

Interactive comment on “Spatial trends in leaf size of Amazonian rainforest trees” by A. C. M. Malhado et al.

A. C. M. Malhado et al.

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Here, we immensely thank the referee J. Lloyd and the anonymous referee for all their constructive comments on our work, and hope we have satisfactorily addressed all comments, as detailed below.

Section 1; Comments by Referee 1- J. Lloyd

1. J. Lloyd (Referee) Paragraph at the end of p2128, start of p2129: This comes across as a little contradictory; first we are told small leaves assist in the avoidance of heat stress and reductions in photosynthesis, then we are told under low nutrient conditions, we have small leaves because there is no point in having larger leaves because increased temperatures cannot benefit photosynthesis. In any case, is that really the whole story for the theory of smaller leaves under oligotrophic conditions. For

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example, is it also related to increased sclerophylly and increased structural defenses for the same C investment?

Malhado et al. (response) We agree that the sentence needs clarifying since these theoretical predictions explicitly assume that all other traits are invariable. We have made this more explicit, modified the sentence dealing with water availability, and have added an additional sentence that deals with the possible effect of other adaptations such as sclerophylly: However, predictions such as those above need to be treated with caution and may not hold true under all circumstances since leaves may have other adaptations (e.g. Sclerophylly) that strongly influence the optimal strategy under any particular set of environmental conditions.

2. J. Lloyd (Referee) The statement of "increased water investment costs would therefore be expected to favour smaller leaves" might also be refined. Presumably, what is meant more here is "reduced water availability", unless the argument is higher root investment results in less C available for foliar development. In short, this paragraph needs a bit of improvement and refinement.

Malhado et al. (response) See above, paragraph has been refined.

3. J. Lloyd (Referee) Last paragraph p2129: Perhaps here it should already be stated here that the general idea is that variation in leaf area per branch (or unit stem area) in predominately accountable for by variations in leaf size rather than leaf number. Indeed, it would be good to know just how much evidence there is for this assumption.

Malhado et al. (response) This is a very interesting correlation but in this paragraph we are specifically discussing branch architecture and leaf size in the terms of allometric relationships (and potentially mediated through a range of physiological constraints - see Midgley & Bond 1989). We agree that exploring the evidence underlying these assumptions would be fascinating but beyond the scope of the introduction to this article.

4. J. Lloyd (Referee) p2133, Section 2.3: Wouldnt maximum tree height (as in the

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RAINFOR database) be more appropriate here. Or are we assuming that for any given species leaf size changes systematically as trees grow taller?

Malhado et al. (response) Yes, this would be a clever solution - however see discussion (point 10) below.

J. Lloyd (Referee) p2134, section 2.4: As far as I know, this is the first time the "Pioneer Index" has been used. Perhaps it would be nice to give some indication of its validity. For example, a simple measure of agreement between the three assessors. Kendal's coefficient of concordance would be one possibility. I am also skeptical about applying standard parametric statistics to such an Index as seems to be done in Section 3.3.

Malhado et al. (response) The pioneer index has already been used in at least one paper (Butt et al., 2008) and has been discussed at length among the RAINFOR/ATDN team. For the purposes of developing the pioneer index, the pioneer concept was defined for the experts as "plants that are specialists in forest gaps and other disturbed areas";. However, we agree that a systematic analysis of the validity of this index would be useful; and is something more productively done by the co-authors of this index. Therefore, we feel that it is beyond the scope of the current paper to produce a sufficiently detailed and robust analysis.

5. J. Lloyd (Referee) p2135, last paragraph: The Quesada (2008) reference should now probably be: bgd-2008-0243 (Quesada et. Al 2009)

Malhado et al. (response) Reference has now been changed.

6. J. Lloyd (Referee) Also, why (on earth) just use sum of bases as the fertility indicator ? Other factors such as "available" P are just as valid, if not more valid fertility indicators. There are also the results from PCA ordinations which have been used with some success as predictors of other leaf properties (as for example in the Fyllas et al. paper in this special issue). A PCA ordination relating primarily to soil fertility is also in the Quesada paper cited above and would probably prove more informative as a predictor

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Malhado et al. (response) It was Quesada himself, the lead author of the soil studies in Amazonia, who thought that the sum of bases was the most appropriate metric – or at least a sufficiently good indicator. The rationale behind this is that the dynamics of P and bases in the soil is correlated. P comes from rocks and are lost in the soil by lixiviation and the left over in the soil might also became a residual. In the bases case, they are not lost at the same way, although their mobility is higher in the soil.

