

1 **A large-scale assessment of plant dispersal mode and seed**
2 **traits across human-modified Amazonian forests**

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31 *Running headline:* Disturbance and recovery of functional traits

32

33 **Key-words:** forest degradation, forest fires, forest regeneration, frugivory, functional traits, resilience,
34 secondary forest, seed size, selective logging.

35

36 **Summary**

- 37 **1.** Quantifying the impact of habitat disturbance on ecosystem function is critical for understanding
38 and predicting the future of tropical forests. Many studies have examined post-disturbance
39 changes in animal traits related to mutualistic interactions with plants, but the effect of
40 disturbance on plant traits in diverse forests has received much less attention.
- 41 **2.** Focusing on two study regions in the eastern Brazilian Amazon, we used a trait-based approach to
42 examine how seed dispersal functionality within tropical plant communities changes across a
43 landscape-scale gradient of human modification, including both regenerating secondary forests
44 and primary forests disturbed by burning and selective logging.
- 45 **3.** Surveys of 230 forest plots recorded 26,533 live stems from 846 tree species. Using herbarium
46 material and literature, we compiled trait information for each tree species, focusing on dispersal
47 mode and seed size.
- 48 **4.** Disturbance reduced tree diversity and increased the proportion of lower wood-density and
49 smaller-seeded tree species in study plots. Disturbance also increased the proportion of stems with
50 seeds that are ingested by animals and reduced those dispersed by other mechanisms (e.g. wind).
51 Older secondary forests had functionally similar plant communities to the most heavily disturbed
52 primary forests. Mean seed size and wood density per plot were positively correlated for plant
53 species with seeds ingested by animals.
- 54 **5. *Synthesis.*** Anthropogenic disturbance has major effects on the seed traits of tree communities,
55 with implications for mutualistic interactions with animals. The important role of animal-
56 mediated seed dispersal in disturbed and recovering forests highlights the need to avoid
57 defaunation or promote faunal recovery. The changes in mean seed width suggest larger
58 vertebrates hold especially important functional roles in these human-modified forests.
59 Monitoring fruit and seed traits can provide a valuable indicator of ecosystem condition,
60 emphasising the importance of developing a comprehensive plant traits database for the Amazon
61 and other biomes.

62

63 **Sumário**

- 64 **1.** Para melhor entender e prever o futuro das florestas tropicais é crítico quantificar o impacto de
65 distúrbios antrópicos sobre as funções ecossistêmicas. Muitos estudos já avaliaram, após eventos
66 de distúrbios, mudanças nas características funcionais da fauna relacionadas com interações
67 mutualísticas com a flora. Porém, o efeito de distúrbios antrópicos nas características funcionais
68 da comunidade arbórea de florestas megadiversas é ainda pouco estudado.
- 69 **2.** Este estudo focou em duas regiões distintas da Amazônia oriental brasileira, e utilizou um método
70 baseado em características funcionais para entender como a dispersão de sementes, dentro de
71 comunidades arbóreas, pode ser modificada ao longo de um gradiente de distúrbio antrópico,
72 incluindo florestas secundárias e florestas primárias afetadas por fogo e corte seletivo.
- 73 **3.** Foram conduzidos inventários florestais em 230 parcelas de estudo, amostrando um total de
74 26.533 indivíduos vivos pertencentes a 846 espécies arbóreas. A partir de material depositado em
75 herbários e informações da literatura, as características funcionais, para cada espécie arbórea,
76 foram compiladas, focando no tipo de dispersão e no tamanho da semente.
- 77 **4.** Os distúrbios antrópicos reduziram a diversidade arbórea e aumentaram a proporção tanto de
78 espécies com baixa densidade de madeira, como de espécies com sementes pequenas. Os
79 distúrbios antrópicos também aumentaram a proporção de árvores com sementes que são
80 ingeridas por animais e diminuíram àquelas dispersas por outros mecanismos, como o vento.
81 Florestas secundárias em estágios mais avançados de sucessão apresentaram comunidades
82 arbóreas funcionalmente semelhantes àquelas de florestas primárias com maior grau de distúrbios
83 antrópicos. A nível de parcela, o tamanho médio das sementes e a densidade da madeira foram
84 positivamente correlacionados para plantas com sementes dispersas por animais.
- 85 **5. Síntese:** Os distúrbios antrópicos influenciaram amplamente as características funcionais de
86 sementes das comunidades arbóreas, com implicações diretas para as relações mutualísticas com a
87 fauna. A elevada importância de animais na dispersão de sementes tanto em florestas primárias
88 que sofreram distúrbios antrópicos assim como em florestas secundárias ressalta a importância de
89 se evitar a defaunação e de promover a recuperação da fauna. As mudanças no tamanho médio da

90 largura da semente sugerem que grandes vertebrados tem um papel funcional especialmente
91 importante em florestas antropizadas. O monitoramento de características funcionais de frutos e
92 sementes pode prover um valioso indicador das condições de ecossistemas, enfatizando a
93 importância da criação de uma base de dados compreensiva para a Amazônia e para outros
94 biomas contendo características funcionais da vegetação.

95

96 **Introduction**

97 Tropical forests are of fundamental importance for global biodiversity (Barlow et al., 2018; Gibson et
98 al., 2011; Slik et al., 2015), human livelihoods (Newton, Miller, Byenkya, & Agrawal, 2016), climate
99 regulation (Silvério et al., 2015) and carbon storage (Pan et al., 2011), yet are increasingly under
100 pressure from anthropogenic impacts (Malhi, Gardner, Goldsmith, Silman, & Zelazowski, 2014). The
101 conversion of closed-canopy forests to agro-pastoral land-uses often makes global headlines because
102 it results in massive loss of total forest area coupled with associated fragmentation effects (Nepstad et
103 al., 2014). However, this loss occurs concurrently with the widespread but cryptic degradation of
104 remaining primary forests through human-driven disturbances that do not lead to a complete removal
105 of the canopy cover, such as selective logging, understory fires and hunting (Peres, Barlow, &
106 Laurance, 2006; Sasaki & Putz, 2009). As a result, 80% of tropical forest landscapes currently exist in
107 a modified state (Potapov et al., 2017), either as secondary forests in recovery following the
108 abandonment of productive land uses (Chazdon et al., 2009), or as varyingly degraded primary forests
109 (Bregman et al., 2016; Thompson et al., 2013).

