

1 **Patch-scale biodiversity retention in fragmented landscapes:**  
2 **reconciling the habitat amount hypothesis with the island**  
3 **biogeography theory**

4  
5 **Running title:** Biodiversity retention in habitat patches

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16

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27

28 **ABSTRACT**

29 **Aim:** To test whether the species richness of understory insectivorous birds on forest islands  
30 induced by a major hydroelectric dam is best explained by either the island biogeography  
31 theory (IBT) or the habitat amount hypothesis (HAH). Given the low dispersal ability of the  
32 focal species group and the hostile water matrix, we predict that the species richness will be  
33 predominantly driven by an island effect as posited by the IBT, rather than a sample area  
34 effect as posited by the HAH.

35 **Location:** Forest islands within the Balbina Hydroelectric Reservoir, central Brazilian  
36 Amazonia.

37 **Taxon:** Birds.

38 **Methods:** We mist-netted birds at 33 forest islands (0.63–1,699 ha), totalling 874 individuals  
39 of 59 species. The size of the local landscape used to calculate the habitat amount was  
40 determined by a multi-scale analysis in which buffers around mist-net lines ranged from 50 to  
41 2,000 m. We applied four tests to examine whether the species richness on forest islands is  
42 predominantly driven by either an island effect (island size) or a sample area effect (habitat  
43 amount).

44 **Results:** From the four tests applied, one was consistent with an island effect, two were  
45 regarded as inappropriate to test the HAH, and one could not be adequately addressed due to  
46 island size being highly correlated with habitat amount in the local landscape (200-m buffer).

47 **Main conclusions:** Some of the proposed ways of testing the HAH may lead to misleading  
48 conclusions. The relative importance of island size in determining the species richness of  
49 understory insectivorous birds on forest islands is higher than that of surrounding habitat  
50 amount, thereby providing stronger support for IBT. We propose a conceptual framework,  
51 based on the degree of matrix permeability and species dispersal ability, to determine to what  
52 extent a patch- or landscape-centric worldview in landscape ecology provides the most  
53 appropriate framework to assess the effects of habitat fragmentation on biodiversity.

54

55 **Key-words:** Amazonia, habitat amount hypothesis, habitat fragmentation, habitat loss,  
56 insularization, island biogeography theory, SLOSS, species richness, species-area  
57 relationship, tropical forest

58

## 59 INTRODUCTION

60 MacArthur & Wilson's (1967) island biogeography theory (hereafter, IBT) has been  
61 widely applied as a paradigmatic conceptual framework in habitat fragmentation ecology,  
62 implying that habitat patches are analogous to oceanic islands surrounded by a hostile matrix  
63 (Haila, 2002; Laurance, 2008). However, such analogy has been repeatedly challenged since  
64 IBT does not account for many factors operating in fragmented landscapes (Laurance, 2008;  
65 Wiens, 2008), which were later incorporated into a landscape ecology framework (Haila,  
66 2002). For example, species move among suitable habitat patches as a function of varying  
67 degrees of terrestrial matrix permeability (Powell et al., 2013), indicating that habitat patches  
68 exert weaker boundaries to local populations and their derivative assemblages compared to  
69 oceanic islands. If habitat patches fail to behave as discrete spatial units, the universally  
70 celebrated species-area relationship (hereafter, SAR) – which is widely observed in  
71 fragmented landscapes (Matthews et al., 2016) – may be governed at spatial scales larger than  
72 that of island effects driven by habitat patch size.

73 With this in mind, Fahrig (2013) proposed the habitat amount hypothesis (hereafter,  
74 HAH), which posits that (1) habitat patches are *not* discrete spatial units, and (2) the habitat  
75 surrounding any given patch is the main source of immigrants. The underlying mechanism of  
76 SARs in fragmented landscapes is therefore predicted to be the sample area effect, rather than  
77 the island effect. Accordingly, sample sites within larger habitat patches harbour more  
78 species because they are also associated with a greater amount of surrounding habitat.  
79 Meanwhile, sample sites associated with the same amount of landscape-scale habitat should  
80 harbour the same number of species, regardless of patch size (Fig. 7 in Fahrig, 2013). Such  
81 notion implies that conservation efforts should primarily focus on increasing the overall  
82 habitat amount (i.e. the proportion of habitat in the landscape) without necessarily  
83 considering its spatial arrangement (i.e. size and isolation of individual habitat patches)  
84 (Seibold et al., 2017).

85 The generalisation of the HAH was initially criticised since its application was  
86 considered to be restricted to small-scale landscapes containing large habitat amounts  
87 (Hanski, 2015), although the HAH was yet to be tested (Fahrig, 2015). Recent empirical  
88 studies carried out in a variety of natural (e.g. forest fragments, fluvial islands, calcareous  
89 grasslands) and experimental fragmented landscapes (e.g. dead-wood microhabitats, moss  
90 fragments), across a wide range of taxonomic groups (e.g. small and arboreal mammals,  
91 birds, vascular plants, saproxylic beetles, and micro-arthropods), have either supported (Melo  
92 et al., 2017; Rabelo et al., 2017; Seibold et al., 2017) or refuted (Evju & Sverdrup-Thygeson,  
93 2016; Haddad et al., 2016; Torrenta & Villard, 2017) the HAH. Therefore, further empirical  
94 studies are needed to appraise the degree to which the HAH can be generalised to different  
95 landscape scenarios and taxonomic groups (Rabelo et al., 2017).

96           The IBT and HAH were originally developed within a context of oceanic islands  
97 (MacArthur & Wilson, 1967) and habitat patches within terrestrial landscapes (Fahrig, 2013),  
98 respectively. These two landscape scenarios may be seen as extremes along a continuum. In a  
99 global synthesis, Matthews et al. (2016) showed that  $z$ -values of SARs are higher in true  
100 islands than in habitat patches. They also reported gradients in  $z$ -values ranging from inland  
101 water-body to oceanic islands, and from forest to mountaintop habitat patches. Hence, the  
102 magnitude of island effects is context-dependent regarding the type of matrix surrounding  
103 habitat patches (Prugh et al., 2008). Patterns of species richness in intermediate landscape  
104 scenarios, such as inland water-body islands and mountaintops, could therefore be explained  
105 by either IBT or HAH.

106           The HAH was erected under the assumption that species perceive the wider  
107 macrohabitat mosaic as functionally connected (Fahrig, 2013). Matrix permeability, as  
108 measured by the structural similarity between habitat patches and any surrounding matrix  
109 (Prevedello & Vieira, 2010), along with inherent differences in species dispersal ability (Lees  
110 & Peres, 2009), would then determine whether species use their habitat primarily at the  
111 patch- or landscape-scale. Accordingly, we hypothesise that patterns of species richness in  
112 fragmented landscapes can be better explained under either the HAH if species exhibit high  
113 levels of dispersal ability across a permeable matrix, or the IBT if species exhibit low  
114 dispersal ability across a hostile matrix.

115           Here, we examined whether the HAH can be extended to anthropogenic archipelagic  
116 landscapes using the number of understory insectivorous bird species on forest islands  
117 induced by a large hydroelectric dam in central Brazilian Amazonia. We focused on  
118 understory insectivorous birds because they are particularly vulnerable to forest loss and  
119 fragmentation (Powell et al., 2015), and exhibit low dispersal ability through non-forest  
120 matrix habitats (Sekercioglu et al., 2002; Laurance et al., 2004). We show that the number of  
121 understory insectivorous bird species on forest islands is best explained by an island effect,  
122 which is consistent with the IBT. Moreover, we propose a conceptual framework, based on  
123 the degree of matrix permeability and species dispersal ability, to determine which point  
124 along the continuum between a patch- and landscape-centric worldview in fragmentation  
125 ecology – represented here by either IBT or HAH – provides the most appropriate guiding  
126 framework for biodiversity studies in fragmented landscapes.

