

## ***Interactive comment on* “Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate” by N. M. Fyllas et al.**

**N. M. Fyllas et al.**

Received and published: 29 September 2009

We would like to thank the referee and editor for their comments on our manuscript. Here we try to respond to the issues raised.

Referee 1 comments

General Comments

This paper is written for a diverse audience ranging from tropical field ecologists to ecophysiologicals and vegetation dynamics modellers. This was the reason for presenting data on and exploring a range of hypotheses from phylogenetic trait variation to pairwise inter- and intra- specific scaling relationships. Nevertheless, we accept Referee 1’s criticisms that our first draft lacked a clear focus for its main audience and the manuscript has thus been revised and shortened. It is now substantially shorter

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Discussion Paper



(less than 10000 words). We have also reduced the number of figures and statistical tests presented as indicated by the reviewer. It still remains a relatively long paper but we believe that this dataset should be presented, analysed and discussed in a holistic manner.

The new manuscript is also reorganised with three clear hypotheses stated at the introduction, which are subsequently tested and discussed under the respective headers.

One of the main concerns raised by Reviewer 1 (see also Technical Comment) was the way sites were classified into low and high fertility groups. In the earlier version of the manuscript a breakpoint in soil fertility was empirically identified using the value of total reserve bases  $S_{rb}$  as described in Quesada et al. 2009. Here a breakpoint in the continuum of soil properties is estimated using broken line regression models (Muggeo, 2008). An example is given in Fig. 1 with a regression of soil P concentration against  $\log_{10}(S_{rb})$ . Broken line models of soil pH, P, N, C, Ca Mg, K cation exchange capacity against  $\log_{10}(S_{rb})$  were fit and the overall breakpoint in soil fertility was estimated as the mean value of the separate cases. This shift in the breakpoint value (from 80 to 130  $\text{mmol kg}^{-1}$ ) leads to a reclassification of only two sites. Subsequently all the analyses using classification of species and/or environmental effects have been repeated and the new estimates are presented in the respective tables.

Referee 1 also suggested that sites should not be divided into a low and a high fertility groups, and if so it would be better to use the PCA scores of the sites instead of their  $S_{rb}$  value. We agree with him/her that soil fertility may be better represented as continuous variable, and in this paper such a measure of soil fertility (first PCA axis) is later used (Section 3.7) as a driver of plot-environmental level variation of leaf traits. However  $S_{rb}$  provides a good measure of soil fertility and it is a property relatively easily quantified and frequently recorded in field studies. Thus it could also be used in other studies as a first estimate of soil fertility without having to measure and analyse the full set of the soil properties recorded here.

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Discussion Paper

---

Interactive  
Comment

We have also made clearer the purpose of classifying sites into low and high fertility groups  $S_{rb}$ ; that is to test if at least at these extremes exists or not a difference in the functional relationship between pairs of key traits. This classification was also implemented in order to allow comparisons with results of other studies (e.g. Townsend et al 2007), where soil type and plant diversity have been shown to significantly affect pairwise relationships as for example leaf N vs P concentrations. In addition by using  $S_{rb}$  as a fertility measure we tried to derive a more objective way of separating between fertile and infertile sites. Likewise, Kattge et al. (2008) have also examined photosynthesis/nitrogen relationships for trees also making distinctions between fertile ("oxisol") versus infertile("non-oxisol") soils. Interestingly using SMA regressions no difference in the slope of the genetic principal axis was found for most pairs, suggesting that the inherent way Amazonian trees are allocating their resources to photosynthetic tissue is common. However a shift along this common axis was identified suggesting that under different soil conditions trees are functioning at discrete ranges of this common axis. As we show in a subsequent paper (Patino et al.) where a full blown PCA (as also requested by referee 1) is done (including other traits such as wood density, Huber values, leaf size, seed size, maximum tree height, etc) this distinction between "low" and "high" fertility soils assumes a new importance as the weightings for some of the main eigenvectors depend on the fertility on which the soil is growing.

Another key concern raised by referee 1, was the validity of the hierarchical/multilevel modelling approach to partition the variance and provide accurate estimates of the foliar properties of interest for the genetic and the environmental component. The hierarchical modelling technique can be used in unbalanced samples (Gelman and Hill, 2006; pp. 246) with even one observation per group (Gelman and Hill, 2006; pp. 276); and this is now explicitly pointed out in the revised manuscript. Moreover, we have additionally verified the technique and its results by conducting a simulation study, where we stipulated a the variance partitioning for a range of traits as well as species and plot level effects, the computer program sampling individuals in a highly unbalanced manner similar to our actual sample. Subsequently we retrieved the (known) genetic and

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

environmental effects for the artificial population, in addition to partitioning the trait variations between species and plots (and with residual effects) using an identical REML approach. This additional analysis is presented in Supplementary information where we show that even with such an unbalanced sample the REML approach is appropriate for estimating the components of interest and further analyse them.

