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Interactive comment on "Soil carbon, nitrogen and phosphorus stoichiometry (C : N : P) in relation to conifer species productivity and nutrition across British Columbia perhumid rainforests" *by* John Marty Kranabetter et al.

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Thank you for the thorough review of our manuscript, we incorporated many of the suggested edits as follows: Reviewer 1

A lot of attention is given to the potentially important role of P. Although the authors have attempted to provide support for their statements on P (co-)limitation based on multiple lines of evidence (relatively high foliar N:P, high soil C:Po vs low soil C:N, low soil Pi, low leaf P, literature + comparison with data from other parts of the island), I am

not yet fully convinced. For example, there was only mediocre evidence for a role of soil C:Po in explaining variation in basal area (and the apparent + effect that occurred may have been caused by a mere confounding effect of soil C:N, as acknowledged by the authors), and no link between leaf P and soil C:Po, in sharp contrast to its analogue with N. I suggest to reinforce the evidence by performing some additional analyses you can do based on the data you already have (e.g. test for effects of Pi, test soil C:N*C:Po if no collinearity, plot foliar N:P vs forest floor and mineral soil C:N), and by referring better to any existing literature discussing P limitation on this region of the island, or other comparable systems.

We would disagree with the reviewer that results regarding organic P weaken the case for P limitations. A decline in element ratios has been typically matched to gains in plant-available nutrients, and consequently has been proposed as fundamental relationship in forest soils (e.g., Mooshammer et al. 2014; Zechmeister-Bolenstern et al. 2015; Spohn 2016). The fact that C:Po and N:Po were poor variables in explaining basal area or foliar nutrition is a very important finding as it underscores the uncertainty as to where these stoichiometry concepts can be successfully applied. This does not undermine the evidence for P deficiencies in these forests, but emphasizes instead how organic P is not behaving as ecological theory postulates. All the other lines of evidence for P limitations (low soil Pi, low foliar P%, high foliar N:P, fertilizer responses etc.) are collectively quite compelling, and underscore how C:Po should by all accounts be a useful metric. As we outlined in the Discussion, it is possible the fairly high values for C:Po, elemental imbalance with microbial biomass, and abiotic immobilization of PO4 have collectively reduced the effectiveness of Po to supply plant-available P in these ecosystems. One could argue that in this case a 'negative' (or nonsignificant) result is as interesting as a 'positive' one would be.

Here and elsewhere was a request for much more attention to inorganic P in the manuscript. We certainly examined soil Pi in our preparations but felt it was a poor covariate. The distribution of Pi was skewed, being generally low for most sites with a few outlier plots with high Pi. This created an issue because the main treatment factors of Spacing and Species were not evenly balanced among the upper range in Pi, leading to possible spurious relationships. Arguably a second covariate should be added to the analysis (e.g., C:N plus Pi) but the statistical model is overwhelmed with two main treatments (Spacing, Species), two covariates and all the interaction terms. We were advised our study design was not suitable for multiple covariates. Given the range in soils and constraints of the study design we felt the questions to be best answered were focused entirely on organic matter stoichiometry and how well these relationships matched the ecological literature (as mentioned above). We only added one Pi statistic in regards to foliar P%, to at least establish some relationship with soil P, but would argue a fuller analysis of Pi would be unwise and possibly misleading. We included a comment in the Discussion on this matter "Ultimately soil C:N and soil Pi together might best explain variations in rainforest productivity but the limitations in study size (64 plots distributed among 4 conifer species and 3 planting densities) prevented an adequate statistical analysis of all main factor interactions for two soil covariates"

The manuscript has a strong focus on these particular perhumid forest ecosystems of western Vancouver Island. The eventual paper might attract a broader audience if more reference is made to other possible P (co-)limited coniferous and temperate ecosystems worldwide. One short section in the Discussion, plus perhaps mentioning it in the Abstract and/or Conclusion may suffice. In the Introduction, the authors explain why the forest ecosystems of Vancouver Island are unique, but still I think some parallels can be made with other forests globally.

