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Landscape-scale changes in forest canopy structure across a partially logged tropical peat swamp

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Abstract

Forest canopy structure is strongly influenced by environmental factors and disturbance, and in turn influences key ecosystem processes including productivity, evapotranspiration and habitat availability. In tropical forests increasingly modified by human activities, the interplaying effects of environmental factors and disturbance legacies on forest canopy structure across landscapes are practically unexplored. We used high-fidelity airborne laser scanning (ALS) data to measure the canopy of old-growth and selectively logged peat swamp forest across a peat dome in Central Kalimantan, Indonesia, and quantified how canopy structure metrics varied with peat depth and under logging. Several million canopy gaps in different height cross-sections of the canopy were measured in 100 plots of 1 km^2 spanning the peat dome, allowing us to describe canopy structure with seven metrics. Old-growth forest became shorter and had simpler vertical canopy profiles on deeper peat, consistently with previous work linking deep peat to stunted tree growth. Gap Size Frequency Distributions (GSFDs) indicated fewer and smaller canopy gaps on the deeper peat (i.e. the scaling exponent of pareto functions increased from 1.76 to 3.76 with peat depth). Areas subjected to concessionary logging until 2000, and informal logging since then, had the same canopy top height as old-growth forest, indicating the persistence of some large trees, but mean canopy height was significantly reduced; the total area of canopy gaps increased and the GSFD scaling exponent was reduced. Logging effects were most evident on the deepest peat, where nutrient depletion and waterlogged conditions restrain tree growth and recovery. A tight relationship exists between canopy structure and the peat deph gradient within the old-growth tropical peat swamp. This relationship breaks down after selective logging, with canopy structural recovery being modulated by environmental conditions.

1 Introduction

The structure of forest canopies is a determinant of fundamental ecological processes governing productivity, nutrient cycling and turnover across tropical landscapes (Asner et al., 1998; Brokaw, 1982; Denslow, 1987; Kellner et al., 2009; Prescott, 2002; Vitousek and Denslow, 1986). For example, the interception and processing of light energy, and thus primary production, is not only affected by total leaf area but also by the layering, positioning and angle of leaves within the canopy (Asner et al., 1998; Ellsworth and Reich, 1993; Montgomery and Chazdon, 2001; Stark et al., 2012); evapotranspiration is also affected by the internal length of hydraulic pathways and roughness of the canopy (Costa and Foley, 1997; Malhi et al., 2002). Canopies provide habitats for epiphytes and a multitude of vertebrates and invertebrates, sometimes strongly dependent on micro-climate controlled by canopy structure (Bergen et al., 2009; Palminteri et al., 2012; Simonson et al., 2014; Vierling et al., 2008). Yet, the complex environmental drivers and spatial disturbance and recovery patterns leading to the observed variety of three-dimensional canopy organisation across landscapes remain poorly understood. In particular, in human-modified tropical forests the interplaying effects of environmental factors and disturbance legacies on forest canopy structure is practically unexplored. In the biodiversity hotspot of Borneo, more than 30 % of forest cover has been lost over the past 40 years, 46 % of remaining forests have been selectively logged (Gaveau et al., 2014), and further tracks of old-growth forest are earmarked for concessionary selective logging (Abood et al., 2014; Gaveau et al., 2014) and/or are affected by illegal logging (Curran et al., 2004; Englhart et al., 2013).

Borneo's tropical peat domes are natural laboratories for exploring changes in forest canopy structure with environment. Trees become shorter, narrower-stemmed, and more densely packed towards the centre of the domes (Anderson, 1961; Page et al., 1999; Whitmore, 1975), where there is a greater accumulation of peat, decreased nutrient availability (Page et al., 1999) and protracted substrate anoxia (Hoekman, 2007; Page et al., 1999; Wösten et al., 2008). Yet this current understanding of forest structural changes is based on a handful of field studies on a limited number of peat domes. Further progress is impeded by access to these remote locations, which are difficult to traverse by foot. While many ecological studies have focused on plant community shifts in environments gradually changing from moist and fertile to dry and nutrient-poor, the ecology of plant communities in increasingly waterlogged and nutrient-poor conditions are much less well studied (Coomes et al., 2013).

The influence of current and past human disturbance can no longer be ignored when studying environmental gradients across tropical forest landscapes. At least 20 % of tropical forests worldwide have been disturbed by selective logging for economically valuable timber (Asner et al., 2009). Logged forests have more open canopies (Asner et al., 2004b) and networks of logging routes (Andersen et al., 2013; Asner et al., 2004b; Gaveau et al., 2014) that allow continuous human access (Laurance et al., 2009) with negative impacts on biodiversity (Burivalova et al., 2014). Set against a backdrop of rapid deforestation (Hansen et al., 2013), selectively logged forests are increasingly important for conservation of biodiversity and ecosystem services (Edwards et al., 2014; Laurance and Edwards, 2014; Putz et al., 2012). It goes without saying that logging modifies canopy structure (Asner et al., 2004b), but satellite studies have had limited power in measuring logging effects as they lack information about the intricate three-dimensional structure of canopies. Airborne Laser Scanning (ALS) has opened new avenues for canopy research, as it provides high-fidelity information on canopy height, layers and the location of canopy gaps over entire landscapes (Drake et al., 2002; Dubayah et al., 2010; Kellner and Asner, 2009; Lefsky et al., 2002). However, ALS studies so far have largely focused on logging impacts on above-ground biomass alone (Andersen et al., 2013; d'Oliveira et al., 2012; Englhart et al., 2013; Kronseder et al., 2012; but see Weishampel et al., 2012).

We quantified landscape-scale changes in canopy structure across a peat swamp forest in Central Kalimantan, Indonesian Borneo using an ALS survey of 750 km^2 of forested swamp. As with most of Borneo, the study area has been impacted by logging. Our study addresses the following questions: (a) do other aspects of canopy structure co-vary with canopy height along the peat depth gradient, (b) how is canopy structure affected under the legacy of logging, and (c) is there evidence from canopy structure that recovery after logging is slowest on the deepest peats where growth is thought to be slowest?

2 Materials and methods

2.1 Study area and logging history

Our study site (ca. 750 km^2) is part of the Mawas Conservation Area (latitude −2.496 to −2.033° N, longitude 114.400 to 114.599° E), in the Indonesian province of Central Kalimantan (Fig. 1). The area covers a peat dome whose depth exceeds 12 m in places (KFCP, 2009) and is bordered by two rivers; the major Kapuas river in the west is adjacent to shallow peat and the smaller Mantangai river in the east cuts through deep peat and must have developed after the dome had formed. Rainfall is 3574 mm year^{-1} (mean from 1990–2011, source: FetchClimate) with a drier season in June–August.

Much of the area was selectively logged from ∼ 1980–2000 (Englhart et al., 2013; Gaveau et al., 2014), and an agricultural development project destroyed most of the southern section of the peatland between 1996 and 1999 (the Mega Rice Project, see Aldhous, 2004). Selective illegal timber extraction has persisted despite the area becoming legally protected for conservation ("hutan konservasi" and "hutan lindung") in 2003 (Englhart et al., 2013; Franke et al., 2012). Where logging records are unavailable, historical satellite imagery is often used to retrace the spread of major logging roads through time (Bryan et al., 2013; Gaveau et al., 2014). We mapped forest cover and human-made linear features corresponding to logging routes (i.e. light railways, trails and canals) using Landsat satellite imagery from 1994 to 2013 processed with ClasLite (Supplement). ClasLite renders sub-pixel fractional cover information that enabled the identification of logging routes characterised by high soil or dead vegetation fractions (Asner, 2009). Our local logging route map is similar to the Borneo-wide map of Gaveau et al. (2014), except that we have included additional logging routes resulting from illegal timber extraction after 2000. Forested areas within 500 m of a logging route were classified as selectively logged; the rationale being that mean canopy height maps (measured from ALS) indicate that logging is restricted to within 500 m of the routes (Supplement). Forest within 5 km of the Kapuas river was all classified as selectively logged as this area is used by local villagers (KFCP, 2009).

