

This is a repository copy of *Contrasting patterns of local richness of seedlings, saplings and trees may have implications for regeneration in rainforest remnants*.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/134645/>

Version: Accepted Version

---

**Article:**

Stride, Gail Louise, Thomas, Chris [orcid.org/0000-0003-2822-1334](https://orcid.org/0000-0003-2822-1334), Benedick, Suzan et al. (4 more authors) (2018) *Contrasting patterns of local richness of seedlings, saplings and trees may have implications for regeneration in rainforest remnants*. *Biotropica*. 889–897. ISSN 0006-3606

<https://doi.org/10.1111/btp.12605>

---

**Reuse**

This article is distributed under the terms of the Creative Commons Attribution (CC BY) licence. This licence allows you to distribute, remix, tweak, and build upon the work, even commercially, as long as you credit the authors for the original work. More information and the full terms of the licence here:

<https://creativecommons.org/licenses/>

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

1 LRH: Stride *et al.*

2 RRH: Fragmentation impacts on Borneo trees

3

4 **Contrasting patterns of local richness of seedlings, saplings and trees may have**  
5 **implications for regeneration in rainforest remnants.**

6 Gail Stride<sup>1</sup>, Chris D. Thomas<sup>1</sup>, Suzan Benedick<sup>2</sup>, Jenny A. Hodgson<sup>3</sup>, Ahmad Jelling<sup>4</sup>, Mike  
7 J.M. Senior<sup>5</sup>, Jane K. Hill<sup>1</sup>

8

9

10 <sup>1</sup> Department of Biology, University of York, York YO10 5DD, UK

11 <sup>2</sup> Faculty of Sustainable Agriculture, Universiti Malaysia Sabah, 90509 Sandakan, Sabah,  
12 Malaysia

13 <sup>3</sup> Department of Evolution, Ecology and Behaviour, University of Liverpool, Biosciences  
14 Building, Crown Street, Liverpool L69 7ZB, UK

15 <sup>4</sup> The Royal Society South East Asia Rainforest Research Programme, Danum Valley Field  
16 Centre, PO Box 60282, 91112 Lahad Datu, Sabah, Malaysia

17 <sup>5</sup> Proforest, South Suite, Frewin Chambers, Frewin Court, Oxford OX1 3HZ, UK

18

19 Received\_\_\_\_; revision accepted\_\_\_\_.

20 **Abstract**

21 Remnants of lowland rainforest remain following deforestation, but the longer-term  
22 effects of fragmentation remain poorly understood, partly due to the long generation  
23 times of trees. We study rainforest trees in three size classes: seedlings (<1 cm dbh),  
24 saplings (1-5 cm dbh) and trees (>5 cm), that broadly reflect pre- and post-fragmentation  
25 communities, and we examine the impacts of fragmentation on forest regeneration in  
26 Sabah, Malaysian Borneo. We found that seedling richness (measured as the number of  
27 genera per plot) in fragments was about 30 percent lower than in plots in undisturbed  
28 forest, and about 20 percent lower than in an extensive tract of selectively logged forest,  
29 providing evidence of recruitment declines in fragments. Seedling richness was lowest in  
30 small, isolated, and disturbed fragments, potentially signalling an extinction debt given  
31 that these fragmentation impacts were not observed in trees. Unlike seedlings, saplings  
32 showed no declines in richness in fragments, suggesting that density dependent mortality  
33 (where rare individuals have a higher survival rate) and/or year-to-year variation in which  
34 species are recruiting could potentially compensate for the reductions in seedling richness  
35 we observed. Longer-term studies are required to determine whether sporadic or failed  
36 recruitment in small fragments will eventually translate into reduced richness of mature  
37 trees, or whether the processes that currently retain high sapling richness will continue in  
38 fragments.

39

40 **Keywords**

41 Biodiversity; Borneo; extinction debt; forest fragments; habitat fragmentation; natural  
42 regeneration; oil palm landscape; tropical trees.

43 THE LONG-TERM EFFECTS OF HABITAT LOSS AND FRAGMENTATION on the floristic diversity of  
44 vegetation remnants remain uncertain, predominantly because plants often have long  
45 generation times. For example, the species richness of plants in temperate grassland and  
46 forest fragments has been found to reflect historic pre-fragmentation conditions rather than  
47 recent habitat availability (Krauss *et al.* 2010), implying century or longer extinction debts  
48 (Tilman *et al.* 1994; Kuussaari *et al.* 2009). These extinction debts may be compounded by  
49 similarly long colonisation lags (Diamond 1972), resulting in highly non-equilibrium  
50 communities in fragments. Thus, the effects of forest fragmentation and isolation on forest-  
51 dependent animal communities, which have been measured on time scales of years to decades  
52 (e.g. Fitzherbert *et al.* 2008; Hill *et al.* 2011), may just be the beginning of more fundamental  
53 changes in forest ecosystems, driven by the dynamics of long-lived and structurally important  
54 plant components of terrestrial ecosystems.

55         Habitat loss has particularly detrimental effects on highly diverse tropical forests,  
56 where the ecosystem biomass is primarily composed of (potentially) long-lived trees (Malhi  
57 *et al.* 2004). Deforestation in the tropics is driven primarily by agricultural expansion  
58 (Henders *et al.* 2015), linked to increasing demand for food from a growing human  
59 population (Koh & Wilcove 2008). Immediately following forest clearance of the  
60 surrounding land, some species will die out immediately in the remaining fragments, and  
61 other species will go extinct as a consequence of stochastic (meta) population dynamics  
62 (Laurance 2008). Systematic changes in community composition will also occur within  
63 fragments, given that species vary in their traits (Ewers & Didham 2006), and that reduced  
64 forest area and increased edge habitat alter the abiotic conditions (Laurance 2000), potentially  
65 leading to reduced species richness and an increased abundance of disturbance-loving species  
66 in fragments (Rutledge 2003). Fragment isolation is related to the amount of forest habitat  
67 within the landscape surrounding a forest fragment, and is the inverse of connectivity.

68 Increasing fragment isolation has the potential to disrupt biological processes such as  
69 pollination and seed dispersal, which could influence seedling recruitment (Aizen &  
70 Feinsinger 1994; Cordeiro & Howe 2001). These effects are generally most severe in small  
71 and isolated fragments (Haddad *et al.* 2015), but individual trees may persist for centuries  
72 without recruiting viable offspring, creating persistent extinction debts (Tilman *et al.* 1994;  
73 Vellend *et al.* 2006). Thus, the eventual impacts of fragmentation are likely to be under-  
74 estimated in short-term studies (Wearn *et al.* 2012), but differences in the species richness of  
75 pre- and post-fragmentation size classes of trees provide an initial assessment of emerging  
76 patterns of diversity change.

77 To assess the likelihood that fragmentation effects will result in recruitment failure  
78 and extinction debt we examine the genus richness of seedlings, saplings and mature trees in  
79 rainforest remnants. We evaluate whether tropical trees are continuing to recruit offspring  
80 within forest fragments that were probably formed about 20 years ago on Borneo, in the  
81 1990s during rapid development of oil palm (*Elaeis guineensis* Jacq.) plantations. Southeast  
82 Asia is one of the most rapidly-changing landscapes globally and, on Borneo, oil palm  
83 plantations have replaced much of the original forest cover in lowland areas (Sodhi *et al.*  
84 2010). Lowland tropical rainforest in Southeast Asia is dominated by a single family, the  
85 Dipterocarpaceae, which form the majority of the standing biomass (Curran *et al.* 1999).  
86 Throughout the aseasonal tropics, dipterocarps recruit seedlings almost exclusively via  
87 synchronised mast fruiting on an irregular supra-annual basis of two to 10 years (Appanah  
88 1993), triggered by the droughts and low night time temperatures of El Niño Southern  
89 Oscillation (ENSO) events (Yasuda *et al.* 1999). The extent to which masting is disrupted by  
90 fragmentation is currently unknown, but given that fragments experience greater drought and  
91 higher temperatures than continuous tracts of forest (Ewers & Banks-Leite 2013), it seems  
92 likely that seed production and seedling survival will be affected. Understanding the impacts

93 of rainforest fragmentation is critical for conserving biodiversity, given that so much of the  
94 remaining forest has been degraded by repeated logging (Reynolds *et al.* 2011), and  
95 fragmentation (Haddad *et al.* 2015). Moreover, isolated fragments of forest are increasingly  
96 important refuges for species in oil-palm dominated agricultural landscapes, making it  
97 important to understand factors affecting their long-term persistence.

98         We examine fragmentation effects by studying the consequences for plant  
99 communities within remaining rainforest patches following their insularisation. Our study  
100 landscape has undergone extensive deforestation, so that remaining patches of natural forest  
101 are surrounded by agricultural land. We enumerate plant richness within forest patches and  
102 examine changes in local (plot-scale) plant communities with respect to fragment size, shape  
103 and degree of isolation from other forest habitat. We compare genus richness of seedlings (<1  
104 cm dbh and <1.5 m height), nearly all of which will have recruited after the forest fragments  
105 were isolated in the 1990s (Connell & Green, 2000), with the genus richness of forest trees.  
106 Trees that were already established at the time of fragmentation will predominantly fall into  
107 our tree (>5 cm dbh) size class category, although some fast-growing stems will have  
108 recruited since fragmentation. Thus, the tree size class provides us with an insight into pre-  
109 fragmentation communities, although there will have been some turnover. We also examine  
110 saplings (1 – 5 cm dbh), anticipating that this size class will comprise many post-  
111 fragmentation individuals, but also some pre-fragmentation individuals. We test the  
112 hypothesis that seedling recruitment is reduced within plots in forest fragments, compared  
113 with plots in continuous forest, and specifically that seedling and sapling genus richness is  
114 reduced in plots in small, isolated and more disturbed fragments. In this way, we assess the  
115 regeneration potential of forest fragments and whether there are extinction debts in tree  
116 communities.

## 117 METHODS

118 STUDY REGION AND SITES.—The study was carried out in Sabah (Malaysian Borneo) during  
119 April-August 2015, in lowland (< 500 m asl) dipterocarp rainforest. We compared plant  
120 communities in 14 forest fragments with 5 sites in an extensive tract of more continuous  
121 forest. The continuous forest sites were located within the Yayasan Sabah Forest  
122 Management Area (YSFMA, ~1,000,000-ha), three sites within fully-protected primary forest  
123 (Danum Valley Conservation Area), and two sites within twice-logged forest (Malua Forest  
124 Reserve), which was selectively logged in the mid-1980s (~120 m<sup>3</sup>/ha timber extracted) and  
125 again in 2005/6 (~35m<sup>3</sup>/ha timber extracted; Reynolds *et al.* 2011; Fig. S1).

126 The fragments of primary forest that we studied were protected as “Virgin Jungle  
127 Reserves” (VJR) in the 1950s for scientific research, were formally gazetted in 1984 and are  
128 managed by the Sabah Forestry Department. These fragment VJRs make up ~1.2 percent of  
129 Sabah’s land area but represent nearly 20 percent of the reserve area in which logging is  
130 prohibited (McMorrow & Talip 2001). These fragment sites were not commercially logged  
131 prior to formation, but most have subsequently experienced low levels of disturbance from  
132 human encroachment (pers. obs.). The 14 fragments range in size from 40 to 120,000-ha (Fig.  
133 S1; Table S1), and were probably formed at least 20 years ago, during the rapid development  
134 of oil palm cultivation in the region in the 1990s (Reynolds *et al.* 2011). Sites were >2 km  
135 apart and fragments were surrounded by mature oil palm plantations at the time of study.

136 FLORISTIC SURVEYS.—A 1 km linear transect was set up at each of the 19 sites. Each transect  
137 comprised five plots spaced 160 m apart along the transect (Fig. S1), with the exception of  
138 site #2 (44-ha; Table S1), where only three plots were possible due to its small size. Transects  
139 in fragments started 100 m from the forest edge to avoid the main edge effects (Ewers &  
140 Didham 2006), and were angled towards the fragment centre. Each plot was 20 x 40 m, and

141 was sampled following a modified Gentry protocol, using a series of subplots to sample  
142 different size classes (Gentry 1982; Fig. S1). Hence our approach was to sample with equal  
143 effort at each site (rather than in proportion to site area), and our analyses compare local  
144 (plot-scale) genus richness among sites.

