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4 Landscape structure shapes tree seedlings' diversity at multiple spatial scales in a fragmented tropical
5 rainforest

6 Short title

7 Landscape structure shapes tree seedlings' diversity in a fragmented tropical rainforest

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20

21 Abstract

22

23 Biotic-dispersed tree seedling species are fundamental for the maintenance of the structure and function
24 of forest patches in fragmented rainforest landscapes. Nonetheless, the effects of landscape structure
25 and the spatial scale at which operates on seedling α - and β -diversity is unknown. Using a multi-scale
26 approach, we assessed the relative effect of landscape composition (i.e., percentage of old-
27 growth/secondary forest cover), configuration (i.e., aggregation/density of forest patches) and
28 connectivity (i.e., structural and functional) on α - and β -diversity of biotic-dispersed seedlings in 16
29 forest patches in the Lacandona rainforest, Mexico. We assessed these effects at 13 spatial scales (from
30 300 to 1500 m radius, at 100 m intervals) for three α - and β -diversity orders (rare, common and
31 dominant species). We found that patch aggregation increased species richness and reduced β -diversity
32 of common and dominant species at similar spatial scales (500 to 600 m). Additionally, functional
33 connectivity had a positive effect on the β -diversity of rare species in the 800 m spatial extent. These
34 effects suggest that landscape configuration and functional connectivity sustain seedling diversity by
35 preserving seed rain richness and the presence of large terrestrial herbivorous mammals. In contrast, the
36 percentage of secondary forest matrix was detrimental for all α -diversity orders and the β -diversity of
37 common and dominant species. Forthcoming conservation strategies should prevent deforestation,
38 increase habitat amount and promote functional connectivity of forest-dependent fauna through matrix
39 management actions.

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42

43 1. Introduction

44

45 The long-term conservation of biodiversity is increasingly relying on novel ecosystems [1],
46 particularly in human-modified tropical landscapes (HMTLs) [2–4]. In tropical rainforests, old-growth
47 forest tree species are the major components of diversity, structure and function of these ecosystems
48 [5,6], whereas the seedling community is the main regenerative pool of forest trees [7,8]. Therefore, it
49 is not surprising that alterations of seedling species' richness (α -diversity) and spatial dissimilarity (β -
50 diversity) lead to the taxonomic, phylogenetic and functional impoverishment of tropical rainforests
51 [9–11]. Accordingly, understanding how landscape structure (composition, configuration and
52 connectivity) affects seedling diversity is crucial for biodiversity conservation in HMTLs [12,13].

53 A variety of studies suggest that seedling diversity is associated with the habitat amount and
54 landscape connectivity of HMTLs [14,15]. The positive association between seeds and seedling α -
55 diversity and the amount of old-growth forest (OGF) suggests a rescue effect of the latter by sustaining
56 the landscape pool of colonizers and long-distance seed dispersal [16,17]. Configurational patterns that
57 increase habitat amount, such as patch aggregation and spatial proximity (structural connectivity), can
58 also perform a rescue effect in highly deforested landscapes [18–20].

59 Furthermore, in HMTLs, seedling β -diversity is sensitive to changes in abundance because of
60 alterations in local seed dispersal and seedling recruitment [16,21,22]. In remaining forest patches, the
61 seed rain is influenced by the surrounding secondary forests (SF), whereas seedling recruitment is
62 sensitive to edge effects and habitat heterogeneity [9,23]. Furthermore, β -diversity is strongly affected
63 by the functional complementarity between mammalian seed/seedling predators and seed dispersers
64 [24,25]. Large-sized herbivorous mammals reduce the number of rare species and the abundance of
65 dominant species at the local the scale, while dispersing the latter at the landscape scale [24,26]. The
66 persistence of herbivorous mammals in HMTLs relies on the functional connectivity provided by a

67 structural contrast of matrix with OGF patches [27,28]. Therefore, assessing functional connectivity is
68 crucial in understanding the role of functional connectivity in seedling β -diversity.

69 Furthermore, determining the relevant scale of landscape effects' biological responses, known
70 as the scale of effect [29], is needed to improve conservation and management strategies. In addition, it
71 is critical to assess the scale of effect between diversity types (α -/ β -diversity) and abundance-based
72 measurements (diversity orders) [30]. It is hypothesized that variables shaped by richness fluctuations
73 are expected to have larger scales of effect than those affected by individuals' abundance [31–33]. So
74 far, only a single study has supported the above in seed rain α -diversity [16]. Thus, determining the
75 scale of effect among diversity types and orders is required to accurately assess the response of tree
76 seedling communities to landscape structure.

77 Multi-scale approaches evaluate the scale of effect of landscape structure on biological
78 responses and the species-landscape relationships [34]. This avoids overlooking the true scale of effect
79 if assessments were performed using very few scales within narrow ranges [29,34]. Only a handful of
80 studies have employed multi-scale approaches for plant communities within HMTLs [16,35], and to
81 our knowledge, there is a lack of studies on seedling communities. In this study, we employed a multi-
82 scale approach to assess the contribution of landscape composition (OGF and SF amount),
83 configuration (the patches' aggregation and fragmentation) and connectivity (structural and functional)
84 on α - and β -diversity of tree seedlings within rainforest patches. We particularly focused on the
85 following question: Which components of landscape structure are influencing seedling α - and β -
86 diversity and at what spatial scale?

87 We tested the following predictions : (1) If α -diversity is more reliant on the rescue effects of
88 landscape structure than β -diversity, we should find a positive association between α -diversity and
89 OGF (i.e., the amount, aggregation and structural connectivity), and a positive effect of patch
90 fragmentation and functional connectivity for β -diversity; (2) If the SF matrix has a poor or detrimental

91 contribution to seedlings diversity, there should be a negative effect of SF on α - and β -diversity; and
92 (3) If the landscape structure is driving the colonization and extinction dynamics at larger spatial scales,
93 then there should be larger scales of effect in richness-based than in abundance-based measures in α -
94 and β -diversity.

95

96 2. Material and methods

97 2.1. Study site

98

99 We conducted the study at the Lacandona rainforest in southeastern Mexico (Figure 1a). The
100 monthly temperature oscillates between 24 and 26 °C, and the annual precipitations ranges from 2500
101 to 3500 mm [36]. This region encompasses the largest rainforest of the Mesoamerican biodiversity
102 hotspot [37,38]. Land-cover change to cattle pastures, however, has reduced its forest cover by more
103 than 50% of its original extension [39,40]. We selected 16 forest patches, ranging from 1 ha to 63 ha
104 (Figure 1b).

105

106 2.2. Tree seedling sampling

107

108 We established ten 1-m² plots arranged in a stratified random manner across a 1-ha block within
109 each forest patch. We placed 1-m² plots at least 100 m away from patch edges to avoid strong edge
110 effects as much as possible [22,41]. Thereafter, within each plot we counted and identified all tree
111 seedlings (10-100 cm height). We identified each seedling to the lowest possible taxonomic level with
112 the help of a local parataxonomist and field guides [42,43]. We took samples for further identification
113 in herbariums (MEXU, ECO-SC-H) when field identification was not possible. Furthermore, we

114 determined the dispersal syndrome (abiotic or biotic; Table S1) of each species, based on their fruits
115 and seed morphology [44–47]. Since in rainforests biotically-dispersed tree species comprise up to 90%
116 of the seed rain [16,48], we developed the analysis using only this species guild. Plant nomenclature
117 followed the Missouri Botanical Garden database Tropicos [49].

