Design matters: an evaluation of the impact of small man-made forest clearings on tropical bats using a before-after-control-impact design

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ABSTRACT

In recent years, large clearings (> 1,000 ha) accounted for gradually smaller amounts of

total annual deforestation in the Brazilian Amazon, whereas the proportion of small

clearings (< 50 ha) nowadays represents more than 80% of annual deforestation.

Despite the ubiquity of small clearings in fragmented Amazonian landscapes, most

fragmentation research has focused on the effects of large-scale deforestation, leading to

a poor understanding of the impacts of smaller barriers on Amazonian vertebrates. We

capitalized on the periodical re-isolation of experimental forest fragments at the

Biological Dynamics of Forest Fragments Project in the Central Amazon as a before-

after-control-impact experiment to investigate the short-term effects of small clearings

on bat assemblages. Over the course of three years we sampled six control sites in

continuous forest, the interiors and edges of eight forest fragments as well as eight sites

in the surrounding matrix. Sampling took place both before and after the experimental

manipulation (clearing of a 100 m wide strip of regrowth around each fragment),

resulting in ~4,000 bat captures. Species were classified as old-growth specialists and

habitat generalists according to their habitat affinities and a joint species distribution

modeling framework was used to investigate the effect of fragment re-isolation on

species occupancy. Following fragment re-isolation, species richness declined in all

habitats other than fragment edges and, although responses were idiosyncratic, this

decline was more pronounced for forest specialist than for generalist species.

Additionally, fragment re-isolation led to a reduction in the similarity between

assemblages in modified habitats (fragment interiors, edges and matrix) and continuous

forest. Sampling of controls in continuous forest both prior to and after re-isolation

revealed that much of the variation in bat species occupancy between sampling periods

did not arise from fragment re-isolation but rather reflected natural spatiotemporal

46 variability. This emphasizes the need to sample experimental controls both before and

47 after experimental manipulation and suggests caution in the interpretation of results

48 from studies in which the effects of habitat transformations are assessed based solely on

49 data collected using space-for-time substitution approaches.

50

51 *Keywords***:** Amazon, BACI, Bayesian inference, fragmentation, hierarchical modeling,

52 joint species distribution modeling.

53

54 **Introduction**

55 Human reshaping of natural ecosystems has unleashed one of the greatest biodiversity

56 crises the planet has ever faced (Ceballos et al., 2015). Habitat loss and fragmentation

57 are among the primary causes of this global demise (Haddad et al., 2015) and their

58 impact is especially worrisome in tropical forests, the most diverse and complex

59 terrestrial ecosystems (Bradshaw et al., 2008; Hansen et al., 2013). A better

60 understanding of the patterns and processes associated with the division of continuous

61 forest into smaller and more isolated fragments is thus critical for the implementation of

62 management programs aimed at abating the ongoing biotic homogenization of wildlife

63 assemblages that persist in fragmented human-altered tropical landscapes.

64 With an area of ~5.3 million km^2 the Amazon forest is the dominant biome in the

65 Neotropics and the largest block of rainforest remaining on Earth (Aragão et al., 2014).

66 Around 60% of this area is located within Brazil and although much of it still

67 constitutes mostly undisturbed evergreen rainforest, the expansion of agricultural

68 activities, logging, ground fires and urbanization have reduced forest cover at an

69 average annual rate of 19,500 km^2 between 1996 and 2005 (Nepstad et al., 2009). By

70 2013 this figure was 5,843 km^2, representing a 70% decrease in the rate of deforestation

(Nepstad et al., 2014). Over recent years, large clearings (>1,000 ha) have accounted for gradually lesser extents of total annual deforestation, whereas the proportion of small clearings (6.25–50 ha) has remained unchanged and nowadays represents more than 80% of annual deforestation (Rosa et al., 2012). Despite this prevalence of small clearings in the Brazilian Amazon and elsewhere in the tropics, most research on forest disturbance has focused on large-scale deforestation, leading to a poor understanding of the impacts of smaller barriers on tropical wildlife (Laurance et al., 2009).

Although observational studies have offered valuable insights into the effects of anthropogenic disturbances on tropical species (e.g. Laurance et al., 2004; Avila-Cabadilla et al., 2009; Rocha et al., 2015), they are typically hampered by the absence of rigorous controls, insufficient replication and lack of baseline data (Ramage et al., 2013; Bicknell et al., 2015; Meyer et al., 2016). Whole-ecosystem fragmentation experiments can overcome some of these drawbacks, offering an opportunity to assess the effects of small man-made clearings on fragment assemblages using before-after-control-impact (BACI) sampling, a potent experimental design in which replicates of treatments and controls are surveyed both prior to and after manipulation (Fayle et al., 2015). This allows for stronger inference than studies that depend on a space-for-time substitution approach (Block et al., 2001; França et al., 2016).

The Biological Dynamics of Forest Fragments Project (BDFFP) in the Brazilian Amazon is the world's largest and longest-running experimental study of forest fragmentation (Haddad et al., 2015). Forest fragments at the BDFFP were isolated from continuous forest by distances of 70-1,000 m in the early 1980s. However, due to secondary regrowth, fragment isolation has been maintained ever since by the clearing of a 100 m wide strip of secondary vegetation around each fragment. This re-isolation takes place at intervals of ~10 years (Laurance et al., 2011) (Fig. 1). The areas of

96   secondary forest cleared around the BDFFP forest fragments range from 6.4 to 42 ha

97   and thus accurately mirror current patterns of deforestation in the Brazilian Amazon

98   (Rosa et al., 2012).

