Response to reviewer 1 (Kyle Dexter)

Thanks for the many interesting and thoughtful comments on the manuscript.

SPECIFIC COMMENTS

(1) Pg 7 106, line 25: While I agree that BCI being unaffected by cyclones allow it to be representative of large areas of lowland tropical forest, I think the caveat should be added that it is an island in the middle of a lake, and thus likely experiences a very different wind regime than most other tropical forests. Further, are we sure that the taxa that occur on BCI are adapted to deal with such a wind regime, which is relatively novel for them? I am not suggesting that other tropical tree communities are at equilibrium in species composition with respect to their environment, but BCI definitely is not. For example, see Feeley et al. (2011. Ecology. 92(4): 871-882), which shows directional changes in the composition of the 50 ha plot.

It would be interesting for the authors to briefly discuss their study and results in light of that paper, either here or in the discussion.

Response: We agree with the reviewer in noting that as BCI is an island in the centre of a lake, we would expect certain differences with other tropical forests. However, we expect these differences to be most significant closest to the shore, and to diminish closer to the center of the island. For this reason a buffer was used to exclude gaps and edge effects within 20 m of the shore. It is also worth noting that the main cause of tree falls on BCI are convective wind storms which are often very localized and can have very different effects across the BCI landscape. Most gaps form during the wet season, when winds off the lake are light (Brokaw 1996; Ecology of a Tropical Forest Chapter 7). Lastly, from our calculations of exposure it seems that including a distance of 1 km from the shore toward the lake to calculate exposure seems to overestimate total exposure. Thus, we expect the results from this study to still be representative of the conditions for many lowland tropical forests.

(2) Pg 7107, line 20: Can we assume that the soils correlate fairly well with the geomorphological units? I see now in section 2.3.3 that soil type was actually the variable used in analyses, rather than geomorphological unit. Perhaps this should be briefly mentioned here.

Response: The soil type is linked more closely to the underlying geology (see Ballie et al. 2006) than to the geomorphological unit (plateau, ridge, slope, valley, shore). We studied soil as an explanatory variable because we expect soil type to affect gap formation through effects on the probability of tree fall related to soil properties, e.g. soil, hydrology, fertility, etc. We expect that the remaining topographic variables, namely slope and topographic exposure, will capture differences amongst geomorphological units.

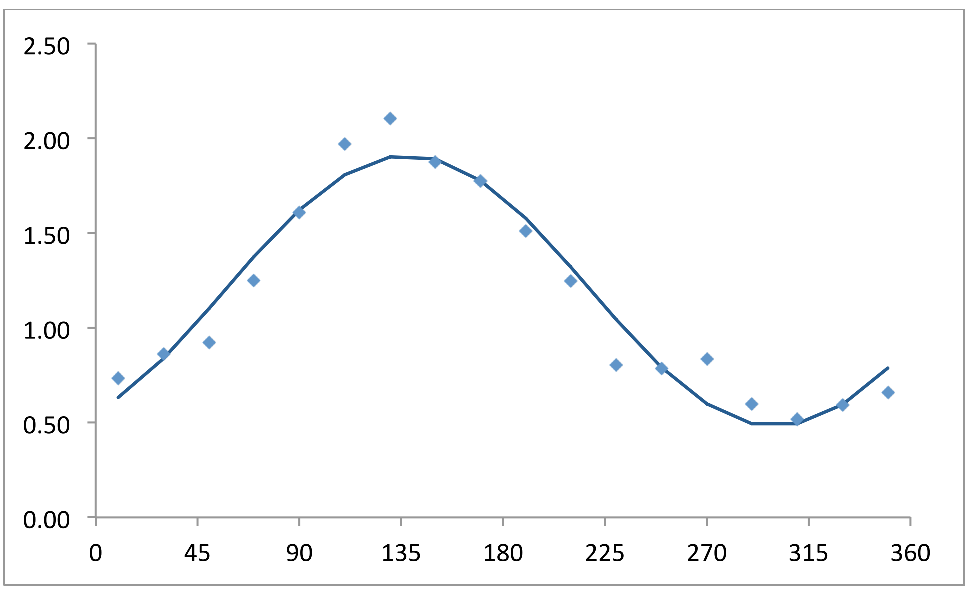
(3) Pg 7112, line 5, pg 7114, line 25, and Figure 5: Aspect is a circularly distributed variable (e.g. values of 1 and 359 are quite close to each other), but it seems that it was modelled as a standard continuous variable. Based on Fig. 5, it looks like no matter how it is modelled, it probably won't be found to have a significant effect on lambda, but it clearly affects gap fraction. While fitting a polynomial works, many other options could be considered and may be better (e.g. check out the package circularin R). These alternative modelling approaches might also be helpful in a multivariate analysis of gap area fraction that I advocate (see comment immediately below).