127

## 128 **MATERIALS AND METHODS**

### 129 **Study area**

130           This study was carried out within the Balbina Hydroelectric Reservoir (BHR) in  
131 central Brazilian Amazonia (1°40' S, 59°40' W; Fig. 1). The BHR spans *ca.* 300,000 ha and

132 was formed by the damming of the Uatumã River in 1987 (Fearnside, 2016), creating over  
133 3,500 land-bridge islands of variable size (range = 0.2–4,878 ha), which are surrounded by a  
134 vast water reservoir often containing dead tree snags rising above the water level (Benchimol  
135 & Peres, 2015a). To offset the environmental impacts of the dam, the left bank of the former  
136 Uatumã River, including all islands, became strictly protected by the 940,358-ha Uatumã  
137 Biological Reserve (IUCN category Ia), the largest of its category in Brazil (Fig. 1).

138 The vegetation is comprised primarily of submontane dense ombrophilous (*terra-*  
139 *firme*) forest, although *igapó* forest subjected to seasonal flooding formerly occurred along  
140 the margins of the Uatumã River before damming. Forest structure varies among islands due  
141 to both island size and associated edge-mediated disturbance: smaller islands are species-poor  
142 and dominated by pioneer tree species, whereas larger islands are species-rich and contain a  
143 higher dominance of large-seeded canopy tree species (Benchimol & Peres, 2015a).  
144 According to the Köppen classification, the climate is equatorial fully humid (Af), with mean  
145 annual precipitation and temperature of 2,464 mm and 26.5 °C, respectively (Alvares et al.,  
146 2013).

147

## 148 **Sampling design**

149 We selected 33 forest islands within the BHR, ranging in size from 0.63 to 1,698.84  
150 ha. Sixteen islands were on the left bank, whereas 17 islands were on the right bank (Fig. 1).  
151 The combined study meta-landscape encompassed 177,720 ha where sample sites were  
152 spaced apart by an average distance of 27.9 km (SD = 15.0 km; range = 2.0–68.4 km).

153 We surveyed birds using mist nets (12 × 2.5 m, *Ecotone* 1016/12) from July to  
154 December in two consecutive years (2015 and 2016). We placed 16 mist nets end-to-end in  
155 the understorey along a continuous near-linear net-line (*ca.* 200 m) whenever possible, but  
156 used a cross-shaped net-line design on islands smaller than 4 ha, thereby ensuring the same  
157 sampling effort across all 33 surveyed islands. Herein, each mist-net line corresponds to one  
158 sample site. Mist nets were operated from 06:00 to 15:00 h for two days at each site each  
159 year, resulting in a total sampling effort of 19,008 net-hours (16 mist nets × 9 hours × 2 days  
160 × 2 years × 33 sites). To avoid double-counting, we ringed birds with coded aluminium rings  
161 and excluded recaptures. Rings were provided by the Brazilian National Center for Bird  
162 Conservation and Research (CEMAVE) under research permits SISBIO 49068 and  
163 CEMAVE 3984.

164

## 165 **Response variable and species group**

166 We used the *number of species* of understory insectivorous birds as the response  
167 variable, and limited our analysis to forest species because the habitat type (i.e. forest) must  
168 be appropriately defined for the focal species group (Fahrig, 2013). We defined forest species  
169 as those classified as having ‘medium’ or ‘high’ levels of forest dependency (*sensu* BirdLife  
170 International, 2018), and insectivorous species as those classified under the ‘invertebrate’  
171 dietary category (*sensu* Wilman et al., 2014). The only forest insectivorous species omitted  
172 from the analysis was the Amazonian Pygmy-Owl (*Glaucidium hardyi*) because surveys were  
173 diurnal, and this species is nocturnal (Wilman et al., 2014). Since understory mist nets  
174 primarily capture understory birds and occasionally those that walk on the ground or forage  
175 at forest strata higher than 2.5 m (Karr, 1981), we considered all species captured as  
176 understory birds to avoid misinterpretation.

177

## 178 **Predictor variables**

179 We extracted data on *island size* and *habitat amount* for all 33 sample sites using a  
180 classified image (Collection 2, 2015, Amazon) derived from 30-m resolution LANDSAT  
181 imagery downloaded from the Brazilian Annual Land Use and Land Cover Mapping Project  
182 (available at <http://mapbiomas.org>). To do so, we used the QGIS software (QGIS  
183 Development Team, 2016) and the *LecoS* plugin (Jung, 2016). Island size corresponds to the  
184 total forest area (in hectares) within an island, and habitat amount corresponds to the  
185 percentage of forest cover within a given surrounding landscape at varying scales. In  
186 extracting the predictor variables, only ‘dense forest’ (pixel value 3) was defined as forest,  
187 because other pixel values effectively represent either heavily degraded forests or non-forest  
188 land cover types.

189

## 190 **Data analysis**

### 191 *Scale of effect*

192 Species-landscape relationships are strongly affected by the scale at which landscape  
193 attributes are measured (Jackson & Fahrig, 2015). We therefore employed a multi-scale  
194 analysis to determine the ‘scale of effect’ – the landscape scale at which the relationship  
195 between the number of species and habitat amount peaks (Jackson & Fahrig, 2015). We  
196 defined the scale of effect as the ‘local landscape’ for understory insectivorous birds at the  
197 Balbina forest archipelago. Our multi-scale analysis examined 40 different buffer sizes  
198 around sample sites (i.e. mist-net lines), ranging from 50 to 2,000 m at 50-m intervals. The  
199 smallest landscape scale (50 m) corresponds to the average between the reluctance of  
200 Amazonian understory birds to cross forest clearings as narrow as 30 m (Laurance et al.,  
201 2004) and an assemblage-wide avian gap-crossing ability of up to 70 m (Lees & Peres, 2009).

202 The largest landscape scale (2,000 m) includes those frequently used in avian fragmentation  
203 studies (Jackson & Fahrig, 2015; Morante-Filho et al., 2015; Aurélio-Silva et al., 2016). For  
204 this analysis, we included all 33 surveyed islands and log-transformed the response and  
205 predictor variables ( $\log_{10} x + 1$ ).

206

#### 207 *IBT vs. HAH*

208 The number of species in fragmented landscapes can be explained by either patch size  
209 (e.g. Torrenta & Villard, 2017) or habitat amount (e.g. Melo et al., 2017), which represent  
210 two worldviews in assessing the total area of suitable habitat. This means that the iconic SAR  
211 (Rosenzweig, 1995) holds true regardless of its spatial drivers (patch size or habitat amount),  
212 but that the underlying mechanism may be either the island effect driven by patch size as  
213 predicted by the IBT, or the sample area effect driven by habitat amount as predicted by the  
214 HAH (Fahrig, 2013). We applied four tests to determine whether the IBT or the HAH is the  
215 most appropriate theoretical framework to explain the number of understorey insectivorous  
216 bird species on forest islands within the BHR.

217

#### 218 Test 1: Multiple linear regression

219 We used multiple linear regression analysis to examine the independent effects of  
220 island size and habitat amount in the local landscape on species richness. This method allows  
221 one to estimate how much of the variation in the response variable (i.e. number of species)  
222 can be attributed solely to a predictor variable (e.g. island size), once the effects of another  
223 predictor (e.g. habitat amount) are controlled for (Legendre & Legendre, 1998).

224 An effect of island size, rather than one of habitat amount, would provide support for  
225 IBT, whereas the reverse would provide support for HAH (Fig. 2). The response and  
226 predictor variables were log-transformed ( $\log_{10} x + 1$ ) prior to analysis. The predictor  
227 variables were also standardised (mean = 0, SD = 1) to allow comparison of regression  
228 slopes. Finally, we examined the strength of correlation values between island size and  
229 habitat amount across the entire spectrum of 40 landscape scales (50–2,000 m) to assess the  
230 suitability of the multiple linear regression test.

