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The impact of logging on vertical canopy structure across a gradient of tropical forest degradation intensity in Borneo

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Abstract

1. Forest degradation through logging is pervasive throughout the world's tropical forests, leading to changes in the three-dimensional canopy structure that have profound consequences for wildlife, microclimate and ecosystem functioning. Quantifying these structural changes is fundamental to understanding the impact of degradation, but is challenging in dense, structurally complex forest canopies.
2. We exploit discrete-return airborne LiDAR surveys across a gradient of logging intensity in Sabah, Malaysian Borneo, and assess how selective logging has affected canopy structure (Plant Area Index, PAI, and its vertical distribution within the canopy).
3. LiDAR products compared well to independent, analogue models of canopy structure produced from detailed ground-based inventories undertaken in forest plots, demonstrating the potential for airborne LiDAR to quantify the structural impacts of forest degradation at landscape scale, even in some of the world's tallest and most structurally complex tropical forests.
4. PAI estimates across the plot network exhibited a strong linear relationship with stem basal area (R^2 = 0.95). After at least 11-14 years of recovery, PAI was ~28% lower in moderately logged plots and ~52% lower in heavily logged plots than in old-growth forest plots. These reductions in PAI are associated with near-complete lack of trees >30-m tall, which has not been fully compensated for by increasing plant area lower in the canopy. This structural change drives a marked reduction in the diversity of canopy environments, with the deep, dark understory conditions characteristic of old-growth forests far less prevalent in logged sites, with full canopy recovery likely to take decades.
5. *Synthesis and Applications.* Effective management and restoration of tropical forests requires detailed monitoring of the forest and its environment. These results demonstrate that airborne LiDAR can effectively map the canopy architecture of the complex tropical forests of Borneo, capturing the three-dimensional impact of degradation on canopy structure at landscape scales, therefore facilitating efforts to restore and conserve these ecosystems.

Keywords: Tropical rainforest, Borneo, canopy structure, lidar, logging, degradation, leaf area index

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1. Introduction

Degradation through logging is pervasive across the tropics, representing an important source of anthropogenic carbon emissions (Houghton, 2013) and land use change towards simplified production landscapes (e.g. oil palm, rubber, pulpwood and coffee) (Gaveau et al., 2016; Ordway & Asner, 2020). The island of Borneo hosts some of the largest tracts of intact forest within SE Asia, but the extent of forests here has declined by >30% from an estimated ~558,000 km^3 in 1973 (Gaveau et al., 2014), with the deforestation front sweeping inland from the low-lying coastal regions (Gaveau et al., 2014). By 2010, >45% of the remaining forest had been subject to some degree of selective logging, including ~60% of the forested area in Sabah (Gaveau et al., 2014).

The direct impact of logging-driven degradation is to change the structure of the forest canopy. Trees that previously dominated the main canopy are removed, while crowns of the residual trees are damaged by felling of neighbouring trees (Pfeifer et al., 2015). Canopy structure contributes towards the regulation of microclimate (Hardwick et al., 2015; Jucker, Hardwick, et al., 2018), light availability (Kumagai et al., 2001; Montgomery & Chazdon, 2001) and canopy biogeochemical fluxes (Ellsworth & Reich, 1993; Flack-Prain, Meir, Malhi, Smallman, & Williams, 2019). To a large extent, it also determines the environmental diversity within landscapes, and therefore biodiversity (e.g. Coomes, Kunstler, Canham, & Wright, 2009; Struebig et al., 2013; Deere et al., 2020). Degradation-driven shifts in canopy architecture therefore have the potential to propagate, affecting many different facets of ecosystem function.

To understand how forest structure responds to anthropogenic degradation – and therefore the wider impacts of degradation on tropical forests – it is critical to quantify the vertical distribution of foliage in the canopy. Foliar density is commonly quantified using Leaf Area Index (LAI, m^2 m^{-2}), defined as the total (one-sided) leaf area per unit ground surface area (Watson, 1947). The vertical distribution of LAI is characterised by the distribution Leaf Area Density, LAD (units: m^2 m^{-3}). The closely related Plant Area Index (PAI) and Plant Area Density (PAD) are estimated where methods do not distinguish between leaves and branches or trunks (Gower, Kucharik, & Norman, 1999). Harvesting vertical columns of foliage through the canopy is difficult and labour-intensive. Consequently, few direct estimates of vertical canopy structure in tropical forests exist (i.e. La Selva Biological Station: Costa Rica: Clark, Olivas, Oberbauer, Clark, & Ryan, 2008; Olivas et al., 2013; Tang et al., 2012; Adolfo Ducke Reserve, Brazil: Stark et al., 2012). Measurements from ground-level are largely indirect, using estimates of gap fraction that do not resolve the vertical distribution of vegetation (Bréda, 2003). It is also difficult to map degradation of canopies in dense tropical forests using optical or radar remote sensing techniques. Disturbances may be too small and regeneration of canopy cover too rapid to be captured by optical remote sensing (Milodowski, Mitchard, & Williams, 2017), which also do not resolve vertical variations within-canopy. The biomass and leaf area density supported by these forests exceed the signal saturation points of widely available radar products (Joshi et al., 2017).

