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Heterogenization of remaining biodiversity in fragmented tropical forests across agricultural landscapes — [Source link](#)

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1 **Heterogenization of remaining biodiversity in fragmented tropical forests**
2 **across agricultural landscapes**

3

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15

16 **Author contributions:**

17 ‘CYV conceived the idea with considerable inputs from RRR, MFS and TS. CYV,

18 MFS and DSBR performed data compilation; MFS and DSBR modeled species

19 distributions; CYV and TS analyzed the data and led the writing of the manuscript; all

20 authors edited the drafts and gave final approval for publication.

21 **Abstract**

22 The increasing worldwide interest on the conservation of tropical forests
23 reflects the conversion of over 50% of their area into agricultural lands and other uses.
24 Understanding the distribution of remaining biodiversity across agricultural landscapes
25 is an essential task to guide future conservation strategies. To understand the long-
26 term effects of fragmentation on biodiversity, we investigated whether forest fragments
27 in southeastern Brazil are under a taxonomic homogenization or heterogenization
28 process. We estimated pre-deforestation species richness and composition based on
29 a Species Distribution Modelling approach, and compared them to the observed
30 patterns of α - and β -diversity. In particular, we asked (i) if changes in β -diversity reveal
31 convergence or divergence on species composition; (ii) if these changes are similar
32 between forest fragments in Strictly Protected Areas (SPAs) (n=20) and within private
33 lands (n=367) and in different regions of the state (West, Center, and Southeast). We
34 detected steep reductions in observed local species richness in relation to our modeled
35 predictions, and this was particularly true among forest fragments in non-protected
36 private lands. The higher observed β diversity indicated an overall biotic
37 heterogenization process, consistent with the idea that the originally diverse
38 vegetation is now reduced to small and isolated patches, with unique disturbance
39 histories and impoverished communities derived from a large regional species pool.
40 Since conservation of biodiversity extends beyond the boundaries of strictly Protected
41 Areas, we advocate forest fragments are valuable for conservation in agricultural
42 landscapes, with particular relevance for private lands, which represent the most
43 exposed and neglected share of what is left.

44

45 **Key words:** Biodiversity conservation, Human-modified landscapes, Protected areas,
46 Private lands

47 INTRODUCTION

48 Tropical forests are known for holding a substantial portion of the world's
49 terrestrial biodiversity (Myers et al. 2000; Chazdon, Harvey, et al. 2009; Slik et al.
50 2015), yet over 50% of its original area was converted into agricultural lands or other
51 uses, with prospects for an increasing agricultural expansion in tropical developing
52 countries (Hansen et al. 2013; Laurance et al. 2014). Understanding the distribution of
53 remaining biodiversity across human-modified landscapes (HMLs) and what has
54 changed after forest conversion are essential questions to guide future conservation
55 strategies (Tabarelli et al. 2010; Melo, Arroyo-Rodríguez, et al. 2013; Laurance et al.
56 2014; Socolar et al. 2016). In HMLs, tropical forest fragments comprehend a variety of
57 different sized habitats, including forests that never experienced clear cutting or severe
58 impacts (*i.e.* primary forests), and the full spectrum of degraded forests that are
59 regenerating after extraction, fire or abandonment of croplands and pastures, among
60 other previous land-uses (*i.e.* secondary forests) (Melo, Arroyo-Rodríguez, et al. 2013;
61 Malhi et al. 2014). A very narrow fraction of these forest fragments are under restrictive
62 protected areas, where biodiversity conservation is tangible to a limited extent (Andam
63 et al. 2008; Joppa et al. 2008; Coetzee et al. 2014). In this context, the variety of forest
64 fragments located within private lands not only represent the largest share of what is
65 left (Gardner et al. 2009; Sparovek et al. 2012; Soares-Filho et al. 2014; Mendenhall
66 et al. 2016), but also the most neglected. These fragments are rarely explicitly targeted
67 in conservation programs, as the focus is usually on avoiding deforestation (Chazdon,
68 Harvey, et al. 2009; Barlow et al. 2016). Several studies have shown that secondary
69 forests may play an important role in conservation (Santos et al. 2007, Chazdon et al.
70 2009; Dent & Wright 2009; Tabarelli et al. 2012), as they hold a depleted but relevant
71 portion of biodiversity even within HMLs. Abundant evidence is available for birds (Karp
72 et al. 2012; Emer et al. 2018), mammals (Galetti et al. 2009; Pardini et al. 2010; Beca
73 et al. 2017) and plants (Arroyo-Rodríguez et al. 2008; Lima et al. 2015; Sfair et al.
74 2016; Farah et al. 2017).

75 The effects of habitat loss and fragmentation on biodiversity have been
76 intensively studied over the past three decades, with a primary focus on more local
77 scales (Karp et al. 2012; Vellend et al. 2013; Dornelas et al. 2014; Malhi et al. 2014;
78 Newbold et al. 2015; Barlow et al. 2016). There has been an increase on studies
79 focusing on broader extensions, based on the assumption that we cannot properly

80 understand the consequences of deforestation if disregarding the influence of entire
81 landscapes over local processes (Malhi et al. 2014). Also, beyond the intuitive interest
82 on species richness loss, an emerging issue of interest is how community composition
83 responds to fragmentation along spatial gradients and periods of time (Arroyo-
84 Rodríguez et al. 2013; Solar et al. 2015; Morante-Filho, Arroyo-Rodríguez, et al. 2015;
85 Collins et al. 2017; Olden et al. 2018). Measures of the variation in species composition
86 among sites (β) can indicate if communities are converging or diverging in response to
87 fragmentation, providing relevant information on the maintenance of regional diversity
88 (Socolar et al. 2016).

89 Some studies have demonstrated that forest fragmentation and degradation
90 result into biotic homogenization (Vellend et al. 2007; Lôbo et al. 2011; Karp et al.
91 2012; Marcelo Tabarelli et al. 2012; Püttker et al. 2015; Zwiener et al. 2017), *i.e.* the
92 convergence of biotas in time and space, in which communities may suffer a
93 simplification of their genetic, taxonomic and functional diversities (McKinney &
94 Lockwood 1999; Olden & Rooney 2006). The rationale is that more ecologically
95 specialized species (“losers”) are locally extinct, while a much narrower sub-set of
96 generalists, with high dispersal abilities (“winners”), override them (Lôbo et al. 2011;
97 Marcelo Tabarelli et al. 2012; Mendenhall et al. 2016). This process results in
98 impoverished communities that represent sub-sets of a larger pool of species,
99 translated by reduced β -diversity and high contribution of the nestedness component
100 on β diversity. The predominance of nestedness suggests conservation efforts might
101 focus on the richest sites, provided they are connected to support viable communities
102 (Howe 2014; Socolar et al. 2016; Emer et al. 2018). An opposite consequence to
103 fragmentation and degradation occurs when communities diverge on composition over
104 time and space (*i.e.* enhanced β diversity) because they suffer different frequencies
105 and levels of disturbances combined with dispersal limitations and environmental
106 heterogeneity, resulting into biotic heterogenization (Dornelas et al. 2014; Solar et al.
107 2015; Sfair et al. 2016; Catano et al. 2017; Collins et al. 2017). In this scenario,
108 widespread regional diversity conservation is only possible if targeting multiple sites.

109 Very few studies of plant community changes in response to fragmentation
110 evaluate β -diversity patterns based on temporal replicates (Lôbo et al. 2011; Dornelas
111 et al. 2014; Haddad et al. 2015; Collins et al. 2017); most of them adopt a space-for-
112 time approach (*e.g.*, disturbed x undisturbed) regardless of the fact that distinct sites

113 could reflect distinct pre-disturbance conditions (Collins et al. 2017). In addition to the
114 lack of temporal replicates, severely deforested landscapes may not be suitable for the
115 space-for-time approach when in the absence of large forest remnants or high forest-
116 covered regions to represent undisturbed ecosystems. For that matter, environmental
117 niche modeling (ENM) and species distribution modeling (SDM) can be useful to
118 provide species' spatial occurrence disregarding the effects of anthropogenic
119 disturbances, which is a major driver of community composition changes (Malhi et al.
120 2014, Catano et al. 2017). Since ENM is based on the niche concept and considers
121 environmental conditions as the primary influence over the establishment of a given
122 species (De Marco Junior & Siqueira 2009), it results in maps representing the
123 geographic space where the abiotic conditions are appropriate (Peterson & Soberon
124 2012). Distinctly from ENM, which disregards dispersal/colonization limitations and
125 biotic interactions, SDM restricts the model calibration to accessible areas, incorporating
126 dispersal issues into analyses and producing maps where a focal species may
127 potentially occur, with varying degrees of suitability (De Marco Junior & Siqueira 2009;
128 Peterson & Soberon 2012). For community-level modeling, further methodologies are
129 available to adjust the over-prediction of the number of species coexisting at a given
130 location (Guisan & Rahbek 2011; Calabrese et al. 2014; Gavish et al. 2017). Therefore,
131 these approaches combined can be used to generate expectations of what
132 communities would look like, in terms of species composition, if they were not disturbed
133 by land use conversion.

