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Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests

Running head: NPP and disturbance in tropical forest

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ABSTRACT

Tropical forests play a major role in the carbon cycle of the terrestrial biosphere. Recent field studies have provided detailed descriptions of the carbon cycle of mature tropical forests, but logged or secondary forests have received much less attention. Here we report the first measures of total net primary productivity (NPP) and its allocation along a disturbance gradient from old-growth forests to moderately and heavily logged forests in Malaysian Borneo. We measured the main NPP components (woody, fine root and canopy NPP) in old-growth (n=6) and logged (n=5) 1 ha forest plots. Overall, the total NPP did not differ between old-growth and logged forest (13.5 ± 0.5 and 15.7 ± 1.5 Mg C ha^{-1} $year^{-1}$, respectively). However, logged forests allocated significantly higher fraction into woody NPP at the expense of the canopy NPP (42% and 48% into woody and canopy NPP, respectively, in old-growth forest vs. 66% and 23% in logged forest). When controlling for local stand structure, NPP in logged forest stands was 41% higher, and woody NPP was 150% higher than in old-growth stands with similar basal area, but this was offset by structure effects (higher gap frequency and absence of large trees in logged forest). This pattern was not driven by species turnover: the average woody NPP of all species groups within logged forest (pioneers, non-pioneers, species unique to logged plots and species shared with old-growth plots) was similar. Hence, below a threshold of very heavy disturbance, logged forests can exhibit higher NPP and higher allocation to wood; such shifts in carbon cycling persist for decades after the logging event. Given that the majority of tropical forest biome has experienced some degree of logging, our results demonstrate that logging can cause substantial shifts in carbon production and allocation in tropical forests.

INTRODUCTION

The tropical forest biome plays a dual role in the global carbon budget. On the one hand, it forms a large terrestrial carbon sink of approximately 1.0±0.5 Pg C yr^{-1} (Pan *et al.*, 2011), accounting for 40% of the global land C sink (Malhi, 2010; Ciais *et al.*, 2013). On the other hand, carbon emissions from tropical forest degradation and deforestation, 1.1±0.8 Pg C yr^{-1}, make up >90% of the total emission from land use and land use change, which currently account for 12% of all anthropogenic carbon dioxide emissions (Ciais *et al.*, 2013) .

Today, approximately 75% (1713 M ha) of the original, pre-industrial tropical forest area remains (FAO, 2015; Keenan *et al.*, 2015). Of the extant tropical forest area, only 30% is relatively undisturbed (Potapov *et al.*, 2008). The remaining area has been modified by humans, mostly through selective logging. Hence, the most pervasive aspect of global change in tropical forests is probably neither deforestation nor climate change, but the increasing transformation (approximately 12 M ha $year^{-1}$; FAO, 2015) of high biomass, slow-turnover, old-growth forests into lower biomass, higher turnover post-disturbance forests (Malhi *et al.*, 2014). Selective logging changes the forest carbon cycle by altering forest structure, dynamics, composition, and microclimate, and, as a result, the functioning of the ecosystem. Standing carbon stocks and the amount of metabolically active tissue decrease, while necromass increases. Gaps left by the removed and dying trees make the physical environment more exposed, altering radiation, temperature, humidity, and soil moisture regimes (Hardwick *et al.*, 2015). In addition to the changes in microclimate, logging operations cause soil disturbance, loss of top soil and soil compaction, especially around logging roads, skid trails and logging platforms, which may cover up to 25% of logged forest areas (Yamada *et al.*, 2014). Competition both above- and below-ground is reduced and resource availability (e.g. light in gaps, extra nutrients from logging residue and decomposing necromass) increases. The selective removal of large, commercially valuable canopy trees that dominate the biomass stock (Sist *et al.*, 2014) changes the size and age structure and species composition of the forest. The colonisation of gaps by pioneer species further alters the community composition (Sist & Nguyen-The, 2002), especially if all canopy species, and therefore their seed source, have been removed. Typically, the community shifts from slow-growing, conservative, shade-tolerant species towards fast-growing, acquisitive, light-demanding species (Bischoff *et al.*, 2005; Carreno-Rocabado *et al.*, 2012; Saner *et al.*, 2012). In the shorter term, logging decreases primary productivity and increases heterotrophic respiration (Huang & Asner, 2010). As the forest starts to recover, however, the woody biomass accumulation rate in logged forest may be several times higher than in old-growth forest (Blanc *et al.*, 2009; Berry *et al.*, 2010).

Almost all studies of biomass production and recovery in logged forests focus only on above-ground woody biomass (e.g. Blanc *et al.*, 2009; Huang & Asner, 2010; Berenguer *et al.*, 2014). Although woody production is a significant proportion of net primary production (NPP), typically 39% ±10% in old-growth tropical forests (Malhi *et al.*, 2011), carbon fixed through photosynthesis is also allocated to production of leaves, roots, flowers, fruits, and other ecosystem components. A more complete understanding of biomass production can be attained through assessment of NPP.

NPP is the amount of carbon assimilated through photosynthesis that is converted into new tissue, root exudates and volatile organic compounds. In old-growth tropical forests, plants use approximately 60-70% of gross primary productivity (GPP) on their own metabolism, releasing the assimilated CO_2 back to the atmosphere through autotrophic respiration (Chambers *et al.*, 2004; Malhi *et al.*, 2009; Malhi, 2012; Anderson-Teixeira *et al.*, 2016). Thus, the carbon use efficiency (proportion of GPP converted to NPP) is estimated to be about 30-40% in old-growth forests, but may be substantially higher in post-disturbance forests where rapid growth and resource acquisition is prioritised over maintenance and defence. A pan-tropical analysis of NPP allocation into canopy, woody, and fine root NPP (which, together, account for ~90% of the total NPP) indicates roughly equal partitioning into these three components in old-growth forests, but site-specific variation is considerable (Malhi *et al.*, 2011).

In recent years, there have been an increasing number of studies of above- and below-ground NPP in tropical old-growth forest sites (e.g. Clark *et al.*, 2001; Aragão *et al.*, 2009; Malhi *et al.*, 2011; Malhi *et al.*, 2015, Moore *et al.* 2017). However, as far as we are aware, there has been no assessment of above- and below-ground NPP for tropical logged forests; the most comprehensive synthesis of the existing empirical data on tropical forest carbon stocks and fluxes to date contains no estimates of total NPP for logged forests and only one estimate of total NPP for a naturally regenerating secondary forest (Anderson-Teixeira *et al.*, 2016). Given that the area of logged and human-modified forest exceeds that of old-growth forests (FAO, 2015), quantifying the carbon dynamics of logged forests is essential for understanding the carbon balance of the tropical forest biome.

In this study we present the first quantification of total net primary productivity and its allocation into woody, canopy and fine root NPP along a disturbance gradient from old-growth to heavily logged forest. Specifically, we addressed the following questions:

- How do total NPP and its allocation to canopy, woody and fine root components vary along a disturbance gradient from old-growth to heavily logged forests?
- Are the high woody growth rates reported for logged forests the result of an increase in NPP or a shift in allocation in favour of woody production, or some combination of these two factors?
- To what extent are the shifts in NPP along the disturbance gradient determined by species turnover, in particular, the presence of pioneer species?

- What is the relative contribution of shifts in tree carbon budgets (changes in productivity and allocation) vs. changes in stand density and structure (gaps, reduced number of large trees) in determining the net change in NPP and its allocation between logged and old-growth forests?

MATERIALS AND METHODS

Study sites

The study sites were located in Malaysian Borneo, in the states of Sarawak and Sabah. This area is a global hotspot of logging and forest conversion. By 2009, 28% of the original forest area of Sabah and Sarawak had been converted to plantations, predominantly oil palm, and 72% of the remaining forest area had been selectively logged (Bryan *et al.*, 2013). Climate in the region is moist tropical, with an annual daily mean temperature of 26.7°C (Walsh & Newbery, 1999). Annual precipitation is approximately 2600-2700 mm (Walsh & Newbery, 1999; Kumagai & Porporato, 2012). There are no distinct dry seasons, but approximately 12% of months experience rainfall of <100 mm month^{-1} (Walsh & Newbery, 1999). The area experiences severe droughts linked to El Niño events approximately every ten years, with some evidence that the drought frequency is increasing (Walsh & Newbery, 1999; Malhi & Wright, 2004; Katayama *et al.*, 2009).

