

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

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

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17 **ACKNOWLEDGEMENTS**

18 We are very grateful to Evanir Damasceno, Tatiane Abreu, Ivana Cardoso and Carla
19 Fonseca for their invaluable field assistance. We also thank Alexander Lees for helping with
20 bird identification, the staff at Reserva Biológica do Uatumã for logistical support, CEMAVE
21 for supplying bird rings, and Lenore Fahrig and the anonymous referees for their valuable
22 comments on the manuscript. This study was funded by the Rufford Foundation (grant
23 17715-1), Reserva Biológica do Uatumã (ICMBio), University of East Anglia, and a
24 NERC/UK grant (NE/J01401X/1) awarded to CAP. ASB is funded by a PhD studentship
25 (grant 200463/2014-4) from Conselho Nacional de Desenvolvimento Científico e
26 Tecnológico (CNPq) – Brazil.

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 understorey insectivorous bird species on forest islands
117 induced by a large hydroelectric dam in central Brazilian Amazonia. We focused on
118 understorey 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 understorey 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 understorey 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 understorey mist nets
174 primarily capture understorey 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 understorey 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 understorey 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 understorey 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 ± 23.4), and the
266 number of species from 0 to 27 (8.8 ± 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.

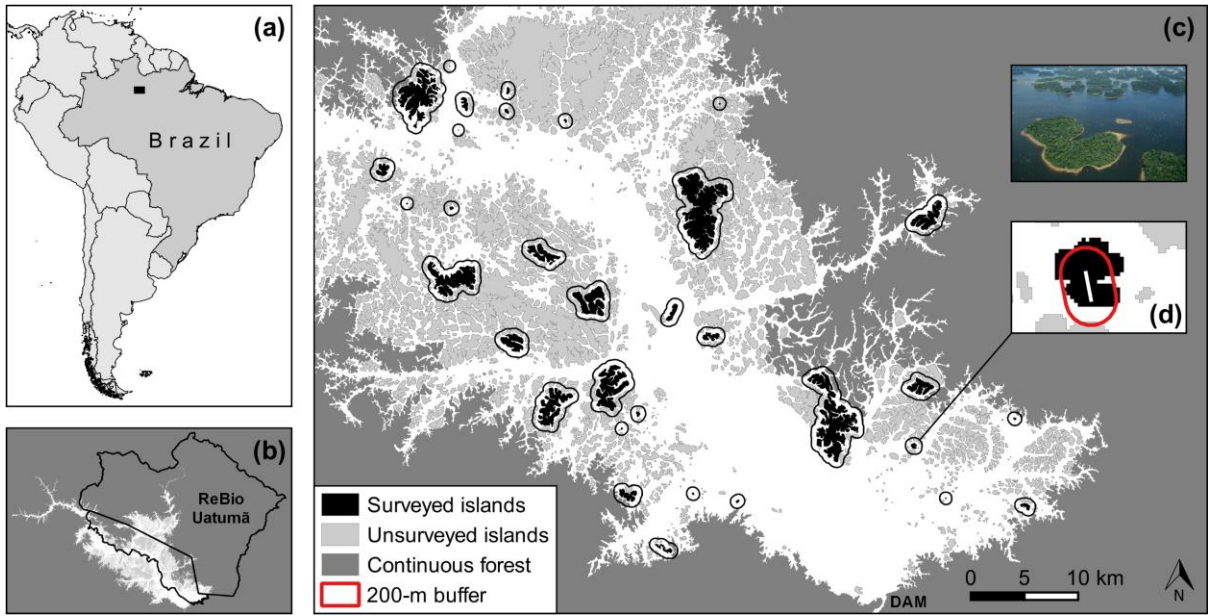
565

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.