99   Bats are the second most diverse mammalian order with over 1,300 recognized species

100 (Fenton and Simmons, 2015). They reach their highest richness in the Neotropics

101 (Altringham, 2011), where they provide key ecological services such as seed dispersal,

102 pollination, and regulation of small vertebrate and invertebrate populations (Kunz et al.,

103 2011). They are sensitive to land-use change (Medellín et al., 2000; García-Morales et

104 al., 2013; Meyer et al., 2016), a feature that, in combination with their high abundance,

105 richness, ecological diversity and relative ease of survey, qualifies them as a good

106 model taxon for investigating the impacts of forest disturbance (Jones et al., 2009).

107 Species vary widely in their sensitivity to forest disturbance, depending on their habitat

108 affinities and species-specific characteristics (García-García et al., 2014; Farneda et al.,

109 2015; Wordley et al., 2017). However, the assessment of faunal responses to forest

110 disturbance is often based on composite biodiversity metrics that may conceal species-

111 level responses and consequently misguide conservation actions and management

112 (Klingbeil and Willig, 2009). The reliance on such metrics often is a consequence of the

113 rarity of old-growth specialist species for which limited data prevents sufficient

114 statistical power for species-specific approaches. Here, we capitalize on the periodical

115 re-isolation of the BDFFP fragments as a BACI experiment to investigate how abrupt

116 changes in fragment-matrix contrast affect Neotropical bats. We use a joint species

117 distribution modeling framework that combines species-specific models into a single

118 hierarchical model thus allowing the assessment of the influence of environmental

119 variables at the level of individual species regardless of their rarity within the

120 assemblage (Warton et al., 2015; Ovaskainen et al., 2017). By combining species-level

121   inference with a robust sampling design, in which surveys in modified habitats as well

122   as in undisturbed reference sites in continuous forest were conducted prior to and

123   following the impact of re-isolation, we were capable of unveiling, for the first time, the

124   short-term effects of the creation of small clearings on tropical bats at both the species

125   and assemblage levels.

126   We hypothesized that fragment re-isolation would reduce species occupancy in

127   fragments and adjoining edge and matrix sites and lead to a decrease in similarity

128   between the assemblages inhabiting these habitats and the ones found in nearby

129   continuous forest (used as experimental controls). We predicted that following fragment

130   re-isolation: i) the reduction in occupancy would be more marked for species classified

131   as old-growth specialists than for habitat generalists; ii) species responses would be

132   idiosyncratic, with re-isolation effects being more prominent in edge and matrix habitats

133   than in fragment interiors and iii) the assemblage similarity between continuous forest

134   and edge and matrix sites would decrease more than the assemblage similarity between

135   continuous forest and fragment interiors.

136

137   **2. Materials and methods**
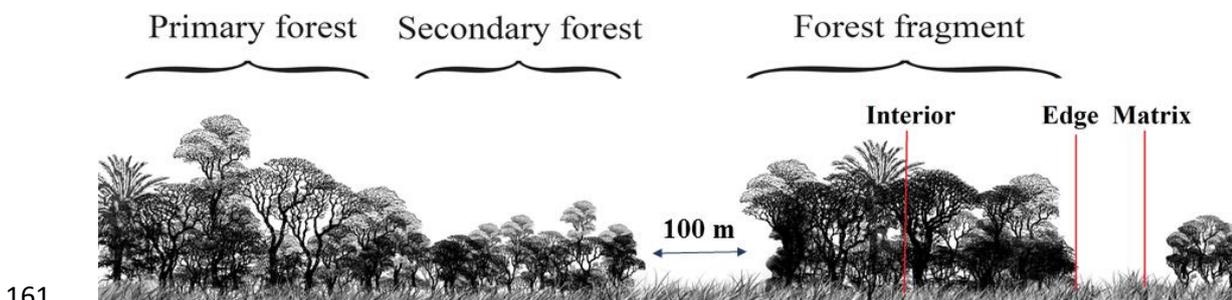
138   *2.1. Study area*

139   The study was conducted at the BDFFP, situated about 80 km north of Manaus (2°30'S,

140   60°W), Amazonas, Brazil (Fig. A.1). The area comprises c. 40 x 10 km of a mosaic of

141   *terra firme* rainforest, secondary regrowth, and primary forest fragments and lies 30–

142   125 m above sea level. The area is characterized by elevated tree species richness (often

143   exceeding 280 species ha-1) (Oliveira and Mori, 1999) and rainfall varies from 1,900 to

144   3,500 mm annually, with a dry season between June and October (Laurance et al.,

145 2011). Fragments used in this study were isolated from continuous forest by distances

146 of 80-650 m in the early 1980s, and are 1, 10 and 100 ha in size. The landscape matrix

147 is composed of ~20-year-old secondary forest dominated mainly by *Vismia* spp. and

148 *Cecropia* spp. (Mesquita et al., 2015).

149

150 *2.2. Fragment re-isolation*

151 Following the initial isolation of the fragments in the early 1980s secondary forest has

152 occupied much of the areas previously cleared. Fragment isolation was thus maintained

153 by clearing and burning of a 100 m wide strip of regrowth around each of the forest

154 fragments at intervals of ~10 years, prior to this study most recently between 1999 and

155 2001 (Laurance et al., 2011). Fragment re-isolation took place again between November

156 2013 and March 2014, by clearing (but not burning) of areas ranging from 6.4 (around 1

157 ha fragments) to 42 ha (around 100 ha fragments) around each of the experimental

158 forest fragments (Fig. 1 and Fig. A.2). During the above-mentioned periods no

159 manipulation took place in the nearby continuous forest, which were used as

160 experimental controls.

162 **Figure 1** – Schematic representation of the sampling design after the experimental re-

163 isolation of fragments by clearing of the surrounding regrowth vegetation.

