Response to Reviewers

Response to Reviewer #1

Reviewer#1: This manuscript presents an analysis of various factors on wood productivity and net primary productivity across a series of plots located on two transects. Although the findings appear robust, logically, and technically correct, I believe the analysis could be improved by better describing key details like the calculation of wood productivity, inclusion of additional covariates (particularly stand structural attributes), and general model behavior as well as fit statistics. In addition, a few paragraphs in the Introduction could be further expanded with key details.

Answer: Thank you for the helpful comments to our manuscript! We have now expanded the Methods section on the measurement of biomass and productivity and include more details on our calculations.

The concept, where the SEM is based on, included elevation, tree diversity, soil and stand properties as predictors of productivity. We included only AGB and WSG (WSG showed a stronger correlation to stand productivity than LAI or stem density) in the SEM. Additional structural variables such as basal area or quadratic mean diameter in the model would have weakened the analysis, as they are closely related to AGB. Model fit statistics are given in the figure legends (Figure 4 and 5).

The discussion of possible abiotic and biotic drivers of forest productivity in the Introduction has been expanded, as recommended.

Reviewer#1: L14: How is “productivity” being defined here? ANPP?

Answer: We changed it to “wood production” (result of the overall analysis of all plots), because ANPP was only analyzed for the Loja transect.

Reviewer#1: L50-53: Seems this paragraph and a few the other ones above it should be further expanded? How widespread are tropical montane forests? Where are they primarily located? Why specifically focus on them?

Answer: We are now introducing tropical montane forests as an ecosystem type in more detail.

Reviewer#1: L57: Don’t understand the use of “rarefied” here.

Answer: We replaced “rarefied number of tree species per plot“ by “tree diversity”, the rarefaction method is explained in detail in the data analysis paragraph.

Reviewer#1: L60: I am confused by the “10 K” Can this be presented differently?

Answer: K (degrees Kelvin) is the SI unit for temperature differences; it should be used instead of °C, when differences are meant.

Reviewer#1: L67: TMF was not previously defined and I assume referring to tropical montane forests?

Answer: We define TMF now earlier in the Introduction.

Reviewer#1: L106: Some additional details would be helpful here. I assume these are predicted biomass values? What was the average remeasurement length? Is annual AGB increment computed from tree rings?

Answer: The plot biomass values were calculated for each plot as the sum of the biomass of the single stems using the Chave et al (2005) equation for tropical wet forests with stem diameter, wood specific gravity (WSG) and tree height as parameters. Re-measurement intervals were between 1 and 5 years, depending on the study sites. We describe the biomass and wood production measurements now in some more detail.

Reviewer#1: L130-133: I am bit confused by this. Personally, I would use AGB to predict WP or NPP, while I would consider WSG to be more of a function of species composition than stand structure? Seems other structural attributes could be computed like total basal area, quadratic mean diameter, and measures of the diameter distribution?

Answer: We also used AGB as a predictor for WP (see Figure 4), in addition, we selected WSG from the stand properties (LAI, stem density, WSG) because it showed a stronger correlation to stand productivity than LAI and stem density. Both basal area and quadratic mean diameter are highly correlated to AGB, and we think that AGB is the most meaningful of these variables.

We changed “stand structural variables” to “stand properties” in the respective sentence.

Reviewer#1: L141: What are RMSEA and CFI?

Answer: RMSEA (root mean square error of approximation) and CFI (comparative fit index) were used to assess the goodness of model fit.

Reviewer#1: Figure 2: Might not include 0 on graphs with narrow distributions like LAI and WSG to better highlight trends.

Answer: The respective figures are improved to make the elevational trend more visible.

Reviewer#1: L276: Your LAI cover a very narrow range and often the strong relationships are observed when values are below 5-6.

Answer: We now discuss at the end of the Discussion the assumed shortcomings of optical LAI estimates in complex forests and refer to stems and branches, which are recorded by the LAI2000 systems as well. Litter trapping studies in several plots in the Loja transect confirm these assumptions about under- and overestimation of LAI by optical methods.