Specific Comments 1. Histograms of trait variation have been moved to supplementary information (SA1). We kept this figure and not deleted it as suggested by the reviewer as it gives a nice overview of the shift in the distribution of traits between fertile and infertile plots.

2. Partition of variance. Please see discussion on why some traits are more genetically and others environmentally controlled in section 4.1.

3 and 4. Family Genus and Species trait variation results are now presented and discussed in Appendix A, thus maintaining the general flow of the manuscript as suggested by Reviewer 1.

5. The relationships presented in Fig. 3 (former Fig. 6) between pairs of genetic component have been selected based on their general interest (N-MA, P-MA and P-N) as well as based on the identified very high correlation (K-P, Mg-Ca). The classification of sites to low and high fertility groups is now done by using the broken line regressions technique discussed above.

6. In Fig. 4 (former Fig. 7) we now use the same panels with Fig. 3 as suggested by Reviewer 1. Additionally in section 3.6 we summarise how often the slope of the principal axis is similar for the genetic and environmental component indicating a similar functional relationship between trait pairs.

7. Table 3. This table has been deleted and now a single line is been used (aggregating fertile and infertile plot) in Table 1 for the plot-environmental component.

8. Former Table 4 is now Table 3.

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

9. The multiple regression along with the spatial autoregressive model results have now been moved to appendix B.

10. Table 4 (former Table 6) and Fig. 5 and 6 have been retained and further discussed in the respective section of the manuscript (4.3 Environmental predictors of foliage properties variation).

11. Results and discussion on N-Fixers are now in Appendix A, along with the presentation of Family, Genera and Species effects.

12. As discussed above and now detailed in the supplementary information, the multilevel random effects models used in this study to partition the variance into a genetic and an environmental component can be applied to unbalanced samples even with only one measurement per species.

13. The manuscript has been restructured and it is now shorter and simpler compared to the earlier version. Three hypotheses have been formed tested and discussed with the respective headers. An additional section has been added in the Discussion which compares the identified axes of coordination for our Neotropical dataset with the ones identified in other worldwide data.

14. The aim of this paper is to explore the variation in some key physiological properties of Amazonian tree species and to identify their main source of variation. Additionally we explored the relationship between key trait pairs and tested for differences in their functional form along soil fertility gradients. A multivariate analysis of this dataset will be presented in two new papers i.e. Patino et al.1 and Fyllas Lloyd and is not included in this study.

N. Fyllas J. Lloyd

#### Reference

Gelman, A. and Hill, J.: Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, 648pp, 2006.

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)

Kattge, J., Knorr, W., Raddatz, T. and Wirth, C.: Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, 15, 9768213;991, 2009.

Muggeo, V.M.R : segmented: An R Package to Fit Regression Models with Broken-Line Relationships *R News*, 8(1), 20-25, 2008.

Quesada, C. A., Lloyd, J., Schwarz, M., Martinelli, L., Patino, S., Baker, T. R., Czimczik, C., Fyllas, N. M, Martinelli, L., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luiz732;ao, F. J., Arneeth, A., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Moraes Filho, J., Paiva, F., Araujo Filho, R., Chaves, E., Cruz Junior, O., Pimentel, T. P. and Paiva, R.: Chemical and physical properties of Amazonian forest soils in relation to their genesis, *Biogeosciences Discuss.*, 2009.

Townsend, A.R. Cleveland, C. C., Asner, G. P. and Bustamante, M. M. C.: Controls over foliar N:P ratios in tropical rain forests. *Ecology* 88, 107-118, 2007.

#### Related papers

Patino, S. et al.: Relationships Among Ecologically Important Dimensions of Plant Trait Variation in 53 Neotropical Forests as Affected by Soils and Climate (in preparation for *Annals of Botany*)

Fyllas, N.M. and Lloyd, J. : Deriving plant functional types for Amazonian forests using numerical techniques (in preparation for *Journal of Ecology*)

---

[Interactive comment on Biogeosciences Discuss.](#), 6, 3707, 2009.

[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)[Discussion Paper](#)