164

165   *2.3. Bat sampling*

166   Field work before and after re-isolation was conducted from August 2011 to June 2013

167   and from April to November 2014, respectively. The bat fauna was sampled in eight

168   forest fragments, categorized according to their area as "1 ha" ($n = 3$), "10 ha" ($n = 3$)

169   and "100 ha" ($n = 2$) and six control sites in continuous forest (CF). Fragments were

170   located at different BDFFP camps (Dimona, Colosso and Porto Alegre), whereas CF

171   interior sites were located in Cabo Frio and Km 41 (Fig. A.1). Mist net sampling was

172   performed in the interiors and at the edges of all fragments, as well as in sites located

173   100 m away from the edge of each fragment, in the adjacent secondary regrowth. The

174   latter, referred to hereafter as "matrix sites", were located at the border of the area of

175   secondary regrowth cleared during the re-isolation of the fragments. At fragment edges,

176   mist-nets were deployed parallel to the border between the fragment and the adjoining

177   matrix (Fig. 1).

178   At each site, bats were sampled eight times before fragment re-isolation (four times in

179   each season) and four times after fragment re-isolation (twice per season). Fourteen

180   ground-level mist-nets (12 x 2.5 m, 16 mm mesh, ECOTONE, Poland) were used in CF

181   and fragment interiors and seven at edge and matrix sites. Nets were opened at dusk and

182   were deployed for six hours, being revised at intervals of ~20 minutes. Total mist net

183   effort was 6,046, 8,025, 3,994 and 4,005 mist-net hours (mnh; 1 mnh equals one 12 m

184   net open for 1 h) for continuous forest, fragment interior, edge and matrix, respectively.

185   Bias in capture rates due to net shyness was avoided by spacing visits to the same site

186   by periods of three to four weeks (Marques et al., 2013). Species were identified

187   following Lim and Engstrom (2001) and Gardner (2007), and taxonomy follows

188   Gardner (2007).

189 With the exception of the mormoopid bat *Pteronotus parnellii* we excluded all non-

190 phyllostomid species from the analysis as they cannot be adequately sampled with mist-

191 nets (Kalko, 1998).

192

193 *2.4. Classification of species habitat affinities*

194 Bat captures from this and previous studies at the BDFFP (Sampaio et al., 2003;

195 Bobrowiec and Gribel, 2010; Rocha et al., 2017a) were compiled into a database

196 amounting to 10,311 captures of 50 species sampled in the understory of CF, fragments

197 and secondary forest across the BDFFP landscape between 1996 and 2014. The joint

198 species distribution model (see section 2.5) was only based on a sub-set of these

199 captures (4,244 individuals). Captures were divided into two categories, namely: CF *vs*

200 forest fragments and secondary forest. Species were then classified according to their

201 habitat affinity into CF specialists, secondary forest specialists, generalists or too rare to

202 classify using the statistical approach described in Chazdon et al. (2011). Classification

203 was conducted in R v.3.0.2 (R Development Core Team, 2013) using function *clamtest*

204 of the *vegan* package (Oksanen et al., 2015) and was based on the super-majority

205 specialization threshold ($K = 2/3$) and a significance level of $P = 0.01$. We

206 conservatively grouped CF specialists and species too rare to classify into a single group

207 and since only two species were assigned to the secondary forest category, they were

208 lumped together with generalists. We therefore considered two groups according to their

209 habitat affinity in our analysis: CF specialists and species too rare to classify (hereafter

210 "specialist species") and generalists and secondary forest specialists (hereafter

211 "generalist species").

212

2.5. Hierarchical joint species distribution model

We evaluated the effect of fragment re-isolation by means of a hierarchical joint species distribution model (Ovaskainen et al., 2017). For the analyses we considered one mist-netting session in one sampling site ($n = 360$ mist-netting sessions) as a sampling unit (the study design is illustrated in Fig. A.3). Due to the high prevalence of zeros in the data, we truncated the counts to presence-absence, and thus considered as the response variable the vector of presence-absences of all the 50 species (Y matrix, Fig. A.3). We assumed a Bernoulli distribution with probit link function. Explanatory variables (X matrix, Fig. A.3) were: i) habitat type (categorical: CF, fragment interior, fragment edge or matrix); ii) survey period (categorical: before or after re-isolation); and iii) log-transformed survey effort. We also included an interaction between survey period and habitat type. Multiple visits to the same site were accounted for by including a site-level random effect in the model, implemented at the community level using a latent factor approach (Ovaskainen et al., 2016a). The species habitat affinity classification described above was included as a trait (T matrix, Fig. A.3) and phylogenetic non-independence was accounted for by structuring the error variance with a phylogenetic correlation matrix derived from a phylogenetic tree under the diffusion model, following Abrego et al. (2017) (C matrix, Fig. A.3). The phylogenetic tree was extracted from Jones et al. (2002). We fitted the model in the Bayesian framework using the Gibbs sampler of Ovaskainen et al. (2016a,b). The model was fitted to the data using the HMSC software for MatLab (HMSC-MatLab), assuming the default priors described in the Supporting Information of Ovaskainen et al. (2017). We ran the model for 50,000 iterations out of which 15,000 were discarded as transient. The MCMC chains mixed well, as illustrated by the MCMC trace plot of the species-specific regression parameters (beta) in Fig. A4.

237   The parameterized model was used to predict the expected mean species richness before

238   and after fragment re-isolation for all species and separately for generalists and

239   specialists. Mean species richness was defined as the model prediction for the number

240   of species expected to be observed during a survey visit and computed as the sum (over

241   the species) of the species-specific occurrence probabilities. Predictions were based on

242   mist-netting effort standardized to the mean value over all visits.