Alternatively, canopy structure may be quantified at high spatial resolution using airborne remote sensing with LiDAR, which directly samples the three-dimensional structure of forest canopies at high spatial resolution (e.g. Stark et al., 2012; Tang et al., 2012; Vincent et al., 2017). To date, airborne LiDAR has not been applied to assess the impact of canopy degradation on the density and vertical structure of the hyper-diverse forests of Borneo. Airborne LiDAR-derived vertical canopy profiles have previously been used to investigate shifts in canopy structure driven by logging and regeneration in Costa Rica (Tang et al., 2012), finding that the PAI of secondary forests recovered to old-growth levels within 20 years. Other studies have examined the degradation driven by fires in Amazonian forests on the canopy profile (Almeida et al., 2016; Brando et al., 2019). However, the structural impact of degradation – and hence its wider environmental impact – is likely to be strongly dependent on the local context, including original old-growth canopy structure, and logging practices, which vary according to regulations and management decisions (Hosonuma et al., 2012). The dearth of studies documenting the basic structural impacts of degradation therefore represents a critical knowledge gap that undermines our ability to assess the resilience of these forests to future change (Mitchard, 2018).

We investigate the impact of degradation, through selective logging, on the canopy PAD profiles of eight 1-ha plots located in Sabah, Malaysian Borneo. These plots span a gradient of logging intensity, from undisturbed, old-growth forest to a series of degraded forest plots subject to different levels of logging (Both et al., 2019; Riutta et al., 2018). Logging predated the LiDAR survey by at least 11-14 years (Pfeifer et al., 2015). The LiDAR survey therefore provides a temporal snapshot of recovery following differing logging intensities. In addition, detailed field inventories of canopy architecture at the sites enable the development of independent models of canopy structure for cross-comparison, in the absence of harvested profiles for a true validation. This evaluation is important. To date, validation of LiDAR-derived tropical canopy profiles against vertically harvested profiles has been limited to two sites: one site in the Amazon, using discrete-return LiDAR (Stark et al., 2012), and one site in Costa Rica, using full-waveform LiDAR (Tang et al., 2012). Together, the gradient in logging intensity and detailed field surveys present a unique opportunity to assess the ability of airborne LiDAR to detect canopy structural changes associated with degradation in structurally complex tropical forests. Specifically, we address the following questions:

1) How does the canopy structure of degraded forests, logged at various intensities, differ from old-growth forests, characterised by the Plant Area Index (PAI), and its vertical distribution (PAD) within the canopy?
2) How do the observed differences in PAI compare against classic structural attributes such as basal area?
3) What are the implications of these structural changes for the diversity of canopy environments within logged forests, compared to old-growth systems?

2. Materials and Methods

For a more detailed description of the methods, please refer to the supplement.

2.1. Field Sites

Our study sites are located in the state of Sabah, Malaysian Borneo (Figure 1), comprising eight 1-ha plots (part of the Global Ecosystems Monitoring (GEM) network (Marthews et al., 2014)) (Table 1). Each plot spans one hactare, comprising a regular lattice of 25 0.04-ha (20-m x 20-m) subplots. Four plots are located in undisturbed old-growth forest: two within the Maliau Basin Conservation Area

(MLA-01, and MLA-02), two within the Danum Valley Conservation area inside the Danum 50 ha CTFS-ForestGEO plot (DAN-04 and DAN-05). The remaining four plots are located within logged forest fragments in the Kalabakan Forest Reserve. All three regions were originally within a connected tract of lowland dipterocarp rainforest.

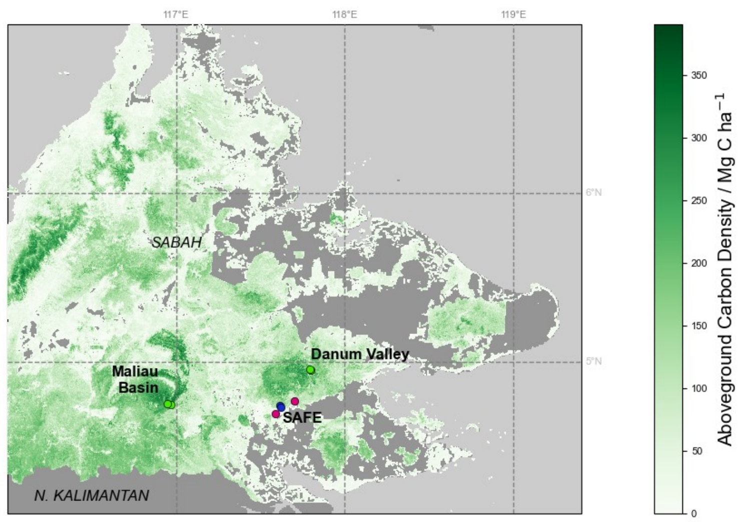

Figure 1 Map of northern Borneo, indicating the locations of the field sites. The plotted Aboveground Carbon Density (ACD) is from the Sabah-wide map published by Asner et al. (2018). Mangroves and plantations have been masked.