2.2 Canopy structure metrics from ALS

ALS data were collected during the dry season of 2011 (15 August to 14 October) with an Optech Orion M200 laser scanner at maximum half scan angle of 11° and with a calculated point density of 2.8 points m^{-2} (full flight specifications given in Table S2). TIFFS was used to filter the point cloud into ground and object returns (Chen et al., 2007) and to create a digital elevation model (DEM) from ground returns and a digital surface model (DSM) from first returns, both with 1 m pixel spatial resolution. Subtracting the DEM from the DSM resulted in a canopy height model (CHM). We used the vertical distribution of object returns in the ALS point cloud as a proxy for the vertical canopy profile (Asner et al., 2008, 2014). Object return heights were normalised against ground returns and we counted the number of returns within volumetric pixels (voxels) of 20 m × 20 m spatial and 1 m vertical resolution, from 0 m up to 40 m above-ground (maximum tree height). Subsequently, the number of returns in each voxel was divided by the sum of all returns in the same vertical column in order to yield a percentage of ALS returns within each slice of the vertical profile (Asner et al., 2008, 2014).

A total of 100 virtual plots of 1 km × 1 km were positioned throughout the research area (Fig. S4). Using the map of logged and unlogged areas (Fig. 1) we laid out plots in random stratified way: 53 plots were located in areas having undergone past concessionary and recent illegal selective logging (henceforth “logged”) and 47 plots in areas unaffected by main logging routes (henceforth “old-growth forest”). Within each plot, the following canopy height and canopy gap metrics were measured using the

ALS point cloud or the CHM (summarised in Table 1). All percentage maps and CHM manipulations and measures were done in ArcGIS 10.2 (ESRI, 2013).

2.2.1 Canopy height metrics

Within each plot, canopy height was extracted from 10 000 random pixels of the CHM, from which the canopy top height (99th quantile of height) and the standardised canopy height (mean height of CHM/99th quantile of height) were calculated. We identified the height of the voxel containing the highest proportion of ALS returns in the vertical frequency distributions of returns (see above, 0–1 m voxels excluded to avoid ground returns), as a proxy for maximum canopy volume (Asner et al., 2008, 2014). The canopy shape parameter is given by the ratio of the height of maximum canopy volume to canopy top height (Asner et al., 2014).

2.2.2 Canopy gap metrics

To identify canopy gaps, we took horizontal cross-sections of the CHM in 1 m increments from 2 up to 12 m above ground (following Kellner and Asner, 2009) and recorded agglomerations of empty pixels surrounded by full pixels. For example, agglomerates of empty pixels in the 5 m height layer indicate gaps extending to ≤ 5 m above ground (Fig. 2a and b). We thus extend the traditional definition of gaps as canopy openings reaching within 2 m of the ground (Brokaw, 1982) to include a wider array of disturbance types (recent tree fall and gaps with regrowth or re-sprouting up to crown-breaking or failure of large branches), but also gaps or openings that result from the spatial organisation of crowns in the canopy (West et al., 2009). We measured gap areas and calculated plot-level mean gap area and gap fraction as total area of gaps per km^2 for each CHM cross-section from 2–12 m. Gaps < 9 m^2 were excluded from further analysis to avoid minor openings between crowns. The upper CHM cross-section considered was 12 m (see Fig. S5 for explanation).

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2.2.3 Gap size frequency distribution

The gap size frequency distribution (GSFD) describes the relationship between the frequency and area of gaps (Fig. 2c–e). Most recent studies using ALS to detect canopy gaps have fitted a power law to describe the GSFD (Asner et al., 2013; Boyd et al., 2013; Espírito-Santo et al., 2014; Kellner and Asner, 2009; Kellner et al., 2011; Lobo and Dalling, 2013). In such a power law, the probability of gap size x is given by:

$$f(x) = cx^{-\alpha} \tag{1}$$

where c is a normalising term. The scaling parameter α quantifies the ratio of large to small gaps; the larger the value of α, the greater the frequency of small gaps. However, power-law functions are “fat-tailed” and tend to overestimate the occurrence of extremely large natural events (Schoenberg and Patel, 2012; see also Anfodillo et al., 2013). For this reason, we used a modified finite pareto function which behaves as a power law and transitions to a negative exponential function at very large gap sizes (Schoenberg and Patel, 2012):

$$f(x) = \left(\frac{\gamma}{x} + \frac{1}{\theta}\right) \cdot \left(\frac{x_{\min}}{x}\right)^{\gamma} \cdot \exp\left(\frac{x_{\min} - x}{\theta}\right), \tag{2}$$

where $x_{\min}$ is the lower truncation point (here $9\,\mathrm{m}^2$ is the smallest gap size considered), γ is the scaling exponent of the pareto function and θ governs the transition from power law to exponential decay. For gap sizes $x \ll \theta$, the function is predominantly power-law-like, whereas for $x \gg \theta$ it is predominantly exponential. It can be shown that $\gamma + 1$ is equivalent to α in Eq. (1) (Supplement), and so for ease of comparison, we will report $\alpha = \gamma + 1$ in this paper.

We used a hierarchical Bayesian model with random plot effect to estimate parameters γ and θ of Eq. (2) at plot-level, using the package RStan (Stan Development Team, 2014; see Supplement for code, priors and model convergence). We assumed normal prior distributions for γ and θ. The mean and 95 % confidence intervals of both parameters were extracted from the posterior distribution. This was repeated for all cross-sections of the CHM from 2–12 m above ground. In the cross-sections of 2–4 m above-ground, the estimated transition parameter θ was smaller than the truncation point $x_{\min}$ (9 m^2) in some plots. This suggested that the distribution was not well described by a power law and results would not be comparable to other studies, thus only results from cross-section at 5 m above-ground and upwards are reported for the GSFD parameters.

2.3 Explanatory variables used in regression models

2.3.1 Peat depth

Peat depth is the main environmental gradient determining forest physiognomy on peat domes (Page et al., 1999). Peat depth for plots was either derived from ground measurements or inferred from the relationships between peat depth and canopy top height ($R^2 = 0.77$) and between peat depth and distance to river ($R^2 = 0.59$) (Fig. S3). These relationships were tested on an independent data set of more than 300 peat depth measurements with associated ALS-derived canopy top height and distance to river measures (Supplement).

2.3.2 Logging

Logging was first included as a categorical variable (i.e. logged vs. unlogged) in regression models, and we also calculated a basic "logging pressure index" (LPI) for each logged plot. Since no official logging records were available, we approximated logging pressure by the density of logging routes detected in historical satellite images (see "Study area"). In the "new routes LPI", the density of logging routes was weighted according to the year those logging routes were first detected: old logging routes received a smaller weight than newer logging routes as we assumed that forest recovery was greater, and logging impact was smaller, along older routes. Different weightings were explored (Supplement). In contrast, the “cumulative LPI” weighted all roads equally. The “new routes” approach assumes that most logging disturbance is happening at logging frontiers while the “cumulative” approach assumes that all existing routes are used at any given time.

2.4 Statistical analyses

2.4.1 Plot matching

Because forest structure is generally closely related to peat depth in tropical peat swamp forests (Page et al., 1999), we needed to compare logged and old-growth plots found on similar peat depths to assess the impact of logging on canopy structure correctly. This motivated us to use a matching approach which selected and weighted plots in order to achieve logged and old-growth plots samples comparable in terms of peat depth. Matching on peat depth to the nearest meter was performed in R using the “*exact matching*” option in the MatchIt package (Ho et al., 2011), yielding a selection of 47 old-growth and 30 logged plots out of the 100 plots described in the “Study area” section. The 23 logged plots that were not matched were mostly on shallow peats around the edge of the peat dome, where hardly any old-growth forest remains. We further restricted the statistical comparison between logged and unlogged plots to peat depths from 6 to 12 m where both treatments were more evenly represented and outlying weight values were avoided; this left us with 45 old-growth and 18 logged matched plots. Since variable numbers of logged and old-growth plots were matched for a given peat depth, the matching algorithm provided weights to be used in weighted regressions. No comparison between old-growth and logged plots was possible on peats shallower than 6 m because those areas were dominated by logged forest only.

