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Interactive comment on "Landscape-scale changes in forest canopy structure across a partially logged tropical peat swamp" *by* B. M. M. Wedeux and D. A. Coomes

B. M. M. Wedeux and D. A. Coomes

bmmw2@cam.ac.uk

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We thank M. Disney, R. Hill, F. Espirito-Santo and M. Hayashi for their comments, which have helped improve the manuscript. We thank the handling associate editor A. Ito for considering the revised manuscript and hope he will now find it suitable for publication.

We respond to the comments in detail below. Additions to the manuscript are marked in blue, both in this response and the manuscript.

Response to F. Espirito-Santo's comments

We thank Dr Espirito-Santo for his thoughtful review, which raises several key issues that apply to our study and to others in the nascent field of structural analyses of forests using LiDAR. Dr Espirito-Santo's review focuses primarily on one aspect of the paper, the gap size frequency distribution, and discusses the implications of our methodological choices for the ecological interpretation of our results. He expresses the view that we should (a) measure gap sizes close to the ground in order to quantify the effects of recent tree-fall events, (b) exclude gaps smaller than about 25 m2 because they are unlikely to have arisen from recent tree-fall events, and (c) include measurements across a larger area than we do at present, in order that the gap-size distribution of recent tree-fall gaps is quantified robustly. If we had intended to quantify the sizes of gaps created by recent tree-fall events then Dr Espirito-Santo's points would have been completely valid. But that was not our intention. The paper focusses instead on characterising the structure of recently logged, regenerating and old growth forests using a variety of metrics, including gap size distributions at different heights in the forest canopies.

We are grateful to Dr Espirito-Santo for raising his concerns. We believe that a laxity of definition is at the heart of this disagreement. Four terms appearing in our manuscript and in the reviews – tree fall gap, canopy gap, forest gap, and tree crown spaces – are used somewhat interchangeably to describe the openness of canopies, and this has created confusion. Dr Espirito-Santo's helpful comments have prompted us to tighten up our wording and explain our intentions more carefully. We do not believe that any reanalyses of data are necessary to address his concerns.

Answering the reviewer's comments in more detail now: 1. We agree with the reviewer that the detection of disturbances created by recent tree fall gaps probably requires monitoring a larger area than 1 km2/100 ha as we did, choosing a larger gap size threshold and should be based on openings that reach down to height cross-sections of 2 m preferably. The definition of a reasonable tree fall gap size must rely on extensive ecological knowledge and surveys in the forest type of interest. Added complexity occurs along edaphic gradients where changes in tree fall gap size and tree fall gap

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frequency have been observed (Kapos et al., 1990). 2. The key point is that we did not intend to measure patterns in recent tree-fall gaps, but rather to provide a broader overview of the canopy structure along the peat dome and after selective logging. This was specified in the title of the paper. In our view, the canopy structure encompasses canopy height, vertical organisation of the canopy, the spatial organisation of crowns in the canopy and open spaces in the canopy at different heights above ground. Those open spaces, which we called 'gaps' in the paper, encompass both openings that result from tree mortality events but also open spaces resulting from the spatial organisation of the crowns in the canopy, which the reviewer calls 'tree crown spaces'. All these canopy openings have an ecological meaning in the sense that they influence the spatial organisation of crowns and the light environment in the forest understory. Previously the methods section of the manuscript said:

10991 l.17: '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 have now added a sentence in the introduction to clarify our definition of 'canopy gap':

10988 l. 22: 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.

We have also made some amendments to the text to reflect the dual origin of canopy gaps:

10998 l. 21 As such, the landscape-scale relationship between forest height and natural disturbance patterns canopy gap structure was lost in selectively logged forests.

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10999 l. 26: 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.

11000 l.5: 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. 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 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).

3. CHOICE OF MINIMUM GAP SIZE: The reviewer correctly points out that including gaps of small sizes modifies the exponent of the power law relationship fitted to the datasets, and tends to make them larger. A review of the recent studies that have used similar LiDAR-based approaches reveals that most studies (Asner et al., 2013; Boyd et al., 2013; Kellner and Asner, 2009; Kellner et al., 2011; Lobo and Dalling, 2013) have used even smaller minimal gap sizes than we did (1 – 2 m2). We chose a minimum gap size of 3 $\times$ 3 m (corresponding to 3 $\times$ 3 pixels in the CHM) in order to avoid openings that might result from local aberrations of the ALS-derived CHM. We clarify this in the manuscript:

10991 l.23: Gaps < 9 m2 were excluded from further analysis to avoid including openings resulting from aberrations in the CHM.