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The logged forest fragments have been subject to varying intensities of selective logging (Ewers et al., 2011). Two plots (SAF-03 and SAF-04) have been selectively logged twice ("moderately logged"). Two plots (SAF-01, SAF-02) have been subject to four rounds of selective logging ("heavily logged"). The first round of logging occurred in the mid-1970s, with an estimated 114 m^3 ha^{-1} was removed under a modified uniform system (Struebig et al., 2013). Subsequent rounds took place during the 1990s and early 2000s, during which an additional 37 m^3 ha^{-1} of timber was removed at moderately logged sites. Lifting of restrictions at heavily logged sites resulted in further rounds of logging, removing a cumulative total of ~66 m^3 ha^{-1} (Struebig et al., 2013). Thus the last date of logging predated the LiDAR survey by 11-14 years (Pfeifer et al., 2015). The normal protocol of 60-year rotations was not followed, as the area had been set aside for conversion to oil palm plantation between 2015-2017 (Ewers et al., 2011), although the oil palm was never planted.

Table 1. Summary characteristics for the 1-ha plots on which this study is based.

GEM plot code (SAFE site names)	**Location**	**Latitude (N) / Longitude (E)**	**Forest Type**	**Basal Area*** / m^2 ha^{-1}	**Max. canopy height**** / m	**LiDAR pulse density** / pulses m^{-2} mean (min, max)
MLA-01 Maliau Belian	Maliau Basin Conservation Area	4.747 / 116.951	Old-growth	41.6 ± 3.6	70.0	24.5 (9.0/34.6)
MLA-02 Maliau Seraya	Maliau Basin Conservation Area	4.737 / 116.951	Old-growth	34.7 ± 2.7	68.7	22.9 (14.8/34.2)
DAN-04 Danum Carbon 1	Danum Valley Conservation Area	4.953 / 117.795	Old-growth	32.0 ± 3.2	58.4	3.3 (2.7/4.1)
DAN-05 Danum Carbon 2	Danum Valley Conservation Area	4.958 / 117.795	Old-growth	30.6 ± 3.4	62.5	9.5 (5.2/18.6)
SAF-03 Fragment E	SAFE landscape, Kalabakan Forest Reserve	4.690 / 117.586	Moderately logged	19.6 ± 1.9	48.6	32.9 (26.7/51.0)
SAF-04 Fragment LF	SAFE landscape, Kalabakan Forest Reserve	4.765 / 117.702	Moderately logged	19.3 ± 1.7	33.0	19.6 (16.4/26.0)
SAF-02 Fragment B North	SAFE landscape, Kalabakan Forest Reserve	4.744 / 117.618	Heavily logged	11.1 ± 1.8	29.5	34.8 (22.3/49.7)
SAF-01 Fragment B South	SAFE landscape, Kalabakan Forest Reserve	4.729 / 117.618	Heavily logged	6.81 ± 1.0	28.5	39.5 (26.6/55.6)

**Basal area for all trees with DBH ≥ 10 cm (Riutta et al., 2018)*
*** 99^{th} percentile of LiDAR first return heights.*

2.2. Field estimation of vertical canopy structure

In each plot, the positions and heights of all trees with a stem diameter at breast height (DBH) ≥ 10 cm were mapped using ground-based Field-Map technology (IFER, Ltd., Jílové u Prahy, Czech Republic). We mapped individual tree crowns by measuring 5-30 spatial positions, representing the boundary of a crown projected onto the horizontal plane. Crown projections were smoothed using the "smooth contour line" feature of Field-Map software v.11.

We use the canopy inventory survey to derive estimates of vertical canopy structure independent of the LiDAR-based methods. Simple canopy volume models are clearly a simplification of true canopy structure. For example, tropical trees in the understory have been found to have deeper crowns than their counterparts in the upper canopy (Montgomery & Chazdon, 2001; Kohyama, Suzuki, Partomihardjo, Yamada, & Kubo, 2003). Nevertheless, field-based canopy crown models provide a useful and independent estimate for validation purposes where direct observations are not available, and have previously been used to help validate LiDAR-based structural metrics (Coops et al., 2007; Knapp, Fischer, & Huth, 2018). For each plot we simulated a forest of ellipsoid model crowns, based on field-measured heights and crown areas, and crown depths determined using a regional allometric scaling relationship derived from the BAAD database (Falster et al., 2015). For comparison with the LiDAR canopy profiles, leaf area was assumed to be uniformly distributed within the crowns (e.g. Knapp et al., 2018); contributions from the trunks were ignored. To account for the predictive uncertainty associated with the allometric relationships, we used a Monte Carlo approach, producing 100 crown models for each plot.

2.3. LiDAR-estimation of canopy structure

NERC's Airborne Research Facility (ARF) undertook an airborne LiDAR survey in November 2014, using a Leica ALS50-II LiDAR sensor on-board a Dornier 228-201 (flight elevation: 1400–2400 m.a.s.l., depending on the site; flight speed:120–140 knots). The average density of the resultant point clouds varied between sites due to differing levels of flight line overlap (Table 1). We classified the points into ground and non-ground returns using LAStools (rapidlasso GmbH, Gilching, Germany) and normalised return heights to height-above-ground.