145 A nested design was used to ensure adequate sampling of different tree size classes  
146 (seedlings, saplings, trees), because a larger sampling area was required for trees and we did  
147 not want to over-sample saplings and seedlings. Seedlings were defined as non-climbing  
148 woody plants <1.5 m in height and <1 cm dbh, and were measured and identified in four 2 m  
149 x 2 m sub- plots distributed evenly within each plot (Fig. S1). All seedlings are expected to  
150 have been recruited since fragmentation during mast fruiting events (e.g. 1997/98 and  
151 2015/16 were particularly strong global ENSO events (Curran *et al.* 1999; Cpc.ncep.noaa.gov  
152 2017). Saplings were defined as non-climbing woody plants 1–5 cm dbh, and they were  
153 enumerated and identified in four 5 m x 5 m subplots within each plot (Fig. S1). Trees >5 cm  
154 dbh were divided into two groups: those 5–30 cm dbh were sampled in one 5 m x 40 m strip  
155 within each plot, and trees >30 cm dbh were enumerated in the full 20 x 40 m plot (Fig. S1).  
156 It is difficult to estimate the age of individual trees due to high levels of inter- and intra-  
157 specific variation in growth rates, depending on life-history strategy and resource availability  
158 (especially light). Therefore we defined size classes to represent individuals that  
159 predominantly germinated prior to fragment formation (“trees”), after fragment formation  
160 (“seedlings”), and an intermediate group (“saplings”) which contains many individuals  
161 germinating after fragment formation, but also includes individuals germinating prior to  
162 fragmentation. Our analyses focus on comparing the genus richness of each size class  
163 (seedlings, sapling, trees) separately among sites. We also computed plot-level plant diversity  
164 using Simpson’s index (supplementary material), which confirmed that our results were not  
165 confounded by variation in stem density across sites (Fig. S4; Table S5), and so we only



166 include analyses of genus richness in the main text. We also performed an individual stem-  
167 based rarefaction analysis of genus richness (see Text S1), by combining data from all plots  
168 at a site (excluding Site 2 with only three plots), which supported our overall conclusions,  
169 and again confirmed that our main findings were not affected by variation in stem density.

170 Plant identification was carried out in the field where possible and confirmed by the  
171 botanist at Danum Valley Field Centre, based on leaf samples and photographs taken in the  
172 field. All but six individuals were named to species or genus level, and unidentified  
173 individuals (representing 0.06% of stems) were removed from the analysis. We carry out all  
174 analyses at genus level given the complexities of plant identification. However, we also  
175 repeated our analyses at species level, and results were qualitatively the same (Fig. S2, Table  
176 S2) implying that finer resolution identification would not have altered our conclusions.

177 SITE AND PLOT CHARACTERISTICS.—In order to relate our findings on plant genus richness to  
178 attributes of the sites where data were collected, we recorded the following site  
179 characteristics. We measured fragment area and perimeter using ArcMap 10.0 and R v. 3.2.2,  
180 after tracing the outline of each fragment from Google Earth satellite imagery. Fragment  
181 shape was calculated from the area ( $m^2$ ) and perimeter (m), where a value of 1 indicates a  
182 circular fragment, and values approaching a maximum of 5 indicate a highly convoluted  
183 shape (Arroyo-Rodríguez & Mandujano 2006; see Text S2 for equation). The connectivity  
184 (i.e. inverse of isolation) of each fragment was calculated from forest land cover data  
185 (Miettinen *et al.* 2012) at a grid cell resolution of 250 m to identify the size of, and distance  
186 to, all forest patches within a 5 km radius of each site (McGarigal & Marks 1995; for  
187 equation, see Text S3). A connectivity value of 0 for a fragment indicates an absence of  
188 patches of forest in the surrounding landscape, and increasing connectivity values indicate a  
189 greater total area of forest cover in the surrounding landscape. This metric represents the

190 degree of isolation of a site by taking into account the amount of forest habitat within the  
191 buffer, and weights it by area and proximity. We tested the sensitivity of our findings to  
192 different buffer widths, using buffer distances of 1 – 10 km, representing a range of seed and  
193 pollinator dispersal distances (Table S6). However, our results were not affected by different  
194 buffer widths and so we only report data for connectivity values based on 5 km buffer in the  
195 main text.

196 In order to characterise the forest in each of the plots within each of the 19 sites (93  
197 plots in total), we measured the following variables: temperature and light intensity (mean  
198 values ( $^{\circ}\text{C}$  and lux) from two Hobo® loggers placed 1.8 m from the ground within each plot,  
199 measured between 10am and 4pm over 2-3 days); photosynthetically active radiation (mean  
200 of four measurements taken within each seedling sub-plot (four sub-plots per plot) using a  
201 Skye Light Meter for Growers Limited); leaf litter depth (mean of four measurements using a  
202 steel ruler); canopy cover (taken in the centre of the plot using a densiometer). We also  
203 counted the number of lianas rooted within seedling sub-plots (Fig. S1). Many of these  
204 predictor variables were correlated with one another, and so we used principal components  
205 analysis (PCA) to reduce these six variables to a smaller number of independent factors, and  
206 the first principal component of this PCA was used in our analyses of seedling, sapling, and  
207 tree genus richness as an index of forest disturbance at sites.

208 DATA ANALYSES.—In order to test the hypothesis that tree recruitment is impaired in forest  
209 fragments compared with continuous forest sites, we first calculated the number of plant  
210 genera per plot, separately for seedlings, saplings and trees (Fig. 2), and compared genus  
211 richness in fragments, logged continuous forest, and primary continuous forest sites using  
212 one-way ANOVAs, followed by post-hoc Tukey HSD tests.

213 In order to test the hypothesis that seedling and sapling genus richness is lowest in  
214 small, isolated and most disturbed fragments, we carried out three general linear mixed  
215 effects models (GLMMs) to evaluate seedling, sapling and tree genus richness (response  
216 variable = number of genera per plot) in relation to four site attributes: size, shape,  
217 connectivity, and disturbance (PCA factor score; PC1). We gave sites in continuous forest a  
218 notional area of 800,000-ha (the area of the Yayasan Sabah Forest Reserve; Reynolds *et al.*  
219 2011), and values of 1 for shape and 17,000,000 for connectivity so that these five sites could  
220 be included in our analyses. We carried out Poisson GLMMs with a log-link function,  
221 including 2-way interactions between the four predictor site attributes (with data analysed at  
222 plot-level; 93 data points), and site identity was included as a random effect to account for  
223 non-independence of plots within sites. Area was log<sub>10</sub>-transformed and connectivity was  
224 cube-root transformed to reduce skew in the data, and all four predictor variables were scaled  
225 to have a mean of 0 and variance of 1 prior to analysis, to aid comparison of their relative  
226 importance on genus richness. The top models were identified using an AIC approach  
227 (Burnham & Anderson 2002), where delta AICc <2 of the best model were included in the  
228 top models, and model averaging was then used to find the importance of each variable and  
229 determine their relative effect sizes: effect sizes whose confidence intervals (CIs) did not  
230 cross zero were assumed to be significant predictors of plant richness. All analyses were  
231 performed using the R package vegan (Oksanen *et al.* 2011) in R v. 3.2.2 (R Development  
232 Core Team 2015).

## 233 **RESULTS**

234 Across the 93 plots at 19 sites, we surveyed 9608 individual plants, representing 222 genera  
235 and 76 families. As is typical for this region, the Dipterocarpaceae family was dominant  
236 across all size classes, and 27 percent of all individuals were represented by this family. The

237 most numerous genus was *Shorea* (Dipterocarpaceae), which formed 30 percent of individual  
238 seedlings, 4 percent of saplings, and 8 percent of trees. The frequency distributions of stem  
239 sizes across the three forest types were similar, although only primary forest contained  
240 individuals over 125 cm dbh (Fig. 1).

241 The first principal component (PC1), constructed from six variables describing site  
242 and plot characteristics, accounted for 32.5 percent of the overall variation, and increased  
243 with increasing light, temperature, and a more open canopy (Fig. S3A). Hence we conclude  
244 that PC1 is a measure of forest disturbance, and PC1 scores were negatively correlated with  
245 site area and connectivity (Fig. S3B), indicating that forest disturbance is greater in small and  
246 isolated forest fragments.

247 VARIATION IN PLANT GENUS RICHNESS AMONG STUDY SITES.—Seedling genus richness was  
248 much lower in plots in fragments compared with plots in primary and logged forest (one-way  
249 ANOVA of genus richness by forest type;  $F_{(2,90)} = 8.55$ ,  $p < 0.001$ ), but there was no  
250 significant difference between seedling genus richness in primary and logged forest.  
251 Fragment seedling genus richness ( $N = 14$  sites; mean = 7.3 genera per plot  $\pm 0.3$  SE) was 29  
252 percent lower than in primary continuous forest ( $N = 3$  sites, mean = 10.3 genera per plot  $\pm$   
253 0.7 SE), and 20 percent lower than in logged continuous forest ( $N = 2$  sites, mean = 9.1  
254 genera per plot  $\pm 1.2$  SE; Fig. 2). However, there was little impact of fragmentation on genus  
255 richness of either saplings ( $F_{(2,90)} = 2.36$ ,  $p = 0.10$ ; fragments, mean richness = 16.9 genera  
256 per plot  $\pm 0.7$  SE; logged forest, mean = 20.5  $\pm 2.0$ ; primary forest, mean = 15.9 genera per  
257 plot  $\pm 1.0$ ) or trees ( $F_{(2,90)} = 0.82$ ,  $p = 0.44$ ; fragments, mean = 16.8 genera per plot  $\pm 0.5$  SE;  
258 logged forest, mean = 18.6 genera per plot  $\pm 1.6$ ; primary forest, mean = 16.5 genera per plot  
259  $\pm 0.8$ ). Thus we conclude that forest fragmentation reduces local seedling genus richness but  
260 has no impact on the genus richness of saplings or trees.

261 EFFECTS OF SITE CHARACTERISTICS ON PLANT RICHNESS.—Outputs from GLMMs revealed  
262 that seedling genus richness was positively associated with site area, and there was an  
263 indication that connectivity, and forest disturbance of sites were also important (Fig. 3). Site  
264 area was the most important variable in the best model (Table 1), and seedling genus richness  
265 was particularly low in small, isolated, highly disturbed sites. Our rarefaction analyses of  
266 seedling data found similar trends (Fig. S5, see Text S1 for further discussion). In contrast to  
267 data for seedlings, and even though we assumed that saplings were predominantly produced  
268 after fragmentation, there was no effect of site area (or any other predictor variable) on  
269 sapling genus richness. This result was robust to varying the stem diameter threshold for our  
270 sapling size class (Table S7), and to the removal of high wood density, slow-growing genera  
271 ( $> 0.75 \text{ g/cm}^3$ ; Table S8). Additionally, results were qualitatively similar when we split our  
272 data set according to the median wood density of all genera we encountered in our study  
273 ( $0.55 \text{ g/cm}^3$ ), indicating that differences in plant growth rates are not having major impacts on  
274 our designation of post- and pre-fragmentation individuals, or our overall findings (Table S9,  
275 see Text S6 for further discussion). We assumed that trees were representative of pre-  
276 fragmentation communities and as predicted, tree genus richness did not vary according to  
277 site area. Tree genus richness did however vary according to levels of forest disturbance at  
278 sites (PC1 score), indicating that sites with more open canopies, higher temperatures and  
279 higher light environments contained fewer tree genera.

## 280 **DISCUSSION**

281 Forest fragmentation significantly reduced the local genus richness of tree seedlings. On  
282 average, only 4.2 seedling genera ( $\pm 0.97 \text{ SE}$ ) were found per  $16 \text{ m}^2$  plot in the smallest  
283 fragment (39.6 ha), compared to 11.8 seedling genera ( $\pm 0.86$ ) per plot in a primary forest site  
284 in continuous forest. The absence of any reduced genus richness in trees may be indicative of

285 an extinction debt in small fragments, although our failure to find any reduction in sapling  
286 genus richness may suggest that there are compensatory processes in operation (see below).