134 In recent years, Brazil has stood out among tropical developing countries
135 for its environmental engagement, which resulted in the exceptional decline in
136 deforestation rates during 2000-2012 (Hansen et al. 2013; Loyola 2014), despite the
137 fact that it already has 30% of its total area occupied by agricultural lands (Martinelli et
138 al. 2010). In Sao Paulo state, southeastern Brazil, which includes two biodiversity
139 hotspots (Atlantic Forest and Cerrado) (Myers et al. 2000; Laurance 2009),
140 deforestation has taken place during the last three centuries (Metzger 2009), and
141 surveys only became a common practice in the last 30 years (Haddad et al. 2015;
142 Renato Augusto Ferreira de Lima et al. 2015). With a very long history of land
143 conversion for agricultural purposes, most remaining vegetation is comprised by small
144 forest fragments (i.e. <50ha) (Ribeiro et al. 2009), representing an unique opportunity
145 to understand the long-term effects of fragmentation on biodiversity. The purpose of

146 our study was to evaluate whether the woody assemblages on forest fragments are
147 under a taxonomic homogenization or heterogenization process in response to habitat
148 fragmentation. For that matter, we estimated pre-deforestation species richness and
149 composition based on a Species Distribution Modelling approach, and compared them
150 to the observed patterns of α - and β -diversity. In particular, we asked (i) if changes in
151 β -diversity indicate convergent or divergent composition; (ii) if these changes are
152 similar between forest fragments under strict protection or within private lands and in
153 different regions of the state. In the hyper-fragmented landscapes of this study, we
154 expected to find lower mean values of α -diversity within private lands relative to strictly
155 Protected Areas. Additionally, because of intrinsic environmental heterogeneity
156 strengthened by fragmentation disturbances, we expected an overall increase in β -
157 diversity, indicating a taxonomic differentiation process. This pattern should be
158 particularly more evident for unprotected forest fragments located within private lands,
159 where fragments are more susceptible to a broader range of recurrent disturbances
160 (Laurance et al. 2014; Malhi et al. 2014).

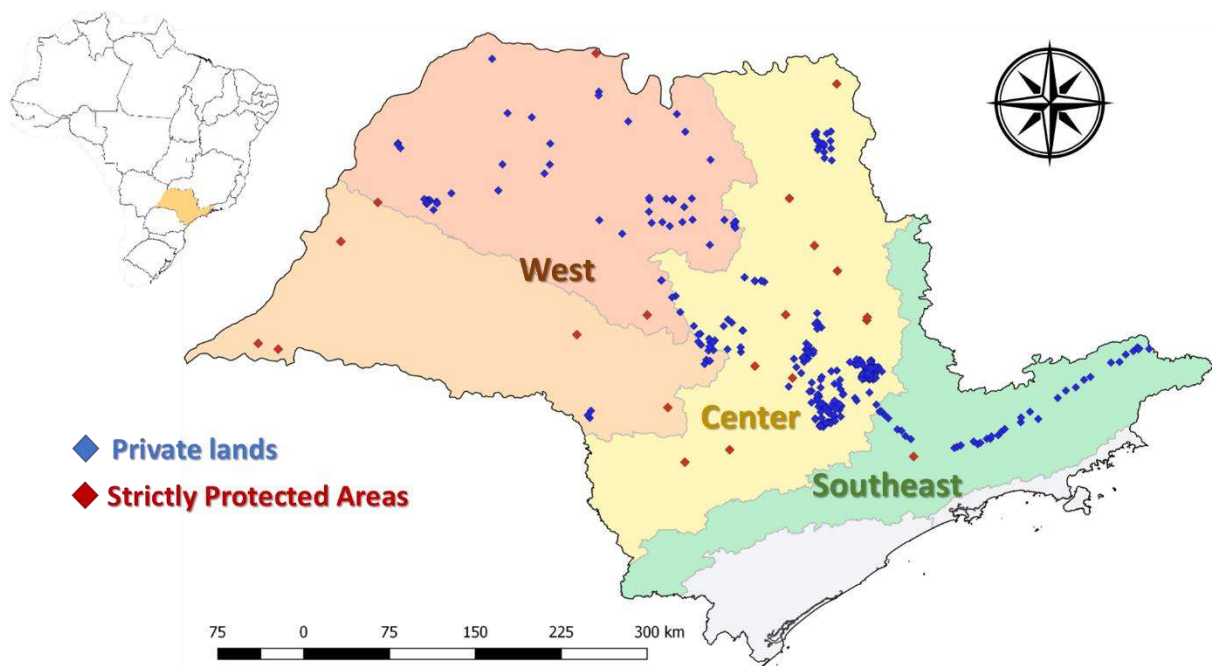
161

162 **METHODS**

163 **Study region**

164 The state of Sao Paulo is located within the range of two current global
165 hotspots, the Atlantic Forest and Cerrado (tropical savannas) (Myers et al. 2000). With
166 a long history of deforestation caused by timber extraction and agricultural cycles
167 (coffee, pasture, orange, sugarcane) (Metzger 2009), the São Paulo state case-study
168 may provide relevant insight about the long-term effects of habitat loss and
169 fragmentation on biodiversity, which can be useful for other tropical regions facing the
170 same threats (Laurance 2009). Both hotspots are poorly protected, with only 1.6% and
171 0.5% of Atlantic Forest and Cerrado's original area protected as strictly Protected
172 Areas (Durigan et al. 2006; Ribeiro et al. 2009; Carranza et al. 2014). The remaining
173 vegetation cover in the interior plateau (*i.e.* excluding coastal areas) ranges from 1 to
174 30% (São Paulo State Forest Inventory 2011), mostly located within private rural
175 properties (Gardner et al. 2009; Sparovek et al. 2012; Soares-Filho et al. 2014;
176 Mendenhall et al. 2016).

177 In order to facilitate analyses' interpretation along the extent region of this
178 study, we adopted the ecological regions defined by Setzer (1966), which divide the
179 state in 6 sub-regions based on climate, soil, topography and vegetation variables
180 (Setzer 1966). We excluded the south and north coastal areas because their forest
181 cover is well above the rest of the state. To meet a minimum of 30 localities per sub-
182 region, we joined Southwest and Northwest into one single "West" sub-region (**Figure**
183 **1**).



184

185 **Figure 1:** Distribution of forest fragments among regions in São Paulo state (Southeastern Brazil),
186 considering those in private lands (n=367) and strictly protected areas (n=20). Mean forest cover based
187 on São Paulo State Forest Inventory (2011): West = 6.5%, Center= 10.9%, Southeast= 27.7%.

188

189 Regarding vegetation, we focused on the predominant seasonal semi-
190 deciduous forest (SSF), considering its transition to evergreen forests or forested
191 savannas (Cerradão) (Oliveira-Filho & Fontes 2000; Durigan & Ratter 2006), and all
192 other forest ecosystems included in this extension: swamp, alluvial and deciduous
193 forests. Despite the fact that these forests are influenced and determined by soil,
194 altitude and climatic conditions (Oliveira-Filho & Fontes 2000), their floristic
195 composition are strongly influenced by the surrounding vegetation (*e.g.* SSF), creating
196 complex transitional mosaics and continuum distribution of species (Kurtz et al. 2015;
197 Oliveira-Filho & Fontes 2000).

198 **Woody plant species occurrence data**

199 We chose to use woody plant species (*i.e.* trees and shrubs) in this study
200 because they represent a fundamental structure and functional component of forest
201 ecosystems, as they support food webs and represent a substantial proportion of
202 tropical diversity (Arroyo-Rodriguez et al. 2015; Slik et al. 2015). Based on a
203 compilation of 367 floristic surveys in private lands (more details in Rodrigues et al.
204 2011 and Farah et al. 2017), we initially defined a species pool of 921 species. To
205 enhance our sample of the environmental space occupied by these species and to
206 improve modelling outcomes, we retrieved complementary national occurrence data
207 for these species from *SpeciesLink* (<http://splink.cria.org.br/>) and NeoTropTree
208 (<http://prof.icb.ufmg.br/treetlan/>) (Oliveira-Filho 2017). Finally, we selected 691
209 species occurring in more than 10 localities along the Brazilian territory, which
210 comprised 114,740 records.