231

#### 232 Test 2: Z-values

233 We used the logarithmic form of the SAR (type IV curve *sensu* Scheiner, 2003) to fit  
234 simple linear regression models (Rosenzweig, 1995) for islands surrounded by either low



235 habitat amounts (up to *ca.* 50% of the landscape; Morante-Filho et al., 2015) or high habitat  
236 amounts, according to the following equation:

$$237 \quad \log_{10}(S + 1) = z \times \log_{10}(A + 1) + \log_{10}(c),$$

238 where  $S$  = number of species,  $z$  = regression slope,  $A$  = island size,  $c$  = regression intercept.  
239 To assess whether the  $z$ -values derived from either SARs were significantly different ( $p <$   
240  $0.05$ ), we performed an ANCOVA model with habitat amount (low or high) as an  
241 independent categorical variable. To support the IBT, the SAR for islands with low habitat  
242 amounts should have a higher  $z$ -value than those with high habitat amounts (Fig. 2).  
243 Conversely,  $z$ -values should be statistically equivalent to support the HAH (Fig. 2).

244

#### 245 Test 3: Species accumulation curves

246 We compared the cumulative number of species on all 33 surveyed islands ordered  
247 according to both increasing (small-to-large) and decreasing (large-to-small) island sizes  
248 (Quinn & Harrison, 1988), which may lead to three possible outcomes. First, the small-to-  
249 large accumulation curve lies below the large-to-small, supporting IBT (Fig. 2). Second, the  
250 curves overlap, supporting HAH (Fig. 2). Third, the small-to-large accumulation curve lies  
251 above the large-to-small, supporting neither IBT nor HAH.

252

#### 253 Test 4: Extrapolation of SAR

254 We fit a SAR model (see Test 2:  $Z$ -values) to all 33 surveyed islands. We further  
255 extrapolated the number of species to a hypothetical island containing the area (+ 1) of all 33  
256 surveyed islands combined (7,841.4 ha), and compared the overall number of species  
257 observed across surveyed islands with the extrapolated value (Yaacobi et al., 2007).  
258 Compared with the extrapolated value, a lower observed number of species would support  
259 IBT (Fig. 2); a statistically equivalent number, HAH (Fig. 2); a higher number, neither IBT  
260 nor HAH.

261

## 262 RESULTS

263 We captured a total of 874 individual understorey insectivorous birds representing 59  
264 species, 49 genera and 19 families across all 33 sample sites (see Table S1 in Supporting  
265 Information). The number of individuals per island ranged from 0 to 84 ( $26.5 \pm 23.4$ ), and the  
266 number of species from 0 to 27 ( $8.8 \pm 7.5$ ; see Table S2).

267

268 **Scale of effect**

269           The correlational peak between the number of species and habitat amount (i.e. the  
270 scale of effect) occurred at 200-m buffers around sample sites ( $r = 0.873$ ; see Fig. S1),  
271 thereby corresponding to the local landscape for understory insectivorous birds at the  
272 Balbina forest archipelago. The fact that this local landscape is intermediate between the  
273 smallest and the largest landscape scales examined here indicates that our multi-scale analysis  
274 included the true scale of effect (Jackson & Fahrig, 2015). Therefore, habitat amount is  
275 defined as the percentage of forest cover only within 200-m buffer local landscapes for all  
276 subsequent analyses.

277

278 **Test 1: Multiple linear regression**

279           A multiple linear regression model including island size and habitat amount showed  
280 that both predictor variables were strongly and positively related to the number of species ( $R^2$   
281  $= 0.80$ ,  $p < 0.001$ ). Partial regressions also showed that habitat amount had a slightly better fit  
282 and higher regression slope than island size (see Fig. S2), which in itself would lend more  
283 support for HAH than IBT. However, island size and habitat amount were positively  
284 correlated across the entire range of 40 landscape scales examined and peaked exactly at the  
285 scale of effect (200-m buffer; see Fig. S3). Due to the high collinearity between predictors ( $r$   
286  $= 0.857$ ), regression coefficients could change depending on the random component in the  
287 response variable (Legendre & Legendre, 1998), thereby precluding us from raising any  
288 conclusions derived from Test 1.

289

290 **Test 2: Z-values**

291           The species-area relationship for islands surrounded by low habitat amounts ( $< 55\%$ )  
292 had a statistically higher  $z$ -value (0.747) than islands surrounded by high habitat amounts ( $>$   
293  $70\%$ ; 0.311), as shown by an ANCOVA test ( $p = 0.009$ ; Fig. 3). This outcome supports an  
294 island effect, rather than solely a sample area effect (Fahrig, 2013), thereby lending stronger  
295 support for IBT.

296

297 **Test 3: Species accumulation curves**

298           Species accumulation curves did not overlap whether sampling sites were ordered  
299 according to increasing (small-to-large) or decreasing (large-to-small) island sizes. The  
300 small-to-large curve lay above the large-to-small curve (Fig. 4), which contradicts both IBT  
301 and HAH.

302

303 Test 4: Extrapolation of SAR

304 We observed a larger number of species ( $59 + 1$ ) across all 33 surveyed islands than  
305 that extrapolated (55.2) to a hypothetical island containing the area (+ 1) of all surveyed  
306 islands combined (7,841.4 ha). However, the difference between the observed and  
307 extrapolated number of species was not significant (Fig. 5), which lends support for HAH.

308

## 309 **DISCUSSION**

310 Compared to the HAH, there was more evidence giving support to the IBT in  
311 explaining the number of understory insectivorous bird species within Amazonian forest  
312 islands in one of the largest hydroelectric reservoirs on Earth. Considering the four tests  
313 applied, Test 2 ( $z$ -values) was consistent with an island effect as posited by the IBT, Tests 3  
314 (SACs) and 4 (extrapolation of SAR) were regarded as inappropriate to test the HAH (see  
315 below), and Test 1 (multiple linear regression) could not be adequately addressed due to a  
316 prohibitively high correlation between island size and habitat amount at the local landscape.  
317 Since both an island effect (e.g. Evju & Sverdrup-Thygeson, 2016) and a sample area effect  
318 (e.g. Rabelo et al., 2017) may explain patterns of species richness in fragmented landscapes,  
319 the key question becomes which of these two theoretical frameworks provides the best fit to  
320 different scenarios in ‘real-world’ fragmented landscapes. This question has critical  
321 implications to biodiversity conservation strategies since empirical evidence primarily  
322 supporting IBT would imply a management focus on the spatial arrangement of remaining  
323 habitat patches, whereas support for HAH would imply a management strategy focused on  
324 retaining the maximum overall amount of habitat regardless of its configuration (Seibold et  
325 al., 2017).

326 The independent effects of predictor variables may be disentangled using statistical  
327 methods such as multiple regression analysis. However, as the degree of collinearity between  
328 predictor variables increases, the accuracy in determining their independent effects decreases,  
329 particularly above a high threshold ( $r > 0.7$ ) from which parameter estimates begin to be  
330 severely distorted in regression-type analyses (Dormann et al., 2013). In our set of sample  
331 sites, the highest correlation between island size and habitat amount occurred exactly at the  
332 scale of effect (i.e. 200-m buffer;  $r = 0.857$ ), which precluded us from directly testing the  
333 predictions of the HAH. Ideally, patch size and habitat amount should be either orthogonally  
334 independent or negatively correlated (Fig. 7 in Fahrig, 2013). However, the pervasive  
335 positive correlation between habitat patch size and habitat amount in landscapes worldwide is  
336 the rule rather than the exception (Fahrig, 2003), and this correlation becomes even stronger  
337 and more ubiquitous for smaller local landscapes (Rabelo et al., 2017). For instance, island

338 size and habitat amount were more likely to be independent in our study system at larger  
339 scales, well beyond a demographically realistic local landscape for our focal species group.

340 The scale of effect is indeed unlikely to be known before sampling design is  
341 established, thereby a multi-scale analysis is necessary to determine the local landscape  
342 (Fahrig, 2013). This implies that sample sites selected *a priori* to control for the positive  
343 correlation between patch size and habitat amount may fail to achieve this goal if the size of  
344 the local landscape is different than initially thought. To illustrate this, consider a set of  
345 sample sites where the size of the focal habitat patches increases while the amount of habitat  
346 remains constant (Fig. 6). If the size of the local landscape derived from a multi-scale  
347 analysis is found to be half of that defined *a priori*, patch size and habitat amount will be  
348 positively correlated (Fig. 6). Therefore, directly testing the HAH under its main assumptions  
349 is expected to be less feasible if the scale of effect is small or not known *a priori*. Despite  
350 these shortcomings, there are alternative ways of testing the HAH (Fahrig, 2013).

