Response to Associate Editor

Associate Editor Decision: Publish subject to minor revisions (review by editor) (08 Jan 2021) by Sara Vicca
Comments to the Author:

Dear authors,

Your revised manuscript has now reviewed by the reviewer, who is very positive about the dataset that you present but pointed out that the manuscript could still be considerably improved by further elucidating the mechanisms behind the observations. I agree with this and think the reviewer provided very useful input for you to further improve the manuscript.

I would also like to add my appreciation about the dataset and especially for including and providing multiple soil data. I did miss some motivation for the choice of soil measurements - why these and not other soil properties and nutrient measurements. Please include that information in the revised manuscript and also indicate (perhaps in the discussion) if there are any potentially important variables that may still be missing from the dataset. From my experience, soil organic matter content is an important variable that is not included in your dataset. Organic layer depth is probably a good proxy and this could be mentioned explicitly in the text. Soil texture is another important soil property that is missing from the dataset. Do you have any indication if texture varied (substantially) across the gradient?

Please consider all suggestions carefully and in case you choose not to implement some of them, provide arguments for that in the response letter.

I look forward to receiving your revised manuscript.

Kind regards,
Sara Vicca

Answer: Thank you for the constructive criticism!

We think, that we already included more soil parameter than most other tropical forest transect studies, But you are right, there are some additional parameters missing that probably might improve our understanding of soil effects on forest productivity. Unfortunately, data on soil texture and soil organic matter content are not available (or only for a subset of plots). We assumed that soil hydrology in this perhumid climate is of secondary importance for tree growth and therefore soil texture might be less important than the studied soil parameters.

We explain in the Methods (and also the Discussion) that we selected the physiologically most meaningful soil chemical properties. These are the five plant macronutrients (N, P, K, Ca, Mg) in their plant-available form (N supply rate, plant-available P, salt-exchangeable Ca, K, Mg), in addition C/N ratio as an indicator of decomposability, and soil acidity.

The following sentence was added to the Methods section: The increase in organic layer depth with elevation in both transects, accompanied by wider C/N ratios and lower pH, is probably related to higher soil organic matter contents and indicates a decrease in nutrient availability as a result of reduced organic matter turnover.

Response to Reviewer #2

Reviewer#2: The revision and response letter addresses all the points raised; thanks very much for the effort, and also for the analysis of an important and fascinating dataset. Overall the ms is improved, but there are some key issues that have not really been elucidated enough here for publication, leaving the analysis much less complete than it should or could be. There is the odd useful but missing reference that I think would be helpful to add, but the main conceptual gap appears to be around the connection of temperature with mechanism and the relationships to traits and diversity.

The authors mention a plot size effect on analyzing diversity/productivity relationships. I thought I had mentioned the paper of Sullivan 2016 (Sci Reps) before, but perhaps not (apologies if not). This is relevant to the introductory material around line 28 and in the discussion, around line 345-355: Sullivan et al. 2016 find (small) plot size can influence inferences from their analysis of diversity and AGB/C storage in tropical forests. This needs to be included/discussed, I think.

Answer: We initially refrained from citing the Sullivan et al. (2016) study here, because it addresses the diversity – biomass relationship (DBR) and not the diversity – productivity relationship (DPR), which is our focus. The relation between aboveground biomass and productivity is weak in tropical forests, as carbon residence time is a key determinant of standing biomass, which varies considerably with climate and soil. We now mention Sullivan et al. (2016) in the Discussion related to plot size effects on the DPR.

Reviewer#2: As for the productivity-temperature-elevation discussion this seems to (i) miss some of the earlierst references to the subject (eg S Bruijnzeel's classic work) and (ii) be a bit simplified to the point that key issues are obscured (or inadvertently lost) in the current text. There is significant advantage in being specific here – eg TMF or tropical lowland forest studies often focus on NPP (or just tree growth, as here), but others also consider GPP, both from an empirical and modelling perspective, and the papers in the introduction (eg Line 44-60) refer to several different versions of 'productivity'.