211 We also gathered available checklists for 20 strictly Protected Areas within
212 the study region (**Figure 1**) following the same criteria regarding forest types as those
213 applied to select forests in private lands. We did not use the strictly Protected Areas
214 localities to build species distribution models due to the lack of precision on their
215 geographical coordinates, varying from a random point within their boundaries to the
216 municipality centroid. We compiled the floristic surveys available at Fundação Florestal
217 (<http://fflorestal.sp.gov.br>) and Instituto Florestal (<http://iflorestal.sp.gov.br>), both
218 related to the São Paulo State Environmental Secretariat, and WWF Protected Areas'
219 Observatory (<http://observatorio.wwf.org.br/>). Species names were standardized using
220 the Plantminer web tool (www.plantminer.com) (Carvalho et al. 2010), based on Flora
221 do Brasil (www.floradobrasil.jbrj.gov.br) (Flora_do_Brasil_2020) and The Plant List
222 (www.theplantlist.org/). Complementary queries were performed on The Missouri
223 Botanical Gardens (www.tropicos.org). According to these databases, we excluded
224 any exotic and unidentified species from final compilation.

225

226 **Environmental data**

227 We compiled 22 environmental predictors with spatial resolution of 1km²
228 and summarized them by using a Principal Component Analysis (PCA) considering

229 1,000 randomly distributed points within Sao Paulo state. Pairs of variables with scores
230 > 111 (absolute value) were verified to avoid multicollinearity (correlation <0.7) finally
231 selecting 6 variables with the highest PCA scores (**Appendix 1**).

232

233 **Environmental Niche Modeling and Species Distribution Modeling**

234 Environmental Niche Models (ENM) are statistical models that relate focal
235 species occurrence to associated environmental conditions, generating correlative
236 rules that allow extrapolation and prediction of occupancy patterns over wide
237 geographic extents, representing a valuable tool for conservationist purposes (De
238 Marco Junior & Siqueira 2009; Angelieri et al. 2016; Gavish et al. 2017; Guisan et al.
239 2013). We applied a Species Distribution Model (SDM) approach by restricting ENM
240 to accessible areas, aiming to presume the distribution range of species if they were
241 not affected by habitat loss, fragmentation and disturbance. In other words, if species'
242 distribution were primarily defined by abiotic conditions (*i.e.*, environmental niche), in
243 the lack of constraints imposed by altered habitat and landscape structure (*e.g.*,
244 fragmentation and patch isolation) (Peterson & Soberon 2012). As ENM and SDM can
245 be based on the same sets of mathematical algorithms, occurrence data and
246 environmental variables (Peterson & Soberon 2012), they are near-synonymous: the
247 main difference is that SDM implies on some sort of restriction over ENM, which will
248 be further detailed; for the purpose of this study, we hereafter will refer to our modeling
249 approach only as SDM.

250 We built the SDM for each species using the Model-R framework (Sánchez-
251 Tapia et al. 2018) with a three-fold cross validation procedure, meaning that two
252 partitions were used for parameter estimation and algorithm training, and one to
253 evaluate the model's accuracy. Random pseudo-absence points ($n_{\text{back}} = 1000$) were
254 sorted within a mean distance buffer, where the radius of the buffer was the mean
255 geographic distance between the occurrence points. If one species' records were less
256 than 20 km apart, they were rarefied to reduce effects of sampling bias and avoid
257 modelling overfitting (Elith et al. 2006; Zwiener et al. 2017).

258 In the Model-R framework, for each partition and algorithm a model was
259 built and its performance was tested by their True Skill Statistics (TSS) (Allouche et al.

260 2006). We previously tested several algorithms - BioClim, GLM, SVM, Random Forest,
261 MaxEnt – and selected the last two based on their overall performance (**Appendix 2**),
262 which was consonant to the results found by Diniz-filho et al. (2009). We then selected
263 Random Forest and MaxEnt partitions with TSS>0.4, and applied a threshold that
264 maximizes two error types: sensitivity (*i.e.* true presences) and specificity (*i.e.* true
265 absences) (Sánchez-Tapia et al. 2018). The resulting binary models were averaged
266 into a final model for each algorithm, and then combined into a final ensemble model
267 with an average threshold that maximizes TSS values (Sánchez-Tapia et al. 2018),
268 resulting in a final map indicating areas of probable presence. These maps were
269 primarily generated for all the Brazilian territory and then cropped for São Paulo State.

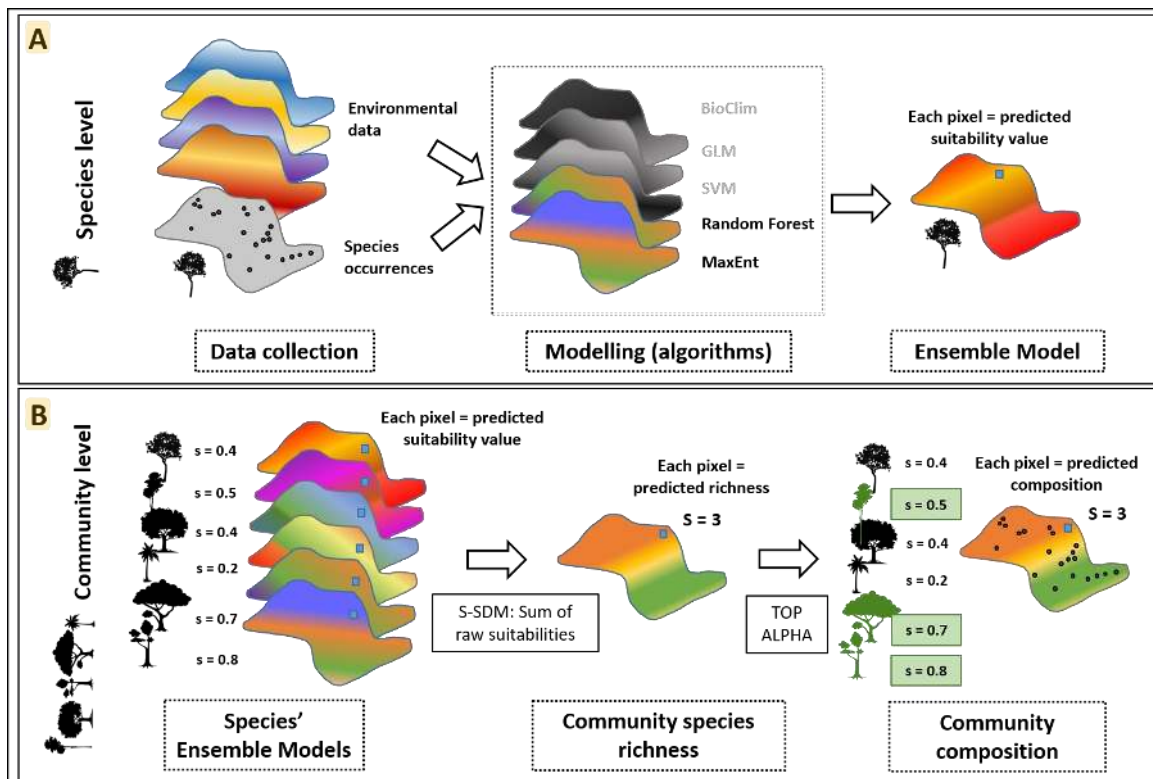
270

271 **Species richness and community composition**

272 Our analyses were based on two different type of information: the observed
273 species richness and community composition in each site and the species richness
274 and community composition predicted by SDM. The observed metrics were adjusted
275 to consider only modelled species, that is, species occurring in more than ten localities,
276 at least 20km apart and with a final ensemble model derived from Random Forest and
277 Maxent algorithms, using their partitions with TSS>0.4 (**Figure 2a**), as previously
278 detailed. This adjustment was necessary in order to make proper comparisons
279 between observed and predicted richness and compositions, and considered a final
280 sub-set of 663 woody species.