Given that Quesada was the ‘owner’ of the RAINFOR soil data and just gave us the data used in the analysis we were somewhat directed. Nowadays, we could indeed make the analyses suggested, but there are people within the RAINFOR network currently doing a detailed study of all traits in the RAINFOR database and it is highly probable that this analysis is currently being done, so we prefer to avoid any conflict.

7. J. Lloyd (Referee) p2136; Section 2.6: It is excellent that attempts have been made to account for spatial autocorrelation, but also what we are looking at here is essentially compositional data. Has some sort of transformation been made to account for this? And if not, then why not ?

Malhado et al. (response) All the frequency data was ArcSine-square root transformed. The compositional data was analysed with both ArcSine-square root transformation and untransformed but this did not influence the results. For this reason we reported the untransformed data.

8. J. Lloyd (Referee) p2137 and elsewhere: I don’t think it excessively pedantic to point out that proportions vary between 0 and 1 and percentages between 0 and 100. Given that one of main advantages of Biogeosciences is that colour figures can be presented at no extra costs, I wonder in the clarity of Figure 2 and other bar charts could be enhanced using colour presentation.

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Malhado et al. (response) Figures redone as requested.

9. J. Lloyd (Referee) p2141; Section 3.3 See my previous comments w.r.t. pioneer index.

Malhado et al. (response) Redone using non-parametric statistics.

10. J. Lloyd (Referee) p2141; Section 3.4 I would certainly like to see the rationale for "controlling for dbh" better explained. If traits are co-ordinated, then why do this? Also, see previous comments about appropriate soil fertility indices. Further, why not test for water availability and moisture effects jointly (and I would suggest perhaps using spearman's rho as is available in SAM? Why one earth should any of this be linear!? Finally, what is the rationale for analysing within different regions as well as across the Basin as a whole Whatever the rationale, then certainly some correction for multiple testing surely has to be made.

Malhado et al. (response) At the time of analyses of the data we felt that controlling for DBH was a logical way to control for differences in composition between plots and regions. However after reflecting deeply on your comments, and taking into consideration that the leaf data is associated with species identities rather than individual trees, it seems probable that partitioning the data in this way is not generating any additional insights; and, indeed, did not reveal any significant patterns. For these reasons we feel it is better to remove it from the analysis.

11. J. Lloyd (Referee) p2143; section 4.1: Doesnot one saying that there are smaller leaves in the Guyana shield region just because of more Fabaceae just add up to saying leaf size is itself ecologically irrelevant?

Malhado et al. (response) No, it just implies that the effects of phylogeny and adaptation are difficult to untangle here. However, the paragraph has been re-written to focus on the special ecology of the Guyana Shield region (see work by ter Steege) that creates a unique environmental template for the vegetation of the area.

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12. J. Lloyd (Referee) Is it also worth noting that ter Steege et al. (2006) did not correct for spatial correlation? Perhaps their results would have been very different if they did?

Malhado et al. (response) Yes, this is true. This point has now been raised at the discussion section 4.1.

13. J. Lloyd (Referee) Although not providing direct support for the work of Webb (1959) and Dolph and Dicter (1980) perhaps it would be good to make clear the magnitude of the precipitation gradients studied here relative to those studies (along with the absolute range). If for example this study had extended to the dry deciduous Chaco forests of Bolivia (for which Killeen and colleagues have full species compositional data and floras from which leaf sizes could be inferred), then perhaps a gradient might would have indeed been found.

Malhado et al. (response) Thank you bringing this to our attention. Our original statement certainly required clarification; which we have now done. We have re-written the paragraph for better comparison with Dolph & Dilcher work. On reflection, we felt that Webb's work did not provide a robust enough comparison with our study and have therefore removed this reference. These changes have allowed us to provide a more nuanced discussion of this issue.

14. J. Lloyd (Referee) The Discussion would also benefit greatly with some consideration of soil nutrient effects (or lack thereof), again with reference to the range observed in Amazonia as compared with other studies (though in this case they are probably larger).

Malhado et al. (response) A critical consideration of the soil data has been added to the discussion.

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