351 First, if patch size *per se* does not affect the number of species, as predicted by the  
352 HAH,  $z$ -values derived from species-area relationships are expected to be the same in  
353 landscapes with either low or high habitat amounts (Fig. 2). We showed that the  $z$ -value for  
354 islands at landscapes isolated by low habitat amounts ( $< 55\%$ ) is statistically higher than that  
355 at landscapes connected by high habitat amounts ( $> 70\%$ ; Fig. 3), which contradicts a  
356 prediction of the HAH. Such a difference could be attributed to the selected cut-off (55%)  
357 that distinguishes low from high habitat amounts. To test whether the difference in  $z$ -values is  
358 sensitive to this threshold, we reran the  $z$ -value test using different cut-offs for habitat amount  
359 (54%, 50%, 48.5%, 45%, 43.1%, 30%; see Supporting Information). The differences in  $z$ -  
360 values held true except when the species-area relationship for islands surrounded by low  
361 habitat amounts was *not* significant. Since all islands were smaller than 10 ha for the lower  
362 cut-offs ( $\leq 45\%$ ), the lack of a relationship may be explained by the small island effect (i.e.  
363 for small islands, the variation in island size does not affect the number of species; Lomolino  
364 & Weiser, 2001). In sum, forest islands surrounded by low habitat amounts had a steeper  
365 decline in species richness as a function of island size reduction (i.e. higher  $z$ -value) than  
366 those surrounded by high habitat amounts whenever the SAR models were significant.

367 The difference between  $z$ -values is attributed to an island effect, which is consistent  
368 with the IBT (Fahrig, 2013). Accordingly, larger and less isolated islands are more species-  
369 rich than smaller and more isolated islands because the former experience lower extinction  
370 (area effect) and higher colonisation rates (distance effect) (MacArthur & Wilson, 1967).  
371 Thus, if islands within their local landscapes were functionally connected as assumed by the  
372 HAH, the number of immigrants reaching focal islands would mainly depend on the amount  
373 of habitat surrounding those islands (sample area effect), thereby compensating species  
374 declines through rescue effects (Fahrig, 2013; see Seibold et al., 2017).

375           Second, the species accumulation curves (SACs) from either small to large patches or  
376 from large to small patches (Fig. 2) should roughly coincide to support HAH since this is  
377 caused by a sample area effect, meaning that the long-celebrated dichotomy between a Single  
378 Large Or Several Small patches (SLOSS) should harbour a similar number of species.  
379 Alternatively, a faster accumulation in the number of species from large to small patches,  
380 compared to that from small to large patches, would be attributed to an island effect (IBT).  
381 The cumulative number of understorey insectivorous bird species at the Balbina forest  
382 archipelago rose faster from small to large patches than from large to small ones, which  
383 supports neither IBT nor HAH.

384           The fact that several small patches (islands) apparently harboured more species than a  
385 single large patch (Fig. 4) is consistent with the literature (Fahrig, 2017). However, we did  
386 not find support for several possible explanations for this pattern at the Balbina forest  
387 archipelago. First, we strictly focused on forest species implying that the pattern was not  
388 confounded by the inclusion of disturbance-adapted species, which would increase the overall  
389 number of species across small patch sites (Lovei et al., 2006). Second, habitat heterogeneity,  
390 regarding vegetation structure in Amazonian *terra firme* forests, is associated with elevation  
391 (Castilho et al., 2006), below-ground vertical distance to the water table (Schietti et al., 2014)  
392 and horizontal distance to perennial streams (Drucker et al., 2008). Thus, several small  
393 patches could harbour more species than a single large patch if they covered wider  
394 topographic and hydrologic gradients, resulting in higher levels of habitat heterogeneity  
395 (Báldi, 2008). However, our islands consist of upland habitat remnants resulting from hilltop  
396 terrains of the once continuous forest. As such, they span similar elevations and streams were  
397 missing from all but two very large islands (Beco do Catitu and Mascote). As a result,  
398 surveyed islands shared relatively low levels of intra-patch habitat heterogeneity regarding  
399 closed-canopy forest structure. Third, the Balbina islands are isolated by a hostile water  
400 matrix which likely hinders the dynamic of colonisation and extinction (Palmeirim et al.,  
401 2017), particularly for species that are unable to either cross wide gaps or use dead tree snags  
402 as stepping stones. Indeed, the disappearance of understorey insectivorous birds from forest  
403 fragments has been largely attributed to dispersal limitation (Sekercioglu et al., 2002), which  
404 along with a severely hostile water matrix explain patterns of bird species occupancy on  
405 forest islands (Moore et al., 2008). The relatively small local landscape threshold (200-m  
406 buffer) for understorey insectivorous birds at the Balbina forest archipelago provides  
407 additional evidence of such dispersal limitation (Jackson & Fahrig, 2012).

408           The most likely explanation for the observed SACs (Fig. 4) relies on a bias associated  
409 with this method. In a SLOSS-type study, Gavish et al. (2012) compared four methods to  
410 examine the effects of habitat loss and fragmentation on the species richness of spiders. They  
411 concluded that only SACs (Quinn & Harrison, 1988) should be avoided as this method was  
412 biased towards detecting more species in several small habitat patches than in a single large

413 patch. This occurs because the method is sensitive to sampling intensity (i.e. proportion of  
414 patch area that is sampled), which could lead to an apparent higher number of species in  
415 small but more intensively sampled patches (Gavish et al., 2012). Since the proportion of the  
416 island area we sampled in smaller islands was immensely higher than in larger islands, the  
417 result of the SACs is likely to be misleading. Moreover, the pattern of SACs was inconsistent  
418 with the HAH even in an experiment designed to decouple the independent effects of patch  
419 size and habitat amount on saproxylic beetles whose revealed strong support for HAH  
420 (Seibold et al., 2017).

421 Third, the extrapolation of the SAR model (Yaacobi et al., 2007) suggests that several  
422 small islands did *not* harbour more understorey insectivorous bird species than a single large  
423 island containing the same aggregate area of several small islands (Fig. 5). This result is  
424 presumably consistent with the HAH (Fahrig, 2013; MacDonald et al., 2018). However, had  
425 this method been suitable to test the HAH, oceanic archipelagos should harbour fewer species  
426 than that predicted by the extrapolation of SAR models derived from their constituent islands.  
427 Indeed, observed and extrapolated values of species richness for most oceanic archipelagos  
428 are statistically the same (75% to 95% of 40 case studies; Santos et al., 2010). Collectively,  
429 this means that neither SACs nor an extrapolation of SAR models seem to be reliable  
430 methods to test the HAH.

431 Testing the HAH is by no means a trivial task for two main reasons. First, as a general  
432 rule, habitat patch size and habitat amount tend to be positively correlated (Fahrig 2003).  
433 However, these two predictors should be either largely orthogonal or negatively correlated to  
434 properly test predictions derived from the HAH (Fig. 7 in Fahrig, 2013). Depending on the  
435 landscape, this constraint may however be overcome if the scale of effect (*sensu* Jackson &  
436 Fahrig, 2015) is known prior to the establishment of the experimental design. Second, species  
437 assemblages are comprised of species with varying degrees of dispersal ability, although  
438 within some groups, such as understorey insectivorous birds, such a trait is broadly similar  
439 across species (Laurance et al., 2004). Thus, the scale of effect for a given species  
440 assemblage will result from a combination of species with either lower or higher dispersal  
441 ability (Lees & Peres, 2009). Therefore, we believe the most robust way forward in testing  
442 the HAH would be to focus on individual species (Hanski, 2015) whose dispersal ability  
443 through the matrix (i.e. landscape vagility) is known *a priori* and derived from *in situ* studies  
444 (e.g. Awade & Metzger 2008).

