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 interplay between environmental factors and disturbance legacies on forest canopy structure across landscapes are practically unexplored. We used 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, consistent 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 illegal 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. With logging, 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 peat depth gradient within the old-growth tropical peat swamp. This relationship breaks down after selective logging, with canopy structural recovery, as observed by ALS, modulated by environmental conditions.

These findings improve our understanding of tropical peat swamp ecology and provide important insights for managers aiming to restore degraded forests.

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, 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 interplay between 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. Peat domes form by accumulation of organic matter over millennia; peat dome complexes can be up to 60 km in diameter, with peat depths reaching up to 20 m in the centre of the dome (Ashton, 2014).Trees become shorter, narrower stemmed, and more densely packed towards the centre of the domes (Anderson, 1961; Bruenig and Droste, 1995; Bunyavejchewin, 1995; 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 very few field studies (Anderson, 1961; Bruenig and Droste, 1995; Bunyavejchewin, 1995; Page et al., 1999; Whitmore, 1975). 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). Optical satellite studies have had limited power in measuring logging effects as they lack information about the intricate three-dimensional structure of canopies, and only recently have researchers used satellite radar data to delineate degraded forests (e.g. Schlund et al., 2014). Airborne Laser Scanning (ALS) has opened new avenues for canopy research, as it provides detailed 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). Here we define canopy gap as an opening in the forest canopy, which can result from tree fall or from the organisation of crowns and can reach to different heights above ground. Previous studies have used ALS to analyse the variation in gap sizes in different forest types within landscapes (Asner et al., 2013, 2014; Boyd et al., 2013; Espírito-Santo et al., 2014; Kellner and Asner, 2009; Kellner et al., 2011) and the impacts of logging on above-ground biomass (Andersen et al., 2013; d'Oliveira et al., 2012; Englhart et al., 2013; Kronseder et al., 2012; but see Weishampel et al., 2012). Changes in canopy structure along continuous environmental gradients within landscapes and the potentially long-term impact of logging on canopy structure remain to be studied.

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 per year (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, a freely-available software that performs spectral un-mixing on satellite images (Supplement). CLASlite renders sub-pixel fractional cover information that enabled the identification of logging routes characterised by high fractions of soil or dead vegetation (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 a recovery of canopy height after 500 m. Furthermore, logging operations were reported to extend to 500 m from railways in PSF (Franke et al., 2012) (Supplement). Forest within 5 km of the Kapuas river, could not be classified as ‘old-growth’ because local villagers have traditional land rights in that area, and make use of the forests (KFCP, 2009). Since 54% of the area was interspersed with logging routes, it was classified as 'logged'.

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 × 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 1×1 km were positioned throughout the research area to yield a good coverage of the landscape and avoid having plots crossing land cover boundaries (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 selected pixels (to optimise computing time and provide a representative sample) of the CHM, from which the canopy top height (99th quantile of height) was calculated. We identified the height of the band 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 m up to 12 m above ground (following Kellner & 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 including openings resulting from aberrations in the CHM. Gaps were truncated at the edge of the plot. The upper CHM cross-section considered was 12 m to avoid the coalescence of gaps from distinct origins and truncation of very large gaps at plot edges, observed above this threshold (see Fig. S5 for a fuller explanation).

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). 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:

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

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 & Patel 2012;see also Anfodillo *et al.* 2013; Kent *et al.* 2015). 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):

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

where x_{min} is the lower truncation point (here 9 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 γ+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 there were insufficient gaps to fit a power law at cross-sections close to the ground, 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). In the research area, peat depth could not be estimated directly from the DEM because the mineral bedrock increases in elevation from South to North (6 to 32 m a.s.l.; source: FetchClimate). We disposed of an independent data set of more than 300 peat depth measurements across the study area and measured canopy top height (99th quantile of height) within a 100 m neighbourhood. We first tested for the effect of logging on canopy top height in this independent dataset by fitting generalised linear models containing peat depth and additive or multiplicative effects of logging as a factor (yes, no). No significant logging effect was detected. We found that canopy top height was closely related to peat depth (R^2=0.79) except on shallow peat within 3000 m of the Kapuas river (Fig. S3a). On shallow peat, distance to river was linearly related to peat depth (R^2 = 0.59; Fig. S3b). Peat depth for our study plots was thus inferred as (Eq. 3):

$$Peat\ depth = \begin{cases} 26.0 - 0.7 \times top.height\ for\ dist.riv > 3000\ m, \\ 0.31 + 0.002 \times dist.riv\ for\ dist.riv \leq 3000m, \end{cases} \quad (3)$$

where *top.height* is canopy top height (99th quantile) and *dist.riv* is distance to the large Kapuas river. The inference of peat depth from canopy top height was thus done from an independent data set to the plot data further used for analyses. This approach was validated, as it yielded a fit going through the origin and with an $R^2 = 0.88$ between predicted and measured peat values in 33 plots where peat data was available.

