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

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

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

Introduction

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

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

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

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

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

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

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

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

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

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

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

Vegetation survey

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

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

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

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

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

Data analysis

Above-ground biomass

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

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

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

Forest heterogeneity

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

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

$$\beta = \gamma / \alpha$$

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

Community similarity

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

Species richness

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

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

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

Scale dependency of the two metrics

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

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

critical in this analysis because we applied a linear model.

RESULTS

Forest structure

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

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

Community similarity and forest heterogeneity

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

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

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

Species richness

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

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

Scale dependency of the two metrics

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

DISCUSSION

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

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

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

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

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

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

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

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

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References

- Akutsu K, Khen CV, Toda MJ (2007) Assessment of higher insect taxa as bioindicators for different logging-disturbance regimes in lowland tropical rain forest in Sabah, Malaysia. *Ecol Res* 22:542-550
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32-46
- Asner GP, Knapp DE, Broadbent EN et al (2005) Selective logging in the Brazilian Amazon. *Science* 310:480-482
- Azevedo-Ramos C, De Carvalho Jr O, Do Amaral BD (2006) Short-term effects of reduced-impact logging on eastern Amazon fauna. *For Ecol Manage* 232:2635
- Baker TR, Phillips OL, Malhi Y et al (2004) Variation in wood density

- 451 determines spatial patterns in Amazonian forest biomass. *Global Chang*
452 *Biol* 10:545-562
- 453 Barlow J, Gardner TA, Araujo IS et al (2007) Quantifying the biodiversity
454 value of tropical primary, secondary, and plantation forests. *Proc Natl*
455 *Acad Sci USA* 104:18555-18560
- 456 Berry NJ, Phillips OL, Lewis SL et al (2010) The high value of logged
457 tropical forests: lessons from northern Borneo. *Biodiversity Conserv*
458 19:985-997
- 459 Berry NJ, Phillips OL, Ong RC et al (2008) Impacts of selective logging on
460 tree diversity across a rainforest landscape: the importance of spatial
461 scale. *Landscape Ecol* 23:915-929
- 462 Bertault JG, Sist P (1997) An experimental comparison of different
463 harvesting intensities with reduced-impact and conventional logging in
464 East Kalimantan, Indonesia. *For Ecol Manage* 94:209-218
- 465 Bicknell J, Peres CA (2010) Vertebrate population responses to
466 reduced-impact logging in a neotropical forest. *For Ecol Manage*
467 259:2267-2275
- 468 Bischoff W, Newbery DM, Lingenfelder M et al (2005) Secondary
469 succession and dipterocarp recruitment in Bornean rain forest after
470 logging. *For Ecol Manage* 218:174-192
- 471 Blaser J, Sarre A, Poore D et al (2011) Status of tropical forest management.
472 ITTO Technical Series 38. International Tropical Timber Organization,
473 Yokohama, Japan
- 474 Brearley FQ, Prajadinata S, Kidd PS et al (2004) Structure and floristics of
475 an old secondary rain forest in Central Kalimantan, Indonesia, and a

476 comparison with adjacent primary forest. For Ecol Manage 195:385-397

477 Cannon CH, Peart DR, Leighton M et al (1994) The structure of lowland

478 rainforest after selective logging in West Kalimantan, Indonesia. For

479 Ecol Manage 67:49-68

480 Cannon CH, Peart DR, Leighton M (1998) Tree species diversity in

481 commercially logged Bornean rainforest. Science 281:1366-1368

482 Castro-Arellano I, Presley SJ, Saldanha LN et al (2007) Effects of reduced

483 impact logging on bat biodiversity in terra firme forest of lowland

484 Amazonia. Biol Conserv 138:269-285

485 Chave J, Andalo C, Brown S et al (2005) Tree allometry and improved

486 estimation of carbon stocks and balance in tropical forests. Oecologia

487 145:87-99

488 Chazdon RL, Colwell RK, Denslow JS et al (1998) Statistical methods for

489 estimating species richness of woody regeneration in primary and

490 secondary rain forests of Northeastern Costa Rica. In: Dallmeier F,

491 Comiskey JA (eds) Forest biodiversity research, monitoring and

492 modeling: conceptual background and old world case studies. Parthenon

493 Publishing, Paris, pp 285-309

494 Chua LSL, Hawthorne WD, Guan SL et al (1998) Biodiversity database and

495 assessment of logging impacts. In: Lee SS, Dan YM, Gauld ID et al (eds)