References:

Chave J et al. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145:87–99

Response to Reviewer #2

Reviewer#2: This paper is a very exciting summary of a large number of 400 m2 forest plots distributed over a large elevation gradient in the Andes. It addresses questions relating to productivity, species diversity and environment. It is rare for a dataset of this size to be assembled, and that alone justifies support for publication, after revision. The focus of the paper starts with a discussion of the diversity-function debate and then moves to a discussion on the determinants of low productivity at high elevation in tropical montane forests. Both subjects are dealt with usefully but I think both need some attention. The theoretical importance of the diversity-function debate is mentioned, but if this line of argument is to be maintained, I think it needs further justification. The debate has practical importance, but the theoretical importance, whilst it exists, receives a fair bit of skepticism in the literature. I don't think this point is central to the main strength of the paper, but I mention it, as the authors may choose to soften the stance on the theoretical importance or to support it more fully. Further on this point, I note that some large observational datasets are referred to, in order to address diversity-function relationships across biome types. I am supportive of this; all approaches to the diversity-function question have some unavoidable flaws in relation to this question but the experimental ones seem most prone to it. On the other hand some key experimental work in the tropics is not mentioned – surely it is of interest to place this discussion in the context of the Sabah Biodiversity Experiment – a large scale experiment in lowland tropical forest? There are few such comparisons in tropical forest to make use of and this feels like a gap.

Answer: Thank you for the detailed suggestions to our manuscript and for this thoughtful comment on the biodiversity-function relationship. We have rewritten part of the Introduction with relation to DPR and have softened the wording in places. We now mention shortcomings of both experimental approaches and observational studies on the DPR. In addition to the Sardinilla experiment (Panama; Schnabel et al. 2019), we now also mention the Sabah Biodiversity Experiment (Tuck et al. 2016) – however, due to the young age of the trees, no analysis of overyielding has apparently been published so far.

Reviewer#2: On the question of causes/predictors of reduced productivity at high elevation, the comparative and interpretive analysis seems a little limited, even though the data are impressive and wide-ranging. The authors note the work of Fyllas 2017 (Ecology Letters), where a modelling approach was taken using annual estimates of GPP along a Peruvian (ie also in the Andes) elevation gradient as validation data. However, Homeier et al miss the first mechanistic modelling study of tropical montane forest productivity differences by elevation, presented by van der Weg et al. 2014 (Ecosystems). The 2014 paper validates model estimates of productivity using fine-scale mechanistically-related detailed sap flux data, whilst the 2017 paper validates mainly against impressive annual GPP estimates based on summed measurements of NPP and respiration. They come to different conclusions. Based on Amax values measured above 20 deg C, Fyllas et al highlight the importance of variation in Amax with elevation and variation in radiation with elevation, whilst van der Weg et al using Vcmax/Jmax, a stomatal model and measured leaf temperature (shown to be frequently well below 20 C in the high elevation site), conclude that variations in temperature and radiation are the most important drivers. The Fyllas conclusion is attractive as it suggests that despite high species turnover, overall Amax 'responds' by increasing at lower temperatures, suggesting a degree of 'optimisation to environment', filtered by species turnover. On the other hand, the mechanistic validation in the van der Weg paper, and its use of real leaf temperatures well below 20 C suggests a key role for temperature not strongly evident in the Fyllas analysis. The paper here (Homeier et al) could contribute strongly to this overall discussion with independent data and analysis. Whilst the density of measurements is not the same as presented in Fyllas, and there is no modelling (which is not necessarily a problem), there is very detailed edaphic information, as well as productivity and information on species identity. It is also clear that there is a huge range in productivity at each elevation among the different forest plots. This may be noise related (smallish plots…but lots of them!) or it may be environmental; I note that the data Fyllas et al use for Amax values suggest a wide range of photosynthetic capacities at each elevation….ie a similar pattern as found here, of much variation at each elevation. In sum, this paper has the potential to make a bigger contribution to this discussion than it currently does. I hope these comments are of use; it is worth expending effort on in a revision because the question is about fundamental tropical ecology (or indeed montane-to-lowland ecology), and had remained in the realm of 'many explanatory factors but we don't know which' until relatively recently.

Answer: Thank you for the detailed suggestions. We have extended the discussion about temperature effects on productivity in TMF by including various additional papers, notably van de Weg et al. 2014 and the modeling study of Fyllas et al. 2017, and also the empirical study of elevational change in photosynthesis of Wittich et al. 2012. In the Discussion section, possible pathways through which temperature could influence tree metabolism are now mentioned and part of the Discussion has been rewritten. As a possible indirect low-temperature effect on physiology, the slowing down of N mineralization and resulting nutrient deficiency is discussed. The possibility that temperature manifests primarily through trait variation due to the elevational species turnover is also mentioned. We added two sentences about the importance of environmental variation within elevation levels to the last paragraph of the discussion.

