Peer Community In
Ecology

Growth trajectories, better than organ-level functional traits, reveal intraspecific response to environmental variation

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François Munoz based on reviews by Georges Kunstler and François Munoz

A recommendation of:
Sébastien Levionnois, Niklas Tysklind, Eric Nicolini, Bruno Ferry, Valérie Troispoux, Gilles Le Moguedec, Hélène Morel, Clément Stahl, Sabrina Coste, Henri Caron, Patrick Heuret. **Soil variation response is mediated by growth trajectories rather than functional traits in a widespread pioneer Neotropical tree** *(2020), bioRxiv, 351197, ver. 4 peer-reviewed by Peer Community in Ecology.* 10.1101/351197

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Functional traits are "morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival" [1]. Most functional traits are defined at organ level, e.g. for leaves, roots and stems, and reflect key aspects of

resource acquisition and resource use by organisms for their development and reproduction [2]. More rarely, some functional traits can be related to spatial development, such as vegetative height and lateral spread in plants. Organ-level traits are especially popular because they can be measured in a standard way and easily compared over many plants. But these traits can broadly vary during the life of an organism. For instance, Roggy et al. [3] found that Leaf Mass Area can vary from 30 to 140 g.m^(-2) between seedling and adult stages for the canopy tree *Dicorynia guianensis* in French Guiana. Fortunel et al. [4] have also showed that developmental stages much contribute to functional trait variation within several Micropholis tree species in lowland Amazonia. The way plants grow and invest resources into organs is variable during life and allows defining specific developmental sequences and architectural models [5,6]. There is clear ontogenic variation in leaf number, leaf properties and ramification patterns. Ontogenic variations reflect changing adaptation of an individual over its life, depending on the changing environmental conditions. In this regard, measuring a single functional trait at organ level in adult trees should miss the variation of resource acquisition and use strategies over time. Thus we should built a more integrative approach of ecological development, also called "eco-devo" approach [7].
Although the ecological significance of ontogeny and developmental strategies is now well known, the extent to which it contributes to explain species survival and coexistence in communities is still broadly ignored in functional ecology. Levionnois et al. [8] investigated intraspecific variation of functional traits and growth trajectories in a typical, early-successional tree species in French Guiana, Amazonia. This species, *Cecropia obtusa*, is generalist regarding soil type and can be found on both white sand and ferralitic soil. The study examines whether there in intraspecific variation in functional traits and growth trajectories of *C. obtusa* in response to the contrasted soil types. The tree communities observed on the two types of soils include species with distinctive functional trait values, that is, there are changes in species composition related to different species strategies along the classical wood and leaf economic spectra. The populations of *C. obtusa* found on the two soils showed some difference in functional traits, but it did not concern traits related to the main economic spectra. Conversely, the populations showed different growth strategies, in terms of spatial and temporal

development. The major lessons we can learn from the study are: (i) Functional traits measured at organ level cannot reflect well how long-lived plants collect and invest resources during their life. The results show the potential of considering architectural and developmental traits together with organ-level functional traits, to better acknowledge the variation in ecological strategies over plant life, and thus to better understand community assembly processes. (ii) What makes functional changes between communities differs when considering interspecific and intraspecific variation. Species turnover should encompass different corteges of soil specialists. These specialists are sorted along economic spectra, as shown in tropical rainforests and globally [2]. Conversely, a generalist species such as *C. obtusa* does occur on contrasted soil, which entails that it can accommodate the contrasted ecological conditions. However, the phenotypic adjustment is not related to how leaves and wood ensure photosynthesis, water and nutrient acquisition, but regards the way the resources are allocated to growth and reproduction over time. The results of the study stress the need to better integrate growth strategies and ontogeny in the research agenda of functional ecology. We can anticipate that organ-level functional traits and growth trajectories will be more often considered together in ecological studies. The integration should help better understand the temporal niche of organisms, and how organisms can coexist in space and time with other organisms during their life. Recently, Klimešová et al. [9] have proposed standardized protocols for collecting plant modularity traits. Such effort to propose easy-to-measure traits representing plant development and ontogeny, with clear functional roles, should foster the awaited development of an “eco-devo” approach.