287 NO EFFECTS OF FRAGMENTATION ON TREE GENUS RICHNESS.— Given the age of our fragments,  
288 we assume that our tree size class would have mostly germinated prior to fragmentation, and  
289 that the genus richness of these trees broadly represents the ‘pre-isolation’ condition of the  
290 forest. Although we did not detect direct effects of fragment size or isolation on our tree size  
291 class, we did find indirect effects because reduced genus richness was associated with  
292 disturbance, and fragments generally contained more disturbed forest; Fig. S3B). Hence trees  
293 were affected by local forest disturbance rather than by the direct effects of fragmentation in  
294 reducing site area and isolation.

295 REDUCED LOCAL GENUS RICHNESS OF SEEDLINGS IN FRAGMENTS.— The reduced number of  
296 seedling genera per plot in (small) forest fragments, compared to continuous forest, could  
297 arise from multiple processes relating both to the biological and physical conditions of the  
298 fragments. Forest fragments experience a change in physical (micro)climatic conditions  
299 associated with increased disturbance and edge effects, particularly through greater wind  
300 disturbance and elevated desiccation (Laurance 2004). This can alter the cues linked to the  
301 initiation of (sporadic) mass flowering (Curran *et al.* 1999) and may hamper the physiological  
302 ability of trees to support fruit development, the germination of seeds, and affect the  
303 establishment and survival of seedlings (Delissio & Primack 2003). Fragmentation may also  
304 lead to the loss of pollinators (Aizen & Feinsinger 1994) and change patterns of seed  
305 predation and dispersal (Cordeiro & Howe 2001). Self-incompatibility mechanisms in  
306 tropical trees may lead to reproductive failure among species with small numbers of  
307 individuals surviving per fragment (Ghazoul *et al.* 1998; Naito *et al.* 2008). Given that  
308 different species of trees will flower and fruit in response to different physical cues, and

309 exhibit different interactions with specialised and generalist natural enemies, it is likely that a  
310 combination of processes may reduce the ‘post-isolation’ genus richness of seedlings in forest  
311 fragments. In addition, our rarefaction analyses, that account for differences in seedling stem  
312 density, also found a trend of decreasing numbers of seedling genera in smaller fragments,  
313 and so it seems likely that regeneration processes are being disrupted in fragments.

314 LONG-TERM VIABILITY OF FRAGMENTS AND CONFLICTING RESULTS FROM SAPLINGS.—As with  
315 seedlings, we expected a high proportion of saplings to have germinated subsequent to  
316 fragmentation, yet we did not find any effects of fragmentation on saplings, despite finding  
317 an effect on seedlings. Isolation of our Virgin Jungle Reserve sites probably occurred at least  
318 20 years before our study. Certain shade tolerant species are able to persist in seedling banks  
319 in the forest understory for a number of years (Brown & Whitmore 1992), and it is likely that  
320 our sapling size class comprises a mixture of individuals that germinated both pre- and post-  
321 fragmentation (Delissio *et al.* 2002). Nonetheless, a portion of saplings will have recruited  
322 post-fragmentation, and hence we expected (but did not observe), some effects of  
323 fragmentation on sapling genus richness. There are a number of possible explanations for this  
324 disparity between seedlings and saplings, which could result from a combination of the  
325 following: 1) more sporadic recruitment of seedlings in small fragments than in continuous  
326 forest; 2) increased density-dependent survival of the rarest seedlings; and 3) delayed  
327 (lagged) impacts of fragmentation on seedling recruitment failure. For example, if different  
328 species are recruited in different years in fragments (more so than in continuous forest) owing  
329 to disruption of flowering or reduced pollination in fragments, then there will be lower  
330 richness in any single seedling size class. However, the sapling size classes in the same plots  
331 are likely to include a wider age range of individuals than seedlings, and hence represent the  
332 survivors from several seedling size classes. The impact of recruiting different species in  
333 different years could be further enhanced if density-dependent mortality of conspecifics takes

334 place, whereby rare species have a higher survival rate (LaManna *et al.* 2017). Survival of  
335 low density species may be elevated in fragments if herbivores and pathogens specialising on  
336 rare species become extinct from small areas of forest (Arnold & Asquith 2002). If sporadic  
337 recruitment and density-dependent processes allow sapling genus richness to be maintained,  
338 then fragmentation may not necessarily have longer-term detrimental impacts on plant  
339 richness. However, high sapling genus richness may reflect time lags between fragmentation  
340 and reduced seedling recruitment, such that surveys immediately post-fragmentation would  
341 not have detected any changes in seedling genus richness. If the first two processes are  
342 operating, then local (plot scale) genus richness of saplings and mature trees may not  
343 inevitably decline over time in small fragments, despite the reduction in seedling genus  
344 richness at any one time. Nonetheless, even if local plot scale genus richness is maintained,  
345 some (mainly rare) species and genera are still likely to be lost from small fragments. These  
346 explanations for the findings we report deserve further research, given that they lead to quite  
347 different expectations about future diversity changes in forest fragments.

348 CONCLUSIONS.—Small, isolated and disturbed forest fragments have lower local seedling  
349 genus richness but similar levels of sapling and tree genus richness, compared with  
350 continuous forest. Whether fragmentation will lead to long-term reductions in the plant  
351 diversity of fragments is not yet clear, given that genus richness is apparently maintained in  
352 the sapling size class post-fragmentation. The longevity of trees extends the window for  
353 conservation action (Wearn *et al.* 2012), and episodic recruitment, density dependence and  
354 lagged effects of fragmentation may buy more time still. The fact that recruitment patterns  
355 differ between fragments and continuous forest sites implies that there will be divergence in  
356 the plant communities of these areas, but it is too early to conclude that fragments will have  
357 reduced diversity in the long term. Hence, local tree genus richness may be maintained in  
358 fragments, regional habitat specialists may only survive in small fragments if continuous



359 forest no longer exists elsewhere, and small fragments may increasingly support unique  
360 biological communities. Thus, rainforest remnants may have inherent conservation value.

### 361 **Author contributions**

362 GS, JKH, and CDT conceived and designed the study; GS and AJ collected field data; GS led  
363 data analysis and wrote the first draft of the manuscript, with substantial contributions from  
364 JKH and CDT to all further revisions. SB, JH and MJMS also contributed to revisions. All  
365 authors gave final approval for publication.

### 366 **Competing interests**

367 The authors declare they have no competing interests.

### 368 **Funding**

369 This research was funded by a NERC studentship awarded to GS via the ACCE DTP (award  
370 ref. 1505102).

371 **Data Availability:** The data used in this study are archived at the Dryad Digital Repository  
372 (doi:10.5061/dryad.3jt6kh3).

373

### 374 **LITERATURE CITED**

375 AIZEN M. A., FEINSINGER P. 1994. Habitat Fragmentation, Native Insect Pollinators , and  
376 Feral Honey Bees in Argentine ‘Chaco Serrano’. *Ecol. Appl.* 4: 378–92. (doi:  
377 10.2307/1941941)

378 APPANAH S. 1993. Mass flowering of dipterocarp forests in the aseasonal tropics. *J. Biosci.*  
379 18: 457–74. (doi: 10.1007/BF02703079)

380 ARNOLD A. E., ASQUITH N. M. 2002. Herbivory in a fragmented tropical forest: Patterns from  
381 islands at Lago Gatun, Panama. *Biodivers. Conserv.* 11: 1663–80. (doi:  
382 10.1023/A:1016888000369)

383 ARROYO-RODRÍGUEZ V., MANDUJANO S. 2006. The importance of tropical rain forest  
384 fragments to the conservation of plant species diversity in Los Tuxtlas, Mexico. *Biodivers.*  
385 *Conserv.* 15: 4159–79. (doi: 10.1007/s10531-005-3374-8)

386 BROWN N., WHITMORE T. 1992. Do dipterocarp seedlings really partition tropical rain forest  
387 gaps? *Philos. Trans. Biol. Sci.* 335: 369–78. (doi: 10.1098/rstb.1992.0028)

388 BURNHAM K., ANDERSON D. 2002. Model selection and multimodel inference: a practical  
389 information-theoretic approach. Springer Science & Business Media. Springer-Verlag New  
390 York.

391 CONNELL J. H., GREEN P. T. 2000. Seedling Dynamics over Thirty-Two Years in a Tropical  
392 Rain Forest Tree. *Ecology*, 81: 568–584. (doi: 10.2307/177449)

393 CORDEIRO N. J., HOWE H. F. 2001. Low Recruitment of Trees Dispersed by Animals in  
394 African Forest Fragments. *Conserv. Biol.* 15: 1733–41. (doi: 10.1046/j.1523-  
395 1739.2001.99579.x)

396 CPC.NCEP.NOAA.GOV. 2017. CPC - Climate Weather Linkage: El Niño Southern Oscillation  
397 [Internet]. [cited 2017 Jul 10]. Available from:  
398 <http://www.cpc.ncep.noaa.gov/products/precip/CWlink/MJO/enso.shtml>

399 CURRAN L. M., CANIAGO I., PAOLI G. D., ASTIANTI D., KUSNETI M., LEIGHTON M., *et al.*  
400 1999. Impact of El Niño and Logging on Canopy Tree Recruitment in Borneo. *Science* 286:  
401 2184–8. (doi: 10.1126/science.286.5447.2184)

402 DELISSIO L. J., PRIMACK R. B. 2003. The impact of drought on the population dynamics of  
403 canopy-tree seedlings in an aseasonal Malaysian rain forest. *J. Trop. Ecol.* 19: 489–500. (doi:  
404 10.1017/S0266467403003547)

405 DELISSIO L. J., PRIMACK R. B., HALL P., LEE H. S. 2002. A decade of canopy-tree seedling  
406 survival and growth in two Bornean rain forests: persistence and recovery from suppression. *J*  
407 *Trop. Ecol.* 18: 645–58. (doi: 10.1017/S0266467402002420)

408 DIAMOND J. M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of  
409 southwest pacific islands. *Proc. Nat. Acad. Sci. USA.* 69: 3199–3203. (doi:  
410 10.1073/pnas.69.11.3199)

411 EWERS R. M., BANKS-LEITE C. 2013. Fragmentation Impairs the Microclimate Buffering  
412 Effect of Tropical Forests. *PLoS One.* 8: e58093. (doi: 10.1371/journal.pone.0058093)

413 EWERS R. M., DIDHAM R. K. 2006. Confounding factors in the detection of species responses  
414 to habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* 81: 117–42. (doi:  
415 10.1017/S1464793105006949)

416 FAHRIG L. 2017. Responses to Habitat Fragmentation Per Se. *Annu. Rev. Ecol. Evol. Syst.*  
417 48: 1–23. (doi: 10.1146/annurev-ecolsys-110316-022612)

418 GENTRY A. 1982. Patterns of neotropical plant species diversity. *Evol. Biol.* 15: 1–84. (doi:  
419 10.1007/978-1-4615-6968-8\_1)

420 GHAZOUL J., LISTON K., BOYLE T. 1998. Disturbance-induced density-dependent seed set in  
421 *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree. *J. Ecol.* 86: 462–73. (doi:  
422 10.1046/j.1365-2745.1998.00270.x)

423 HADDAD N. M., BRUDVIG L. A., CLOBERT J., DAVIES K. F., GONZALEZ A., HOLT R. D., *et al.*  
424 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv.* 1:  
425 e1500052–e1500052. (doi: 10.1126/sciadv.1500052)

426 HENDERS S., PERSSON U. M., KASTNER T. 2015. Trading forests: land-use change and carbon  
427 emissions embodied in production and exports of forest-risk commodities. *Environ. Res. Lett.*  
428 IOP Publishing 10: 125012. (doi: 10.1088/1748-9326/10/12/125012)

429 HILL J. K., GRAY M. A., KHEN C. V., BENEDICK S., TAWATAO N., HAMER K. C. 2011.  
430 Ecological impacts of tropical forest fragmentation: how consistent are patterns in species  
431 richness and nestedness? *Philos. Trans. R. Soc. B.* 366: 3265–76. (doi:  
432 10.1098/rstb.2011.0050)

433 KOH L. P., WILCOVE D. S. 2008. Is oil palm agriculture really destroying tropical  
434 biodiversity? *Conserv Lett.* 1: 60–4. (doi: 10.1111/j.1755-263X.2008.00011.x)

