



TITLE:

Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales

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4 **Title:** Effects of selective logging on tree species diversity and composition
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25

26 **Abstract** Reduced-impact logging (RIL) is known to be beneficial in
27 biodiversity conservation, but its effects on tree diversity remain unknown.
28 Pattern of tree diversity following disturbance usually varies with spatial
29 scale of sampling (i.e. plot size). We examined the impacts of RIL on species
30 richness and community composition of tree species at different spatial scales,
31 and the scale (plot size) dependency of the two metrics; species richness vs.
32 community similarity. One 2-ha and three to four 0.2-ha plots were
33 established in each of primary, RIL and conventionally logged (CL) forest in
34 Sabah, Malaysia. Species richness (the number of species per unit number of
35 stems) was higher in the RIL than in the CL forest at both scales. The
36 relationship between species richness and logging intensity varied with plot
37 size. Species richness was greater in the RIL than in the primary forest at the
38 2-ha scale, while it was similar between the two forests at 0.2-ha scale.
39 Similarly, species richness in the CL forest demonstrated a greater value at
40 the 2-ha scale than at the 0.2-ha scale. Greater species richness in the two
41 logged forests at the 2-ha scale is attributable to a greater probability of
42 encountering the species-rich, small patches that are distributed
43 heterogeneously. Community composition of the RIL forest more resembled
44 that of the primary forest than that of the CL forest, regardless of plot size.
45 Accordingly, species richness is a scale-dependent metric, while community
46 similarity is a more robust metric to indicate the response of tree assemblage
47 to anthropogenic disturbance.

48

49 **Keywords** Borneo; forest heterogeneity; non-metric multi-dimensional
50 scaling (NMDS); PERMANOVA; species-accumulation curves

51 **Introduction**

52 Forests degraded due to anthropogenic disturbances are rapidly expanding
53 in area in the tropics (Asner et al. 2005; Wright 2005). Degraded tropical
54 forests usually have higher species richness than monocultural plantations
55 and agricultural lands (Gibson et al. 2011, Lawton et al. 1998). On the other
56 hand, strictly protected areas that are expected to conserve biodiversity are
57 rather limited in area (Rodrigues et al. 2004), leading to a growing interest
58 in the conservation value of degraded tropical forests (Berry et al. 2010,
59 Edwards et al. 2010). A key driver of forest degradation in Southeast Asian
60 tropics is unregulated selective logging, which often damages more than
61 50% of the original forest biomass, and causes surface-soil disturbance
62 (Bertault and Sist 1997; Cannon et al. 1994; Pinard and Putz 1996; Putz et
63 al. 2008a; Sist et al. 1998). Understanding the responses of biodiversity to
64 selective logging in the tropics is crucial for predicting and managing
65 biodiversity in our rapidly changing global environment.

66 To mitigate the detrimental impacts of selective logging on forests,
67 “reduced-impact logging” (RIL) has recently been applied to some of
68 natural production forests in the tropics (Kleine and Heuvel dop 1993; Lagan
69 et al. 2007; Putz et al. 2008a). RIL is a modification of selective logging,
70 including pre-harvest inventory, mapping of all canopy trees, directional
71 felling, liana cutting and planning of skid trails, log decks and roads. In
72 comparison with unregulated conventional logging (CL), RIL is beneficial
73 not only in maintaining future crop trees (Peña-Claros et al. 2008; Rockwell
74 et al. 2007) and forest biomass (Bertault and Sist 1997; Johns et al. 1996;
75 Miller et al. 2011; Pinard and Putz 1996; Putz et al. 2008b; Sist et al. 1998),

76 but also in biological diversity, such as dung beetles (Davis 2000), flying
77 insects (Akutsu et al. 2007), soil macrofauna (Hasegawa et al. 2006) and
78 forest-dwelling vertebrates (Imai et al. 2009). Many other taxa, such as ants,
79 arachnids, bats, birds, fishes and animals, also are not adversely affected by
80 RIL (Azevedo-Ramos et al. 2006; Bicknell and Peres 2010; Castro-Arellano
81 et al. 2007; Dias et al. 2010; Edwards et al. 2012; Felton et al. 2008; Presley
82 et al. 2008; Samejima et al. 2012; Wunderle et al. 2006). However, the
83 effects of RIL on tree species diversity of tropical rain forests remain
84 largely unknown, despite that the diversity of trees is fundamental to the
85 structure and functions of the forests. The diversity of trees may also
86 determine the diversity of other taxonomic groups, because trees provide
87 resources and habitat structure for dependent species.

88 To date, only three studies have examined the effects of RIL on tree
89 species diversity (Foody and Cutler 2003; Medjibe et al. 2011; Webb and
90 Peralta 1998). However, two studies compared tree diversity of RIL with
91 that of primary forest (Medjibe et al. 2011; Webb and Peralta 1998), and
92 only one study compared tree diversity of RIL with that of both primary and
93 CL forest by using quite a small (0.05 ha in area) plot (Foody and Cutler
94 2003). Given that widespread commercial logging of high-value timber in
95 the tropics still rely mainly upon conventional techniques (Blaser et al.
96 2011), comparison of logging impacts on tree diversity between RIL and CL
97 is urgently needed.