2.4.2 Generalized linear models

We tested the effect of peat depth and logging as explanatory variables of canopy height metrics (canopy top height, standardised canopy height, canopy shape) and gap metrics (mean gap area, gap fraction in all 2–12 m CHM cross-sections, and α, θ in cross-sections 5–12 m) as response variables using generalized linear models. Mean gap area was log-transformed prior to analysis, to improve homoscedasticity of the residuals. The standardised canopy height, the canopy shape and the gap fraction were logit-transformed as they were bound between 0 and 1 (Warton and Hui, 2011). All other analyses assumed normal distributions. Three alternative models were compared: M1 as a simple linear model containing peat depth only; M2 was M1 with an additive effect of logging as a treatment (yes, no), i.e. assuming a constant effect of logging along the peat dome; and M3 was M2 with an interaction effect between peat depth and logging, indicating that the effect of logging treatment is dependent on peat depth. Regressions were weighted by plot weights provided by the matching algorithm. We selected the best-supported models based on AICc, reporting either the model with smallest AICc or another simpler model with a difference in AICc < 2, a threshold below which alternative models are considered equally well supported (Burnham and Anderson, 2002). We fitted only M1 on plots with peat depths < 6 m where logged forest prevailed and no comparison between old-growth and logged forest could be done.

To test whether logging pressure had an effect on forest structure within logged regions of the forest, generalized linear models were fit to canopy structure metrics of logged plots, using peat depth and "logging pressure index" (LPI) as explanatory variables. Note that LPIs did not significantly co-vary with peat depth ($r = 0.05$–0.25).

3 Results

3.1 Canopy height and structure in old-growth forest along the peat dome

Along the whole peat depth gradient and in both old-growth and logged plots, canopy top height decreased by 1 m for each meter of added peat depth (Fig. 3a, Supplement). Canopy top height was not affected by logging, suggesting that some large trees (presumably of low commercial value) were left within the plots. The fact that canopy top height was unaffected by logging meant that we could infer peat depth from canopy top height in plots where this information was missing (Supplement).

Standardised canopy height, measured from the CHM, did not change along the peat depth gradient in old-growth forest (grey line, Fig. 3b) suggesting that mean canopy height decreased in parallel to canopy top height (Fig. 3a). The canopy shape parameter, derived from the complete ALS point cloud, increased with peat depth in old-growth forest (Fig. 3c) indicating that the main canopy volume came increasingly closer to the top of the canopy. Visual inspection of the vertical profiles (Fig. 3d) for old-growth forest indicated that this was mostly driven by a decrease in canopy top height and the loss of a small peak at 30 m above-ground likely formed by emergent trees.

Canopy gap metrics of old-growth forest also significantly changed along the peat depth gradient. Gap metrics in cross-sections around 8 m above-ground were the most responsive to peat depth and logging effects. The canopy vertical profiles (Fig. 3d) reveal that gaps at 8 m above-ground are clearly located below the bulk of the canopy volume and thus are more likely to have been created by tree mortality rather than just being open spaces between crowns. We hence use the 8 m cross-section to illustrate findings and give full details for all cross-sections in Tables S3 and S4. The mean gap size and gap fraction of old-growth forests decreased with increasing peat depth (grey lines in Fig. 4a and b) in the 8 m-height cross-section. The GSFD scaling coefficient (α) became larger with increasing peat depth, indicating an increasing proportion of small gaps (Fig. 4c). The GSFD transition parameter θ did not significantly decrease with peat depth in the 8 m cross-section although this was observed at lower cross-sections (Fig. 4d, Table S3). On average, 6 % of the total gap area was located above θ in the 8 m cross-section, giving support for the finite scaling distribution used here. Weak negative correlations were found between α and θ in cross-sections ≥ 6 m height (Pearson correlation coefficient $r = -0.25$ to -0.35); indicating that θ was greatest in sites containing large gaps. From cross-sections ≥ 9 m height, θ was not different from zero (Table S3) and the GSFD was described by a power law.

Canopy top height was also a good explanatory variable for canopy gap changes along the peat dome (recalling that peat depth is negatively related with canopy top height) and was linearly related to mean gap size (Fig. 5a, $R^2 = 0.82$, $p < 0.001$) and to α (Fig. 5b, $R^2 = 0.75$, $p < 0.001$) (Table S5).

3.2 Logging effects on canopy structure

Selective logging altered both canopy height and canopy gap sizes along the peat dome, especially for higher cross-sections (model M2 or M3 selected). As already described, logging did not influence canopy top height (Fig. 3a). However a marked decrease of standardised canopy height was observed (Fig. 3b), implying the removal of canopy trees in logged plots. Surprisingly though, similar effects were not apparent in canopy shape (Fig. 3c). In the 8 m cross-section, logged plots had larger gaps, a higher gap fraction and a higher proportion of large gaps (smaller α) (red lines, Fig. 4a–c). The transition parameter θ was not significantly larger in logged plots (Fig. 4d). Logging effects were usually observed in height cross-sections from 5 m, and with greater variance among plots with increasing height above-ground (Fig. S6 and Table S3).

Because of unequal effects on canopy top height and gaps, we no longer observed the tight relationships (marked decrease in R^2) among canopy top height, mean gap area (Fig. 5a, $R^2 = 0.28$, $p < 0.001$) and α (Fig. 5b, $R^2 = 0.38$, $p < 0.001$) which we found in old-growth forest (Table S5).

There was limited evidence that logging route density within logged areas had an influence on canopy structure. The logging pressure indexes (LPI) did not explain differences in standardised canopy height, canopy shape parameter, gap fraction, α or

θ in areas we had identified as logged. However, we found that the cumulative LPI increased mean gap size by $< 10\,\%$ in the 2 and 3 m cross-sections (Table S6). This indicates that heavier logging in areas with dense logging route networks increased the average size of gaps reaching to the ground irrespective of logging route age.

3.3 Recovery after logging is slowest on the deepest peats

Logging had a constant effect on standardised canopy height across the peat dome (Fig. 3b; model M2 selected), but had differential effects on canopy gap metrics except θ (Fig. 4a–c; model M3 selected). Significant interactions between logging and peat depth effects were detected for mean gap area, gap fraction and α in the 8 m cross-section. In all cases, canopy structure showed a greater logging effect when on deeper peat. In other words, the canopy of logged peat swamp forest on intermediate peat depth (6 m) had already recovered to structural characteristics similar to those of old-growth forest while logged forests on deep peat (12 m) exhibited a more strongly altered canopy structure (larger gaps in average, higher gap fraction, larger proportion of large gaps) relative to old-growth forest (Fig. 4a–c).

4 Discussion

Major changes in canopy structure across the tropical peat swamp forest landscape closely followed the peat depth gradient. The canopy of selectively logged forests remained open 11 years after concessionary logging had ended, although structural recovery depended strongly on peat depth. As such, the landscape-scale coordination between forest height and natural disturbance patterns was lost in selectively logged forests.

4.1 Forest height and canopy structure along the peat dome

We observed a strong decrease in canopy top height (from about 34 to 23 m) with peat depth, consistent with field observations (Anderson, 1961; Page et al., 1999; Whitmore, 1975) and ALS results from other Southeast Asian peat domes (Kronseder et al., 2012; Boehm, Liesenberg and Limin, 2013), although for unknown reasons the neighbouring Sebangau peat dome bears tall forest (45 m) on deep peat (Page et al., 1999). Tropical peat swamp forests exhibit limited height development in comparison to neighbouring lowland dipterocarp forests, where emergent trees typically reach up to 60 m in height (Ashton et al., 1992). The canopy vertical profile revealed that the canopy structure becomes simpler with increasing peat depth as the emergent layer is lost and the main canopy volume is increasingly allocated to the top of a shorter forest. Emergent trees are sometimes lost on nutrient-poorer soils (Whitmore, 1975; Kapos et al., 1990; Paoli et al., 2008 but see Ashton et al., 1992) and shallow rooting depth as a result of substrate waterlogging is likely to limit tree height development (Crawford et al., 2003). Similar patterns are observed in flooded vs. *terra firme* neotropical forest types (Asner et al., 2013; Boyd et al., 2013; Coomes and Grubb, 1996).