118

119 2.3. Diversity estimation

120

121 We assessed the sampling completeness with the sample coverage estimator of Chao and Shen
122 [50]. We combined the data of the 10 sampling plots within each patch and estimated the proportion of
123 the total number of individuals that belong to the species represented in the sample [51]. The sample
124 coverage among patches was high ($91.07 \pm 7.47\%$; mean \pm SD), indicating that our sampling effort was
125 adequate for estimating species diversity [52]. We then estimated true diversity using Hill numbers
126 [30,53]. We employed the Hill numbers of order zero (0D ; species richness), which gives a
127 disproportionate weight to rare species, one (1D ; exponential Shannon index) to represent the number
128 of typical species, and two (2D ; inverse Simpson index) to represent the number of very abundant
129 species [53–56]. We calculated the gamma diversity of each patch (γ_{patch}) and the mean alpha diversity
130 of plots (α_{plot}) of the three diversity orders following the formula of Jost [30]. Afterward, we estimated
131 the beta diversity between plots (${}^q\beta_{plot} = {}^q\gamma_{patch}/{}^q\alpha_{plot}$) to indicate the “effective number of completely
132 distinct communities” within each patch [30]. These β -diversity values range between one (when all
133 communities are identical) and N (N = the number of plots when all communities are completely
134 different from each other). We used the package *vegan* [57] for the entire procedure.

135

136 2.4. Landscape metrics and multi-scale assessment

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138 We employed a multispectral SPOT-5 satellite image recorded in March 2013 to carry out a
 139 supervised classification using the GRASS GIS software [58] for the entire procedure. The overall
 140 classification accuracy was 79%. We then calculated six landscape metrics (Table 1) relevant to the
 141 diversity of seed and plant communities [16,35]. The composition metrics included the percentages of
 142 old-growth forest (OGF) and secondary forest (SF) covers, whereas the configuration metrics were the
 143 density (PD) and aggregation (AI) of OGF patches. We selected the mean Euclidean-nearest neighbor
 144 distance between patches (ENN) for estimating structural connectivity and the percentage of
 145 contrasting edges (EC) as a measure of functional connectivity.[16,19,27,35,59–63]

146

147 Table 1. Description, metric type and ecological relevance of the landscape metrics employed in the
 148 study

Metric	Description	Metric type	Ecological relevance	References
Old-growth forest (OGF)	Percentage of landscape area covered by old-growth forest	Composition	Indicator of the landscape-scale habitat amount. It is positively associated with propagules' availability, seeds dispersal and abundance/richness of seed/seedling predators	[16,27,59–65]
Secondary forest (SF)	Percentage of landscape area covered by secondary forest	Composition	Measurement related to impacts on the dynamics and trajectories of floristic change within forest patches via shifts in edge effects and seed rain diversity	[9,66–69]
Patch density (PD)	Number of forest patches per landscape area	Configuration	Fragmentation metric positively associated with both edge effects on the tree/seedling community and with	[19,27,35,59,60,63]

	(n/ha)		landscape connectivity for a variety of seed dispersal vectors (i.e., frugivorous bats/birds, and arboreal/terrestrial mammals) in the tropics	
Aggregation index (AI)	Percentage of like-adjacencies between forest patches. Maximum aggregation indicates a single, compact patch	Configuration	A proxy of habitat amount/homogeneity in landscapes with low amounts of forest cover, influencing edge effects, local dispersal patterns and landscape complementation/supplementation dynamics	[19,66,70,71]
Euclidean-nearest neighbor distance (ENN)	Mean distance between forest patches within the landscape	Connectivity	Metric commonly employed to estimate structural connectivity (patch isolation). Patch isolation can have strong effects on seed dispersal success, altering tree/seedlings richness and floristic differentiation among patches	[19,20,59,61,72]
Edge contrast index (EC)	Average degree of edge contrast between forest patches and its immediate neighborhood	Connectivity	High percentages of contrasting edges reduce trees/seedlings survival and limit functional connectivity of seed dispersers in the tropics	[9,16,27,35,63,66,69,70,73]

149

150

151 We calculated the EC using quality values that describe the permeability of matrix covers for
152 terrestrial mammals. The permeability values were based on the assumption that overall species'
153 presence declines along a gradient of habitat loss and relates the percentage of each land-cover type
154 within the landscape matrix to its relative quality [3,27]. We ranked the relative quality of each land-
155 cover type based on the suitability of vegetation structure for mammals' feeding, movement and/or
156 habitat on a seven-point scale: 1 (water bodies, with the lowest suitability); 2 (anthropogenic cover); 3
157 (cattle pasture); 4 (arboreal crops); 5 (semiaquatic vegetation); 6 (secondary forest); and 7 (old-growth
158 forest, representing the highest suitability). To obtain a more robust and realistic representation of
159 landscape structure effects, we estimated the area-weighted mean of the EC index [74].

160 We estimated these metrics within 13 circular buffers (of a 300 to 1500-m radius, at 100 m
161 intervals) from the center of each focal forest patch (Figure 1c). The number and range of the buffers'
162 sizes comprise the reported scale of effect for a variety of patterns in understory vegetation, seed rain,
163 and bird and mammal communities in HMTLs [27,35,60,62]. Although the overlapping between
164 buffers of nearby sampling points increased at larger spatial extents, the degree of spatial
165 autocorrelation in the model residuals is not necessarily associated with the extent of landscape overlap
166 but rather with the proximity between sampling sites [75,76]. According to Moran's I autocorrelation
167 tests, we did not find spatial autocorrelation between the distance of sampling sites and the diversity
168 patterns assessed (Table S2).

169

170 2.5. Statistical analyses

171

172 We assessed the scale of effect of each landscape metric using linear models. We previously
173 verified the variables' normality with a Shapiro-Wilk test [77]. We fitted each diversity pattern with a
174 single landscape metric for each buffer size and assessed its predictive power with a leave-one-out

175 cross-validation (LOOCV). Next, we calculated the proportion of the variation that can be predicted by
176 the model using the LOOCV coefficient of determination (R^2_{CV}) as follows:

177

178

$$R^2_{CV} = 1 - \frac{MSE}{\frac{1}{n} \sum_{i=1}^n (y_i - \bar{y})^2}$$

179

180 where y_i is the diversity value for the i^{th} patch and n is the number of patches. The R^2_{CV} ranges
181 between $-\infty$ (indicating the model has a worse prediction power than the null model) and one
182 (indicating the model predicts the validation data perfectly), and can be used to compare between
183 response variables and scales of measurement [78]. We identified the scale of effect of each landscape
184 metric by plotting the R^2_{CV} of each model at each scale in function of buffer size and selected those
185 with the strongest response [34].

186 We then evaluated the effects of the selected landscape metrics on diversity patterns through
187 multiple linear models. We estimated the variance inflation factor (VIF) of landscape metrics
188 beforehand with the *car* package [79]. Since we did not find significant collinearity ($VIF \geq 4$) between
189 the explanatory variables [80], we employed the *dredge* function of the *MuMIn* package [81] to create
190 combinations up to three explanatory variables plus the null model (only the intercept). We ranked the
191 models using the Akaike's information criterion corrected for small samples (AICc) and selected those
192 models with a AICc difference lower than two ($\Delta AICc < 2$) as the best supported by the data [82].

193 Finally, we assessed the importance and the relative effect of each landscape metric measured at
194 the scale of effect on each diversity value using an information-theoretic approach and multimodel
195 inference [82]. For this, we selected a subset of models that had the 95% probability of containing the

196 best model using the summed Akaike weights (w_i) of ranked models until $\sum w_i \leq 0.95$. We employed
197 the w_i of the model's subset to calculate the relative importance and the model-averaged parameter
198 estimates of each explanatory variable. We carried out all statistical analysis in the R 3.5.2 statistical
199 computing environment [83].