496 Conservation, management and development of forest resources. Forest

497 Research Institute Malaysia, Kuala Lumpur, pp 30-40

498 Condit R, Hubbell SP, Lafrankie JV et al (1996) Species-area and

499 species-individual relationships for tropical trees: a comparison of three

500 50-ha plots. J Ecol 84:549-562

- 501 Connell JH (1978). Diversity in tropical rain forests and coral reefs.
502 Science 199:1302-1310
- 503 Davis AJ (2000) Does reduced-impact logging help preserve biodiversity in
504 tropical rainforests? A case study from Borneo using dung beetles
505 (Coleoptera: Scarabaeoidea) as indicators. Environ Entomol 29:467-475
- 506 Dias MS, Magnusson WE, Zuanon J (2010) Effects of reduced-impact
507 logging on fish assemblages in central Amazonia. Conserv Biol
508 24:278-286
- 509 Dumbrell AJ, Clark EJ, Frost GA et al (2008) Changes in species diversity
510 following habitat disturbance are dependent on spatial scale: theoretical
511 and empirical evidence. J Appl Ecol 45:1531-1539
- 512 Edwards DP, Larsen TH, Docherty TDS et al (2010) Degraded lands worth
513 protecting: the biological importance of Southeast Asia's repeatedly
514 logged forests. Proc R Soc B-Biol Sci 278:82-90
- 515 Edwards DP, Woodcock P, Edwards FA et al (2012) Reduced-impact logging
516 and biodiversity conservation: a case study from Borneo. Ecol Appl 22:
517 561-571
- 518 Felton A, Wood J, Felton AM et al (2008) Bird community responses to
519 reduced-impact logging in a certified forestry concession in lowland
520 Bolivia. Biol Conserv 141:545-555
- 521 Foody GM, Cutler MEJ (2003) Tree biodiversity in protected and logged
522 Bornean tropical rain forests and its measurement by satellite remote
523 sensing. J Biogeography 30:1053-1066
- 524 Gibson L, Lee TM, Koh LP et al. (2011) Primary forests are irreplaceable
525 for sustaining tropical biodiversity. Nature 478:378-381

- 526 Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and
527 pitfalls in the measurement and comparison of species richness. *Ecol Lett*
528 4:379-391
- 529 Gutiérrez-Granados G, Pérez-Salicrup DR, Dirzo R (2011) Differential
530 diameter-size effects of forest management on tree species richness and
531 community structure: implications for conservation. *Biodivers Conserv*
532 20:1571-1585
- 533 Hall JS, Harris DJ, Medjibe V et al (2003) The effects of selective logging
534 on forest structure and tree species composition in a Central African
535 forest: implications for management of conservation areas. *For Ecol*
536 *Manage* 183:249-264
- 537 Hamer KC, Hill JK (2000) Scale-dependent effects of habitat disturbance on
538 species richness in tropical forests. *Conserv Biol* 14:1435-1440
- 539 Hasegawa M, Ito MT, Kitayama K et al (2006) Logging effects on soil
540 macrofauna in the rainforests of Deramakot Forest Reserve, Sabah,
541 Malaysia. In: Lee YF, Chung AYC, Kitayama K (eds) *Proceedings of the*
542 *2nd workshop on synergy between carbon management and biodiversity*
543 *conservation in tropical rain forests*. Forest Research Centre, Forestry
544 Department, Sabah, pp 53-60
- 545 Hill JK, Hamer KC (2004) Determining impacts of habitat modification on
546 diversity of tropical forest fauna: the importance of spatial scale. *J Appl*
547 *Ecol* 41:744-754
- 548 Imai N, Samejima H, Langner A et al (2009) Co-benefits of sustainable
549 forest management in biodiversity conservation and carbon sequestration.
550 *PLoS One* 4:e8267