243   To examine how fragment re-isolation affected assemblage turnover, we calculated

244   assemblage similarity among the control (CF) and modified habitats (fragment interior,

245   fragment edge and matrix) as the correlation between model-predicted log-transformed

246   occurrence probabilities (Ovaskainen and Soininen, 2011; Appendix B). We performed

247   these analyses for all species and separately for generalists and specialists.

248

249   **3. Results**

250   We captured 4,244 bats (3,079 individuals of 41 species before re-isolation and 1,165

251   individuals of 35 species after re-isolation). Twenty-seven species were classified as

252   specialists whereas 23 were classified as generalists (Table A.1 and Fig. A.5; see

253   section 2.4 for classification details).

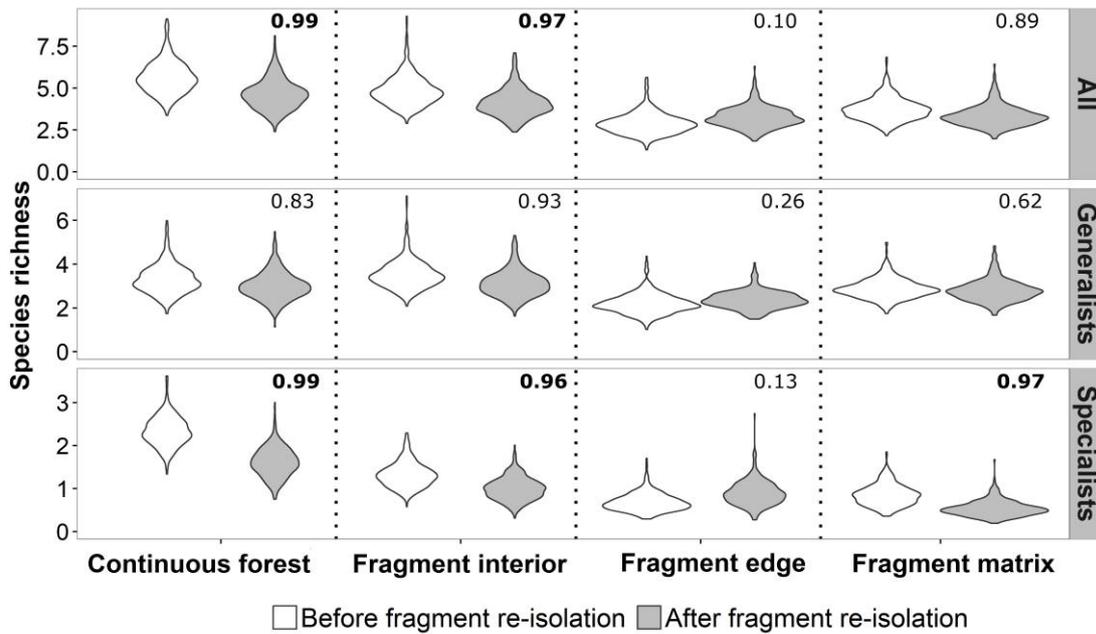254   *3.1 Occupancy responses to fragment re-isolation*

255   *3.1.1. Changes in species richness*

256   Model-predicted numbers of species captured per sampling visit indicated that CF was

257   the most species-rich habitat both before and after experimental manipulation, yet also

258   the one showing the largest declines (5.64 ± 0.95 [mean ± SD] before; 4.62 ± 0.88 after)

259   (Fig. 2). Among the habitats exposed to experimental manipulation, species richness

260   was the highest in fragment interiors (4.85 ± 0.89 before; 4.11 ± 0.81 after), followed by

261   matrix (3.74 ± 0.67 before; 3.34 ± 0.63 after) and edge sites (2.88 ± 0.62 before; 3.26 ±

262   0.62 after). When separating the species by their habitat affinity, specialists exhibited

263   the same pattern of decreasing species richness from CF to fragment interiors, matrix

264   and edge habitats, however, after fragment re-isolation generalists were more species-

265   rich at edges than in the matrix (Fig. 2).

266   Overall, species richness was higher before than after fragment re-isolation. This pattern

267   was consistent in CF, fragment interiors and, to a lesser extent, the matrix (18%, 15%

268   and 11% decrease in species richness following fragment re-isolation). The sole

269   exception, though with limited statistical support, were the fragment edges, for which

270   the model estimated a 13% increase in species richness following re-isolation (Fig. 2).

271   The between-period change in species richness was more pronounced for specialist

272   species than for generalists (Fig. 2). Whereas for generalists the support for a decline in

273   species richness in any of the considered habitats was low (posterior probability <

274   95%), specialist species were significantly less likely to be captured after fragment re-

275   isolation in all habitats, except fragment edges. For the latter, and similarly to

276   generalists, model predictions were higher after fragment re-isolation (8 and 31%

277   increase for generalists and specialists, respectively), however, with no significant

278   differences (Fig. 2).

Figure 2 – Patterns of species richness at continuous forest and fragment interior, edge and matrix sites of the Biological Dynamics of Forest Fragments Project before and after fragment re-isolation. Plotted are the predictions for the mean number of species expected to be observed during a survey visit for all species combined and separately for generalist and specialist bats. Inserts represent the posterior probabilities for the predictions being lower after fragment re-isolation than before re-isolation; values showing high statistical support (posterior probability > 95%) are highlighted in bold. The classification of the species into generalists and specialists is reported in Table A.1.