200

201 3. Results

202

203 We recorded a total of 1334 tree seedlings from 29 families, 51 genera and 72 species in 160 m²
204 (Table S3). Most seedlings were biotically-dispersed species (1258; 94.3%), belonging to 24 families,
205 42 genera and 58 species. Mean species density of the biotically-dispersed seedlings was 11.37 ± 2.96
206 species/10 m² (range 6–16 species; mean \pm standard error), whereas seedling density was 78.62 ± 34.03
207 ind/10 m² (range 10–129 individuals). The most abundant species was *Inga punctata*, which
208 represented 33 % of all individuals sampled, followed by *Ampelocera hottlei* (13%) and *Brosimum*
209 *alicastrum* (11%). Less than half of the species (ca. 31%) were restricted to one patch, and only two
210 species, *I. punctata* and *Trophis racemosa*, were found in 14 and 12 patches, respectively. Variations
211 within α - and β -diversity orders are shown in Figure S1.

212

213 3.1. Scale of effect and importance of landscape structure on seedling diversity

214

215 We found α -diversity was affected by composition and structural connectivity metrics,
216 regardless of diversity orders (Table S4). The AI and SF affected α -diversity in the 600-m buffer,
217 whereas OGF and ENN effects occurred in smaller and larger buffer sizes, respectively (Figure S2).

218 The AI and PD metrics affected ${}^1\beta$ and ${}^2\beta$ at the 500-m buffer, whereas the latter metric influenced ${}^0\beta$ at
 219 the 1400 m buffer (Table S4). The EC affected ${}^0\beta$ and ${}^2\beta$ in the same buffer size, whereas the scale of
 220 effect of SF varied greatly between ${}^0\beta$ and ${}^1\beta$ (Figure S3).

221 When assessing the importance and contribution of the above metrics, we found that the best-
 222 fitting models of α -diversity included the positive effects of AI and the negative effects of SF (Table 2).
 223 The former metric was the second most important variable only for ${}^0\alpha$ (Figure 2c), whereas SF was
 224 strongly ($\sum w_i > 0.75$; Figure 2a) and significantly associated with all α -diversity orders (Figure 2c). For
 225 β -diversity, we found that AI and SF metrics had negative effects for ${}^1\beta$ and ${}^2\beta$, whereas EC was
 226 negatively associated with ${}^0\beta$ (Table 2). The importance of these metrics was high and significant for
 227 their respective β -diversity orders (Figure 2b and 2d).

228

229 Table 2. Best-supported linear models ($\Delta AICc < 2$) that explain α - and β -diversity patterns in
 230 fragmented tropical forest in southern Mexico. The positive (+) and negative (-) symbols denote the
 231 significant effects ($P < 0.05$) of landscape metrics in the models (values reported in Table S5). The
 232 models' log-likelihood (LL), the Akaike weight (w_i), the coefficient of determination (R^2) and the
 233 coefficient of prediction (R^2_{cv}) are shown. The landscape metrics are the aggregation index (AI), the
 234 edge contrast index (EC), the mean distance between patches (ENN), the percentage of old-growth
 235 forest (OGF), and the percentage of secondary forest (SF). The subscript numbers indicate the scale of
 236 effect of each variable.

Diversity	LL	AICc	w_i	R^2	R^2_{cv}	AI ₅₀₀	AI ₆₀₀	EC ₈₀₀	ENN ₁₂₀₀	FC ₄₀₀	PD ₁₄₀₀	SV ₄₀₀
${}^0\alpha$	-8.38	28.39	1	0.6	0.48		+					

	-1.84	15.31	0.29	0.67	0.57		-	
${}^1\alpha$	-1.93	15.50	0.26	0.67	0.58		+	
	-3.81	15.62	0.25	0.61	0.55			
	-2.23	16.09	0.20	0.65	0.57			+
${}^2\alpha$	2.41	6.80	0.64	0.74	0.65		-	
	0.02	7.95	0.36	0.67	0.63			
${}^0\beta$	-11.04	30.08	0.50	0.40	0.28		-	
	-9.76	31.17	0.30	0.45	0.22		-	+
	-10.17	31.98	0.20	0.42	0.32		-	+
${}^1\beta$	-8.77	29.18	1	0.68	0.64	-		
${}^2\beta$	-4.47	20.57	0.69	0.70	0.65	-		
	-3.09	22.17	0.31	0.72	0.59	-	-	

237

238

239 4. Discussion

240

241 4.1. Landscape effects on α -diversity

242

243 As predicted, α -diversity was strongly and positively associated with habitat amount and

244 declined as SF increased in the surrounding matrix. Nonetheless, habitat amount was related to AI

245 rather than OGF. In addition, the AI and SF affected the three α -diversity orders in the 600-m buffer.
246 Thus, α -diversity alterations by the above metrics and scales of effect suggest that species arrival is
247 influenced by small-scale drivers that affect the local seed rain.

248 Firstly, the relationship between AI and habitat amount, as well as the observed scale of effect,
249 is not surprising. In highly disturbed landscapes, the scale of effect is expected to be smaller since
250 biological responses are predicted to depend on small-scale variables, such as the mean patch size
251 [31,84]. The mean patch size is positively related to the AI in landscapes where forest cover is low (<
252 10%), sustaining the habitat of forest-dependent birds [18,85]. Accordingly, the AI maintains the
253 habitat amount of seed sources and dispersers in the 600-m buffer size, where the OGF is low
254 (24.97 ± 10.68). This is supported by the positive effects of fragmentation within similar buffer sizes on
255 specialist birds (564 m), primates (594-956 m) and seed rain (800 m) in HMTLs [16,60,62,86]. These
256 species can optimize their foraging by including nearby patches within their home range as they
257 become spatially closer [61,87]. Thus, seedling α -diversity persists through species colonization and/or
258 recolonization from nearby patches (i.e. landscape supplementation dynamic) [70,88].

259 Although having non-significant effects, the scales of effect of OGF (300-500-m; Table S4) are
260 like those observed for birds (564 m and 1261 m) and primates (200-600-m) [60,62]. Moreover, the
261 scale of effect of a negative association between ENN and seedling richness (1200 m; Table S4) is
262 consistent with the positive effect of OGF on seed rain richness (1244 ± 142 m; mean \pm SE) [16]. This
263 supports the role of habitat amount in driving seedling richness through seed dispersers at smaller
264 spatial scales and through colonization and/or extinction dynamics at larger spatial scales [16].

265 Secondly, the negative effect of SF on α -diversity is associated with the replacement of old-
266 growth forest tree species by secondary forest species in the seed rain [9,23,68]. Furthermore, the
267 richness decline of old-growth forest species is also associated to the limited movement of bird
268 dispersers through SF within similar buffer sizes (500-564 m) [60,87]. Following seedling

269 establishment, microclimatic alterations at forest edges promote the recruitment of disturbance-tolerant
270 species and the mortality of shade-tolerant seedlings [22,68]. Thus, our results suggest that the
271 secondary forest matrix reduced seedlings α -diversity through limiting seed arrival and the seedling
272 survival of shade-tolerant species, while promoting the proliferation of disturbance-tolerant species,
273 such as *I. punctata*.

274

275 4.2. Landscape effects on β -diversity

276

277 The negative association between $^{1}\beta$ - $^{2}\beta$ -diversity and SF and AI indicates that matrix
278 composition and patch clumping have homogenizing effects on seedling assemblages through
279 abundance alterations. We suggest this homogenization is driven by the input of successional-tree
280 species at larger spatial scales and the reduction of habitat heterogeneity, seed dispersal and seedling
281 predation at smaller scales.

282 The scale of effect of SF (1300-m) indicates that secondary forests are influencing tree and
283 seedling composition, a process observed elsewhere [9,23,67,68]. In the Amazon rainforest, the
284 abundance of successional tree species increases in patch edges adjacent to secondary vegetation [67].
285 The convergence and/or divergence of tree assemblages among patches and their long-term trajectories
286 of floristic change are driven by the extension and composition of the surrounding forest regrowth
287 [67,68,89]. The latter are shaped by land-use history, abandonment age, forest area, and surrounding
288 land-use types [90–92]. Our results, and the homogeneous land-use types in our study site (extensive
289 cattle ranching), suggests that SF is converging seedling composition through the input of successional-
290 tree species at larger scales. This supports the role of the SF as a strong driver of biotic homogenization
291 [9,13].