Detailed points

Reviewer#2: Line 28. What about reference to the Sabah Biodiv Expt? Can you make more of the comparison of the diversity-function relationship at high vs low diversity? Also, is it useful to refer to Sullivan 2016 Scientific Reps (biomass and diversity…very slightly different question as biomass is not 'function' but it does discuss plot size)

Answer: The Sabah Biodiv Experiment is mentioned now (Tuck et al. 2016), even though we are not aware of a study reporting productivity data that prove overyielding in this experiment.

Reviewer#2: Line 37-45. Missing the van der Weg 2014, which used data and modelling in early trop montane forest data+modelling analysis. It shows temp and radiation dependence mechanistically, and water use is validated using sap flux data. It also demonstrates importance of low leaf temps affecting function. The analysis in these lines mentions some key comparative flux and parameter data (eg Girardin 2014 Malhi 2017), but omits the Fyllas 2017 paper mentioned above. A bigger discussion is needed somewhere here to set this paper up more comprehensively.

Answer: The van de Weg et al. 2014 paper is now mentioned in the Discussion, as is the Fyllas et al. paper. The overview of possible abiotic and biotic controls of TMF productivity has been expanded in the Introduction.

Reviewer#2: Line 47. I note the use of the Chisholm 2013 reference, but I think this analysis/discussion needs to take into account dynamics too, if only briefly. ABG does always reflect productivity - see Baker 2004, Galbraith et al. 2013, Malhi et al. 2015); residence time is important, as is recruitment. So the point made here needs to be made in relation to this wider discussion on determinants of ABG.

Answer: The relation between ABG and ANPP and the role of woody tissue residence time are now dealt with in more detail in the Introduction. It is mentioned that the relation is often weak (even though some studies reported an AGB effect on wood production).

Reviewer#2: Line 59. The choice and effectiveness of small plots needs a fuller discussion than reference only to Chisholm. For example, if diversity effects are only likely to emerge at small scale, what does this mean for their fundamental role?

Answer: We now discuss the advantages of small plots in rugged terrain, with respect to the chance of detecting diversity effects and concerning time consumption and the resulting potential to monitor a larger number of plots in total. At the end of the Discussion, we mention that diversity effects that manifest in 0.04 ha plots may be of low relevance for the landscape level.

Reviewer#2: Line 135. It's great to see a careful path analysis approach being taken here to distinguish different drivers. However, can you explain how the original model structure affected the ultimate outcomes? Might you have had a different outcome had your starting point (structure) been different or have your methods fully accounted for this? (apologies if I've missed this point).

Answer: The reviewer is right, SEM model structure affects the outcome. Therefore we carefully developed a structure that, based on the available data and our knowledge, represented the best combination of predictors for productivity (elevation, tree diversity, soil and stand properties). We iteratively removed insignificant paths from the starting model to test whether incorporation of those paths improved the model fit (described in the last paragraph of the data analysis chapter).

Reviewer#2: Line 160. Are there any recruitment data to advance the C dynamics analysis?

Answer: For our study we focused on stem diameter growth of the surviving trees, assuming an equivalence of stem mortality and recruitment. We think that to determine reasonable rates of mortality and recruitment would require bigger plots.

Reviewer#2: Line 164. LAI measurements are really important but difficult to make. Are you sure the differences you see in LAI are related to leaf area and not a change in stem density/canopy structure? High stem density would increase Plant Area Index (ie leaves and wood) even if LAI did not increase. I know this is hard to separate, but some comment/discussion/caveat would be useful.

Answer: We now discuss at the end of the Discussion the assumed shortcomings of optical LAI estimates in complex forests and refer to stems and branches, which are recorded by the LAI2000 system as well. Litter trapping studies in several plots in the Loja transect confirm these assumptions about under- and overestimation of LAI by optical methods.

Reviewer#2: Fig 2. There are strong signals of variation in mean values with elevation in some of the key metrics (eg WP, Stem density). But there is also very large variation at each elevation. Is this discussed? The variation by elevation is larger than the overall mean signal in the regression; this has also been observed in ecophys measurements elsewhere (eg Bahar et al. 2016 New Phytologist).

Answer: We fully agree. This is an important topic, and we have addressed variation in fine root traits at a given elevation in the Loja transect in a separate paper that went online in New Phytologist recently (Pierick et al. 2020). We added two sentences about the importance of environmental variation within elevation levels to the last paragraph of the discussion.

Reviewer#2: Line 193. As per the second paragraph above, the Fyllas 2017 paper notes that there is large turnover in species but argues that there are directional changes in mean trait values with elevation and these become determining of productivity along with radiation....how can we link these different findings?