98 Tree species richness (number of tree species at a single site) in
99 selectively logged forests may vary depending on the spatial scale of
100 sampling (Dumbrell et al. 2008; Hamer and Hill 2000; Hill and Hamer

101 2004). Selectively logged forests consist of a mosaic of patches affected by
102 different intensities of disturbance, such as remnant stands, gaps due to
103 harvesting and road construction, and regenerating patches with varying
104 successional stages. A small plot can encounter only one or a few patch
105 types within a heterogeneous logged-over forest. On the other hand, a large
106 plot is potentially able to encounter all different patch types within the
107 forest. Because logging creates new habitats for the species not found in a
108 primary forest, deploying a large plot overestimates species richness in a
109 logged-over forest. Accordingly, plot size, which determines the number of
110 different patch types encountered in a given area, can in turn affect species
111 richness in that area. However, previous studies assessing tree species
112 richness in selectively logged forests have used either small (mostly less
113 than 0.2 ha in area) or large plots (1 ha in area in a few studies; Berry et al.
114 2008; Chua et al. 1998; Kirika et al. 2010; Medjibe et al. 2011; Ouédraogo
115 et al. 2011, Souza et al. 2012). Deploying both small and large plots is
116 necessary to reliable evaluation of logging impacts on tree species richness.

117 The ideal metric of biodiversity must be independent of spatial scale
118 of sampling (Chazdon et al. 1998). Sheil and Burslem (2003) reported that
119 tree species richness in tropical forests following habitat disturbance varied
120 with spatial scale. On the other hand, community similarity (difference of
121 community composition between sites) is receiving increasing attention as a
122 useful metric to assess the effects of forest managements on biodiversity,
123 rather than species richness (Barlow et al. 2007; Su et al. 2004). Despite
124 that, no assessment of the scale-dependent response of tree community
125 similarity to habitat disturbance has yet been conducted. Understanding the

126 scale dependency of the two major metrics following disturbance can
127 improve the interpretation of the outcome of tropical biodiversity studies,
128 in which sampling size and evaluation metrics largely differ among
129 different studies.

130 We established one 2-ha and three to four 0.2-ha plots in each of
131 primary, RIL and CL forest in Bornean lowland tropical rain forests to
132 examine the effects of RIL on tree species richness and composition at
133 different spatial scales. We also compared the scale (plot size) dependency
134 of the two metrics (species richness vs. community similarity) to consider
135 which metric is more appropriate for evaluation of the forest-management
136 effects on tropical biodiversity.

137

138 **Material and methods**

139 Study site

140 This study was carried out in Deramakot Forest Reserve and Tangkulap Forest
141 Reserve in Sabah, Malaysia (5°14-30'N, 117°11-36'E). The mean annual
142 temperature of the area is 27°C and the mean annual precipitation is *c.* 3500
143 mm, with little seasonal variation. The region is characterized by Tertiary
144 sedimentary rocks. The altitude in the reserves is between 20 and 300 m asl.
145 The vegetation is a mixed dipterocarp lowland tropical rain forest. Deramakot
146 (551 km²) and Tangkulap (275 km²) are located adjacent to each other.

147 Deramakot and Tangkulap were originally licensed for logging
148 starting in 1956 and the 1970s, respectively. Subsequently, conventional
149 logging commenced there (Sabah Forestry Department 2005). During
150 1959-1968, timber, with a mean volume of 109 m³/ha, was harvested in

151 Deramakot (Sabah Forestry Department 2005). In 1989, Deramakot was
152 chosen by the Sabah State Government as a model site to develop a
153 sustainable forest management system and all logging activities were
154 suspended thereafter. A new management system with RIL was implemented
155 in 1995. Deramakot is now divided into 135 compartments of varying sizes
156 (approx. 500 ha each), and about two to four compartments are harvested
157 annually using RIL with a planned rotation period of 40 yr (Lagan et al. 2007).
158 17 of these compartments (3,473 ha in area) are reserved for conservation
159 (not to produce logs).

160 Based on the guidelines of RIL, all harvestable trees must be measured
161 before harvesting and located on a detailed map and appropriate routes for
162 skidders are designed to minimize the damage to non-target trees. The trees
163 harvested are limited to those in the range of 60-120 cm diameter at breast
164 height (dbh), and trees that are near streams, on steep terrain, with hollows,
165 or of fruiting species for wildlife are excluded from harvesting. A
166 compartment will be harvested only when the harvestable timbers exceed 25
167 m³/ha. Tangling lianas are cut before harvesting and targeted trees are
168 harvested with a directional felling technique. Harvesting and road
169 construction cease during periods of heavy rainfall to reduce soil erosion.
170 Gap size of each harvesting must be less than 0.1 ha. Dipterocarpaceae is one
171 of the major targeted tree families for harvesting. In Deramakot, a total of
172 24,934 trees (2.36 trees /ha) with a volume of 145,399 m³ (13.74 m³/ha) were
173 harvested during 1995-2006 (Samejima et al. 2012).

174 Tangkulap Forest Reserve was repeatedly logged using a conventional
175 logging technique until 2001, when the government suspended all logging

176 activities. There are no reliable statistics for the log production in Tangkulap.
177 According to the analysis of logging history in the two reserves using Landsat
178 satellite data (Imai et al. 2009), much heavier logging have occurred in
179 greater areas in Tangkulap compared with Deramakot during 1985-2002. This
180 difference of degradation status between Deramakot and Tangkulap resulted
181 from the differences of the two logging methods (i.e. RIL and CL) and
182 harvested volume between the two reserves. We used these forests as a model
183 site to examine the impacts of RIL on species richness and community
184 composition of tree species at different spatial scales, and the scale (plot size)
185 dependency of the two metrics; species richness vs. community similarity.