3.1.2. Species-specific responses to fragment re-isolation

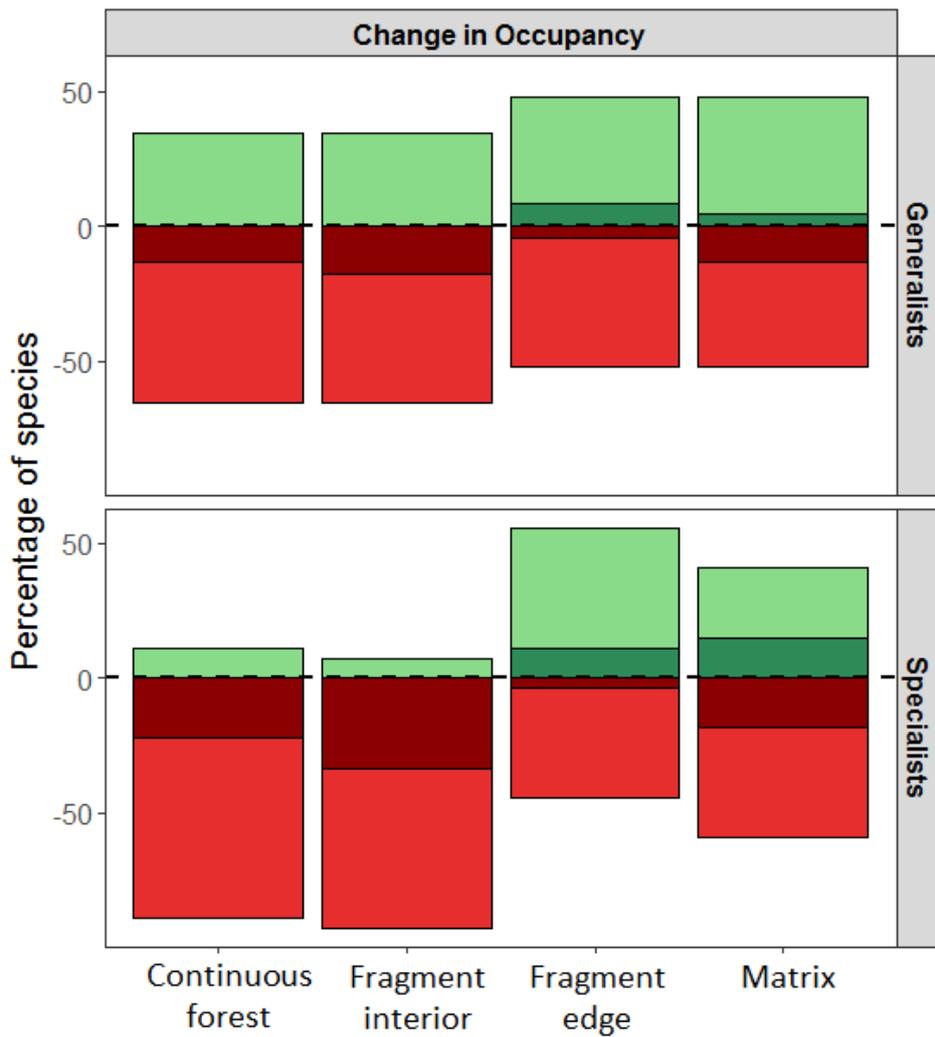For both generalists and specialists, more species declined in occupancy than increased following fragment re-isolation (Fig. 3). Model predictions revealed high statistical support (posterior probability > 95%) for the decline in occupancy probability of 13% of the generalist and 19% of the specialist species in CF. The only habitats to exceed CF

295 in the number of species exhibiting significant negative changes were fragment

296 interiors, for which 13% of the generalists and 22% of the specialists exhibited high

297 statistical support for a decrease in occupancy following fragment re-isolation (Fig. 3).

298 For both generalists and specialists, a greater number of species exhibited high support

299 for positive than negative changes in occupancy in edge sites (9% *vs* 4% for generalists

300 and 11% *vs* 4% for specialists, respectively). Yet, this pattern was reversed in matrix

301 sites, with more generalists and specialists exhibiting high support for a decrease rather