Recent applications of airborne laser scanning (ALS) have identified power-law GSFDs in the Neotropics (Asner et al., 2013, 2014; Boyd et al., 2013; Espírito-Santo et al., 2014; Kellner and Asner, 2009; Kellner et al., 2009; Lobo and Dalling, 2013) and Hawaii (Kellner and Asner, 2009; Kellner et al., 2011). Our analysis of an Indomalayan tropical peat swamp forest landscape finds a very wide range of scaling exponents α ranging from 1.66 to 3.76 across all old-growth sites and canopy cross-sections, following an inverted U-shaped pattern indicating high proportions of large gaps at low and high cross-sections (but see Kellner and Asner, 2009; Boyd et al., 2013). The largest α yet reported in the literature is found in short forest on deep peat, indicating that this forest type's gap regime is dominated by very small gaps and likely infrequent disturbance events. The large range of α values (range width of 2.1 vs. 0.2 to 1.8 in other studies; Asner et al., 2013; Boyd et al., 2013; Kellner and Asner, 2009; Kellner et al., 2011; Lobo and Dalling, 2013) across the peat dome may reflect a strong control of environmental gradients over forest dynamics. This aspect of peat swamp forest ecology deserves future scrutiny through the establishment of permanent plots (Lawson et al., 2014) and repeated ALS surveys.

Changes in the vertical forest structure along the peat dome were associated with a decrease in mean gap size, gap area fraction and the proportion of large gaps. We know of only limited evidence from three field-based studies (Bruenig and Droste, 1995; Kapos et al., 1990; Schaik and Mirmanto, 1985) and one ALS-based study (Kellner et al., 2011) reporting lower gap fractions and smaller average gap sizes in nutrient-poor soils than in higher fertility conditions. Several processes may contribute to the changing canopy gap patterns along the peat dome. First, smaller gap sizes may be due to a loss of large emergent trees on nutrient-poor substrate (Kapos et al., 1990; Paoli et al., 2008), as shorter trees will create smaller canopy openings when dying (Numata et al., 2006). Accordingly, we found a close link of mean gap size and α with canopy top height along the peat depth gradient (Fig. 6). Secondly, small proportions of large gaps (larger α) on deep peats might result from trees dying "on their feet" in low stature forest (Coomes and Grubb, 1996), while tall trees forming structured canopies on shallow peats are more likely to damage neighbouring trees when falling over due to natural mortality or exogenous disturbance factors such as wind or lightning (Bruenig and Droste, 1995; Kapos et al., 1990). Such large gaps are additionally more likely to experience post-disturbance contagion with higher mortality of exposed neighbouring trees through co-damage or stability loss (Jansen et al., 2008). Thirdly, we assume a functional component by which tropical peat swamp forests communities see a shift towards more conservative adaptations (Whitmore, 1975) leading to slow individual turnover on low-fertility substrate (Kellner et al., 2011). Functional and structural adaptations lead to different modes of gap formation on different soil types (Coomes and Grubb, 1996; Jans et al., 1993). A positive feedback loop is created since small gaps tend to be closed by shade-tolerant saplings or lateral regrowth, while larger

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openings are recolonized by short-lived pioneer and light-demanding species (Sist and Nguyen-Thé, 2002).

Environmental gradients are natural laboratories to explore environmental controls over forest structure using ALS. Changes in forest canopy structure along the peat depth gradient are similar to those observed along a substrate age gradient in Hawaii where nutrient limitation switches from N to P over time, with highest resource availability at intermediate soil ages (Kellner et al., 2011): along both gradients the forests are tallest where nutrients are most plentiful within the landscape, and the taller forests have more structured canopies (emergent layer and main canopy) and large canopy gaps. Canopy height decreases with altitude along an Amazon-to-Andes elevation gradient (Asner et al., 2014), but the changes in canopy structure are quite distinct from those observed in the peat swamp and soil chronosequence: the shorter forests here are sparse in trees, and dominated with a dense fern and bamboo understory, the latter having very open canopies with most canopy volume close to the ground and high proportions of large gaps. Combining ALS-derived forest structure measurements with ground data of major environmental drivers opens new avenues for researchers to explore processes at more ecologically meaningful scales than that allowed by plot studies

4.2 Persistent and uneven legacies of logging on peat swamp forest canopy structure

Anthropogenic disturbance events such as selective concessionary and illegal logging leave long-lasting legacies of altered dynamics, carbon stocks and species composition in tropical forests often visible more than 20 years after activities have stopped (Numata et al., 2006; Sist and Nguyen-Thé, 2002; Slik et al., 2002). Consistent with this, we detected pervasive alteration of forest canopy structure 11 years after selective concessionary logging had stopped and interestingly, recovery was modulated by environmental conditions along the peat dome.

Logged forests harboured an altered vertical structure and larger gaps, a higher gap fraction and lower α from about 6 m above ground relative to old-growth forest on similar peat depth. Canopy top height remained unaltered after selective logging probably because some tall low-value timber trees remain unharvested. Surprisingly, the relative vertical distribution of canopy volume was not affected either, but the standardised canopy height was reduced by tree removal under logging.

Canopy structure in logged sites did not generally relate to the "logging pressure index" (LPI), except that larger gaps close to the ground were found in areas with dense logging route networks. This effect did not vary with the age of logging routes which suggests that existing logging routes take long to recover structurally or continue to be used for illegal timber harvesting. Usually, canopy recovery depends strongly on time since logging and on logging intensity (Asner et al., 2004b, 2006; Sist et al., 1998). Logging infrastructure and routes, used here to infer the presence and timing of logging, might however not always be a good predictor of logging effect severity (Asner et al., 2004b). Subsequent ALS research should preferably be carried out in logging concessions where timing and intensity of logging are well documented (see e.g. Andersen et al., 2013; d'Oliveira et al., 2012). Since the logging pressure was relatively homogenous along the peat depth gradient and did not affect canopy structure, we can interpret observed differences in canopy gap patterns between logged and old-growth plots as mostly related to inherent differential forest recovery rates along the peat dome.

Canopy structural responses to selective logging were influenced by peat depth; a likely explanation is slower recovery rates of forests growing on nutrient-depleted and waterlogged substrates in the centre of peat domes. Gap metrics were most sensitive to differential recovery across the peat dome. In particular, a clear segregation in GSFD scaling exponent α was observed between old-growth and logged plots on deep peat; large differences in the scaling relationships of undisturbed vs. disturbed systems have previously been related to low resilience in disturbed systems (Kerkhoff and Enquist, 2007). Those forest communities adapted to extreme environmental conditions are unlikely to recover fast following logging because species might have conservative adaptations and grow slowly. Thus recolonization of canopy openings would be very slow.

5 Concluding remarks

The ability of ALS to measure gaps reaching down to different layers of the forest vertical profile provides unique information on canopy gaps at different recovery stages (Boyd et al., 2013; Espírito-Santo et al., 2014). Such gaps are hard to detect using optical satellite imagery as these data do not allow vertical penetration. For instance, Franke et al. (2012) report that canopy disturbance of peat swamp forest from selective logging and small logging trails became invisible in satellite images only a year after they were active, likely due to leaf cover rather than biomass recovery (Asner et al., 2004a).

The absence of pervasive logging damage close to the ground (2 to about 7 m above-ground) indicates that regrowth, either by saplings, resprouting of damaged trees or by lateral filling, has occurred to a certain degree across the studied peat swamp, which is positive news for conservation and rehabilitation endeavours in the area (BOS Foundation, 2008). Tropical peat swamp forests stabilize deep peat deposits beneath them (Moore et al., 2013) acting as globally important carbon stores whose conservation is key to climate change mitigation (Murdiyarso et al., 2010; Page et al., 2002, 2011). However, concessionary and illegal logging remain widespread (Miettinen et al., 2012; Abood et al., 2014; Gaveau et al., 2014). The links between forest disturbance and peat stability yet remain to be addressed. In any case, open canopies after logging lead to higher light penetration (Numata et al., 2006), drier and warmer understory conditions (Hardwick et al., 2015) making deadwood in logged forests more prone to fire (Siegert et al., 2001) – a major issue in tropical peatlands (Page et al., 2002). Our study demonstrates that ALS can provide improved assessments of logging legacies in different tropical forest types, underpinning effective and adapted management and conservation plans.

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References

Abood, S. A., Lee, J. S. H., Burivalova, Z., Garcia-Ulloa, J., and Koh, L. P.: Relative contributions of the logging, fiber, oil palm, and mining industries to forest loss in Indonesia, Conserv. Lett., 8, 58–67, 2014.