435 KRAUSS J., BOMMARCO R., GUARDIOLA M., HEIKKINEN R. K., HELM A., KUUSSAARI M., *et al.*  
436 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different  
437 trophic levels. *Ecol. Lett.* 13: 597–605. (doi: 10.1111/j.1461-0248.2010.01457.x)

438 KUUSSAARI M., BOMMARCO R., HEIKKINEN R. K., HELM A., KRAUSS J., LINDBORG R., *et al.*  
439 2009. Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* 24: 564–  
440 71. (doi: 10.1016/j.tree.2009.04.011)

441 LAMANNA J. A., MANGAN S. A., ALONSO A., BOURG N. A., BROCKELMAN W. Y.,  
442 BUNYAVEJCHEWIN S., *et al.* 2017. Plant diversity increases with the strength of negative  
443 density dependence at the global scale. *Science* 356: 1389–92. (doi:  
444 10.1126/science.aam5678)

445 LAURANCE W. 2000. Do edge effects occur over large spatial scales? *Trends Ecol. Evol.* 15:  
446 134–5. (doi: 10.1016/S0169-5347(00)01838-3)

447 LAURANCE W. F. 2004. Forest-climate interactions in fragmented tropical landscapes. *Philos.*  
448 *Trans. R. Soc. B.* 359: 345–52. (doi: 10.1098/rstb.2003.1430)

449 LAURANCE W. F. 2008. Theory meets reality: How habitat fragmentation research has  
450 transcended island biogeographic theory. *Biol. Conserv.* 141: 1731–44. (doi:  
451 10.1016/j.biocon.2008.05.011)

452 MALHI Y., BAKER T. R., PHILLIPS O. L., ALMEIDA S., ALVAREZ E., ARROYO L., *et al.* 2004.  
453 The above-ground coarse wood productivity of 104 Neotropical forest plots. *Glob. Chang.*  
454 *Biol.* 10: 563–91. (doi: 10.1111/j.1529-8817.2003.00778.x)

455 MCGARIGAL K., MARKS B. 1995. FRAGSTAT: Spatial pattern analysis program for  
456 quantifying landscape structure. United States Dep Agric Pacific Northwest Res Station. 120  
457 pages.

458 MCMORROW J., TALIP M. A. 2001. Decline of forest area in Sabah, Malaysia: Relationship to  
459 state policies, land code and land capability. *Glob. Environ. Chang.* 11: 217–30. (doi:  
460 10.1016/S0959-3780(00)00059-5)

461 MIETTINEN J., SHI C., TAN W. J., LIEW S. C. 2010. Land cover map of insular Southeast Asia  
462 in 250-m spatial resolution. *Remote Sens. Lett.* 2012 Jan 3: 11–20. (doi:  
463 10.1080/01431161.2010.526971)

464 NAITO Y., KANZAKI M., IWATA H., OBAYASHI K., LEE S. L., MUHAMMAD N., *et al.* 2008.  
465 Density-dependent selfing and its effects on seed performance in a tropical canopy tree

466 species, *Shorea acuminata* (Dipterocarpaceae). *For. Ecol. Manage.* 256: 375–83. (doi:  
467 10.1016/j.foreco.2008.04.031)

468 OKSANEN A. J., BLANCHET F. G., KINDT R., LEGENDRE P., MINCHIN P. R., HARA R. B. O., *et*  
469 *al.* 2015. *vegan: Community Ecology Package*. R package version 2.3-1. [http://CRAN.R-](http://CRAN.R-project.org/package=vegan)  
470 [project.org/package=vegan](http://CRAN.R-project.org/package=vegan)

471 R CORE TEAM. 2015. *R: A language and environment for statistical computing*. R Foundation  
472 for Statistical Computing, Vienna, Austria.

473 REYNOLDS G., PAYNE J., SINUN W., MOSIGIL G., WALSH R. P. D. 2011. Changes in forest land  
474 use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the Danum  
475 Valley region. *Philos. Trans. R. Soc. B.* 366: 3168–76. (doi: 10.1098/rstb.2011.0154)

476 RUTLEDGE D. 2003. Landscape indices as measures of the effects of fragmentation : can  
477 pattern reflect process? *DOC Sci. Intern. Ser.* 98: 1–27.

478 SODHI N. S., KOH L. P., CLEMENTS R., WANGER T. C., HILL J. K., HAMER K. C., *et al.* 2010.  
479 Conserving Southeast Asian forest biodiversity in human-modified landscapes. *Biol.*  
480 *Conserv.* 143: 2375–84. (doi: 10.1016/j.biocon.2009.12.029)

481 STRUEBIG M. J., KINGSTON T., ZUBAID A., MOHD-ADNAN A., ROSSITER S. J. 2008.  
482 Conservation value of forest fragments to Palaeotropical bats. *Biol. Conserv.* 141: 2112–26.  
483 (doi: 10.1016/j.biocon.2008.06.009)

484 TILMAN D., MAY R. R. M., LEHMAN C. L., NOWAK M. A. 1994. Habitat destruction and the  
485 extinction debt. *Nature* 371: 65–6. (doi: 10.1038/371065a0)

486 VELLEND M., VERHEYEN K., JACQUEMYN H., KOLB A., VAN CALSTER H., PETERKEN G., *et al.*  
487 2006. Extinction debt of forest plants persists for more than a century following habitat  
488 fragmentation. *Ecology*. 87: 542–8. (doi: 10.1890/05-1182)

489 WEARN O. R., REUMAN D. C., EWERS R. M. 2012. Extinction Debt and Windows of  
490 Conservation Opportunity in the Brazilian Amazon. *Science* 337: 228–31. (doi:  
491 10.1126/science.1219013)

492 YASUDA M., MATSUMOTO J., OSADA N., ICHIKAWA S., KACHI N., TANI M., *et al.* 1999. The  
493 mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *J. Trop. Ecol.*  
494 15: 437–49. (doi: 10.1017/S0266467499000930)

495 **TABLES**

496 TABLE 1. Top ranked GLMMs of factors affecting tree, sapling and seedling richness in 93  
 497 plots nested within 19 sites. Candidate models are ranked according to the Akaike's  
 498 information criterion (AICc). Corresponding degrees of freedom (df), log-likelihood  
 499 estimation (logLik), difference between AICc and lowest AICc value ( $\Delta_i$ ) in model set,  
 500 Akaike weight ( $w_i$ : the probability that each model is the best approximating model), and  
 501 marginal ( $R^2m$ ) and conditional ( $R^2c$ ) r-squared values are presented. Only models with  $\Delta_i < 2$   
 502 were included in the averaged top models.

<b>Response</b>								
<b>variable</b>	<b>Candidate models</b>	<b>df</b>	<b>logLik</b>	<b>AICc</b>	$\Delta_i$	$w_i$	$R^2m$	$R^2c$
Seedling richness	Area	3	-222.38	451	-	0.55	0.15	0.19
	Area + Connectivity	4	-222.11	452.7	1.65	0.24	0.16	0.19
	Area + Disturbance	4	-222.28	453	1.99	0.20	0.15	0.19
Sapling richness	-	2	-285.96	576	-	0.42	0	0.16
	Disturbance	3	-285.46	577.2	1.14	0.24	0.02	0.16
	Shape	3	-285.76	577.8	1.75	0.18	0.01	0.16
	Connectivity	3	-285.80	577.9	1.82	0.17	0.01	0.16
Tree richness	Disturbance	3	-265.77	537.8	-	0.51	0.05	0.10
	Disturbance + Shape	4	-265.26	539	1.17	0.28	0.07	0.10
	-	2	-267.70	539.5	1.72	0.21	0	0.10

503

504

505



506 **FIGURE LEGENDS**

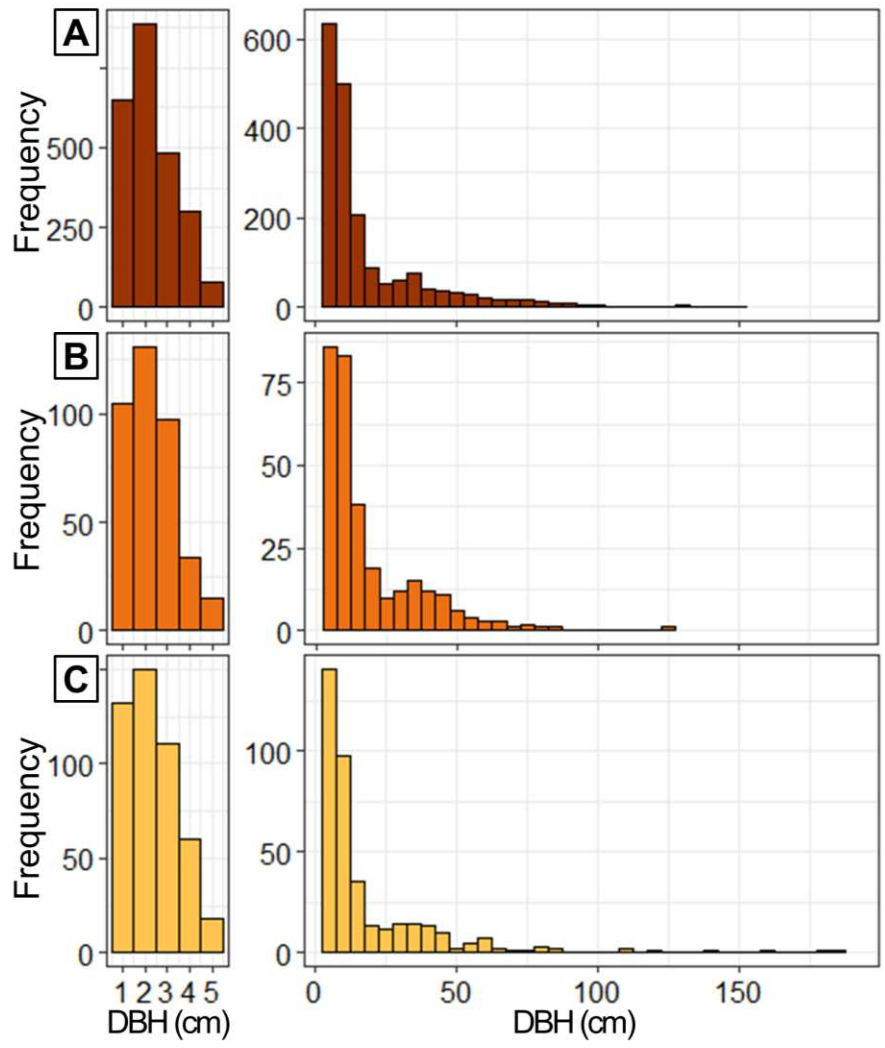
507 FIGURE 1. Overall frequency distribution of sapling (left) and tree (right) stem sizes in (A)  
508 forest fragments (brown bars, n = 68 plots), (B) logged forest (orange bars, n = 10 plots), and  
509 (C) primary forest (yellow bars, n = 15 plots) sites.

510 FIGURE 2. Effect of fragmentation on size class richness in primary, logged, and fragmented  
511 forest sites. Mean of standardised plant genus richness values ( $\pm$  SE) of size classes in plots  
512 located in primary continuous forest (yellow bars; n = 15), previously logged continuous  
513 forest (orange bars; n = 10), and forest fragments (brown bars; n = 68). ANOVA of plant  
514 richness by forest type:  $p \leq 0.001 = ***$ .

515 FIGURE 3. Effect of site characteristics on size class richness. A. Effect size of variables  
516 included in averaged models. Effect sizes whose 95% confidence intervals did not cross zero  
517 were assumed to be significant, and are shaded in grey. B. Impact of area, connectivity,  
518 fragment shape, and forest disturbance (principal component) on richness of trees, saplings,  
519 and seedlings. Brown symbols (fragments), orange symbols (logged forest) and yellow  
520 symbols (primary forest) show genus richness values of plots, and hollow circles are site  
521 means with standard error. Black line is fitted for variables where the slope was significantly  
522 different from zero in averaged top models; dotted line is fitted where variable was included  
523 in averaged top models but was not significant.