292 Additionally, the scale of effect of the negative association between AI and $^{1}\beta$ - $^{2}\beta$ -diversity
293 suggests a homogenizing effect of the habitat and inter-patch seed dispersal in the absence of terrestrial
294 mammals. According to the “biotic differentiation hypothesis” the limited exchange of seeds and the
295 differences of disturbance regimes across disaggregated forest patches promote a floristic
296 differentiation in highly deforested landscapes [59,68]. The establishment of a wider array of species is
297 facilitated due to the greater variety of conditions and a less evenly distributed number of individuals
298 among dominant species [18,59]. Furthermore, the inverse relationship between $^{0}\alpha$ -diversity and $^{1}\beta$ - $^{2}\beta$ -
299 diversity through AI within similar buffer sizes (600-m and 500-m, respectively), suggests the absence
300 of terrestrial mammals. Exclusion experiments have shown that terrestrial seed and seedling predators
301 reduce seedling $^{0}\alpha$ -diversity and the abundance of dominant species at the local scale [24,93].
302 Herbivorous mammal foraging also promotes β -diversity of dominant species through seed dispersal at
303 larger spatial scales [24,26,94]. Terrestrial mammals’ richness is positively associated with OGF in
304 similar buffer sizes than the observed AI effects (564 m) [27]. The above suggests an insufficient
305 habitat amount for frugivore and browsing mammals at these spatial scales. Alongside terrestrial
306 mammals decline, the positive effects of forest fragmentation on generalist and birds and bats sustain
307 seedling $^{0}\alpha$ -diversity through local seed dispersal (Section 4.1).

308 Furthermore, EC affected $^{0}\beta$ -diversity exclusively, supporting our assumption about the role of
309 functional connectivity for sustaining β -diversity at local scale. This is consistent with the relationship
310 between tree $^{0}\beta$ -diversity decline and dispersal constraints of shade-tolerant species in highly
311 fragmented landscapes [59]. In addition, the scale of effect of EC (800-m) is within the range observed
312 for matrix quality effects on patch occupancy by terrestrial mammals in HMTLs [27,28,95]. These
313 findings support the assumption the matrix drives functional connectivity of seed dispersers at smaller
314 spatial scales [16]. It is noteworthy that the observed scale of effect of EC (800-m) is similar to those of

315 matrix contrast observed for understory plants (797.88-m) and seed rain abundance (800±128 m) in
316 other HMTLs of Mexico [16,35].

317

318 4.3. Conclusions and conservation implications

319

320 Our findings strengthened the evidence suggesting that conservation actions should be focused
321 on preventing forest loss and promoting functional connectivity for maintaining forest regeneration
322 [14,16,35]. The spatial extents for these actions should range to 500 and 800-m around patches.
323 Accordingly, we recommend that policy interventions require preserving small OGF patches and
324 diversifying the agricultural matrix. Implementing laws that restrict forest clearing and that promote
325 sustainable forest management through payment for ecosystem services' schemes can prevent further
326 deforestation and the maintenance of remaining patches [1,96,97].

327 Additionally, our results also support the positive effects of fragmentation [19] for seedling β -
328 diversity. Accordingly, promoting configurational patterns that increase habitat amount and improving
329 matrix quality can be achieved through land-sharing schemes of smallholder agriculture [19,98]. This is
330 supported by trend scenarios where crop intensification, the reduction of cattle ranching expansion, and
331 the diversification of small-scale agroecosystems can reduce forest biodiversity loss in HMTLs
332 [96,99,100].

333 Although our study was restricted to a single region, the study site represents a scenario of
334 severely deforested and fragmented landscapes (less than 25% of forest cover), where the surrounding
335 matrix is very homogeneous. Deforestation trends indicate that these landscapes will dominate HMTLs
336 in the short term, even in the most conservative scenarios [101]. Therefore, our findings are
337 representative of the ongoing conditions of HMTLs

338 Furthermore, the strong association between α -diversity with landscape composition and
339 configuration; and β -diversity with landscape configuration and connectivity is consistent with
340 landscape structure effects on birds and arboreal and terrestrial mammals [27,60,62,87,95]. These
341 faunal assemblages regulate key ecological interactions, particularly seed dispersal and seed/seedling
342 predation [24,93,102]. Therefore, the decline of forest-dependent fauna could alter seedling diversity
343 and its long-term ecological functions, potentially compromising the ecosystem integrity of HMTLs.
344 The above highlights the critical role of maintaining the original fauna by increasing habitat amount
345 and functional connectivity. Nonetheless, connectivity assessments regarding these fauna assemblages
346 are scant, and the components of matrix vegetation involved in functional connectivity are unknown.
347 This topic represents a very important avenue for future research.

348

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350

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360 References

361

- 362 1. IPBES. Global assessment report on biodiversity and ecosystem services of the
363 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Brondizio
364 ES, Settele J, Díaz S, Ngo HT, editors. Bonn, Germany: IPBES Secretariat; 2019.
- 365 2. Alroy J. Effects of habitat disturbance on tropical forest biodiversity. *Proc Natl Acad Sci*.
366 2017;114: 6056–6061. doi:10.1073/pnas.1611855114
- 367 3. Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA, Peres CA, et al. Prospects for
368 tropical forest biodiversity in a human-modified world. *Ecol Lett*. 2009;12: 561–582.
369 doi:10.1111/j.1461-0248.2009.01294.x
- 370 4. Kim DH, Sexton JO, Townshend JR. Accelerated deforestation in the humid tropics from the
371 1990s to the 2000s. *Geophysical Research Letters*. John Wiley & Sons, Ltd; 2015. pp. 3495–
372 3501. doi:10.1002/2014GL062777
- 373 5. Denslow JS. Tropical Rainforest Gaps and Tree Species Diversity. *Annu Rev Ecol Syst*.
374 1987;18: 431–451. doi:10.1146/annurev.es.18.110187.002243
- 375 6. Galetti M, Bovendorp RS, Guevara R. Defaunation of large mammals leads to an increase in
376 seed predation in the Atlantic forests. *Glob Ecol Conserv*. 2015;3: 824–830.
377 doi:10.1016/j.gecco.2015.04.008
- 378 7. Webb CO, Peart DR. Seedling Density Dependence Promotes Coexistence of. *Ecology*.
379 1999;80: 2006–2017.
- 380 8. Harms KEE, Wright SJJ, Calderón O, Hernández A, Herre EA a. Pervasive density-dependent
381 recruitment enhances seedling diversity in a tropical forest. *Nature*. 2000;404: 493–5.

382 doi:10.1038/35006630

383 9. Tabarelli M, Peres CA, Melo FPL. The “few winners and many losers” paradigm revisited:
384 Emerging prospects for tropical forest biodiversity. *Biol Conserv.* 2012;155: 136–140.