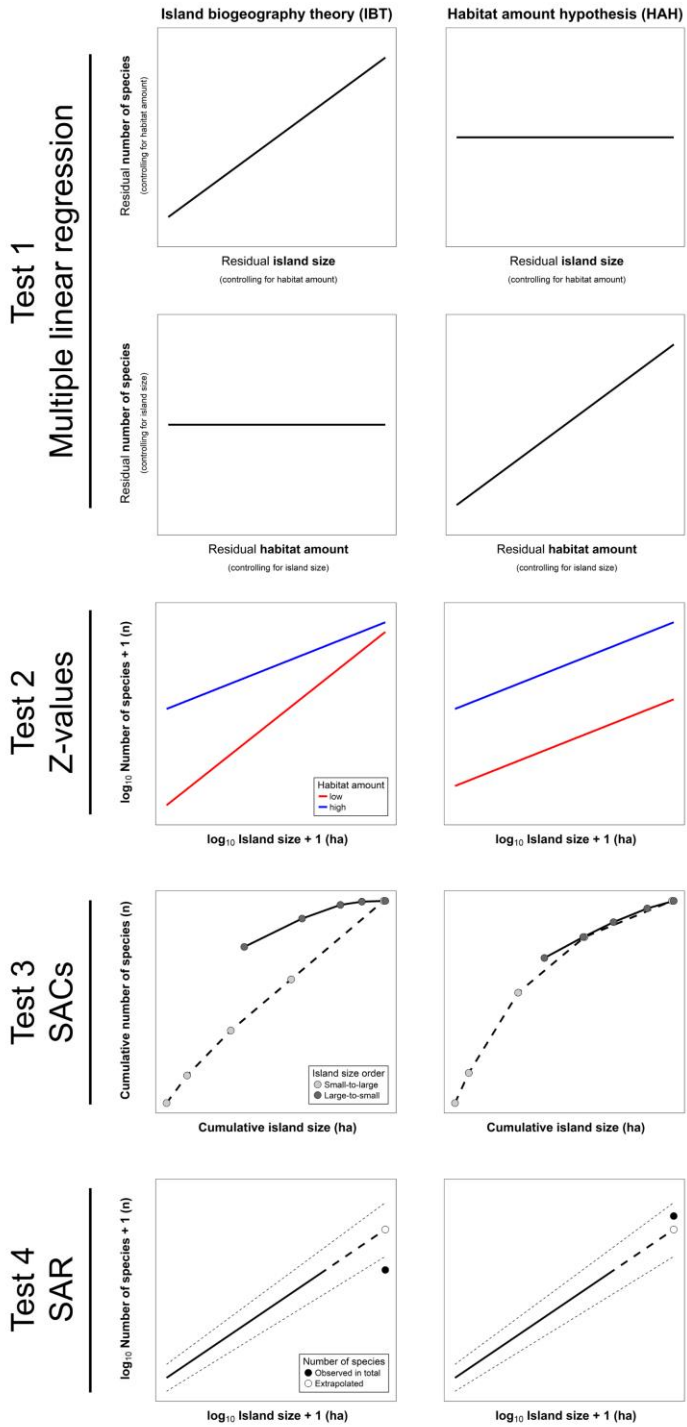
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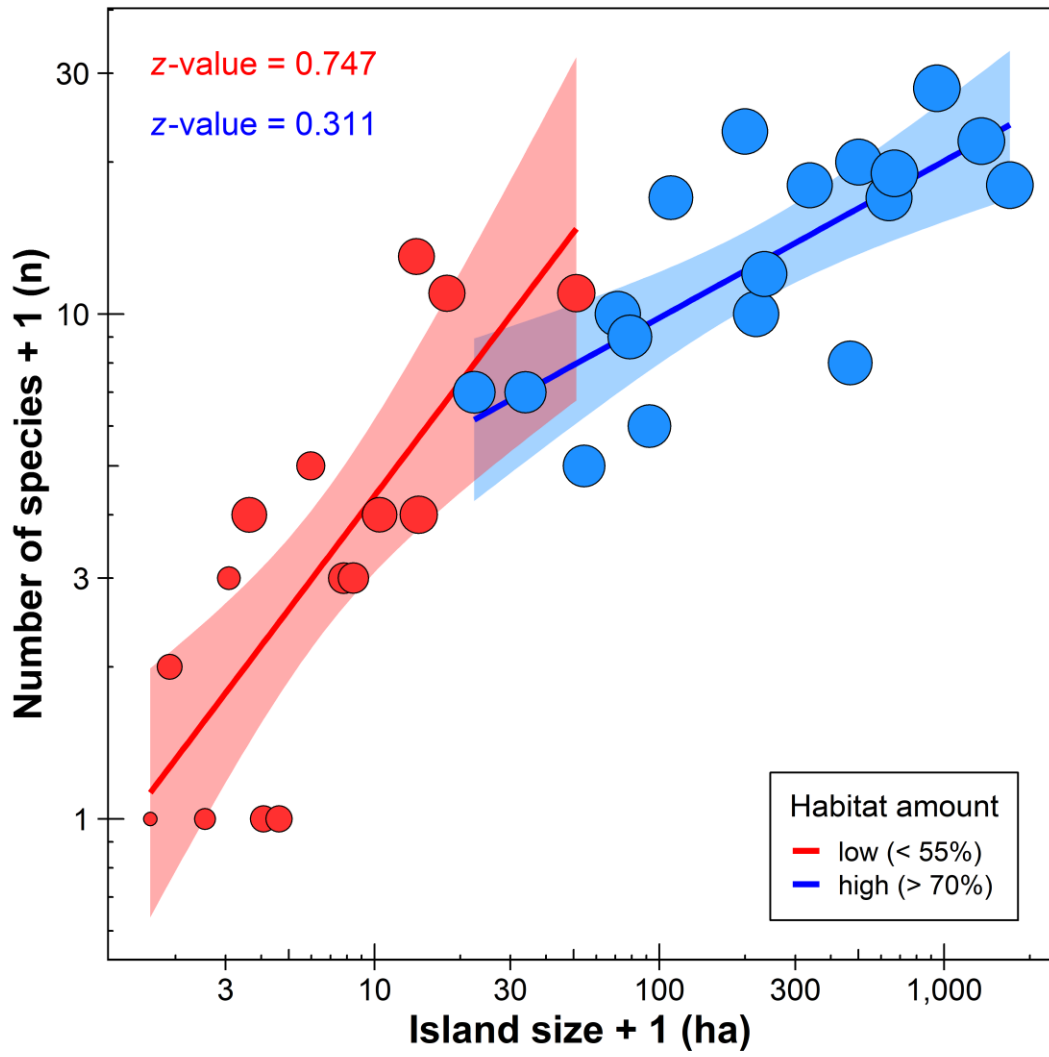
580 Figure 1