Aldhous, P.: Land remediation: Borneo is burning, Nature, 432, 144–146, 2004.

Andersen, H. E., Reutebuch, S. E., McGaughey, R. J., D'Oliveira, M. V. N., and Keller, M.: Monitoring selective logging in western Amazonia with repeat lidar flights, Remote Sens. Environ., 151, 157–165, 2013.

Anderson, J. A. R.: The Ecological Types of the Peat Swamp Forests of Sarawak and Brunei in Relation to their Silviculture, Ph.D. thesis, University of Edinburgh, Edinburgh, UK, 1961.

Anfodillo, T., Carrer, M., Simini, F., Popa, I., Banavar, J. R., and Maritan, A.: An allometry-based approach for understanding forest structure, predicting tree-size distribution and assessing the degree of disturbance, P. Roy. Soc. B-Biol. Sci., 280, 20122375, doi:10.1098/rspb.2012.2375, 2013.

Ashton, P. S., Hall, P., and Ashton, S.: Comparisons of structure among mixed dipterocarp of north-western forests Borneo, J. Ecol., 80, 459–481, 1992.

Asner, G. P.: Automated mapping of tropical deforestation and forest degradation: CLASlite, J. Appl. Remote Sens., 3, 033543, doi:10.1117/1.3223675, 2009.

Asner, G. P., Wessman, C. A., and Archer, S.: Scale dependence of absorption of photosynthetically active radiation in terrestrial ecosystems, Ecol. Appl., 8, 1003–1021, 1998.

Asner, G. P., Keller, M., Pereira, R. J., Zweede, J. C., and Silva, J. N. M.: Canopy damage and recovery after selective logging in Amazonia: field and satellite studies, Ecol. Appl., 14, 280–298, 2004a.

Asner, G. P., Keller, M., and Silva, J. N. M.: Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon, Global Chang. Biol., 10, 765–783, 2004b.

Asner, G. P., Broadbent, E. N., Oliveira, P. J. C., Keller, M., Knapp, D. E., and Silva, J. N. M.: Condition and fate of logged forests in the Brazilian Amazon., P. Natl. Acad. Sci. USA, 103, 12947–12950, 2006.

Asner, G. P., Hughes, R. F., Vitousek, P. M., Knapp, D. E., Kennedy-Bowdoin, T., Boardman, J., Martin, R. E., Eastwood, M., and Green, R. O.: Invasive plants transform the three-dimensional structure of rain forests., P. Natl. Acad. Sci. USA, 105, 4519–4523, 2008.

Asner, G. P., Rudel, T. K., Aide, T. M., Defries, R., and Emerson, R.: A contemporary assessment of change in humid tropical forests., Conserv. Biol., 23, 1386–1395, 2009.

Asner, G. P., Kellner, J. R., Kennedy-Bowdoin, T., Knapp, D. E., Anderson, C., and Martin, R. E.: Forest canopy gap distributions in the southern peruvian Amazon., PLoS One, 8, e60875, doi:10.1371/journal.pone.0060875 , 2013.

Asner, G. P., Anderson, C. B., Martin, R. E., Knapp, D. E., Tupayachi, R., Sinca, F., and Malhi, Y.: Landscape-scale changes in forest structure and functional traits along an Andes-to-Amazon elevation gradient, Biogeosciences, 11, 843–856, doi:10.5194/bg-11-843-2014, 2014.

Bergen, K. M., Goetz, S. J., Dubayah, R. O., Henebry, G. M., Hunsaker, C. T., Imhoff, M. L., Nelson, R. F., Parker, G. G., and Radeloff, V. C.: Remote sensing of vegetation 3-D structure for biodiversity and habitat: Review and implications for lidar and radar spaceborne missions, J. Geophys. Res., 114, G00E06, doi:10.1029/2008JG000883, 2009.

BOS Foundation: Brief Summary of Mawas Conservation Program Initiatives, available at: http://redd-database.iges.or.jp/redd/download/project?id=13 (last access: 13 July 2015), 2008.

Boyd, D. S., Hill, R. A., Hopkinson, C., and Baker, T. R.: Landscape-scale forest disturbance regimes in southern Peruvian Amazonia, Ecol. Appl., 23, 1588–1602, 2013.

Brokaw, N. V. L.: The definition of treefall gap and its effect on measures of forest dynamics, Biotropica, 14, 158–160, 1982.

Bruenig, E. F. and Droste, H. J.: Structure, dynamics, and management of rainforests on nutrient-deficient soils in Sarawak, in: Ecology, Conservation, and Management of Southeast Asian Rainforests, edited by: Primack, R. B. and Lovejoy, T. E., Yale University, New Haven and London, 41–53, 1995.

Bryan, J. E., Shearman, P. L., Asner, G. P., Knapp, D. E., Aoro, G., and Lokes, B.: Extreme differences in forest degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei, PLoS One, 8, e69679, doi:10.1371/journal.pone.0069679, 2013.

Burivalova, Z., Şekercioğlu, Ç. H., and Koh, L. P.: Thresholds of logging intensity to maintain tropical forest biodiversity, Curr. Biol., 24, 1893–1898, 2014.

Burnham, K. P. and Anderson, D. R.: Model Selection and Multimodel Inference, 2nd edn., SPRINGER, New York, 2002.

Chen, Q., Gong, P., Baldocchi, D., and Xie, G.: Filtering airborne laser scanning data with morphological methods, Photogramm. Eng. Rem. S., 73, 175–185, 2007.

Coomes, D. A. and Grubb, P. J.: Amazonian caatinga and related communities at La Esmeralda, Venezuela: forest structure, physiognomy and floristics, and control by soil factors, Vegetatio, 122, 167–191, 1996.

Coomes, D. A., Bentley, W. A., Tanentzap, A. J., and Burrows, L. E.: Soil drainage and phosphorus depletion contribute to retrogressive succession along a New Zealand chronosequence, Plant Soil, 367, 77–91, 2013.

Costa, M. H. and Foley, J. A.: Water balance of the Amazon Basin: dependence on vegetation cover and canopy conductance, J. Geophys. Res., 102, 23973–23989, 1997.

Crawford, R. M. M., Jeffree, C. E., and Rees, W. G.: Paludification and forest retreat in northern oceanic environments, Ann. Bot.-London, 91, 213–226, 2003.

Curran, L. M., Trigg, S. N., McDonald, A. K., Astiani, D., Hardiono, Y. M., Siregar, P., Caniago, I., and Kasischke, E.: Lowland forest loss in protected areas of Indonesian Borneo, Science, 303, 1000–1003, 2004.

d'Oliveira, M. V. N., Reutebuch, S. E., McGaughey, R. J., and Andersen, H. E.: Estimating forest biomass and identifying low-intensity logging areas using airborne scanning lidar in Antimary State Forest, Acre State, Western Brazilian Amazon, Remote Sens. Environ., 124, 479–491, 2012.

Denslow, J. S.: Tropical rainforest gaps and tree species diversity, Annu. Rev. Ecol. Syst., 18, 431–451, 1987.

Drake, J. B., Dubayah, R. O., Clark, D. B., Knox, R. G., Blair, J. B., Hofton, M. A., Chazdon, R. L., Weishampel, J. F., and Prince, S. D.: Estimation of tropical forest structural characteristics using large-footprint lidar, Remote Sens. Environ., 79, 305–319, 2002.

Dubayah, R. O., Sheldon, S. L., Clark, D. B., Hofton, M. A., Blair, J. B., Hurtt, G. C., and Chazdon, R. L.: Estimation of tropical forest height and biomass dynamics using lidar remote sensing at La Selva, Costa Rica, J. Geophys. Res., 115, 1–17, 2010.

Edwards, D. P., Tobias, J. A, Sheil, D., Meijaard, E., and Laurance, W. F.: Maintaining ecosystem function and services in logged tropical forests., Trends Ecol. Evol., 29, 511–520, 2014.

Ellsworth, D. S. and Reich, P. B.: Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest, Oecologia, 96, 169–178, 1993.

Englhart, S., Jubanski, J., and Siegert, F.: Quantifying dynamics in tropical peat swamp forest biomass with multi-temporal LiDAR datasets, Remote Sens., 5, 2368–2388, 2013.