- 551 Johns JS, Barreto P, Uhl C (1996) Logging damage during planned and
552 unplanned logging operations in the eastern Amazon. *For Ecol Manage*
553 89:59-77
- 554 Kirika JM, Bhning-Gaese K, Dumbo B et al (2010) Reduced abundance of
555 late-successional trees but not of seedlings in heavily compared with
556 lightly logged sites of three East African tropical forests. *J Trop Ecol*
557 26:533-546
- 558 Kleine M, Heuvel dop J (1993) A management of planning concept for
559 sustained yield of tropical forests in Sabah, Malaysia. *For Ecol Manage*
560 61:277-297
- 561 Lagan P, Mannan S, Matsubayashi H (2007) Sustainable use of tropical
562 forests by reduced-impact logging in Deramakot Forest Reserve, Sabah,
563 Malaysia. *Ecol Res* 22:414-421
- 564 Lawton JH, Bignell DE, Bolton B et al (1998) Biodiversity inventories,
565 indicator taxa and effects of habitat modification in tropical forest.
566 *Nature* 391:72-76
- 567 Lemmens RHMJ, Soerianegara I, Wong WC (1995) Timber trees: minor
568 commercial timbers, *Plant Resources South-east Asia* 5(2). Backhuys
569 Publishers, Leiden, pp 655
- 570 Magurran AE (2004) *Measuring biological diversity*. Blackwell Science Ltd,
571 Oxford, pp 256
- 572 Makana JR, Thomas SC (2006) Impacts of selective logging and agricultural
573 clearing on forest structure, floristic composition and diversity, and
574 timber tree regeneration in the Ituri Forest, Democratic Republic of
575 Congo. *Biodivers Conserv* 15:1375-1397

- 576 Medjibe VP, Putz FE, Starkey MP et al (2011) Impacts of selective logging
577 on above-ground forest biomass in the Monts de Cristal in Gabon. For
578 Ecol Manage 262:1806-1799
- 579 Miller SD, Goulden ML, Hutyra LR et al (2011) Reduced impact logging
580 minimally alters tropical rainforest carbon and energy exchange. Proc
581 Natl Acad Sci USA 108:19431-19435
- 582 Molino JF, Sabatier D (2001) Tree diversity in tropical rain forests: a
583 validation of the intermediate disturbance hypothesis. Science
584 294:1702-1704
- 585 Oey DS (1951) Perbandingan berat dari djenis2 kaju Indonesia dan
586 pengartian beratnja kaju untunk keperluan praktek. Penjelidikan
587 Kehutanan, Bogor, pp 183
- 588 Okuda T, Suzuki M, Adachi N et al (2003) Effect of selective logging on
589 canopy and stand structure and tree species composition in a lowland
590 dipterocarp forest in peninsular Malaysia. For Ecol Manage 175:297-320
- 591 Ouédraogo DY, Beina D, Picard N et al (2011) Thinning after selective
592 logging facilitates floristic composition recovery in a tropical rain forest
593 of Central Africa. For Ecol Manage 262: 2176–2186
- 594 Peña-Claros M, Fredericksen TS, Alarcón A et al (2008) Beyond
595 reduced-impact logging: silvicultural treatments to increase growth rates
596 of tropical trees. For Ecol Manage 256:1458-1467
- 597 Pinard MA, Putz FE (1996) Retaining forest biomass by reducing logging
598 damage. Biotropica 28:278-295
- 599 Plumptre AJ (1996) Changes following 60 years of selective timber
600 harvesting in the Budongo Forest Reserve, Uganda. For Ecol Manage

601 89:101-113

602 Presley SJ, Willig MR, Wunderle Jr JM et al (2008) Effects of
603 reduced-impact logging and forest physiognomy on bat populations of
604 lowland Amazonian forest. *J Appl Ecol* 45:14-25

605 Putz FE, Sist P, Fredericksen T et al (2008a) Reduced-impact logging:
606 challenges and opportunities. *For Ecol Manage* 256:1427-1433