581



582

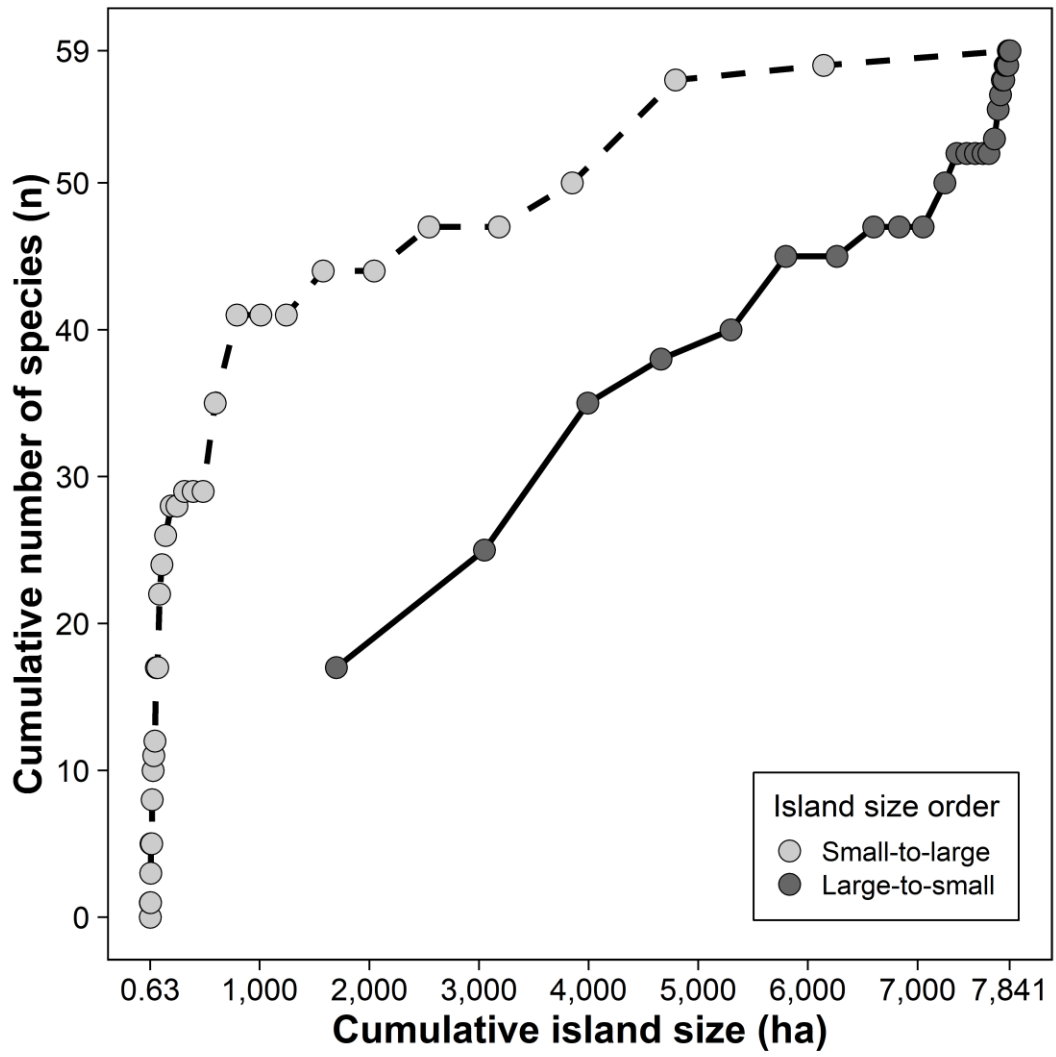
583 Figure 2

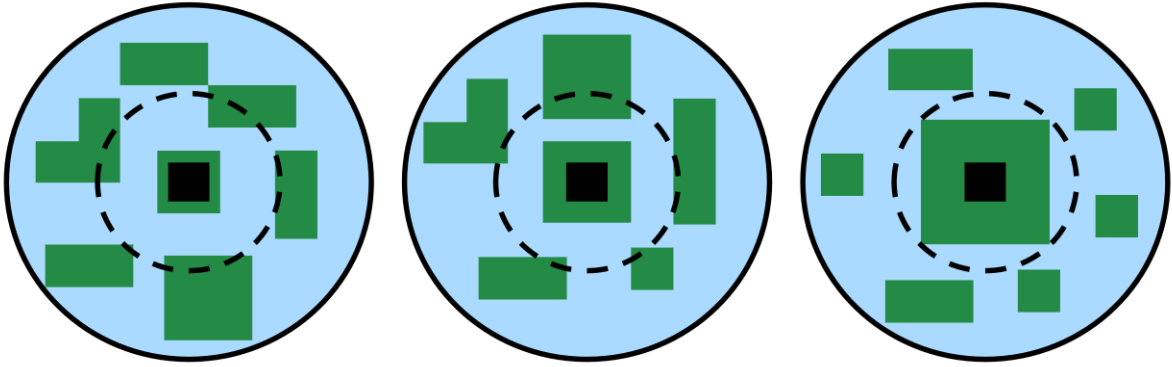


584

585 Figure 3

586

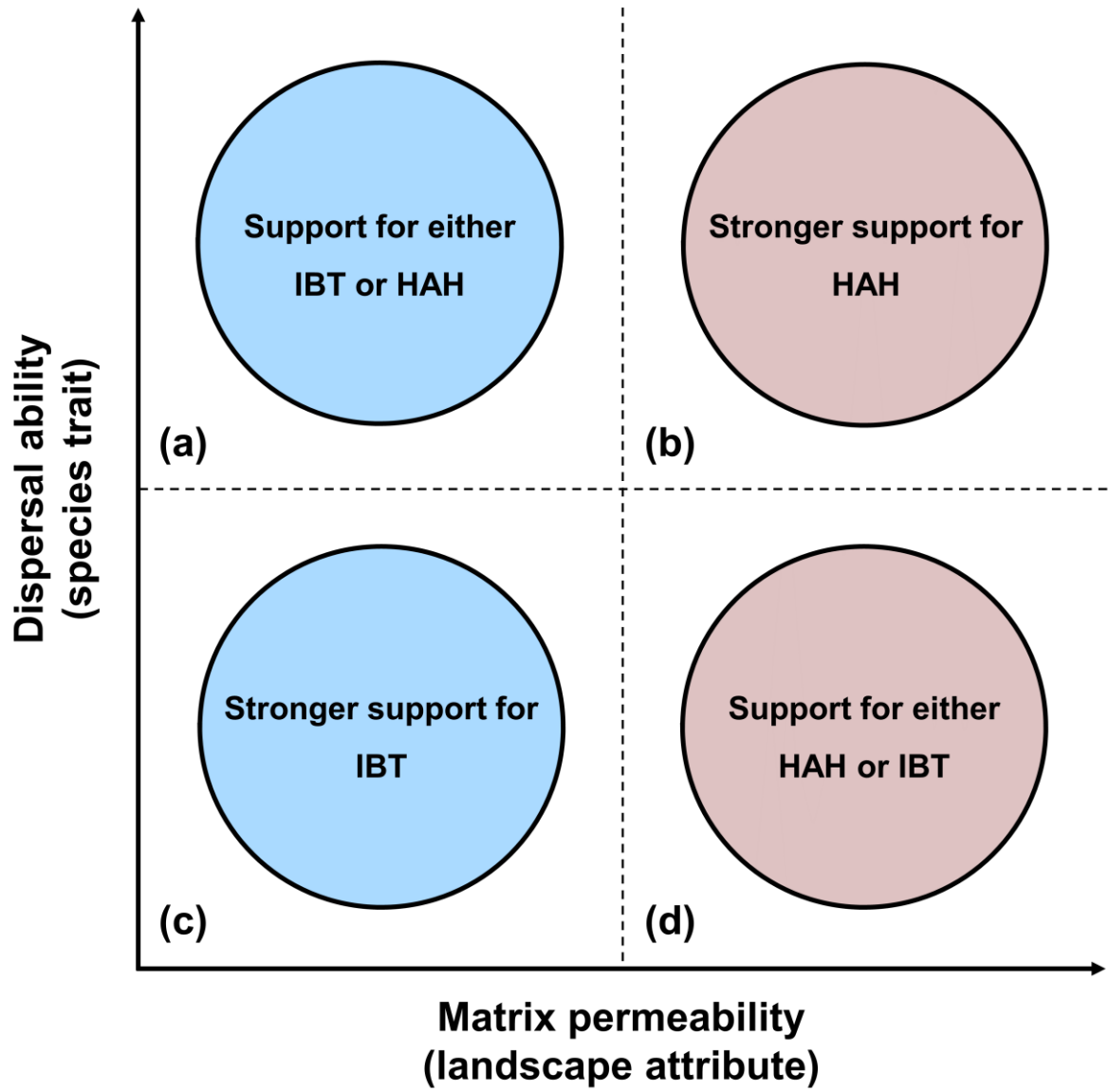




593

594 Figure 6

595



596

597 Figure 7

598 **REFERENCES**

- 599 Alvares, C.A., Stape, J.L., Sentelhas, P.C., Gonçalves, J.L. de M., & Sparovek, G. (2013)
600 Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, **22**, 711–
601 728.
- 602 Aurélio-Silva, M., Anciães, M., Henriques, L.M.P., Benchimol, M., & Peres, C.A. (2016)
603 Patterns of local extinction in an Amazonian archipelagic avifauna following 25 years of
604 insularization. *Biological Conservation*, **199**, 101–109.
- 605 Awade, M. & Metzger, J.P. (2008) Using gap-crossing capacity to evaluate functional
606 connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral*
607 *Ecology*, **33**, 863–871.
- 608 Báldi, A. (2008) Habitat heterogeneity overrides the species–area relationship. *Journal of*
609 *Biogeography*, **35**, 675–681.
- 610 Benchimol, M. & Peres, C.A. (2015a) Edge-mediated compositional and functional decay of
611 tree assemblages in Amazonian forest islands after 26 years of isolation. *Journal of*
612 *Ecology*, **103**, 408–420.
- 613 Benchimol, M. & Peres, C.A. (2015b) Predicting local extinctions of Amazonian vertebrates
614 in forest islands created by a mega dam. *Biological Conservation*, **187**, 61–72.
- 615 Benchimol, M. & Peres, C.A. (2015c) Widespread forest vertebrate extinctions induced by a