Espírito-Santo, F. D. B., Gloor, M., Keller, M., Malhi, Y., Saatchi, S., Nelson, B., Junior, R. C. O., Pereira, C., Lloyd, J., Frolking, S., Palace, M., Shimabukuro, Y. E., Duarte, V., Mendoza, A. M., López-González, G., Baker, T. R., Feldpausch, T. R., Brienen, R. J. W., Asner, G. P., Boyd, D. S., and Phillips, O. L.: Size and frequency of natural forest disturbances and the Amazon forest carbon balance, Nat. Commun., 5, 3434, doi:10.1038/ncomms4434, 2014.

replace by ESRI 2013, ArcGIS Desktop: Release 10.2., Redlands, CA: Environmental Systems Research Institute, 2013.

FetchClimate: FetchClimate Explorer version 1.2 alpha, Microsoft Research, available at: http://fetchclimate2.cloudapp.net (last access: 13 July 2015), 2012.

Franke, J., Navratil, P., Keuck, V., Peterson, K., and Siegert, F.: Monitoring fire and selective logging activities in tropical peat swamp forests, IEEE J. Sel. Top. Appl., 5, 1811–1820, 2012.

Gaveau, D. L. A., Sloan, S., Molidena, E., Yaen, H., Sheil, D., Abram, N. K., Ancrenaz, M., Nasi, R., Quinones, M., Wielaard, N., and Meijaard, E.: Four decades of forest persistence, clearance and logging on Borneo, PLoS One, 9, e101654, doi:10.1371/journal.pone.0101654 , 2014.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., and Townshend, J. R. G.: High-resolution global maps of 21st-century forest cover change, Science, 342, 850–853, 2013.

Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., and Ewers, R. M.: The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives changes in microclimate, Agr. Forest Meteorol., 201, 187–195, 2015.

Ho, D. E., Imai, K., King, G., and Stuart, E. A.: MatchIt: nonparametric preprocessing for parametric causal inference, J. Stat. Softw., 42, 1–28, 2011.

Hoekman, D. H.: Satellite radar observation of tropical peat swamp forest as a tool for hydrological modelling and environmental protection, Aquat. Conserv., 17, 265–275, 2007.

Jans, L., Poorter, L., Rompaey, R. S. A. R. Van and Bongers, F.: Gaps and forest zones in tropical moist forest in Ivory Coast coast, Biotropica, 25, 258–269, 1993.

Jansen, P. A., Van der Meer, P. J., and Bongers, F.: Spatial contagiousness of canopy disturbance in tropical rain forest: an individual-tree-based test, Ecology, 89, 3490–3502, 2008.

Kapos, A. V., Pallant, E., Bien, A., and Freskos, S.: Gap frequencies in lowland rain forest sites on contrasting soils in Amazonian Ecuador, Biotropica, 22, 218–225, 1990.

Kellner, J. R. and Asner, G. P.: Convergent structural responses of tropical forests to diverse disturbance regimes, Ecol. Lett., 12, 887–897, 2009.

Kellner, J. R., Clark, D. B., and Hubbell, S. P.: Pervasive canopy dynamics produce short-term stability in a tropical rain forest landscape, Ecol. Lett., 12, 155–164, 2009.

Kellner, J. R., Asner, G. P., Vitousek, P. M., Tweiten, M. A., Hotchkiss, S., and Chadwick, O. A.: Dependence of forest structure and dynamics on substrate age and ecosystem development, Ecosystems, 14, 1156–1167, 2011.

Kerkhoff, A. J. and Enquist, B. J.: The implications of scaling approaches for understanding resilience and reorganization in ecosystems, Bioscience, 57, 489–499, 2007.

KFCP: Kalimantan Forests and Climate Partnership (KFCP), design document, available at: http://redd-database.iges.or.jp/redd/download/project;jsessionid=F5414B40A100A330B258A615F97995C8?id=57 (last access: 13 July 2015), 2009.

Kronseder, K., Ballhorn, U., Böhm, V., and Siegert, F.: Above ground biomass estimation across forest types at different degradation levels in Central Kalimantan using LiDAR data, Int. J. Appl. Earth Obs., 18, 37–48, 2012.

Laurance, W. and Edwards, D. P.: Saving logged tropical forests, Front. Ecol. Environ., 12, 147–147, 2014.

Laurance, W. F., Goosem, M., and Laurance, S. G. W.: Impacts of roads and linear clearings on tropical forests, Trends Ecol. Evol., 24, 659–669, 2009.

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Lefsky, M. A., Cohen, W. B., Parker, G. G., David, J., and Harding, D. J.: Lidar remote sensing for ecosystem studies, Bioscience, 52, 19–30, 2002.

Lobo, E. and Dalling, J. W.: Effects of topography, soil type and forest age on the frequency and size distribution of canopy gap disturbances in a tropical forest, Biogeosciences, 10, 6769–6781, doi:10.5194/bg-10-6769-2013, 2013.

Malhi, Y., Pegoraro, E., Nobre, A. D., Pereira, M. G. P., Grace, J., Culf, A. D., and Clement, R.: Energy and water dynamics of a central Amazonian rain forest, J. Geophys. Res., 107, 1–17, 2002.

Miettinen, J., Shi, C., and Liew, S. C.: Two decades of destruction in Southeast Asia's peat swamp forests, Front. Ecol. Environ., 10, 124–128, 2012.

Montgomery, R. A. and Chazdon, R. L.: Forest structure, canopy architecture, and light transmittance in tropical wet forests, Ecology, 82, 2707–2718, 2001.

Moore, S., Evans, C. D., Page, S. E., Garnett, M. H., Jones, T. G., Freeman, C., Hooijer, A., Wiltshire, A. J., Limin, S. H., and Gauci, V.: Deep instability of deforested tropical peatlands revealed by fluvial organic carbon fluxes, Nature, 493, 660–663, 2013.

Murdiyarso, D., Hergoualc'h, K., and Verchot, L. V: Opportunities for reducing greenhouse gas emissions in tropical peatlands, P. Natl. Acad. Sci. USA, 107, 19655–19660, 2010.

Numata, S., Yasuda, M., Okuda, T., Kachi, N., and Supardi, M. N. N.: Canopy gap dynamics of two different forst stands in a Malaysian lowland rain forest, J. Trop. For. Sci., 18, 109–116, 2006.

Page, S. E., Rieley, J., and Shotyk, W.: Interdependence of peat and vegetation in a tropical peat swamp forest, Philos. T. Roy. Soc. B, 354, 1885–1897, 1999.

Page, S. E., Siegert, F., Rieley, J. O., Boehm, H.-D. V, Jaya, A., and Limin, S.: The amount of carbon released from peat and forest fires in Indonesia during 1997, Nature, 420, 61–65, 2002.

Page, S. E., Rieley, J. O., and Banks, C. J.: Global and regional importance of the tropical peatland carbon pool, Glob. Chang. Biol., 17, 798–818, 2011.

Palminteri, S., Powell, G. V. N., Asner, G. P., and Peres, C. A.: LiDAR measurements of canopy structure predict spatial distribution of a tropical mature forest primate, Remote Sens. Environ., 127, 98–105, 2012.

Paoli, G. D., Curran, L. M., and Slik, J. W. F.: Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo, Oecologia, 155, 287–299, 2008.

Prescott, C. E.: The influence of the forest canopy on nutrient cycling, Tree Physiol., 22, 1193–1200, 2002.

Putz, F. E., Zuidema, P. A., Synnott, T., Peña-Claros, M., Pinard, M. A., Sheil, D., Vanclay, J. K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J., and Zagt, R.: Sustaining conservation values in selectively logged tropical forests: the attained and the attainable, Conserv. Lett., 5, 296–303, 2012.

Schoenberg, F. P. and Patel, R. D.: Comparison of pareto and tapered Pareto distributions for environmental phenomena, Eur. Phys. J.-Spec. Top., 205, 159–166, 2012.

Siegert, F., Ruecker, G., Hinrichs, A., and Hoffmann, A. A.: Increased damage from fires in logged forests during droughts caused by el Nino, Nature, 414, 437–440, 2001.