Response: In agreement with the referee's comments, we have used a circular function to model for aspect's effect on the gap fraction (see below). However, it is still not possible to create a multivariate model for the gap area fraction as explained in relation to the next comment.

Scale: 25 m^2

Model: $y = 1.20 + 0.32 \sin(0.02\ x) - 0.64 \cos(0.02\ x)$

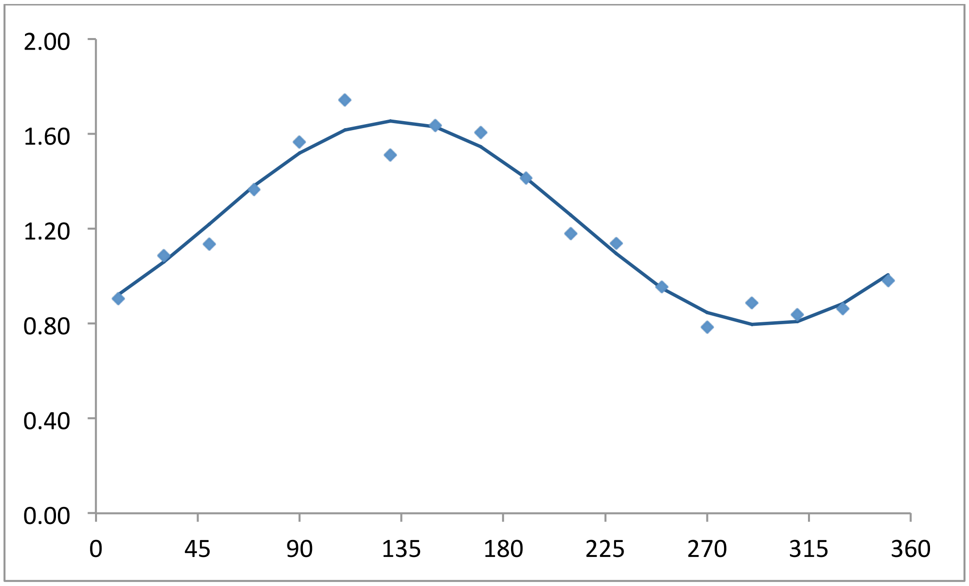
$R^2 = 0.94$



Scale: 100 m^2

$y = 1.22 + 0.24 \sin(0.02\,x) - 0.35 \cos(0.02\,x)$

$R^2 = 0.96$



(4) Pg 7112, section 2.4.2 and pg 7116, section 3.2: Why was a multivariate analysis not conducted for gap area fraction? It would be good to assess potential interactions between the explanatory variables for this response variable as well. This needs to be done.

Response: It would be very interesting indeed to have a multivariate model for the gap area fraction, however, the nature of the gap area fraction statistic, combined with the scale of the study site, does not allow for these analyses. The approach used to fit a multivariate model for lambda allows for enough replication by using a gap-based approach in a Bayesian modeling framework. Such approach cannot be used for modeling gap fraction, as the calculation of gap fraction is intrinsically linked to an area; thus, for gap fraction to be calculated for a subset of gaps, a plot has to be created. Dividing the BCI landscape systematically into plots presents the following problems: i) for a small plot size (<10ha), there are issues with the sample size for gaps and edge effects appear (there is the issue of gaps that are intersected by the edge of the plot); ii) for a large plot size (50-100ha), the extent of the landscape does not provide enough replication for all the combinations of the explanatory variables and there is the issue of capturing the variability of these variables across each plot.