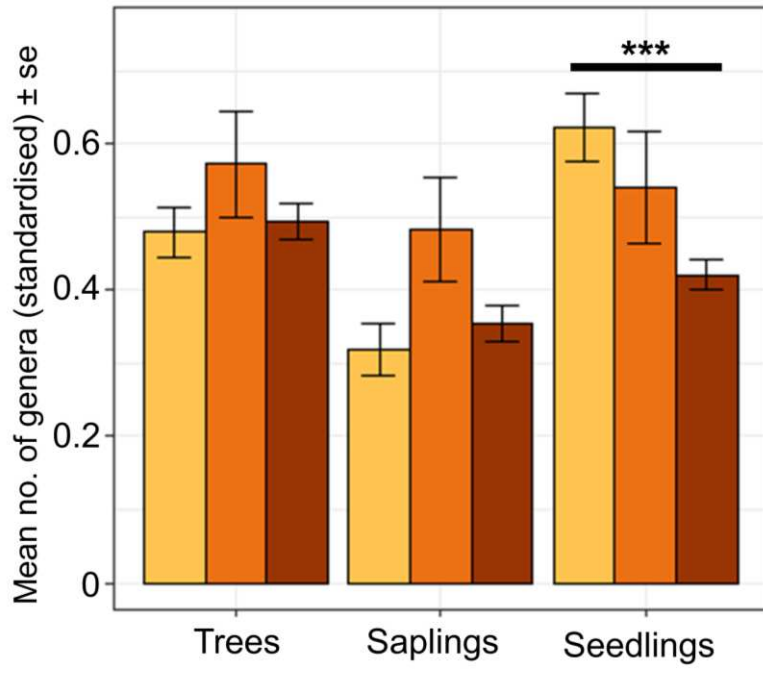
524

525



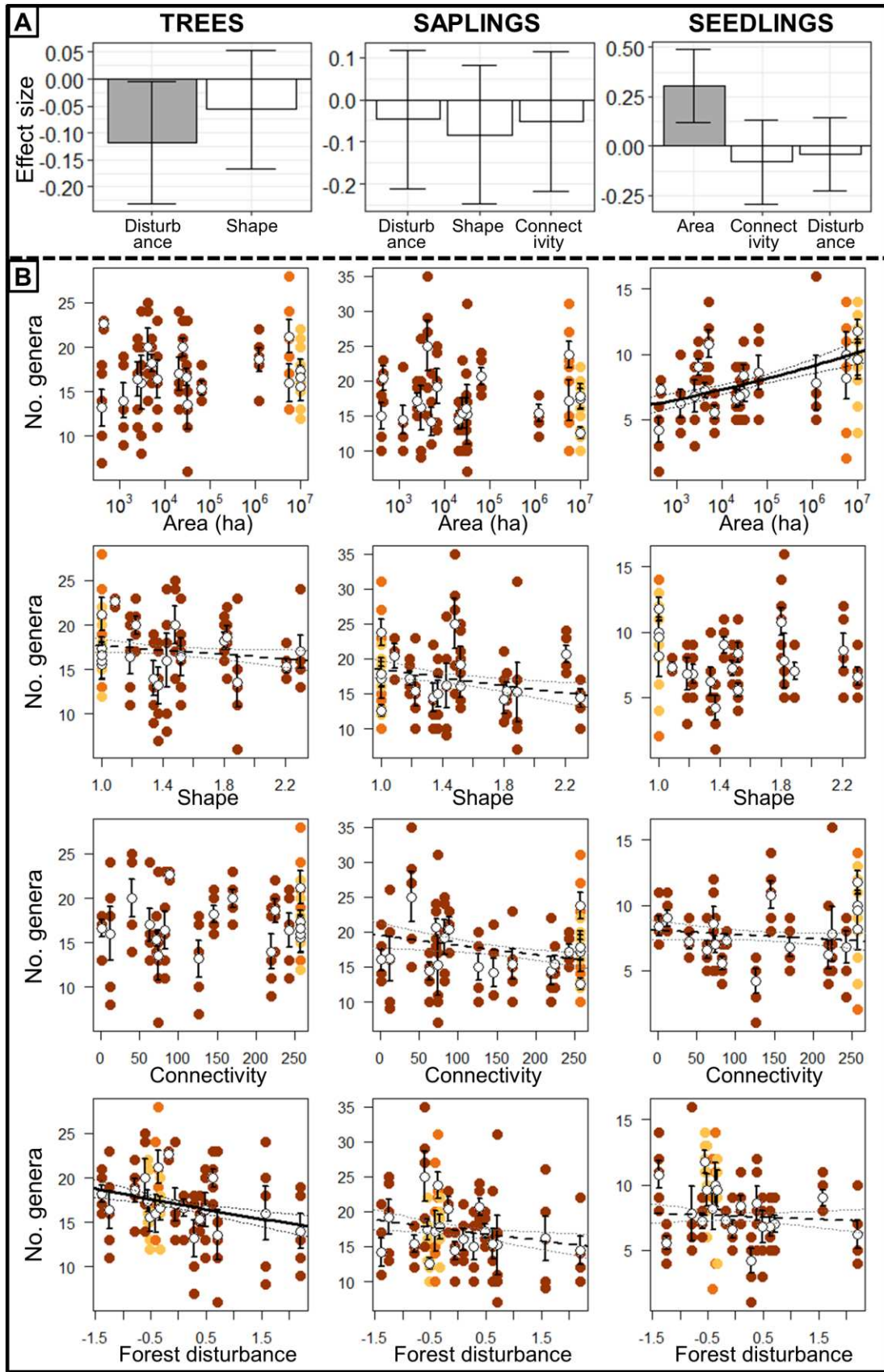
526

527 FIGURE 1.



528

529 FIGURE 2.



530

531 FIGURE 3.

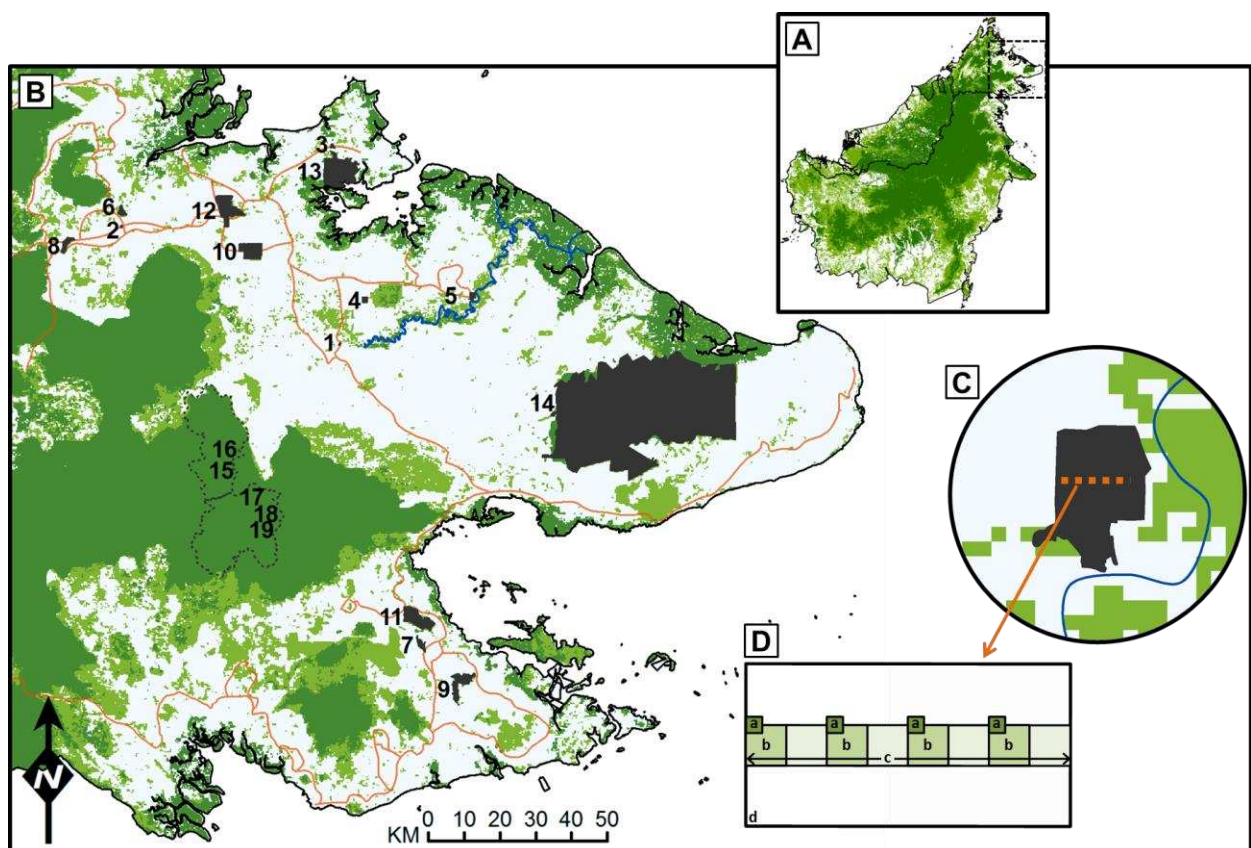
532 **Supporting Information**

533

534 **Contrasting patterns of local richness of seedlings, saplings and trees may have**  
535 **implications for regeneration in rainforest remnants.**

536 Gail Stride, Chris D. Thomas, Suzan Benedick, Jenny A. Hodgson, Ahmad Jelling, Mike J.M.  
537 Senior, Jane K. Hill

538

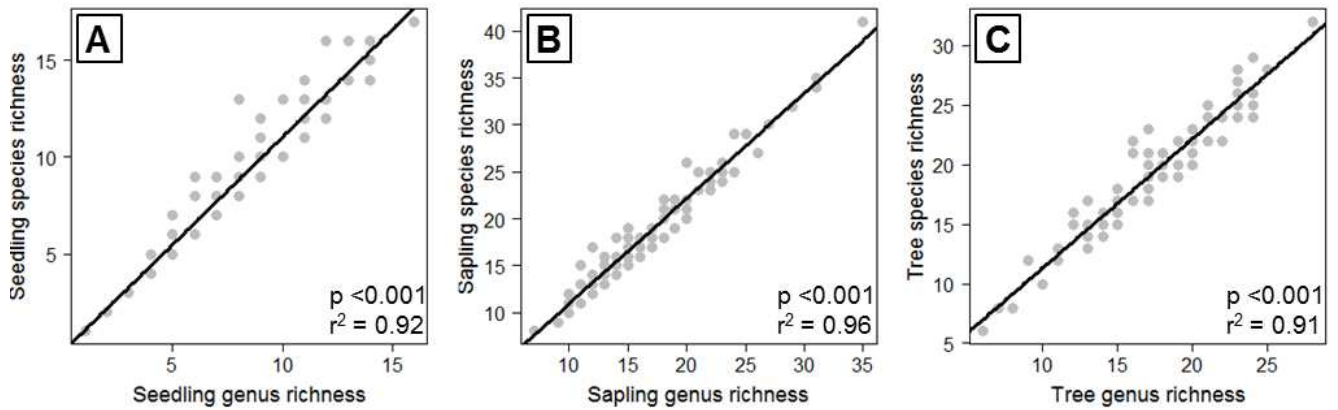


539

540 **Figure S1.** (A) Study area location on Borneo and (B) location of sites. Sites are numbered in  
541 order of increasing size; dark green areas indicate forest; light green areas indicate  
542 regenerating or degraded forest; white areas indicate agricultural land predominantly covered  
543 by oil palm; sites 15 – 19 within dotted areas are continuous forest sites. Forest cover data  
544 were obtained from Miettinen *et al.*, 2010. (C) Five plots along a transect in a forest fragment  
545 site. (D) Nested sampling design (subplot area in brackets): a = seedling plots (4 x (2 x 2 m)),

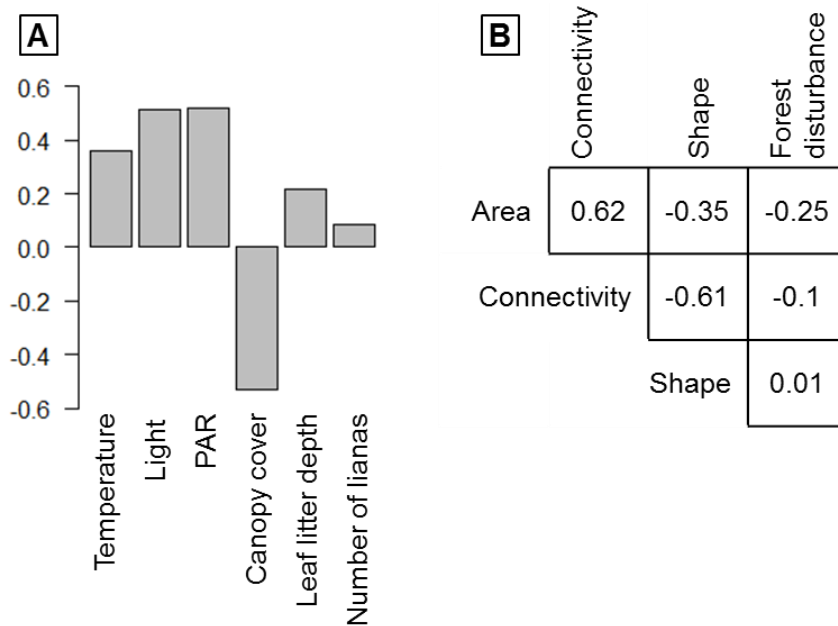
546 b = saplings 1-5 cm dbh (4 x (5 x 5 m)), c = trees 5 – 30 cm dbh (5 x 40 m), d = trees >30 cm  
 547 dbh (20 x 40 m).