Simonson, W. D., Allen, H. D., and Coomes, D. A.: Applications of airborne lidar for the assessment of animal species diversity, Methods Ecol. Evol., 5, 719–729, 2014.

Sist, P. and Nguyen-Thé, N.: Logging damage and the subsequent dynamics of a dipterocarp forest in East Kalimantan (1990–1996), Forest Ecol. Manag., 165, 85–103, 2002.

Sist, P., Dykstra, D. P., and Fimbel, R.: Reduced Impact Logging Guidelines for Lowland and Hill Dipterocarp Forest in Indonesia, CIFOR, Bogor, Indonesia, 1998.

Slik, J. W. F., Verburg, R. W., and Keßler, P. J. A.: Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia, Biodivers. Conserv., 11, 85–98, 2002.

Stan Development Team: RStan: the R interface to Stan, Version 2.5, available at: http://mc-stan.org/rstan.html (last access: 13 July 2015), 2014.

Stark, S. C., Leitold, V., Wu, J. L., Hunter, M. O., de Castilho, C. V, Costa, F. R. C., McMahon, S. M., Parker, G. G., Shimabukuro, M. T., Lefsky, M. a, Keller, M., Alves, L. F., Schietti, J., Shimabukuro, Y. E., Brandão, D. O., Woodcock, T. K., Higuchi, N., de Camargo, P. B., de Oliveira, R. C., Saleska, S. R., and Chave, J.: Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment, Ecol. Lett., 15, 1406–1414, 2012.

Van Schaik, C. P., and Mirmanto, E.: Spatial variation in the structure and litterfall of a Sumatran rain forest of a spatial variation in the structure and litterfall Sumatran rain forest, Biotropica, 17, 196–205, 1985.

Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S., and Clawges, R. M.: Lidar: shedding new light on habitat characterization and modeling, Front. Ecol. Environ., 6, 90–98, 2008.

Vitousek, P. M. and Denslow, J. S.: Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest, J. Ecol., 74, 1167–1178, 1986.

Warton, D. I. and Hui, F., K. C.: The arcsine is asinine: the analysis of proportions in ecology, Ecology, 92, 3–10, 2011.

Weishampel, J. F., Hightower, J. N., Arlen, F., and Chase, D. Z.: Use of airborne LiDAR to delineate canopy degradation and encroachment along the Guatemala-Belize border, Trop. Conserv. Sci., 5, 12–24, 2012.

West, G. B., Enquist, B. J., and Brown, J. H.: A general quantitative theory of forest structure and dynamics, P. Natl. Acad. Sci. USA, 106, 7040–7045, 2009.

Whitmore, T. C.: Tropical Rain Forests of the Far East, Clarendon Press, Oxford, 1975.

Wösten, J. H. M., Clymans, E., Page, S. E., Rieley, J. O., and Limin, S. H.: Peat–water interrelationships in a tropical peatland ecosystem in Southeast Asia, Catena, 73, 212–224, 2008.

Table 1. List and description of canopy structure metrics used in this study.

Metric	Description
Canopy top height (m)	99th quantile of the canopy height distribution measured in 10 000 pixels (1 m^2) in each plot.
Standardised canopy height	Ratio of the mean canopy height (measured from CHM) to the canopy top height.
Canopy shape	Ratio of the height at which the highest percentage of ALS returns are measured to canopy top height.
Mean gap area (m^2)	Mean of all gap sizes measured in a given cross-section of a given plot.
Gap fraction (%)	Total gap area in a given cross-section as a percentage of the total plot area (km^2).
Scaling exponent α of the GSFD	Scaling parameter determining the decrease in frequency of gaps as gap size increases. It also relates to the ratio of large to small gaps (Lobo and Dalling, 2013).
Transition parameter θ of the GSFD	Parameter governing the transition from power law to exponential (Schoenberg and Patel, 2012).

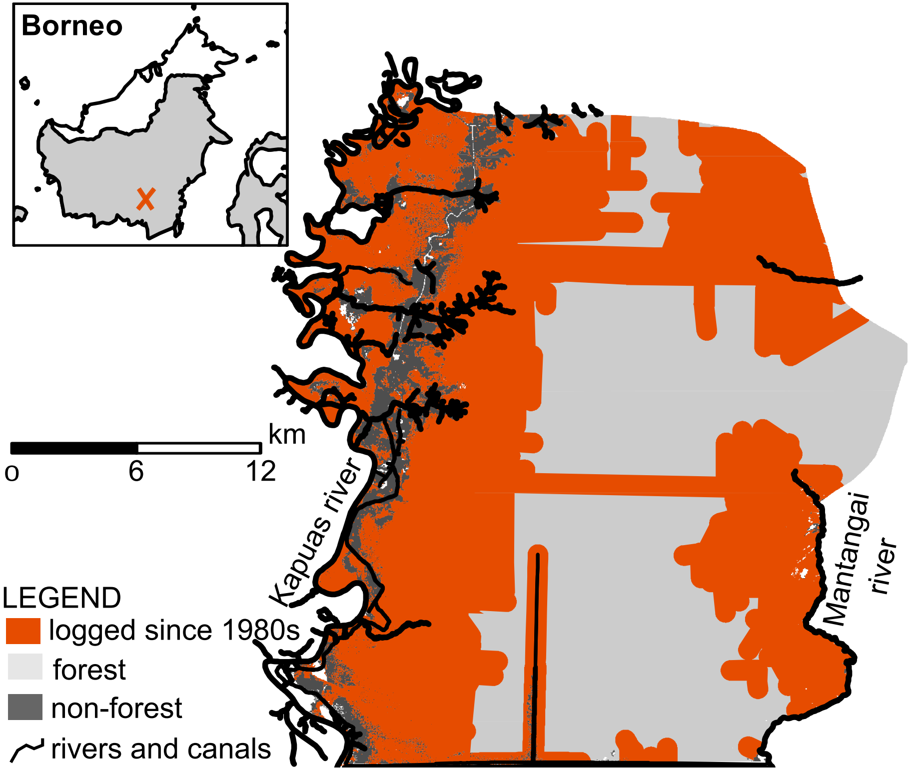

Figure 1. Map of old-growth (light grey), selectively logged forest (red) and non-forest (dark grey) within the 750 km^2 Mawas peat swamp forest, Indonesian Borneo (location shown in inset). Full red zones indicate areas affected by selective concessionary timber extraction until 2000 and illegal selective logging thereafter as estimated from logging routes detected in historical satellite imagery (Supplement).