186

187 Vegetation survey

188 Eleven research plots of 0.2 ha were established in Deramakot and Tangkulap
189 during May 2003-March 2005 (Seino et al. 2006). In Deramakot, four plots
190 were established in a primary forest located within the conservation area.
191 Conventional logging method has been applied even in the current
192 conservation area until the 1980s, and there are still evidences of the past
193 logging activities (e.g. old bulldozer paths, old stumps, and absence of
194 emergent trees) in the vicinity of our plots. However, we considered our four
195 plots are in unlogged patches of primary forest, because of the absence of any
196 evidence of past logging activities within the plots. In Deramakot, we also set
197 up four plots in the forest logged by RIL during 1995-2000. In Tangkulap,
198 three plots logged by CL were established. The three CL plots were once
199 logged before 1988, and again logged during 1995-1999, based on the
200 observation of Landsat scenes (Aoyagi R. pers. comm.). Thus, the two logged

201 forests were logged during the similar period; RIL and CL forest were logged
202 5-13 and 5-10 yr before our investigation, respectively. Eleven 0.2-ha plots
203 were laid out primarily as 100 × 20 m. Three out of the four plots in primary
204 forest and one out of the three plots in CL forest were laid out as 50 × 40 m,
205 because of the limited availability of gentle topography. Mean (\pm SD)
206 distances among the 0.2-ha plots are 435 ± 209 , 1130 ± 646 and 756 ± 175 m
207 for primary, RIL and CL forest, respectively. During November
208 2006-February 2008, we enlarged one representative 0.2-ha RIL plot and one
209 representative 0.2-ha CL plot to 2 ha in area (200 × 100 m). We additionally
210 established a new 2-ha plot in primary forest, because the four 0.2-ha primary
211 plots are in small patches of residual forest and therefore cannot be enlarged
212 without including degraded patches. Each plot consists of 10 × 10-m subplots.

213 All trees ≥ 10 cm dbh were measured in each plot. We also
214 established a hundred 5 × 5-m plots within a 2-ha plot (allocated alternately
215 to each 10 × 10-m subplot), and measured dbh of small trees with 5-10 cm
216 dbh. Buttressed trees were measured at well above (*c.* 50 cm) protrusions.
217 All trees were identified by botanical experts of the Herbarium, Forest
218 Research Centre, Sabah Forestry Department, Sandakan. Voucher specimens
219 were collected from the trees that could not be identified in situ. Specimens
220 taken were compared with herbarium collections. Samples that could not be
221 identified to species were distinguished as morphospecies.

222 Plot shape may affect tree species richness, because a rectangular
223 plot may sample a greater number of species than a square plot of the same
224 area (Condit et al. 1996). However, when we tested the effects of plot shape
225 (100 × 20 m vs. 50 × 40 m) using subplots within a 2-ha plot, the mean

226 number of tree species ≥ 10 cm dbh did not significantly differ between ten
227 100×20 -m subplots and ten 50×40 -m subplots (Student's t -test, $P > 0.5$
228 for all, only 1.1-1.9 species greater in 100×20 -m subplots). This is
229 probably because the aspect ratio of our study plots was relatively low
230 {only from 1.25 (50×40 m) to 5 (100×20 m)}. We therefore suggest that
231 the use of different plot shapes does not affect tree species richness in our
232 study.

233

234 Data analysis

235 *Above-ground biomass*

236 Above-ground biomass (AGB) was estimated according to the allometric
237 equation obtained by Chave et al. (2005) as:

$$238 \quad \text{AGB} = \rho \times \exp(-1.499 + 2.148 \ln(D) + 0.207 (\ln(D))^2 - 0.0281 (\ln(D))^3)$$

239 where D is dbh (cm) and ρ is the wood-specific gravity (g/cm^3). We
240 obtained the wood-specific gravity ρ for the observed species/genera from
241 various sources (Lemmens et al. 1995; Oey 1951; Soerianegara and
242 Lemmens 1993; Sosef et al. 1998). In cases, where a range of wood density
243 values were reported, we used a median value. Where wood density data
244 were unavailable for a species, the average across all species in that genus
245 was applied (see Baker et al. 2004; Slik 2006). In the few cases, where trees
246 could not be identified at the genus level or where no literature record was
247 available, we used the mean wood specific gravity of that plot.

248

249 *Forest heterogeneity*

250 To evaluate the forest heterogeneity within a 2-ha plot in each forest type,

251 we calculated a commonly-used measure of β -diversity (Whittaker 1960)
252 within a 2-ha plot:

$$253 \quad \beta = \gamma / \alpha$$

254 We calculated the number of species at the scale of 40×50 m within each of
255 the 2-ha plots (i.e. ten 0.2-ha subplots by sequentially shifting 40×50 -m
256 quadrat per 2-ha plot), and obtained β by dividing the total number of
257 species in each 2-ha plot (γ) by the mean number of species per 0.2-ha
258 subplots (α).

259

260 *Community similarity*

261 We tested the differences in tree community composition among forest types
262 using ordinations and permutational multivariate analysis of variance
263 (PERMANOVA; Anderson 2001). The Chao dissimilarity (distance)
264 function and the relative basal area of each species in eleven 0.2-ha plots (n
265 = 11) and three 2-ha plots separated at the scale of 40×50 m within each of
266 the 2-ha plots ($n = 30$) were used to calculate the distance matrix. The
267 PERMANOVA used the “adonis” procedure in the vegan package in R.
268 Ordinations were plotted with non-metric multidimensional scaling
269 (NMDS) using the vegan’s “metaMDS” procedure.