548  
 549



550  
 551 **Figure S2.** Correlation between number of species and number of genera of (A) seedlings,  
 552 (B) saplings, and (C) trees identified in each plot (n = 93 plots). Black line is fitted using  
 553 generalized linear regression, and  $R^2$  value is adjusted  $R^2$ .

554



555  
 556 **Figure S3. A)** Variable scores in the first axis of a Principal Components Analysis  
 557 characterising forest disturbance, accounting for 32.5% of the variation (among plots) in the

558 data. Scores increased with higher light and PAR, higher temperature, and lower canopy  
559 cover, which we interpreted as being indicative of a higher level of disturbance. **B)** Matrix of  
560 Pearson correlation coefficients calculated between key variables, with 95% confidence  
561 intervals: positive correlations are indicated in blue, negative correlations in red. Non-  
562 significant correlations indicated by red cross.

563

564

565

566

567

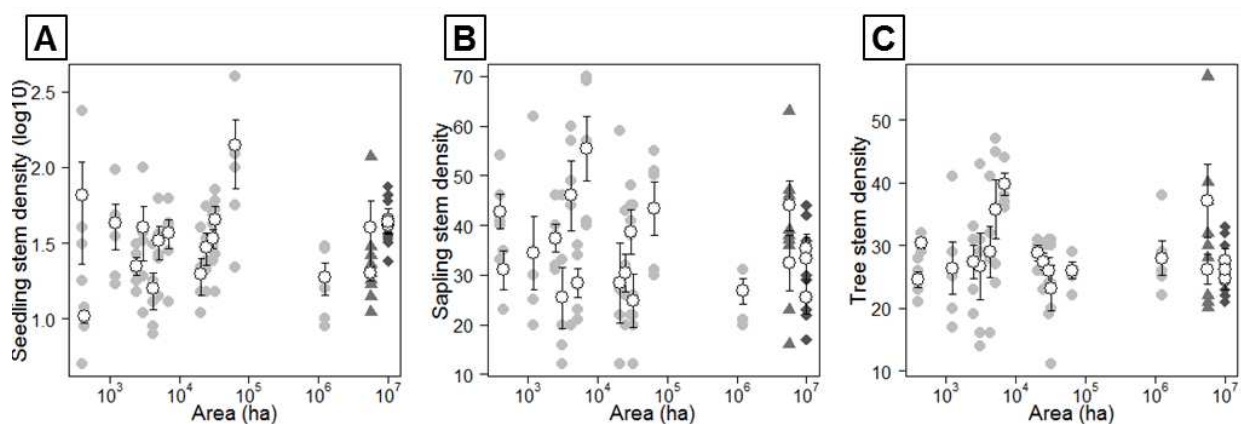
568

569

570

571

## 572 Influence of stem density on genus richness



573

574 **Figure S4.** Variation in stem density of (A) seedling, (B) sapling, and (C) tree size classes

575 with site area. Light grey circle (fragments), darker grey triangles (logged forest) and dark

576 grey diamond (primary forest) show number of stems per plot, and black symbols are site



577 means with standard error. There was no significant relationships between stem density and  
578 either area, connectivity, or shape (univariate GLMMs).

579

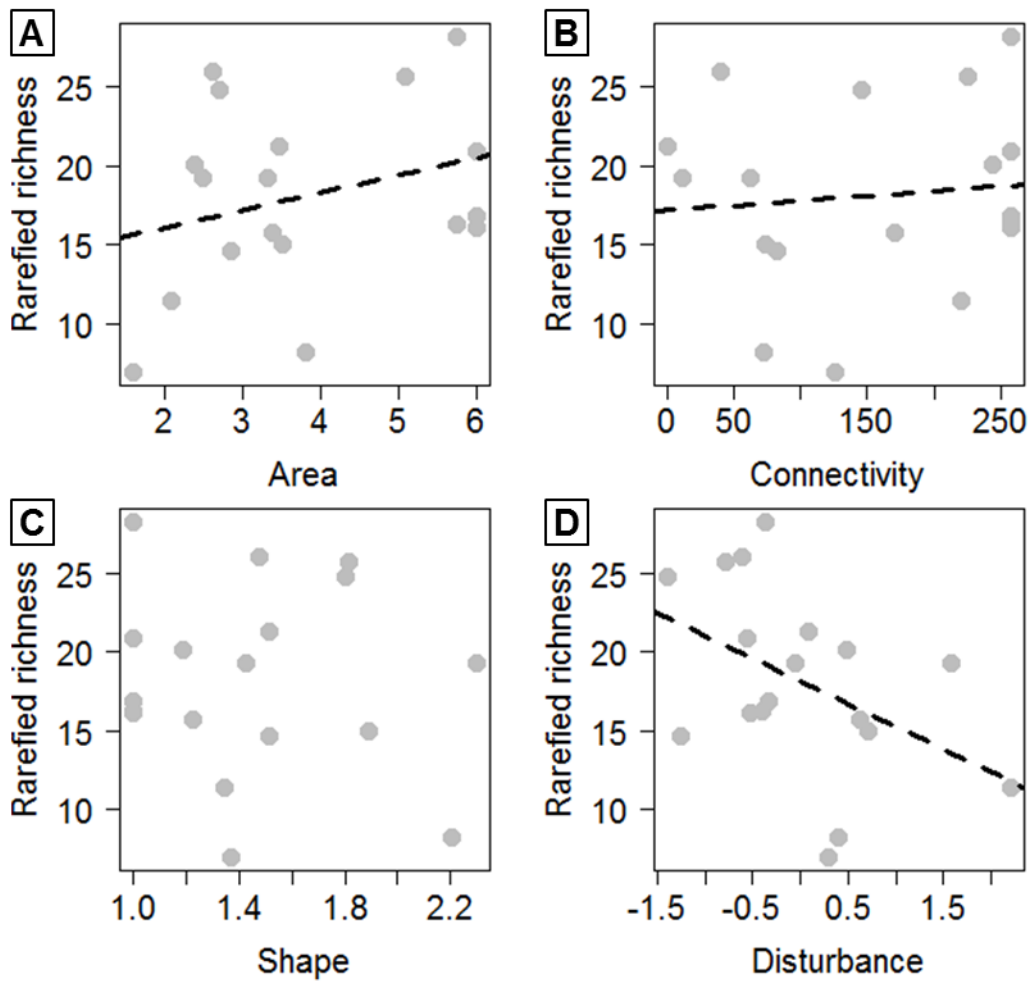
#### 580 **Text S1 Rarefaction analysis**

581 Our sampling strategy and main findings pertain to analysis of plot-level local richness. We  
582 carried out several analyses to explore whether variation in stem density might affect our  
583 findings about fragmentation effects. Given that we only found significant effects of site  
584 characteristics for seedlings, we only carried out rarefaction analyses for seedling data.

585 However, there were too few stems per plot for a meaningful rarefaction analysis (< 10 stems  
586 per plot in many plots), and so we carried out rarefaction analysis at site-level. We combined  
587 plot-level data within each site and removed Site #2 (Sapi A; which only had three plots),  
588 rarefied each sample to 50 stems, and regressed these values against each predictor variable.

589 We show trend lines for area, connectivity, and disturbance, as these variables were important  
590 in top models of seedling genus richness. Although no univariate regressions were  
591 significant, the same trends that were seen in the analysis in the main text were evident  
592 (Figure S5). These findings support our results in the main text (Figures 2 and 3) that  
593 seedling genus richness was lower in smaller and more disturbed forest fragments.





594

595 **Figure S5.** Rarefied seedling genus richness plotted against site characteristic predictor  
 596 variables: (A) area (log10 ha), (B) connectivity, (C) shape, and (D) disturbance. Fitted lines  
 597 are shown where the relationship was important in top models of seedling genus richness in  
 598 the main text.

599

600

601

602

603

604 **Text S2.** Equation used to calculate the shape index of each site.

605 
$$= p_{ij} / 2\sqrt{a_{ij}} \pi$$

606  $a_{ij}$  = area (m<sup>2</sup>) of patch<sub>ij</sub>

607  $p_{ij}$  = perimeter (m) of patch<sub>ij</sub>

608

609 Shape = 1 when the patch is circular, and approaches a maximum of 5 when perimeter is very  
610 convoluted (Forman & Godron, 1986).

611

612

613 **Text S3.** Equation used to calculate the connectivity of each site.

$$= \sum_{s=1}^n \frac{a_{ijs}}{h_{ijs}^2}$$

614

615

616  $a_{ijs}$  = Area (m<sup>2</sup>) of patch<sub>ijs</sub> within specified neighbourhood (m)\* of patch<sub>ij</sub>

617  $h_{ijs}$  = Edge-to-edge distance between patch<sub>ijs</sub> and focal patch<sub>ij</sub>

618

619 Connectivity = 0 when there are no neighbouring patches of forest within specified

620 neighbourhood\*, and increases as forest patches become closer, larger and less fragmented.

621 \*1 – 10 km

622

623

624

625

626 **Table S1.** Summary information for study sites, providing information on location, size,

627 shape and connectivity of each site. FF = forest fragment; LF = twice-logged continuous

628 forest; PF = primary continuous forest.

629

Site #	Site name	Type	Area (ha) <sup>a</sup>	Shape Index <sup>b</sup>	Connectivity <sup>c</sup>	Latitude	Longitude
1	Pin Supu	FF	39.58	1.37	2021014.2	5.40	117.95
2	Sapi A	FF	43.85	1.09	686479.5	5.70	117.40
3	Labuk Rd	FF	121.5	1.34	10652909.4	5.89	117.93
4	Materis	FF	245.6	1.19	14388115.8	5.51	118.02
5	Keruak	FF	307.2	1.43	1740.0	5.51	118.29
6	SapiC	FF	419.2	1.48	62003.4	5.72	117.41
7	Kunak	FF	512.3	1.80	3071774.1	4.66	118.15
8	USP	FF	694.7	1.52	558054.8	5.66	117.27
9	Kalumpang	FF	2069	2.30	248812.5	4.58	118.26
10	Luangmanis B	FF	2473	1.23	4936762.4	5.65	117.73
11	Madai	FF	3015	1.52	0.2	4.74	118.13
12	Luangmanis A	FF	3228	1.89	395896.2	5.72	117.69
13	Sepilok	FF	6441	2.21	373502.0	5.86	117.94
14	Tabin	FF	123000	1.82	11321427.8	5.21	118.50
15	Malua A	LF	1000000	1.00	17000000	5.10	117.67
16	Malua B	LF	1000000	1.00	17000000	5.12	117.67
17	BRL	PF	1000000	1.00	17000000	5.03	117.75
18	Danum	PF	1000000	1.00	17000000	4.97	117.79
19	Tembaling	PF	1000000	1.00	17000000	4.95	117.81

630

631 <sup>a</sup>Fragment area calculated using Google Earth imagery; continuous forest sites assigned a  
632 value of 800,000 ha, the area of the YSFMA.

