Response Letter

Title: Multiple soil nutrient competition between plants, microbes, and mineral surfaces: Model development, parameterization, and example applications in several tropical forests

General Response:

We would like to thank the two anonymous referees and T. Wutzler for their constructive comments. Special concerns came from the two anonymous reviewers about the "constant enzyme abundance assumption". In this revision, we modified our model so that plants are able to dynamically adjust their nutrient carrier enzyme abundance according to their fine root biomass. Sensitivity analysis, model calibration, and evaluations were completely re-done. Since the fertilization experiments we examined were short-term (24 or 48 hours), plants were not able to adjust their competitiveness and we therefore did not see large difference between the new and original models. However, allowing the plants to adjust their competitiveness did affect plant nutrient uptake over longer time periods (*e.g.*, seasonal). The model modifications suggested by the reviewers give the model great potential to better represent nutrient competition among various nutrient consumers.

The response letter is organized by (1) reviewers' major comments in blue; (2) authors' response in black. Minor reviewer comments (*e.g.*, typo) are not listed here. We have carefully checked the entire paper and incorporated those specific minor comments.

Reviewer #1

1. SOM modelling as it is done in most ecosystem models with first-order decay kinetics has been criticised for being too simplistic with a strict artificial division of available N between microbes, plant uptake, de/nitrification and other losses. Zhu et al. address this issue by introducing a soil nutrient competition model N-COM. At a first glance the model seems very interesting and comprehensive, but the way it has been tested and calibrated in the manuscript leaves many questions unanswered.

Response:

Thanks for your positive comments. According to your comments, we improved our manuscript accordingly. Please see our responses below and revised manuscript for more details.

2. In the abstract the authors state that their results imply a certain competitiveness order for NH4, NO3, and POx. I would argue that this order comes mainly from calibrating the model to data than as an independent modelling result.

Response:

You are correct that the reported competiveness is a modeling result. The important distinction for our results and paper is that competitiveness is defined so that it can be calibrated based on observational data, rather than being imposed as a fixed value or order (as is done by most large scale models). We believe this feature is one of the promising aspects of the N-COM model. For this study, the calibrated "competitiveness" is for tropical ecosystem only. The relative "competitiveness" will change due to changes in *e.g.*, plant root architecture, mycorrhizal fungi association, decomposing microbial community, soil pH, and soil order. N-COM facilitates representing the impacts of these factors on nutrient consumers' dynamic competitiveness. We added more discussion about this issue in **section 3.1**.

3. It has been shown (FACE MIP project; Medlyn et al. 2015 and series of articles) that ecosystem models differ in their representation of many different processes with contracting responses to perturbations to the system. So to say that nutrient competition is critical for the ESMs is a little too strong, as I thing many other process brought to light in Medlyn et al. (2015) will have larger impacts.

Response:

Model-data inter-comparison at FACE sites (FACE MIP) is a valuable project resulting in several interesting publications (Walker 2014; Zaehle et al., 2014; Medlyn et al., 2015). These papers showed that no tested ecosystem model was able to reproduce observed carbon and nitrogen dynamics at ORNL and DUKE FACE sites. Their results implied that new theory and modeling methods were needed, especially for modeling how ecosystems respond to elevated CO_2 conditions.

We acknowledge that many other mechanisms besides nutrient competition are important for ESM performance. Therefore, we modified our introduction, by saying that "nutrient competition is critical for ESMs to simulate ecosystem responses to nutrient perturbation".

4. The model at a first glance looks interesting (Eqn 13-21, A6-14 and B8), but the decision to keep the enzyme abundance of all consumers at a constant value (4068 L14) makes me disappointed. So by not activating a flexible [E] I think this study is missing a lot, which the manuscript is mentioning when stating that robust competition representation for climate-scale models will require representation of dynamic changes in plant allocation (4063 L3).

Response:

To address this concern, we modified the assumption of "constant enzyme abundance assumption". In the revised manuscript, we assumed that plant nutrient carrier enzyme abundance is proportional to fine root biomass. During wintertime, fine root biomass declines because the production rate is lower than mortality. In contrast, during the growing season, a large portion of NPP is allocated to fine root production in tropical forests, enhancing plant nutrient competitiveness. In this way, plants are able to adjust their nutrient competitiveness through the imbalance of fine root carbon allocation and mortality. Enabling the changes of enzyme abundance gives the model potential to better represent soil nutrient dynamics and carbon-nutrient interactions.