385 doi:10.1016/j.biocon.2012.06.020

386 10. Park DS, Razafindratsima OH. Anthropogenic threats can have cascading homogenizing effects
387 on the phylogenetic and functional diversity of tropical ecosystems. *Ecography (Cop).* 2019;42:
388 148–161. doi:10.1111/ecog.03825

389 11. Galetti M, Dirzo R. Ecological and evolutionary consequences of living in a defaunated world.
390 *Biol Conserv.* 2013;163: 1–6. doi:10.1016/j.biocon.2013.04.020

391 12. Perfecto I, Vandermeer J. Biodiversity conservation in tropical agroecosystems: A new
392 conservation paradigm. *Ann N Y Acad Sci.* 2008;1134: 173–200. doi:10.1196/annals.1439.011

393 13. Arroyo-Rodríguez V, Melo FPL, Martínez-Ramos M, Bongers F, Chazdon RL, Meave JA, et al.
394 Multiple successional pathways in human-modified tropical landscapes: new insights from forest
395 succession, forest fragmentation and landscape ecology research. *Biol Rev.* 2017;92: 326–340.
396 doi:10.1111/brv.12231

397 14. Santo-Silva EE, Almeida WR, Melo FPL, Zickel CS, Tabarelli M. The nature of seedling
398 assemblages in a fragmented tropical landscape: Implications for forest regeneration. *Biotropica.*
399 2013;45: 386–394. doi:10.1111/btp.12013

400 15. Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, et al.
401 Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation*
402 *Biology.* John Wiley & Sons, Ltd (10.1111); 2002. pp. 605–618. doi:10.1046/j.1523-
403 1739.2002.01025.x

404 16. San-José M, Arroyo-Rodríguez V, Jordano P, Meave JA, Martínez-Ramos M. The scale of

- 405 landscape effect on seed dispersal depends on both response variables and landscape predictor.
406 *Landsc Ecol.* 2019; 1–12. doi:10.1007/s10980-019-00821-y
- 407 17. Charles LS, Dwyer JM, Chapman HM, Yadok BG, Mayfield MM. Landscape structure mediates
408 zoochorous-dispersed seed rain under isolated pasture trees across distinct tropical regions.
409 *Landsc Ecol.* 2019; 1–16. doi:10.1007/s10980-019-00846-3
- 410 18. Radford JQ, Bennett AF, Cheers GJ. Landscape-level thresholds of habitat cover for woodland-
411 dependent birds. *Biol Conserv.* 2005;124: 317–337. doi:10.1016/j.biocon.2005.01.039
- 412 19. Fahrig L. Ecological Responses to Habitat Fragmentation Per Se. *Annu Rev Ecol Evol Syst.*
413 2017;48: annurev-ecolsys-110316-022612. doi:10.1146/annurev-ecolsys-110316-022612
- 414 20. Fahrig L. Rethinking patch size and isolation effects: The habitat amount hypothesis. Triantis K,
415 editor. *J Biogeogr.* 2013;40: 1649–1663. doi:10.1111/jbi.12130
- 416 21. Benitez-Malvido J, Martinez-Ramos M. Influence of Edge Exposure on Tree Seedling Species
417 Recruitment in Tropical Rain Forest Fragments1. *Biotropica.* 2003;35: 530–541.
418 doi:10.1111/j.1744-7429.2003.tb00609.x
- 419 22. Benitez-Malvido J. Impact of forest fragmentation on seedling abundance in a tropical rain
420 forest. *Conserv Biol.* 1998;12: 380–389. doi:10.1046/j.1523-1739.1998.96295.x
- 421 23. Laurance WF, Nascimento HEM, Laurance SG, Andrade AC, Fearnside PM, Ribeiro JEL, et al.
422 Rain forest fragmentation and the proliferation of successional trees. *Ecology.* 2006;87: 469–
423 482. doi:10.1890/05-0064
- 424 24. Villar N, Siqueira T, Zipparro VB, Farah F, Schmaedecke G, Hortenci L, et al. The cryptic
425 regulation of diversity by functionally complementary large tropical forest herbivores. Edwards
426 D, editor. *J Ecol.* 2019; 1365-2745.13257. doi:10.1111/1365-2745.13257

- 427 25. Kurten EL. Cascading effects of contemporaneous defaunation on tropical forest communities.
428 Biol Conserv. 2013;163: 22–32. doi:10.1016/j.biocon.2013.04.025
- 429 26. Fragoso JM V, Silvius KM, Correa JA. Long-distance seed dispersal by tapirs increase seed
430 survival and aggregates tropical trees. Ecology. 2003;84: 1998–2006. doi:10.1890/01-0621
- 431 27. Garmendia A, Arroyo-Rodríguez V, Estrada A, Naranjo EJ, Stoner KE. Landscape and patch
432 attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. J
433 Trop Ecol. 2013;29: 331–344. doi:10.1017/S0266467413000370
- 434 28. Cassano CR, Barlow J, Pardini R. Large Mammals in an Agroforestry Mosaic in the Brazilian
435 Atlantic Forest. Biotropica. 2012;44: 818–825. doi:10.1111/j.1744-7429.2012.00870.x
- 436 29. Jackson HB, Fahrig L. Are ecologists conducting research at the optimal scale? Glob Ecol
437 Biogeogr. 2015;24: 52–63. doi:10.1111/geb.12233
- 438 30. Jost L. Partitioning diversity into independent alpha and beta components. Ecology. 2007;88:
439 2427–2439. doi:10.1890/06-1736.1
- 440 31. Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L. What determines the spatial extent of
441 landscape effects on species? Landsc Ecol. 2016;31: 1177–1194. doi:10.1007/s10980-015-0314-
442 1
- 443 32. Martin AE. The Spatial Scale of a Species' Response to the Landscape Context Depends on
444 which Biological Response You Measure. Curr Landsc Ecol Reports. 2018;3: 23–33.
445 doi:10.1007/s40823-018-0030-z
- 446 33. Suárez-Castro AF, Simmonds JS, Mitchell MGE, Maron M, Rhodes JR. The Scale-Dependent
447 Role of Biological Traits in Landscape Ecology: A Review. Curr Landsc Ecol Reports. 2018;3:
448 12–22. doi:10.1007/s40823-018-0031-y

- 449 34. Jackson HB, Fahrig L. What size is a biologically relevant landscape? *Landsc Ecol.* 2012;27:
450 929–941. doi:10.1007/s10980-012-9757-9
- 451 35. Hernández-Ruedas MA, Arroyo-Rodríguez V, Morante-Filho JC, Meave JA, Martínez-Ramos
452 M. Fragmentation and matrix contrast favor understory plants through negative cascading effects
453 on a strong competitor palm. *Ecol Appl.* 2018;28: 1546–1553. doi:10.1002/eap.1740
- 454 36. Pennington TD, Sarukhán J. Árboles tropicales de México. Manual para la identificación de las
455 principales especies. 3rd ed. Mexico City: Universidad Nacional Autónoma de México; 2005.
- 456 37. González-Espinosa M, Ramírez-Marcial N, Ruiz-Montoya L. Diversidad biológica en Chiapas.
457 Colegio de la Frontera Sur: Consejo de Ciencia y Tecnología del Estado de Chiapas, Plaza y
458 Valdéz, editors. México; 2005.
- 459 38. Myers N, Mittermeier R a, Mittermeier CG, da Fonseca G a, Kent J. Biodiversity hotspots for
460 conservation priorities. *Nature.* 2000;403: 853–8. doi:10.1038/35002501
- 461 39. Kolb M, Galicia L. Scenarios and story lines: drivers of land use change in southern Mexico.
462 *Environ Dev Sustain.* 2018;20: 681–702. doi:10.1007/s10668-016-9905-5
- 463 40. Carabias J, De la Maza J, Cadena R. Conservación y desarrollo sustentable en la Selva
464 Lacandona: 25 años de actividades y experiencia. Mexico City: Natura y Ecosistemas
465 Mexicanos; 2015.
- 466 41. Sánchez-Gallen I, Álvarez-Sánchez FJ, Benítez-Malvido J. Structure of the advanced
467 regeneration community in tropical rain forest fragments of Los Tuxtlas, Mexico. *Biol Conserv.*
468 2010;143: 2111–2118. doi:10.1016/j.biocon.2010.05.021
- 469 42. Martínez E, Ramos-A. CH, Chiang F. Lista florística de la Lacandona, Chiapas. *Bot Sci.* 1994;0:
470 99–177. doi:10.17129/botsci.1430