Five plots formed a disturbance gradient from heavily to moderately logged forest sites, located in Kalabakan Forest Reserve, Sabah (Table 1). Six plots were located in old-growth forest (two in Danum Valley Conservation area, Sabah; two in Maliau Basin Conservation Area, Sabah; and two in Lambir Hills National Park, Sarawak) where there was no evidence of logging or human disturbance of vegetation (apart from indirectly through heavy defaunation in Lambir; Harrison *et al.*, 2013) (for map, see Fig. S1). All plots had a planimetric area of 1 ha, divided into 25 subplots of 20 m × 20 m. The logged plots in Kalabakan Forest Reserve and the old-growth plots in Maliau are part of the Stability of Altered Forest Ecosystem (SAFE) Project, a large-scale forest fragmentation experiment (Ewers *et al.*, 2011; www.safeprojet.net).

The forests in the region are extremely species rich. Lambir has the highest recorded tree species diversity in the Paleotropics (Lee *et al.*, 2002). In all plots, Euphorbiaceae and Dipterocarpaceae were the most species-rich families among trees >10 cm DBH, with the Dipterocarpaceae dominating in overall biomass. In the old-growth plots, the most common genera were the Dipterocarps *Shorea* and *Parashorea* in Maliau, *Shorea* and *Dryobalanops* in Lambir, and *Shorea* and *Diospyros* (Ebenaceae) in Danum, while in the logged plots the most common genera were *Macaranga* (Euphorbiaceae), *Shorea* (Diptocarpaceae) and *Syzygium* (Myrtaceae).On average 46% (range: 27% to 58%) of the basal area in the logged plots comprised of species that were also found in old-growth plots (Table S1). The basal area proportion of pioneer species (Table S1) in the logged plots ranged from 7% to 57% (Table 1).

In the SAFE Project area, the forest had been selectively logged two (SAF-03, SAF-04) or four (SAF-01, SAF-02, SAF-05) times. The first round of logging took place in mid-1970s, followed by one to three repeated rounds during 1990-2008. Approximately 113 m^3 ha^{-1} of timber was removed during the first rotation and an additional cumulative volume of 37 to 66 m^3 ha^{-1} during the subsequent rotations, which is similar to the mean extracted volume of 152 m^3 ha^{-1} within a larger, 220 000 ha area in Sabah (Fisher *et al.*, 2011; Struebig *et al.*, 2013). Converted to biomass, this sums to approximately 46 to 54 Mg C ha^{-1} extracted during the 30-year period. However, total biomass loss was several times higher (estimated to be 94-128 Mg C ha^{-1}; Pfeifer *et al.*, 2016), due to collateral damage, increased mortality after the logging (Pearson *et al.*, 2014; Shenkin *et al.*, 2015), and abandonment of some of the felled trees in the forest (data not available for SAFE, but in Indonesian Borneo typically 25% of the stems; Griscom *et al.*, 2014). As the area is earmarked for conversion to oil palm plantation in 2015-2017 (Ewers *et al.*, 2011), the prescribed logging rotation of sixty years was not followed, and repeated rounds of logging have left parts of the area highly degraded (Reynolds *et al.*, 2011) (the plots will not be converted, but will remain inside forest fragments, except SAF-05 Plot). The logging targeted – but was not limited to – medium-density hardwoods (genera *Dryobalanops* and *Dipterocarpus*) and lighter hardwoods (*Shorea* and *Parashorea*). There was a high level of small scale spatial variation in logging intensity, due to differences in topography, proximity to roads, and available timber, which created a gradient from heavily to moderately logged sites. Pre-logging biomass of the plots was obtained from digitised forest inventory maps from the 1970s, provided by the Natural Forest Research Programme of the Forest Research Centre, Sabah Forestry Department (Fig. 1). The original data was based on the first Sabah forest inventory in 1969-1972 which used the combination of aerial photos (1:25000), and stratified field sampling (Forestal International, 1973; Munang, 1978). Our study plots were assumed to have the pre-logging biomass of the segment they belonged to. In addition, to describe the change in forest structure and composition, we used four metrics to characterise the level of disturbance within each plot: basal area, canopy gap fraction (estimated from hemispherical photos), number of stems >50 cm diameter, and pioneer proportion (Table 1, Table S1).

The soils are orthic Acrisols or Ultisols in the Sabah plots and humult Utisols or udult Utisols in the Sarawak plots (for a comprehensive description of the soil types, see Marsh & Greer, 1992; Sylvester *et al.*, 2009; Kho *et al.*, 2013; Nainar *et al.*, 2015). There were no clear differences between sites (SAFE, Danum, Maliau and Lambir) or forest types (logged, old-growth) in soil nutrient concentrations or physical properties (Table S2, Fig. S2). Despite the geographic proximity of the logged plots, there was more variation in the soil characteristics among the logged plots than among the old-growth plots.

NPP estimates

The plots are part of the pantropical GEM (Global Ecosystems Monitoring) Intensive Carbon Plot network (http://gem.tropicalforests.ox.ac.uk/; Marthews *et al.*, 2012). We quantified the following NPP components: woody NPP (stems, coarse roots and branches), canopy NPP (leaves, twigs and reproductive parts) and fine root NPP. NPP data for the SAFE, Maliau and Danum (Sabah) plots were collected in 2011-2016, over a 24 month period in each plot, and tree census was carried out at least twice. NPP data for the Lambir (Sarawak) plots were collected for 15 months during 2008-2010, and trees were censused every five years between 1992 and 2008; these Lambir NPP data have already been published elsewhere (Kho *et al.*, 2013).

Woody NPP

Woody NPP was quantified as the sum of stem NPP, coarse root NPP and branch turnover NPP. All stems of trees and lianas >10 cm diameter at 1.3 m height (DBH) were tagged and the diameter was measured to the nearest millimetre. Measurement height was adjusted if the stem was not smooth at 1.3 m (buttresses, branching etc.). Small stems of trees and lianas of 2-10 cm DBH were tagged and measured in five subplots per plot in SAFE and in Maliau and in all subplots in Lambir and Danum. All plots were re-censused at least once. Stem height was estimated visually for all trees and calibrated against clinometer measurements for a subsample of 200 stems ranging from 6 to 63 m height. Height was not estimated during the recensus, as the change in height was considered too small to be detected reliably. Instead, a diameter to height relationship was estimated (exponential rise to maximum function, R^2 =

0.66 - 0.97, depending on the plot) and the height increment, as percentage change in height corresponding to the change in diameter, was derived from the curve for each stem.

Above-ground woody biomass was estimated using allometric equations for moist tropical forest, with diameter, height and wood density as inputs (Chave *et al.*, 2005). Wood density for each species (or in the absence of species ID, average by genus or family) was derived from the global wood density database (Chave *et al.*, 2009; Zanne *et al.*, 2009) or from local measurements (Kho *et al.*, 2013). We assumed a carbon content of 47.4% of dry biomass for all woody components (Martin & Thomas, 2011). Coarse root biomass was estimated using an allometric relationship between DBH and coarse root biomass (Eq. 1, Eq. 2), based on a root excavation study in a lowland dipterocarp forest in Pasoh Forest Reserve in Peninsular Malaysia (Niiyama *et al.*, 2010):

$$\text{Coarse root biomass (stems} \geq 2.5 \text{ cm DBH)} = 0.023 \times \text{DBH}^{2.59} \qquad \text{(Eq. 1)}$$

$$\text{Coarse root biomass (stems} < 2.5 \text{ cm DBH)} = 0.079 \times \text{DBH}^{1.04} \qquad \text{(Eq. 2)}$$

where coarse root biomass per stem is in kg and DBH in cm.

Stem and coarse root NPP were calculated as the increase in biomass in surviving trees between two subsequent censuses plus biomass of new recruits minus biomass loss through mortality. We assumed that stems that had died between censuses and new recruits that reached the DBH threshold between censuses did so, on average, in the middle of the census interval.

Branch turnover NPP was estimated in 25 quadrats of 2 m × 2 m in the plots in Sabah, and in four transects of 100 m × 1 m in the plots in Sarawak. All branches >2 cm diameter were collected every three to six months, weighed in the field and classified into five decay classes (Harmon *et al.*, 1995). The first survey quantified the stock, rather than production of the new material. Sub-samples from each decay class in each quadrat were brought back to the laboratory to determine the dry mass and mean wood density of each class. The dry mass of the pieces belonging to classes 2-5 were converted to recently fallen (class 1) mass, using a conversion factor (Eq 3):

$$\text{MassRF\_class(i)} = \text{Mass\_class(i)} \times \text{Density\_class1} / \text{Density\_class(i)} \qquad \text{(Eq. 3)}$$

where the MassRF_class(i) is the mass in decay classes 2-5 converted into recently fallen mass, Mass_class(i) is the measured mass in decay classes 2-5, and Density_class1 and Density_class(i) is the wood density in decay class 1 and wood density in decay classes 2-5, respectively. In subsequent censuses any fallen branches from dead trees were excluded, as we were interested in the branch turnover term.