110 The detrimental impacts of human modification on biodiversity and carbon stocks in tropical forests
111 are increasingly well known (Barlow et al., 2016; Berenguer et al., 2014; Chazdon et al., 2009), but
112 the effects on key ecological functions remain unclear (Chapin, 2003; Chazdon, 2003). Such effects
113 are difficult to measure directly, but one indirect method involves assessing the ability of an
114 ecosystem to retain species with functional traits (Petchey & Gaston, 2006; Violle et al., 2007). These
115 traits can support key ecological processes even if species richness is reduced (Fonseca & Ganade,
116 2001; Peterson, Allen, & Holling, 1998; Tilman et al., 1997), and therefore provide important insights
117 into ecosystem resilience (Nimmo, Mac Nally, Cunningham, Haslem, & Bennett, 2015). Plant
118 functional traits have provided the key to understanding how hyperdiverse tropical forest communities
119 respond to environmental change: for example, stem traits such as wood density are linked to drought
120 and fire resilience (Brando, Oliveria-Santos, Rocha, Cury, & Coe, 2016; Phillips et al., 2009), while
121 leaf traits such as specific leaf area are strongly related to plant growth rates and life spans (Poorter &
122 Bongers, 2006). In contrast, plant reproductive traits (e.g. flowers, fruits and seeds) have received

123 little attention, despite their importance to mutualistic interaction networks and tree recruitment in
124 tropical forest systems.

125 Seed traits, such as seed mass and dimensions, are important determinants of the plant-animal
126 interactions central to seed dispersal, yet are understudied compared to stem and leaf traits. Seed traits
127 are yet to be considered in large-scale trait-based assessment of tropical forests (e.g. Gillespie Eco-
128 evolutionary Models - GEMs; Delong & Gibert, 2016) or individual-based simulations of tropical
129 forest plant communities (e.g. Traits-based Forest Simulator - TFS; Fyllas et al., 2014). Nonetheless,
130 there is growing evidence that seed traits are likely to respond to human disturbance, with
131 implications for ecological processes linked to rainforest stability and resilience (Galetti et al., 2013).
132 For example, tropical forests can experience an increase in the number of abiotically-dispersed
133 pioneer species and a reduction in the number of large-seeded animal-dispersed species when habitat
134 is fragmented (Laurance et al., 2006) or key seed dispersing animals are hunted out (Terborgh et al.,
135 2008). These changes may be mirrored in selectively logged or wildfire-affected forests (Barlow &
136 Peres, 2008; Cochrane & Schulze, 1999; Gerwing, 2002; Slik, Verburg, & Keßler, 2002) where
137 compositional shifts converge towards early successional communities (Berenguer et al., 2014, 2018).
138 The negative outcomes of forest disturbance are partially reversed by succession in secondary forests,
139 which become functionally more similar to primary forests over time (Arroyo-Rodríguez et al., 2017;
140 Howe, 2016).

141 Changes in plant traits can be mediated through interactions with fauna, as many tropical forest
142 vertebrates depend upon fruit as a food resource (e.g. Bregman, Sekercioglu, & Tobias, 2014), and the
143 vast majority of neotropical plants rely on animals to disperse their seeds (Fleming & Kress, 2011;
144 Howe & Smallwood, 1982). The loss of large-bodied frugivorous taxa is associated with altered
145 composition of plant communities and an increase in abiotically dispersed species across tropical
146 Africa, Asia and the Americas (Bovo et al., 2018; Harrison et al., 2013; Peres, 2000; Terborgh et al.,
147 2008; Wright, 2003; Wright, Hernández, & Condit, 2007). Two large-scale assessments have linked
148 this to reductions in above-ground vegetative biomass, based on the weak positive association
149 typically found between larger seeds and higher wood density species (Bello et al., 2015; Peres,

150 Emilio, Schiatti, Desmoulière, & Levi, 2016), although this relationship varies geographically across
151 Amazonia (ter Steege et al., 2006).

152 Despite clear evidence of the importance of dispersal mode and seed traits, we still lack a large-scale
153 understanding of variation in these traits across human-modified tropical landscapes, where floral
154 composition is a complex product of the direct effects of human-induced changes to forest structure
155 (logging or fire-induced mortality) and landscape configuration (edge effects, reduced habitat patch
156 size, increased isolation), and the indirect effects of defaunation and changes in seed dispersal and
157 predation – all of which may be magnified or ameliorated by feedbacks inherent in the fruit-frugivore
158 mutualism (Ganzhorn, 1995). As such, a large-scale assessment of dispersal mode and seed traits can
159 provide important insights into the functional status of human-modified tropical forests, their potential
160 resilience, and policy interventions that may enhance recovery.

161 We address this knowledge gap by analysing the dispersal mode and seed size of over 26,000 stems
162 measured in 230 0.25 ha plots across two landscapes in the Brazilian Amazon. Plots were spread
163 across forest classes that encompass disturbed and undisturbed primary forests, and a chronosequence
164 of secondary forests that have previously been completely clear cut. First, we ask, how disturbance
165 within primary forests and the process of succession within secondary forests affects the relative
166 frequency of seed dispersal modes (see Table S1 for definitions). Second, we test how plot-level seed
167 size in human-modified Amazonian forests compares to undisturbed forests. We focus on seed size in
168 gut-dispersed species because of the importance of its relationship with gape size in frugivores
169 (Levey, 1987; Wheelwright, 1985). Third, we examine whether any variation in dispersal mode and
170 seed traits can be explained by our measures of disturbance history, landscape configuration, and local
171 environment. Finally, we examine the strength of the relationship between seed size and wood
172 density, a widely used stem trait that is strongly related to disturbance and recovery (Berenguer et al.,
173 2018) and is of critical importance for timber stocks and carbon storage (Baker et al., 2004; Chave et
174 al., 2006). The strength and direction of the relationship between wood density and seed size is central
175 to simulated models of defaunation and carbon stocks (Bello et al., 2015; Peres et al., 2016; Wright et

176 al., 2007), but these links have not been assessed in primary forests affected by either selective
177 logging or understorey fires, nor in regenerating secondary forests that have been previously clear cut.

