolo and Metzger, 2011; Martensen et al., 2012; Coudrain et al., 2014; Villard and Metzger,

2014; Martín-Queller et al., 2017). This could be the case in the Atlantic Forest, where forest-dependent small mammals tend to have more restricted inter-patch movements (Crouzeilles et al., 2010; Delciellos et al., 2017). Conversely, in naturally open landscapes inter-habitat patch movements of small mammals are likely larger, reducing the importance of patch isolation. This could be the case of Melo et al. (2017), studying small mammal species in the Brazilian savanna, the Cerrado. They selected the appropriate scale of effect according to Fahrig (2013) and found support for the HAH in detriment to both patch size and isolation. Melo et al. (2017) measured patch isolation as the mean distance from their sampling units (transects) to the three nearest habitat patches. Still, there is more sampling error in this measure of isolation than in habitat amount, which bias the results in favour of the HAH.

In contrast to our results, the HAH was rejected in at least four study systems across the world, where habitat configuration effects were determined controlling for habitat amount. For vascular plants in calcareous grasslands in Norway, the model including habitat amount and patch size was nearly six times more plausible than the model with habitat amount alone. However, there was < 1% of land cover in a 3 km-radius surrounding the studied habitat patches (Ejvu and Sverdrup-Thygeson, 2016). For vascular plants in experimental grasslands of Savannah River Site Corridor Experiment (USA) and for microarthropods in the Moss Fragmentation Experiment (UK), the species-area relationship for fragmented habitats had significantly higher slope, and the magnitude of the difference in slopes increased over time, demonstrating an important effect of habitat configuration on species richness independent of habitat amount (Haddad et al., 2017, in contrast to Rabelo et al., 2017 using the same approach). Richness and density of vascular plants and grassland plant specialists in central Sweden also support IBT over HAH, although the entire region had only 4% of grassland (Lindgren and Cousins, 2017). Therefore, one possible reason for the weak support of HAH in at least some of these studies could be the relatively discontinuous or small range of variation in habitat amount in the study areas. Habitat amount should be more important when the whole gradient of habitat amount (from 0 to 100%) is considered, or when the percentage cover of original habitat is > 50% of the landscape, while habitat configuration becomes more important with < 50% of habitat amount in the landscape (Andrén, 1994; Fahrig, 2003; Villard and Metzger, 2014).

When considering the whole range of the habitat amount in landscapes, from 0 to 100%, a major effect of habitat amount is likely to be found, in support of the HAH, as observed in this study and others that support HAH. This generalization offers simplicity to decision-making regarding conservation and restoration actions. However, patch isolation may offer similar simplicity to decision-making, and rigorous tests of the HAH vs. IBT must consider accurate estimates of patch isolation, measured at its own scale of effect, otherwise comparisons may be biased favouring HAH. In addition, patch isolation may be more determinant of species richness and habitat availability when habitat amount is < 50% (Villard and Metzger, 2014), typical of most current landscapes. Future studies should consider patch isolation or measures of landscape connectivity (e.g. Saura and de la Fuente, 2017) as potential alternatives, escaping from the simplistic duality HAH vs. IBT.

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