616 mega hydroelectric dam in lowland Amazonia. *PLOS ONE*, **10**, e0129818.
- 617 BirdLife International (2018) IUCN Red List for birds. *Downloaded from*
618 *http://www.birdlife.org in April 2018.*
- 619 Blake, J.G. & Loiselle, B.A. (2001) Bird assemblages in second-growth and old-growth
620 forests, Costa Rica: Perspectives from mist nets and point counts. *The Auk*, **118**, 304–
621 326.
- 622 Castilho, C.V. de, Magnusson, W.E., de Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Lima,
623 A.P., & Higuchi, N. (2006) Variation in aboveground tree live biomass in a central
624 Amazonian forest: Effects of soil and topography. *Forest Ecology and Management*,
625 **234**, 85–96.
- 626 Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G.,
627 Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E.,
628 Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., & Lautenbach, S. (2013)
629 Collinearity: a review of methods to deal with it and a simulation study evaluating their
630 performance. *Ecography*, **36**, 27–46.
- 631 Drucker, D.P., Costa, F.R.C., & Magnusson, W.E. (2008) How wide is the riparian zone of
632 small streams in tropical forests? A test with terrestrial herbs. *Journal of Tropical*
633 *Ecology*, **24**, 65–74.
- 634 Evju, M. & Sverdrup-Thygeson, A. (2016) Spatial configuration matters: a test of the habitat
635 amount hypothesis for plants in calcareous grasslands. *Landscape Ecology*, **31**, 1891–
636 1902.