633 <sup>b</sup>Shape index calculated as in Arroyo-Rodriguez et al., 2006 (see Text S1 for further details)

634 <sup>c</sup>Connectivity (5km buffer) calculated as in FRAGSTATS (McGarigal & Marks, 1995; see  
635 Text S2 for further details)

636

637

638

639

640 **Table S2.** Model-averaged coefficients of variables used to predict species richness of

641 seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are

642 derived from GLMMs with site identity fitted as a random effect; adjusted standard errors

643 (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of  
 644 each variable are presented. Significant predictors are highlighted in bold.

Response variable	Predictor	$\beta$	SE	Lower CI	Upper CI	RI
Seedling species richness	Intercept	2.15	0.04	2.07	2.23	
	<b>Area</b>	<b>0.38</b>	<b>0.09</b>	<b>0.20</b>	<b>0.57</b>	<b>1.00</b>
	Connectivity	-0.06	0.11	-0.28	0.15	0.29
Sapling species richness	Intercept	2.93	0.04	2.85	3.02	
	Disturbance	-0.11	0.09	-0.28	0.06	0.30
	Shape	-0.05	0.09	-0.23	0.12	0.16
	Connectivity	-0.04	0.09	-0.21	0.14	0.15
Tree species richness	Intercept	2.94	0.03	2.88	2.99	
	<b>Disturbance</b>	<b>-0.13</b>	<b>0.06</b>	<b>-0.25</b>	<b>-0.02</b>	<b>1.00</b>
	Shape	-0.10	0.06	-0.22	0.02	0.70
	Disturbance:Shape	-0.19	0.19	-0.55	0.18	0.16
	Connectivity	-0.06	0.07	-0.20	0.07	0.14
	Area	-0.05	0.06	-0.17	0.08	0.12

645  
 646  
 647

648 **Table S3.** Mean number of species, genera, and families in each size class, and total number  
 649 of stems, with standard errors (SE), per site (average of 3 – 5 plots per site). Sites are  
 650 arranged in order of increasing area (Table S1).

651

Site #	Size Class	Species ( $\pm$ SE)	Genera ( $\pm$ SE)	Families ( $\pm$ SE)	Abundance ( $\pm$ SE)
1	Seedlings	4.2(0.97)	4.2(0.97)	3.8(0.86)	66(42.91)
2	Seedlings	8.33(0.67)	7.33(0.33)	6.67(0.33)	10.33(0.88)
3	Seedlings	7(0.84)	6.2(1.07)	5.2(0.80)	43(14.40)
4	Seedlings	6.8(1.20)	6.8(1.20)	6(1.14)	22.4(2.93)
5	Seedlings	9.4(0.51)	9(0.63)	7.2(0.20)	40(15.72)
6	Seedlings	7.4(0.75)	7.2(0.58)	6.4(0.40)	15.8(4.19)
7	Seedlings	11.4(1.03)	10.8(1.07)	10(1.14)	32.8(8.10)
8	Seedlings	6.4(0.93)	5.6(0.51)	4.8(0.20)	37.2(8.14)
9	Seedlings	6.8(0.73)	6.6(0.68)	5.2(0.73)	19.8(5.44)
10	Seedlings	7.4(0.87)	6.8(0.73)	6(0.63)	29.8(7.01)
11	Seedlings	9(0.71)	8.4(0.75)	7.6(0.40)	34(4.93)
12	Seedlings	7.6(0.87)	7(0.63)	6.4(0.68)	45.2(10.46)
13	Seedlings	9.4(1.25)	8.6(1.29)	6.2(1.24)	139.8(67.09)
14	Seedlings	8(2.28)	7.8(2.08)	6.4(1.03)	18.8(4.53)
15	Seedlings	9.2(1.93)	8.2(1.66)	6.4(1.21)	40(19.75)

16	Seedlings	11.2(1.98)	10(1.70)	7.8(1.16)	20(2.12)
17	Seedlings	12.8(1.02)	11.8(0.86)	9.6(0.75)	41.8(5.12)
18	Seedlings	12.8(1.11)	9.6(1.21)	8.2(1.20)	44.8(8.39)
19	Seedlings	11.6(1.83)	9.6(1.50)	7.6(1.21)	43.6(5.84)
1	Saplings	16.4(2.38)	15(1.84)	12.4(1.47)	42.8(3.48)
2	Saplings	22.67(2.85)	20.33(1.76)	16(2.08)	31(4.00)
3	Saplings	15.2(2.18)	14.4(2.04)	11.2(1.20)	34.4(7.34)
4	Saplings	19.2(0.97)	17.2(0.97)	13.4(0.60)	37.4(2.75)
5	Saplings	16.8(3.38)	16.2(3.17)	12.4(2.16)	25.4(6.24)
6	Saplings	28(4.37)	25(3.58)	18.6(1.86)	46(7.09)
7	Saplings	15.8(2.06)	14.2(2.06)	11.6(1.44)	28.4(2.94)
8	Saplings	21.2(2.65)	19.2(2.48)	14.6(1.78)	55.4(6.50)
9	Saplings	15.2(1.50)	14.4(1.33)	11.2(1.50)	28.4(8.03)
10	Saplings	17(2.17)	15.4(2.16)	11.8(2.03)	30.4(3.80)
11	Saplings	17.8(1.77)	16(1.52)	12.8(0.73)	38.6(4.47)
12	Saplings	16.8(4.60)	15.2(4.27)	11.6(2.80)	24.8(5.31)
13	Saplings	23.2(1.88)	20.6(1.21)	16(1.10)	43.4(5.33)
14	Saplings	17.8(0.86)	15.4(1.17)	12.2(1.39)	26.8(2.58)
15	Saplings	18.4(3.26)	17.2(2.92)	12.8(1.88)	32.4(5.64)
16	Saplings	26.4(2.25)	23.8(1.88)	18(1.34)	44(5.07)
17	Saplings	19.6(1.81)	17.4(1.47)	13.2(1.24)	35.4(2.82)
18	Saplings	13.6(1.03)	12.6(0.81)	9.4(0.51)	25.4(3.30)
19	Saplings	20.2(2.15)	17.8(1.74)	12.2(1.39)	33.4(4.27)
1	Trees	14.6(2.48)	13.2(2.08)	10.6(1.69)	24.6(1.21)
2	Trees	26(1.15)	22.67(0.33)	16(0.58)	30.33(0.88)
3	Trees	15.6(2.06)	14(1.95)	11.8(1.59)	26.4(4.19)
4	Trees	18.8(2.22)	16.4(1.94)	13(0.71)	27.4(2.71)
5	Trees	17.8(3.94)	16(3.03)	11.8(2.37)	26.6(5.32)
6	Trees	22.2(2.42)	20(2.07)	15.6(1.21)	29(4.02)
7	Trees	20.2(1.24)	18.2(0.97)	14(0.45)	35.8(4.62)
8	Trees	18.6(2.62)	16.4(2.14)	13.4(1.81)	39.8(1.74)
9	Trees	19(1.55)	17(1.87)	12.6(1.72)	28.8(1.16)
10	Trees	20.8(1.24)	20(1.00)	14(0.84)	27.4(1.33)
11	Trees	18.4(1.17)	16.6(0.93)	13.8(0.66)	26(2.17)
12	Trees	14.4(2.91)	13.6(2.79)	10.2(2.06)	23.2(3.65)
13	Trees	16.6(1.21)	15.4(0.75)	11.4(0.87)	26(1.34)
14	Trees	20(1.30)	18.6(1.33)	14.2(0.97)	28(2.74)
15	Trees	17.2(2.08)	16(2.14)	11.6(1.69)	26.2(2.42)
16	Trees	24(2.17)	21.2(1.85)	15.2(0.97)	37.2(5.84)
17	Trees	19.8(0.92)	17.4(1.21)	12.6(0.93)	27.6(1.86)
18	Trees	18.2(1.77)	15.6(1.60)	12.4(0.93)	24.8(1.88)
19	Trees	19.4(1.08)	16.6(1.33)	13.8(1.07)	26.2(1.59)

652 **Text S4 Influence of soil nutrients on size class richness**

653 We measured the following soil characteristics: soil pH (pH-meter in slurry of water and

654 soil), soil nitrogen, carbon and C:N ratio (using dry combustion C/N analyser), and soil

655 phosphorus (using acid-digestion method described in Grimshaw, 1989). Soil characteristics  
 656 were measured from four soil cores per plot, that were bulked for each plot prior to analysis  
 657 at the Forest Research Centre, Sepilok. The soil data were included initially in our analyses,  
 658 but were not found to be important in predicting diversity differences among plots and sites,  
 659 and hence they were excluded from the subsequent analyses.

660

661 **Table S4.** Mean site values with standard errors (SE) for soil nutrient data collected in each  
 662 site. Sites are arranged in order of increasing area.

Site #	pH ( $\pm$ SE)	Total P ( $\pm$ SE)	Total N ( $\pm$ SE)	Total C ( $\pm$ SE)	C:N ratio ( $\pm$ SE)
1	4.31 (0.11)	88.61 (6.53)	0.08 (0.02)	1.39 (0.00)	20.28 (4.19)
2	3.72 (0.09)	126.33 (10.68)	0.10 (0.02)	2.03 (0.26)	23.11 (4.33)
3	4.63 (0.20)	188.34 (19.83)	0.13 (0.03)	1.43 (0.22)	11.81 (1.31)
4	4.64 (0.15)	208.18 (13.47)	0.10 (0.02)	1.40 (0.17)	14.93 (0.88)
5	6.26 (0.45)	281.50 (25.48)	0.32 (0.07)	3.95 (0.98)	12.58 (1.11)
6	4.13 (0.04)	49.03 (8.95)	0.05 (0.01)	1.16 (0.09)	27.95 (6.16)
7	4.84 (0.32)	54.12 (11.04)	0.14 (0.02)	1.93 (0.25)	14.28 (1.37)
8	4.00 (0.16)	75.68 (19.54)	0.13 (0.01)	2.88 (0.62)	22.11 (4.49)
9	5.27 (0.23)	71.63 (4.65)	0.05 (0.00)	1.26 (0.07)	23.56 (1.01)
10	3.94 (0.05)	66.82 (10.28)	0.05 (0.01)	1.34 (0.15)	29.96 (3.13)
11	4.37 (0.08)	280.51 (11.70)	0.21 (0.02)	1.76 (0.14)	8.42 (0.79)
12	5.26 (0.41)	208.31 (35.81)	0.13 (0.01)	1.62 (0.14)	12.11 (0.44)
13	4.00 (0.05)	84.18 (22.16)	0.07 (0.02)	1.30 (0.12)	23.70 (6.24)
14	4.80 (0.14)	348.93 (41.68)	0.15 (0.01)	1.56 (0.16)	10.11 (0.29)
15	3.81 (0.08)	137.99 (7.11)	0.10 (0.02)	1.60 (0.19)	17.85 (2.33)
16	3.88 (0.18)	174.97 (9.39)	0.16 (0.02)	2.08 (0.21)	14.00 (1.56)
17	4.33 (0.13)	316.90 (73.58)	0.13 (0.03)	1.78 (0.13)	15.69 (2.28)
18	3.80 (0.09)	254.11 (23.84)	0.14 (0.03)	1.86 (0.18)	15.25 (2.41)
19	4.63 (0.28)	192.06 (32.32)	0.08 (0.02)	1.33 (0.20)	18.26 (3.27)

663

664

665

666 **Table S5. Reciprocal Simpson diversity.** Parameters are derived from GLMMs with site  
 667 identity fitted as a random effect; adjusted standard errors (SE), 95% lower and upper

668 confidence intervals (CI), and the relative importance (RI) of each variable are presented.

669 Significant predictors are highlighted in bold.

Response variable	Predictor	$\beta$	SE	Lower CI	Upper CI	RI
Seedling Simpson diversity	Intercept	0.29	0.04	0.22	0.36	
	Area	0.04	0.09	-0.13	0.21	0.46
	Connectivity	-0.03	0.06	-0.15	0.08	0.47
	<b>Area:Connectivity</b>	<b>-0.37</b>	<b>0.16</b>	<b>-0.69</b>	<b>-0.05</b>	<b>0.33</b>
	Disturbance	0.08	0.05	-0.02	0.17	0.55
	Shape	0.03	0.07	-0.10	0.17	0.27
Saplings Simpson diversity	Intercept	0.10	0.01	0.09	0.11	
	Connectivity	0.01	0.01	-0.02	0.03	0.21
	Disturbance	0.01	0.01	-0.02	0.03	0.24
Trees Simpson diversity	Intercept	0.09	0.00	0.08	0.09	
	Shape	0.01	0.01	-0.01	0.03	0.38
	<b>Disturbance</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.01</b>	<b>0.17</b>

670

671

672

673 **Text S5 Influence of changing buffer size for calculation of connectivity metric**

674 Altering the buffer width from 1 to 10 km, had little or no effect on the outcome of the

675 model. Variables were standardised before being included in the GLMM and this meant there

676 was little variation in values of connectivity, regardless of buffer size.

