Interactive comment on “Coordination of physiological and structural traits in Amazon forest trees” by S. Patiño et al.

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General Comments:

This manuscript presents a comprehensive analysis of a very impressive dataset on functional trait measures for Amazonian trees. Extending on some of the trait or tissue-specific analyses that have formed the basis for other papers, including those appearing in a special issue of this journal (e.g., Patino et al. 2009 for wood density; Fyllas et al. 2009 for leaf chemistry and morphology; Malhado et al. 2009 for leaf size; Baker et al. 2009 for species maximum height), this paper seeks to examine patterns of trait correlations and the factors contributing to the distribution of different ecological strategies of trees across the Amazon basin. The manuscript adds at least two novel components. First, it integrates leaf and wood traits that had previously been analyzed separately...
in this dataset. Second, it adds new trait data, including a novel index integrating leaf area and wood density, and height and seed mass information at higher taxonomic levels. I commend the authors on the work they have accomplished. Not only are the data amazing but the group is also proven in innovative approaches to data analyses, resulting in a wealth of information of potential interest.

I have three major comments that are inter-related, so I will present them rapidly and then make broad suggestions for improving the manuscript. First, echoing the first reviewer, I think the current submission suffers from the very strengths of the data – with so much to present, the specific research questions and their originality are not clear without several reads. I find this unfortunate as it may discourage many readers from discovering the jewels that sometimes remain hidden. A second and related point is that the writing and organization is often muddled and difficult to read. I believe this is in large part due to a lack of clear orientation and structure to respond to specific questions; in many places as well this simply requires better proofreading and editing which can be improved following specific comments by the first reviewer and below. A third point is that the originality of the manuscript above and beyond what has been published with this dataset (and others) is not always clear. At times, it is presented as the addition of novel traits, at times as more sampled individuals, and at times as a broader approach. I think in fact a clear decision on the questions and original contribution envisioned will help to streamline the manuscript and restructure it into a clear and readable piece of work.

To solve these issues, I would suggest a broad restructuring of the manuscript. I understand that part of the novelty in the approach presented by Fyllas et al. (2009) and continued here, is integrating environmental measures with multivariate analyses of trait coordination. Nevertheless, it remains unclear if the central point is to focus on trait coordination while controlling for environment, or rather to examine the effect of environmental variation on suites of traits. I believe the current analyses are most consistent with the former, particularly, as I note below, because the issue of within-
species variation is not dealt with as explicitly here as it was in Patino et al. (2009). A potential framework would therefore centralize the definition of coordinated traits, asking what are the major axes of trait variation in the dataset, especially when including life history traits such as seed mass and height (invoking the LHS scheme of Westoby). This would play to the original contributions of novel traits. Then, a second question would be the extent to which these sets of coordinated traits are influenced by environmental variation. For the latter, it would be most useful to treat both changes in floristic composition and within species variation (as in Patino et al. 2009), neither of which is addressed adequately here. I would also suggest laying out specific hypotheses for this second part about what may drive changes in trait coordination across the gradient (e.g., environmental filtering vs. biogeographic differences in floristic composition).

Within any chosen framework, I would also like to see the following points addressed more explicitly.

The seed size and height data, which form a large basis of the originality of this submission, are not collected with the same precision as all of the other data in the analysis. This is troubling for at least three reasons. First, it unavoidably limits the extent to which within-species analyses can be performed, as the metrics are generally species-level estimates. The implications of this should be discussed, especially given that the very mechanisms invoked to explain basin-wide variation in trait coordination (forest turnover rates with edaphic constraints, cf. Quesada et al. 2009) may also affect the maximum height or even the seed mass-fecundity allometry of a given species. Second, the seed data were applied as genus-level means and for many large genera present in this dataset (e.g., Pouteria, Ocotea, Eschweilera) there is rather broad variation in seed mass that may mask or even invert the patterns reported here. Third, the maximum height data were recorded from a variety of sources and a variety of sites, often from herbarium records that are known to be imprecise (rounded to nearest 5 or 10m). Please discuss the precision and provide the proportion of species for which higher-level taxonomic means were substituted as described in Baker et al. 2009.
Then, please add more discussion of the extent to which these imprecisions may bias the interpretations of trait coordination that you report.

I would prefer that the authors not refer to taxonomic contributions to trait variation as ‘genetic’ controls. Although the attribution is technically true and was published in the earlier Fyllas et al. 2009 paper, it connotes equivalence between taxonomic distances and more precise phylogenetic distances, which clearly vary for the same taxonomic scale among different clades.