To quantify PAD distributions from airborne discrete LiDAR data, we use a variant of the 1D Beer-Lambert approximation for light propagation through a turbid medium (MacArthur & Horn, 1969; Stark et al., 2012). Beer-Lambert models have been widely applied to estimate canopy PAD profiles from using both full-waveform (e.g. Tang et al., 2012) and discrete-return LiDAR (e.g. Stark et al., 2012). The resultant profiles have been validated against directly harvested foliage profiles in tropical forests in both the Brazilian Amazon (Stark et al., 2012) and Costa Rica (Tang et al., 2012).

The basic premise of the Beer-Lambert approximation is that for a laterally homogeneous canopy, with vertical distribution of plant density PAD(z), where z is the depth into the canopy from its top, the PAD for a given layer of thickness $\Delta z = |z_i - z_{i-1}|$ can be estimated based on the vertical column of LiDAR returns:

$$PAD = \frac{1}{\kappa \Delta z} ln\left(\frac{\sum_{z=0}^{z=z_{i-1}} w_i}{\sum_{z=0}^{z=z_i} w_i}\right) \qquad (1),$$

where w_i represents the points, weighted by the number of returns associated with their respective LiDAR pulse (e.g. Armston et al., 2013); κ is a correction factor accounting for canopy characteristics, such as clumping of vegetation within the canopy (Ni-Meister, Jupp, & Dubayah, 2001), and the leaf angle distribution (Detto, Asner, Muller-Landau, & Sonnentag, 2015). The number of returns entering the top of a canopy layer determines the numerator in the log-term; the number of returns penetrating into underlying layers defines the denominator. We use a layer thickness, Δz, of 1-m. We do not account for the azimuth of the returns.

We lack direct estimates of PAI for calibration of κ. However, Schneider et al. (2019) have published vertical profiles of PAI for an old-growth dipterocarp-dominated stand at Lambir Hills, also in Borneo based on a combination of ground-based and tower-mounted terrestrial lidar, with a cumulative PAI above 2-m of ~8.4 m^2m^{-2}. As the forest at Lambir Hills is similar in character to the old-growth forests in Maliau Basin and Danum Valley (Riutta et al., 2018), we assume a value of κ (0.50) that results in a mean estimated PAI for our old-growth plots that matches this value. This assumption means the reported PAI estimates carry additional uncertainty, and complicate interpretation of absolute PAI values against other studies. However, for a given model, we anticipate that the relative changes observed across the degradation gradient are more robustly comparable.

We provide a sensitivity analysis of the LiDAR metrics to pulse density and spatial resolution in the supplement.

2.4. Comparison against inventory-based crown volume distributions

To compare the similarity of the LiDAR-derived PAD profiles against the crown volume distributions derived from the field inventory we employ a simple profile overlap test. The individual 1-ha PAD and crown volume profiles are normalised by dividing through by the total plot PAI and crown volume respectively. We calculate profile overlap based on the percentage overlap between the two profiles. In the absence of harvested foliage profiles for validation, this approach provides a simple test of agreement between independent approaches to estimate the vertical distribution of vegetation in the canopy, noting that there is significant uncertainty attached to the field-based distributions.

2.5. Assessing the diversity of canopy environments

To assess the diversity of canopy environments across the degradation gradient, we use the canopy Shannon Index, which has previously been used to relate the canopy structural diversity to tropical forest dynamics (Stark et al., 2012). The Shannon Index increases with the number of canopy layers, and as PAD is distributed more evenly between layers:

$$Shannon\ Index = \sum_{i=1}^{N} PAD_i ln(PAD_i) \quad (2).$$

3. Results

3.1. LiDAR-derived PAI and vertical PAD distributions

LiDAR-estimated PAI is substantially lower in forest plots degraded by logging compared to reference old-growth plots (Table 2). The gradient in degradation intensity is marked by a trend of decreasing PAI as logging intensity increases, following a linear relationship with basal area ($R^2 = 0.95$; Figure 2). In Maliau Basin, PAI reached 8.7 $m^2\ m^{-2}$, with similar PAI measured in the other old-growth plots. PAI declined by 28% and 52% in moderately and heavily logged forests respectively, compared to the mean old-growth forest PAI.

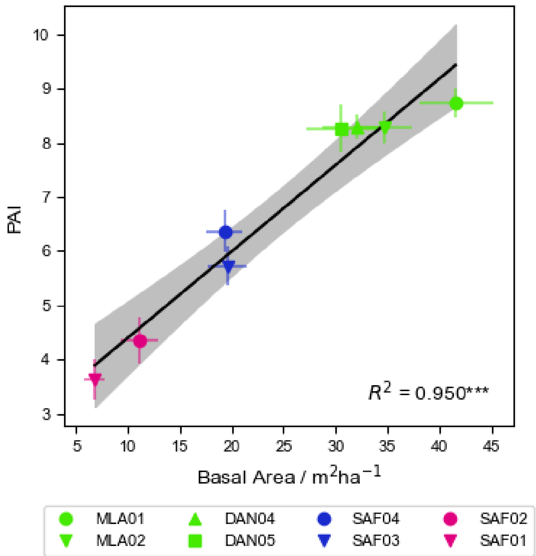

Figure 2. Comparison of the LiDAR-estimated PAI and plot basal area (basal area data from Riutta et al (2018)). Points indicate 1-ha means of 0.04 ha subplots, plotted with standard errors. Colours indicate degradation intensity: green – old-growth; blue – moderately logged; magenta – heavily logged.