281 Species richness based on SDM can be predicted either by stacking
282 individual species-level models (Stacking SDM, S-SDM) or by modelling α -diversity
283 itself (Macroecological Models, MEM) (Gavish et al. 2017; Calabrese et al. 2014;
284 D'Amen et al. 2015; Guisan & Rahbek 2011). Since stacking binary presence/absence
285 SDM tend to overpredict richness, as it does not account for biotic interactions or filters
286 (Gavish et al. 2017; Guisan & Rahbek 2011), Calabrese *et al.* (2014) proposed S-SDM
287 corrections to reduce these overpredictions and concluded that if stacked correctly, S-
288 SDM are no worse than MEM. According to their findings, a corrected S-SDM approach
289 involves summing-up the raw predicted suitabilities for each locality instead of
290 summing-up their binary values (Calabrese et al. 2014; D'Amen et al. 2015) (**Figure**
291 **2b**). Hence, we inputted an average of the raw suitability values into the areas of

292 probable presence defined on the final ensemble models; the predicted community
 293 species richness is the sum of these values considering any given location (i.e. pixel).



294

295 **Figure 2:** Steps for species distribution modeling and for predicting community
 296 richness and composition at a given point (i.e. pixel). (A) Step 1: Species distribution
 297 modeling for each of the 663 species, considering Random Forest and MaxEnt
 298 algorithms and their partitions with True Skill Statistics (TSS) ≥ 0.4 . The final ensemble
 299 model indicate, for each pixel, the suitability of occurrence for one given species. (B)
 300 Step 2: The predicted community species richness at a given point results from the
 301 sum of the raw probabilities of occurrence (i.e., suitabilities not converted to binary
 302 values by any threshold) of targeted species. Step 3: The community composition
 303 results from the TOP ALPHA approach, which consists on ranking the species
 304 according to their suitabilities of occurrences and selecting species with the highest
 305 values until attaining the predicted richness (step 2).

306

307 Following the estimation of potential richness, we predicted site-level
 308 composition by adopting the “top alpha” approach (Gavish et al. 2017), where we
 309 ranked the species’ suitabilities of occurrence per site from the highest to the lowest
 310 values – based on their individual ensemble SDM – and then selected the top number
 311 of species that equals to the predicted potential richness per site (D’Amen et al. 2015;
 312 Gavish et al. 2017) (**Figure 2b**).

313

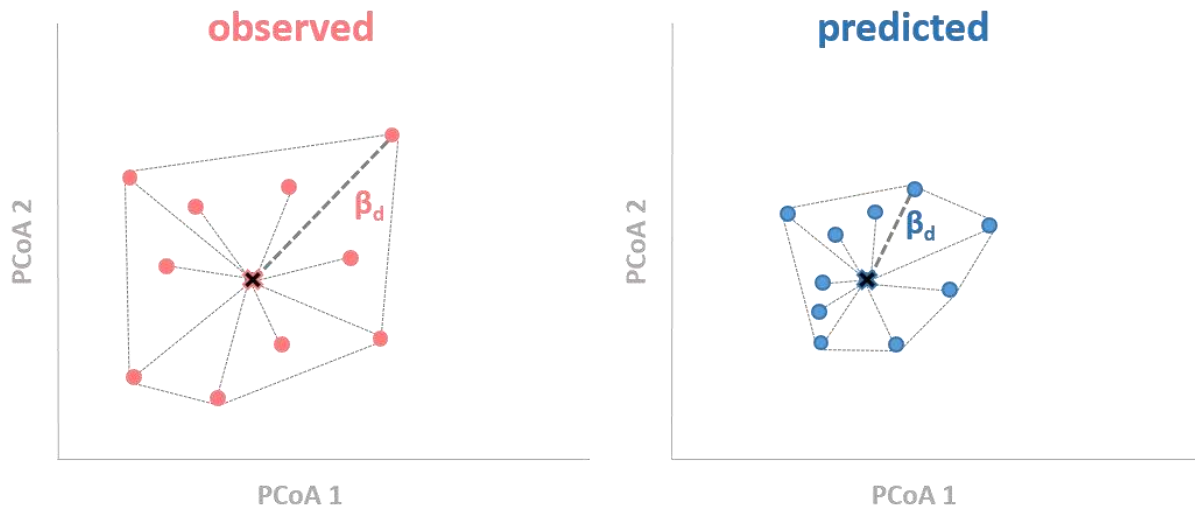
314 β -diversity analyses

315 The compositional variation among communities from site-to-site (β -
316 diversity) relates local diversity (α) to the regional species pool (γ) (Anderson et al.
317 2010). When evaluating the effects of habitat loss and fragmentation, changes on the
318 organization of biodiversity over space and time can reveal if biological
319 homogenization or heterogenization is taking place, an essential information to guide
320 conservation planning over regional diversity (Socolar et al. 2016; Arroyo-Rodríguez
321 et al. 2013; Püttker et al. 2015). Despite the valuable contribution from evaluating β -
322 diversity, its interpretation must be very cautious, as there are several ways to measure
323 and compare it (Koleff et al. 2003; Baselga et al. 2007; Jost 2007; Chao et al. 2012;
324 Jost et al. 2010; Anderson et al. 2006, 2010; Tuomisto 2010).

325 There is extensive debate regarding the interrelationships among α , β and
326 γ -diversity, in addition to measures for partitioning it (*i.e.* multiplicative or additive) and
327 statistical approaches to properly analyze β -diversity (Anderson et al. 2010). A
328 particular concern for our study is the fact that a great variety of metrics to estimate β -
329 diversity depend on α and γ diversity – and therefore on scale and sample size.
330 Considering that our samples represent a compilation of floristic surveys using distinct
331 methods and sampling effort, we decided to use a β -diversity metric that weights on
332 composition dissimilarities more than on richness differences (Koleff et al. 2003). For
333 that matter, we calculated pairwise Sorensen (β_{SOR}) and Simpson indices (β_{SIM}) among
334 sites, which indicate the overall variation on the species composition between pairs of
335 sites (β_{SOR}) and the variation related to its turnover component (β_{SIM}), reflecting the
336 replacement of species (Baselga 2010; Baselga et al. 2015; Socolar et al. 2016).

337 To evaluate differences between observed and predicted β -diversity, we: (i)
338 ran a Principal Coordinate Analysis (PCoA) based on the Simpson (β_{SIM}) observed
339 dissimilarity matrix (as the turnover component was the main contribution to total beta
340 diversity; see below); (ii) estimated the distance of each site (forest fragment) to the
341 group centroid in the multivariate ordination space generated by the PCoA (β_{d} , **Figure**
342 **3**); (iii) repeated steps (i) and (ii) using the SDM predicted species composition; and
343 (iv) compared mean observed β_{d} with mean predicted β_{d} with permutational paired t-
344 test. In this test, observed β_{d} values were paired with predicted β_{d} ones. β_{d} is
345 analogous to the local contribution to beta diversity (LCBD) proposed by Legendre and

346 De Cáceres (2013), since higher values of β_d represent higher distinctiveness of one
347 site (forest fragment) within a group. This metric with standard effect size allowed us
348 to test the null hypothesis that beta diversity does not differ among observed and
349 predicted communities.

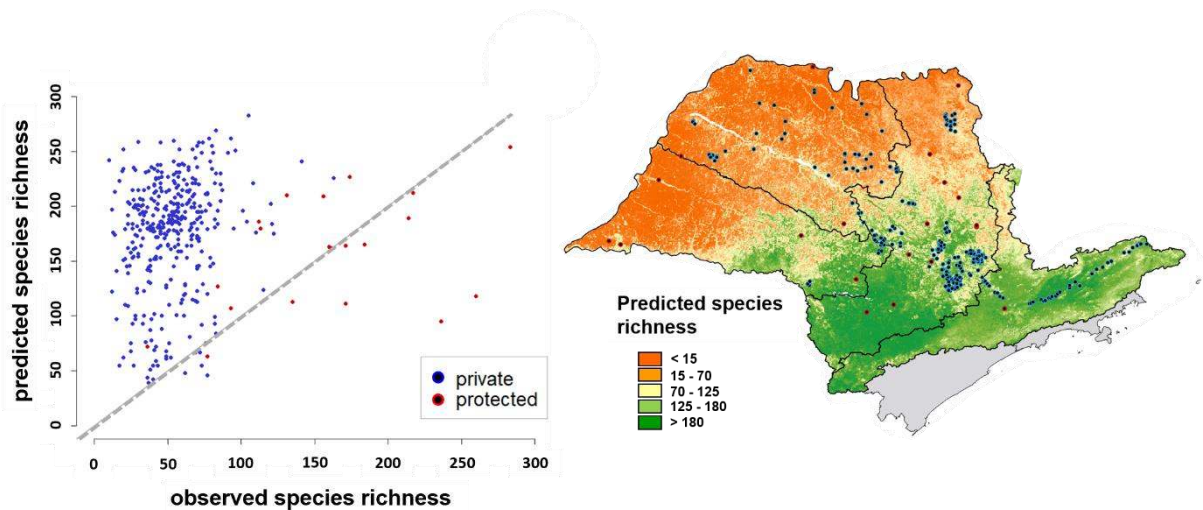


350
351 **Figure 3:** Hypothetical example of a multivariate ordination space describing the
352 distance (β_d) of a unit to the group centroid (central cross), considering the observed
353 (red) and the predicted (blue) species composition.