4. CHOICE OF HEIGHT CROSS-SECTIONS REPORTED: The 12 m cut-off was selected because gaps identified in lower height tiers were found to merge above that height (Fig. S5); this is because we are taking slices through the canopy at a height above many tree crowns. Many of these large gaps are truncated by plot edges so their true size is unknown, creating biases if we would use them to create gap size distributions. We clarified the main text:

10991 l.25: 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).

The studies we cite have used different height cross-sections. A recent publication (Lobo and Dalling, 2014) demonstrates that the choice of the height threshold influences the coefficients of the gap size distribution. Therefore, we provide the coefficients at different height cross-sections, to facilitate comparisons with other studies.

The presentation of the 8-m cross-section results in the graphics were based on the fact that the differences between logged and old-growth forest were most marked there. To facilitate the visualisation of results, we opted against presenting the results for all height cross-sections in the main text (but we do in the supplementary material). We inform the reader that the results at the 8 m cross section reveal the most differences among peat depths and disturbance classes and is therefore used to illustrate the findings presented in the text. Differences were also visible in other height tiers, particularly at 7 to 10 m height, and these are provided in the supplement. We write:

10996 l. 18-23: 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.

5. CHOICE OF PLOT SIZE: We chose the size of plots (1 km2) based on reaching a balance between covering the whole research area and having enough data points at different peat depths, in order to be able to fit regressions subsequently. Doubling the size of plots, as the reviewer suggests, would lead to an increase in variation of forest and canopy structure within each plot and fewer data points along the peat depth gradient, which would compromise the fit of the regressions. Furthermore, we noted that more than a third of plots (out of 100 in total), had fewer than 10 gaps at the 2 m height threshold. Doubling the plot size would not have ensured a good fit of the power law for that height tier.

Furthermore, (Lobo and Dalling, 2014) tested the effect of plot size (10, 50, 100 ha) on gap size frequency distribution in BCI, where they note that the disturbance regime is dominated by small gaps. They find that the gap size does not influence the fit and the coefficients of the gap size frequency distribution, but confidence intervals around estimated coefficients are tighter when plot size is larger. According to that study our coefficient estimates should be accurate, but there were simply not enough gaps close to the ground to fit the power law.

We added this justification in the text 10990 l.22: 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).

We also added a few lines on the study of Lobo and Dalling (2014) in the discussion, where we compare the canopy structure along the peat depth gradient to other gradients:

11001 l.15: 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.

Technical corrections:

[Reviewer comment] 10986-L10: I agree that there area many canopy gaps in different height cross-sections of the lidar tree heights. The question is: are they millions of canopy gaps or millions of tree crown spaces? If you cut-off of the minimum gap size-area is based on ground observation (_ 25 m2), there area few gaps in a 100 ha forest plot. As I mentioned before, I feel that the authors have incorporated more information about crown spaces rather than forest gaps.

[Author response]: Addressed under point 2 of response to general comments above.

[Reviewer comment] 10986-L15: the exponent of the gap frequency distribution (1.76-3.76) is high because there is a huge number of small gaps incorporated in the statistical model. If you apply a minimum gap size-area threshold that matches ground observations (ex. BCI data or any other ecological study reporting a minimum gap size-area), the exponent of this power-law distribution will decrease; perhaps exponents will be around 1.2. I believe that this power law fit may be heavily weighted to small holes in the forest canopy that are not gaps in an ecological sense.

[Author response]: We agree that our 'gap size frequency distribution' is populated by both open spaces corresponding to tree fall gaps and top open spaces between crowns. We also agree that the presence of many small gaps influences the estimated exponent of the distribution. As we noted under point 3 of the response to general comments, most other studies have also chosen small gaps, so our coefficients are

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comparable to those reported in other studies. We suggest that the variation in power law exponents with different gap sizes is an interesting area for future research. (see also the response to comment on 10991 – L23)

[Reviewer comment] 10987-from L1 to L23: This introduction is not well organized. The authors started with a discussion about forest structure, moved to light attenuations in the canopy, changed for biodiversity, mentioned land-use processes and finished with a description of Borneo. All those topics described at the begging of the introduction! Please, rephrase and focus only in few key points.

[Author response] We used the first paragraph of the introduction to provide an overview of the main knowledge gaps and the relevant topics for the paper. We thus prefer to keep the paragraph as it is.

[Reviewer comment] 10988-L18: "It goes without saying. . ." Remove it? Rephrase? or Start from "Satellite studies have had . . .."

[Author response]: We followed the reviewer's advice and removed this part of the sentence.

[Reviewer comment] 10989 – L23: "processed with ClasLite" . Ok, but the real analysis behind of this method is not ClasLite. It is an "un-mixing image spectrometry approach". I suggest you mention it. ClasLite is just an unmixing image algorithm. There are several others available.

[Author response]: We have modified the sentence to give more information about CLASlite: 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 unmixing on satellite images (Supplement).