677

678 **Table S6.** Influence of change buffer size for calculation of connectivity metric.

679

Buffer size (km)	Response variable	Predictor	$\beta$	SE	Lower CI	Upper CI
1	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.30	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree	Intercept	2.83	0.03	2.77	2.89

	genera richness	Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
2	Seedling	Intercept	2.06	0.04	1.98	2.15
	genera richness	Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.30	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling	Intercept	2.83	0.04	2.75	2.92
	genera richness	Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree	Intercept	2.83	0.03	2.77	2.89
	genera richness	Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
3	Seedling	Intercept	2.06	0.04	1.98	2.15
	genera richness	Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling	Intercept	2.83	0.04	2.75	2.92
	genera richness	Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree	Intercept	2.83	0.03	2.77	2.89
	genera richness	Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
4	Seedling	Intercept	2.06	0.04	1.98	2.15
	genera richness	Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling	Intercept	2.83	0.04	2.75	2.92
	genera richness	Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree	Intercept	2.83	0.03	2.77	2.89
	genera richness	Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
5	Seedling	Intercept	2.06	0.04	1.98	2.15
	genera richness	Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling	Intercept	2.83	0.04	2.75	2.92
	genera richness	Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree	Intercept	2.83	0.03	2.77	2.89
	genera richness	Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05



6	Seedling genera richness	Intercept	2.06	0.04	1.98	2.15
		Area	0.31	0.09	0.12	0.49
		Connectivity	-0.08	0.11	-0.29	0.13
		Disturbance	-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
	7	Seedling genera richness	Intercept	2.06	0.04	1.98
Area			0.31	0.09	0.12	0.49
Connectivity			-0.08	0.11	-0.29	0.14
Disturbance			-0.04	0.09	-0.23	0.14
Sapling genera richness		Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
Tree genera richness		Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
8		Seedling genera richness	Intercept	2.06	0.04	1.98
	Area		0.31	0.09	0.12	0.49
	Connectivity		-0.08	0.11	-0.29	0.14
	Disturbance		-0.04	0.09	-0.23	0.14
	Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
	Tree genera richness	Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
	9	Seedling genera richness	Intercept	2.06	0.04	1.98
Area			0.31	0.09	0.12	0.49
Connectivity			-0.08	0.11	-0.29	0.14
Disturbance			-0.04	0.09	-0.23	0.14
Sapling genera richness		Intercept	2.83	0.04	2.75	2.92
		Disturbance	-0.08	0.08	-0.25	0.08
		Shape	-0.05	0.08	-0.22	0.11
		Connectivity	-0.05	0.08	-0.21	0.12
Tree genera richness		Intercept	2.83	0.03	2.77	2.89
		Disturbance	-0.12	0.06	-0.23	0.00
		Shape	-0.06	0.06	-0.17	0.05
10		Seedling genera richness	Intercept	2.06	0.04	1.98
	Area		0.31	0.09	0.12	0.49

	Connectivity	-0.08	0.11	-0.29	0.14
	Disturbance	-0.04	0.09	-0.23	0.14
Sapling genera richness	Intercept	2.83	0.04	2.75	2.92
	Disturbance	-0.08	0.08	-0.25	0.08
	Shape	-0.05	0.08	-0.22	0.11
	Connectivity	-0.05	0.08	-0.21	0.12
Tree genera richness	Intercept	2.83	0.03	2.77	2.89
	Disturbance	-0.12	0.06	-0.23	0.00
	Shape	-0.06	0.06	-0.17	0.05

680  
681  
682

683

684 **Table S7. Influence of changing size class upper/lower bounds on sapling and tree size**  
685 **classes.** Model-averaged coefficients of variables used to predict genus richness of seedling  
686 (< 1cm dbh), sapling (1 – 2.5 cm dbh), and tree (>10 cm dbh) size classes in 93 plots nested  
687 within 19 sites. Parameters are derived from GLMMs with site identity fitted as a random  
688 effect; adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the  
689 relative importance (RI) of each variable are presented. Significant predictors are highlighted  
690 in bold.

691

Response variable	Predictor	$\beta$	SE	Lower CI	Upper CI	RI
Seedling genera richness	Intercept	2.06	0.04	1.98	2.15	
	<b>Area</b>	0.31	0.09	0.12	0.49	<b>1.00</b>
	Connectivity	-0.08	0.11	-0.29	0.13	0.24
	Disturbance	-0.04	0.09	-0.23	0.14	0.20
Sapling genera richness	Intercept	2.44	0.05	2.33	2.54	
	Disturbance	-0.10	0.11	-0.31	0.11	0.27
	Connectivity	-0.06	0.11	-0.27	0.15	0.21
Tree genera richness	Intercept	2.23	0.03	2.17	2.30	
	<b>Disturbance</b>	-0.19	0.07	-0.34	-0.05	<b>1.00</b>
	Area	-0.03	0.07	-0.18	0.11	0.27

692  
693  
694

**Text S6. Wood density as a proxy for growth-rate of genera**

695 In order to test the robustness of our results to the removal of slow-growing genera, we used  
696 wood density as a proxy for growth rate (Slik, 2005). We obtained wood density on dry  
697 weight ( $\text{g/cm}^3$ ) data from The Global Wood Density database (Chave & al., 2009). We then  
698 removed high wood-density ( $>0.75 \text{ g/cm}^3$ ), slow-growing genera and repeated our analyses,  
699 but found no qualitative difference in our results (i.e. lower richness of seedlings in  
700 fragments, but no effects of fragmentation on saplings or trees). These analyses support our  
701 assumption that size is a reasonable proxy for pre- and post-fragmentation individuals.  
702 We also carried out our analyses of fragmentation effects separately for high and low wood  
703 density groups, and we split our data set according to the median wood density of all genera  
704 we encountered in our study ( $0.55 \text{ g/cm}^3$ ). We found significantly fewer low wood density  
705 tree genera present in plots in primary forest than in logged or fragmented forest (ANOVA of  
706 tree richness by forest type; high wood density:  $F(2,90) = 2.57, p = 0.08$ ; low wood density:  
707  $F(2,90) = 4.55, p = 0.01$ ), however findings from our ANOVA analyses of tree, sapling and  
708 seedling richness were qualitatively similar to our original analysis i.e. both low and high  
709 wood density seedlings have lower richness in fragments (ANOVA of seedling richness by  
710 forest type; high wood density:  $F(2,90) = 5.60, p = 0.005$ ; low wood density:  $F(2,90) = 4.60,$   
711  $p = 0.01$ ; ANOVA of sapling richness by forest type high wood density:  $F(2,90) = 2.87, p =$   
712  $0.06$ ; low wood density:  $F(2,90) = 0.23, p = 0.80$ ). Our findings from our GLMMs with  
713 respect to examining site characteristics important for richness were also qualitatively similar  
714 for the low and high wood density groups. As previously, there was no effect of site area on  
715 either high or low wood density sapling richness and so we conclude that differences in plant  
716 growth rates are not having major impacts on our designation of post- and pre-fragmentation  
717 individuals, or our overall findings.

718

719 **Table S8. Influence of removal of high wood-density (>0.75 g/cm<sup>3</sup>), slow-growing genera**  
720 **on size classes.** Model-averaged coefficients of variables used to predict genus-level richness  
721 of seedling, sapling, and tree size classes in 93 plots nested within 19 sites. Parameters are  
722 derived from GLMMs with site identity fitted as a random effect; adjusted standard errors  
723 (SE), 95% lower and upper confidence intervals (CI), and the relative importance (RI) of  
724 each variable are presented. Significant predictors are highlighted in bold.

<b>Response variable</b>	<b>Predictor</b>	<b>β</b>	<b>SE</b>	<b>Lower CI</b>	<b>Upper CI</b>	<b>RI</b>
Seedling genera richness	Intercept	2.00	0.04	1.92	2.08	
	<b>Area</b>	0.28	0.09	0.10	0.46	<b>1.00</b>
	Connectivity	-0.06	0.09	-0.24	0.13	0.21
	Disturbance	-0.05	0.11	-0.27	0.16	0.22
Sapling genera richness	Intercept	2.76	0.04	2.68	2.84	
	Disturbance	-0.07	0.08	-0.23	0.09	0.21
	Connectivity	-0.06	0.08	-0.21	0.10	0.19
	Shape	-0.04	0.08	-0.20	0.12	0.17
Tree genera richness	Intercept	2.76	0.03	2.70	2.82	
	<b>Disturbance</b>	-0.13	0.06	-0.24	-0.01	<b>0.80</b>
	Shape	-0.05	0.06	-0.17	0.06	0.27

725

726

727 **Table S9.** Model-averaged coefficients of variables used to predict genus-level richness of  
728 low and high wood-density seedling, sapling, and tree size classes in 93 plots nested within  
729 19 sites. Parameters are derived from GLMMs with site identity fitted as a random effect;  
730 adjusted standard errors (SE), 95% lower and upper confidence intervals (CI), and the  
731 relative importance (RI) of each variable are presented. Significant predictors are highlighted  
732 in bold.

<b>Response variable</b>	<b>Predictor</b>	<b>β</b>	<b>SE</b>	<b>Lower CI</b>	<b>Upper CI</b>	<b>RI</b>
Seedling genera richness (low wood density)	Intercept	1.16	0.06	1.04	1.27	
	<b>Area</b>	<b>0.30</b>	<b>0.12</b>	<b>0.06</b>	<b>0.53</b>	<b>1.00</b>
	Shape	-0.07	0.13	-0.33	0.18	0.28
Sapling genera richness (low wood density)	Intercept	1.85	0.05	1.75	1.96	
	Connectivity	-0.21	0.14	-0.48	0.06	0.44

wood density)	Shape	-0.20	0.14	-0.46	0.07	0.54
	Area	-0.13	0.11	-0.35	0.09	0.22
	Disturbance	-0.07	0.10	-0.27	0.13	0.09
Tree genera richness (low wood density)	Intercept	1.89	0.04	1.81	1.98	
	Area	-0.14	0.09	-0.32	0.04	0.41
	Connectivity	-0.09	0.09	-0.27	0.08	0.17
	Disturbance	-0.07	0.09	-0.25	0.11	0.13
	Shape	0.06	0.09	-0.11	0.24	0.13
Seedling genera richness (high wood density)	Intercept	1.54	0.06	1.41	1.66	
	<b>Area</b>	<b>0.31</b>	<b>0.14</b>	<b>0.04</b>	<b>0.59</b>	<b>1.00</b>
	Connectivity	-0.11	0.16	-0.43	0.20	0.20
	Disturbance	-0.07	0.14	-0.34	0.20	0.17
	Shape	0.06	0.13	-0.20	0.32	0.17
Sapling genera richness (high wood density)	Intercept	2.36	0.05	2.27	2.45	
	Disturbance	-0.11	0.09	-0.30	0.07	0.31
	Area	0.09	0.09	-0.10	0.27	0.24
Tree genera richness (high wood density)	Intercept	2.33	0.03	2.26	2.39	
	<b>Disturbance</b>	<b>-0.18</b>	<b>0.07</b>	<b>-0.32</b>	<b>-0.05</b>	<b>1.00</b>
	<b>Shape</b>	<b>-0.13</b>	<b>0.07</b>	<b>-0.27</b>	<b>0.00</b>	<b>0.72</b>

733

734

735 **References**

- 736 1. Slik, J. W. F. (2005) Assessing tropical lowland forest disturbance using plant  
737 morphological and ecological attributes. *For. Ecol. Manage.* 205, 241–250.
- 738 2. Chave J, Coomes DA, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards  
739 a worldwide wood economics spectrum. *Ecology Letters* 12(4): 351-366.  
740 <https://doi.org/10.1111/j.1461-0248.2009.01285.x>

741

742