270

271 *Species richness*

272 We estimated the number of tree species by using rarefaction, which is used
273 to calculate the number of species expected in a subsample selected at
274 random from a total sample (Gotelli and Colwell 2001; Magurran 2004). We
275 ran 100 randomizations using the data of the number of trees ≥ 10 cm dbh for

276 each species at 10 × 10-m subplots by EstimateS ver. 8 (available online at
277 <http://viceroy.eeb.uconn.edu/estimates>) to produce species-area curves. The
278 species-individual curves were obtained by converting the cumulative area
279 to cumulative numbers of individuals. Estimated number of species for 70
280 stems in the 0.2-ha plots and for 850 stems in the 2-ha plots were separately
281 calculated by interpolation from the species-individual curves; 70 and 850
282 were the number of individuals in the site with the smallest total number of
283 individuals at each plot size.

284 Differences in vegetation properties (stem density, basal area, AGB,
285 observed and estimated number of species) among forest types were tested
286 by an analysis of variance (ANOVA). When the ANOVA *P* value was < 0.05,
287 the Tukey-Kramer *post hoc* test was performed to determine which pairs of
288 means differ significantly.

289

290 *Scale dependency of the two metrics*

291 To examine the scale dependency of the two metrics, we tested which
292 metrics (species richness and community similarity) better correlated with
293 AGB at both 0.2-ha and 2-ha scales. Estimated AGB in each plot was
294 considered as a surrogate of the degree of forest degradation. Estimated
295 number of species in each plot was used as an index of species richness,
296 because it can compare expected species richness between data of different
297 sample sizes (Gotelli and Colwell 2001; Magurran 2004). NMDS axis 1
298 score in each plot was used as an index of community similarity.

299 Unfortunately, we established only one 2-ha plot per forest type due
300 to impenetrability in our study site. However, the lack of replicates is not

301 critical in this analysis because we applied a linear model.

302

303 **RESULTS**

304 Forest structure

305 Stem density in 0.2-ha plots tended to be lower in CL than in the other two
306 forests ($P < 0.1$), but did not differ between primary and RIL forest (Table
307 1). Stem density in 2-ha plots decreased with increasing logging intensity
308 (Table 1). Densities of trees ≥ 60 cm dbh in 0.2-ha plots and trees with 5-10
309 cm dbh in 2-ha plots were lower in CL than in the other two forests (Fig. 1,
310 $P < 0.05$ for both).

311 In 0.2-ha plots, AGB, maximum dbh and total basal area were lower
312 in CL than in the other two forests, but did not differ between primary and
313 RIL forest (Table 1). These structural properties showed a similar pattern
314 also in 2-ha plots to that shown in 0.2-ha plots.

315

316 Community similarity and forest heterogeneity

317 Dipterocarp species dominate primary and RIL forest, while pioneer species
318 (mostly *Macaranga* spp.) were abundant in CL forest (Table 1). Community
319 composition consistently differed between CL and the other two forests at
320 both 0.2-ha (PERMANOVA, $P < 0.05$) and 2-ha scales ($P < 0.001$) (Table 2).
321 While community composition of RIL forest also differed from that of
322 primary forest at 2-ha scale ($P < 0.001$), it did not differ from that of
323 primary forest at 0.2-ha scale ($P > 0.05$). Primary and CL forest were
324 plotted at the opposite extremes along the NMDS axis 1 consistently at both
325 scales (Fig. 2a,b). RIL forest was plotted at similar positions with primary

326 forest at 0.2-ha scale (Fig. 2a) while at an intermediate position at 2-ha
327 scale (Fig. 2b).

328 Forest heterogeneity within a 2-ha plot, measured with Whittaker's
329 β -diversity, increased with increasing logging intensity (4.1, 4.6 and 4.8 in
330 primary, RIL and CL forest, respectively).

331

332 Species richness

333 We recorded 1324 stems of 360 species in 0.2-ha plots and 2992 stems of
334 544 species (3614 stems \geq 5 cm dbh of 589 species) in 2-ha plots. Observed
335 number of families and genera were lower in CL than in the other two
336 forests in 0.2-ha plots, while it did not largely differ among forest types in
337 2-ha plots (Table 1). Observed number of species per unit area was lower in
338 CL than in the other two forests, but did not differ between primary and RIL
339 forest, regardless of plot size and tree size class (Table 1, Fig. 3a-c,g-j).

340 Species richness (estimated number of species) in 0.2-ha plots was
341 also lower in CL than in the other two forests (Table 1). Species richness in
342 2-ha plots was greater in RIL, intermediate in primary, and lower in CL
343 forest. Species richness of primary forest was 1.6 times greater at 0.2-ha
344 scale (50.1 vs. 31.1 species), while only 1.06 times greater at 2-ha scale
345 than that of CL forest (257 vs. 243 species). Such higher species richness of
346 the two logged forests at 2-ha scale compared at 0.2-ha scale is due to the
347 difference in species richness of small trees between 0.2-ha and 2-ha scale.
348 In 2-ha plots, species richness of trees with 5-20 cm dbh did not differ
349 between primary and CV forest (Fig. 3m,n), and that with 10-20 cm dbh was
350 rather higher in RIL than in primary forest (Fig. 3m).