We modified our model and re-did the model calibration and evaluation again. We found that although the new model was theoretically more robust, the posterior model was similar to previous versions in terms of simulating nutrient competition in the short-term (24 or 48 hours) fertilization experiments. Plant competitiveness changes could not be so rapid. Therefore the advantage of "dynamic enzyme abundance assumption" was not realized for these short simulations. However, as mentioned above, these changes do result in dynamic relative competitiveness over seasonal to annual time frames

5. VMAX is mentioned throughout the paper, but isn't the constant to calibrate k in eqn B8, if flexible [E] is to be used? Will the calibrated values of VMAX and KM be valid under flexible [E]?

Response:

If [E] is flexible, then VMAX must be treated as the product of two independent variables. One is the reaction rate for one unit enzyme (*k*), the other is the enzyme abundance [E]. In the revised N-COM model, [E] is scaled by fine root biomass. Therefore, we only need to calibrate the enzyme base reaction rate (*k*).

6. The model was spun up for 100 years for the Puerto Rico simulation (4074 L19). I would like some more explanations on the spin up procedure (SOM build up? N/P uptake? etc) and the need for it as this is the only place it is mentioned in the manuscript.

Response:

Sorry for the confusion. We took soil organic matter stock (carbon) from a CLM4.5 restart file (which is in steady state). Other state variables were obtained from literature for tropical forest sites, but not particularly for Puerto Rico or Hawaii tropical forests (*e.g.*, free phosphate was from Panama site (Wright et al., 2011), organic nitrogen and phosphorus were inferred based on SOM CNP stoichiometry (Parton et al., 1988), adsorbed phosphorus and parent material phosphorus were from Yang et al., 2014).

In order to eliminate the impact of our imposed initial conditions on the fertilization experiments, we ran the model from the initialization state for 100-years and then applied the fertilizer into the soil. In the revised manuscript, we summarized this model spin-up procedure.

7. The change of coarse woody debris turnover time by 50% (4075 L18) is significant and its consequences to the C, N and P cycles/stocks should be covered.

Response:

That's a good idea. For the revised version of N-COM, the posterior model had longer woody debris turnover time but shorter litter turnover time. The whole soil organic carbon decay was not significantly changed, however. In the revised manuscript, we added more discussion about calibrated model parameters (compared with their prior) and their impact on the system C, N, and P cycles (particularly for those parameters closely associated with nutrient dynamics).

8. Figure 5 shows the result of the Hawaiian chronosequence experiment. It looks like modelled microbes is taking up close to nothing at all three sites and mineral all available P. Could this figure become clearer or is it that mineral is so competitively strong that they get 100% in the model?

Response:

First of all, the minerals are very competitive, and they can quickly establish equilibrium between adsorbed and free phosphate. Therefore, the large adsorption flux would limit microbial P immobilization.

Secondly, the response of microbial P immobilization to P fertilization is also limited by underestimation of microbial P demand. For our CENTURY type decomposition model, stoichiometric differences between soil organic matter and microbes are not considered. The observed difference between microbial and soil C/P ratios can be as large as 6-fold (Mooshammer et al., 2014; Xu et al., 2013). Were that the case in the observations we applied, the potential soil P demand calculated based on microbial C/P ratio should be 6 times higher than that based on soil organic matter C/P ratio. We have added some discussion on this issue in **section 3.4**.

9. For NH4 at the Puerto Rico site, plant and microbe is opposite strong at taking up NH4. Could this be adjusted if [E] became flexible?

Response:

You are right, if [E] becomes flexible, the tree may adjust its competitiveness when the environmental conditions are favorable. Since the fertilization experiment was conducted during growing season we expect to see that plants have higher competitiveness than during the non-growing season.

10. I also miss how the model would affect plant growth, heterotrophic respiration, N fluxes compared to a normal first-order decay kinetics model. Have this test been done? If so could a section describe the differences in their behaviour? Or even add it to Figure 5 for comparison.

Response:

At this point, we have used the model as a diagnostic tool. Many variables were taken from CLM4.5 simulations, as described in Methods. Our ongoing work is to integrate the competition scheme in CLM4.5, so that we can run the full model to predict how nutrient competition affects plant growth, soil respiration, etc.