Canopy NPP

Fine litter fall (leaves; twigs, woody tissue and branches≤2 cm diameter; reproductive parts; undefined fine debris) was used as a proxy for canopy production. Litter was collected every 14 to 21 days from 50 cm × 50 cm litter traps, 1 m above the ground (n=25 per plot), dried at 70°C until constant weight, and sorted into components. Litter carbon content was assumed to be 50%.

Fine root NPP

Fine root NPP was measured using cylindrical root in-growth cores of 12 cm diameter and 30 cm depth, made of wire mesh (n=16 per plot in Sabah, n=9 per plot in Sarawak). At the installation, all roots were extracted and the core was filled with the root free soil. The root mass at the first installation quantified the root stock rather than production. The cores were then harvested every three months, roots extracted, cleaned, dried (70°C until constant weight) and weighed. Roots in each core were searched in the forest for a fixed time (4×5 min or 4×10 min) and the total root mass in the sample was estimated from a cumulative root mass over time curve (Metcalfe *et al.*, 2007; Kho *et al.*, 2013), solved to 120 minutes. This method allows the root search time to be kept within a reasonable limit in the field while taking into account that a small fraction of roots is likely to remain unextracted. Root dry mass was converted into carbon by assuming a carbon content of 50%. Based on fine root mass in the top 30 cm soil layer, we estimated the fine root mass to 1 m depth by applying a correction factor of 1.125, derived from a root depth profile determined in Pasoh Forest Reserve in Peninsular Malaysia (Yoda, 1978; Kho *et al.*, 2013).

Missing components of NPP

Somewhat inevitably, any estimate of NPP may be biased towards underestimation because it neglects several small NPP terms, such as NPP lost as volatile organic emissions, non-measured litter trapped in the canopy, NPP lost to herbivory, or dropped from understorey plants below the litter traps. At a site in central Amazonia, volatile emissions were found to be a minor component of the carbon budget (0.13±0.06 Mg C ha^{-1} year^{-1}; Malhi *et al.*, 2009). Kurokawa and Nakashizuka (2008) estimated a leaf herbivory rate of 4.9% for Lambir, equivalent to 0.2-0.3 Mg C ha^{-1} year^{-1} (Kho et al., unpublished analysis). For below-ground NPP, the allocation to root exudates and to mycorrhizae is neglected, but can account for 5-10% of NPP in tropical forests (Doughty et al, 2017). Kho et al. (unpublished analysis) estimate an allocation to mycorrhizae of 1.3-1.4 Mg C ha^{-1} year^{-1}. These terms are challenging to measure, and here we focus on canopy, woody and fine root productivity, which are likely to account for over 85% of NPP, while recognising that these missing components do exist. The three missing terms above are likely to account for 10-13% of total NPP in Lambir (Kho et al., unpublished analysis), with transport to mycorrhizae being the most important.

Data analysis

The focus of this paper was to quantify the spatial variation in NPP (within and among plots, and between old-growth and logged forest) rather than to examine temporal trends. Therefore, all temporal replicates of each spatial replicate were pooled to derive a mean value for that sampling unit over the study period. These values were then used in the analyses.

The impact of logging disturbance on NPP was examined in two ways: by comparing the two forest types (old-growth and logged) by plot and by looking at the data along a finer scale disturbance gradient, wherein parts of each plot may represent a different level of disturbance. At the plot scale, the differences in total NPP and its components between forest types were tested using generalised least squares models, with forest type as a fixed factor (site was tested as a random effect, but did not improve the models). The models were run using R (R Core Team, 2014), with the package 'nlme' (Pinheiro *et al.,* 2014). To test whether the relative allocation into the main NPP components (woody, canopy and fine root NPP) and canopy NPP allocation into different litter fractions (leaf, twigs, reproductive and undefined debris) differed between the forest types, we used a linear model for compositional data (Pawlowsky-Glahn & Buccianti, 2011), in the R package 'compositions' (van den Boogaart, 2008; van den Boogaart *et al.*, 2014).

Along the disturbance gradient, differences in NPP and its allocation are influenced by factors of two different types: (i) a change in total NPP (which we will term *'the productivity effect'*) and/or shift in allocation patterns *('the allocation effect')* in the plants; and (ii) changes in stand structure and density ('*the structure effect'*). The structure effect may result from the reduction in the number of stems, particularly large stems, which may reduce overall NPP and also affect allocation patterns if allocation shows allometric relationships with tree size, and/or from an almost complete loss of stems and NPP in very open and degraded patches, such as old logging platforms. To assess the magnitude and relative importance of these effects, we conducted an analysis at sub-plot level, controlling for variation in stand basal area. At the subplot scale, basal area correlated with the mean and maximum diameter of stems >10 cm DBH (Fig. S3). For a given basal area, both the mean and maximum diameter were slightly lower in logged forest than in old-growth forest (a difference of 1.2 cm, $p=0.007$ and 4.5 cm, $p=0.047$ for mean and maximum diameter, respectively). However, there was a large overlap in the data distribution across the basal area range, compared to which the observed differences were small, indicating that at a similar basal area, the stand structure in the two forest types is comparable.

Variation in NPP along the disturbance gradient was partitioned into productivity effect, allocation effect and structure effect as follows: The total basal area range at the subplot scale within the dataset (each 20 m × 20 m subplot forming one data point) was 0-102 m^2 ha^{-1}, and the overlapping basal area range for logged and old-growth forest was of 7-51 m^2 ha^{-1}. For the overlapping range, we assumed that the structure effect caused no variation in NPP between the forest types. Therefore, the difference in total NPP between the forest types within that range was used as an estimate for the productivity effect. The difference in total NPP at the non-overlapping basal area range (<7 m^2 ha^{-1} or >51 m^2 ha^{-1}) was used as an estimate for the structure effect. At the NPP component (canopy, woody and fine root) scale, allocation effect had to be taken into account, in addition to the productivity and structure effects. The allocation effect was quantified by comparing the differences in NPP with observed allocation and assuming no difference in allocation (logged forest canopy, woody and fine root NPP recalculated, assuming the observed logged forest total NPP, but old-growth forest allocation pattern). In these analyses, old-growth forest was used as reference, against which the effects of logging were quantified. The area proportions of the overlapping and non-overlapping basal area zones were taken into account when calculating the overall importance of the productivity, allocation and structure effects.

NPP along the basal area gradient was modelled using a general additive mixed effects model (GAMM), with basal area of trees >10 cm DBH as an additive smoother and plot as a random effect. The data followed a gamma distribution (NPP values are non-negative, variance increases with increasing mean). The models were run using R packages 'nlme' (Pinheiro *et al.*, 2014) and 'mgcv' (Wood, 2011), following the protocols outlined by Zuur *et al.* (2009). We compared models with a single overall smoother or a separate smoother by forest type, and the best model in each case was chosen using an information theoretic approach (Burnham and Anderson 2002) by comparing the possible models using Akaike's Information Criterion (Akaike 1974), corrected for small sample sizes (AIC_C) (R package 'AICcmodavg'; Mazerolle, 2015).

To assess the extent to which the difference in logged forest and old-growth forest NPP were caused by tree species turnover, the species were classified into shared (present in both logged and old-growth plots) and unique (present in only one forest type) species and into pioneers and non-pioneers (Table S1). We then compared the woody NPP by these species groups (mixed effects model with the group as a fixed factor, diameter as a covariate and plot as a random effect), and the relationship between the pioneer basal area and pioneer woody NPP at each plot and subplot. The number of pioneer stems in the old-growth plots (n=11 for all six plots combined, <1% of the stems) was too small to be included in the analysis. Note that the canopy NPP and fine root NPP cannot be partitioned into species groups due to method constraints – several species contribute to the values derived from each spatial replicate (litter traps and root in-growth cores).

RESULTS

Carbon stocks and forest structure

Logged forest only had a third of the old-growth forest woody biomass (above-ground woody + coarse root biomass), 87±15 vs. 268±34 Mg C ha^{-1}, respectively (Fig. 1). In the moderately logged plots the smaller biomass was mainly due to the absence of large (>50 cm DBH) stems. However, in the most heavily logged plots the biomass was lower across all diameter classes (Fig. 2; Fig. S4). In contrast, the mean pre-logging (1970s) biomass of the logged forest (176±19 Mg C ha^{-1}) was similar to the current biomass in the old-growth forest ($F_{1,9}$=274.3, p=0.745). The partitioning of woody biomass between above- and below-ground components was similar in both forest types, with 20%±1.4% and 19% ±0.9% partitioned below ground in logged and old-growth forest, respectively.