A related point is a reiterated suggestion to analyze and discuss within species variation in the dataset. I recognize that some of this will be of limited novelty (as seed size and height would be excluded), but it would permit a novel and important extension of the analyses in Patino et al. 2009 in a way that to my knowledge has not been treated with the leaf data.

I think too much attention and space (particularly figures and discussion) are spent explaining bivariate relationships in the dataset. I agree that bivariate relationships help to explain physiological tradeoffs represented by the dataset, but I think that they could be chosen for specific examples of a multivariate analysis that is most appropriate to the research questions as I have interpreted them.

I gratefully acknowledge that this review was prepared following discussions with my colleague, Claire Fortunel (claire.fortunel@ecofog.gf).

I also apologize for delays due to my late review, and I invite the authors to contact us with any questions.

Cordially,

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Specific Comments and Technical Corrections:

In addition to the comprehensive list of corrections pointed out by an earlier reviewer, I
would add the following:

Abstract:

Page 5084, line 3-4: What do you mean by “plants modulate their structural investments to best maintain and utilise their physiological capabilities”? This sentence is a bit confusing since plant physiology doesn’t depend on structural investments alone and plant traits cover various aspects of plant morphology, physiology and phenology.

Page 5084, line 6: you say that you added trait data (leaf area to sapwood area ratio, leaf and leaflet area) for 1040 species in 53 plots, but at the end of the introduction (page 5088, lines 16-17) you say that these traits were measured on 661 species in 52 plots, while in the discussion you talk about 1021 species and 53 plots (page 5103, line 10). Which are the correct numbers in the present paper, and what data is novel relative to that presented in Patino et al. 2009, Fyllas et al. 2009, Malhado et al. 2009, and Baker et al. 2009?

Page 5084, lines 7-9: It’s nice to have trait abbreviations from the abstract, though it’ll be nice if you could use common abbreviations (e.g. LMA for leaf mass per unit area) and also use something else than S for seed mass (S being used to designate vessel size to number ratio in wood by Zanne et al. 2010).

Page 5084, lines 14: The leaf economics spectrum (LES) as defined by Wright et al. 2004 included LMA, LL, LNC, LPC, Amass and Rmass. As such it is a combination of your first two axes, so you can’t say that your 2nd axis is a “classic LES”. Moreover, remove “increased individual” and “higher”. Simplify by saying that LA and Φ were newly identified as part of your 2nd axis.

Page 5084, lines 21: Remove “also”.

Page 5084, lines 26-28: This sentence is unclear. Clarify what you mean to say on trait coordination.

Introduction
Page 5085, line 8: What do you mean by “identifying important evolutionary adaptations”? Traits can be random, conserved or overdispersed in the phylogeny and you can conclude on their pertinence to study evolutionary aspects until you test that.

Page 5087, lines 4-8: You introduce the very important aspect of intra-specific variability in traits, but you haven’t tested it in your study. I strongly suggest adding this analysis during revisions.

Page 5088, lines 19-27: The end of the introduction doesn’t clearly state what the expectations/hypotheses are. The reader doesn’t know what original results to expect from the paper.

Materials and methods:

Page 5090, line 2-4: Following above comment, please provide more information on the precision of the seed mass and maxheight variables.

Page 5090, line 5: Replace “related” by “physiological”.

Page 5091, lines 2-7: Please provide some summary information from the Quesada et al. papers regarding relationships of climate variables to soil factors.

Page 5091, line 24: From what you said before, you actually ran the model on 4 traits? leaf area to sapwood area ratio, leaf and leaflet area, and branch xylem density?

Page 5091, line 25: In the formula, why leave out the interactions among the terms?

Results

Page 5094, lines 24-25: we would expect the opposite pattern, i.e. lower leaf carbon content but higher leaf nutrients contents in more fertile environments.

Page 5095, lines 2-13: It is confusing for the reader that most results of trait variance partitioning are in Fyllas et al. 2009 and Patino et al. 2009 papers. It would be appropriate to quickly summarize the results for these traits (leaf nutrients, LMA, wood
density) here, especially since the PCA on traits and environmental factors show that most traits varied with environmental factors (Table 4).

Page 5095, section 3.4: If you focus on the taxonomic component of traits, why discuss trait variations between fertile and infertile soils in this section?