- 471 43. Sousa M. Adiciones al género *Inga* para la flora Mesoamericana. *Acta botánica Mex.* 2009;89:
472 25–41.
- 473 44. Ibarra-Manríquez G, Cornejo-Tenorio G. Diversidad de frutos de los árboles del bosque tropical
474 perennifolio De México. *Acta botánica Mex.* 2010;104: 51–104.
- 475 45. Ibarra-Manríquez G, Martínez Ramos M, Oyama K. Seedling functional types in a lowland rain
476 forest in Mexico. *Am J Bot.* 2001;88: 1801–1812. doi:10.2307/3558356
- 477 46. Durán-Fernández A, Aguirre-Rivera JR, García-Pérez J, Levy-Tacher S, De Nova-Vázquez JA.
478 Inventario florístico de la comunidad lacandona de Nahá, Chiapas, México. *Bot Sci.* 2016;94:
479 105–121. doi:10.17129/botsci.248
- 480 47. Ibarra-Manriquez G, Oyama K. Ecological Correlates of Reproductive Traits of Mexican Rain
481 Forest Trees. *Am J Bot.* 1992;79: 383. doi:10.2307/2445150
- 482 48. Jordano P. Fruits and frugivory. 2nd ed. In: Fenner M, editor. *Seeds: the ecology of regeneration*
483 *in plant communities.* 2nd ed. Wallingford, U.K.: CABI Publishing; 2000. pp. 125–166.
- 484 49. Missouri Botanical Garden. Tropicos.org. 2019 [cited 4 Jun 2019]. Available:
485 <https://www.tropicos.org/>
- 486 50. Chao A, Ma KH, Hsieh TC, Chiu C-H. User's Guide for Online Program SpadeR (Species-
487 richness Prediction And Diversity Estimation in R). Taiwan; 2016.
- 488 51. Chao A, Lee SM. Estimating the number of classes via sample coverage. *J Am Stat Assoc.*
489 1992;87: 210–217. doi:10.1080/01621459.1992.10475194
- 490 52. Chao A, Jost L. Coverage-based rarefaction and extrapolation: Standardizing samples by
491 completeness rather than size. *Ecology.* 2012;93: 2533–2547. doi:10.1890/11-1952.1
- 492 53. Jost L. Entropy and diversity. *Oikos.* 2006;113: 363–375. doi:10.1111/j.2006.0030-

- 493 1299.14714.x
- 494 54. Jost L. The relation between evenness and diversity. *Diversity*. 2010;2: 207–232.
495 doi:10.3390/d2020207
- 496 55. Tuomisto H. A diversity of beta diversities: Straightening up a concept gone awry. Part 1.
497 Defining beta diversity as a function of alpha and gamma diversity. *Ecography (Cop)*. 2010;33:
498 2–22. doi:10.1111/j.1600-0587.2009.05880.x
- 499 56. Chao A, Chiu CH, Hsieh TC. Proposing a resolution to debates on diversity partitioning.
500 *Ecology*. 2012;93: 2037–2051. doi:10.1890/11-1817.1
- 501 57. Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. vegan:
502 Community Ecology Package. 2.3-3. 2019. Available: [https://cran.r-](https://cran.r-project.org/web/packages/vegan/index.html)
503 [project.org/web/packages/vegan/index.html](https://cran.r-project.org/web/packages/vegan/index.html)
- 504 58. GRASS Development Team. Geographic Resources Analysis Support System (GRASS GIS)
505 Software, Version 7.2. 2017. Available: <http://grass.osgeo.org>
- 506 59. Arroyo-Rodríguez V, Rös M, Escobar F, Melo FPL, Santos BA, Tabarelli M, et al. Plant β -
507 diversity in fragmented rain forests: Testing floristic homogenization and differentiation
508 hypotheses. Kitzberger T, editor. *J Ecol*. 2013;101: 1449–1458. doi:10.1111/1365-2745.12153
- 509 60. Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, de Freitas SM, Fahrig L.
510 Impact of landscape composition and configuration on forest specialist and generalist bird
511 species in the fragmented Lacandona rainforest, Mexico. *Biol Conserv*. 2015;184: 117–126.
512 doi:10.1016/j.biocon.2015.01.014
- 513 61. Ordóñez-Gómez JD, Arroyo-Rodríguez V, Nicasio-Arzeta S, Cristóbal-Azkarate J. Which is the
514 appropriate scale to assess the impact of landscape spatial configuration on the diet and behavior
515 of spider monkeys? *Am J Primatol*. 2015;77: 56–65. doi:10.1002/ajp.22310

- 516 62. Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernández G. Drivers of the spatial
517 scale that best predict primate responses to landscape structure. *Ecography (Cop)*. 2018;41:
518 2027–2037. doi:10.1111/ecog.03632
- 519 63. Galán-Acedo C, Arroyo-Rodríguez V, Estrada A, Ramos-Fernández G. Forest cover and matrix
520 functionality drive the abundance and reproductive success of an endangered primate in two
521 fragmented rainforests. *Landsc Ecol*. 2019;34: 147–158. doi:10.1007/s10980-018-0753-6
- 522 64. Umetsu F, Paul Metzger J, Pardini R. Importance of estimating matrix quality for modeling
523 species distribution in complex tropical landscapes: a test with Atlantic forest small mammals.
524 *Ecography (Cop)*. 2008;31: 359–370. doi:10.1111/j.0906-7590.2008.05302.x
- 525 65. San-José M, Arroyo-Rodríguez V, Sánchez-Cordero V. Association between small rodents and
526 forest patch and landscape structure in the fragmented Lacandona rainforest, Mexico. *Trop
527 Conserv Sci*. 2014;7: 413–432. doi:10.1177/194008291400700304
- 528 66. Harper KA, Macdonald SE, Burton PJ, Chen J, Euskirchen NIES, Brososke KD, et al. Edge
529 Influence on Forest Structure and Composition in Fragmented Landscapes. *Conserv Biol*.
530 2005;19: 768–782.
- 531 67. Nascimento HEM, Andrade ACS, Camargo JLC, Laurance WF, Laurance SG, Ribeiro JEL.
532 Effects of the Surrounding Matrix on Tree Recruitment in Amazonian Forest Fragments.
533 *Conserv Biol*. 2006;20: 853–860. doi:10.1111/j.1523-1739.2006.00344.x
- 534 68. Laurance WF, Nascimento HEMM, Laurance SG, Andrade A, Ewers RM, Harms KE, et al.
535 Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. Bennett
536 P, editor. *PLoS One*. 2007;2: e1017. doi:10.1371/journal.pone.0001017
- 537 69. Ewers RM, Banks-Leite C. Fragmentation impairs the microclimate buffering effect of tropical
538 forests. *PLoS One*. 2013;8: e58093. doi:10.1371/journal.pone.0058093

- 539 70. Dunning JB, Danielson BJ, Pulliam HR. Ecological processes that affect populations in complex
540 landscapes. *Oikos*. 1992;65: 169–175. doi:10.2307/3544901
- 541 71. He HS, DeZonia BE, Mladenoff DJ. An aggregation index (AI) to quantify spatial patterns of
542 landscapes. *Landsc Ecol*. 2000;15: 591–601. doi:10.1023/A:1008102521322
- 543 72. Rayfield B, Fortin MJ, Fall A. Connectivity for conservation: A framework to classify network
544 measures. *Ecology*. 2011;92: 847–858. doi:10.1890/09-2190.1
- 545 73. Stevens SM, Husband TP. The influence of edge on small mammals: evidence from Brazilian
546 Atlantic forest fragments. *Biol Conserv*. 1998;85: 1–8. doi:10.1016/S0006-3207(98)00003-2
- 547 74. Li BL, Archer S. Weighted mean patch size: A robust index for quantifying landscape structure.
548 *Ecol Modell*. 1997;102: 353–361. doi:10.1016/S0304-3800(97)00071-9
- 549 75. Zuckergberg B, Desrochers A, Hochachka WM, Fink D, Koenig WD, Dickinson JL. Overlapping
550 landscapes: A persistent, but misdirected concern when collecting and analyzing ecological data.
551 *J Wildl Manage*. 2012;76: 1072–1080. doi:10.1002/jwmg.326
- 552 76. Cleary KA, Waits LP, Finegan B. Agricultural intensification alters bat assemblage composition
553 and abundance in a dynamic Neotropical landscape. *Biotropica*. 2016;48: 667–676.
554 doi:10.1111/btp.12327
- 555 77. Crawley MJ. *The R Book*. 2nd ed. John Wiley & Sons, Ltd.; 2013.
- 556 78. Gallardo-Cruz JA, Meave JA, González EJ, Lebrija-Trejos EE, Romero-Romero MA, Pérez-
557 García EA, et al. Predicting tropical dry forest successional attributes from space: Is the key
558 hidden in image texture? *PLoS One*. 2012;7: e30506. doi:10.1371/journal.pone.0030506
- 559 79. Fox J, Weisberg S. *An R Companion to Applied Regression*. 2nd ed. Thousand Oaks: SAGE
560 Publications; 2011.