Component and total net primary productivity

The logged forest plots had higher woody NPP than old-growth forest plots ($F_{1,9}$ =11.35, p=0.008), owing to the higher woody NPP in the small and intermediate diameter classes (Fig. 2; Fig. 3b; Fig. S4). Individual trees across all diameter classes showed higher growth in the logged plots compared with the old-growth plots (Fig. 2c). However, in the logged plots the number of large trees, and thus their contribution to the plot level woody NPP, was small, (Fig. 2a, Fig. 2c). All tree species groups in the logged plots had a higher woody NPP per stem than the groups in the old-growth plots (pair-wise comparisons, all p-values <0.01), including those species that were found in both forest types (Fig. 4). Within each forest type, the groups did not differ from one another (all p-values >0.05).

Canopy NPP was lower in logged forest ($F_{1,9}$ =24.91, p<0.001), while fine root NPP was similar in both forest types ($F_{1,9}$ =0.832, p=0.385) (Fig. 3a,c). In logged forest, on average 87%±2.1% of the canopy NPP was allocated to leaves, 8.5%±1.4% to twigs and 1.7%±0.7% to reproductive parts, while 2.5%±0.2% of the sample mass was unidentified debris (most likely to be leaf material). The corresponding values in the old-growth forest were 78%±4.2% (leaves), 12%±1.9% (twigs), 1.7%±1.7% (reproductive) and 6.4%±1.3% (debris). The allocation of the canopy components into different fractions did not differ between the forest types ($F_{2,9}$=1.980, p=0.206 and $F_{2,9}$=3.337, p=0.088, with debris included and excluded, respectively).

Total NPP was similar in both forest types ($F_{1,9}$=1.791, p=0.214), on average 15.7±1.50 Mg C ha^{-1} $year^{-1}$ in logged forest and 13.5±0.51 Mg C ha^{-1} $year^{-1}$ in old-growth forest (Fig. 3d).

NPP allocation to canopy, woody, and fine root NPP

At the plot scale, NPP allocation differed significantly between logged and old-growth plots (Fig. 3d, Fig. 5) ($F_{2,8}$=18.227, p=0.001). There was a clear shift in allocation from canopy to woody NPP in the logged forest (66%±2.2% allocated to woody NPP, 23%±1.6% to canopy NPP), compared with old-growth forest (42%±4.2% to woody NPP, 48%±3.6% to canopy NPP). Allocation to fine roots was similar in both forest types (11%±1.6% in logged, 10%±1.5% in old-growth forests).

Productivity, allocation and structure effects

The patterns in NPP at the basal area range where logged and old-growth forest data overlap (thus, assuming that no difference in NPP between the two forest types was caused by structure effect) were used for distinguishing the productivity and allocation effects. When controlled for basal area within this range (7-51 m^2 ha^{-1}), total NPP was approximately 41% higher in logged forest than in old-growth forest when averaged across subplots (Fig. 6). In addition, the allocation to different NPP components differed between the forest types. Across the overlapping basal area range, logged forest had 150% higher woody NPP and 46% higher fine root NPP than old-growth forest. Logged forest canopy NPP, on the other hand, was 38% lower.

The shapes of the basal area response curves illustrate structure effects (Fig. 6). These were particularly clear in logged forest, especially regarding canopy and woody NPP: canopy and woody NPP were low when basal area was small, and increased sharply and linearly with increasing basal area (though there is probably important herbaceous layer NPP in these gaps, which we do not account for). The threshold appeared at the basal area of approximately 10 m^2 ha^{-1} for canopy and woody NPP (a threshold that may suggest canopy closure), after which the slope became less steep. As a result, total NPP in logged forest also followed this pattern. However, fine root NPP showed a more consistently linear relationship with basal area and no clear basal area threshold. The old-growth forest plots did not have subplots with low basal areas, and in these plots all responses were relatively linear, or in the case of the canopy NPP, showed little relationship with basal area. Hence, canopy NPP was relatively insensitive to forest structure above a threshold basal area of canopy closure in both logged and old-growth forests, while woody, fine root and total NPP showed a greater sensitivity to basal area in logged forests than in old-growth forests. Slopes of linear regressions when basal area >10 m^2 ha^{-1} did not differ between logged and old-growth forest for canopy NPP ($p=0.840$), was marginally significant for woody NPP ($p=0.053$), and did differ for fine root NPP ($p=0.028$) and total NPP ($p=0.022$) (the results were similar when basal area threshold was increased to >20 m^2 ha^{-1}).

The relative importance of the productivity, allocation and structure effects on the variation in NPP between logged and old-growth forest is summarised in Figure 7. Compared with old-growth forest, the productivity effect increased the logged forest NPP by 31%. However, this effect was partly offset by the structure effect (logged forest plots having many subplots with very low basal area and no subplots with very high basal area; see data distribution rugs in Fig. 6), which lowered the logged forest NPP by 15%. The net effect was that NPP was only slightly (not significantly) higher in the logged forest at the 1 ha plot scale (Fig. 3d), although the difference between the two forest types within the overlapping basal area range was more marked. Woody NPP showed the largest difference between the forest types, being 83% higher in logged forest than in old-growth forest (Fig. 7) as a result of positive productivity and allocation effects. Canopy NPP, on the other hand, was smaller in logged forest (allocation effect -61%). Fine root NPP was similar in both forest types (slightly higher in logged forest but not significant at the plot scale).

DISCUSSION

NPP and its allocation along the disturbance gradient from old-growth to heavily logged forest

To our knowledge, these are the first comprehensive NPP estimates for human-modified tropical forests, describing all the main NPP components. In these forests, total NPP was similar in both forest types, although logged forests showed more variation, both within and among plots. In a previous publication, NPP estimates in the two plots in Lambir were put into pan-tropical context (see Table 3 in Kho *et al.*, 2013), showing that NPP in Bornean old-growth forests is higher (this study: 13.5 Mg C ha^{-1} year^{-1}, with SE of 0.519 Mg C ha^{-1} year^{-1}) than the tropical average (11.2 ± 0.73 Mg C ha^{-1} year^{-1}), but not exceptionally so.

Despite similar productivity in logged and old-growth forests, the legacy of logging was evident in the significantly reduced woody carbon stocks in logged forests. The absence of the largest trees contributed most to the lower carbon stocks in logged plots, but it is noteworthy that the carbon stock and the number of stems was lower even in the smallest diameter classes in the heavily logged plots compared with old-growth plots, which is similar to the pattern observed in Indonesian Borneo (Cannon *et al.*, 1994). The logged plots had experienced on average a 50% reduction in their woody carbon stocks. This is representative for the larger Yayasan Sabah Forest Management Area, which covers nearly a third of the forest area in Sabah (Fisher *et al.*, 2011; Reynolds *et al.* 2011), similar to the values reported elsewhere in Sabah (53%, Berry *et al.*, 2010), and in line with other parts of Borneo, where remaining basal area has been recoded as 14 m^2 ha^{-1} (SD =7) and 18 m^2 ha^{-1} (SD=10) in sparse and dense canopy fagments, respectively (Cannon *et al.*, 1994). Although the logging intensity in this study and in South East Asia in general is probably higher than the global average, the biomass loss is comparable to what has been reported in Brazil (35-57%, Berenguer *et al.*, 2014) and Africa (20-72%, Valentini *et al.*, 2014; Cazolla Gatti *et al.*, 2015).

Although the total NPP did not differ between forest types, there was a very clear difference in NPP allocation: logged forest allocated considerably more to woody NPP than to canopy NPP (66%±2.2% to woody, 23%±1.6% to canopy), compared with old-growth forests (42%±4.2% to woody, 48%±3.6% to canopy). A similar shift between canopy and woody allocation was reported when comparing young naturally regenerating regrowth forests with old intact forests (Anderson-Teixeira *et al.*, 2016). Since the results demonstrate a clear allocation shift between logged and old-growth forest, this highlights the importance of measuring all main NPP components, rather than using only one of them as a proxy for total NPP. In old-growth tropical forests, canopy NPP was found to be the best predictor of the total NPP both at Amazonian (Aragão *et al.*, 2009; Girardin *et al.*, 2010) and pan-tropical scales (Malhi *et al.*, 2011), with allocation to canopy showing less variation than the allocation to other NPP components. Although this was the case for the old-growth plots in this study as well, the results from the logged plots of this study and from regrowth forests globally (Anderson-Teixeira *et al.*, 2016) show that disturbance can markedly change these patterns.