We added comments in the Discussion on how our results are fairly well aligned with temperate rainforests of New Zealand, and also added a second reference (Xu et al. 2013) with global C, N and P datasets to facilitate comparison of these sites with ecosystems elsewhere.

Line 5 – Consider changing the title to reflect the main conclusion of this work, e.g. the different responses among tree species to variation in soil stoichiometry, or on the

possible importance of P (the latter only if evidence is strong enough, see my other comments).

We changed the title to emphasize the contrasting patterns in conifer productivity. Since foliar nutrition was a secondary objective (along with conifer species effects on soils) we thought it best to remove that word from the title.

Line 6 – I assume that "nutrition" refers to foliar stoichiometry?

Yes, but nutrition has now been removed from the title

Line 26 – "We described the nature of soil organic matter (...)": this is a bit confusing, could also refer to SOM properties not measured in this study. I suggest you immediately indicate that you determined the forest floor thickness, and forest floor + soil nutrient concentrations and stoichiometry.

We changed this to nutrient concentrations as suggested. Forest floor depth was measured but did not contribute much to our analysis so we felt it was unnecessary to include that detail in the Abstract.

Line 31 – At this point, it is not clear whether you refer to forest floor or mineral soil C:N. In practice, both explained well spatial variation in basal area. I suggest to specify that. We made it clear that both substrate C:N were related to basal area as suggested.

Line 36 – "(...) no evidence via foliar nutrition for increased P availability with declining element ratios (...)": this refers to the lack of a relationship between foliar P and soil C:Po ratio. Looking at Table 4 and Fig. 5b, this seems to be correct definitely when combining species. But maybe there is a significant correlation between foliar P and soil C:Po within species? Foliar stoichiometry is typically strongly taxonomy-dependent (Sardans et al., 2015).

Under Methods we note that the model was first run with all interactions and then the insignificant terms removed to solve for the remaining terms (we inadvertently did not specify Species $\times$ Soil in the first draft, it is included now). We at no time found a significant Species $\times$ Soil interaction for foliar nutrients. To emphasize this point we included the interaction p values for each of the foliar nutrients throughout Results.

Line 36 – Throughout the manuscript, C:Po ratio is used instead of C:P ratio. The rationale behind this is mentioned in the text, and the text also explains that results for C:Po and C:P are very similar. I suggest to at least once also mention C:P in the Abstract, and making clear that in this case results are very analogous anyway.

A comment was added to include C:Ptotal as suggested.

Line 40 – A lot of attention is given to the potentially important role of P, but it was not possible to detect a clear effect of soil C:Po ratio on foliar P, nor productivity. My feeling is that this is to a great extent because N is still the primary nutrient limiting productivity across most of the gradient, yet I agree that P may become more important as a limiting factor at plots with low C:N. Since soil P availability is strongly influenced by soil pH, and pH seems to have been measured at all plots, you may consider testing relationships between productivity and pH, foliar P and pH, soil C:Po and pH, soil Pi and pH, ... Since curves of P availability vs pH typically show an optimum, first try fitting a quadratic function (although pH is generally low in this dataset and may eventually be below the optimum anyway).

Nitrogen varied widely to include both low N availability to high N availability (foliar N% of 0.9 to 1.5%). In contrast, P was almost a 'blanket' constraint across the landscape, as indicated by a large number of plots with low Pi and moderate foliar P% (often 0.10 - 0.13%). What the reviewer is suggesting in regards to pH and P optima would have been more suitable to an earlier publication (2019. New Phytologist 221, 482-492) on Vancouver Island where we compared a more balanced array of plots across wet to dry maritime forest soils with low to high Pi. Our focus in this manuscript is largely the quality of soil organic matter and how well these element ratios reflect forest productivity and nutrition. Details on soil Pi were included to fully characterize the soils, but a full analysis of inorganic P optima is beyond the scope of this study.

Line 80 – "Baseline relationships in soil resource stoichiometry and ecosystem productivity should also consider the interaction of tree species.": I agree, and this is also the case for foliar stoichiometry. While different species are shown in Fig. 5, the analyses in Table 4 do not test for the interaction between soil stoichiometry and species. Why?