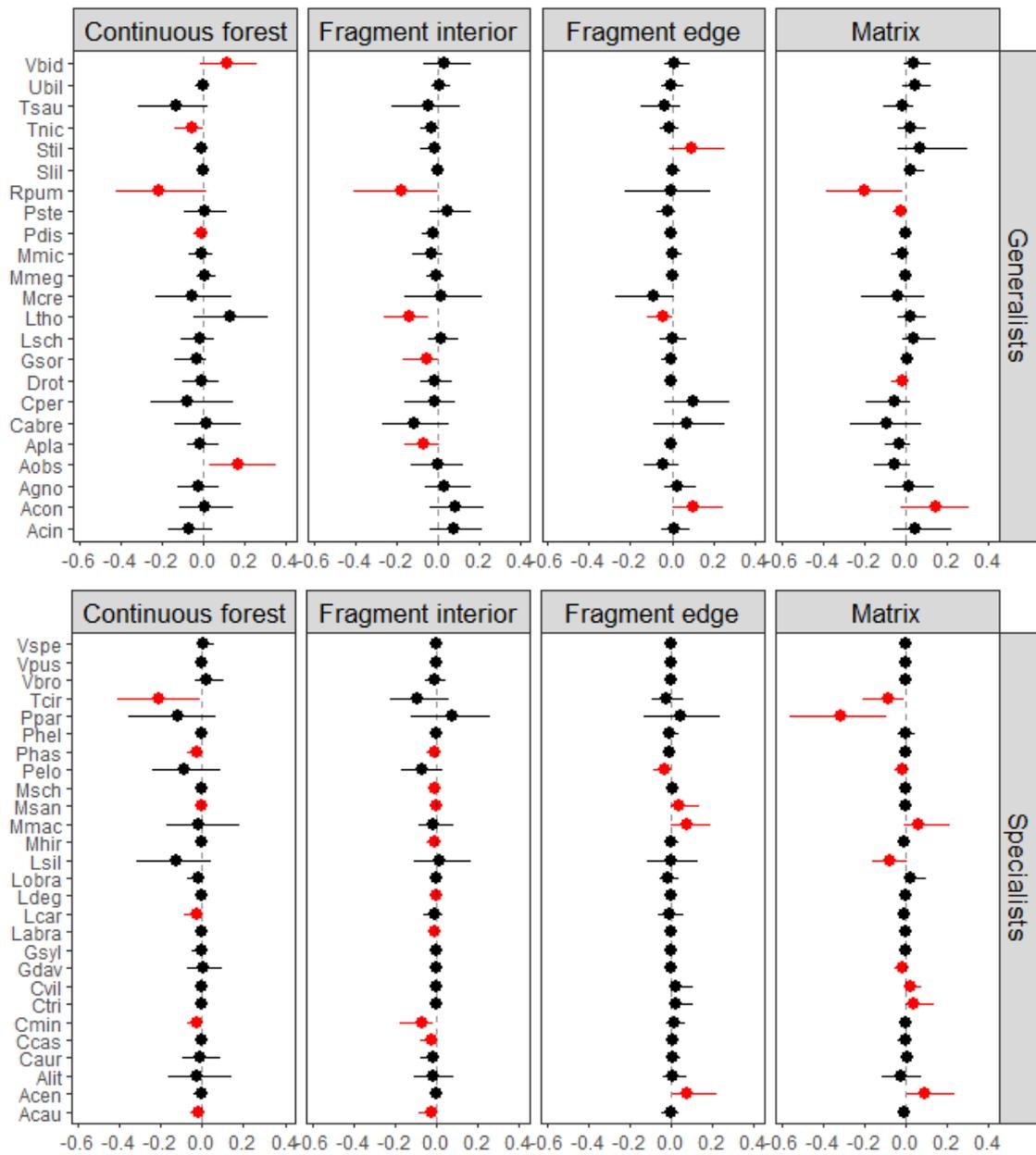302 than an increase following re-isolation (Fig. 3).

303 For generalists, high support for increases in occupancy was only found for *Artibeus*

304 *obscurus* and *Vampyressa bidens* in CF, for *Artibeus concolor* and *Sturnira tildae* in

305 fragment edges and for *A. concolor* in matrix sites (Fig. 4). The more pronounced

306 declines among generalists were found for *Rhinophylla pumilio* in CF, fragment

307 interiors and matrix, followed by *Trinycteris nicefori* in CF, *Lonchophylla thomasi,*

308 *Glossophaga soricina* and *Artibeus planirostris* in fragment interiors and *Mimon*

309 *crenulatum* in fragment edges. On the other hand, for specialists, high support for

310 positive between-period changes was only found for *Micronycteris sanborni*,

311 *Mesophylla macconnelli* and *Ametrida centurio* in edge, and for *A. centurio*, *M.*

312 *macconnelli, Chiroderma trinitatum* and *C. villosum* in matrix sites. For this group, the

313 more significant negative changes were found for *Pteronotus parnellii, Lophostoma*

314 *silvicolum* and *Trachops cirrhosus* in matrix sites, *T. cirrhosus* in CF and *Choeroniscus*

315 *minor* in fragment interiors (Fig. 4).

316

Figure 3 – Percentage of generalist and specialist species with negative (red) and positive (green) changes in occupancy after fragment re-isolation at the Biological Dynamics of Forest Fragments Project. Dark colours represent species with high statistical support (posterior probability > 95%) whereas light colours stand for species with low statistical support (posterior probability < 95%). Predictions account for within-habitat differences in capture effort between the two period.

323

324

325 **Figure 4 - Changes in species occupancy probability associated with fragment re-**

326 **isolation of forest generalist and specialist bat species across the different habitat**

327 **types sampled at the Biological Dynamics of Forest Fragments Project.** Plotted are

328 the species-specific differences in the predictions of mean occupancy per survey visit

329 before and after fragment re-isolation (and corresponding 95% quantile). Species with

330 high statistical support (posterior probability > 95%) are highlighted in red. Species

331 abbreviations are reported in Table A.1.

332

3.2. Changes in assemblage similarity

Model predictions indicate that within-habitat assemblage similarity before and after

fragment re-isolation was highest for CF (0.8), followed by fragment interiors (0.74),

fragment edges and matrix (0.62) (Table A.2).

Assemblage similarity between CF and fragment interiors, edge and matrix decreased

following fragment re-isolation. These declines in assemblage similarity were more

discernible for specialist than for generalist species and, for both groups, the reduction

in assemblage similarity was more pronounced at fragment edges and matrix sites than

in fragment interiors (Table 1).

342

343 **Table 1 - Assemblage similarity between continuous forest and modified habitats**

344 **(fragment interiors, fragment edges and matrix sites), before and after fragment**

345 **re-isolation.** Similarity between two assemblages was defined as the correlation

346 between model-predicted occurrence probabilities (log-transformed). The values in the

347 table show posterior mean similarities between assemblages in CF and modified

348 habitats for the two study periods.

	Fragment interior		Fragment edge		Matrix	
	Generalists	*Specialists*	*Generalists*	*Specialists*	*Generalists*	*Specialists*
Before re-isolation	0.90	0.82	0.67	0.72	0.62	0.72
After re-isolation	0.76	0.70	0.38	0.30	0.34	0.36
% change[1]	16%	15%	43%	58%	45%	50%
Posterior probability[2]	0.87	0.86	0.94	**0.97**	0.93	**0.97**

349

350 [1] Percent change in assemblage similarity before and after fragment re-isolation.