178

179 **Materials and methods**

180 *Study sites*

181 Forest inventories were conducted in the municipalities of Paragominas (PGM; 2°59'S, 47°21'W) and
182 Santarém-Belterra-Mojuí dos Campos (STM; 2°26'S, 54°42'W), Pará state, in the eastern Brazilian
183 Amazon. The availability of a gradient of varyingly-disturbed primary and varyingly-aged secondary
184 (6-22+ years) forests at the landscape scale, coupled with the diverse range of native fruit-frugivore
185 interactions, makes these two regions an ideal setting to investigate how human modification of
186 forests affects plant functional traits related to seed dispersal. In each region, 18 drainage catchments
187 (mean area \pm SD = 4,667.6 \pm 752.2 ha) were selected along a deforestation gradient, with forest cover
188 ranging from 6% to 100% in each catchment (Gardner et al., 2013). Within each catchment, 0.25 ha
189 plots (250 x 10 m) were distributed in proportion to the prevailing land uses (i.e. a catchment with
190 more forest cover had more study plots). A total of 230 plots (57.5 ha) were surveyed across the two
191 regions (PGM: 120, STM: 110; Table 1) in 2010 and 2011. No signs of pre-Columbian settlements,
192 such as *terra pretas* (McMichael et al., 2012), were found in any of our plots (Berenguer et al., 2014).

193 All plots were located in evergreen *terra firme* forests at least 1500 m apart and at least 100 m from
194 forest edges to reduce edge effects (M Tabarelli, Lopes, & Peres, 2008). See Gardner et al. (2013) and
195 Berenguer et al. (2014) for a study site map and further explanation of sampling design. A
196 combination of physical evidence and Landsat images (see Berenguer et al., 2014 for details) was
197 used to assign each plot to one of six different forest classes along a disturbance gradient: undisturbed
198 primary (U); disturbed primary – burned (D_B); disturbed primary – logged (D_L); disturbed primary
199 – burned-and-logged (D_BL); secondary – old [>20 years] (S_O); and secondary – young [≤ 20 years]
200 (S_Y). Within each plot, all live tree stems (including palms) ≥ 10 cm diameter at breast height
201 (DBH) were measured, identified by experienced botanists, and, in case of doubt, samples were

202 compared with reference material in the regional herbaria of Embrapa Amazônia Oriental and the
203 Museu Paraense Emílio Goeldi, Belém, Brazil. A total of 26,533 stems were measured (PGM: 14,063,
204 STM: 12,470; Table 1) and 99.4% of all stems were identified to species level. We excluded 39 Brazil
205 nut tree stems (*Bertholletia excelsa* H. & B., Lecythidaceae) from the secondary forest plots as their
206 very large diameters suggested they were uncut during the clear-cut process due to legal protection.
207 Tree species were classified into families according to the APG III system (APG III, 2009).
208 Nomenclature was verified and standardised using The Plant List (2013).

209

210 *Trait measurements*

211 We collected data on a range of fruit and seed traits of relevance to seed dispersal from a combination
212 of herbarium collections, scientific literature and online databases. We included a total of 24,400
213 records (15,693 fruit; 8,707 seeds) from individually examined specimens (recording lengths and
214 weights) at three of the most important herbaria in the Brazilian Amazon: (1) Embrapa Amazônia
215 Oriental, Belém, (2) Museu Paraense Emílio Goeldi, Belém, and (3) Orsa Florestal, Monte Dourado
216 (Table S2). We also extracted fruit trait data from literature sources (see Table S3 for details),
217 including six books and nine journal articles, in addition to literature sources contained within Frubase
218 (Jordano, 1995). Further records were obtained for 201 species using online sources including the
219 Kew Seed Information Database (SID; <http://data.kew.org/sid/>) and the New York Botanical Garden
220 (NYBG) C. V. Starr Virtual Herbarium (<http://sweetgum.nybg.org/science/vh/>). Full details of fruit
221 and seed traits compiled, as well as measurement protocols, are provided in Table S4.

222 Where available in each source, we recorded information on dispersal mode, fruit type, dehiscence,
223 presence of fleshy tissue or aril, fruit colour, fruit shape, fruit dimensions, fruit mass, seed shape, seed
224 colour, seed dimensions, seed mass, number of seeds, diaspore type, and animal dispersers (Table S3).
225 Dispersal modes from the literature were collapsed to the following categories: (1) endozoochorous
226 (gut-dispersed) *sensu stricto* (i.e. definite endozoochory); (2) endozoochorous (gut-dispersed) *sensu*
227 *lato* (i.e. possible endozoochory); (3) eynzoochorous (scatter-hoarded); and (4) non-zoochorous

228 (Table S1). In cases where the dispersal mode was not stated or ambiguous (~10% of species, 5% of
229 stems), we used functional traits to assign fruits to a predominant dispersal mechanism (Thomson et
230 al., 2010; van der Pijl, 1982). Only 17 species (2.0%) and 489 stems (1.8%) were unclassified in terms
231 of dispersal mode, and only 22 species (2.6%) and 466 stems (1.8%) unclassified for fruit type.

232 Fruit and seed dimensions (length, width and depth) and mass were treated as continuous variables.
233 We focused on seed width (defined as the maximum distance along a plane passing through the
234 second-longest axis) in gut-dispersed endozoochorous species (using the ‘*lato*’ definition of possible
235 endozoochory) as the most appropriate measure of seed size because our question regarding the
236 effects of disturbance and recovery upon seed size is based on the association between seed size and
237 the gape size of animal dispersal agents (Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning,
238 2016; Donoso, Schleuning, García, & Fründ, 2017; Mazer & Wheelwright, 1993; Wheelwright,
239 1985). This approach was further supported by the positive relationships between seed width and dry
240 seed mass, and other dimensions of both seeds and fruits (i.e. length, weight) for subsets of the species
241 where more than one dimension was available (Figure S1). Furthermore, although dry seed weights
242 provide a good indicator of resources available for seedling establishment (Leishman & Westoby,
243 1994), seed width is less likely to be affected by water content. We obtained a seed width value for
244 771 (94.8%) of endozoochorous tree species (PGM: 596, STM: 686), and for 25,491 (96.1%) of tree
245 stems.

246 In addition to data on fruit and seed traits, we extracted wood density data for tropical South America
247 from the Global Wood Density Database (Zanne et al., 2009). For stems not identified to species level
248 (0.6%), we used the mean seed width dimensions and wood densities for the appropriate genus or
249 family, accordingly, and for unidentified stems (<0.2%) we used mean dimensions across all stems in
250 the same vegetation plot (see Berenguer et al., 2014 for details).