- 637 Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology,*
638 *Evolution, and Systematics*, **34**, 487–515.

- 639 Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis.
640 *Journal of Biogeography*, **40**, 1649–1663.
- 641 Fahrig, L. (2015) Just a hypothesis: A reply to Hanski. *Journal of Biogeography*, **42**, 993–
642 994.
- 643 Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of*
644 *Ecology, Evolution, and Systematics*, **48**, 1–23.
- 645 Fearnside, P.M. (2016) Environmental and Social Impacts of Hydroelectric Dams in
646 Brazilian Amazonia: Implications for the Aluminum Industry. *World Development*, **77**,
647 48–65.
- 648 Freeman, M.T., Olivier, P.I., & van Aarde, R.J. (2018) Matrix transformation alters species-
649 area relationships in fragmented coastal forests. *Landscape Ecology*, **33**, 307–322.
- 650 Gavish, Y., Ziv, Y., & Rosenzweig, M.L. (2012) Decoupling fragmentation from habitat loss
651 for spiders in patchy agricultural landscapes. *Conservation Biology*, **26**, 150–159.
- 652 Haddad, N.M., Gonzalez, A., Brudvig, L. a., Burt, M. a., Levey, D.J., & Damschen, E.I.
653 (2016) Experimental evidence does not support the Habitat Amount Hypothesis.
654 *Ecography*, **125**, 336–342.
- 655 Haila, Y. (2002) A conceptual genealogy of fragmentation research: From island
656 biogeography to landscape ecology. *Ecological Applications*, **12**, 321–334.
- 657 Hanski, I. (2015) Habitat fragmentation and species richness. *Journal of Biogeography*, **42**,