- 561 80. Kutner MH, Nachtsheim C, Neter J, Li W. Applied linear statistical models. 5th ed. McGraw-
562 Hill; 2005.
- 563 81. Barton K. MuMIn: Multi-Model Inference. R Packag version 1421. 2018.
- 564 82. Burnham KP, Anderson DR. Model Selection and Multimodel Inference: A Practical
565 Information-Theoretic Approach (2nd ed). Ecological Modelling. Springer-Verlag; 2002.
566 doi:10.1016/j.ecolmodel.2003.11.004
- 567 83. R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna,
568 Austria; 2018. Available: <https://www.r-project.org/>
- 569 84. Ricci B, Franck P, Valantin-Morison M, Bohan DA, Lavigne C. Do species population
570 parameters and landscape characteristics affect the relationship between local population
571 abundance and surrounding habitat amount? Ecol Complex. 2013;15: 62–70.
572 doi:10.1016/j.ecocom.2013.02.008
- 573 85. Bennett AF, Radford JQ, Haslem A. Properties of land mosaics: Implications for nature
574 conservation in agricultural environments. Biol Conserv. 2006;133: 250–264.
575 doi:10.1016/j.biocon.2006.06.008
- 576 86. Jesus FM, Pivello VR, Meirelles ST, Franco GADC, Metzger JP. The importance of landscape
577 structure for seed dispersal in rain forest fragments. Partel M, editor. J Veg Sci. 2012;23: 1126–
578 1136. doi:10.1111/j.1654-1103.2012.01418.x
- 579 87. Kormann UG, Hadley AS, Tschardt T, Betts MG, Robinson WD, Scherber C. Primary
580 rainforest amount at the landscape scale mitigates bird biodiversity loss and biotic
581 homogenization. Maron M, editor. J Appl Ecol. 2018;55: 1288–1298. doi:10.1111/1365-
582 2664.13084
- 583 88. Tschardt T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, et al. Landscape

- 584 moderation of biodiversity patterns and processes - eight hypotheses. *Biol Rev.* 2012;87: 661–
585 685. doi:10.1111/j.1469-185X.2011.00216.x
- 586 89. Ewers RM, Andrade A, Laurance SG, Camargo JLJL, Lovejoy TE, Laurance WF. Predicted
587 trajectories of tree community change in Amazonian rainforest fragments. *Ecography (Cop).*
588 2017;40: 26–35. doi:10.1111/ecog.02585
- 589 90. Zermeño-Hernández I, Méndez-Toribio M, Siebe C, Benítez-Malvido J, Martínez-Ramos M.
590 Ecological disturbance regimes caused by agricultural land uses and their effects on tropical
591 forest regeneration. Hölzel N, editor. *Appl Veg Sci.* 2015;18: 443–455. doi:10.1111/avsc.12161
- 592 91. Zermeño-Hernández I, Pingarroni A, Martínez-Ramos M. Agricultural land-use diversity and
593 forest regeneration potential in human- modified tropical landscapes. *Agric Ecosyst Environ.*
594 2016;230: 210–220. doi:10.1016/j.agee.2016.06.007
- 595 92. Chazdon RL. Tropical forest recovery: Legacies of human impact and natural disturbances.
596 *Perspect Plant Ecol Evol Syst.* 2003;6: 51–71. doi:10.1078/1433-8319-00042
- 597 93. Camargo-Sanabria AA, Mendoza E, Guevara R, Martínez-Ramos M, Dirzo R. Experimental
598 defaunation of terrestrial mammalian herbivores alters tropical rainforest understorey diversity.
599 *Proc R Soc B Biol Sci.* 2014;282. doi:10.1098/rspb.2014.2580
- 600 94. Fragoso JM V., Huffman JM. Seed-dispersal and seedling recruitment patterns by the last
601 Neotropical megafaunal element in Amazonia, the tapir. *J Trop Ecol.* 2000;16: 369–385.
602 doi:10.1017/S0266467400001462
- 603 95. Thornton DH, Branch LC, Sunkist ME. The relative influence of habitat loss and
604 fragmentation: Do tropical mammals meet the temperate paradigm? *Ecol Appl.* 2011;21: 2324–
605 2333. doi:10.1890/10-2124.1
- 606 96. DeClerck FAJ, Chazdon R, Holl KD, Milder JC, Finegan B, Martinez-Salinas A, et al.

- 607 Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and
608 future. *Biol Conserv.* 2010;143: 2301–2313. doi:10.1016/j.biocon.2010.03.026
- 609 97. Ricketts TH, Daily GC, Ehrlich PR, Michener CD. Economic value of tropical forest to coffee
610 production. *Proc Natl Acad Sci U S A.* 2004;101: 12579–12582. doi:10.1073/pnas.0405147101
- 611 98. Pazos-Almada B, Bray DB. Community-based land sparing: Territorial land-use zoning and
612 forest management in the Sierra Norte of Oaxaca, Mexico. *Land use policy.* 2018;78: 219–226.
613 doi:10.1016/j.landusepol.2018.06.056
- 614 99. Chazdon RL, Harvey CA, Komar O, Griffith DM, Ferguson BG, Martínez-Ramos M, et al.
615 Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical
616 landscapes. *Biotropica.* 2009;41: 142–153. doi:10.1111/j.1744-7429.2008.00471.x
- 617 100. IPBES. The Regional Assessment Report on Biodiversity and Ecosystem Services for the
618 Americas. Rice J, Seixas CS, Zaccagini ME, Bedoya-Gaitán M, Valderrama N, editors. Bonn,
619 Germany; 2018.
- 620 101. Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödiger E, et al. Global patterns of
621 tropical forest fragmentation. *Nature.* 2018;554: 519–522. doi:10.1038/nature25508
- 622 102. Breitbach N, Laube I, Steffan-Dewenter I, Böhning-Gaese K. Bird diversity and seed dispersal
623 along a human land-use gradient: high seed removal in structurally simple farmland. *Oecologia.*
624 2010;162: 965–76. doi:10.1007/s00442-009-1547-y

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631 Figure 1. Location of the study area in the Lacandona forest in Chiapas in southeastern Mexico (a). We
632 show the location of the 16 study forest fragments (black) in the Marqués de Comillas region (b). The
633 13 buffer sizes around the geographic center of the focal patch are also indicated (c).

634

635 Figure 2. Importance and relative effects of the landscape metrics included in 95% set of models for α -
636 (a and c) and β -diversity (b and d) in a fragmented tropical forest in southeastern Mexico. The
637 importance of each variable is represented by the sum of the Akaike weights ($\sum w_i$). The effects of each
638 covariate were estimated through a model-averaged parameter estimate of information-theoretic-based
639 model selection and multimodel inference. The whiskers represent the unconditional standard error
640 (USE) and the highlighted bars indicate the influential variables (those for which the USE did not
641 include zero). The landscape metrics are the aggregation index (AI), the edge contrast index (EC), the
642 mean distance between patches (ENN), the percentage of old-growth forest (OGF), and the percentage
643 of secondary forest (SF). The subscript numbers indicate the scale of effect of each variable.