354

355 RESULTS

356 For the 663 woody species considered in this study, overall comparisons
357 revealed that predicted richness at the site level (α -diversity) was 3.8 times higher than
358 observed richness. This ratio was much lower when considering only strictly Protected
359 Areas, ranging around 1.0. In fact, the few forest fragments that presented increased
360 observed species richness in relation to predicted richness were mostly represented
361 by Protected Areas (**Figure 4**) (**Appendices 3 and 4**).



362

363 **Figure 4: (a)** Scatterplot relating the predicted and observed species richness at the
 364 site level, considering both protection types (strictly Protected Areas and Private
 365 lands). Dots below the line represent forest fragments with higher observed richness
 366 than predicted. **(b)** Predicted species richness map, calculated by summing the raw
 367 suitability of occurrence for each of the 663 woody species of this study regions.

368

369 Partition of total beta diversity (β_{SOR}) indicated a consistent higher contribution
 370 of turnover (β_{SIM}) to overall dissimilarity within regions and protection categories (**Table**
 371 **2**) (**Appendix 5**).

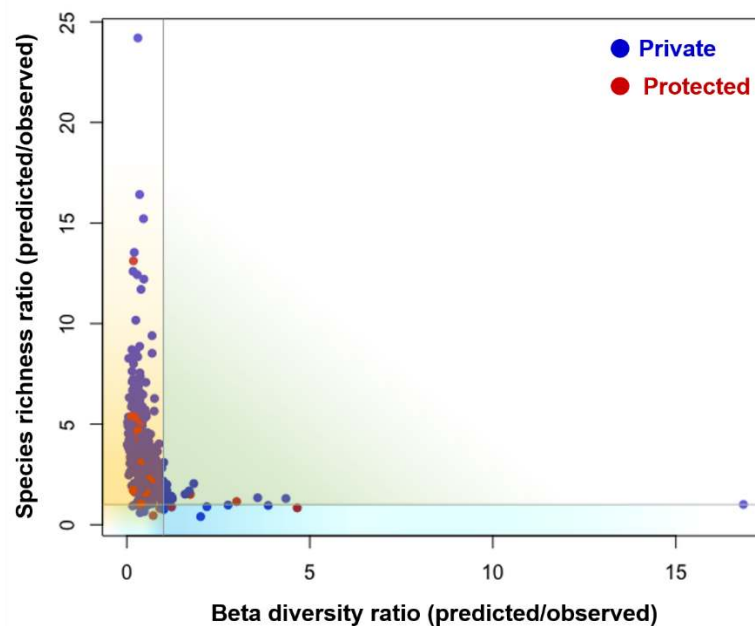
372 **Table 2:** Mean \pm standard deviation of total beta diversity (B_{SOR}) and its components
 373 turnover (B_{SIM}) and nestedness (B_{NES}) for distinct regions and categories,
 374 considering the observed (red) and the predicted (blue) species composition.

		B _{SOR}	B _{SIM}	B _{NES}	B _{SOR}	B _{SIM}	B _{NES}
	Center	0.73 \pm 0.12	0.63 \pm 0.17	0.10 \pm 0.11	0.35 \pm 0.21	0.27 \pm 0.19	0.08 \pm 0.07
Regions	Southeast	0.74 \pm 0.09	0.68 \pm 0.11	0.05 \pm 0.06	0.48 \pm 0.16	0.43 \pm 0.16	0.04 \pm 0.03
	West	0.76 \pm 0.12	0.65 \pm 0.16	0.11 \pm 0.11	0.48 \pm 0.16	0.32 \pm 0.16	0.16 \pm 0.11
Protection categories	Protected	0.61 \pm 0.15	0.48 \pm 0.16	0.13 \pm 0.11	0.58 \pm 0.17	0.48 \pm 0.18	0.11 \pm 0.08
	Private	0.76 \pm 0.12	0.69 \pm 0.15	0.07 \pm 0.08	0.46 \pm 0.23	0.36 \pm 0.21	0.10 \pm 0.09

375

376

377 We found that sites with lower predicted than observed β_{SOR} (ratio < 1) also
 378 had higher predicted than observed species richness (ratio > 1) (**Figure 5**), which
 379 indicates a correlation between local species loss and heterogenization.



380

381 **Figure 5:** Scatterplot relating the predicted/observed species richness ratio (vertical
 382 axis) and total beta diversity (β_{SOR}) ratio (horizontal axis). Sites (dots) above vertical
 383 value=1 and below horizontal value=1 (yellow quadrant) experienced local species
 384 loss and heterogenization (higher observed β_{SOR}) in comparison to predictions. Green
 385 quadrant represent sites that experienced local species loss and homogenization
 386 (lower observed β_{SOR}).

387

388 The mean observed distance to centroid (β_d) was significantly higher than the
 389 predicted β_d for all regions and for private lands, with strictly protected areas being the
 390 only exception (**Table 3; Figure 6**).

391 **Table 3:** Minimum, mean \pm standard deviation and maximum values of distance to
 392 centroid (β_d) for distinct regions and categories, considering the observed (red) and
 393 the predicted (blue) species composition.

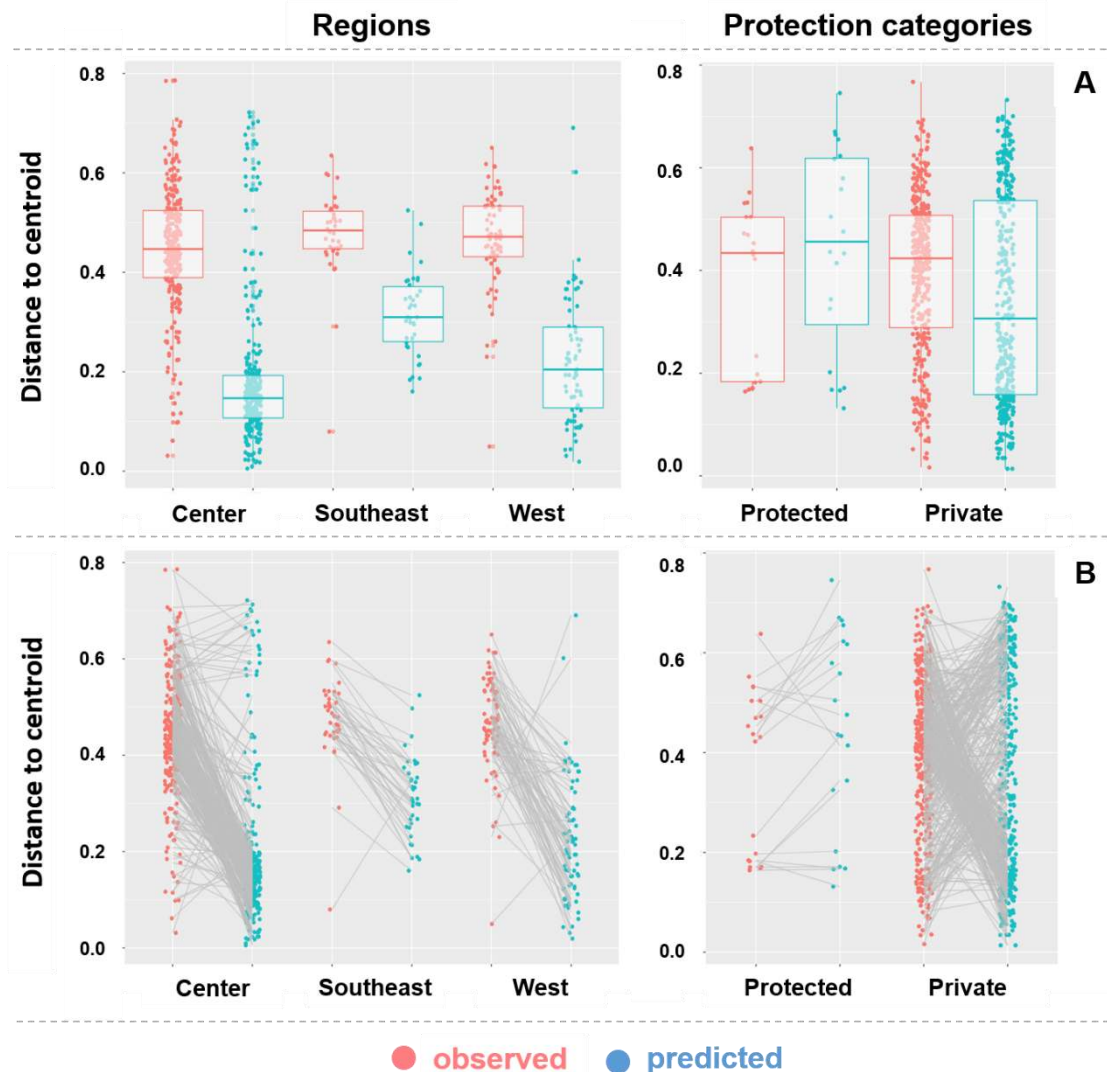
		Min.	Mean \pm SD	Max.	Min.	Mean \pm SD	Max.	t-value	P
	Center	0.03	0.45 \pm 0.12	0.79	0.01	0.18 \pm 0.15	0.72	26.18	<0.0001
Regions	Southeast	0.08	0.47 \pm 0.09	0.63	0.16	0.32 \pm 0.08	0.52	9.8	<0.0001
	West	0.05	0.46 \pm 0.10	0.65	0.02	0.22 \pm 0.13	0.69	12.28	<0.0001
Protection categories	Protected	0.16	0.37 \pm 0.16	0.64	0.13	0.44 \pm 0.19	0.75	0.29	0.75
	Private	0.02	0.39 \pm 0.15	0.78	0.01	0.34 \pm 0.20	0.73	31.79	<0.0001