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 unlogged 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, 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 canopy shape and the gap fraction were logit-transformed as they were bound between 0 and 1 (Warton and Hui, F., 2011). All other analyses assumed normal distributions, as supported by visual inspection of residuals. 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, $p > 0.05$).

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). In an independent data set of more than 300 peat depth measurements and associated canopy top height measurements, canopy top height was not affected by logging (Supplement), 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). The canopy shape, derived from the complete ALS point cloud, did not change along the peat depth gradient in old-growth forest (grey line, Fig. 3b) suggesting that the height of the main canopy volume decreased in parallel to canopy top height (Fig. 3a).

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. 3c) 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–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, decreased significantly with peat depth for cross-sections up to 8-m height above ground (Fig. 4d, Table S3), but the trend was not statistically significant in the 8-m cross-section (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. Negative correlations between α and θ in cross-sections $\geq$ 6 m height (Pearson correlation coefficient r = -0.25–-0.35, p = 0.02 – 0.67) indicated that θ was greatest in sites containing large gaps. From cross-sections $\geq$ 9 m height, θ was not different from zero (Table S3) and the GSFD was described by a power law.

Canopy top height accounted for a large proportion of the variation in canopy gap metrics along the peat dome (recalling that peat depth is negatively related with canopy top height and mean gap area) 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 canopy shape was observed (Fig. 3b), indicating the removal of canopy volume in logged plots. 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 as an explanatory variable and mean gap area (Fig. 5a, $R^2 = 0.28$, $p < 0.001$) or α (Fig 5 b, $R^2 = 0.38$, $p < 0.001$) which we found in old-growth forest (Table S5). This explains the absence of relationship between peat depth and gap metrics in the first half of the peat depth gradient (Figs 4a-d).

There was limited evidence that logging route density within logged areas had an influence on canopy structure. The logging pressure indices (LPI) did not explain differences in canopy shape parameter, gap fraction, α or θ in areas that we had identified as logged. However, we found that the cumulative LPI increased mean gap size by < 10% in the 2-m 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 canopy shape across the peat dome (Fig. 3b; model M2 selected), but had differing 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 gaps 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 gap 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 structure of selectively logged forests remained altered after concessionary logging had ended, although structural recovery depended strongly on peat depth. As such, the landscape-scale relationship between forest height and canopy gap structure 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 m 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 & 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 (Figure S6c). 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, which might result from small spaces between evenly distributed small crowns 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. These gap patterns may arise from both changes in the organisation of crowns in the canopy as well as from changing disturbance patterns along the edaphic gradient. First, smaller gap sizes may be due to a loss of large emergent trees and even canopies filled with small crowns on nutrient-poor substrate (Kapos et al., 1990; Paoli et al., 2008). These shorter trees will additionally 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 (smaller α) on deep peats might result from trees dying 'on their feet' in low stature forest (Coomes and Grubb, 1996). Large proportions of large gaps (larger α) on shallow peats suggest that trees forming structured canopies 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 also 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 forest 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 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. The use of different definitions of canopy gaps renders comparison of results difficult (Lobo & Dalling, 2014). While GSFD coefficients are insensitive to plot size, especially in forests dominated by small gaps such as PSF, they vary widely with different height thresholds and spatial resolution of the canopy model (Lobo & Dalling, 2014). We chose a small minimum gap size and different height thresholds following the majority of studies recently published (Kellner & Asner, 2009; Kellner et al., 2011; Asner et al., 2013; Boyd et al., 2013; Lobo & Dalling, 2013). If a consensus is found, combining ALS-derived forest structure measurements with ground data of major environmental drivers could open new avenues for researchers to explore ecological processes, e.g. disturbance dynamics, at spatial scales at which such processes take place, rather than being confined to small-scale 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 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, but the relative vertical distribution of canopy volume 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 have slow structural recovery 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). PSF on deep peat were deemed unsuitable for commercial logging operations due to low density of poles and fragility of the system (Bruenig & Droste, 1995). Yet we detected concessionary logging railways on deep peat in our study area, and we are developing new techniques to better monitor illegal logging (unpublished data). 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 canopy structure did not respond to variation in logging pressure, 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 RapidEye satellite images with 5 m spatial resolution 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 m to about 5 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 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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Tables

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

Metric	Description
Canopy top height (m)	99^{th} quantile of the canopy height distribution measured in 10,000 pixels (1 m^2) in each plot.
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 legends

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).

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 m^2) as darkened areas in horizontal cross-sections of the CHM at 5, 8 and 11 m above ground. Examples of variation of the GSFD with (c) height aboveground, (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.

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 in an independent data set (section 2.3.1, 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).