(5) Pg 7116, line 20: Don't forget that in many gaps, regeneration comes from damaged trees that survived (i.e. resprouts).

Response: In agreement with the referee's comment we will modify the sentence to:

Small gaps are more likely to be filled by growth from adjacent trees, resprouts from surviving trees, and seedlings of shade tolerant tree species

(6) Pg 7117, line 25: Perhaps it could also be that, on steep slopes, trees fall before they can get too big, thus preventing big gaps (same goes for gap area fraction in section 4.2). Perhaps this could be checked by assessing a relationship between tree DBH and canopy height with slope.

Response: The referee makes a valid point, however the pattern across BCI is quite the opposite: there is a shift in the canopy height distribution towards higher canopy height as slope increases, while the observed pattern of smaller gaps at greater slopes is maintained.

Distribution of slopes and canopy heights across the BCI landscape.

			Canopy Height (m)			
Slope (o)	Area (Ha)	Freq. (%)	Mean (m)	SD (m)	Min (m)	Max (m)
0 - 2	373.3	26	20.3	7.1	0	47.0
2 - 4	392.4	27	21.8	7.0	0	51.2
4 - 6	236.9	17	23.3	7.1	0	52.7
6 - 8	147.6	10	24.1	7.0	0	50.2
8 - 10	94.0	7	24.9	7.0	0	49.5
10 - 14	106.3	7	25.7	6.9	0	52.1
> 14	83.8	6	27.0	6.7	0	53.2

In terms of the connection between DBH and slope, this can only be verified through the contrast between monitoring plots, as DBH of trees is not recorded across the whole of BCI's landscape; when comparing the 50-ha monitoring plot which is mostly comprised of old-growth forest with a neighboring 25-monitoring plot over old secondary forest, the pattern is consistent with that between canopy height and slope across the island.

(7) Pg 7118, lines 14-15: This could be explained in a little more detail. Perhaps soil type did not have a strong effect because it covaries somewhat with forest age (based on looking at Fig. 1, the authors' comment here, and the comment in line 25 on this page).

That age stayed in the overall model and soil type did not does not definitively negate a role for soil type (i.e. because of possibly significant covariance). As topography (other than slope) had little effect on lambda on its own, I am less worried about its covariance with forest age.

Response: It cannot be denied that soil and forest age covary, however, the hierarchical approach followed in the multivariate analyses, by which each variable is considered separately and then the remaining additional variables are added one by one in all possible combinations, combined with the comparison of DIC weights allows us to infer that forest age has a higher explanatory power on the variation of lambda than soil type.

In agreement with the referee's comment, this does not negate an effect of soil type, which might very well be present; it only means that the effect of soil type is smaller relative to slope and forest age.

Response to anonymous reviewer 2

We appreciate all the insights and suggestions about the manuscript.

SPECIFIC COMMENTS

(1) Forest age is a fundamental variable addressed by the paper, and the authors allude to a long history of research on BCI enabling them to map forest age at a high degree of spatial resolution (Figure 1a). However it is unfortunate that there is no description or critique of the techniques used by previous authors to determine forest age, which is required to justify confidence in the high spatial resolution inferred by this study (Enders 1935 is not available to me). It is particularly important to convince readers that previous researchers did not infer forest age based on forest structural criteria (which is a perfectly valid technique, but would then require circular reasoning for Lobo & Dalling to use the forest age data in models explaining one element of forest structure). There is also an unexplained disparity between the age classifications claimed by the original authors (apparently five age classes) and the coarser resolution adopted in this paper (old growth vs old secondary). If you're confident in the original authors' classifications, why abandon the opportunity to analyse at higher temporal resolution ? If you're not confident in those classifications, then is the 1 m2 spatial resolution justified ?