394

395

396 Individual β_d values varied within regions and protection categories from
 397 almost zero to almost 0.8, especially in the central region (**Figure 6a**). Despite this
 398 variation, most observed-predicted pairs of sites showed an increase in β_d
 399 predicted to observed values (**Figure 6b**), indicating a clear trend for biotic
 400 heterogenization in the different regions. After splitting the data into protection

401 categories (all regions pooled), we found that the higher beta-diversity in the observed
402 data was due to an increase in β_d values in private lands, as there was no difference
403 between observed and predicted values in strictly protected areas. These results were
404 confirmed by the paired t-test (**Table 3**).



405

406 **Figure 6:** (a) Boxplots representing individual distances to centroid (β_d values)
407 considering the observed (red) and predicted (blue) datasets of different regions and
408 protection categories. Each point represents the distance from one site (forest
409 fragment) to the group centroid in a β_{sim} -based ordination space. (b) Grey lines
410 connect pairs of observed and predicted β_d values.

411

412 DISCUSSION

413 We detected a general loss on observed local diversity in relation to our
414 modeled predictions and this was particularly true among forest fragments in private

415 lands, where we registered consistent reductions in species richness. The higher β
416 diversity registered for the observed dataset imply an overall biotic heterogenization.
417 However, our study also exposes the complexity of this process, with evidence
418 indicating that both homogenization (positive observed-predicted pairwise slopes) and
419 heterogenization (negative observed-predicted pairwise slopes) are taking place in
420 these hyper-fragmented landscapes. Even though distinct regions of São Paulo state
421 were gradually occupied and converted along time – from the eastern coast towards
422 western countryside – all of them presented the same pattern: observed and predicted
423 beta diversity were significantly different, with lower mean values for the latter. This is
424 probably because of the results found among private lands, which represent almost
425 95% of our samples and drove the pattern registered for all state regions (*i.e.*,
426 heterogenization). As an exception, strictly Protected Areas had lower local species'
427 loss with no significant differences between observed and predicted β diversity,
428 suggesting they may be fulfilling, to some extent, their protection purpose.

429 Biodiversity changes in tropical ecosystems are extremely complex to
430 evaluate and understand, as they are scale and context dependent, differ among
431 taxonomic groups and ecosystems, and often respond differently to similar
432 environmental changes (Vellend et al. 2013; Dornelas et al. 2014; Newbold et al. 2015;
433 McGill et al. 2015; Boesing et al. 2018; Catano et al. 2017; Magurran et al. 2018). For
434 instance, recent studies found no evidence for systematic loss in local diversity
435 (Vellend et al. 2013; Dornelas et al. 2014), while several others indicate this is not true
436 for the tropics, where a variety of taxa experienced steep local species decreases in
437 human modified landscapes (Haddad et al. 2015; Mendenhall et al. 2016; Beca et al.
438 2017; Ceballos et al. 2017; Farah et al. 2017; Galetti et al. 2017; Barlow et al. 2018;
439 Bovendorp et al. 2018). Whereas the unprecedented level of forest degradation,
440 fragmentation and intensive land use have an undeniable contribution to immediate
441 and long-term local diversity loss (Haddad et al. 2015; Barlow et al. 2018), less is
442 known regarding how these disturbances modify and drive the community composition
443 along time and space, regardless of the recent growing interest and evidence on these
444 compositional shifts (Dornelas et al. 2014; Haddad et al. 2015; McGill et al. 2015;
445 Collins et al. 2017; Olden et al. 2018).

446 The comparison between observed and predicted species composition
447 revealed the idiosyncratic responses of β -diversity (*i.e.* homogenization and

448 heterogenization) in agricultural landscapes, which can be explained by several
449 mechanisms suggested by the literature. Studies that observed biotic homogenization
450 associate β diversity reduction to niche-selection processes, suggesting ecological
451 filtering overrides environmental heterogeneity (Vellend et al. 2007; Lôbo et al. 2011;
452 Marcelo Tabarelli et al. 2012; Arroyo-Rodríguez et al. 2013; Morante-Filho, Arroyo-
453 Rodríguez, et al. 2015; Püttker et al. 2015; Zwiener et al. 2017). This statement
454 assumes non-random local species extinctions occur because habitat fragmentation
455 affects species differently, according to traits such as rarity, life span, dispersal, and
456 reproductive mode (Haddad et al. 2015), supporting the proliferation of widespread,
457 short-lived and small-seeded species (*e.g.* pioneer species, generalists or “winners”
458 as defined by Tabarelli et al. 2012a) in detriment of rare and shade-tolerant species
459 (*e.g.* specialists or “losers”) (Lôbo et al. 2011; Marcelo Tabarelli et al. 2012; Arroyo-
460 Rodríguez et al. 2013; Morante-Filho, Arroyo-Rodríguez, et al. 2015; Zwiener et al.
461 2017). Additionally, non-random plant extinctions may also be related to selective
462 logging, which overharvest valuable hardwood species, and to the disappearance of
463 large and medium frugivores through overhunting and habitat loss, with cascading
464 effects over plant-frugivore interactions, species persistence, ecosystem services and
465 functioning in human-modified landscapes (Bello et al. 2015; Bovendorp et al. 2018).
466 All of these mechanistic explanations may be related to the homogenization registered
467 in our study region, where forest fragments are usually small and therefore exposed to
468 edge effects, with depleted plant-animal interactions – especially large-sized species
469 (Beca et al. 2017, Emer et al. 2018), and subject to recurrent fire and other
470 disturbances (Farah et al. 2017).

471 Overall, however, our results showed that biotic heterogenization is the
472 predominant process in our study region, accordingly to studies that found
473 compositional shifts heading towards divergent communities (Smart et al. 2006;
474 Dornelas et al. 2014; Solar et al. 2015; Sfair et al. 2016; Collins et al. 2017). In fact, a
475 meta-analysis carried by Catano *et al.* (2017) found 21 cases of heterogenization
476 among 22 studies evaluating herbaceous plants in disturbed/undisturbed grasslands
477 and savannas. Assuming the long history of forest degradation and fragmentation in
478 our study region as the main driver acting upon forest fragments, we refer to some
479 mechanisms that may explain why the studied communities were more heterogeneous
480 than compared to our modeled predictions. First, there is a combination of long-term