Answer: We added a key publication of Bruijnzeel & Veneklaas (1998). Moreover, we rewrote part of the Introduction section, which focuses on assumed temperature effects on productivity. We stress that temperature may have direct and indirect effects on productivity. All cited work refers to NPP, and not GPP, now.

Reviewer#2: One advantage of being specific is that it allows the author to dissect better the drivers of reduced productivity (at higher elevation), especially when linking tree growth and gross primary productivity (=gross photosynthesis, GPP). This is can be powerfully done using a combination of data and mechanistic modelling. Line 46 introduces modelling work but refers only to that of Fyllas 2017. The Fyllas study uses a mechanistic model, but validates only based on annual-scale estimates of summed components of the carbon cycle. The modelling study of van der Weg 2014 is not mentioned except in reference to LMA, and yet this earlier modelling paper (the first to use a mechanistic analysis to identify temperature as the main driver of differences in GPP with elevation in TMF) validates model results based on high-frequency sap flux data as well as annual-scale component-summed carbon cycle analysis. That is, it provides validation data at a timescale relevant to the processes being driven by variation in the environment, and via the relevant mechanisms. Both the Fyllas and van der Weg papers use photosynthetic physiology at the core of their models but they come up with different interpretations of the main driver of change productivity (GPP) with elevation. As indicated in the first review, this needs to be discussed because the van der Weg findings are consistent with those in this submitted paper (ie that temperature is a dominant driver) but the Fyllas paper suggests that any effects of temperature are expressed through trait variation.

Taking the analysis presented in this submitted manuscript on Ecuadorian data a step further, the work of Wittich 2012 is cited as showing that light-saturated assimilation rates (called Amax) are lower at higher elevation, ie this is consistent with the results presented in this submitted paper (of lower wood production (WP)) at higher elevation...but I don't know if the Wittich values are temperature-corrected, or if they are cited at ambient temperature (ie T differing by elevation).

Answer: The Amax measurements of Wittich et al. (2012) were taken at ambient temperature of the respective elevation (typical temperature at noon on a sunny day); thus they reflect the elevational temperature decrease. The community means of Amax did not show a clear elevational trend from 1000 to 3000 m (similar to the study of Fyllas et al. 2017), suggesting partial of full biochemical compensation of the temperature decrease, perhaps through a higher Rubisco concentration at higher elevation. However, Wittich et al. found a significant Amax decrease from 2000 to 3000 m, i.e. in the uppermost transect, which coincides with a significant decrease in foliar N and P concentrations in this transect section (which is only partly compensated by a LMA increase with elevation). In addition, leaf longevity increases toward higher elevation in this transect (Moser et al. 2007), which usually coincides with reduced foliar N and lower Amax. Both the Fyllas et al. and the Wittich et al. study suggest that temperature effects on the photosynthtic apparatus are mainly expressed through species turnover and related change in leaf traits. However, while the Wittch et al. data indicate only a small, and the Fyllas et al. data no, elevational change in Amax (measured at ambient temperatures), a pantropical literature review covering ca. 170 species from 18 sites (included in Wittich et al. 2012) suggests that Amax decreases by on average 1.3 µmol m^{-2} s^{-1} per km elevation in tropical mountains. Our conclusion is that local edaphic (soil fertility) and climatic factors (such as cloudiness or very high precipitation, causing temporal soil anoxia) may have a large influence on elevational patterns in phytosynthetic capacity. The Andes in Peru and Ecuador may differ from Central American, African or SE Asian tropical mountains in this respect. Our results do not allow more detailed conclusions on direct and/or indirect temperature effects on NPP, as temperature most likely influences various processes simultaneously, notably photosynthesis, respiration, stem growth, nutrient and water acquisition and morphology (temperature effects on wood and leaf properties).