251

252 *Data analyses*

253 To assess variation in plant traits across human-modified tropical forests, we calculated the proportion
254 of stems in each study plot that belonged to each broad category of seed dispersal mode and fruit type
255 (Table S1). We used a chi-squared test (Type II Wald) with Tukey comparisons to evaluate
256 differences in the proportion of stems per plot in each seed dispersal and fruit type category across the
257 different forest classes, and also the number of species per plot in each seed dispersal category. We
258 used an ANOVA to similarly test differences in seed width. To assess variation in (a) the proportion
259 of endozoochorous stems (*sensu lato*) per plot, and (b) seed width amongst endozoochorous species
260 across forest disturbance classes, we used generalised linear mixed models (GLMMs) with binomial
261 or Gaussian distributions for proportional and seed width data, respectively. To account for potential
262 spatial autocorrelation and biogeographic differences, we included 'catchment' as a nested random
263 factor and examined correlograms of Moran's I against distance. We adjusted all binomial models that
264 showed overdispersion by adding an observation-level random effect (Bolker et al., 2009; Harrison,
265 2015). For species count data, we used a negative binomial distribution because there was high
266 overdispersion with a Poisson distribution. To assess any disproportionate influence of palms, we
267 repeated the GLMMs excluding palm stems (14 species, 409 individuals).

268 We used basal area as our main proxy for both primary forest disturbance and secondary forest
269 recovery, because forest biomass (which is largely defined by stem basal area; Berenguer et al., 2015)
270 increases over time in secondary and disturbed primary forests (Ferreira et al., 2018; Lennox et al.,
271 2018) while basal area declines with the intensity of edge effects, selective logging and wildfires
272 (Berenguer et al., 2014). Potential predictors were selected from a comprehensive range of
273 environmental variables (Berenguer et al., 2014; Gardner et al., 2013) to cover both local and
274 landscape-level conditions: basal area, soil clay content, distance to nearest primary forest edge, plot
275 slope, surrounding area of primary forest cover, and surrounding area of undisturbed primary forest
276 cover (Table 2). We constructed separate models for disturbed and secondary forest plots because two
277 of the landscape level variables (edge distance and undisturbed forest cover) were not relevant for
278 secondary forest patches and were therefore calculated only for primary forests. All combinations of
279 first-order models were ranked using Akaike Information Criteria (AICc) values for small samples

280 sizes, averaging all models with $\Delta\text{AICc} < 4.0$ and calculating the relative importance of each predictor
281 variable by summing AICc weights (Burnham & Anderson, 2002). We also present diversity results
282 to explore whether ecosystem function tracks or precedes species loss (SI Methods). Finally, we
283 tested for relationships between seed width and wood density (and basal area), both at the community
284 level (using mean values per plot weighted by individual density) and species level (using mean
285 values per species).

286 All analyses were conducted in R version 3.3.2 (R Core Team, 2016); models were built using the
287 packages *lme4* (Bates, Mächler, Bolker, & Walker, 2015), *lmerTest* (Kuznetsova, Brockhoff, &
288 Christensen, 2017), and *glmmTMB* (Brooks et al., 2017), and model selection was conducted using the
289 package *MuMIn* (Bartoń, 2016). We standardised the continuous explanatory variables using the *sta*
290 function from the package *vegan* (Oksanen, Blanchet, & Kindt, 2013) and checked the adjustment of
291 all models using the package *DHARMA* (Hartig, 2019). We conducted the Moran's I tests and
292 correlograms using the *spdep* (Bivand & Wong, 2018) and *ncf* (Bjørnstad, Ims, & Lambin, 1999)
293 packages.

294

295 **Results**

296 *Prevalence of dispersal modes and fruit types*

297 We sampled a total of 26,533 live tree stems ≥ 10 cm DBH distributed across 230 forest plots,
298 including 846 species from 293 genera in 72 families (Table 1). Animal-dispersal (zoochory) was the
299 dispersal mode for the majority of both species (720; 85.1%) and stems (22,578; 85.1%; Table S5).
300 Gut-dispersal (endozoochory) comprised the majority of these, and levels of endozoochory (*sensu*
301 *lato*) were significantly higher in secondary forest plots, and primary forest plots that were both
302 burned and logged, compared to undisturbed primary forest ($\chi^2 = 69.45$, $p < 0.001$; Figure 1). The most
303 common fruit types were berry-like, capsule-like and drupe-like, with the relative proportion of all
304 fruit types varying significantly across forest classes (Figure S2). When compared to undisturbed
305 forests, disturbed primary and secondary forest plots often contained elevated levels of compound

306 fruits (e.g. Moraceae, Siparunaceae, Urticaceae) and syncarpia (e.g. Annonaceae), and reduced levels
307 of berries and capsules. The number of gut dispersed species across forest classes (Figure S3) closely
308 matched the pattern for overall species richness (Figures S4-5).

309

310 *Seed size in endozoochorous stems*

311 Our use of seed width as an overall indicator of seed size was supported by strong positive
312 relationships across species between fruit weight and length, and seed weight and length, based on our
313 measurements of carpotec specimens (Figure S1A-D), and between seed weight and seed length using
314 measurements from literature sources (Figure S1E). The seed width of gut-dispersed tree stems was
315 significantly lower in secondary and disturbed burned-and-logged primary forests than in undisturbed
316 primary forests (ANOVA: $F_{5,244} = 32.7$, $p < 0.001$), and significantly lower in young secondary forests
317 than in all disturbed forests (Figure 1). Mean seed width was significantly smaller in burned-and-
318 logged forest than in forest that had been either logged only or burned only but old secondary forests
319 were not significantly different from either young secondary forests or burned-and-logged forests.

320

321 *Drivers of change in dispersal mode and seed size*

322 Basal area - our main proxy for forest condition (Figures S6-7) - was the only significant variable
323 influencing the proportion of endozoochorous-dispersed stems, with a strong negative effect in
324 models for primary forests (Figure 2A). Basal area was also the most important variable influencing
325 seed width, with a strong positive effect in models for disturbed primary forests (Figure 2C). Local
326 variables, including soil clay content and slope, and landscape variables, including the proportion of
327 primary and undisturbed forest within 1 km buffers, had weak and non-significant effects in all
328 models. We found no significant spatial autocorrelation overall; in all models tested, the correlograms
329 showed a few distance classes with significant spatial autocorrelation (Figure S8) but these classes
330 were not enough to create a significant spatial bias in our mixed model frameworks (Table S6).