Response: It appears from the reviewer's comments that there might be some misunderstanding as to the spatial resolution and nature of the different variables used in this study. The study involves categorical variables, such as forest age and soil type, as well as numerical variables, such as canopy height, slope, topographic exposure and aspect. Not all variables are recorded at *the same spatial resolution and with the same accuracy. Specifically, canopy height, which is used to then define gaps and gap areas, is available at the 1 m spatial resolution. Results from a prior study by (Lobo and Dalling, in review) indicate that using the finest resolution available to derive gap areas provides a significant improvement over coarser spatial resolutions and ground-based assessments (also see Kellner et al 2009 and Kellner and Asner 2009).*

The original classification for forest age uses historical information on forest structure as well as forest compositional information to differentiate the 5 classes. Thus, we decided to use a simplified classification of forest age into the two age classes that is supported by historical records. For example, an aerial photograph taken of BCI in 1922 shows a clear distinction between tall (old growth) forest, and short regrowth. While this is a classification based on structure, these historical records provide an unambiguous basis for delimiting old growth and secondary forest.

Finally, as to the spatial resolution of variables used in the model, please note that variables have been introduced into the model at the spatial resolution at which they seem to have an effect on gaps. For example, slope is available at the 1 m scale, but the model for lambda uses slope at 10 m scale, as it is at this scale that it has an effect on the gap distribution.

(2) Pg 7107, line 20: Can we assume that the soils correlate fairly well with the geomorphological units? I see now in section 2.3.3 that soil type was actually the variable used in analyses, rather than geomorphological unit. Perhaps this should be briefly mentioned here.

Response: The soil type is linked more closely to the underlying geology (see Baillie, I., Elsenbeer, H., Barthold, F., Grimm, R., Stallard, R.: A semi-detailed soil survey of Barro Colorado Island, Panama, Smithsonian Tropical Research Institute, 54 pp., 2006.) than to the geomorphological unit (plateau, ridge, slope, valley). We studied soil as an explanatory variable because we expect soil type to affect gap formation through effects on the probability of tree fall related to soil properties, e.g. soil texture and depth, fertility and soil moisture holding characteristics. We also explored how topographic variables, namely slope and topographic exposure, influence gap characteristics independently of soil type.

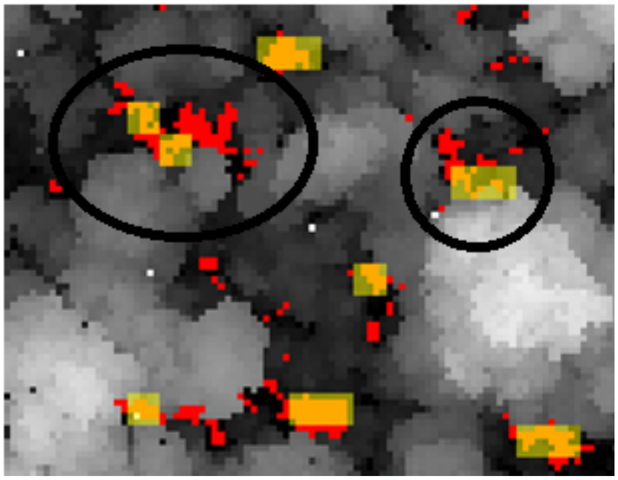
(3) Second, I'm puzzled as to why the authors chose a canopy height threshold of 5 m for defining gaps. I appreciate the choice is essentially arbitrary, and as they point out one limitation of prior work is that different authors have used different height thresholds, but at least one well-cited author (Brokaw) applies a threshold of 2 m and it's a shame this paper doesn't take the open opportunity to determine the sensitivity of their conclusions to variation in this threshold – an obvious methodological assumption that could be tested.