Allocation to fine roots was low in all sites, on average 10%±1.0%. This is consistent with reports from other sites in Asia (Hertel *et al.*, 2009; Swamy *et al.*, 2010; Kira *et al.*, 2013), while allocation to fine roots is markedly higher in the Neo-tropical sites (global compilation by Malhi *et al.*, 2011 and references therein). Allocation to fine roots was isometric, showing little variation across plots or along the disturbance gradient. Overall, we find no evidence of changes in relative investment in fine roots after logging, as might be expected if a flush of nutrients caused a decreased need for root foraging, or conversely if a surge in growth caused increased demand for nutrients. Results from old-growth forests in Amazonia also found little evidence for shifts in nutrient allocation towards roots in nutrient poor soils (Aragão *et al.*, 2009; Malhi *et al.*, 2015), suggesting little support for nutrient acquisition optimization models for predicting fine root NPP.

Higher woody growth rate in logged forest: Increase in NPP or shift in allocation?

Logged tropical forests typically have higher woody growth rates than old-growth forests: 50% higher stem growth rate and recruitment (Bischoff *et al.*, 2005) and up to five times higher above-ground biomass production (Berry *et al.*, 2010) has been reported. This could be due to either increased NPP or a shift in allocation in favour of woody production. Our analysis shows that in these forests in Borneo, the higher woody productivity is equally a result of both processes. Hence, trees grow faster in logged forests both because they have higher NPP, and because the invest more of their NPP in stem growth (at the expense of leaf growth and defence) to compete for light.

The increased NPP could be caused by an increase in total canopy photosynthesis/gross primary productivity (GPP), and/or by an increase in the carbon use efficiency (CUE; the ratio NPP/GPP) in more disturbed sites. Studies in Amazonia show that more dynamic and disturbed forests appear to have a higher CUE, reflecting increased plant prioritisation in favour of NPP rather than maintenance respiration (Malhi *et al.*, 2015). In logged forests, the prioritisation in favour of rapid growth to reach canopy gaps is likely to lead to less proportional investment in maintenance and defence. It is also possible that the nutrient availability and/or mineralisation rates are higher as a result of the logging residue and changes in microclimate, which may boost leaf nutrient content and maximum photosynthesis rates. However, we find no consistent differences in soil nutrient concentrations in logged forests (Fig. S2).

The observed shift in allocation in favour of woody production is also consistent with this functional shift. After logging, the priority of successful trees is to grow crowns to capture now abundant within-forest light, to shade competitors and to avoid being shaded themselves (Chen *et al.*, 2013), which favours increased investment in stem growth. Allocation to leaves decreases when light availability increases – such as in logged forests that have gaps and recovering areas where the canopy is not yet fully closed (Poorter *et al.*, 2012).

The roles species turnover and pioneer species in logged forest NPP

In this study, the proportion of pioneers in the logged plots was high (on average, 30% of basal area, 33% of stems). However, the comparison by species groups showed that all species, not only pioneers, grew significantly faster in logged forests than in old-growth forests, indicating that the reduced competition and higher availability of light were more important factors than species identity in explaining the difference in NPP between the forest types. Similarly, in a previous study in Malaysia, growth rate differences among tree species were shown to be much more strongly influenced by light interception index, crown illumination index and crown area than by wood density (King *et al.* 2015).

Relative contributions of productivity, allocation, and structure effects in determining the net change in NPP between logged and old-growth forests

The subplot-scale analysis showed that after reaching canopy closure, logged forests were considerably more productive than old-growth forests of similar basal area. Overall, the productivity effect increased the logged forest NPP by 31%. This is consistent with the well-documented age-related decline in forest productivity in temperate and boreal forests, where NPP shows a rapid increase in young stands, peaks in intermediate age classes and a slowly declines towards old stands (e.g. Gower *et al.*, 1996; Ryan *et al.*, 1997; Pregitzer & Euskirchen, 2004). The selectively logged forests of this study are not, however, directly comparable to chronosequence studies, due to their high within-plot variability, patchy structure and the mixture of old trees and new recruits. In this study, the growth of individual trees was highest in the most heavily logged plots across all diameter classes, including the largest (and, potentially, oldest) trees. This indicates that, in addition to age, the altered resource availability and growth strategies (investing in growth rather than in maintenance and defence) also contributed to the higher productivity.

However, the higher productivity rates in logged forests in this study applied only if the structure effect were not taken into account. The structure effect was strongest in the areas of most sparse tree cover (basal area <10 m^2 ha^{-1}). These areas may either be logging gaps, such as roads and landing sites, which regenerate slowly (Pinard *et al.*, 2000), or tree fall gaps resulting from persistently higher mortality rates due to past logging. In these gaps, the NPP of individual trees, and thus the NPP per unit basal area, may be high due to abundant light, low below-ground competition, and, typically, dominance of fast-growing pioneer species (Huang & Asner, 2010). However, such areas have low NPP per unit ground area because of the small number of trees — using a banking analogy, a small amount of capital earns only a small interest, even if the interest rate is high. The low NPP in the sparse tree cover areas largely counterbalanced the positive productivity effect, resulting in a similar average NPP in logged and old-growth forests at the 1-ha plot scale. The steep decline in NPP when basal area was <10 m^2 ha^{-1} makes the area proportion of gaps one of the main factors affecting logged forest NPP. Based on high-resolution remote sensing data, Bryan *et al.* (2013) classified 32% of the logged forest area in Sabah as severely degraded. In our study, the area proportion of very sparse tree cover areas (basal area <10 m^2 ha^{-1}) in the logged plots was similar (37%), indicating that the results are likely to be representative across the wider landscape.

Similar to total NPP, the component (canopy, woody and fine root) NPP in logged forest showed a positive productivity effect and negative structure effect. A similar productivity effect has been reported in other studies, where the magnitude of total NPP or GPP was the best predictor of the component NPP (Litton *et al.*, 2007; Wolf *et al.*, 2011). However, for the component NPP, potential allocation shifts must be taken into account to fully understand the differences between logged and old-growth forest. For logged forest canopy NPP, the negative allocation effect was stronger than the positive productivity effect, while logged forest woody NPP was increased as much by the positive allocation effect as by the positive productivity effect. This demonstrates that allocation effects may be equally or more important than changes in overall productivity and stand structure in determining the magnitude of woody growth, or root or canopy production.

The data presented here give new insights into how disturbance affects productivity and allocation. As logged forests become an increasingly prevalent part of the tropical forest biome, these shifts in productivity and allocation represent a profound human impact on the carbon cycling of the tropical biosphere, which is almost certainly larger than the impacts to date caused by atmospheric and climate change.

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FIGURE LEGENDS

Figure 1. Above-ground woody biomass (positive values) and coarse root biomass (negative values) of living stems in logged and old-growth plots. Error bars are ±1 SE. The white bars for the logged plots denote the pre-logging biomass in the 1970s, obtained from historical records, ±20% uncertainty (below-ground stock estimated assuming the same allocation as post-logging).

Figure 2. a) Diameter distribution, **b)** above-ground woody biomass, and **c)** above-ground woody net primary productivity (AGW NPP) by stem diameter class in heavily logged (SAF-01, SAF-02, SAF-05), moderately logged (SAF-03, SAF-04) and old-growth (DAN-04, DAN-05, MLA-01, MLA-02, LAM-06, LAM-07) plots. Mean values are shown; for individual plots, see Fig. S4. Inset in **(c)**: mean annual diameter growth by 5 cm diameter classes in the three forest types. Classes with n≥5 stems are shown.

Figure 3. Canopy (**a**), woody (**b**), fine root (**c**) and total (**d**) net primary productivity (NPP) by plot and by forest type. Error bars are ±1 SE.

Figure 4. Average woody NPP (±1 SE) per stem by species groups across 10 cm diameter classes. Classes with n≥5 are shown. Species were classified into shared (found both in logged and old-growth plots) and unique (found only in one forest type) species and into pioneers and non-pioneers (Table S1). Species groups: LSN – logged, shared, non-pioneer; LUN – logged, unique, non-pioneer; LUP – logged, unique, pioneer; OSN – old-growth, shared, non-pioneer; OUN – old-growth, unique, non-pioneer.

Figure 5. Relative allocation (% of total) of net primary productivity (NPP) into canopy, woody and fine root NPP in individual plots and mean by forest type.