331 Results were unaffected when excluding palm stems from the analyses (Figure S9), with the exception

332 of clay becoming a significant predictor of the proportion of endozochorous-dispersed stems in
333 secondary forests (Figure S9, panel B).

334

335 *Relationships between functional traits*

336 The mean value of wood density across forest classes was qualitatively similar to mean seed width
337 (Figure S10) and was significantly lower in disturbed primary and secondary forests than in
338 undisturbed primary forests. The similarity of the responses of wood density and seed width was
339 reflected by a strong positive relationship (Pearson's: $r = 0.84$, $p < 0.001$) between their plot-level
340 mean trait values for the endozochorous species – but this relationship was not significant for
341 synzochorous species and was negative for non-zochorous species (Figure 3D-F). Species-level
342 correlations between seed width and wood density were much weaker, and also varied according to
343 seed dispersal mode (Figure 3A-C).

344

345 **Discussion**

346 Our results demonstrate that the effect of tropical forest disturbance extends beyond species loss to
347 include changes in the prevalence of functional traits related to seed dispersal. In particular, through
348 our focus on plant traits, we found that, counterintuitively, disturbance lead to tree communities in
349 which a greater proportion of species and individuals rely on animal dispersal – but with a loss of
350 functional breadth, and a significant shift towards small-seeded species. This complex process of
351 community disassembly following forest degradation from e.g. fire and logging is contrasted by the
352 reassembly observed in secondary succession. We discuss our results on the effects of disturbance and
353 recovery on seed dispersal modes and seed size in terms of implications for both frugivores and forest
354 resilience.

355

356 *What does an altered seed dispersal network mean for disturbed forest recovery?*

357 Our results show that human disturbance has led to a shift in both dispersal mode and seed traits in
358 these tropical forests. There are likely to be multiple drivers of these changes. For example, hunting
359 can reduce seed dispersal by large birds and mammals (Terborgh et al., 2008), and there may be an
360 interaction between structural disturbance and hunting pressure. Selective logging may also influence
361 patterns, as many of the valuable timber species such as *Manilkara* spp., *Brosimum* spp have
362 endozoochorous fruits. However, other valuable species such as *Dinizia excelsa* are not animal
363 dispersed (Peres & Van Roosmalen, 2002; Rosin, 2014). Isolating these disturbance-specific
364 relationships will likely be difficult in human-modified landscapes where forests are responding to
365 multiple drivers of change.

366 While there was a positive influence of secondary forest stage on seed widths, these remained far
367 below the seed widths in primary forests even after more than 20 years of succession. There are three
368 reasons that could explain this pattern. First, an increase in the dispersers of small-seeds could lead to
369 an increased recruitment of small-seeded trees in forests after human disturbance. Many small-bodied
370 frugivore taxa are common in disturbed forests (Lopes & Ferrari, 2008; Medellín, Equihua, & Amin,
371 2000), e.g. both bats and birds are known to be particularly important seed dispersal agents of key
372 pioneer tree species such as *Cecropia* spp. and *Vismia* spp. (Medellin & Gaona, 1999), and small
373 frugivorous birds have been shown to increase in abundance after a single wildfire, feeding off and
374 helping disperse the abundant small-seeded Rubiaceae and Melastomataceae that dominated the
375 understorey (Barlow & Peres, 2004).

376 Second, the lack of larger-seeded fruiting species could fail to attract the largest dispersers –
377 preventing the immigration of zoochoric large-seeded species which are known to rely upon large-
378 bodied frugivores as seed dispersal agents (Doughty et al., 2016; Galetti et al., 2018), and even
379 limiting their effective dispersal if present. This introduces a possible destabilising feedback where
380 changes in plant communities negatively impact animal communities, and those impoverished animal
381 communities subsequently lead to further alteration of plant communities. With simultaneous losses in
382 both plant and animal communities, future ecosystem function could appear appropriately balanced
383 but this perspective would ignore the problem of the shifting baseline. Considering that intact baseline

384 is crucial to more fully address the concept of resilience i.e. maximising the scope for current and
385 future recolonization of degraded areas by primary forest species. Third, our focus on dispersal traits
386 in stems >10cm DBH means we may have missed the presence of slow-growing large-seeded species
387 that have not yet met the size threshold for inclusion. Indeed, the successional trajectory of forest
388 recovery means that these smaller stems often hold wood density values closer to primary forests than
389 larger stems (Berenguer et al. 2018), suggesting that a more detailed assessment of the dispersal traits
390 of small stems would provide additional insights into secondary forest recovery.

391 Of course, we have only examined one side of the complex seed dispersal network, and have not
392 considered other components that determine successful plant recruitment such as Janzen-Connell
393 effects (Connell, 1971; Janzen, 1970) or edge effects (Marcelo Tabarelli, Lopes, & Peres, 2008).
394 Spatial scale is likely to be important; faster colonisation of dispersal-limited species might be
395 expected in secondary forest patches surrounded by primary forest. However previous land-use
396 intensity is also key (Jakovac, Peña-Claros, Kuyper, & Bongers, 2015), and can be even more
397 important than distance to mature forest (Fernandes Neto, Costa, Williamson, & Mesquita, 2019). The
398 implications for seed dispersal are also complicated by potential trophic cascades and the relative
399 effectiveness of seed dispersal agents across different plant species (Schupp, Jordano, & Gómez,
400 2010). This includes consideration of the importance of rodents as seed predators (Wright et al.,
401 2000), with evidence that smaller-seeded species are less protected from rodents (Dirzo, Mendoza, &
402 Ortíz, 2007; Fricke & Wright, 2016). The continuing challenge in interpreting the effects of
403 disturbance on seed dispersal is to disentangle these dual, interacting effects upon plant and animal
404 communities (Poulsen, Clark, & Palmer, 2013). Although more narrowly defined seed dispersal
405 modes may allow more precise insights into the effect of disturbance on tropical flora, this remains
406 very challenging due to the substantial degree of overlap in generalist fruit-frugivore networks
407 (Bascompte & Jordano, 2007) and the continued shortage of information on what constitutes effective
408 seed dispersal (Howe, 2016).