Response: This is a good suggestion and we will comment on the sensitivity of our findings to the canopy height threshold in a revision to the paper. We excluded it from this manuscript because we have completed a detailed analysis testing the effects of canopy height threshold on gap disturbance metrics in another paper (Lobo and Dalling, in review). The results from that study *show that for BCI, the gap size distribution can be studied as fractal with respect to canopy height. Thus, it is possible to interpret the results from the canopy height threshold with respect to this pattern. The 5 m threshold for canopy height was chosen because we are interested in interpreting canopy gaps with respect to the recruitment of gap-dependent species; this is done in a separate manuscript, where we compare our results with those of Hubbell et al. (1999), who also used a 5 m canopy height threshold for defining gaps. Additionally, our field observations indicate that a 2 m threshold for canopy gap detection is too conservative, and does not correlate well with tree recruitment.*

(4) The method for defining gap area also needs more complete description and justification. In the sentence "all contiguous 1 m2 quadrats with a canopy height ..", does the definition of contiguous imply that the quadrats are adjacent and share a common edge, while adjacent quadrats that only share a common corner are not contiguous. Thus a quadrat can only be contiguous with a maximum of four adjacent quadrats, and not eight ? On the ground, real gaps are often broken up by relict trees and overtopping crowns that break-up their contiguity based on vertical-projection methods for defining gaps (which is why some authors extend their concept of a gap to include an area up to the base of adjacent large trees). Again, testing the sensitivity of the models to different approaches to defining gaps would have provided interesting methodological context.

Response: Our definition of gaps aggregates quadrats that share a common edge but not a corner. We agree with the referee that the method for defining gaps affects the results. As mentioned earlier, different methods for defining gaps and their consequences for the gap size distribution are studied in a different manuscript (Lobo and Dalling, in review)

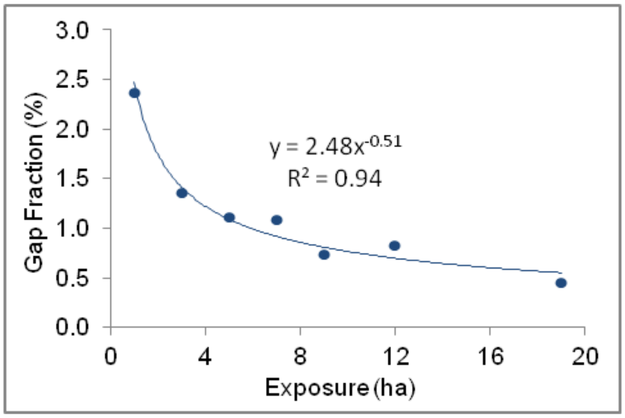
However, with respect to the reviewer's comments, much of the variation in gap area that could be caused by the definition of 'adjacent' is avoided by using a spatial resolution of 1 m in the measurements of canopy height. Even when gaps are highly irregularly shaped, there is a strong likelihood that at least one of the 1 m^2 pixels will share an edge with an adjacent pixel 'connecting' parts of a gap. The problem of arbitrarily dividing single gaps that lack connection points becomes more severe with larger pixel sizes. This is apparent in the figure below where the total gap area for the two gaps circled in black is much larger using the 1m^2 resolution (red pixels), than 25m^2 pixels (yellow pixels), and where in the case of the left-hand gap, the gap would be sub-divided into two smaller adjacent gaps using 25 m^2 pixels.



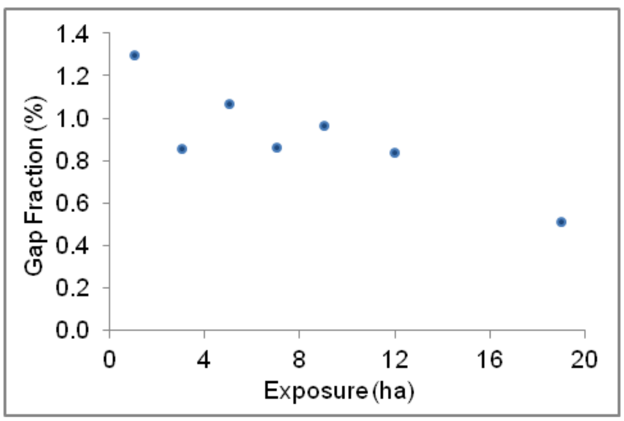
Pg 7119, line 20: Were not the lake vs. terrestrial exposure analyses intended to help sort this out? Results concerning these two measures were not given for the gap area fraction.

Yes, that was the original purpose, but as results did not provide any clarity to the interpretation of exposure they were not included in the article for simplicity. See remaining graphs below

Exposure to Terrain



Exposure to Lake



Total Exposure