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Montpellier, 4th of June 2019

Subject: Answer to Round #2 after major revisions

Dear Editor,

We are pleased to send back our manuscript (<https://doi.org/10.1101/351197>) after major revisions on the text. We thank the reviewer for providing another remarkable review of our work, with suggestions which allowed us to improve the manuscript. In the text below we address each point of the reviewer and include further explanations of the modified text where necessary. As the number of modifications in the text is important, we also provided the word file with all comments, and all the history of modifications in comparison to the past version.

On behalf of all the authors, I state that all the material is original and that no part has been submitted for publication elsewhere. All authors have agreed to submission. We declare to not have any source of conflict of interest.

We thank both reviewers and the editing staff for the suggestions and ideas that have improved our manuscript and we look forward to hearing from you.

Yours sincerely,

Sébastien LEVIONNOIS

Number of words (main body)	7282
Number of references	87
Number of figures	3
Number of tables	4
Supporting information	4 appendices and 4 figures

Round #2

Decision

by François Munoz, 2019-09-15 23:19

Manuscript: <https://doi.org/10.1101/351197>

Revision needed

My congratulations to the authors for their thorough revision work, which has substantially improved the manuscript.

I still see a few points that could be improved in a new, rather moderate revision.

The main point will be to make even clearer the central hypothesis that there is some trade-off between organ-level functional traits and growth strategies. In the present version of the manuscript, the rationale is that organ-level traits cannot grasp how species resource use and growth vary with soil type. It would be useful to have 1-2 more sentences making even more explicit the idea that functional traits and growth strategies are not opposed but complementary aspects. Investment in leaf and stem organs needs to be seen over the whole tree life-span and will depend on how the tree develops in space and time.

We re-arrange the 6th paragraph of the introduction in this perspective. Notably with these sentences:

“Easy-to-measure, organ-level, functional traits commonly used in trait-based ecology are appropriate to capture a snapshot image of the resource-acquisition strategy (Baraloto *et al.* 2010). They are generally assumed to be proxies of the individual performance, and therefore to indirectly impact fitness (Violle *et al.* 2007). But functional traits generally measured in trait-based ecology fail to take into account the growth strategy, which integrates the long-term response of the individual to its environment.”

“Here, we combine functional trait approaches with a whole-tree developmental approach based on retrospective analysis to gain complementary aspects of tree phenotypic responses.”

In the same line, the authors stress that a main originality here is to be the first incorporating both tree architectural and functional traits. However it may be not the most interesting, salient point (cf. beginning of Discussion). The most important issues are (i) to question the way environmental constraints influence differently ecophysiological response traits at organ level vs. whole-tree developmental and performance strategy, (ii) these influences differ at between and within-species levels.

We pointed to these salient point in the introductive paragraph of the discussion:

“Here, our integrated approach, combining functional trait and architectural development, showcases how environmental constraints can impact differently on (i) the response of traits between the organ level and the resource-acquisition axis, and (ii) the whole-tree level and the resource-use axis, at least at the intraspecific level. Our study also demonstrated that environmental constraints can also have different effects on traits at the intraspecific and the interspecific level.”

The concept of "performance trait" seems to be quite central (e.g., P10L33, and later on), but it not explained/introduced clearly enough. >From what I understand, the growth and architectural traits represent performance, as indexes of the ability of trees to develop and produce biomass. Most of the functional traits considered here can represent response traits, but it could be made clearer what it implies compared to performance traits in the present ecological context.

This has been made clearer at the end of the introduction (7th parapgraph):

“Therefore, the accumulation of growth and branching over time can be expressed as a growth trajectory, and represents the ability of trees to develop and produce biomass. Such growth trajectory can be seen as a performance trait, as growth is one of the three main components of individual performance directly impacting fitness (Violle *et al.* 2007).”

As also in the first paragraph of the Materials and Methods part: *Terms and definitions*.

In addition, there are clearly two kinds of architectural traits: (i) traits related to developmental units (internode number and length), (ii) trait related to whole-tree level development. It may be made clearer how addressing architectural properties at these two levels convey complementary insights.