409

410 *Will disturbed forests help conserve Amazonia's diverse frugivorous fauna?*

411 Fruits and seeds represent a key resource for a wide range of vertebrate taxa in tropical forests,
412 including bats (Muscarella & Fleming, 2007), birds (Kissling, Böhning-Gaese, & Jetz, 2009), fish
413 (Goulding, 1980; Horn et al., 2011), primates (Hawes & Peres, 2014a), reptiles (Valido & Olesen,
414 2007) and ungulates (Bodmer, 1990), and these resources are partitioned to some degree amongst
415 frugivore taxa (Gautier-Hion et al., 1985; Hawes & Peres, 2014b). The high proportion of smaller-
416 seeded stems producing endozoochorous fruits in disturbed primary and secondary forests reinforces
417 the suitability of these forests for smaller-bodied taxa such as small passerine birds and bats
418 (Edwards, Massam, Haugaasen, & Gilroy, 2017; Medellin & Gaona, 1999; Muscarella & Fleming,
419 2007). However, it is not clear if these small seeded resources can sustain large-bodied frugivores
420 specialising on large-seeded plants; although these species can naturally ingest both small and large
421 seeds, and the relationship between animal body mass and the average size of ingested seeds may not
422 always be positive (Chen & Moles, 2015), there may be a size threshold under which it becomes
423 inefficient to eat small fruits. Moreover, large-bodied frugivores may face other environmental filters
424 (such as branch connectivity and strength) that prevent them from moving through or foraging in
425 disturbed or secondary forest.

426

427 *Will changes in plant traits influence carbon storage?*

428 Animal-plant interactions have an important but hitherto neglected influence on carbon cycling
429 (Schmitz et al., 2018), and large-scale models have simulated the loss of carbon stocks under
430 defaunation in undisturbed forests (Bello et al., 2015; Peres et al., 2016). Our results lend some
431 support to this, as the relationships between seed size and the wood density at the plot level were very
432 strong. However, these were far weaker at the species level – suggesting that while disturbed primary
433 and regenerating secondary forests have lower values for wood density and smaller seeds, the
434 similarity in response is driven by the relative abundance of species in plots (Chapin, 2003) rather
435 than any clear trade-offs in these traits at the species level (e.g. Díaz et al., 2016). This is interesting
436 because it suggests that it is not just the change in community composition, through the loss or gain of
437 particular plant species, that drives changes in a particular trait, but rather the more complex changes

438 in community structure. This shift in the community structure of disturbed primary forests, with a
439 time-lagged turnover from disturbance-sensitive species to disturbance-tolerant species (Edwards et
440 al., 2011; Moura et al., 2014), and associated changes in particular functional traits (including fruit
441 and seed traits), means that ecosystem function can be heavily impacted, even if species richness is
442 maintained at close to pre-disturbance levels.

443 The strength of this association between wood density and seed size raises the possibility that any
444 processes that limit the dispersal of large-seeded species could negatively influence the recovery of
445 high wood density forests. This could have longer term implications for both the carbon storage and
446 drought sensitivity of forests: wood density is the most important predictor of carbon storage in forest
447 after tree size (Chave et al., 2006) and a key determinant of drought sensitivity (e.g. Phillips et al.,
448 2009). While we do not have enough data to examine these issues in detail, the potential influence of
449 defaunation on the post-disturbance recovery trajectory of disturbed tropical forests (Bregman et al.,
450 2016) represents a crucial research aim given very few primary forests in the eastern Amazon have
451 escaped some degree of disturbance (Barlow et al., 2016; Tyukavina, Hansen, Potapov, Krylov, &
452 Goetz, 2016) and the growing importance of secondary forests (Vieira, Gardner, Ferreira, Lees, &
453 Barlow, 2014). While uncertainty remains, it is therefore prudent (from both biodiversity and carbon
454 storage perspectives) to maintain intact forests, including extensive unlogged areas (Barlow et al.,
455 2016; Watson et al., 2018).

456

457 **Conclusions**

458 Our results demonstrate that tropical forest disturbance has pervasive effects that extend beyond the
459 loss of species richness, and include major implications for seed dispersal and mutualistic networks.
460 In particular, disturbance drives a significant shift in tree communities towards small-seeded species,
461 with an increased proportion of species and individuals relying on animal dispersal. Similar effects are
462 observed in secondary forests recovering from clear-felling, with older secondary forests having plant
463 communities comparable to those found in the most heavily disturbed primary forests. These findings

464 highlight the importance of developing a more comprehensive plant traits database that goes beyond
465 leaf and stem traits to consider seasonal or reproductive traits (flowers, fruits and seeds). They also
466 suggest that animal-plant interactions could provide new insights into ecosystem function and
467 resilience in human-modified tropical forests.

468

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485

486 **Author contributions**

487 JB and ICGV conceived this study; EB collected field data; AC, JAT, AW and ICGV collected or
488 coordinated lab data; JEH and AW collected literature data; JEH, LFSM and JB analysed the data;

489 JEH and JB led the writing of the manuscript. All authors contributed critically to the drafts and gave
490 final approval for publication.

491

492 **Data accessibility**

493 Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.kd51c5b2g> (Hawes
494 et al., 2020). Fruit and seed measurements from herbarium collections were also contributed to the
495 TRY Plant Trait Database (Kattge et al., 2020).

496

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843

844 **Tables**

845

846 **Table 1.** Number of plots (N) surveyed and numbers of stems and species of live tree ≥ 10 cm DBH

847 per region in each forest class.

Forest class	Paragominas			Santarém		
	N plots	Stems	Species	N plots	Stems	Species
Undisturbed primary	13	1,829	271	17	1,996	363
Disturbed primary						
Burned	0	0	0	7	790	260
Logged	44	5,473	460	26	3,118	498
Burned-and-logged	44	5,167	390	24	2,799	418
Secondary						
Old (>20 years)	5	581	107	20	2,516	276
Young (≤ 20 years)	15	1,013	142	17	1,251	150
Total	120	14,063	607	110	12,470	701