445

446 **Moving beyond: a conceptual framework to assess the role of patch size and habitat**  
447 **amount in explaining species responses to habitat fragmentation**

448

449 We can reasonably expect that local assemblage structure is primarily governed by  
450 patch-level characteristics in a hypothetical situation in which species seldom if ever exit the  
451 patch, due to low dispersal ability, low matrix permeability, or both (Moore et al., 2008).  
452 Conversely, landscape-level characteristics should matter most in a hypothetical situation in  
453 which species often move among patches within the local landscape, due to high dispersal  
454 ability, high matrix permeability, or both (Walter et al., 2017). Hence, the degree to which  
455 either a patch- or landscape-centric worldview is most pertinent in fragmentation ecology  
456 studies should be determined by the species vagility within the local landscape, which is  
457 largely a combination of matrix permeability (a landscape attribute) and dispersal ability (a  
458 species trait) (Fig. 7). Accordingly, increasing support for IBT should be expected for a  
459 species assemblage with low dispersal ability in patches surrounded by an impermeable  
460 matrix (Fig. 7c; this study; Palmeirim et al., 2017). Conversely, increasing support for HAH  
461 would be expected for a species assemblage in which high dispersal ability is prevalent and  
462 habitat patches are surrounded by a permeable matrix (Fig. 7b; Melo et al., 2017). Under  
463 intermediate scenarios (Fig. 7a and 7d), the most appropriate theoretical framework – IBT or  
464 HAH – would depend on the relative contributions of matrix permeability and species  
465 dispersal ability. For instance, support for HAH would be expected if species successfully  
466 move among patches even if they are surrounded by an impermeable matrix (Fig. 7a; Storck-  
467 Tonon & Peres, 2017), whereas support for IBT would be expected if species fail to move  
468 among patches even if they are surrounded by a relatively permeable matrix (Fig. 7d;  
469 Munguía-Rosas & Montiel, 2014).

470 A recent empirical study testing the HAH (MacDonald et al., 2018) provides further  
471 support for our conceptual framework. Accordingly, the inclusion of highly mobile species in  
472 the species pool led to stronger support for HAH in explaining the number of butterfly  
473 species on islands within a natural archipelagic landscape (Fig. 7a), whereas excluding highly  
474 mobile species led to stronger support for IBT (Fig. 7c). Our conceptual framework also  
475 accounts for dynamic matrix habitats that change over time. As such, for a given forest  
476 landscape dominated by a regenerating vegetation matrix that accumulates aboveground  
477 phytomass, a patch-centric approach should be gradually replaced by a landscape-centric  
478 approach as the matrix becomes more permeable, ultimately enhancing species vagility of  
479 even the most sedentary species (Powell et al., 2013). The Biological Dynamics of Forest  
480 Fragments Project (BDFFP) in central Brazilian Amazonia is an iconic example of a dynamic  
481 tropical landscape, in which a cattle pasture matrix surrounding primary forest fragments has  
482 been fully replaced by an ageing secondary forest over the past *ca.* 35 years (Stouffer et al.,  
483 2011). As the structural contrast between forest fragments and their adjacent matrix  
484 decreases, forest species can resume movements between forest fragments (Stouffer et al.,  
485 2011), exploit newly available matrix resources (Blake & Loiselle, 2001), and incorporate  
486 matrix habitats into their territories (Stouffer et al., 2006). In such situation, a dichotomous

487 classification of the landscape into either habitat or non-habitat is at best misleading (Stouffer  
488 et al., 2006), and a landscape-centric approach would be most appropriate.

489 At the Balbina forest archipelago, the structural contrast between habitat patches  
490 (forest islands) and the matrix (open-water) could not be greater, and is aggravated by the fact  
491 that matrix recovery, by definition, cannot occur within hydroelectric reservoirs with stable  
492 water levels. Such harsh landscape scenario restricts populations of species with low  
493 dispersal ability to fewer islands compared to species that can traverse the matrix. Indeed, the  
494 inherent swimming capacity – a measure of dispersal ability on open-water – of large  
495 vertebrate species at the Balbina forest archipelago is positively related to species island  
496 occupancy (Benchimol & Peres, 2015b). Based on both patch- and landscape-scale  
497 predictors, that study also found island size to be the single best predictor of island occupancy  
498 for most species. Likewise, island size was a powerful predictor of species richness of  
499 terrestrial and arboreal vertebrates ( $r^2 = 0.910$ , Benchimol & Peres, 2015c), birds ( $r^2 = 0.808$ ,  
500 Aurélio-Silva et al., 2016), lizards ( $r^2 = 0.870$ , Palmeirim et al., 2017) and frogs ( $r^2 = 0.891$ ,  
501 Lima et al., 2015) within Amazonian forest archipelagos. Given this bulk of evidence  
502 showing a strong island size effect on species richness, a patch-centric approach (IBT) is  
503 likely to be the most appropriate in true archipelagic landscapes. Nevertheless, species with  
504 high dispersal ability (e.g. orchid bees, Storck-Tonon & Peres, 2017; butterflies, MacDonald  
505 et al., 2018) may still be able to cross hostile expanses of water, which would justify a  
506 landscape-centric approach (HAH).

507

## 508 CONCLUSIONS

509

510 We tested the habitat amount hypothesis (HAH) under one extreme of the continuum of  
511 matrix permeability and species dispersal ability (Fig. 7c) and found stronger support for the  
512 island biogeography theory (IBT). Meanwhile, we hypothesise that stronger support for HAH  
513 is expected under the opposite extreme of this continuum (Fig. 7b), and to either IBT or HAH  
514 under intermediate scenarios (Fig. 7a and 7d). This notion implies that most species  
515 responses to habitat fragmentation lie somewhere along these extremes. Hence, IBT and  
516 HAH should not be seen as a mutually exclusive dichotomy, but instead a continuum in  
517 explaining patterns of species retention in habitat patches. The conceptual framework we  
518 propose (Fig. 7) also considers fragmented landscapes with dynamic (e.g. vegetation  
519 regrowth following land abandonment) or managed matrices (e.g. restored habitats following  
520 human intervention). In such landscapes, patch-centric patterns of occupancy (IBT) should  
521 gradually transition into those dominated by entire landscapes (HAH) given the role of matrix  
522 type in mediating species-area relationships (Freeman et al., 2018). Conversely, matrix



523 habitat degradation would revert the emphasis back to prime habitat patches. Although  
524 ameliorating the harshness of water matrices is virtually impossible, other hostile matrix  
525 habitats, such as bauxite mining (Kennedy & Marra, 2010), can be managed to enhance  
526 functional connectivity among habitat patches (Fig. 7 in Villard & Metzger, 2014). Finally,  
527 we conclude that the most appropriate worldview in fragmentation ecology (IBT or HAH) is  
528 not only context-dependent but also dynamic. Therefore, the best conservation strategy –  
529 focusing on either the spatial arrangement of remaining habitat patches or the overall habitat  
530 amount in the landscape – is neither static nor can be generalised to a wide spectrum of  
531 landscape scenarios and taxonomic groups.

532

533 **FIGURE LEGENDS**

534 Figure 1. (a) Location of the study area in central Brazilian Amazonia, indicated by a solid  
535 rectangle containing (b) the Balbina Hydroelectric Reservoir (BHR) landscape, showing the  
536 boundaries of the Uatumã Biological Reserve, a strictly-protected area safeguarding most of  
537 this landscape; (c) larger inset map showing the spatial distribution of the 33 surveyed  
538 islands; and (d) the 200-m buffer area (red polygon) around a mist-net line (white line)  
539 representing the local landscapes derived for the understory insectivorous birds examined  
540 here. Photo credit: Eduardo M. Venticinque.

541

542 Figure 2. Possible conceptual relationships of the four empirical tests applied to determine  
543 whether either the island biogeography theory (IBT; graphs on the left) or the habitat amount  
544 hypothesis (HAH; graphs on the right) is the most appropriate theoretical framework to  
545 explain the number of understory insectivorous bird species on forest islands within the  
546 Balbina Hydroelectric Reservoir in central Brazilian Amazonia.