Table 2. Summary of PAI estimates across the degradation gradient. Profile overlap represents the percentage overlap between normalised crown volume profiles and LiDAR PAD profiles.

Plot	**Forest Type**	**Crown Volume / m^3 ha^{-1}**	**LiDAR-based PAI / $m^2 m^{-2}$**	**Profile overlap / %**
		Mean ± S.D. (100 iterations)	Mean + S Err (assuming $\kappa = 0.44$)	
MLA-01	Old-growth	14.9 ± 1.0	8.7 ± 0.3	84.3
MLA-02	Old-growth	12.7 ± 0.5	8.3 ± 0.3	81.0
DAN-04	Old-growth	10.0 ± 0.6	8.3 ± 0.2	80.7
DAN-05	Old-growth	11.6 ± 1.0	8.3 ± 0.4	76.1
SAF-03	Moderately logged	4.8 ± 0.2	5.7 ± 0.4	86.9
SAF-04	Moderately logged	8.9 ± 0.3	6.4 ± 0.4	87.2
SAF-02	Heavily logged	4.0 ± 0.1	4.3 ± 0.4	83.5
SAF-01	Heavily logged	3.5 ± 0.2	3.6 ± 0.4	79.5

Vertical PAD profiles also revealed striking structural changes in the canopy across the degradation gradient. Old-growth forest plots were characterised by structurally complex canopies, stretching to 70-m in height. In contrast, there was an almost complete loss of canopy material >30-40-m in moderately logged plots (SAF-03, SAF-04), and >20-30-m in heavily logged plots (SAF-01, SAF-02) (Figure 3; equivalent plots for DAN-04 and DAN-05 presented in Figure S1). Across all forest plots, PAD is distributed throughout the canopy, but highest in the mid-lower canopy (<30-m height). PAD contrasted strongly with the distribution of the original point clouds (Figure 3), reflecting the increased probability of interception of LiDAR pulses higher in the canopy.

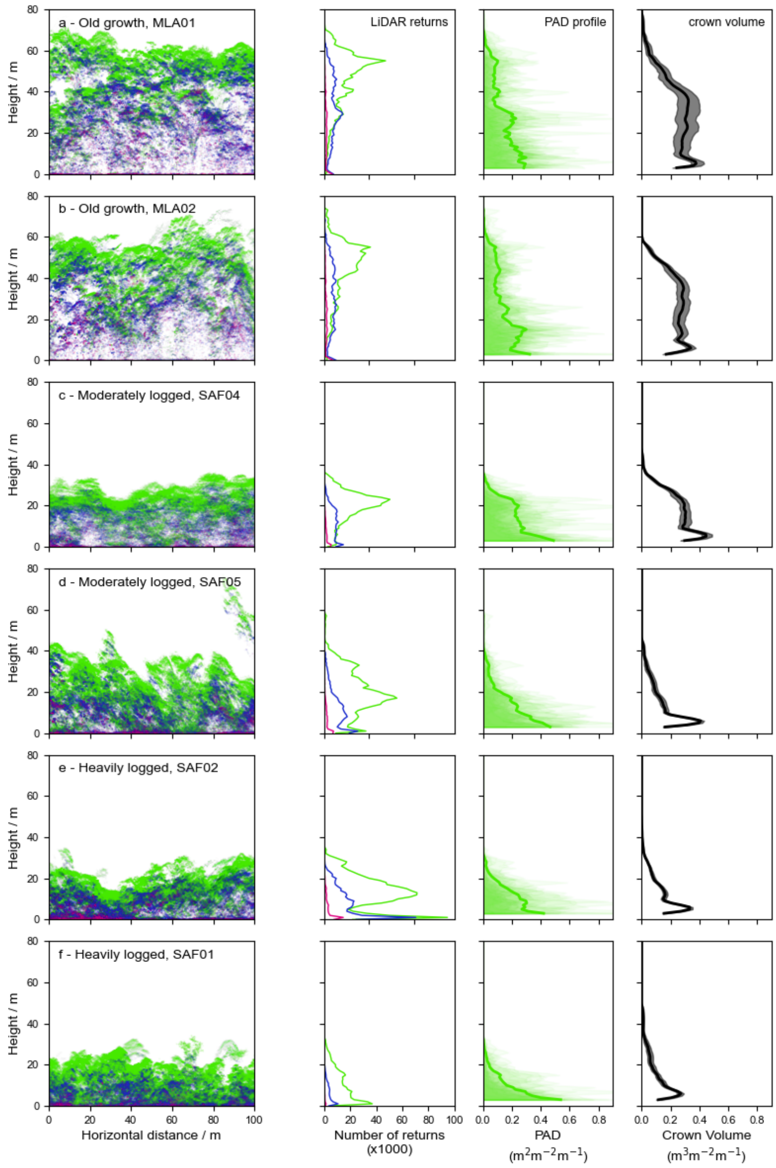

Figure 3. Point clouds and vertical canopy profiles for six of the 1-ha plots illustrating changes in vertical canopy structure across the degradation gradient. From left to right: LiDAR point cloud coloured according to return number, k (first returns – green, second returns – blue, third returns – magenta); vertical profile of LiDAR returns by return number, k; Plant Area Density (PAD) distributions modelled from the LiDAR; crown volume profiles (mean ± 95% confidence interval) estimated from field measurements. For the PAD profiles, thick lines represent 1-ha averages of 0.04-ha subplot profiles, subplots are plotted as semi-transparent histograms, giving an indication of structural variability.

3.2. Cross-comparison of LiDAR-estimated PAD profiles with field-based canopy models

Aggregated crown volume estimates across the degradation gradient ranged from ~3.5 m^3 m^{-2} in the most heavily logged plots to >10-$m^3 m^{-2}$ in the old-growth plots. Canopy volumes corresponded closely with LiDAR-based PAI estimates (R^2 = 0.89; Table 2). Vertical crown volume distributions mirrored the first-order patterns observed in the LiDAR-derived PAD distributions, with the loss of crown volume >30-40-m in the moderately logged plots, and further declines in crown volume >20-30-m for heavily logged plots (Figure 3). The morphology of the 1-ha crown volume distributions was similar to the LiDAR-derived PAD profiles at heavily logged and moderately logged plots (Profile Overlap >76%; Table 2). While differences were greater at old-growth plots, crown volume was distributed throughout the vertical profile, and highest in the mid- and lower canopy, consistent with the LiDAR estimates.

3.3. Shifts in the diversity of canopy environments

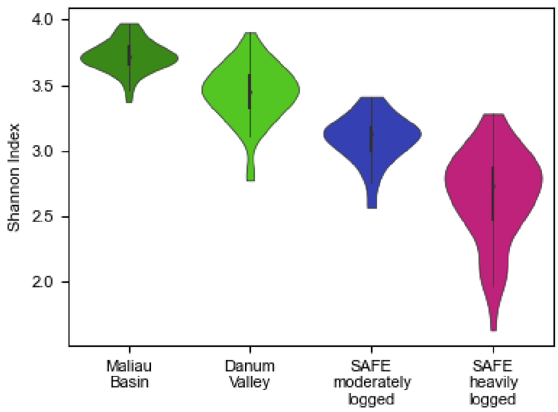

Figure 4. Changing canopy complexity across the degradation gradient at SAFE, as measured using the Shannon Index.

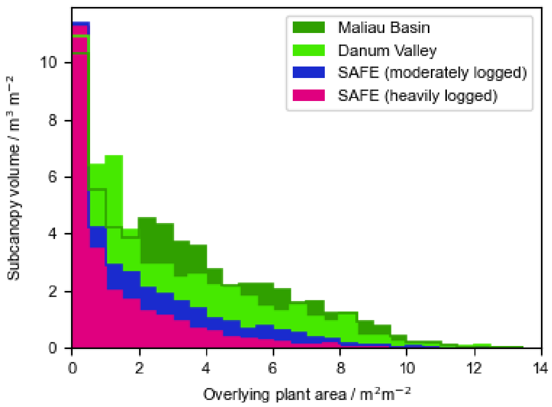

Figure 5. Comparison of the distribution of sub-canopy volume with varying cumulative overlying plant area, highlighting the decline in the length of the light gradient within the canopy as logging intensity increases..

Shannon Index distributions show that the diversity of canopy environments is diminished in logged forest, relative to old-growth forest (Figure 4). To a large part, this is driven by lower overall canopy height, and loss of associated structure above ~30-m, limiting the number of sub-canopy environments. The difference in the availability of sub-canopy environments across the degradation gradient is illustrated by considering the variation in sub-canopy volume as a function of cumulative overlying PAD (Figure 5). Recasting the canopy profiles like this reveals both logged forest and old-growth forest have similar canopy volumes at their surfaces (i.e. little overlying vegetation), where light is abundant. In contrast, there is divergence in the availability of understory environments. Old-growth forest is characterised by deep, shaded understories, with two-three times greater sub-canopy volumes than logged forests for a given level of overlying canopy PAD; understory volumes are most greatly reduced in heavily logged forests.

4. Discussion

4.1. Canopy structure in Borneo's old-growth forest

Old-growth forest plots within the Maliau Basin and Danum Valley Conservation Areas were characterised by high vegetation densities (PAI >8, assuming $\kappa = 0.50$), with the tallest trees reaching >70-m, overtopping a dense understory <~30-m. Profiles retrieved for the old-growth plots in Maliau

Basin and Danum Valley show significant variation both within and between plots (Figures 4, S6); however, they all share the common feature of gradually increasing PAD with canopy profile depth, and notable increases in understory PAD (below 20-30-m). This general pattern is consistent with canopy profiles published at another old-growth forest site in Western Borneo based on a combination of terrestrial LiDAR surveys undertaken at ground level and above the canopy (from a tower) (Lambir Hills; Schneider et al., 2019). Our PAD profiles do not discriminate leaves from woody vegetation (branches, twigs, trunks), which may contribute to around ~20% of the total PAI in tropical forests (Olivas et al., 2013), and will contribute particularly to increased PAD estimates in the understory (Schneider et al., 2019).

Our analysis in Borneo contrasts with canopy profiles in old-growth forest elsewhere in Equatorial regions. Canopy PAD profiles reported for old-growth forests in Central Amazonia (direct harvest and discrete return LiDAR; Stark et al., 2012), Costa Rica (direct harvest: Clark et al., 2008; full-waveform LiDAR: Tang et al., 2012), and French Guiana (3D inversion of small-footprint waveform LiDAR; Vincent et al., 2017), often exhibit closed canopies with peaks in PAD at ~25-30-m, and differing levels of understory density. Across these Neotropical sites, canopy heights are limited to between 30- and 50-m, thus foliage density is distributed along a shorter vertical dimension compared to Bornean old-growth forests. Variability in old-growth canopy structure may limit the extent to which we can translate the ecological impacts of degradation from one region to another.

4.2. Logging intensity drives first-order changes in canopy structure

Logging practices in Borneo typically involve removal of the largest trees (Slik et al., 2013). This logging strategy results in a steep decline in the abundance of large-basal area trees relative to smaller sized stems (Riutta et al., 2018). The impact of this logging strategy on canopy structure is striking. PAI drops as a function of logging intensity, and is >50% lower at the most heavily logged sites relative to the average for pristine old-growth forest (Figure 2). The tallest cohort of trees, contributing PAD above ~30-m height, is virtually absent from logged plots, an effect that has persisted more than a decade after the final round of logging. We know the impact of logging on canopy structure extends beyond the trees removed; felling frequently causes substantial collateral damage to surrounding trees (Pfeifer et al., 2015). There is also a significant shift in allocation of productivity to stem-wood production at the expense of canopy allocation in the logged forest plots (Riutta et al., 2018). However, our results indicate that the removal of large trees appears to be the principal mechanism driving the first-order changes in PAD distributions. Full recovery to pre-disturbance canopy structure will therefore likely take decades (Cannon, Peart, Leighton, & Kartawinata, 1994), requiring reestablishment of the largest stems. Importantly, this loss of PAD from the mid-upper canopy has not yet been compensated by a similar increase in understory PAD (at least above the 2-m threshold employed in this study). We caveat this conclusion with the uncertainty attached to lower canopy PAD estimates, which are particularly pronounced for the old-growth sites (see supplement). The consequences of this loss of foliage from the canopy include reduced shade and buffering of sub-canopy microclimate (Hardwick et al., 2015; Jucker, Hardwick, et al., 2018), and lower productivity (Riutta et al., 2018).

The picture emerging from our logged plots in Borneo is one of slow canopy recovery. These plots provide a snapshot of forest recovery following two to four rounds of selective logging, 11-14 years after logging finished (Pfeifer et al., 2015; Riutta et al., 2018). Neither PAI, vertical profiles, nor structural diversity, have recovered in this period. This contrasts against relatively rapid rates of recovery of PAI observed at La Selva, Costa Rica (Tang et al., 2012). The forest at La Selva comprises a mixture of old-growth, selectively logged forests (>30 years post-logging (Clark et al., 2004)) and secondary forest recovering from clear-felling. Using full-waveform airborne LiDAR to map PAD profiles and PAI, Tang et al. (2012) found the PAI of selectively logged forests were close to old-growth values (within 10%), although direct comparisons are complicated by differences in the time since logging ceased. However, the secondary forest chronosequence suggests swift recovery rates: median PAI in young secondary forests at La Selva (age 6-17 years) was ~40% lower than old-growth forest, but returned close to old-growth values within ~20 years of clear-felling (Tang et al., 2012). Differences in recovery rates may reflect the differences in old-growth forest structure (e.g. height of dominant species), but also regional differences in logging practices and intensity (Hosonuma et al., 2012). Further exploration of factors driving differential recovery rates is critical to understanding the long-term impacts of logging, and the resilience of degraded tropical forests.

4.3. Logging generates decades-long shifts in available sub-canopy environments

Logging results in a significant contraction in the length of the light gradient and diversity of canopy environments (Figures 4, 5). In particular, the absence of a deep, shaded understory represents a fundamental difference between logged and old-growth forest. The shifts in canopy structure observed here are intuitive and consistent with a model of canopy dynamics whereby: following disturbance, a thicket of light-demanding vegetation becomes established, from which pioneer trees, such as *Macaranga spp*., emerge through rapid vertical growth, combining with remnant trees to form a new canopy (Slik, Verburg, & Kessler, 2002). As light availability is reduced, the density of light-demanding vegetation in the understory declines, and although shade-tolerant trees may be present, as recruits or pre-disturbance remnants, growth is slower (Nicotra, Chazdon, & Iriarte, 1999), occurring sporadically in response to new canopy openings, while the canopy continues to stretch upwards (Farrior, Bohlman, Hubbell, & Pacala, 2016). The absence of extensive deeply shaded understorey environments in logged forests (Figure 5) may limit habitat availability for specialists of these low light conditions (Deere et al., 2020). Our findings suggest that restoration of old-growth structure is only complete once PAD has recovered. Recovery involves vertical packing of the understory with species that can survive and grow even in the deepest shade (Kabakoff & Chazdon, 1996), and establishment of tall emergent trees. Based on the timescale of recovery at this snapshot (at least 11-14 years), full recovery of canopy diversity at logged sites is likely to take several decades.