This has been made clearer at the end of the introduction (7th parapgraph):

“Therefore, the accumulation of growth and branching over time can be expressed as a growth trajectory, and represents the ability of trees to develop and produce biomass. Such growth trajectory can be seen as a performance trait, as growth is one of the three main components of individual performance directly impacting fitness (Violle *et al.* 2007). Moreover, the analysis of the fluctuation of elementary units (internode length, annual shoot length, number of branches...) through tree’s lifespan conveys complementary insights on the determinants of variation of growth trajectory across trees, and further help to characterize different growth strategies.”

In the discussion, it is noted that the developmental strategies grasped by architectural traits allow a more integrative view on tree performance, but you could also stress that measuring functional traits at a single ontogenic stage may miss important plasticity of the functional traits during ontogeny. It could be a point (iii) on P15-16.

As suggested by the reviewer we added this 3rd point:

“The leaf and wood functional traits we measured can be subjected to strong variation with the succession of tree ontogenetical stages. This ontogenetical effect can be related to changes in local environment with tree growth such as light (Roggy *et al.* 2005; Coste *et al.* 2009; Dang-Le *et al.* 2013). This ontogenetical effect can also be related to mechanical and hydraulic constraints with self-support and long-transport distance (Ryan *et al.* 2006; Niklas 2007; Oldham *et al.* 2010; Bettiati *et al.* 2012; Rungwattana Kanin *et al.* 2017; Prendin *et al.* 2018). Two-to-3 fold variation with ontogeny in leaf and wood functional traits has been demonstrated across several studies (Roggy *et al.* 2005; Coste *et al.* 2009; Dang-Le *et al.* 2013; Rungwattana Kanin *et al.* 2017; Lehnebach *et al.* 2019). As we consider the trajectory of internode length variation as a performance trait, the trajectory of leaf trait variation with ontogeny can be considered as an integrated functional trait with its own functional significance regarding environmental filtering with soil types. Alternatively, it can be hypothesised that environmental filtering with soil types decisively occurs at seedling and sapling stages, therefore leaf functional traits expressed at these stages would be more responsive.”

In addition,

- The first point of the Abstract seems to be a bit too general.
We added one sentence to complete this first point:
“Trait-environment relationships have been described at the community level across tree species. However, whether interspecific trait-environment relationships are maintained consistent at the intraspecific level is yet unknown. Moreover, we do not know how consistent is the response between organ vs whole-tree level”.
- Since the second point does not expose the ecological hypotheses considered and tested here, it sounds a bit too descriptive.
As suggested by the reviewer, we made more explicit our expectation:
“We expect soil types to affect both, functional traits in relation to resource acquisition strategy as already described at the interspecific level, and growth strategies due to resource limitations with reduced growth on poor soils.”
- In Discussion, consider adding a few word about the possible role of growth strategies underground.
As suggested by the reviewer few sentences on this point in the second part of the Discussion:
“Architectural analysis and deciphering growth strategies can also be applied to roots (Atger and Edelin 1994; Charles-Dominique et al. 2009). Root vs shoot allocation pattern can differ with the environment (Freschet et al. 2018). The root growth strategy directly drives to rooting depth, root lateral expansion, and root density (i.e. number of roots and root lengths per unit of soil volume), which will finally determine soil foraging capacity, water absorption capacity, and belowground intra- and interspecific competition.”
- We can note that the differences between WS and FS differ between sites, which may be a major limitation of the study. I would add at the end of the abstract a sentence stating that "Apart from soil differences, much variation was found across sites, which calls for further investigation of the factors shaping growth trajectories in tropical forests".
Thanks for this suggestion. This has been added.

Further comments/suggestions:

P3L3: "are maintained" sounds weird here.

We agree with the reviewer, and we modified by “are consistent”.

P3L9: "early successional forest stages"

We thank the reviewer for this correction.

P3L9-L11: Something is missing here regarding the hypotheses tested here: should we expect influence of soil types on functional traits and growth strategies, and why?

We agree with the reviewer and we added the following sentence: “We expect soil types to affect both, functional traits in relation to resource acquisition strategy as already described at the interspecific level, and growth strategies due to resource limitations with reduced growth on poor soils”.

P3L12: "weak" does not mean no effect. You can underline that "major" functional traits related to basic economic spectra are not involved here, although there is marked interspecific trait variation across soil types.