658 989–993.
- 659 Jackson, H.B. & Fahrig, L. (2012) What size is a biologically relevant landscape? *Landscape*
660 *Ecology*, **27**, 929–941.
- 661 Jackson, H.B. & Fahrig, L. (2015) Are ecologists conducting research at the optimal scale?
662 *Global Ecology and Biogeography*, **24**, 52–63.
- 663 Jung, M. (2016) LecoS – A python plugin for automated landscape ecology analysis.
664 *Ecological Informatics*, **31**, 18–21.
- 665 Karr, J.R. (1981) Surveying birds in the tropics. *Studies in Avian Biology*, **6**, 548–553.
- 666 Kennedy, C.M. & Marra, P.P. (2010) Matrix mediates avian movements in tropical forested
667 landscapes: Inference from experimental translocations. *Biological Conservation*, **143**,
668 2136–2145.
- 669 Laurance, S.G.W., Stouffer, P.C., & Laurance, W.F. (2004) Effects of road clearings on
670 movement patterns of understory rainforest birds in central Amazonia. *Conservation*
671 *Biology*, **18**, 1099–1109.
- 672 Laurance, W.F. (2008) Theory meets reality: How habitat fragmentation research has
673 transcended island biogeographic theory. *Biological Conservation*, **141**, 1731–1744.
- 674 Lees, A.C. & Peres, C.A. (2009) Gap-crossing movements predict species occupancy in
675 Amazonian forest fragments. *Oikos*, **118**, 280–290.
- 676 Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. Elsevier Science, Amsterdam, The
677 Netherlands.
- 678 Lima, J.R., Galatti, U., Lima, C.J., Fáveri, S.B., Vasconcelos, H.L., & Neckel-Oliveira, S.