Page 5096, line 10: It’s the opposite! Replace “lower fertility” by “higher fertility”.

Page 5096, lines 14-21: Simplify these 2 sentences.

Page 5097, lines 9-10: Is $\Phi$ conserved or variable?

Page 5099, line 6: You cite fig. 8a-c before mentioning fig. 7.

Page 5099, lines 9-10: Is there a significant difference of correlation with these two axes between species associated with fertile vs. infertile environments?

Page 5100, line 6: Here is fig. 7!

Page 5102, line 7: There is not middle panel in fig. 8.

Discussion

Page 5103, lines 1-4: What is considered as a site here? Plot level? Region level?

Page 5103, line 9: The effort of finely measuring leaf and wood traits is hindered by the fact that the same effort wasn’t put up for height or seed mass.

Page 5103, line 12: Replace “genotype” by “species” or “taxon”.

Page 5103, lines 25-28: The cited references confirm your results on the relationship between wood density and LMA, however they studied relatively few species (6 for Bucci et al. 2004, 32 for Ishida et. al 2008, 15 species for Meinzer et al. 2008), while studies of similar range than yours (2134 species in Wright et al. 2007, 668 species in Baraloto et al. 2010) actually didn’t find this relationship.

Page 5105, lines 9-12: You can’t conclude on “growth response” if you don’t make the
comparison of trait variation along environmental gradients within species, because the trait shift may simply be the result of species turnover.

Page 5105, line 19: Remove “the”.

Page 5105, line 23-5106, line 4: Baraloto et al. 2010 found that wood density wasn’t significantly correlated with LNC, LPC and LKC (Pearson correlation coefficients were -0.2, -0.14 and -0.09 respectively).

Page 5106, lines 22-25: Rephrase that sentence.

Page 5107, line 5: Remove one of the two “that”.

Page 5107, lines 5-19: Are you implying that environmental factors filtered species differently across the Amazon or that biogeographical processes caused the actual species distributions?

Page 5107, lines 25-26: Can you generalize that much the link between mesophyll thickness and photosynthesis from a 5-species study? All the more that, LMA being the opposite of SLA, it is more often associated with lower photosynthesis.

Page 5108, line 26-Page 5109, line 3: Develop the “heat budget” and “herbivory” hypotheses.

Page 5109, lines 4-18: What relationships were you expecting between leaf size and soil fertility? Since you made no hypotheses in the introduction, the reader doesn’t know what’s new here.

Page 5109, line 28: Isn’t it somewhat circular to test the correlation between $\Phi$ and LA since you’re using LA to calculate $\Phi$?

Page 5109, line 29: Replace fig. 6 by fig. 5.

Pages 5112-5114, section 4.1.3: Seed mass was determined at the genus level in this study, so interpretations as to how seed mass correlates with other traits or how seed
mass varies along environmental gradients should be leveled.

Page 5114, line 24-Page 5115, line 16: Most of this is Material and Methods.

Page 5116, line 22: Can you actually say that species have a high axis 1? It doesn’t make much sense. As the other reviewer suggested, try using understandable and simple sentences.

Page 5116, line 25: As mentioned for the abstract, the leaf economics spectrum defined by Wright et al. 2004 included LMA, LL, LNC, LPC, Amass and Rmass. It is thus a combination of your first two axes, so you can’t say that your 2nd axis is a “classic LES”.

Page 5117, lines 19-21: LA was included in Baraloto et al. 2010, so not sure what is implied here. Could you test your correlations with the same set of traits to verify if you would have found the same axes?

Page 5118, line 26: Delete “the” and “,”.

Page 5121, line 18-Page 5122, line 10: This part of the discussion means what - That there should be a minimum suite of traits to test for multivariate correlations?

Page 5122, line 14: Replace “is” by “in”.

Page 5122, line 20: Couldn’t find section 4.4.

Page 5123, line 13: Measuring LDMC in the field for such a large number of species seems hard to achieve since LDMC requires the measurement of leaf fresh mass, which is limiting in the field because of rapid water loss after sampling.

Page 5114, lines 4-10: Inconsistent writing. Leaf nutrients (N, P, K) mirror soil fertility.

Page 5125, line 15: You suppose the effect of intra-specific variation, but again what about species turnover?

Page 5126, lines 10-15: The LES defined by Wright et al. 2004 included photosynthetic
capacities but also leaf construction cost.

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