As mentioned above, all interaction terms were tested and we found no significant Species $\times$ Soil terms for foliar nutrients. We now include the interaction p values for each of the foliar nutrients under Results.

Line 110 - A lot of attention is paid to the different responses among species, and a distinction between ECM and ARB trees is made. Moreover, in the discussion, a link with CSR strategies is made. I agree with the authors that these differential responses should be discussed, and I support the idea of explicitly stating a hypothesis or objective on this aspect. However, I would like to see a bit more of an explanation (in Intro and/or Discussion) of why you expect responses to differ between ECM and ARB. Some elements are in the text, but for example, in general, ectomycorrhizae are rather associated with enhanced N uptake, whereas arbuscular mycorrhizae rather for the uptake of P, which may influence (hypothesized) slopes like those in Fig. 4b. Having said that, these ECM-N vs AM-P links may be an overgeneralization; you for instance already mention the potential role of arbuscular mycorrhizae in N uptake in the manuscript.

An excellent review by Hodge (2017) demonstrates ample evidence for both mycorrhizal types to access inorganic and organic sources of nutrients. I suspect the distinction currently in vogue with differential mycorrhizal abilities is overstressed, as reviewer alludes to. We added the Hodge reference to the Discussion to make the point that the coexistence of ARB and ECM conifers demonstrates some shared competence in nutrient uptake from these soils.

Lines 118-124 – Add this information to Table 1 (or make a Table S1 in SI and refer to it). Then it is clear which site has what conditions. While this is not relevant to the main messages of the manuscript, it may be practical in case researchers want to use the data of the paper in the future, e.g. for reviews, meta-analyses, ...

A Supplemental Table was added to the manuscript with a more thorough description of landforms and ecological classification as suggested.

Line 140 – Add forest floor depths to Table 1 or S1.

This was added to S1 as suggested.

Line 156 – ! molar ratios ! In terrestrial ecology, some studies use mass-based ratios, others use molar. Please clarify that molar ratios were used at least in the description of every table and figure.

Molar was added to Tables and Figures

Line 232-233 – Foliar N:P ratios are used in the manuscript as one line of evidence suggesting P (co-)limitation. However, caution is needed when using such critical N:P ratios, since they depend on species. Also, I did not immediately find the proposed threshold of 16 in the given reference Güsewell et al., 2004. As explained under "general comments", please try to find some stronger evidence for (co-)limitation of P. Then for me, mentioning a critical foliar N:P ratio can remain in the manuscript if justified (but you note the taxonomy-dependence), but it should be one piece of the evidence, together with other arguments.

A number of papers have discussed this critical N:P ratio and the reviewer is correct, it was not addressed as directly in Gusewell. I have added the Reich and Oleskyn 2004 paper to reference this proposed threshold in N:P (which suggests 14, rather than 16, to delineate N-only constrained ecosystems; this change was made). I believe we have stressed a number of lines of evidence for P limitations as the reviewer suggested, and we have not over-relied upon a hypothetical threshold in foliar N:P.

Line 236 – For clarity, consider subdividing Discussion into sections with titles, like in Results or referring to the three objectives.

Subheadings were added as suggested

Line 238 – Like in the Introduction, the authors refer here to "high C and N regimes". In contrast to what was written in the Introduction, however, the sentence here discusses TOTAL N, whereas in the Introduction, reference is rather made to the AVAILABILITY of N. I suggest to (i) rephrase the vague mentioning of "high regimes" (e.g. total C and N concentrations were high), and (ii) not use total N as an argument to suggest that P may be as or even more limiting than N. Only a small proportion of the total N is plant-available, in the form of small organic molecules, ammonia and/or nitrate.

True, we revised to total C and N concentrations rather than regime as suggested. Our comment that stands are co-limited by N and P was based mostly on the interpretation of foliar nutrients, not total N.

Line 256-258 – The cited synthesis paper (Booth et al., 2005) indeed focuses on the link between C:N and N availability, among other things. It however not explicitly refers to the influence on soil C:N ratio on stand productivity and/or foliar N. I suggest adding a few references of gradients/large-scale studies exploring Productivity/foliar N _ soil C:N ratio, e.g. Alberti et al., 2014; Van Sundert et al., 2018, ... –> "The clear relationship between mineral soil and forest floor C:N with stand productivity and foliar % was consistent with many other biomes (NEW REFERENCES) and (...) with declining soil C:N (Booth et al., 2005)."

These two references were added as suggested

Line 276 – "(...) we found it more effective to gauge P availability through soil Pi concentrations (as the only significant correlate with foliar P %)": overall, the evidence for P (co-)limitation based on soil C:Po is limited (except from the facts that C:Po was comparatively high, and it had a significant + influence on basal area in Table 3, but a confounding effect with soil C:N cannot be excluded). Table 4 confirms the potential of Pi to explain variation in foliar P instead. So, why didn't you further check whether Pi was perhaps a better indicator of the soil P status than soil Po or C:Po? Would spatial variation in Pi, even within plots, be too high, and also seasonal variation, as can be argued for available N (depending on the application)? I suggest you to either perform additional analyses using Pi, or explain in the manuscript why it is not a suitable indicator.

We felt Pi was generally an unsuitable soil covariate for our analysis as discussed earlier. We maintain that questions related to organic matter stoichiometry are much better suited to the nature of this dataset. A larger geographical area in the region that encompassed a more balanced array of plots between low and high Pi soils would be better suited to this line of enquiry.

Line 336 – I strongly support your reference to additional nearby fertilizer application studies. However, to what extent are soils on N Vancouver Island comparable to W Vancouver Island, where the current study was performed? Earlier in the Discussion, you note based on your own data that the East of the island at least has soils differing from those in the West, as reflected in different foliar P.

The fertilizer study took place in very similar perhumid rainforest sites (the CWHvm, 01 HwBa-Blueberry site series) on the north Island. I revised this comment to note the relevance as suggested.

Line 352 – See also my earlier comment. Inorganic P was generally in low supply, and contributed a relatively minor proportion of total P. Please perform additional analyses on basal area vs Pi etc., or explain why this would not be a good idea. Table 2 – Please include Pi or argue why not. Table 3 – Please include Pi or argue why not.

Please note that the objectives of our study were to better characterize organic matter quality (C:N, C:Po N:Po) and test whether these gradients in element ratios would parallel the trends postulated by the ecological literature. To fully explore how all soil properties might influence tree growth (Pi, but also Ca, K, Mg, B, Cu, Fe, pH etc.) would be much better suited to a simpler design (e.g., one tree species at one planting density replicated across 50 test sites). We recognize that regionally the role of Pi

could be substantial, and have commented on that, but we are unable to prove that with any confidence with this data set.

Table 3 – Why exactly was the 0-20 cm interval used for sampling mineral soil? Is this roughly corresponding to the main rooting zone? Please specify in the M&M section.

This depth captures enough of the critical rooting zone to adequately quantify site effects. A comment was added as suggested.

Table 4 – It would be interesting to see how foliar and soil stoichiometry relate within species. Separate species were visualized in Fig. 5, but separate analyses (or analogous: soil*species interaction) were not performed. You could show that not only the link basal area _ soil stoichiometry depends on species, but also foliar stoichiometry _ soil stoichiometry. If you make a new table for this, perhaps place it in SI, and refer briefly to it.

Table 4 lists the final model for foliar attributes so, as mentioned previously, the Species $\times$ Soil interaction terms were listed in Results.

Figure 4b – I do not understand why mineral soil C:N was preferred here as a predictor over forest floor C:N. Table 3 suggests both are good explanatory variables. Please add and discuss panels using forest floor C:N, or explain why mineral soil C:N is the better alternative.

Depicting both mineral soil and forest floor C:N results seemed redundant as they were strongly correlated and produced very similar model outputs in relation to basal area. To streamline the manuscript we will include forest floor as a Supplemental Figure.

Figure 4b – Add test statistics (P, R2, ...)