607 Putz FE, Zuidema PA, Pinard MA et al (2008b) Improved tropical forest
608 management for carbon retention. *PLoS Biol* 6:e166

609 Rockwell CA, Kainer KA, Staudhammer CL et al (2007) Future crop tree
610 damage in a certified community forest in southwestern Amazonia. *For*
611 *Ecol Manage* 242:108-118

612 Rodrigues ASL, Andelman SJ, Bakan MI et al (2004) Effectiveness of the
613 global protected area network in representing species diversity. *Nature*
614 428:640-643

615 Sabah Forestry Department (2005) Forest management plan 2: Deramakot
616 Forest Reserve, Forest management unit no.19. Sandakan

617 Samejima H, Ong R, Lagan P et al (2012) Camera-trapping rates of
618 mammals and birds in a Bornean tropical rainforest under sustainable
619 forest management. *For Ecol Manage* 270:248-256

620 Seino T, Takyu M, Aiba SI et al (2006) Floristic composition, stand
621 structure, and above-ground biomass of the tropical rain forests of
622 Deramakot and Tangkulap Forest Reserve in Malaysia under different
623 forest managements. In: Lee YF, Chung AYC, Kitayama K (eds)
624 *Proceedings of the 2nd workshop on synergy between carbon management*
625 *and biodiversity conservation in tropical rain forests. Forest Research*

- 626 Centre, Forestry Department, Sabah, pp 29-52
- 627 Sheil D, Burslem DFRP (2003) Disturbing hypotheses in tropical forests.
- 628 Trends Ecol Evol 18:18-26
- 629 Sist P, Nolan T, Bertault JG et al (1998) Harvesting intensity versus
- 630 sustainability in Indonesia. For Ecol Manage 108:251-260
- 631 Slik JWF (2006) Estimating species-specific wood density from the genus
- 632 average in Indonesian trees. J Trop Ecol 22:481-482
- 633 Slik JWF, Verburg RW, Keßler PJA (2002) Effects of fire and selective
- 634 logging on the tree species composition of lowland dipterocarp forest in
- 635 East Kalimantan, Indonesia. Biodivers Conserv 11:85-98
- 636 Soerianegara I, Lemmens RHMJ (1993) Timber trees: major commercial
- 637 timbers, Plant Resources South-east Asia 5(1). Backhuys Publishers,
- 638 Leiden, pp 605
- 639 Sosef MSM, Hong LT, Prawirohatmodjo S (1998) Timber trees:
- 640 lesser-known timbers, Plant Resources South-east Asia 5(3). Backhuys
- 641 Publishers, Leiden, pp 859
- 642 Souza AF, Cortez LSR, Longhi SJ (2012) Native forest management in
- 643 subtropical South America: long-term effects of logging and multiple-use
- 644 on forest structure and diversity. Biodivers Cons 21:1953-1969
- 645 Su JC, Debinski DM, Jakubauskas ME et al (2004) Beyond species richness:
- 646 community similarity as a measure of cross-taxon congruence for
- 647 coarse-filter conservation. Conserv Biol 18:167-173
- 648 Verburg R, Van Eijk-Bos C (2003) Effects of selective logging on tree
- 649 diversity, composition and plant functional type patterns in a Bornean
- 650 rain forest. J Veg Sci 14:99-110

651 Webb EL, Peralta R (1998) Tree community diversity of lowland swamp
652 forest in Northeast Costa Rica, and changes associated with controlled
653 selective logging. *Biodivers Conserv* 7:565-583

654 Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and
655 California. *Ecol Monogr* 30:279-338

656 Wright SJ (2005) Tropical forests in a changing environment. *Trends Ecol*
657 *Evol* 20:553-560

658 Wunderle Jr JM, Henriques LMP, Willig MR (2006) Short-term responses of
659 birds to forest gaps and understory: an assessment of reduced-impact
660 logging in a lowland Amazon forest. *Biotropica* 38:235-255

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

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

	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 ***

Figure captions

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

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

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

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

Fig. 1

Fig. 2

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743 Fig. 3

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Fig. 4