547

548 Figure 3. Divergent species-area relationships for understory insectivorous birds surveyed at  
549 33 islands surrounded by either low ( $r^2 = 0.598, p < 0.001, n = 15$ ) or high ( $r^2 = 0.547, p <$   
550  $0.001, n = 18$ ) habitat amounts. Circle sizes scale to the landscape-scale habitat amount, with  
551 smaller and larger circles representing islands surrounded by either low or high habitat  
552 amounts, respectively. Note the different  $z$ -values for these two landscape scenarios ( $p =$   
553  $0.009$ ) and the base 10 logarithmic scales along both axes.

554

555 Figure 4. Species accumulation curves of understory insectivorous birds for islands ordered  
556 according to either increasing (light grey circles, dashed line) or decreasing (dark grey  
557 circles, solid line) island size.

558

559 Figure 5. Species-area relationship for understory insectivorous birds surveyed at 33 islands.  
560 The white circle shows the extrapolated number of species (55.2) to a hypothetical island  
561 containing the area (+ 1) of all 33 surveyed islands combined (7,841.4 ha), whereas the black  
562 circle shows the total number of species observed in this study (59 + 1). Dashed lines show  
563 the 95% confidence intervals of the predicted line. Note the base 10 logarithmic scales along  
564 both axes.

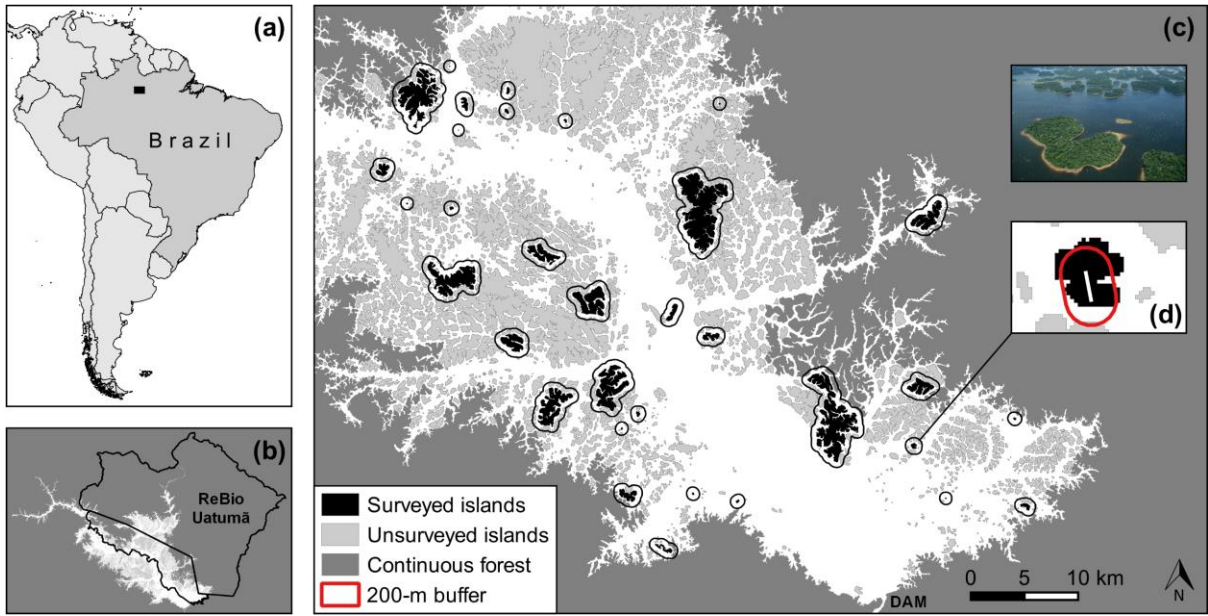
565

566 Figure 6. Sampling design established to control for the positive correlation between patch  
567 size and habitat amount. The solid black circle corresponds to the local landscape defined  
568 *a priori* (i.e. before the scale of effect is known). The dashed black circle corresponds to the  
569 local landscape derived from a multi-scale analysis (i.e. post data analysis). The difference  
570 between the two landscapes scales (solid and dashed black circles) implies that even a well-  
571 designed study may fail to control for the collinearity between predictors. Figure modified  
572 from Fahrig (2013).

573

574 Figure 7. Conceptual framework based on both the degree of matrix permeability and species  
575 dispersal ability in determining whether the island biogeography theory (IBT) or the habitat  
576 amount hypothesis (HAH) is the most appropriate guiding theoretical framework for  
577 biodiversity studies in fragmented landscapes.

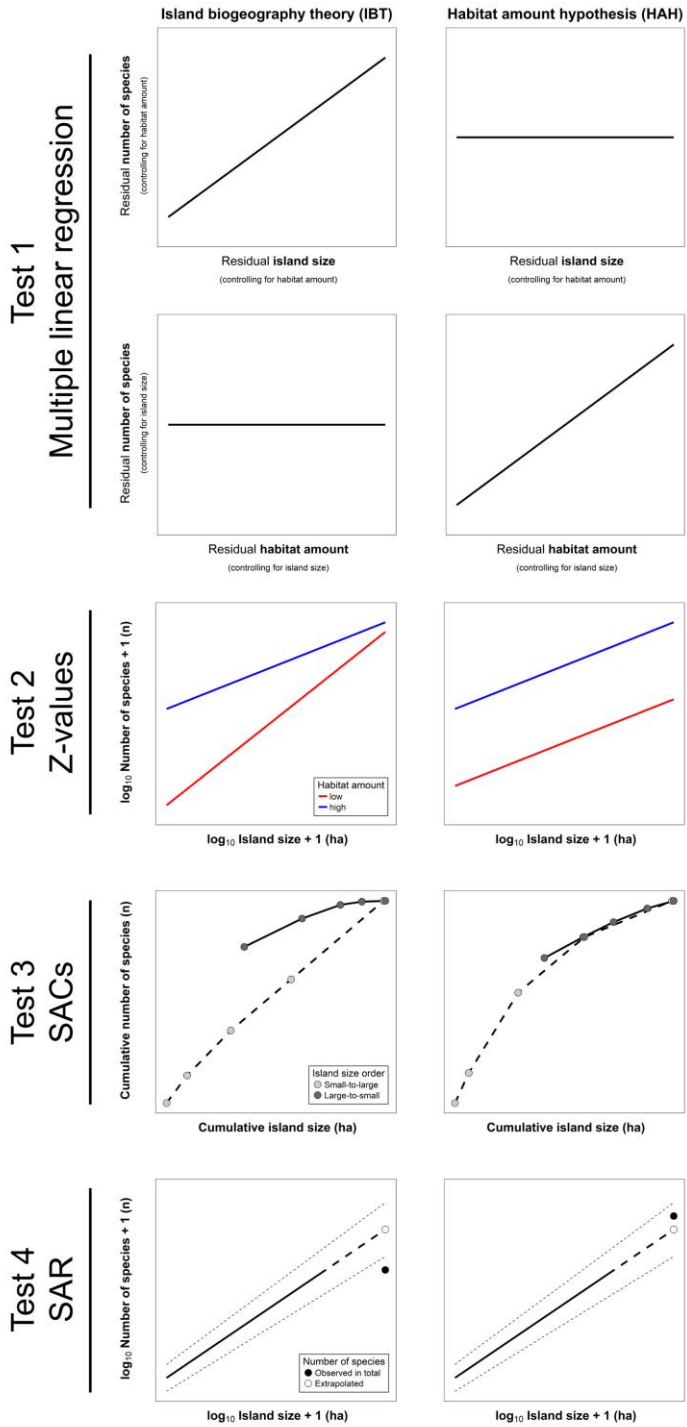
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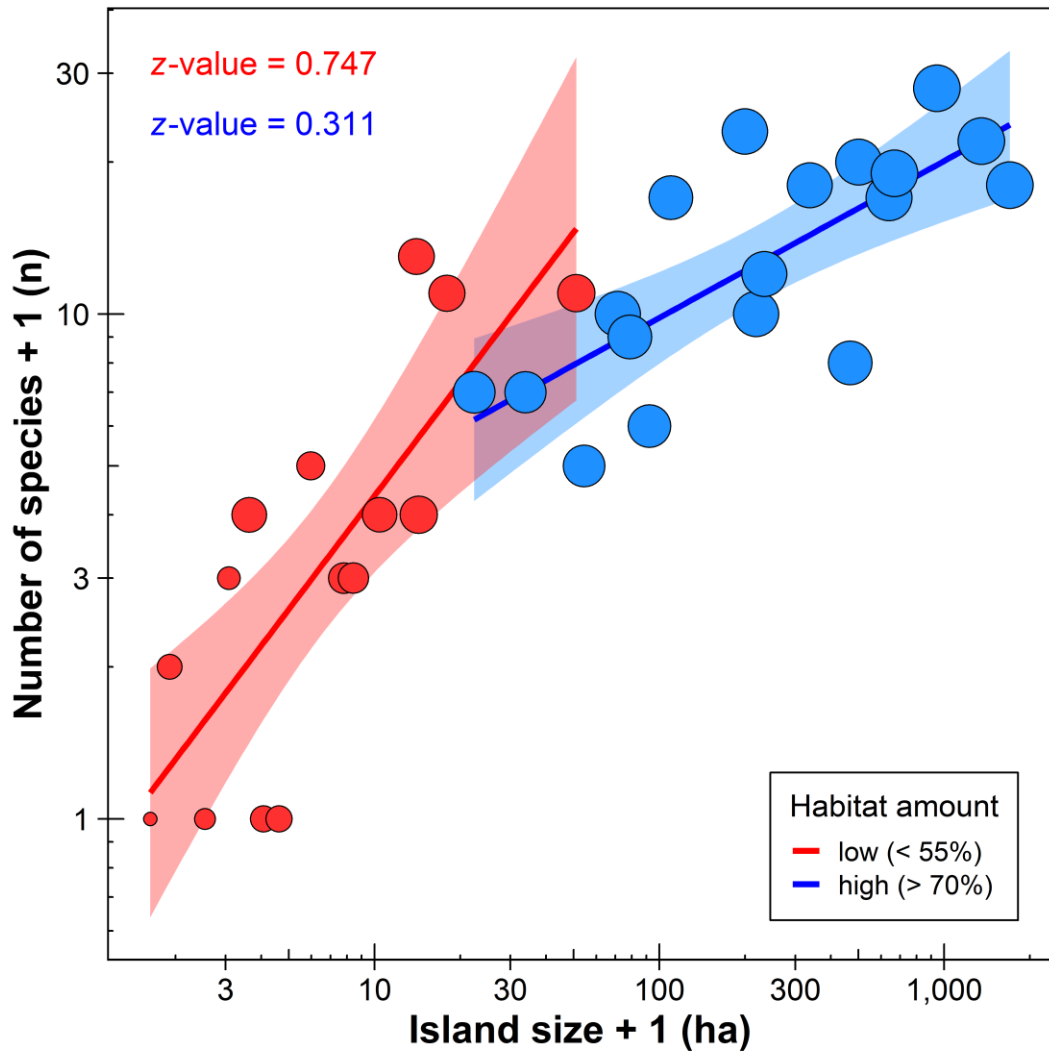
580 Figure 1