Reviewer#2: However, this outcome (Wittich) appears to be inconsistent with the results presented by Fyllas et al 2017 who argue that Amax is constant with elevation and that this constancy is achieved through species turnover. In the Fyllas argument, the changes in species composition with elevation/ temperatures lead, on average, to a higher photosynthetic capacity at higher elevation (ie biochemical capacity, Vcmax25 – see Bahar et al. 2016 New Phytologist and van der Weg 2012 Oecologia for the data on Vcmax25), and whilst the temperature is lower, the effect on Amax (via higher Vcmax) is for Amax to be constant across elevations. For this reason, Fyllas et al argue that radiation and leaf photosynthetic traits drive productivity, not temperature (temperature is inferred to be an indirect driver of average trait variation). The data used by Fyllas are taken at leaf temperatures that do not go very cold even though we know leaves at high elevation spend much time well below 20 C (see van der Weg 2014), so the Wittich analysis might be of much interest to the analysis presented in this paper from Ecuadoran sites, depending on how temperature is handled (remember that 24 hr (/12 hr!) photosynthesis is what determines overall assimilation totals not the maximum observed value of net photosynthesis, Amax, or the maximum photosynthetic capacity, Vcmax25) .

Answer: As the Wittich et al. data were taken at characteristic noon temperature conditions at the different elevations, we feel that they are relevant in the context of net primary production. We are aware that Amax data are poor estimates of daily canopy carbon gain. In another study on the carbon balance of the Ecuadorian forests along the elevation transect, we have roughly estimated canopy carbon gain by accounting for reduced photosynthesis due to cloudiness and lower temperatures in morning and evening hours (Leuschner et al. 2013).

Reviewer#2: Finally, there is a diversity question. The authors show that species diversity is very weakly related to WP in their data. The analysis also shows (and states) that variation in WP is large at each site (possibly larger than overall mean change in WP with elevation?...as also seen in Vcmax25 data, Bahar 2016, referred to above); and the argument is presented that this variation in WP reflects local variation in the environment/diversity. However, their discussion could be enhanced quite a bit by considering species composition and relations to diversity in mean traits (apols if this distinction is made and I've missed it). The Fyllas argument suggests that changes in mean traits do strongly drive variation in WP, and that the traits change with species turnover, ie species composition. Thus, it may be that raw species diversity does not explain variation in WP very well, but other elements of that diversity, ie mean trait change, conceivably might.

Overall, it seems that there is a key element missing here in synthesizing evidence for the mechanistic explanation of the observed variation in WP with elevation (ie, the argument that temperature drives the observed differences – ie, a/the principal focus of the paper). One part of it is explaining the different modelling approaches/conclusions and the other is relating this to evidence from the cited leaf physiology studies and the related mechanistic (/modelling) analysis, both in terms of the full variation in temperature at each elevation and in terms of the effect on diversity in traits (as well as species). I hope this extended comment is useful to the authors, as the data they have are fascinating and have the capacity to shed additional light on this overall discussion about a large fundamental question in forest ecology, and especially so given their additional nutrient information.

Answer: We agree that mean trait change is a major driver of change in productivity and other ecosystem processes along elevation gradients. This is shown by the recently published study on root traits along the Ecuador transect (Pierick et al. 2020, New Phytol) – the study also demonstrates the large effect of phylogeny on functional traits. However, the Amax data of Wittich et al. suggest that the NPP decrease is partly caused by a reduced photosynthetic gain, which contrasts with the constant Amax values in the Peru transect. We explain the differences by local edaphic and possibly climatic pecularities, and possibly by the effect of phylogeny, i.e. trait differences. This is expressed now in the Discussion. In addition, the Introduction was also partly rewritten to address this point.

Reviewer#2: Line 48. Should Tanner et al. 1998 be cited here in addition to the other place(s) where it is already?

Answer: Thank you. Was added.

Reviewer#2: Line 51. Should van der Weg 2014 be cited here in addition to the other place(s) where it is already?

Answer: Thank you. Was added.

Reviewer#2: Line 53, 69, elsewhere. It's not clear where mechanism and correlation are separated. This may be a timescale issue. The fertility discussion seems to be mainly by correlation but the impacts on photosynthesis need to be mechanistic; they are linked of course.