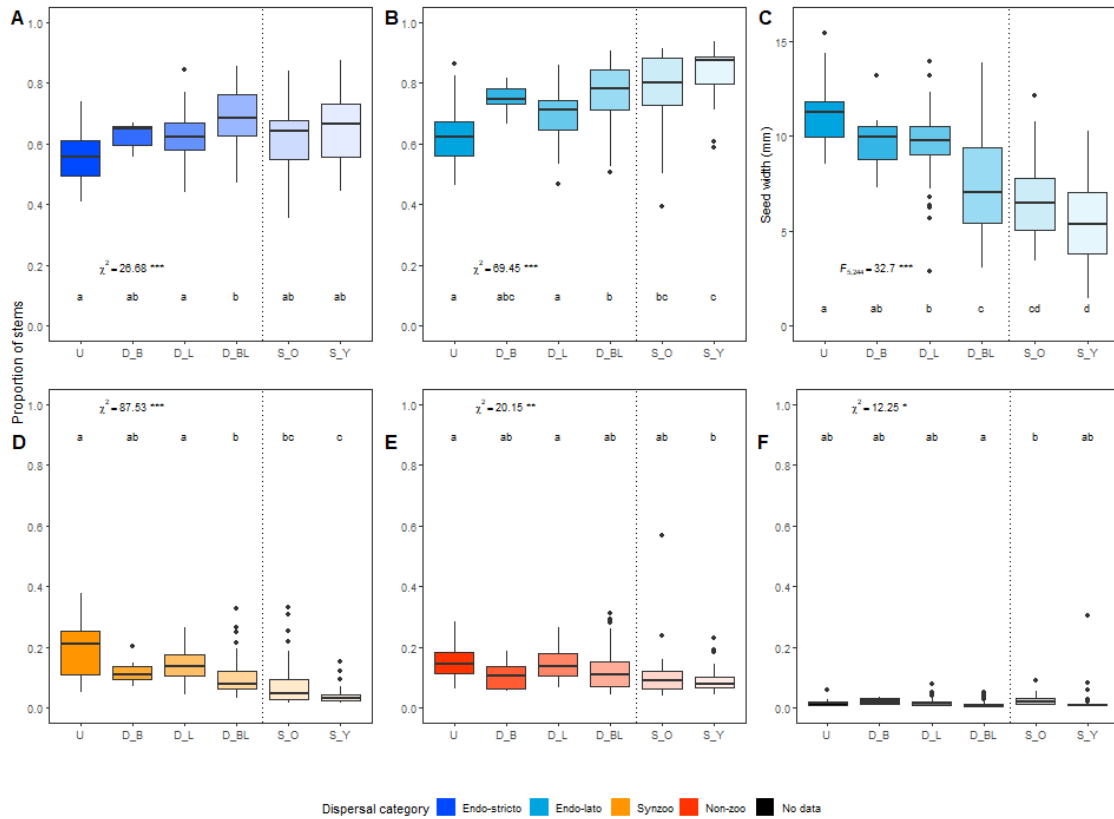
848

849 **Table 2.** Summaries of the environmental variables used in this study; further details of sampling
 850 methods are described in Gardner et al. (2013) and Berenguer et al. (2014).

Code	Variable	Proxy for	Methodology	Sample scale	Models
BA	Basal area	Forest age/disturbance		Plot	Disturbance, Recovery
CC	Clay content	Soil conditions	Soil granulometry using densimeter	Plot	Disturbance, Recovery
ED	Edge distance	Local landscape context		Plot	Recovery
S	Slope	Soil conditions		Plot	Disturbance, Recovery
PF	Primary forest cover (including disturbed forests)	Forest condition	Vegetation classification based on LANDSAT imagery	1 km radius buffer around each transect	Disturbance, Recovery
UF	Undisturbed forest cover (no evidence of logging or wildfires)	Land-use history/wider landscape context	Vegetation classification based on LANDSAT imagery	1 km radius buffer around each transect	Recovery