581



582

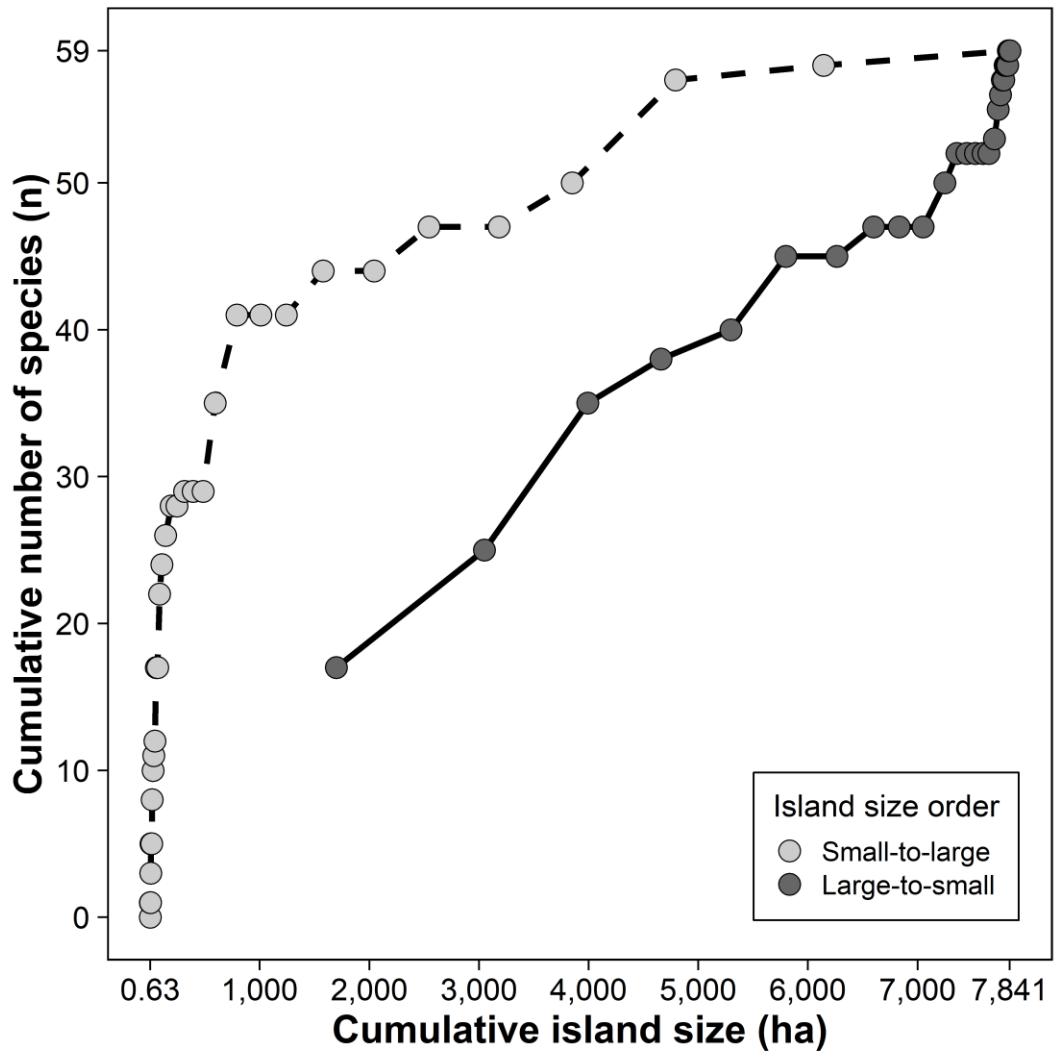
583 Figure 2



584

585 Figure 3

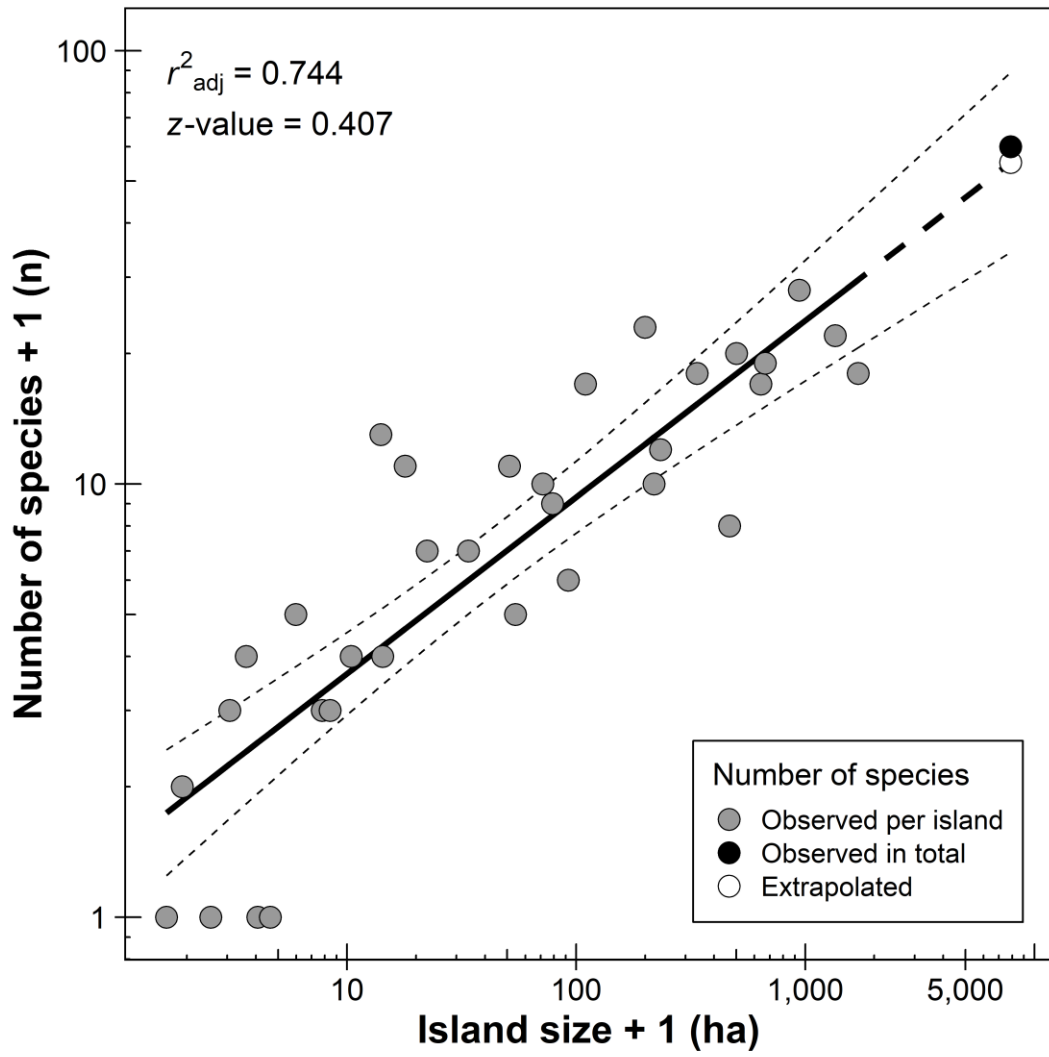
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588 Figure 4