- 679 (2015) Amphibians on Amazonian land-bridge islands are affected more by area than
680 isolation. *Biotropica*, **47**, 369–376.
- 681 Lomolino & Weiser (2001) Towards a more general species-area relationship: diversity on all
682 islands, great and small. *Journal of Biogeography*, **28**, 431–445.
- 683 Lovei, G.L., Magura, T., Tothmeresz, B., & Kodobocz, V. (2006) The influence of matrix
684 and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in
685 habitat islands. *Global Ecology and Biogeography*, **15**, 283–289.
- 686 MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton
687 University Press, Princeton, New Jersey, USA.
- 688 MacDonald, Z.G., Anderson, I.D., Acorn, J.H., & Nielsen, S.E. (2018) Decoupling habitat
689 fragmentation from habitat loss: butterfly species mobility obscures fragmentation
690 effects in a naturally fragmented landscape of lake islands. *Oecologia*, **186**, 11–27.
- 691 Matthews, T.J., Guilhaumon, F., Triantis, K.A., Borregaard, M.K., & Whittaker, R.J. (2016)
692 On the form of species-area relationships in habitat islands and true islands. *Global
693 Ecology and Biogeography*, **25**, 847–858.
- 694 Melo, G.L., Sponchiado, J., Cáceres, N.C., & Fahrig, L. (2017) Testing the habitat amount
695 hypothesis for South American small mammals. *Biological Conservation*, **209**, 304–314.
- 696 Moore, R.P., Robinson, W.D., Lovette, I.J., & Robinson, T.R. (2008) Experimental evidence
697 for extreme dispersal limitation in tropical forest birds. *Ecology Letters*, **11**, 960–968.
- 698 Morante-Filho, J.C., Faria, D., Mariano-Neto, E., & Rhodes, J. (2015) Birds in anthropogenic
699 landscapes: The responses of ecological groups to forest loss in the Brazilian Atlantic
700 Forest. *PLOS ONE*, **10**, e0128923.
- 701 Munguía-Rosas, M.A. & Montiel, S. (2014) Patch size and isolation predict plant species
702 density in a naturally fragmented forest. *PLOS ONE*, **9**, e111742.
- 703 Palmeirim, A.F., Vieira, M.V., & Peres, C. A. (2017) Non-random lizard extinctions in land-
704 bridge Amazonian forest islands after 28 years of isolation. *Biological Conservation*,
705 **214**, 55–65.
- 706 Powell, L.L., Cordeiro, N.J., & Stratford, J. A. (2015) Ecology and conservation of avian
707 insectivores of the rainforest understory: A pantropical perspective. *Biological
708 Conservation*, **188**, 1–10.
- 709 Powell, L.L., Stouffer, P.C., & Johnson, E.I. (2013) Recovery of understory bird movement
710 across the interface of primary and secondary Amazon rainforest. *The Auk*, **130**, 459–
711 468.
- 712 Prevedello, J.A. & Vieira, M.V. (2010) Does the type of matrix matter? A quantitative review
713 of the evidence. *Biodiversity and Conservation*, **19**, 1205–1223.
- 714 Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., & Brashares, J.S. (2008) Effect of habitat area
715 and isolation on fragmented animal populations. *Proceedings of the National Academy
716 of Sciences*, **105**, 20770–20775.
- 717 QGIS Development Team (2018) QGIS Geographic Information System. Version 2.14.22.
718 Open Source Geospatial Foundation Project. URL <http://qgis.osgeo.org>.
- 719 Quinn, J.F. & Harrison, S.P. (1988) Effects of habitat fragmentation and isolation on species