851

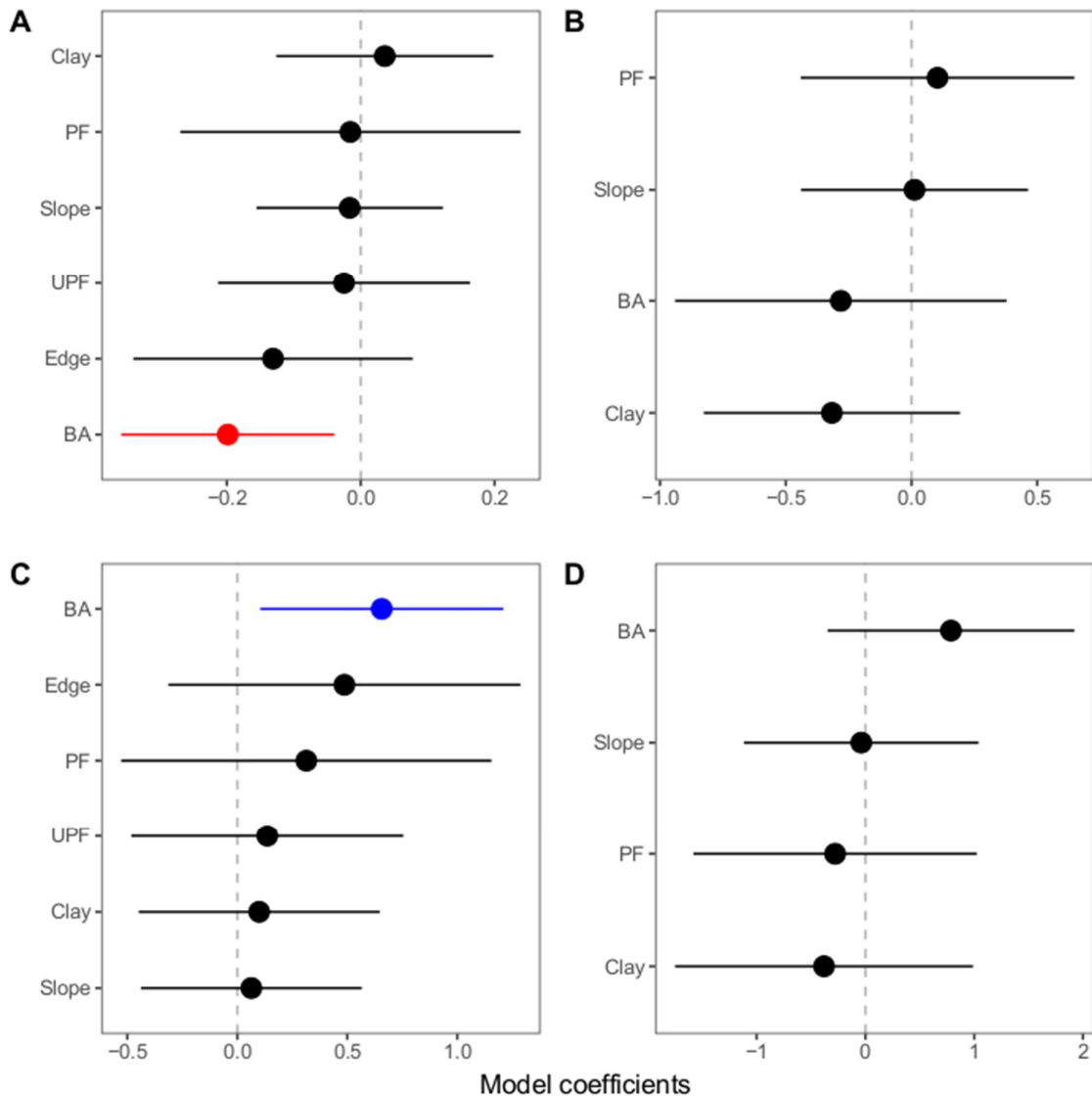
852 **Figures**



853

854 **Figure 1.** Proportion of tree stems (N = 26,533) per dispersal category (A-B, D-F), and mean seed
 855 width (mm) for endozoochorous (*lato*) stems (C), sampled across forest classes in both study regions
 856 (N = 230 plots). Shading represents forest classes along the disturbance gradient: U = undisturbed;
 857 D_B = disturbed – burned; D_L = disturbed – logged; D_BL = disturbed – burned-and-logged; S_O =
 858 secondary – old; and S_Y = secondary – young. Boxplots represent first and third quartiles, whiskers
 859 extend up to 1.5 times the inter-quartile range, points beyond are plotted individually, letters above
 860 represent Tukey subsets, significance: * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

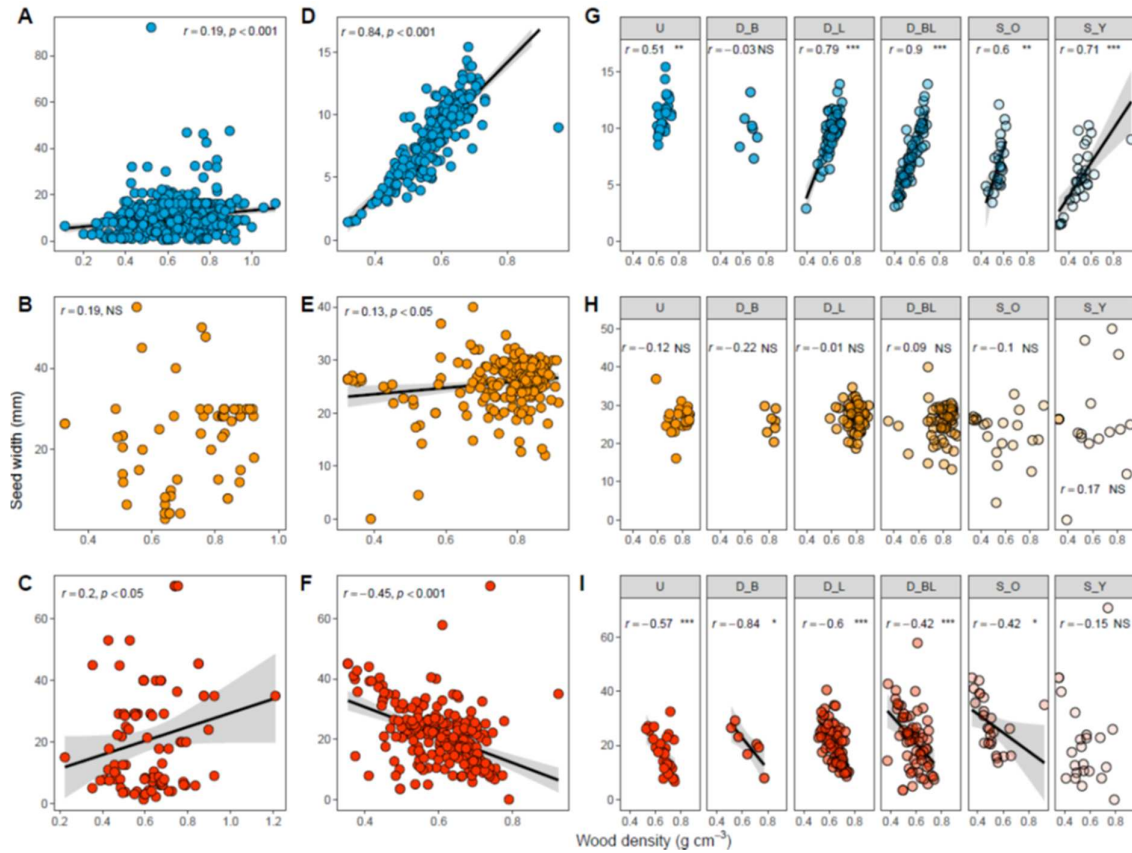
861



863

864 **Figure 2.** Coefficients (\pm 95% CIs) from model averaging process (all candidate models with Δ AICc
 865 $<$ 4.0 and with standardised predictors) for the mean percentage per forest plot of all live trees \geq 10
 866 cm DBH that have an endozoochorous (*lato*) dispersal mode in (A) disturbed primary and (B)
 867 regenerating secondary forests, and the seed width (mm) for those endozoochorous trees \geq 10 cm
 868 DBH in (C) disturbed primary and (D) regenerating secondary forests. BA = basal area, Clay = clay
 869 proportion of soil, Edge = distance to forest edge, PF = % primary forest within a 1 km radius, Slope
 870 = slope of terrain, UPF = % undisturbed forest within a 1 km radius.

871



872

873 **Figure 3.** Relationships between seed width (mm) and wood density (g cm⁻³) for individual tree
 874 species (A, B, C), mean values across all forest plots (D, E, F), and for plots in each forest class (G, H,
 875 I): U = undisturbed; D_B = disturbed – burned; D_L = disturbed – logged; D_BL = disturbed –
 876 burned-and-logged; S_O = secondary – old; and S_Y = secondary – young. Colours represent
 877 dispersal categories: blue = endozoochorous (*lato*), yellow = synzoochorous, and red = non-
 878 zoochorous trees ≥ 10 cm DBH. For significant correlations (Pearson's, r), lines and shading represent
 879 linear models with 95% confidence intervals, significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p <$
 880 0.001.