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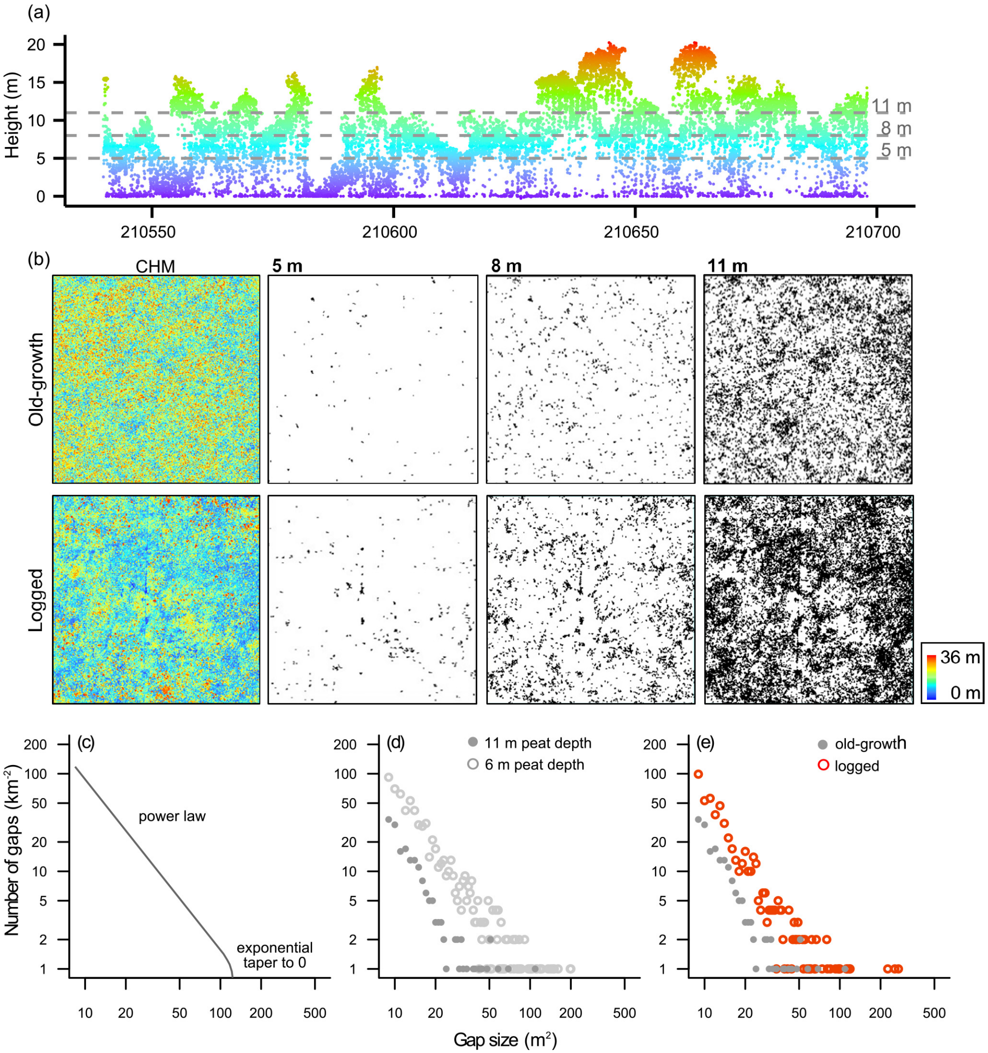
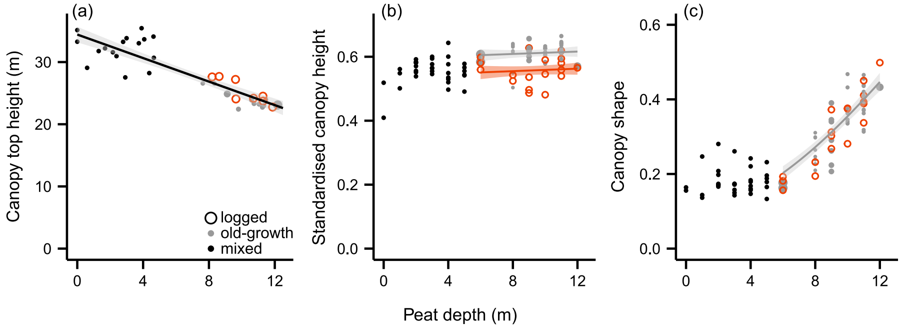


Figure 2. Detection of canopy gaps of a forest using airborne laser scanning (ALS) **(a, b)** and examples of gap size frequency distributions (GSFD) **(c–e)**. **(a)** ALS point cloud along a transect allows distinguishing emergent crowns and canopy gaps reaching to different heights above ground. **(b)** Canopy gap detection in different cross-sections of the ALS-derived canopy height model (CHM) in an old-growth (top row) and a logged (bottom row) peat swamp forest plot (1 km^2). Columns to the right show canopy gaps ($\geq 9\,\mathrm{m}^2$) as darkened areas in horizontal cross-sections of the CHM at 5, 8 and 11 m above ground. **(c)** Shape of the finite pareto distribution used to describe the GSFD and examples of variation of the GSFD with **(d)** peat depth and with **(e)** logging, both in the 8 m cross-section. The number of gaps of a given size is given by the probability distribution multiplied by the total number of gaps.



(d) **Canopy density profiles**

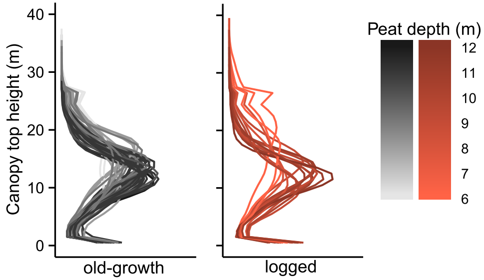


Figure 3. Changes in canopy top height and vertical structure with peat depth in old-growth, logged and mixed peat swamp forest plots (top panels) and canopy density profiles derived from ALS for old-growth and logged plots on different peat depths (bottom panels; the area below each curve is 1). For canopy top height only plots with direct peat measurements are shown and a single regression line is fitted as logging does not affect this metric (Supplement). Logged forest dominated the first half of the peat depth gradient (0–5 m peat depth) preventing any comparison between old-growth and logged plots on the shallower peats. Fitted regression lines are plotted with 95 % confidence intervals.

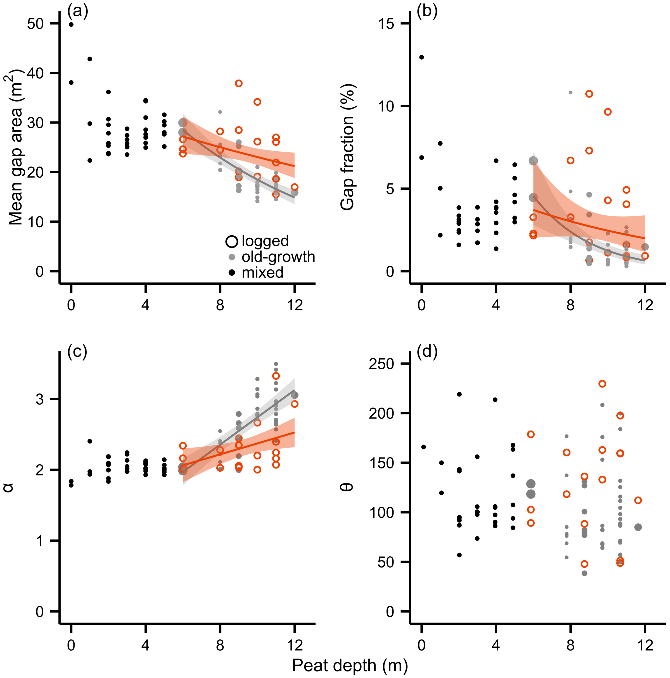


Figure 4. Changes in **(a)** mean gap area, **(b)** gap fraction, **(c)** scaling exponent α of the GSFD and **(d)** transition parameter θ of the GSFD with peat depth in old-growth, logged and mixed peat swamp forest plots. Data are shown for the 8 m cross-section of the CHM. Logged forest dominated the first half of the peat depth gradient (0–5 m peat depth) preventing any comparison between old-growth and logged plots. Fitted regression lines are plotted with 95 % confidence intervals.

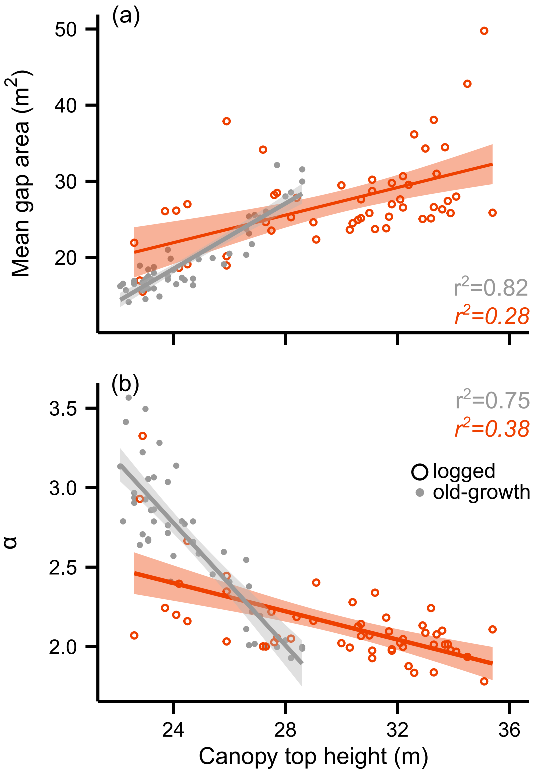


Figure 5. (a) Mean gap sizes and **(b)** scaling exponent α of the GSFD in relation to canopy top height in old-growth and logged peat swamp forest plots. Data are shown for the 8 m cross-section. Fitted regression lines are plotted with 95 % confidence intervals and the R^2 of the regression is given (italic for logged).