4.4. Implications for remote sensing of degradation in tropical forests

The relative changes in PAI observed (Figure 2) are over three times greater than those suggested by previous estimates of PAI across the degradation gradient at SAFE, estimated using 5-m resolution RapidEye imagery calibrated against PAI estimates from hemispherical photographs (Pfeifer et al., 2016). Pfeifer et al. (2016) suggest a more moderate decline of ~15% across the degradation gradient. This result may reflect saturation of PAI estimates in hemispherical photographs in tropical forests (Vincent et al., 2017), reducing the apparent impact of degradation on PAI. The close, linear correspondence between LiDAR-estimated PAI and basal area across the gradient highlights LiDAR's value for studies assessing the environmental impacts of degradation in dense tropical forests. Given the close relationship between basal area and standing carbon stocks, PAI-based basal area models may facilitate efforts to map Aboveground Carbon Density (Asner & Mascaro, 2014; Jucker, Asner, et al., 2018).

4.5. Management implications

Selective logging is pervasive through many of the world's tropical forests (Asner et al., 2005; Gaveau et al., 2014). The impact of the attendant degradation is spatially heterogeneous and of varying intensity (Berry, Phillips, Ong, & Hamer, 2008). Given that canopy structure underpins many aspects of ecosystem function (e.g. energy balance, photosynthesis, transpiration) and is a key determinant of habitat diversity, effective management of these forests requires detailed knowledge of how canopy structure varies in space and time (Struebig et al., 2013). We demonstrate that canopy profiles derived from airborne LiDAR capture the structural impacts of degradation at high resolution and accuracy. Importantly, LiDAR products enable an assessment of three-dimensional and sub-canopy variation in foliage density that will improve understanding of local variations in microclimate (Hardwick et al., 2015), light environment (Kumagai et al., 2001; Montgomery & Chazdon, 2001), productivity (Riutta et al., 2018), and the way that different plant and animal species make use of these forest environments (Deere et al., 2020). This study highlights the role of LiDAR, through mapping of the full canopy profile of plant area density, to delineate areas of forest that promote positive ecosystem functions, such as biodiversity retention, at landscape-scale. LiDAR mapping therefore has clear potential to help prioritise regions for conservation and restoration, and to maximise the benefits of such interventions (Deere et al., 2020).

5. Conclusions

We used airborne LiDAR to quantify canopy architecture adjustments associated with logging and at least 11-14 years of recovery in Borneo's ultra-complex tropical forest. We found a decline in PAI of ~28% in sites logged twice, and ~52% at sites logged four times, relative to old-growth forest. This sharp decline is associated with the near-complete loss of PAD above ~30-m, with further reductions in PAD above 10-15 m at high logging intensities. One impact of these structural changes is a drop in the diversity of canopy environments, in particular, the loss of a deep, shaded understory. These results are consistent with shifts in allocation away from foliage and into stems in logged forests (Riutta et al., 2018), and suggest that full recovery of foliage density, and its vertical distribution, are likely to take decades, leaving a long-lived legacy of logging in recovering forests in Borneo.

PAI estimates across the eight plots exhibited a strong linear relationship with independent measurements of basal area (R^2 = 0.95), highlighting the value of LiDAR to quantify degradation impacts in dense, complex tropical forests and improve estimates of aboveground carbon stocks (Asner & Mascaro, 2014; Jucker, Asner, et al., 2018). The sensitivity of LiDAR-based PAD distributions to logging-driven changes in canopy structure will facilitate landscape-level descriptions of forest condition in high-biomass tropical forests. LiDAR mapping can therefore facilitate management of these forests by helping prioritise conservation and restoration efforts in a manner that maximises the benefits to ecosystem services (Deere et al., 2020). The dominant drivers of degradation (timber logging, fuelwood extraction, fire) vary from region to region (Hosonuma et al., 2012), with potentially distinct impacts on canopy structure (e.g. Tang et al., 2012; Almeida et al., 2016; Brando et al., 2019). Future studies should expand the use of airborne LiDAR across a wider range of environmental settings to understand the detectability and impact of natural and human disturbance on canopy structure, and the consequent effects on wider ecosystem functions.

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~~Finally, we are very grateful for the comments from the Associate Editor and two anonymous reviewers.~~

~~Source code~~Data Availability Statement

Source code (python): https://github.com/DTMilodowski/LiDAR_canopy_structure_JAppEcol

Authors' contributions

DTM & MW designed the research, with input from DAC, TJ and TS; DTM conducted the analysis; DAC and TJ provided the LiDAR point cloud data; TR and DFRPB provided the stem inventories; MS and JK undertook the ground-based canopy surveys; YAT, MW, DAC, RME, YM and DFRPB organized the wider research initiative; DTM wrote the paper, with input from MW and TS and contributions from all co-authors.

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