351 [2] Posterior probability of assemblage similarity being higher before than after fragment
352 re-isolation; values showing high statistical support (posterior probability > 95%) are
353 highlighted in bold.

4. Discussion

Although the consequences of forest disturbance on forest-associated wildlife have been intensively studied (Barlow et al., 2016; Meyer et al., 2016), previous studies have been predominantly observational and consequently limited in their capacity to disentangle spatial and temporal heterogeneity from disturbance effects (França et al., 2016). This limitation has led to recent calls for studies following the quasi-experimental framework of BACI designs (Bicknell et al., 2015; França et al., 2016). Here, we present evidence, by means of a BACI study, that relatively small man-made clearings had a weaker influence on the occupancy of Neotropical bats inhabiting the interiors and edges of forest fragments and matrix sites than temporal heterogeneity due to natural rates of occupancy turnover across the landscape. Yet, we found a considerable increase in spatial turnover following fragment re-isolation, as evidenced by a decrease in assemblage similarity between CF and modified habitats (fragments and matrix). Therefore, despite high natural spatiotemporal variability in bat species occupancy, our results suggest that even small clearings affect the spatial composition of bat assemblages in a regenerating fragmented landscape.

Bat responses to clearings are affected by time since vegetation removal (Kirkpatrick et al., 2017). In this study, sampling was conducted immediately after re-isolation and consequently we might have been unable to detect some effects that might take longer to manifest themselves (i.e. there could be time lags). Yet, since a longer time period between fragment re-isolation and sampling could have masked re-isolation-induced responses due to vegetation regrowth in cleared areas (Kirkpatrick et al., 2017), we consider that the time between re-isolation and sampling was suitable for our objective of investigating how Neotropical bats are affected by abrupt changes in fragment-matrix contrast.

4.1. Species richness responses to fragment re-isolation

Our results revealed that for all habitats other than edges, species richness declined after fragment re-isolation. This decline was more pronounced for forest specialist than for generalist species. The magnitude of these declines in fragment interiors and the matrix was however similar to the decline observed in CF, our experimental controls. This suggests that observed occupancy declines were unlikely the result of re-isolation, but rather reflect marked interannual variation in species occupancy or detectability.

Tropical assemblages exhibit profound spatiotemporal variation in response to resource availability (Haugaasen and Peres, 2007; Beja et al., 2010; Castro and Espinosa, 2015). Although seasonal differences in species richness, abundance and composition have been repeatedly documented across the tropics for many taxa, including bats at the BDFFP and elsewhere (Ramos Pereira et al., 2010; Bobrowiec et al., 2014; Cisneros et al., 2015; Ferreira et al., 2017; Rocha et al 2017b), evidence for supra-annual fluctuations is scarce (Aguirre et al., 2003; Hodgkison et al., 2004; Kingston, 2013). Annual oscillations can however lead to misleading interpretations of ecological patterns, especially if data collection is conducted over small time windows (Meyer et al., 2016; Banks-Leite et al., 2012). By including experimental controls in our study design both before *and* after fragment re-isolation we were able to detect that even undisturbed sites underwent a significant decline in mean species occupancy, therefore precluding the possibly deceptive interpretation that the clearing of the 100 m strip of regrowth around the fragments had negatively impacted fragment and matrix species richness. Yet, some tropical vertebrates are known to make greater use of forest fragments during periods of low resource availability in order to expand their foraging areas or use them as stepping stones to disperse to areas of higher food availability (Maldonado-Coelho and Marini, 2004). Elevated use of secondary forest habitats, where

404 fruit availability can be less seasonal, during periods of higher resource scarcity has also

405 been reported for Neotropical frugivorous birds (Barlow et al., 2007). Consequently,

406 under the absence of the experimental manipulation in forests fragments and

407 surrounding matrix, a decrease in resource availability in CF could have led to

408 displacement towards these habitats. However, since all sampled fragments were re-

409 isolated we could not address this hypothesis.

410 Mounting evidence suggests that Neotropical bats respond, sometimes markedly, to

411 habitat edges (Gorresen and Willig, 2004; Faria 2006; Meyer and Kalko, 2008;

412 Klingbeil and Willig, 2009; Ferreira et al., 2017; Rocha et al., 2017a). Following

413 fragment re-isolation, edges were the only habitat not to experience a decline in species

414 richness. In fact, even though statistical support was limited, we observed an increase in

415 the mean number of both generalist and specialist species captured per survey visit after

416 fragment re-isolation. Declines in species richness at edges have been suggested to be

417 linked to the avoidance of these habitats by animalivorous bats which might relate to

418 changes in the densities of preferred prey or to flight constraints imposed by increased

419 vegetation clutter typical of forest edges (Meyer and Kalko, 2008; Rocha et al., 2017a).

420 This avoidance may be further accentuated by clutter constraints to echolocation due to

421 the masking of echoes from prey by echoes reflecting from surrounding vegetation

422 (Schnitzler and Kalko, 2001) and by reduced access to prey due to denser vegetation

423 (Rainho et al., 2010). Vegetation-free forest streams and man-made tracks also appear

424 to constitute important flyways for bats (Palmeirim and Etherdige, 1985; Adams et al.,

425 2009; Webala et al., 2010; de Oliveira et al., 2015; Kirkpatrick et al., 2017). The

426 removal of the vegetation surrounding the fragments might therefore have freed bats

427 from the restrictions imposed by a denser understory, reflected in the observed increase

428 in species richness. However, bat activity is affected by the size of areas devoid of

429 vegetation, with activity being lower in larger cleared areas (Kirkpatrick et al., 2017).