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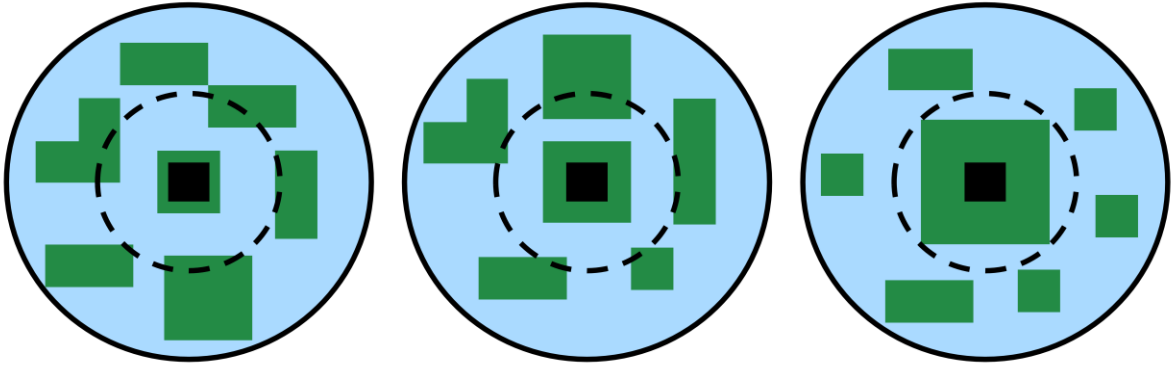


590

591 Figure 5

592

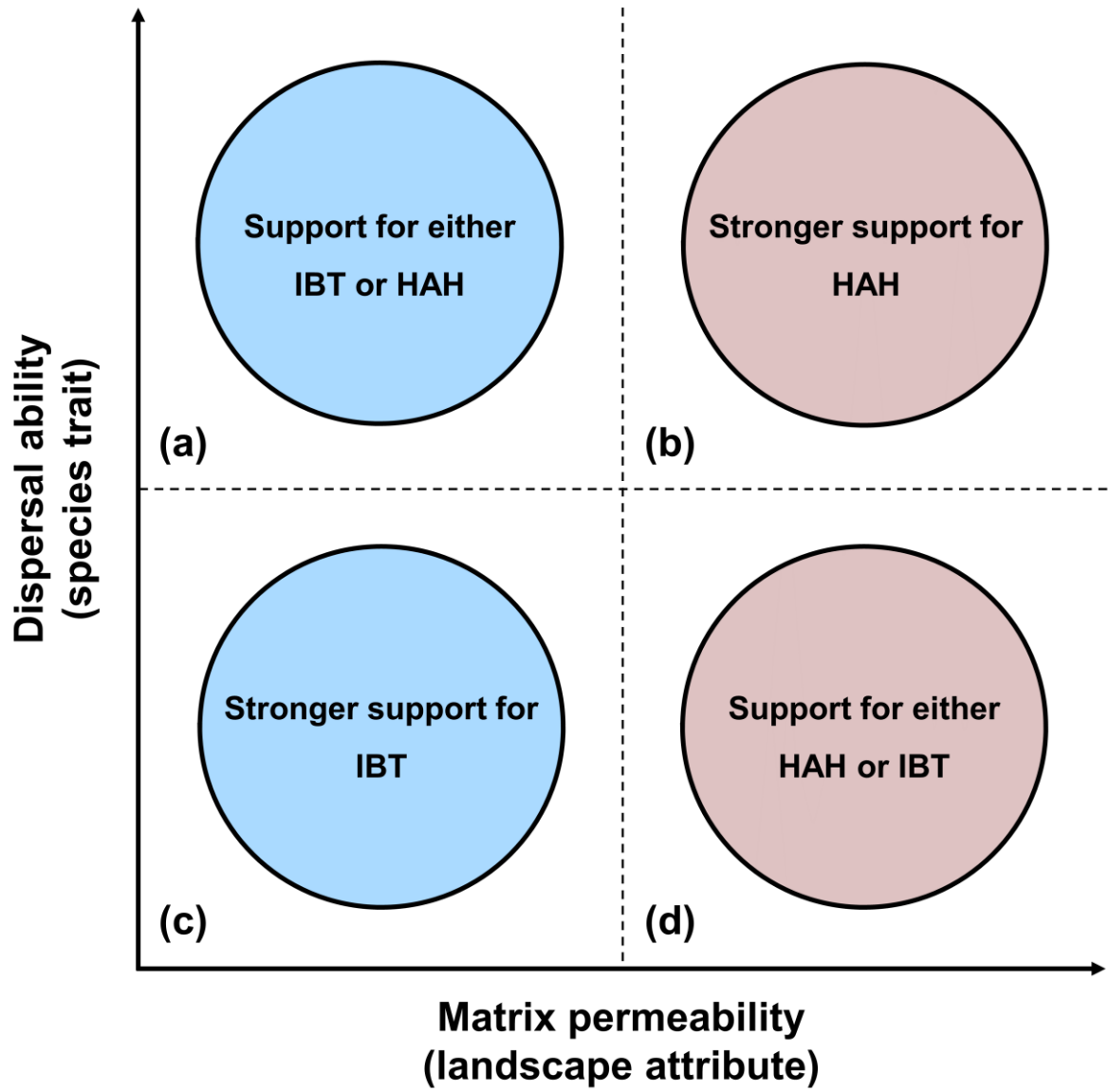




593

594 Figure 6

595



596

597 Figure 7

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