References

[1] Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. Oikos, 116(5), 882-892. doi: 10.1111/j.0030-1299.2007.15559.x [2] Díaz, S. et al. (2016). The global spectrum of plant form and function. Nature, 529(7585), 167-171. doi: 10.1038/nature16489 [3] Roggy, J. C., Nicolini, E., Imbert, P., Caraglio, Y., Bosc, A., & Heuret, P. (2005). Links between tree structure and functional leaf traits in the tropical forest tree Dicorynia guianensis Amshoff (Caesalpiniaceae). Annals of

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Revision round #2

2019-09-15

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.

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.

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.

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.

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.

In addition,

- The first point of the Abstract seems to be a bit too general.
- Since the second point does not expose the ecological hypotheses considered and tested here, it sounds a bit too descriptive.

- In Discussion, consider adding a few word about the possible role of growth strategies underground.
- 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".

Further comments/suggestions:

P3L3: "are maintained" sounds weird here.

P3L9: "early successional forest stages"

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?

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.

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.

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.

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

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

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

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

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

P11L20: what "drive" means here?

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

P11L26: WSG may also be related to mechanical properties.

P11L28: remove "positioned"

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

P12L6: strange use of "relied on".

P12L8: "at stand level"

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

P12L18: missing ")".

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

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.

P13L9-12: what does "filtered" mean?

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

P13L31: "related variable" "were not significantly"

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?

P14L6-7: "covered the largest variayion of growth trajectories": how is it quantified?

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

P14L26: what is the percentage of subsequent axes?

P14L27: "was driven"

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.

P15L3-4: "tree architectural development" the same as "growth trajectory" used elsewhere? Please use consistent terminology to avoid confusion.

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.

P17L1-3: because of substantial site effects, you may propose as a perspective to select new sites.

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.

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.

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

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

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

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.

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Author's reply:

Sébastien LEVIONNOIS CNRS PhD student UMR EcoFoG Campus agronomique, Avenue de France BP 709 – 97387 Kourou Cedex French Guiana, France
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

Download author's reply (PDF file)

Revision round #1

2019-07-29

The manuscript has now been reviewed by an external referee and me.

It has been very difficult to find reviewers who accept to evaluate the manuscript (28 have been invited!), and I apologize for the delay resulting from this issue. Several of the contacted people mentioned that they did not feel competent enough to understand and evaluate the relevance of the analyses on architecture. I think it reflects the need to make the manuscript more accessible to a broad audience of ecologists.

Therefore, I recommend substantially revising the manuscript following these general guidelines: - to better underline the general context, questions and ecological mechanisms addressed in the study. Specifically, the beginning of the introduction is much focused on the specific environmental context of Amazon forests, while you should first introduce your questions on the role of ITV in terms of traits and growth trajectories in a more general context. - to shorten the presentation of results on architectural analysis, and to keep the main aspects that are most relevant to understand the ecological value of the architectural patterns related to environment, - to discuss more specifically the ecological mechanisms underlying the fact that environment influences or not growth patterns and functional traits. The logic of Discussion section should be improved, in order to make clearer your conclusions on the nature and role of ITV.

My review below further includes more specific comments and suggestions. They are coherent with and complement the comments of the second reviewer.

If you wish to submit a revised version of your manuscript, please provide point-by-point answer to the comments and detailed explanation of the changes made in the revised manuscript.