Answer: That was changed in the respective sentences and should be clearer now.

Reviewer#2: Line 80. The 'predestined' term might be replaced by '...which makes them attractive for the study of..'.

Answer: Thank you – was changed accordingly.

Reviewer#2: Line 89. The mention of assumed diversity effects is good, as we are not sure if they are real or if they only seem to occur in small plots. Perhaps this can refer to the preceding discussion as well, to tie up the idea of 'assumed diversity effects'?

Answer: The suggested diversity effects are critically introduced in the Introduction.

Reviewer#2: Line 262. Zimmermann 2010 (Glob Biogeochem Cycl) reports soil moisture data for a similar Andean elevation gradient that suggest little moisture limitation across elevations because of high rainfall, as here – it looks like it would be useful for you to cite here to substantiate your (reasonable) assumption.

Answer: We added the reference of Zimmermann et al.(2010) to Introduction and Discussion.

Reviewer#2: Line 288. Need to refer to more modelling/data studies than just Fyllas here?

Answer: We added two other references (Finegan et al. 2015, Malhi et al. 2017).

Reviewer#2: Line 318. How does WSG mediate this effect on productivity? Can the authors suggest a process or mechanism? Leaving it open like this seems insufficient. Variation in WSG is often associated with variation in moisture constraints because of the link between WSG and hydraulic vulnerability (in some studies)…but the authors don't mention this. In this wet TMF environment, is it nutrients/growth rate, or even herbivory pressure, or just taxonomic identity that are related to the variance in WSG?

Answer: We added the following sentences here: A recent study in South-east Asian tropical forests showed that WSG does neither have a direct mechanistic effect on biomass production (Kotowska et al., 2020) nor on tree water consumption, even though harder wood tends to be associated with lower growth rates (Muller-Landau, 2004; Hoeber et al., 2014). Yet, WSG is known to be associated with most structural and functional wood properties (Chave et al., 2009), and it may also be related to anatomical attributes such as pit membrane characteristics that influence sap flux density, which itself is positively related to productivity (Kotowska et al., 2020).

Reviewer#2: Line 329. Can you shorten the text here by saying that the difficulty of LAI estimation may lead to both under-estimation where leaf clumping is dominant, or over-estimation where stem density is high?

Answer: We shortened the paragraph accordingly.

Reviewer#2: Line 349. Useful to refer here to the Sullivan 2016 work here on plot size/diversity/carbon storage.

Answer: We added the sentences: Similar to the DPR, a significant positive diversity – aboveground biomass relationship was observed in tropical lowland forests only in small plots (0.04 ha), while it disappeared at larger scale (1 ha) (Sullivan et al., 2017). Moreover this study showed that the diversity influence on AGB was small: Doubling species richness at 0.04 ha increased biomass only by 6.9%.

Reviewer#2: Line 368. The analysis here is clear in that it interprets temperature as a key driver of WP-elevation variance. But in the element where future needs are considered it could usefully also refer to a need to understand variation in overall traits – either trait diversity or change in mean trait values, and how they affect major ecosystem processes including productivity, in relation to temperature effects on the core driving processes themselves (ie as well as the species diversity question).

Answer: We added a sentence in the Conclusion referring to the need for more trait-related data.

References:

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Kotowska, M., Link, R., Röll, A., Hertel, D., Hölscher, D., Waite, P.-A., Moser, G., Tjoa, A., Leuschner, C., and Schuldt, B. (2021) Effects of wood hydraulic properties on water use and productivity of tropical rainforest trees. Frontiers in Forests and Global Change, 3, 598759.

Leuschner C, Zach A, Moser G, Homeier J et al. (2013) The carbon balance of tropical mountain forests along an altitudinal transect. In: Bendix J. et al. (eds) Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecol. Stud. 221. Springer, Berlin, pp. 117-139.

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Muller-Landau, H. C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. Biotropica 36, 20-36.

Bruijnzeel, L.A., Veneklaas, E.J. (1998) Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. Ecology, 79, 3-9.