Answer: Thank you, this fits perfectly with what we found for leaf traits in the manuscript by Homeier et al. (to be submitted). We mention now the assumption that trait variation due to elevational species turnover explains a large part of the temperature effect on productivity (and photosynthesis). We mention the Fyllas et al. paper here as well.

Reviewer#2: Line 237. The role of low leaf temperatures needs further consideration in affecting rates of carbon gain, not just radiation levels.

Answer: We agree. See response above. The somewhat contradictory evidence with respect to direct and indirect temperature effects on tree metabolism in Andean TMF is discussed in more detail now in both the Introduction and the Discussion.

Reviewer#2: Line 243. This soils dataset is very substantive and provides detailed driver information for the path analysis. It may be possible to use this to help the contrast with or discussion of preceding analyses on this general productivity/elevation subject.

Answer: Our finding that not only N and P, but likely also basic cations are influencing productivity in an independent manner, is now discussed with respect to the widespread assumption of P limitation in lowland forests and N limitation in high-elevation forests.

Reviewer#2: Line 250. Do you have soil respiration data or root productivity data to back this up (ie higher allocation of C to root production/symbionts)?

Answer: We do not have such data for the complete plot set investigated here. But earlier publications on fine root biomass, fine root production (using both minirhizotron observations and sequential coring approaches) and elevational allocation shifts in the Loja transect help to interpret the findings presented here. We mention now these publications.

Reviewer#2: Line 265. I wonder if an analysis of productivity vs biomass would help here too – ie productivity does not determine biomass in all circumstances because of other fluxes/processes affecting C residence time.

Answer: Since we were primarily interested in productivity as a dependent variable, we did not study effects of productivity on AGB (which are of course existing) but rather AGB effects on productivity. We feel that studying the NPP-AGB relation in more detail would inflate the manuscript; it should better be performed in a separate analysis together with mortality data.

Reviewer#2: Line 268, it seems natural to consider a comparison with the effects of fertlisation in the Andes reported by Fisher et al. 2013, Oecologia, as well as this 1989 reference.

Answer: The fertilization experiments in Andean forests of Peru and Ecuador are mentioned now.

Reviewer#2: Line 274 – as before, please consider LAI vs PAI differences, causative factors.

Answer: See above. We discuss the potential LAI measurement errors at the end of the Discussion.

Reviewer#2: Line 280. I wonder whether this section could be given a bit more depth by including a discussion on the relationship between trait diversity and species diversity? Might we expect a stronger response at low species diversity because trait diversity may increase rapidly as you add species at first, but if trait diversity is ultimately lower than species diversity we might expect the function-diversity graph to saturate more quickly using traits? Also of course there is the wider discussion on how the relationship (with species) varies under harsh and less harsh environments (eg. Paquette et al. 2011, Glob Ecol and Biogeog).

Answer: It would be interesting to see how tree species richness translates into functional diversity in our transects. Unfortunately, functional trait data is so far only available for a small fraction of the tree species from both transects. We added three sentences, offering saturating functional diversity and increasing functional redundancy as a possible explanation for the weak diversity effect.

Reviewer#2: Line 291. Again, might some discussion on traits be useful here too?

Answer: See above.

References:

Pierick, K., Leuschner, C., and Homeier, J.: Topography as a factor driving small-scale variation in tree fine root traits and root functional diversity in a species-rich tropical montane forest. New Phytologist. DOI: 10.1111/nph.17136, 2020.

Schnabel, F., Schwarz, J. A., Dănescu, A., Fichtner, A., Nock, C. A., Bauhus, J., and Potvin, C.: Drivers of productivity and its temporal stability in a tropical tree diversity experiment. Global Change Biology, 25(12), 4257-4272, 2019.

Tuck, S. L., O'Brien, M. J. O., Philipson, C. D., Saner, P., Tanadini, M., Dzulkifli, D., et al.: The value of biodiversity for the functioning of tropical forests: insurance effects during the first decade of the Sabah biodiversity experiment. Proc. R. Soc. B 283, 20161451, 2016.

van de Weg, M. J., Meier, P., Williams, M., Girardin, C., Malhi, Y., Silva-Espejo, J., and Grace, J.: Gross primary productivity of a high elevation tropical montane cloud forest. Ecosystems 17, 751-764, 2014.

Wittich, B., Horna, V., Homeier, J., and Leuschner, C.: Altitudinal change in the photosynthetic capacity of tropical trees: a case study from Ecuador and a pantropical literature analysis. Ecosystems, 15(6), 958-973, 2014.