The aims of this study are to (1) point out the importance of nutrient competition, (2) propose a feasible model structure for competition modeling, and (3) test the concepts against fertilization experiments. More detailed analyses at the whole ecosystem level are ongoing and will be reported in future publications.

Reference

Wright, S. Joseph, et al. "Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest." *Ecology*92.8 (2011): 1616-1625.

Parton, William J., John WB Stewart, and C. Vernon Cole. "Dynamics of C, N, P and S in grassland soils: a model." *Biogeochemistry* 5.1 (1988): 109-131.

Yang, X., et al. "The role of phosphorus dynamics in tropical forests–a modeling study using CLM-CNP." *Biogeosciences* 11.6 (2014): 1667-1681.

Walker, Anthony P., et al. "Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO2 enrichment experiments: Model performance at ambient CO2 concentration." *Journal of Geophysical Research: Biogeosciences* 119.5 (2014): 937-964.

Zaehle, Sönke, et al. "Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate Free-Air CO2 Enrichment studies."*New Phytologist* 202.3 (2014): 803-822.

Medlyn et al., 2015

Mooshammer, Maria, et al. "Stoichiometric imbalances between terrestrial decomposer communities and their resources: mechanisms and implications of microbial adaptations to their resources." *Frontiers in microbiology* 5 (2014).

Xu, Xiaofeng, Peter E. Thornton, and Wilfred M. Post. "A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems."*Global Ecology and Biogeography* 22.6 (2013): 737-749.

Reviewer #2

1. Zhu et al. (2015) did an excellent job at developing the N-COM model. I enjoyed reading their manuscript starting with their motivation on why current ESMs do not represent the competition between different microbial groups, plants and soil matrix for nutrients realistically. Their innovative ECA approach (Equilibrium Chemistry Approach) is very well suited for dealing with the multiple interactions between nutrients, plants, microbial groups and soil minerals. Overall, the manuscripts is well structured and a delight to read. It will be exciting to see N-COM implemented in a microbe mediated SOM decomposition model.

Response:

Thanks so much for your positive feedbacks.

2. From the description in section 2.3 you cannot tell, if the Bayesian calibration of N-COM is entirely proper. It seems that you ran one Monte Carlo Markov Chain for 50000 iterations. You claim that you reached convergence, but you could provide the readers with a trace plot of the MCMC (e.g. in the Appendix).

Response:

To address this reviewer concern, we added a tracer plot (Figure A1) that shows the evolution of model parameters during MCMC sampling. We also performed two replicated MCMC calibrations (with different random number seeds).

We noticed that the some of the parameters were not well constrained, which was reflected in their relatively large posterior uncertainty and small uncertainty reduction. We argued that the non-convergence resulted from data paucity rather then a short MCMC chain. For example, k_{NO3}^{plant} is the least constrained parameter because there were no NO_3^- pool size data. We have added more discussion about this issue in **Section 3.1**.

3. In section 3.1, you state that the posterior parameters were irregularly distributed. Nevertheless, you fitted a normal distribution to the posterior sample (n = 1000) of parameters. You can, however, directly use your sample from the posterior to make inferences about the mean and standard deviation (or maybe better median and interquartile range). I would recommend to use the second halves (your last 25000 *iterations) of your chains to directly calculate your* $\sigma_{posterior}$ *for the estimation of the uncertainty reduction.*

Response:

Thanks for your recommendation. In the revised manuscript, we used the last 25000 samples of the MCMC chain to infer our posterior model parameters (mean and standard deviation).

4. In Figure 2, your binning of the posterior sample is quite broad. Could you use smaller bins and maybe use a larger sample from your MCMC (e.g. second halves of the chains) to construct this plot?

Response:

We updated Figure 2: (1) prior model parameters distributions (log-normal) were plotted for comparison; (2) posterior model parameters were divided into more bins. We also added another figure (Fig. A2) to show the fitting of posterior model parameters to Gaussian distribution, based on which the mean and variance were obtained.

5. I would welcome some additional discussion, if a dynamic simulation of enzyme abundances for the different consumers could result in a time-varying apparent relative competitiveness. For the purpose of the present study, you assumed that all consumers have the same enzyme abundances (P4068,L15). Does this assumption simply eliminate the time-component from competition between the different consumers? Does this mean that with your approach you are able to represent the long-term competition between consumers?

Response:

To address this, and the other two reviewer similar concerns, we modified our model structure so that plants and decomposing microbes were able to adjust their nutrient carrier enzyme abundance (as described above). The enzyme abundance of plants and decomposing microbes were scaled by the fine root biomass or potential immobilization rate, respectively.

6. 1. You could try to improve how you introduce the structure of the five SOC pools. In Equation 4 you introduce $F^{move}_{C\,i,j}$ *, but the link to* f_{ij} *and* g_i *(Table 2) could be presented more clearly to the reader.*

Response:

Sorry for the confusion. Following Equation 4, we added more detailed description about how to calculate $F^{move}_{C\,i,j}$ based on f_{ij} and g_i.

7. In Figure 1, you use the terms "MIC NH4 uptake" and "MIC NO3 uptake"; in the text, however, you mostly use the term "immobilization". It would be great if you updated Figure 1 to match the terminology used throughout the paper.

Response:

Thanks. To ensure consistency, we updated the entire manuscript (including Figure 1). "Microbial NH4 and NO3 updates" were replaced by "NH4 and NO3 immobilization".

8 other minor comments

In line 21, p 4064, you state that carbon has the units "g C m-3 ", while in Table 2 it is "g C m-2 ". Please clarify.

Response:

In line 21, p 4064, that was a typo, we have corrected it. The model is not vertically resolved. All the fluxes and state changes are calculated in terms of "$g\ m^{-2}$".

Reviewer #3

1. The paper presents an interesting ecosystem modeling study dealing with multiple elements and competition. This issue is timely and interesting to a broad community. I read the paper initially with great interest. The ECA formulation of resource uptake probably has large potential to construct adequate models in competition settings. However, by progressing to the results section, and frequently going back to the methods to understand the results, I became disappointed about the model performance and also doubting about the claims of the paper.

Response:

Thanks for the general positive comments. We have modified our model based on your comments. Please see the following responses.

2. In the supplement, the authors write that "soil CNP stoichiometry is flexible and depends on the predicted immobilization rates". This assumption need to be defended very well. If I understand correctly, there are no stoichiometric constraints on SOM decomposition and only the product stoichiometry is adjusted due to the currently available nutrient uptake flux. However, decomposition is done by microbial biomass with rather strict homeostatic constraints. From a model designed to study competition for nutrients, I would expect to deal with stoichiometric constraints and resulting changes in other processes such as decomposition with inhibition or overflow respiration. Maybe it was not well explained, as stoichiometry factors are referred to as subsets of the parameters on page 4071.

Response:

The original N-COM version assumed that soil CNP stoichiometry is flexible within upper and lower bounds. Therefore, the model has some stoichiometry constraints on SOM decomposition.

For the revised N-COM model, we adopted the fixed CNP stoichiometry. We agree that fixed SOM stoichiometry could better deal with the soil CNP imbalance during decomposition if the nutrient immobilization could not satisfy the nutrient demand.

3. I am missing information how the nutrient immobilization flux F immob from appendix A is distributed to the changes of the different SOM pools F immob j (eq. 5 and 6). Why is there another subscript i in F immob ji ? From eq. A6-A8 I first got confused that immobilization fluxes do not depend on the inorganic pool. The amount of substrate, surprising to me, is presented as part of the relative competitiveness (eq. 13ff). Can this be presented better? Further, did I understand correctly that NH4 and NO3 are not in direct competition for satisfying the N demands?

Response:

Sorry for the confusion. $F^{immob}{}_{ij}$ means the immobilization flux occurred when carbon flowed from upstream (i^{th} pool) to down stream (j^{th} pool).

The potential immobilization flux (Equation A6 – A9) is calculated as the total nutrient demand during SOM decomposition. The soil has to immobilize those nutrients to satisfy the soil CNP stoichiometry. However, the soil may not be able to get those nutrients due to the competition stress from other nutrient consumers. Therefore, the immobilization rates are not dependent on the inorganic pool directly, but are constrained by the inorganic pool size indirectly.

Equation 13 – 22 are improved in terms of formulation of competition. Further, we added Equation 23 – 28, 32 – 33 to facilitate the explanation of our competition equations.

We assumed that soil microbes have no preference in nutrient uptake (NH_4^+ versus NO_3^-). The microbes will take up both NH_4^+ and NO_3^- according to their availability in the soil (Equation A7-A8).

4. The assumption of the enzyme baseline seems rather strict. On the other hand, with fitting all the Km coefficients, the concentrations become rather arbitrary because they could cancel with the Km. What would be the consequences on the results by doubling one of the enzyme concentrations?

Response:

We also realized that “constant enzyme abundance assumption” might be too strict. In the new model, for example, the plant nutrient carrier enzyme abundance is updated dynamically based on fine root biomass. That means that during the growing season, plant will produce more enzymes. At the same time, if microbial enzyme abundance does not change, plants will become more aggressive and take up more nutrients than predicted by the original N-COM model. Doubling the plant enzyme abundance will enhance plant competitiveness, but not exactly double, because of competition with other consumers.

5. The competition between microbes, plants, and mineral surfaces is probably very different in rhizosphere, litter layer and bulk soil, with depth, and also at smaller scales down to aggregates. The microbial properties (all the KMs) are probably very heterogeneous in space too. I am missing some critical discussion on this heterogeneity.

Response:

To address this concern, we added text in the Methods describing that the model did not discriminate bulk soil, rhizosphere soil, or the litter layer. In order to be consistent with CLM4.5 model structure, the competition model is designed for the whole soil column (mixed environment of rhizosphere and bulk soil). We agree that heterogeneity is one of the important factors that controls competition. We had some discussion about soil heterogeneity in **section 3.4**. In the revised manuscript we added more detailed discussion in **section 3.1**.

6. I am missing the specification of the likelihood or cost function. Especially with several data streams there are several crucial choices to make. How was convergence of the limiting distribution checked?

Response:

Apologies for the missing explanation. We have added an equation to describe the cost function in the revised manuscript (Eqn. 29).

The convergence of the model parameters was checked visually. We plotted out the evolution of model parameters during MCMC calibration in the Figure A1. Most of the model parameter converged, and have a Gaussian distribution (Figure A2).

7. Fig 2 is too small and the binning of the histogram is done in a way that does not allow many conclusions. All that I get is the impression that the MC calibration did not *successfully converge to the limiting distribution and that the presented sample is far from assumed Gaussian.*

Response:

Figure 2 has been updated: (1) add more bins for posterior parameters and (2) add prior distribution for comparison. We have added new figures to show that most of model parameters were converged to a Gaussian distribution (Figure A1 and A2).

8. The presented way of inspecting uncertainty reduction is rather longwinded and errorprone. I would not trust the conclusions from first specifying priors by factors of one estimate (p4072,l14), then specifying a σprior, and then inferring a σposterior from fitting a normal distribution to the posterior samples presented in Fig.2. I suggest plotting the prior distribution of the range of relevant posterior together with a reasonable histogram and/or density line of the posterior.

Response:

Thanks for the suggestion. In Figure 2, we plotted the prior and posterior distribution together for the purpose of comparison. The estimation of prior parameter uncertainty was also improved. We first assumed that the model parameters could vary within [10% 500%] of their prior values. We then fit them to lognormal distribution, and infer σ_{prior} from the distribution's variances.

9. Since, the parameters are restricted to positive values and are constrained by 10% to 500%, it will be more reasonable to use a log-normal distribution as prior and fit to the posterior, or alternative do the calibration on log-transformed parameters. To me the resulting prior and posterior sigma would be more meaningful.

Response:

We re-did the model calibration by assuming the prior model parameters were lognormally distributed between 10% and 500% of their prior values. We also updated the parameter uncertainty reduction based on the new prior and posterior parameters variance.

10. The authors claim (p 4084), that with more temporally resolved observations the model could be constrained better. From Fig. 4, however, I get the impression that the model structure was not able to already fit the given observations (although the observation uncertainties necessary for evaluation are not presented).

Response:

The model structure has been improved with: (1) fixed SOM CNP stoichiometry and (2) flexible abundance of plants' nutrient carrier enzyme. The calibration was also improved by adopting a lognormal distribution for prior parameters. We showed that our posterior model could reasonably reproduce the observed tropical ecosystem C/N/P dynamics, which imply the efficacy of our model calibration and the accuracy of our model structure.