[Reviewer comment] 10990 – from L3 to L5. I appreciated that the authors tried to quantify the intensity of logging using lidar data. However, I do not see why 500 m appeared to be more reasonable. Any buffer is subjective, but the support material (Figure S2) is not too much informative. The easiest way to see any spatial trend is to use “semivariograms” from geostatistics. Again, this is not critical – it is only a suggestion!

[Author response]: We agree that the choice of a buffer is complex and here further complicated by the natural variability of canopy height along the peat dome. We shall test the effectiveness of semivariograms in future studies and thank the reviewer for the suggestion. We have based the choice of 500 m on ground observations reported by (Franke et al., 2012) and a seeming recovery of canopy mean height at 500 m from railways. We have reformulated the sentence to make it more nuanced and include the information about ground observations: 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).

[Reviewer comment] 10990 – L23. This is critical. 100 ha is very small to quantify forest gaps. If the authors increase the sample area for 200 ha, you will find enough data at 2 m aboveground (tree-fall gaps without regrowth). It is also another additional suggestion. Overall, all statistic analyses of this paper were well done.

[Author response] We have responded to this in point 5 of the response to the general comments. Increasing the size of the plots would include much more variation of canopy structure within the plot and reduced the number of observations along the peat depth gradient. Furthermore, we noted that more than a third of plots (out of 100 in total), had less than 10 gaps at 2 m height threshold. Doubling the plot size would thus not always ensure a good fit of the power law.

[Reviewer comment] 10991 – L23. Now, this is VERY critical! Gaps < 9 m2, are not gaps and I agree with the authors. However, I have not found a single publication about the minimum size-area of tree-fall gap in the ecological literature smaller than 20-25 m2. I think the majority of your data (Gaps < 9 m2) are not gaps in the ecological sense. Perhaps they are tree crown spaces related to sunflecks processes in forests. I think that the minimum gap size-area threshold should be increased for 20-25 m2. Using a large minimum gap size area threshold all lidar forest gaps (holes) are tree-fall disturbances (albeit Brokaw 1992).

[Author response] We have addressed this issue in points 2 and 3 of the response to general comments. The issue is a confusion as to the definition of 'gap'. In our paper, we use the word gap to generally refer to canopy openings. In that sense, even open spaces between crowns are gaps.

[Reviewer comment] 10992 – L13. I appreciated the test of this "modified finite pareto function", but the model is more complex now. What is the ecological meaning of this transition parameter (_) for forest gaps? It is not clear in the article.

[Author response] The point we try to advocate, is that power laws fitted on naturally occurring data should be finite. This is a field for further research and different models have been used in that context, see e.g. (Anfodillo et al., 2012; Kent et al., 2015).

[Reviewer comment] 10993 – L1-L7. The reason that the authors used a cross section starting at 5 m aboveground is because the sample area is very small (100 ha). The data does not show any trend of power-law because there is not enough data at 2 m aboveground. It does not mean that tree-fall gaps do not follow a power law distribution at 2 m height. If you increase your sample area for 200 ha and consider a reasonable minimum gap size-area (20-25 m2) the data will follow a power-law distribution even in 2 m aboveground.

[Author response]: We agree with the first point of this comment and have rephrased as follows: '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.'

As to the second part of the comment: we note that this would not be the case in our forest type, because more than a third of the plots had less than 10 gaps of more than 9 m2 in the 2 m cross-section. It is unlikely that under the parameters suggested by the reviewer, we would find enough gaps to robustly fit a power law.

[Reviewer comment] 10993 – from L11 to L14. I also appreciated the ground collections of peat depth. However, I just did not understand why the authors did not used the digital terrain model (DTM) directly to test the prediction of peat depth. Terrain information is more correlated with soil propriety than vegetation information. I am aware that the study site is very flat, but lidar remote sensing is very powerful to quantify small changes in the forest floor. DTM from my understanding are more meaningful to understand peat depth in the soils than a lidar canopy height model.

[Author response] In our research area, the DTM is not a suitable proxy for peat depth because the mineral bedrock increases in elevation (6 to 32 m a.s.l.) from South to North. Considering that the peat depth reaches maximal values of 12 m depth, it is clear that the peat dome is being elevated with the underlying bed rock. As a consequence, areas with shallow peat may be found at higher elevations than areas with the deepest peat. We added a sentence to clarify this:

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).

[Reviewer comment] 10996 – L25. "The GSFD scaling coefficient (exponent?) became larger with increasing peat depth, indicating a increasing proportion of small gaps". Is it really related to tree-fall gaps or increasing in crown spaces of the forest canopy? From my previous field experiences, flooded forests have more opened crowns than other areas. I guess the same thing happens for areas with large peat depth.