- 720 richness: evidence from biogeographic patterns. *Oecologia*, **75**, 132–140.
- 721 Rabelo, R.M., Bicca-Marques, J.C., Aragón, S., & Nelson, B.W. (2017) Are fluvial islands
722 “real” islands for arboreal mammals? Uncovering the effect of patch size under the
723 species-area relationship. *Journal of Biogeography*, 1–11.
- 724 Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press,
725 Cambridge, UK.
- 726 Santos, A.M.C., Whittaker, R.J., Triantis, K.A., Borges, P.A. V, Jones, O.R., Quicke, D.L.J.,
727 & Hortal, J. (2010) Are species-area relationships from entire archipelagos congruent
728 with those of their constituent islands? *Global Ecology and Biogeography*, **19**, 527–540.
- 729 Scheiner, S.M. (2003) Six types of species-area curves. *Global Ecology and Biogeography*,
730 **12**, 441–447.
- 731 Schiatti, J., Emilio, T., Rennó, C.D., Drucker, D.P., Costa, F.R.C., Nogueira, A., Baccaro,
732 F.B., Figueiredo, F., Castilho, C. V., Kinupp, V., Guillaumet, J.-L., Garcia, A.R.M.,
733 Lima, A.P., & Magnusson, W.E. (2014) Vertical distance from drainage drives floristic
734 composition changes in an Amazonian rainforest. *Plant Ecology & Diversity*, **7**, 241–
735 253.
- 736 Seibold, S., Bässler, C., Brandl, R., Fahrig, L., Förster, B., Heurich, M., Hothorn, T., Scheipl,
737 F., Thorn, S., & Müller, J. (2017) An experimental test of the habitat-amount hypothesis
738 for saproxylic beetles in a forested region. *Ecology*, **98**, 1613–1622.
- 739 Sekercioglu, C.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., & Sandi, R.F. (2002)
740 Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the*
741 *National Academy of Sciences*, **99**, 263–267.
- 742 Storck-Tonon, D. & Peres, C. A. (2017) Forest patch isolation drives local extinctions of
743 Amazonian orchid bees in a 26 years old archipelago. *Biological Conservation*, **214**,
744 270–277.
- 745 Stouffer, P.C., Bierregaard, R.O., Strong, C., & Lovejoy, T.E. (2006) Long-term landscape
746 change and bird abundance in Amazonian rainforest fragments. *Conservation Biology*,
747 **20**, 1212–1223.
- 748 Stouffer, P.C., Johnson, E.I., Bierregaard, R.O., & Lovejoy, T.E. (2011) Understory bird
749 communities in Amazonian rainforest fragments: Species turnover through 25 years
750 post-isolation in recovering landscapes. *PLOS ONE*, **6**, e20543.
- 751 Torrenta, R. & Villard, M.-A. (2017) A test of the habitat amount hypothesis as an
752 explanation for the species richness of forest bird assemblages. *Journal of*
753 *Biogeography*, **44**, 1791–1801.
- 754 Villard, M.-A. & Metzger, J.P. (2014) Beyond the fragmentation debate: a conceptual model
755 to predict when habitat configuration really matters. *Journal of Applied Ecology*, **51**,
756 309–318.
- 757 Walter, S.T., Browne, L., Freile, J., Olivo, J., González, M., & Karubian, J. (2017)
758 Landscape-level tree cover predicts species richness of large-bodied frugivorous birds in
759 forest fragments. *Biotropica*, **49**, 838–847.
- 760 Wiens, J.A. (2008) Habitat fragmentation: Island v landscape perspectives on bird
761 conservation. *Ibis*, **137**, S97–S104.

762 Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., & Jetz, W. (2014)
763 EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals.
764 *Ecology*, **95**, 2027–2027.

765 Yaacobi, G., Ziv, Y., & Rosenzweig, M.L. (2007) Habitat fragmentation may not matter to
766 species diversity. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2409–
767 2412.

768

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774 extinction risk in experimental island landscapes.

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