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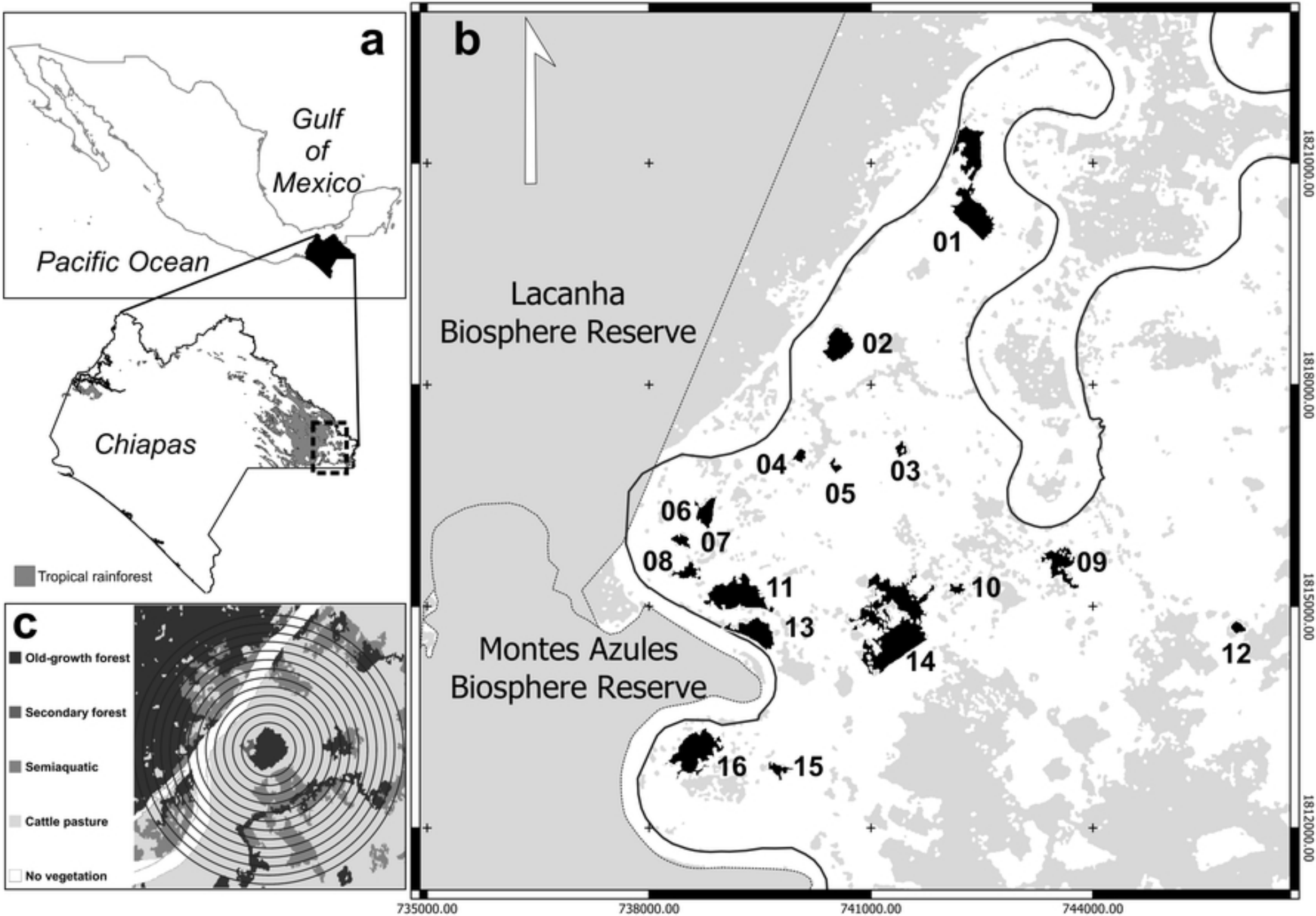


Figure 1

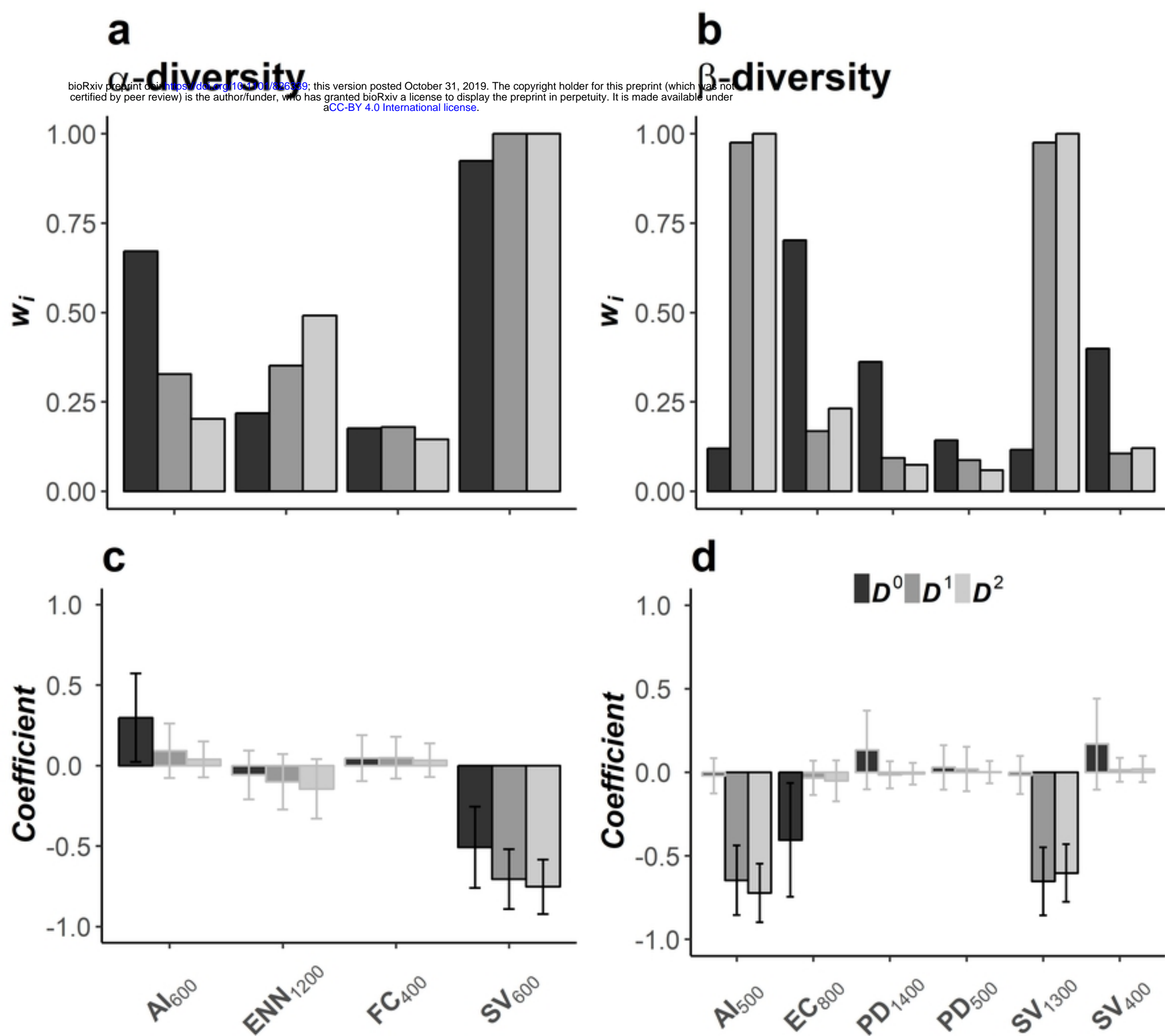


Figure 2