481 disturbances that impose constant selection pressures (*e.g.*, edge effects) with
482 occasional and contingent perturbations (*e.g.*, fires, windstorms etc.), resulting in
483 unique disturbance histories and shifts in the physical environment (*e.g.* microhabitat
484 conditions), that most likely enhance pre-disturbance compositional differences
485 (Haddad et al. 2015; Catano et al. 2017). Second, forest fragments in private lands are
486 more susceptible to disturbances due to the lack of formal and effective protection,
487 proven by their altogether smaller patch sizes (Ribeiro et al. 2009). They also represent
488 a greater variety of conditions that range from mature forests experiencing post-
489 fragmentation changes to regenerating secondary forests (Laurance et al. 2014; Malhi
490 et al. 2014; Farah et al. 2017). In common, they share reduced local species richness,
491 which together with a large regional species pool (*i.e.*, γ diversity) may create a
492 sampling effect; *i.e.*, a higher probability of more distinct composition between sites
493 when a small portion of the species pool (*i.e.*, low α diversity) is expected to occur in
494 any random community, inflating β diversity (Karp et al. 2012; Newbold et al. 2015).
495 The third explanation is particularly relevant in the studied hyper-fragmented
496 landscapes, where dispersal limitation due to patch isolation might play a dominant
497 role in making those communities such heterogeneous. This is supported by the strong
498 positive relation between local species richness and seed arrival in plant communities
499 (Myers & Harms 2009) and because dispersal limitation play a stronger role in
500 determining community assembly in tropical forests (Myers et al. 2013). More
501 specifically, Catano's *et al.* (2017) findings on how disturbance and dispersal interact
502 and alter community composition support that increased β -diversity in disturbed
503 landscapes occurs when dispersal is limited, challenging the hypothesis that
504 disturbances always homogenizes communities compositions through deterministic
505 environmental filtering, that is, selecting those species best able to survive within HMLs
506 (Vellend et al. 2007; Lôbo et al. 2011; Arroyo-Rodríguez et al. 2013; Püttker et al.
507 2015). Finally, other plausible mechanisms acting upon these forest fragments may be
508 related to the reduction in the number of individuals and thus in community size, turning
509 them more susceptible to ecological drift and other stochastic forces (Orrock & Watling
510 2010), and to competitive release arising from the removal of dominant species
511 (Catano et al. 2017).

512 Given that, by definition, proper evaluation of biotic homogenization or
513 heterogenization processes depend on quantifying changes in β diversity through

514 space and time (McKinney & Lockwood 1999; Olden & Rooney 2006; Olden et al.
515 2018), the use of Species Distribution Model proved valuable for predicting community
516 composition in the absence of habitat loss and fragmentation, serving as a temporal
517 surrogate in our study. However, we must acknowledge that our modeling approach
518 imposed some restrictions, notably the non-inclusion of rare or poorly-sampled species
519 and biotic interactions. That said, we do not expect that the overall trend registered
520 here - biotic heterogenization - would be affected by the absence of rare species
521 because their inclusion would most likely increase the differences among communities,
522 while biotic interactions were addressed by choosing a method to adjust or at least
523 reduce an overprediction bias related to the lack of biotic interactions (Calabrese et al.
524 2014; Gavish et al. 2017; Guisan & Rahbek 2011; D'Amen et al. 2017). Another caveat
525 is that the reduced local species richness among private lands may be related, to some
526 extent, to sampling effort. Since the floristic assessments that compose most of the
527 dataset used here aimed to quickly characterize the regional flora for restoration
528 purposes (Rodrigues et al. 2011), we applied preliminary analysis of incidence-based
529 estimated richness (e.g., Chao 2, Jackknife 1 and Jackknife 2 (Magurran 2013)) that
530 indicated satisfactory sampling effort for both private lands and strictly protected areas.
531 Furthermore, we chose β diversity metrics that focused on compositional changes to
532 alleviate the contribution of α diversity and eventual uneven sampling effort (Koleff et
533 al. 2003). With those considerations, we are confident that our results are consistent
534 and would not be much different from what we have shown here.

535 Our study highlights the complexity and idiosyncrasies of community
536 compositional shifts in hyper-fragmented landscapes, where both homogenization and
537 heterogenization processes were detected, with the latter prevailing as an overall
538 trend, especially in non-protected private lands. From an applied perspective, the
539 implication of biotic homogenization or heterogenization alone is not sufficient to
540 underpin conservation strategies, as its interpretation is not straightforward – human
541 disturbances can cause β diversity to increase, decrease or remain unchanged
542 (Socolar et al. 2016; Olden et al. 2018). However, the heterogenization process in our
543 study is coupled with a scenario where (i) the originally diverse vegetation is now
544 extremely reduced and fragmented, with small and isolated patches distributed within
545 an intensive agricultural matrix; (ii) forest fragments, especially in private lands,
546 represent unique disturbance histories that result in varying quality habitats, and often

547 in reduced local diversity derived from a large regional species pool (γ diversity); (iii)
548 community composition accumulate great variation among patches (high β diversity),
549 predominantly from turnover (*i.e.* replacement of species). Bringing these facts
550 together and recognizing that conservation of biodiversity extends far beyond the
551 boundaries of strictly Protected Areas, we advocate that all forest fragments are
552 valuable for conservation in HMLs, with particular relevance for private lands, which
553 represent the most exposed and neglected share of what is left (Gardner et al. 2009;
554 Mendenhall et al. 2016; Farah et al. 2017). Based on our results and supported by
555 many other studies, we understand there is enough information to develop an
556 evidence-based approach that should be considered in future management and
557 conservation plans. To foster and sustain biodiversity conservation in HMLs, we thus
558 recommend: (i) effective protection of strictly Protected Areas, which usually represent
559 the largest regional core areas (Joppa et al. 2008) and where compositional shifts
560 apparently are more stable; (ii) active restoration of forest fragments to enhance their
561 alpha diversity, through the management of hyper abundant species (*e.g.*, lianas)
562 (César et al. 2016; Estrada-Villegas & Schnitzer 2018) and reintroduction of lacking
563 groups of species (Garcia et al. 2014; Viani et al. 2015) (iii) active restoration of
564 corridors where the vegetation is degraded and natural regeneration is unlikely, aiming
565 to enhance forest cover and connectivity among forest fragments, allowing species to
566 disperse and persist (Howe 2014; Emer et al. 2018). Finally, considering the growing
567 development of more sustainable agricultural practices (Ferreira et al. 2012, Gonthier
568 et al. 2014) and alternatives for ecological restoration with profitable purposes (Pedro
569 H. S. Brancalion et al. 2012), we encourage the establishment of policies that foster a
570 feasible production model, aligned with the conservation of the remaining biodiversity.

571

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872 **APPENDICES**

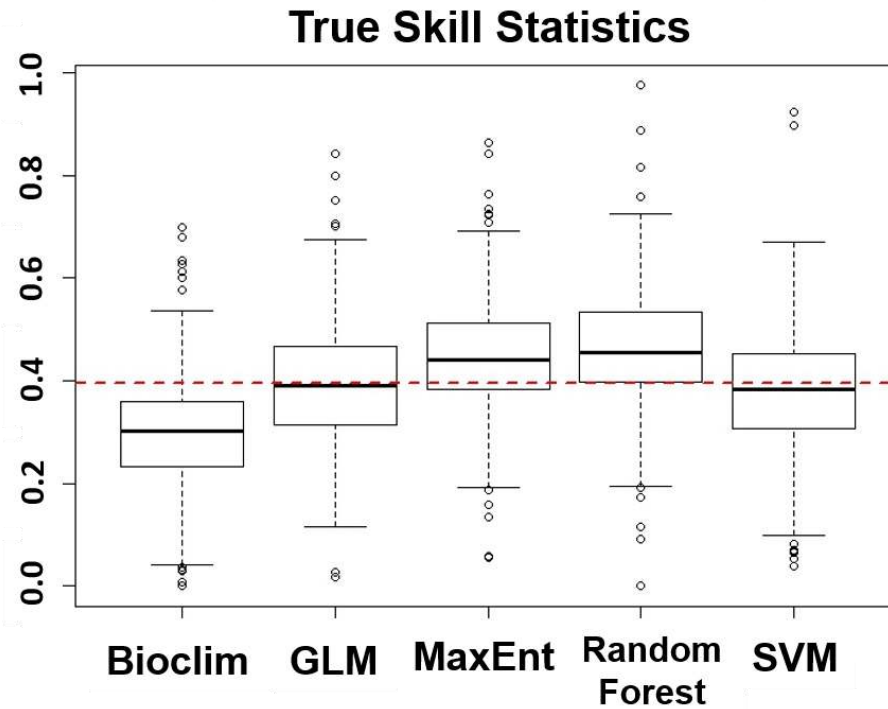
873 **Appendix 1:** Environmental layers used in the Principal Component Analysis (PCA)
 874 and (*) selected for modelling