351 Scale dependency of the two metrics

352 A significant relationship between species richness and AGB (as the degree
353 of forest degradation) was obtained at only one out of the three plot designs
354 (i.e. replicated 0.2-ha plots) (Fig. 4a). By contrast, there was a consistent
355 linear relationship between NMDS axis 1 scores (as community similarity)
356 and AGB irrespective of plot design (Fig. 4d-f).

357

358 **DISCUSSION**

359 Species richness in RIL forest was consistently higher than that in CL forest
360 at both spatial scales, and rather higher than that in primary forest at 2-ha
361 scale. Conventional logging in Tangkulap has caused a greater disturbance,
362 which have led to the loss of late-successional species. Logging following
363 the RIL guidelines in Deramakot extracted a reduced volume of timber and
364 reduced collateral damages to the residual stands (Lagan et al. 2007). Such
365 efforts may create favorable habitats for pioneer species, while maintain the
366 late-successional species, leading to the greater species richness in RIL than
367 in the other two forests. This may correspond with the intermediate
368 disturbance hypothesis (Connell 1978), which predicts local species
369 diversity to be maximal at an intermediate level of disturbance, due to the
370 coexistence of late-successional and pioneer species. Accordingly, RIL does
371 not appear to reduce tree species richness substantially, nor does it promote
372 the prolific colonization of pioneer species.

373 Relationships between tree species richness and logging intensity
374 varied with plot size. There was no difference in species richness between
375 primary and RIL forest at 0.2-ha scale, but rather higher richness in RIL

376 than in primary forest at 2-ha scale. Species richness of primary forest was
377 1.6 times greater at 0.2-ha scale, but only 1.06 times greater at 2-ha scale
378 than that of CL forest. Logged forests consist of both patches with low
379 species richness (due to the degradation or the dominance of a few pioneer
380 species recruited) and patches with relatively high species richness (due to
381 the coexistence of late-successional and pioneer species at small size class).
382 In degraded forest landscapes, the latter patches may occupy a small area
383 and be distributed heterogeneously. Probability of encountering such
384 patches with high species richness will decrease when sampled with smaller
385 plots. This is one major reason why the two logged forests showed
386 relatively higher species richness at 2-ha scale compared at 0.2-ha scale.

387 Previous studies have demonstrated inconsistent responses of tree
388 species richness to selective logging, with unchanged (Bischoff et al. 2005;
389 Foody and Cutler 2003; Hall et al. 2003; Kirika et al. 2010; Medjibe et al.
390 2011; Slik et al. 2002; Verburg and van Eijk-Bos 2003), decreased (Brearley
391 et al. 2004; Gutiérrez-Granados et al. 2011; Makana and Thomas 2006;
392 Okuda et al. 2003), and increased (Berry et al. 2010; Cannon et al. 1998;
393 Plumptre 1996) richness following logging. Most studies used a single plot
394 size, and compared species richness between unlogged and logged forests
395 without the variation of logging intensity (but see Kirika et al. 2010;
396 Molino and Sabatier 2001; Verburg and van Eijk-Bos 2003). Selective
397 logging actually has a wide variation in the volume of timber extracted and
398 the severity of damage caused by the removal of individual trees and road
399 construction (Cannon et al. 1994). Our results indicate that responses of
400 tree species richness to logging intensity can covary with plot size. These

401 two uncontrolled factors (logging intensity and plot size) among different
402 studies may be the possible reasons for the inconsistent responses of tree
403 species richness to selective logging.

404 Unlike species richness, community composition of RIL forest more
405 resembled that of primary forest than that of CL forest regardless of plot
406 size. Therefore, community similarity consistently showed a linear
407 relationship with the degree of forest degradation irrespective of plot design
408 (Fig. 4). Community similarity is a sensitive and consistent metric to
409 evaluate the effects of logging on tree assemblage, rather than species
410 richness per se, which inevitably combines the responses of two contrasting
411 regeneration guilds (pioneer and late-successional species), provides no
412 information on such species identity, and is highly dependent on spatial
413 scale of sampling.

414 In conclusion, RIL can conserve the richness and community
415 composition of tree species at a similar level with primary forest. These
416 positive effects are a co-benefit of RIL, because RIL is primarily a forestry
417 practice to sustainably produce timber. Unfortunately, unregulated selective
418 logging is still common in the tropics (Blaser et al. 2011). If RIL were
419 adopted in much larger areas of natural production forests, a substantial
420 reduction of logging damage on tree assemblage can be expected while
421 timber is sustainably produced. Our results also demonstrated different
422 scale-dependent responses between the two metrics (species richness and
423 community similarity) to logging intensity. We suggest that research on the
424 forest-management adequacy should include several metrics including
425 community similarity at different spatial scales, rather than just evaluating

426 changes in a single metric relating to species richness at a single spatial
427 scale.

428

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676 **Table 1** Forest structure and tree species diversity of three to four 0.2-ha
 677 plots and one 2-ha plot in primary, reduced-impact logged (RIL), and
 678 conventionally logged (CL) forest. Stem density, above-ground biomass
 679 (AGB), maximum dbh, basal area, observed number of families, genera
 680 and species, and estimated number species (per 70 stems in 0.2-ha plots
 681 and per 850 stems in 2-ha plots) are shown. Parentheses indicate values
 682 for trees ≥ 5 cm dbh. Forests sharing the same letters do not differ
 683 significantly at $P < 0.05$. Pioneer species: five *Macaranga* species (*M.*
 684 *conifera*, *M. gigantea*, *M. hypoleuca*, *M. pearsonii*, *M. bancana*) and two
 685 *Croton* species (*C. argyratus*, *C. oblongus*) of Euphorbiaceae, and two
 686 Rubiaceae species (*Neolamarckia cadamba*, *Neonauclea* sp.)

| | 0.2-ha plots | | | 2-ha plots | | |
|---------------------------------|------------------------|-------------------------|------------------------|------------|-----------|-----------|
| | Primary | RIL | CL | Primary | RIL | CL |
| Stem density (/ha) | 623 ±97 | 613 ±72 | 457 ±85 | 607 | 504 | 428 |
| AGB (Mg/ha) | 499 ^a ±60 | 341 ^a ±52 | 163 ^b ±84 | 378 | 290 | 216 |
| Maximum dbh (cm) | 114 ^a ±12 | 106 ^a ±10 | 63 ^b ±9 | 129 | 145 | 92 |
| Basal area (m ² /ha) | | | | | | |
| Total | 41.2 ^a ±4.6 | 32.7 ^a ±4.5 | 19.0 ^b ±7.4 | 34.2 | 28.6 | 23.3 |
| Dipterocarp | 19.9 ^a ±3.7 | 13.2 ^b ±3.4 | 5.1 ^c ±0.8 | 17.6 | 12.4 | 8.5 |
| Pioneer | 1.3 ^b ±0.5 | 2.3 ^b ±1.9 | 8.1 ^a ±3.7 | 0.4 | 2.4 | 4.2 |
| Observed no. families | 30.3 ^a ±1.9 | 29.0 ^a ±2.0 | 20.7 ^b ±2.1 | 52 (52) | 51 (53) | 48 (51) |
| Observed no. genera | 51.5 ^a ±5.4 | 51.5 ^a ±4.5 | 30.0 ^b ±4.6 | 135 (144) | 124 (134) | 121 (131) |
| Observed no. species | 82.5 ^a ±9.3 | 79.5 ^a ±10.3 | 39.3 ^b ±6.4 | 296 (319) | 298 (340) | 243 (263) |
| Estimated no. species | 50.1 ^a ±9.1 | 49.5 ^a ±5.9 | 31.1 ^b ±6.3 | 257 | 282 | 243 |

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688 **Table 2** PERMANOVA test results for community-composition
689 differences between primary, reduced-impact logged (RIL) and
690 conventionally logged (CL) forest. The r^2 values are shown for all
691 pairwise comparisons between forest types. Significant differences are in
692 bold. $P = * < 0.05$, $** < 0.01$, $*** < 0.001$

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| | 0.2-ha plots | 2-ha plots |
|-------------------------|----------------|-----------------|
| Among the three forests | 0.19 ** | 0.35 *** |
| Primary-RIL | 0.15 | 0.31 *** |
| Primary-CL | 0.31 * | 0.39 *** |
| RIL-CL | 0.36 * | 0.18 *** |

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708 **Figure captions**

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710 **Fig. 1** Frequency distribution of dbh for trees ≥ 5 cm dbh at one 2-ha plot
 711 (black bars) and trees ≥ 10 cm dbh at three to four 0.2-ha plots (dotted
 712 bars) in primary (a), reduced-impact logged (RIL) (b) and conventionally
 713 logged (CL) forest (c). Values for trees ≥ 60 cm dbh are also shown in an
 714 inset. Error bars indicate SD.

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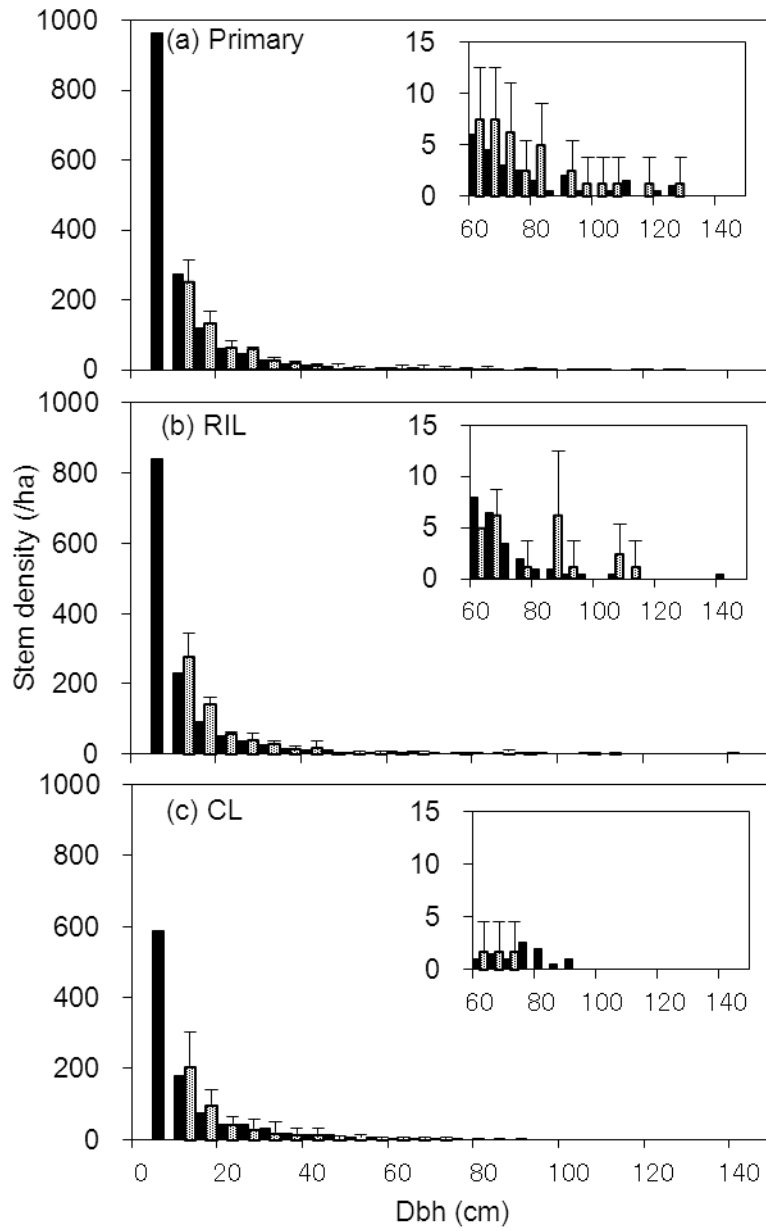
716 **Fig. 2** An ordination of tree community composition of primary,
 717 reduced-impact logged (RIL) and conventionally logged (CL) forest in
 718 the eleven 0.2-ha plots (a) and thirty 0.2-ha subplots in the three 2-ha
 719 plots (b) on the coordinate of axis 1 and axis 2 of NMDS analysis. Stress
 720 values are also shown.

721

722 **Fig. 3** Species accumulation curves of three to four 0.2-ha plots (a-f) and
 723 one 2-ha plot (g-n) in each of primary, reduced-impact logged (RIL) and
 724 conventionally logged (CL) forest by tree size class. Error bars indicate
 725 SD. Species-area curves: a-c,g-j; species-individual curves: d-f,k-n

726

727 **Fig. 4** Relationships between above-ground biomass (AGB) and estimated
 728 number of species (a-c) and NMDS axis 1 scores (d-f) in the three
 729 sampling designs; three to four 0.2-ha plots and a 2-ha plot in primary,
 730 reduced-impact logged (RIL) and conventionally logged (CL) forest, and
 731 ten 0.2-ha subplots within each 2-ha plot. Relationships significant at $P <$
 732 0.05 only are shown.

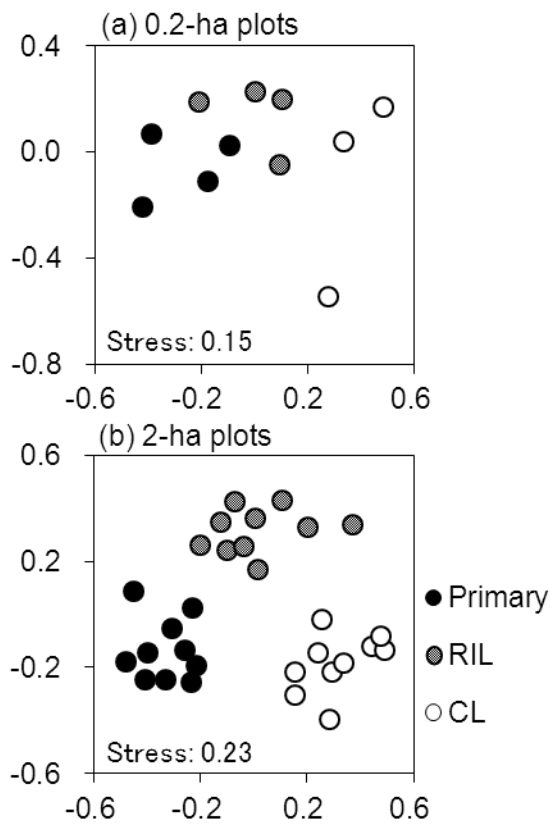


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735 Fig. 1

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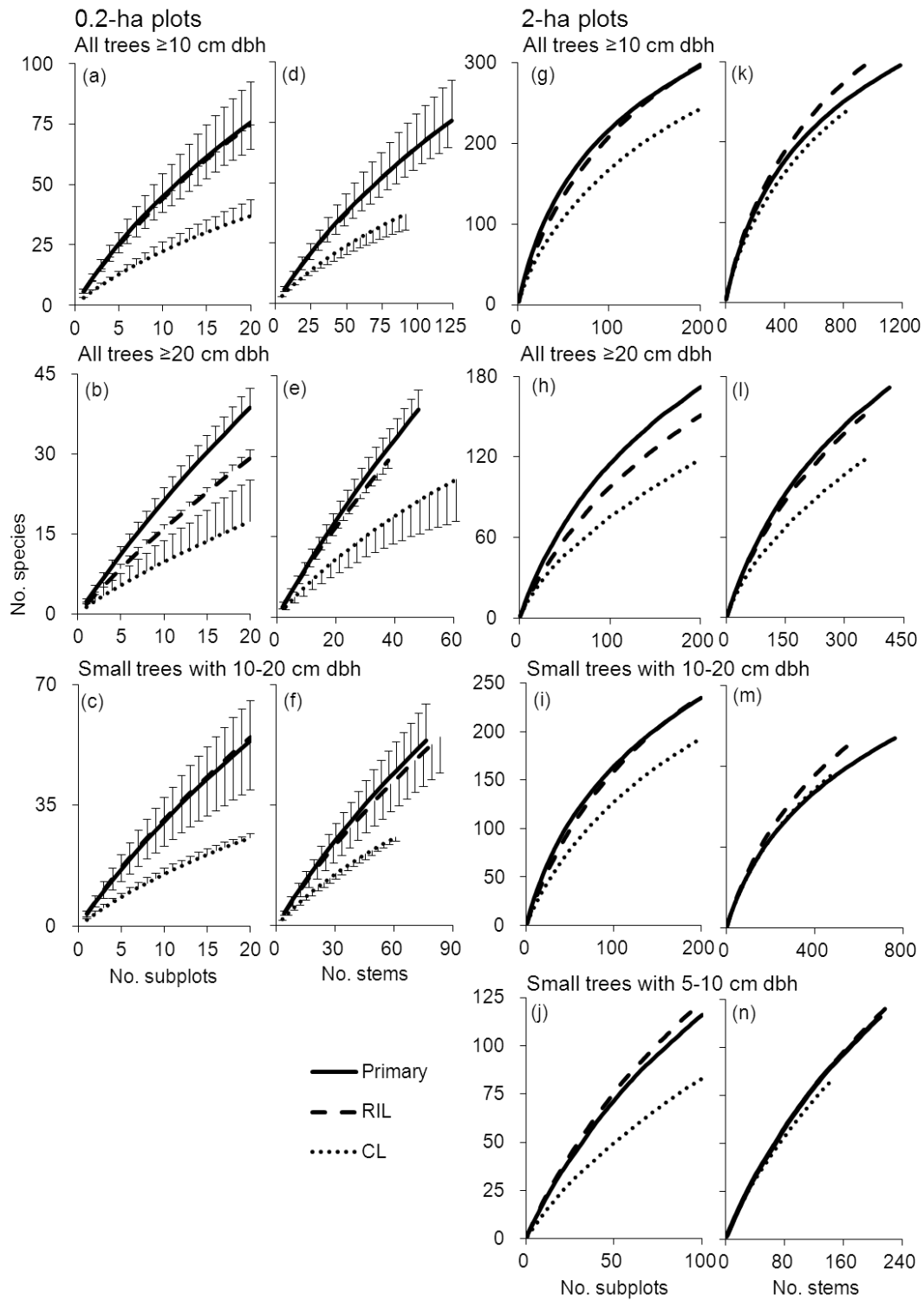


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739 Fig. 2

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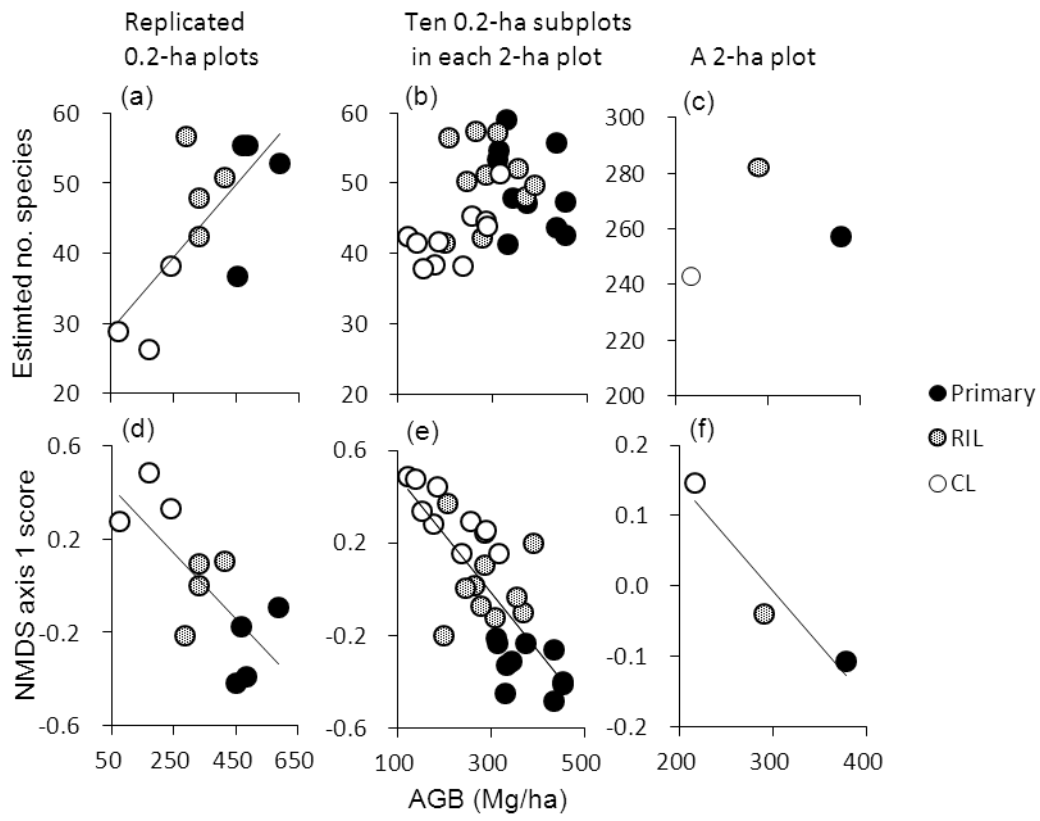


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747 Fig. 4