We agree with the reviewer,, thus we replaced “Functional trait responses to soil types were weak” by “Functional traits were not involved in soil response”.

P3L18: "detect" is not best wording here. It is better to explain the ecological meaning of the response in terms of growth trajectories. You can note that growth strategies allow characterizing and understanding the responses of trees to environmental constraints in a more holistic way.

As suggested by the reviewer, we replaced “detect” by “characterise”.

P3L20: opposing the "architectural approach" to the "functional approach" is not very appropriate. They convey different and complementary insights on the way trees acquire and manage resources over their lifetime.

We agree with the reviewer, thus we underlined the complementarity of both approaches: “The intraspecific variability is higher for growth trajectories than functional traits for *C. obtusa*, revealing the complementarity of the architectural approach with the functional approach to gain insights on the way trees manage their resources over their lifetime”.

P6L11-15: 1-2 references would be needed here.

As suggested by the reviewer, we added 5 references for this part of the introduction.

P7L12-16: I feel it would be more logical to present the 2 points in reverse order. In addition, unclear what "mediated" means.

This has been modified as suggested by the reviewer. Moreover, to follow the logic, associated parts of the discussion have also been inverted. The word “mediated” has been abandoned, thus the related question has been reworded.

P10L33: the concept of "performance trait" is quite central here, and would deserve clearer explanation in the Introduction.

We gave more details at the end of the introduction

P11L15-16: consider reformulating "are modifying their growth strategy".

We modified as follow: “to understand how the trees undergo changes in growth strategy”.

P11L16and20: repeated use of "look at", not very nice wording.

We agree and we replaced “looked at” by “analysed”.

P11L20: what "drive" means here?

We agree that “drive” is sufficiently precise, thus we replaced it by “determine”.

P11L24: "were also measured" Unclear what "whole-tree-level traits" means, since functional traits are measured at organ level (next sentences).

Thank you, we corrected accordingly.

We completed the first paragraph of Materials and Methods “*Terms and definitions*“, and precised the terminology and we modified the text accordingly

P11L26: WSG may also be related to mechanical properties.

We added this information accordingly with “mechanical strength”

P11L28: remove "positioned"

We removed this word accordingly.

P11L29: why talking about "senescence" here? The possible influence of senescence has not been evoked before.

Senescence is applied here to the ageing of the leaf. One can ask why we just measured leaves on A1 axis for the third or fourth nodes, if we do not explain.

P12L6: strange use of "relied on".

We agree with the reviewer and we replaced "relied on" by "conducted"

P12L8: "at stand level"

Thank you, we corrected accordingly.

P12L12-16: I appreciate the concision here, but it is too hard to understand for people not aware of the approach.

We tried to better illustrate what "low-level frequency and high-level frequency fluctuations" refer to.

Citations (Guédon et al 2007 and Zalamea et al 2008) are also here to bring more details to the reader on the methodology

P12L18: missing ")".

Thank you, we corrected accordingly.

P13L3-4: is temporal autocorrelation acknowledged when calculating distances among trajectories?

No, not directly

P13L9-11: I don't get how the effects of seasonality and ontogeny are addressed, insofar as a single leaf is sampled on individuals. Are these effects measured on different trees at different ontogenic stages and/or in different environmental conditions? One more sentence would be useful to clarify the point.

This part of the M&M has been completed accordingly.

P13L9-12: what does "filtered" mean?

This sentence is no longer valid since we now conduct LMER analysis with ontogeny (tree age) as fixed parameter

P13L24-25: more simply, "Fig.1 show significant differences in trajectories..."

Thank you, we modified the sentence accordingly.

P13L31: "related variable" "were not significantly"

Thank you, we modified the sentence accordingly

P14L1: it seems that the variation of annual shoot length is directly related to the variations of internode length and number of internodes per annual shoot?

Yes indeed. We discuss this point in the discussion :

"Regarding the growth strategy, soil type showed a significant effect on both internode length and annual shoot length in Counami, but not in Sparouine. When the soil effect was strong enough, the differences in annual shoot length between soil types corresponded mainly to variations in internode length rather than variations in number of nodes per annual shoot. Reducing the number of nodes per annual shoot would imply the increase of the phyllochron, thus reducing the number of leaves produced per year."