Description	Short name		Source
Slope (declividade)	declividade_br		Ambdata
Height above nearest drain (HAND 50)	hand50_br		Ambdata
Altitude	altitude_br		Ambdata
Depth to bedrock (R horizon) up to 200 cm	Depth		SoilGrids
Soil organic carbon content (fine earth fraction) g/ kg	Carbon_cnt	*	SoilGrids
Clay content (0–2 µm) mass fraction (%)	Clay		SoilGrids
Silt content (2–50 µm) mass fraction (%)	Silt	*	SoilGrids
Sand content (50–2000 µm) mass fraction (%)	Sand		SoilGrids
Cation exchange capacity of soil in cmolc/kg	Cation		SoilGrids
Soil organic carbon stock in tonnes per ha	Carbon_stc		SoilGrids
Soil pH x 10 in H2O	pH_H2O	*	SoilGrids
Soil pH x 10 in KCl	pH_KCl		SoilGrids
Aridity Index	AI		CGIAR CSI
Actual Evapotranspiration	AET		CGIAR CSI
Potential Evapotranspiration	PET		CGIAR CSI
Precipitation (mm)	precip	*	WorldClim v.2
Solar radiation (kJ .m ⁻² .day ⁻¹)	srad	*	WorldClim v.2
Average temperature (°C)	tavg	*	WorldClim v.2
Maximum temperature (°C)	tmax		WorldClim v.2
Minimum temperature (°C)	tmin		WorldClim v.2
Water vapor pressure (kPa)	vapr		WorldClim v.2
Wind speed (m .s ⁻¹)	wind		WorldClim v.2

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877 **Appendix 2:** Boxplots (median \pm quartiles) of the True Skill Statistics (TSS)
 878 comparing partitions of previously tested algorithms used to generate the Species
 879 Distribution Models. Dashed red line indicates the selection criteria (TSS=0.4) applied
 880 to choose algorithms that composed the final ensemble model (MaxEnt and Random
 881 Forest).

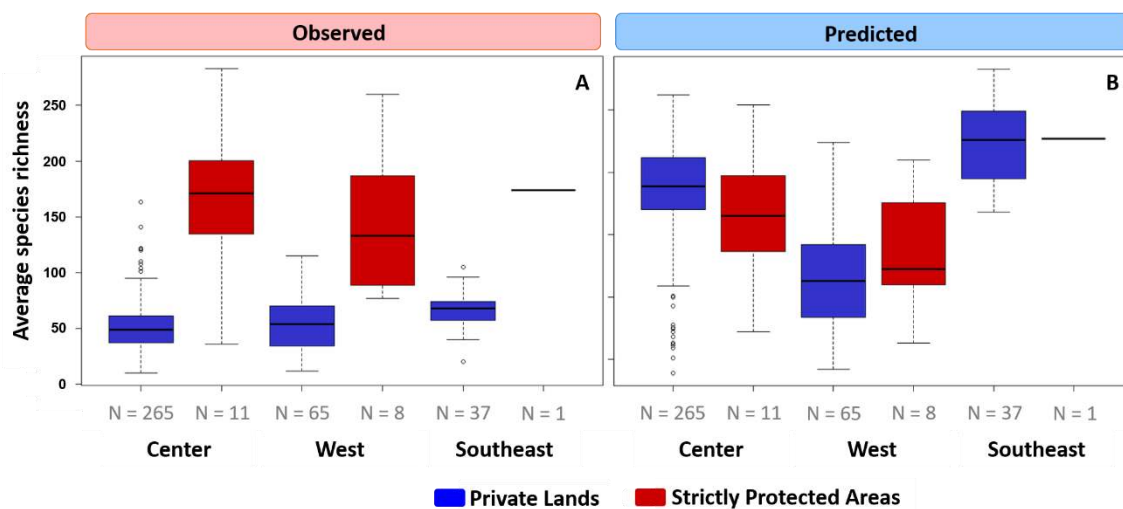


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885 **Appendix 3:** Boxplots (median \pm quartiles) comparing protection categories and
 886 regions of São Paulo state considering (a) the observed and (b) the predicted species
 887 richness per forest fragment. N = sampled forest fragments.



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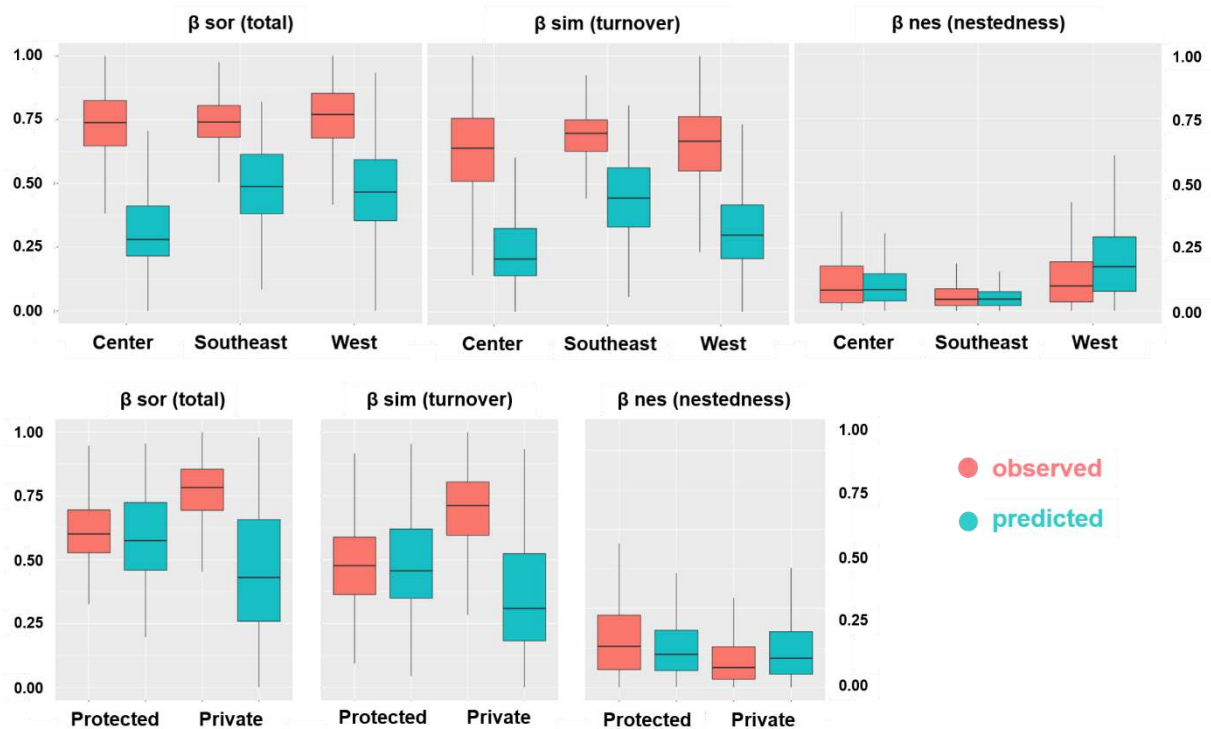
890 **Appendix 4:** Minimum, mean \pm standard deviation and maximum values for species
 891 richness for distinct regions and categories, considering the observed (red) and the
 892 predicted (blue) species composition, and their ratio (grey). N = sampled forest
 893 fragments.

Region	Type	N	S_Obs			S_SDM			ratio SDM/OBS		
			min	mean \pm SD	max	min	mean \pm SD	max	min	mean \pm SD	max
Southeast	Private	37	20	65 \pm 17	105	168	221 \pm 30	283	2	4 \pm 2	12
	Protected	1	-	174	-	-	227	-	-	1	-
	ALL	38	20	68 \pm 24	174	168	221 \pm 30	283	1	4 \pm 2	12
Center	Private	265	10	51 \pm 22	163	39	185 \pm 41	262	1	4 \pm 3	24
	Protected	11	36	167 \pm 67	283	72	165 \pm 54	254	0	1 \pm 0	2
	ALL	276	10	56 \pm 34	283	39	184 \pm 41	262	0	4 \pm 3	24
West	Private	65	12	52 \pm 22	115	42	115 \pm 47	224	1	3 \pm 2	10
	Protected	8	77	144 \pm 65	260	63	136 \pm 48	210	0	1 \pm 0	2
	ALL	73	12	62 \pm 41	260	42	118 \pm 47	224	0	3 \pm 2	10

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896 **Appendix 5:** Boxplots (median \pm quartiles) of total beta diversity (B_{sor}) and its
 897 components turnover (B_{sim}) and nestedness (B_{nes}) for distinct regions and
 898 categories, considering the observed (red) and the predicted (blue) species
 899 composition.



900