The p test statistics here refer to the model output generated by Proc Mixed in Table 3. There are no individual R2 for these relationships, and furthermore we averaged the output across planting densities to help depict the key relationship between projected basal area and soil C:N by species. I added Table 3 to the caption to clarify where this model output came from.

Figure 5 - Why was foliar N and P chosen, and not foliar C:N and C:P (here and throughout the whole manuscript)?

Nutritional data in forest ecology has long been interpreted via concentrations rather element ratios (e.g. Carter 1992) and we chose to continue with this approach as it is far more informative (e.g, foliar P of 0.12% has much more interpretive value than a foliar C:P of 850). We included a comment on this in the Introduction but added average C concentrations of the foliage under Results in case readers want to be able to calculate element ratios.

Figure 5 – Figs. 4 and 5 confirm to me the role of N as a primary determinant of forest structure and function. In order to find stronger evidence for the role of P, you may consider (i) testing the interaction soil C:N*soil C:Po on basal area, and perhaps other response variables, and (ii) plotting foliar N:P (within and among species) vs mineral/forest floor C:N. My feeling is that (i) may fail, because soil C:N and C:Po may induce collinearity in the statistical model. If so, try checking the single influence of soil C:Po for data points only where C:N is low (_ high N availability). For (ii), we may expect an increase in foliar N:P, and thus P (co-)limitation, with decreasing soil C:N.

We indeed played with many of these multiple covariates but upon plotting residuals and discussions with our statistician we felt the study design was not robust enough to expand upon one soil covariate. Species interactions in particular can be potentially spurious with this many model terms for a relatively small data set. In regards to foliar N:P, we found weak patterns in relation to C:N but our analysis was constrained by some of the difficulties in getting adequate foliage for every plot. We felt it best to limit our discussion to the simpler, broader trends in foliar N and P in relation to soil C:N, C:Po and N:Po.

Figure 5b – I would be curious to see this graph with Pi as an explanatory variable (cf. Table 4).

We added that Figure as a Supplemental since the lack of relationship between foliar P and soil C:Po is the more critical finding.

TECHNICAL CORRECTIONS Line 5 – Perhaps the abbreviation C:N:P is not necessary in the title, or only provide the abbreviation and not the full words at this place.

C:N:P was removed from the title as suggested

Line 35 – "(...) no evidence via foliar nutrition (...)": please rephrase, Line 36 - "(...) no evidence via foliar nutrition for increased P availability with declining element ratios as we did for N.": "declining element ratios" is vague; this refers to soil C:Po ratio in the first place. Please rephrase.

Line 35 and 36 were simplified to 'no increase in foliar P concentrations with declining element ratios. . .'

Line 52 – "the N regime in certain soils can be extremely rich": somewhat weird way of expressing that some soils can be rich in available N = exhibit high N availability. Please rephrase.

In ecological classification the word 'rich' in terms of nutrient regime is used regularly but in any case we revised this to 'high'

Line 63 – Remove the word "global".

OK

Line 80 – "Baseline relationships in soil resource stoichiometry and ecosystem productivity should also consider the interaction of tree species.": you mean the statistical interaction between soil stoichiometry with species. As written now, with the word "of", it may seem as if the paragraph would discuss biological interactions between species. I suggest to replace "of" by "with".

OK

Line 188 – Sometimes P-values are given along with the correlations in brackets, sometimes not. Please add P-values everywhere.

The Pearson r values for the comparison of soil C and C:N were redundant as all the correlation statistics are in Table 2 so this text was removed. The comparison of substrates (Fig. 3) was not part of Table 2 so for these we have kept the p and r values

Line 277 – Remove the "%", from the data it is clear that foliar P is expressed in % (also apply this to analogous cases elsewhere).

This was done

Line 317 – "The small difference in forest floor N concentrations under Douglas-fir": you mean it was higher than for the other species. Please rephrase.

OK

Line 601 – At some places in the manuscript, Latin names were used, yet at others, tree species were named in English. Please use one of the two throughout the manuscript, including Tables and Figures.

All text in the manuscript is now with Latin names as suggested

Figure 1 – Please add "mineral" to the titles of both vertical axes.

OK

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