[Author response] We have clarified what we mean by 'gap', which hopefully addresses the first concern. Secondly, the peat swamp forest behaves differently than the flooded forests found in the Amazon, e.g. igapó or várzea. In these forests, cyclic flooding from nearby rivers cause a lot of tree mortality and turnover resulting in open canopies. In the peat swamp forest however, the rain-fed water table and nutrient-poor substrate lead to slow growth, and the forest grows stunted with many small and densely packed stems. As a result, the canopy is interspersed with few and small openings or gaps.

We have also exchanged 'exponent' with 'coefficient', as suggested by the reviewer: The GSFD scaling coefficient became larger. . .

[Reviewer comment] L10997 – from L1 to L2. I do not agree. I think the selection of 8 m cross section was based on lack of data (frequency of tree-fall gaps). Again, 100 ha is very small to detect recent gaps at 2 or 5 m aboveground. Only around 8 m aboveground the frequency of gaps are reasonable to test statistical power-law model.

[Author response] We are certain that there was enough data to fit the finite power law distribution from the 5 m cross-section. The median number of gaps at the 5-m cross-section was 262 (vs 42 in the 2-m cross-section for which we did not report power law distribution coefficients).

[Reviewer comment] L10997 – from L8 to L10. This was a fantastic result even using a lidar height threshold of 8 m! However, be aware that at 8 m your results are from disturbances and regrowth. Different processes!

[Author response] We appreciate the positive comment about this finding as we also think that the link between canopy top height and gap sizes is a novel finding and should be further investigated in future research. We agree that the structure of the canopy around 8 m results of a mix of new tree fall gaps, old tree fall gaps that have experienced regrowth up to a certain height as well as space between crowns.

[Reviewer comment] L10998 – L19. The canopy of selective logged forests remained open 11 years after concessionary. It is from your observation or from some reference? I found difficult to believe, but I guess the intensity of logging was very high there.

[Author response] We make this claim based on our finding that the canopy of logged forests had more gaps or openings than that of old-growth forest. However, we agree that the statement is somewhat misleading in that it suggests that there are significantly more gaps going down to the ground, which is not the case, only the upper canopy structure is affected. We have rephrased: 'The canopy structure of selectively logged forests remained altered after concessionary logging had ended,. . .'

[Reviewer comment] L10999 – L1. Nice result! My only problem here is why the authors did not use the digital terrain model to estimate peat depth?

[Author response] Same as response to comment relative to 10993 – from L11 to L14 (see above).

[Reviewer comment] L10999 – L24. U-shaped pattern? Just because Kellner used this terminology, it does not mean that you should adopt. Because you did not illustrate a U-shape graph of the gap frequency distribution aboveground this terminology is not useful...

[Author response] This statement refers to Figure S6 in the supplement, which we indeed omitted to inform. The pattern is indeed unclear and we chose to delete this information. The sentence now reads: 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 (Figure S6c) indicating high proportions of large gaps at low and high cross-sections (but see Kellner and Asner 2009; Boyd et al. 2013).

[Reviewer comment] L10999 – L16. Small proportions of large gaps or high frequency of tree crown spaces (small gaps < 20 m2) on deep peats?

[Author response] We think that this comment refers to 101000 l.16 rather than 10999 l.16? Given a fixed gap area, which is low on deep peats as revealed by a small gap fraction, stating 'small proportions of large gaps' is equivalent to saying 'large proportions of small gap'. We split the sentence in two and reworded it to make the contrast between both halves clearer: 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). High proportions of large gaps (larger α) on shallow peat suggest that 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).

[Reviewer comment] L10999 – L25. Pervasive? I do not see why. It was based on tree-fall gaps disturbances or tree crown spaces?

[Author response] Since we tested the effect of logging statistically against plots that originally had a similar canopy structure, alterations to the canopy of logged forests are caused by tree felling and regrowth patterns following logging. We removed the word 'pervasive': 'Consistent with this, we detected pervasive alteration of forest canopy structure 11 years after selective concessionary logging had stopped and interestingly,...'

[Reviewer comment] L1003 – from L12 to L14. The absence of tree fall gaps in those areas from 2 to 7 m aboveground is because of the size of the sample (100 ha) and not because of the absence of tree-fall gaps at the landscape scale.

[Author response] This statement is based on the whole study, not just the gap size frequency distribution. Indeed, we also tested for differences in mean gap area and gap fraction, which were not affected by a limitation of detection of a high number of gaps and were not different in logged and old-growth plots. It is however more correct to say that there were no large effects up to 5 m aboveground (see Table S3). The sentence now reads: 'The absence of pervasive logging damage close to the ground (2 m to about 5 m above-ground) indicates that regrowth,...'

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