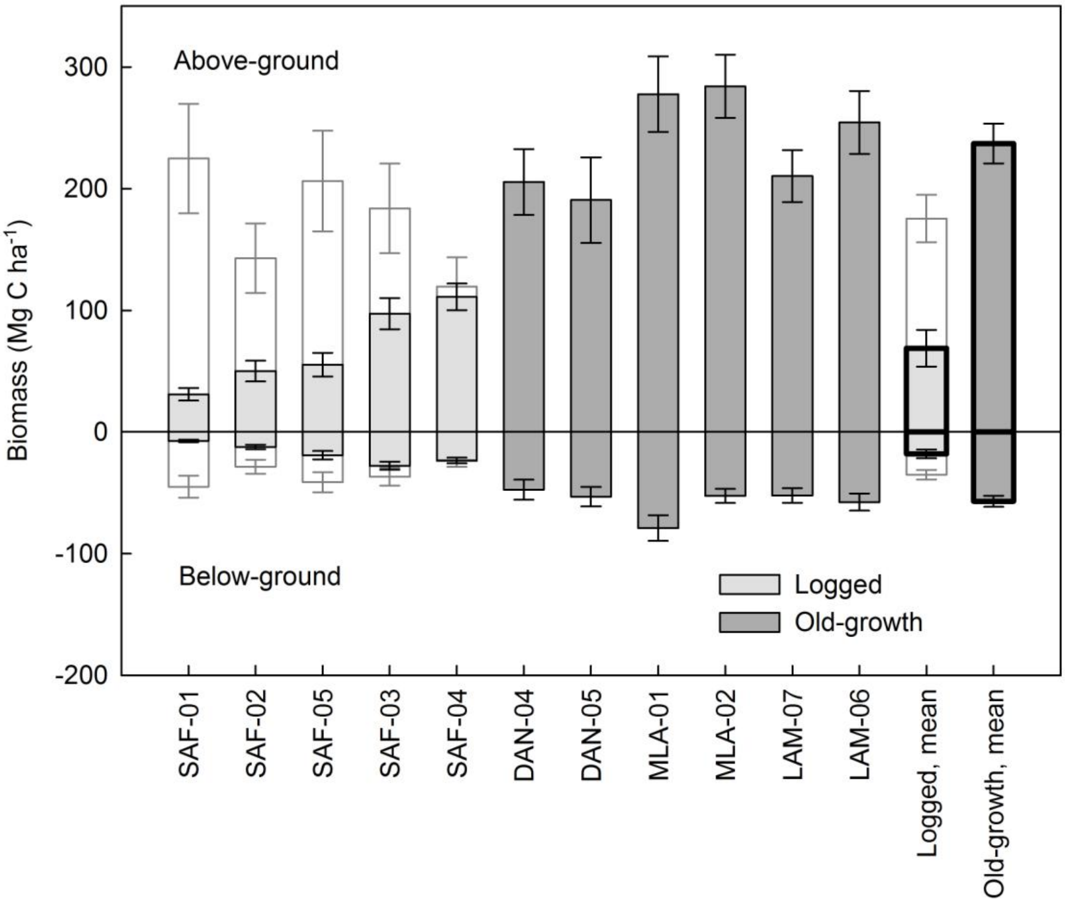
Figure 6. a) Canopy, **b)** woody, **c)** fine root and **d)** total net primary productivity (NPP) as a function of basal area of stems >10 cm diameter in logged and old-growth forest. The lines are cubic regression spline smoothers from general additive models with ± 95% confidence bands. The inward and outward rugs on the x axes denote the distribution of the basal area data in logged and old-growth forest, respectively. To see the figure with data points overlaid, see Fig. S5.

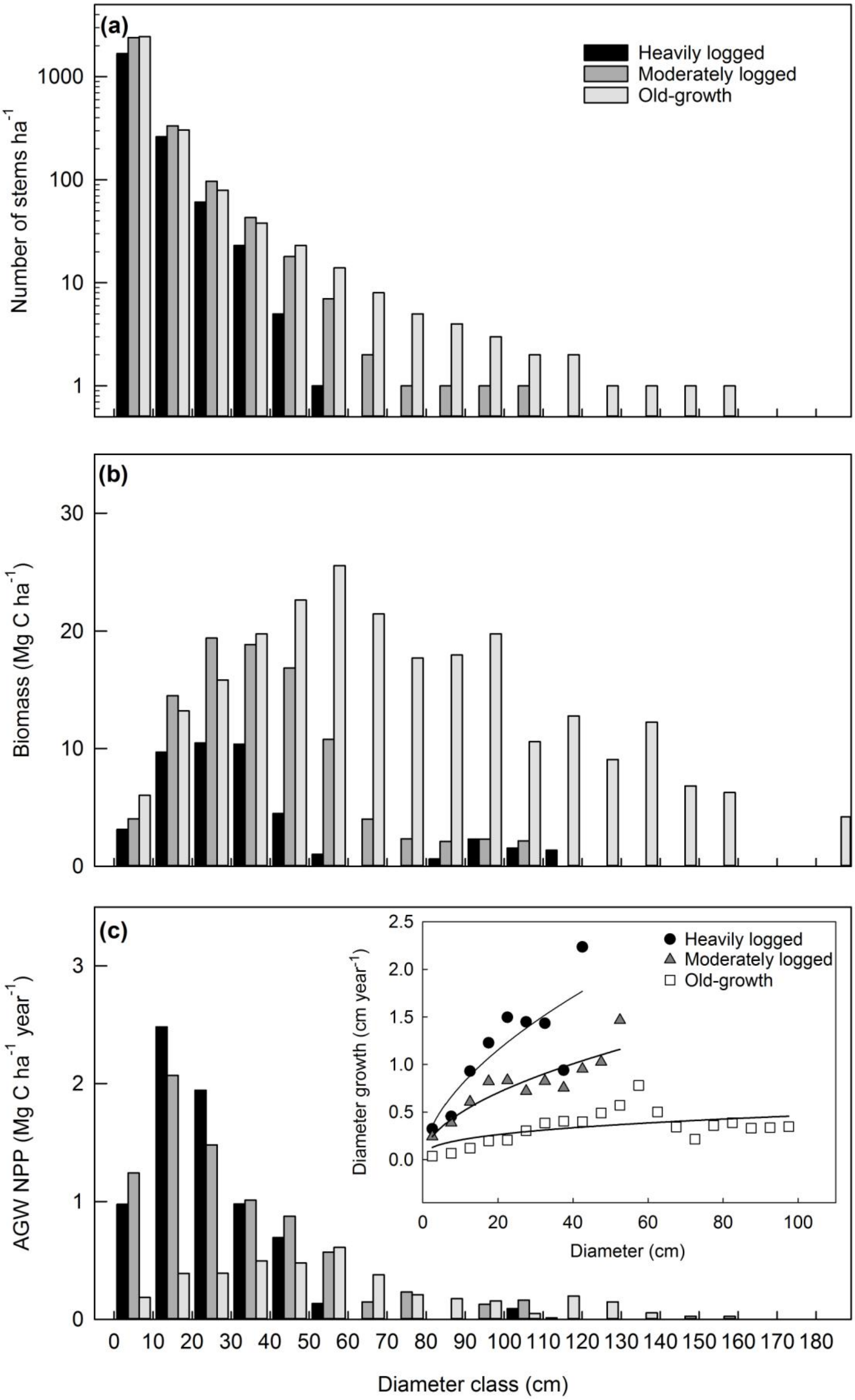
Figure 7. The percentage change in net primary productivity (NPP) in logged forest, compared with old-growth forest. The net effect is partitioned to productivity effect, allocation effect and structure effect, the sum of which equals the net effect. Error bars are ±1 SE.

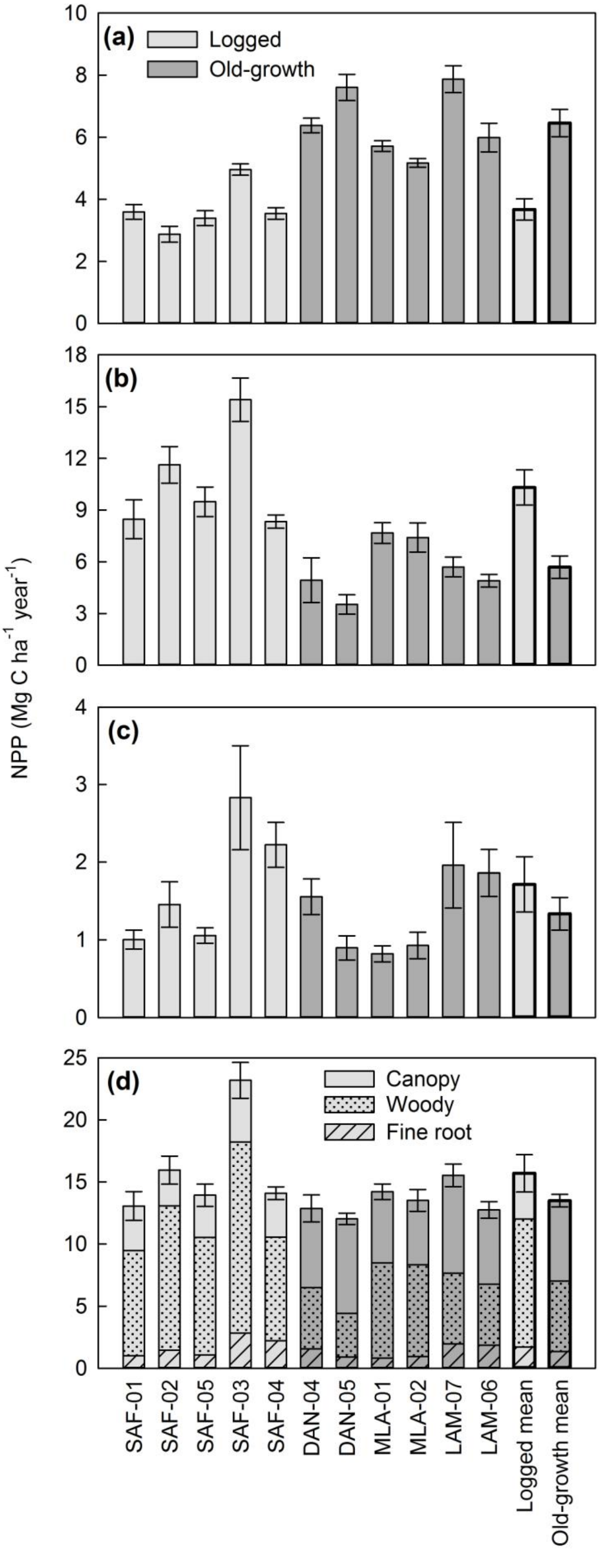
Table 1. Characteristics of the study plots. The logged plots are ranked from most to least intensively logged. Mean of individual subplots ±1 SE. Plot codes are as designated in the forestplots.net database

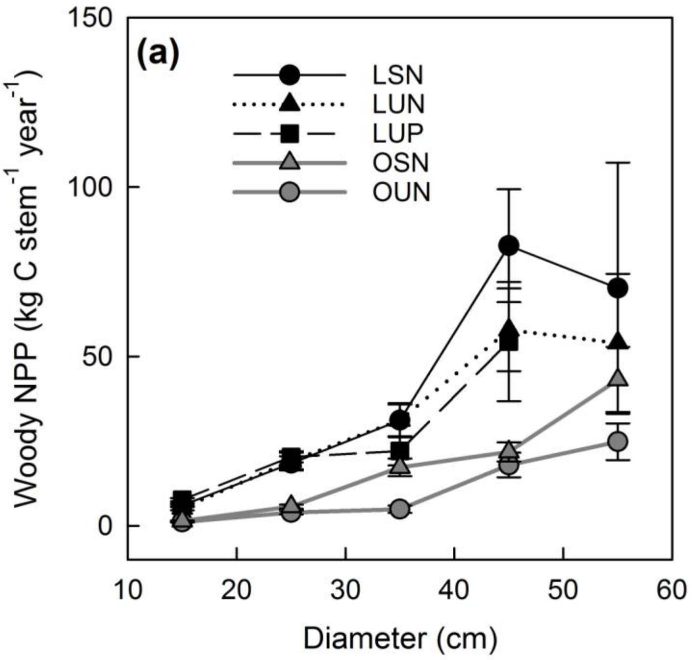
Plot name and plot code	Plot location	Disturbance	Soil type; topography	Basal area of trees >10 cm DBH (m^2 ha^{-1})	Mean canopy gap fraction (%)	Number of big trees (DBH >50 cm ha^{-1})	Pioneer tree species (% of basal area)
B South (SAF-01)	SAFE Project, Sabah (4.732°, 117.619°)	Heavily logged	Clay; mostly flat with a moderate slope on one edge	6.81 ±1.00	15.0 ±2.14	1	28.1 ±4.3
B North (SAF-02)	SAFE Project, Sabah (4.739°, 117.617°)	Heavily logged	Clay; undulating	11.1 ±1.81	13.4 ±1.51	0	57.2 ±5.8
Tower (SAF-05)	SAFE Project, Sabah (4.716°, 117.609°)	Heavily logged	Clay; undulating	13.9 ±1.70	12.2 ±2.07	6	34.5 ±6.6
E (SAF-03)	SAFE Project, Sabah (4.691°, 117.588°)	Moderately logged	Clay; steep slope	19.6 ±1.88	11.2 ±1.29	10	21.5 ±5.0
LF (SAF-04)	SAFE Project, Sabah (4.765°, 117.700°)	Moderately logged	Partly sandy loam, partly clay; flat	19.3 ±1.70	12.8 ±1.03	11	6.9 ±2.2
Danum Carbon 1 (DAN-04)	Danum Valley Conservation Area, Sabah (4.951°, 117.796°)	Old-growth	Clay; steep slope	32.0 ±3.30	10.5 ±1.00	34	0.7 ±1.0
Danum Carbon 2 (DAN-05)	Danum Valley Conservation Area, Sabah (4.953°, 117.793°)	Old-growth	Clay; flat	30.6 ±3.37	11.3 ±1.5	26	0.1 ±0.0

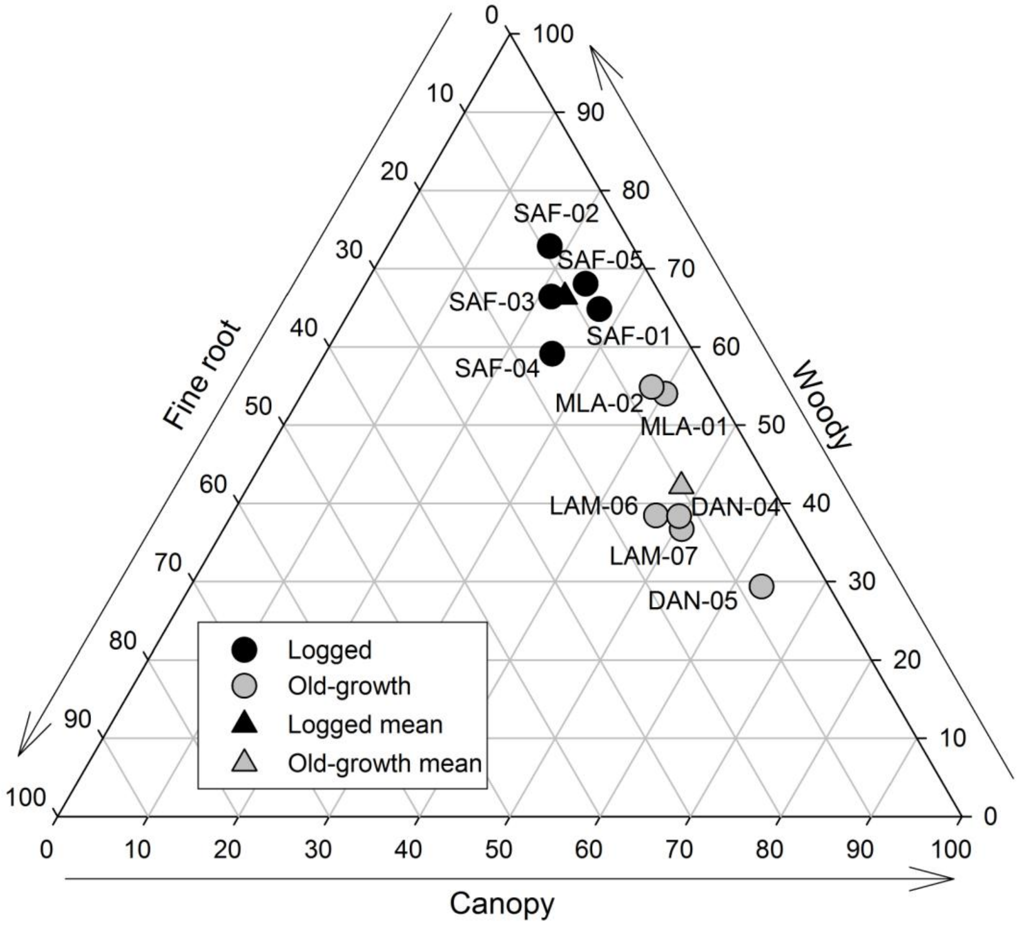
Belian (MLA-01)	Maliau Basin Conservation Area, Sabah (4.747°, 116.970°)	Old-growth	Clay; undulating	41.6 ±3.59	8.70 ±0.62	47	0.2 ±0.3
Seraya (MLA-02)	Maliau Basin Conservation Area, Sabah (4.754°, 116.950°)	Old-growth	Clay; moderate slope	34.7 ±2.74	7.04 ±0.55	56	1.7 ±1.2
Lambir Clay (LAM-07)	Lambir Hills National Park, Sarawak (4.183°, 114.022°)	Old-growth	Clay; valley	31.8 ±3.85	10.5 ±0.45	35	0.1 ±0.3
Lambir Sand (LAM-06)	Lambir Hills National Park, Sarawak (4.188°, 114.019°)	Old-growth	Sandy loam; undulating with steep slopes	41.1 ±2.45	9.52 ±0.22	46	0.3 ±1.0

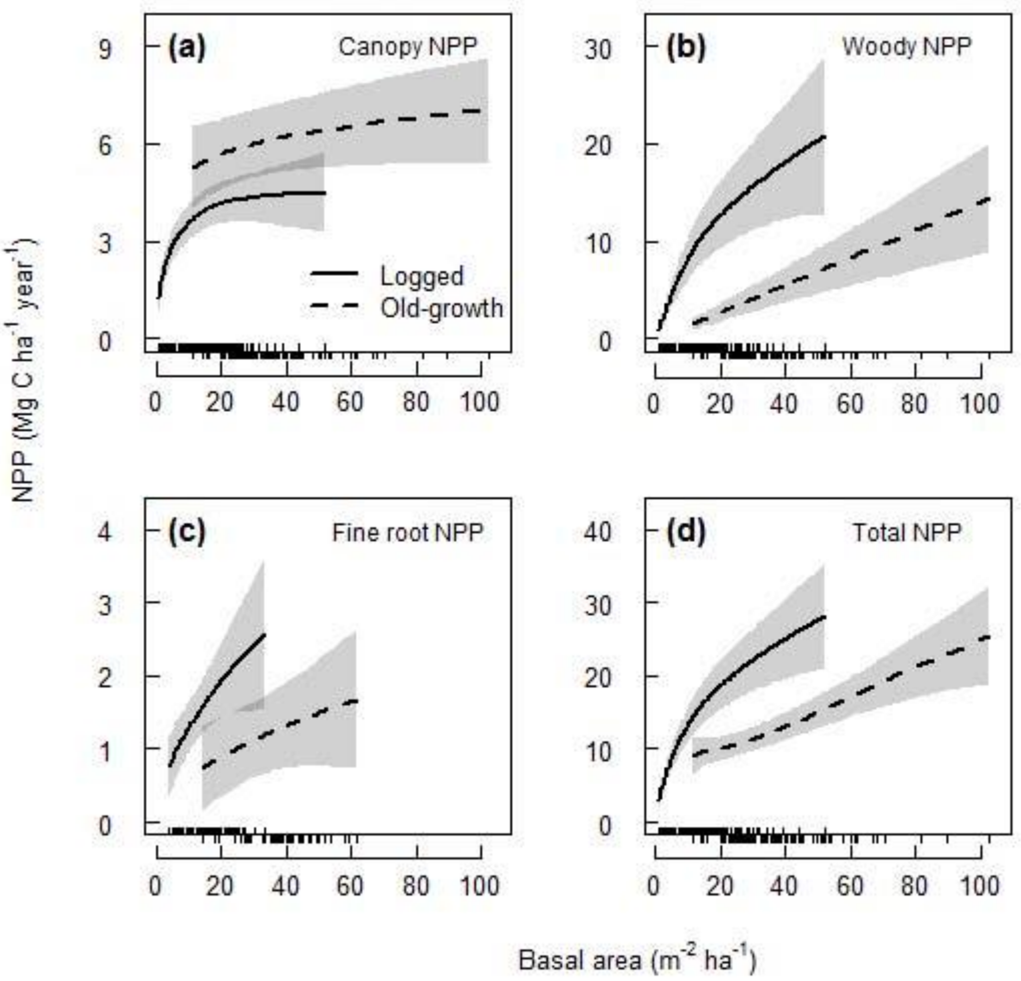

Above-ground
Below-ground
Biomass (Mg C ha^{-1})
300
200
100
0
-100
-200
Logged
Old-growth
SAF-01
SAF-02
SAF-05
SAF-03
SAF-04
DAN-04
DAN-05
MLA-01
MLA-02
LAM-07
LAM-06
Logged, mean
Old-growth, mean

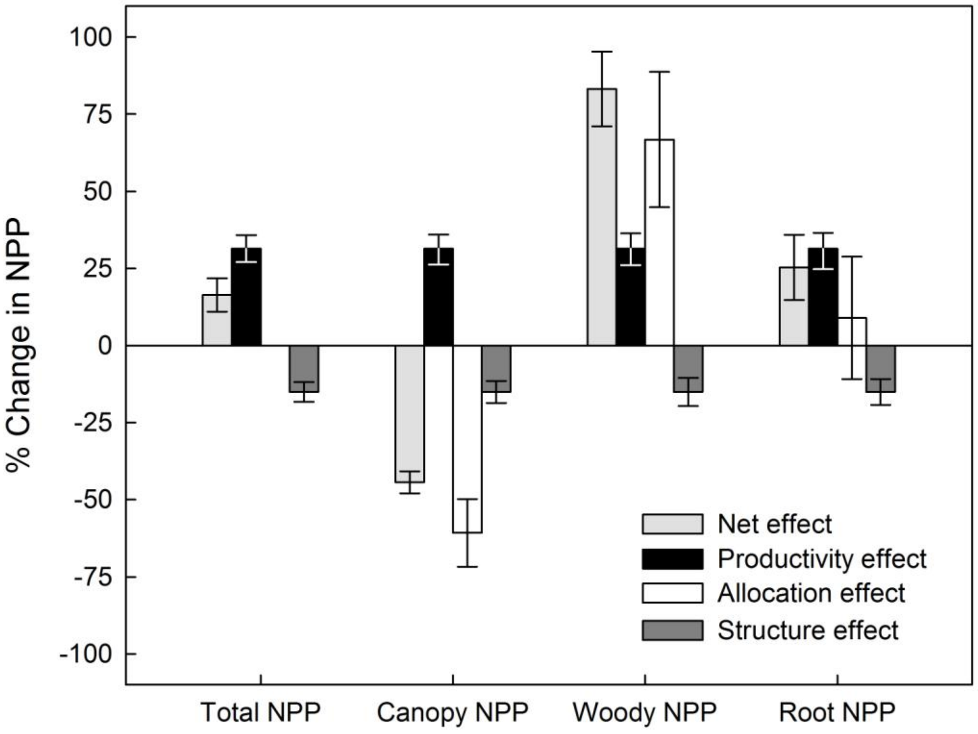

(a)
Heavily logged
Moderately logged
Old-growth
Number of stems ha^{-1}
1000
100
10
1
(b)
Biomass (Mg C ha^{-1})
30
20
10
0
(c)
AGW NPP (Mg C ha^{-1} year^{-1})
3
2
1
0
Heavily logged
Moderately logged
Old-growth
Diameter growth (cm year^{-1})
2.5
2.0
1.5
1.0
0.5
0.0
0
20
40
60
80
100
Diameter (cm)
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
Diameter class (cm)


(a)
Logged
Old-growth
(b)
(c)
(d)
Canopy
Woody
Fine root
NPP (Mg C ha^{-1} year^{-1})
10
8
6
4
2
0
18
15
12
9
6
3
0
4
3
2
1
0
25
20
15
10
5
0
SAF-01
SAF-02
SAF-05
SAF-03
SAF-04
DAN-04
DAN-05
MLA-01
MLA-02
LAM-07
LAM-06
Logged mean
Old-growth mean


(a)
LSN
LUN
LUP
OSN
OUN
Woody NPP (kg C stem^{-1} year^{-1})
0
50
100
150
10
20
30
40
50
60
Diameter (cm)


Fine root
Woody
Canopy
0
10
20
30
40
50
60
70
80
90
100
SAF-02
SAF-05
SAF-03
SAF-01
SAF-04
MLA-02
MLA-01
LAM-06
DAN-04
LAM-07
DAN-05
● Logged
○ Old-growth
▲ Logged mean
△ Old-growth mean


NPP (Mg C ha^{-1} year^{-1})
(a)
Canopy NPP
9
6
3
0
Logged
Old-growth
(b)
Woody NPP
30
20
10
0
(c)
Fine root NPP
4
3
2
1
0
(d)
Total NPP
40
30
20
10
0
0
20
40
60
80
100
Basal area (m^{-2} ha^{-1})


% Change in NPP
100
75
50
25
0
-25
-50
-75
-100
Total NPP
Canopy NPP
Woody NPP
Root NPP
Net effect
Productivity effect
Allocation effect
Structure effect