Preprint DOI: https://doi.org/10.1101/351197

Reviewed by Georges Kunstler, 2018-09-04 10:10

This manuscript explores the intraspecific variability of both functional traits and growth and architecture trajectories between two soil types of contrasted fertility in a generalist tree species in French Guiana. The contrast between poor white sand soils and more fertile soils (such as Ferralitic soil) is a very important contrast structuring the diversity of tropical forests, with a substantial species turnover between these two soil types. These turnovers largely result from specialist species that are restricted to one soil type. There are large differences in traits composition between these two soil types, with a trade-off between growth vs. defense against herbivore (Fine et al. 2004 Science). There is a small number of with-sand endemic species that represent a high proportion of the forest in these poor soils, but there are also several generalist species that can be found at low abundance in these communities (Fine and Baraloto 2016 Biotropica). This manuscript explores what are the mechanisms that allow these generalist species to establish in the harsh condition of the white-sand communities. The hypothesis tested with Cecropia obtuse is that intraspecific traits variability within these species mirror the interspecific traits variability and thus allow the species to establish in both high and low fertility soils. The authors analyze both the leaf and wood traits and reconstruct growth and architectural trajectories of the trees to test their response to soil type. They show that soil types have little effect on leaf and wood traits but impact the growth and architectural trajectories. This is a nice example of the analysis of tree architecture to reconstruct individual growth trajectories. Overall I find the study interesting and based on solid analysis, but the text is sometimes unclear and need improvement. Below I give some general comments:

• I'm not a native English speaker, but I think the English need to be improved.

- The presentation of the statistical methods is sometimes unclear. I think it would help to give an introduction sentence for each method explaining the overall goal of the analysis. The appendix S2 provides a better explanation than the main text. For instance, the section Page 11 lines 9 to 18 is unclear and need to be clarified. If I understand well you try to find regular pattern showing the impact of the dry season to date the internode, is it right?
- Given that you have soil information for each individual (or cluster of individuals) it would be interesting to include soil effect as a continuous variable based on the key fertility variables (or PCA of soil data) rather than just using the contrast WS vs FS.
- In regard to the discussion on whether the intraspecific variability of generalist is larger than specialist, Sides et al. (2014) American Journal of Botany could be an interesting reference to add.
- Several sections of the introduction and the discussion emphasize the role of genetic adaptation whereas you have no data on this topic in your MS. I would downscale these sections.

Minor comments

- Page 1 line 15: “UMR LerFoB” change to “UMR Silva”, no?
- Page 2 line 6: “.measured “ delete the point.
- Page 3 line 9: delete “and on” and replace by “over”?
- Page 3 line 12: “temporal-scaled retrospective analysis” “temporal-scaled” is unclear delete?
- Page 3 lines 13: “soil phenotypic variability” unclear.
- Page 4 line 6: the references are variable in structure along the manuscript you need to correct that. In addition on the line, you use both “Steege” and “ter Steege” you need to be consistent.
- Page 4 line 18: Delete “across-community” and replace by interspecific.

• Page 5 line 14: “a mosaic of the genetic and functional divergences of populations” corrects this sentence.

• Page 5 line 33: correct for “are INTRASPECIFIC functional traits variability shaped by …”

• Page 6 lines 12-14: Several papers have explored the ontogenetic plasticity of traits (for instance LUSK, C. H. (2004), Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. Functional Ecology, 18: 820-828.).

• Page 6 line 21: “caveats” is it really the good word here?

• Page 6 line 28: “functional ecology-based approach” unclear.

• Page 6 lines 30-31: Sentence “The ITV …. On genotype” sentence unclear.

• Page 8 lines 33- 34: “a single colonization pulse” for both soil types?

• Page 10 lines 22-24. Sentence unclear.

• Page 10 lines 27-31: The way you computed leaf lifespan is unclear please clarify.

• Page 11 line 27: Why is it pertinent for old trees?

• Page 11 line 31: change “in (Davis, 1970)” to “in Davis (1970)”.

• Page 12 lines 14-16. The sentence “As for classical k-means … of partitions choice.” sentence unclear clarify.

• Page 12 line 20. PCA of which variables, traits only or soil as well?

• Page 12 lines 21-25: you have two sentences repeating the same idea.

• Page 13 line 19: Appendix S5 or S2?

• Page 15 line 34: “bi- or an annual periodicity” correct.

• Page 18 line 34: “is allowed” change to “could result from two non-exclusive…” ?

• Page 19 line 30: Delete the first name from the reference.

• Page 29 line 1: “dimension architectural traits” only “architectural traits”?

Reviewed by François Munoz, 2018-10-29 07:53

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Author's reply:

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