P14L6-7: "covered the largest variation of growth trajectories": how is it quantified?
It was quantified as the range of tree height across trees for a given age. But for Counami, it is true it is not so different. Moreover this result is not currently discussed in this paper, therefore I remove this part.

P14L13-14: please indicate which test allows identifying the ecological meaning of the groups.
We completed the sentence accordingly.

P14L26: what is the percentage of subsequent axes?
The percentages have been added accordingly.

P14L27: "was driven"
Thank you, we corrected accordingly.

P14L28: here "condition" is a combination soil types by sites, which acknowledges environmental variation across sites. But earlier in the paper, the sites seemed to represent replicates. Needs clarification.
We think the annotation "soil types x sites" is misleading, evoking interaction between terms. we changed it.
Moreover, we effectively tried to replicate sites to test the effect of soil. But finding accessible *Cecropia* trees, sufficiently numerous, with both soil types on a given site remains quite challenging. We found two sites with such conditions, but at the cost of a significant geographic distance that we cannot ignore.

P15L3-4: "tree architectural development" the same as "growth trajectory" used elsewhere?
Please use consistent terminology to avoid confusion.
Architectural development is more general than growth trajectory because it integrates other processes than growth such as flowering, branching etc.
We added definitions at the end of the introduction :
"We measured commonly used functional leaf and wood traits, coupled with growth trajectory (i.e. fluctuation and accumulation of growth over time) and architectural development (i.e. integration of growth, branching, and flowering processes) analyses for *C. obtusa* individuals from two sites with both soil types in French Guiana."

P15L8: "rather weak" is quite vague. It seems that the authors would like to have a clear dichotomy between significant effects on architecture against non-significant effects on "classical" functional traits, but in fact there is some effect on functional traits. I would suggest underlying in this paragraph that, although some functional traits respond, they are not the most important/classical traits involved in major economic spectra, which are known to be related to interspecific functional changes across soils.
We agree with the reviewer and we rewrote the sentence accordingly.

P17L1-3: because of substantial site effects, you may propose as a perspective to select new sites.
Thank you for the suggestion, we added a sentence accordingly.

P17L19-22: this point on fitness differences does not make clear sense. Fitness differences between co-occurring trees should impact their coexistence, but fitness differences across populations do not have clear impact on local survival and coexistence.

But precisely we do not have idea on the genetic structure according to soil type. For a given site, sampled trees may represent a single genetic population, thus phenotypic variation would be only due to phenotypic plasticity. This is why we used “under the assumption that FS and WS trees form a unique population” at the end of this sentence

P18L1: "degree of habitat divergence" is vague. The whole paragraph should be made shorter and clearer. Also it should be better connected and less redundant with the paragraph L30ff. We agree with the reviewer, we modified the sentence accordingly. We also shorted the paragraph.

P18L12: meaning of "homologous" not clear. In addition the term "functional response" is not obvious here.

This part of the discussion is now at first.

We agree with the reviewer and we entitled this part of the discussion as: “*Soil-response of functional traits is not the same between intra- and interspecific levels*”

P18L26-29: what about the potential ontogenic variation of functional traits?

This point is discussed according to the general comment “In the discussion, it is noted that the developmental strategies grasped by architectural traits allow a more integrative view on tree performance, but you could also stress that measuring functional traits at a single ontogenic stage may miss important plasticity of the functional traits during ontogeny. It could be a point (iii) on P15-16.”

A third point of discussion has been added accordingly

P19L1-20: this paragraph is long, insofar as the ideas here, although interesting, remain hypothetical and speculative.

We agree with the reviewer that this paragraph is firstly speculative. However, biotic interactions are not investigated in our study, whereas *Cecropia* –with myrmecophytism- is a nice model for investigating biotic interactions in the perspective of ecological processes. This is what we wanted to underlined here.

We agree with reviewer that the overall Discussion is quiet. If the reviewer think it is really inconvenient, we will finally agree with him to delete this paragraph for the final form of the manuscript.

P19L26: not comfortable with the use of "negative results" here. The fact that there is contrasting within and between species functional variation is not a negative result.

We agree with the reviewer, we changed by the less connected word “signal”