430 This possibly relates to increased perceived predation risk (Baker et al., 2013) and

431 suggests that our results for both edge and matrix sites are sensitive to the size of the

432 cleared areas.

433

434 *4.2. Species-specific responses*

435 The assessment of the effects of forest disturbance on bat assemblages has been

436 somewhat limited by the evaluation of pooled responses at the ensemble- or

437 assemblage-levels through measures such as species richness, evenness or assemblage

438 structure (e.g. Avila-Cabadilla et al., 2009; Mendenhall et al., 2014; Arroyo-Rodríguez

439 et al., 2016; Rocha et al., 2017a). Due to the high species richness, such pooling of

440 species may blur the detection of species-specific trends associated with the wealth of

441 responses to environmental changes found in tropical communities, even among closely

442 related species (Elmqvist et al., 2003). A major impediment to species-level

443 assessments relates to the difficulty in obtaining information for rare species, which

444 abound in tropical ecosystems and are often of greater conservation concern. Here,

445 species-level assessments were achieved by means of a novel joint species distribution

446 model framework which, by incorporating species-specific responses into a single

447 hierarchical model, allowed the detection of the relationship between habitat covariables

448 and species responses at both the species and community levels (Ovaskainen et al.,

449 2017).

450 Strong statistical support for an increase in occupancy in the second sampling period

451 (after fragment re-isolation) was only found for 9 of the 50 species analysed. Of these,

452 *Artibeus obscurus* and *Vampyressa bidens* were the sole species for which there was

22

453　strong statistical support for an increase in CF whereas all remaining species were found

454　to increase either in edge or matrix sites. Interestingly, only two of the species

455　(*Micronycteris sanborni* and *Sturnira tildae*) for which strong statistical support for an

456　increase in occupancy was observed are not a canopy frugivore (Bernard, 2001). Indeed,

457　two species with canopy affinities (*Chiroderma trinitatum* and *C. villosum*) were only

458　captured after fragment re-isolation and a third one, *Ametrida centurio*, was captured

459　twice as often during the four visits to each of the edge and matrix sites after re-isolation

460　than in the 8 visits preceding manipulation (Table A.1). Canopy foraging bats have been

461　suggested to make more use of open areas than species that forage in the understory

462　(Cosson et al., 1999; Kalko and Handley, 2001; Marques et al., 2015). This perception

463　of increased use of open spaces by canopy species may however correspond to an

464　artefact, relating to an anti-predator shift in the use of the vertical space in areas of

465　reduced canopy cover. This "vegetation hugging" behaviour, in which prey species

466　travel close to vegetation to avoid the higher predation risk associated with crossing

467　open spaces has been observed for several European vespertilionids (e.g. Schaub and

468　Schnitzler, 2007) but had to date not been reported in the tropics or for frugivores (Lima

469　and O'Keefe, 2013). Also, canopy bats could be less reluctant to cross forest gaps than

470　understory species as the latter are less familiar with lack of forest cover (Cosson et al.,

471　1999).

472　The most pronounced decline in occupancy following fragment re-isolation was found

473　for *P. parnellii* in matrix habitats. The species is a high duty-cycle insectivorous bat

474　with an echolocation characterized by long constant frequency signals, which allows for

475　efficient prey detection in cluttered environments (Hiryu et al., 2016). Amazonian

476　populations were found to present higher activity in habitats with more clutter, which

477　also presented higher insect biomass (de Oliveira et al., 2015). By affecting vegetation

478 density, the clearance of regrowth vegetation surrounding the fragments might have

479 reduced matrix suitability for the species, leading to a pronounced decline in occupancy.

480

5. Conclusions

482 Our study presents experimental evidence that even relatively small clearings have

483 pervasive impacts on species-rich Amazonian bat assemblages. However, these effects

484 did not manifest as major changes in local diversity (measured as the mean number of

485 species captured per survey visit) but mainly as changes in assemblage composition.

486 These results align with the recent finding by Dornelas et al. (2014) that following

487 anthropogenic modification many assemblages undergo biodiversity change, but not

488 necessarily species loss. Our findings also align with results by Wilson et al. (2016)

489 suggesting that assemblage composition may be a better predictor of how fragmentation

490 affects biotic communities than species richness. Practitioners and researchers alike

491 should therefore include metrics of assemblage composition when investigating

492 temporal change across modified landscapes. Increased use of BACI approaches should

493 also be encouraged as it allows separating the confounding effects of natural temporal

494 heterogeneity from disturbance responses.

495 The experimental clearings targeted by this study are somewhat more similar to large

496 natural forest gaps (e.g. windthrows), in which tumbled trees lie scattered and rotting,

497 encouraging quick secondary forest regrowth, than to anthropogenic clearings. Yet, in

498 the Amazon, ranchers frequently clear secondary vegetation surrounding forest

499 fragments to promote pasture areas for cattle (Laurance et al., 2007). The fragment re-

500 isolation examined in this study somewhat mimics this re-opening of fragment edges by

501 ranchers, offering important insights into the consequences of this common scenario of

502   land-use change. Additionally, the results presented here are important given that linear

503   forest clearings originating from infrastructures such as roads, railroads and powerlines

504   nowadays constitute omnipresent features of human-modified tropical landscapes.

505

518

519   **References**

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776 **Appendix A. Supplementary figures and tables**

777 **Appendix B. Calculation of the assemblage similarity values**

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779 Supplementary data associated with this article can be found, in the online version at: