Multiple soil nutrient competition between plants, microbes, and mineral surfaces:

Model development, parameterization, and example applications in several tropical forests

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Abstract

Soil is a complex system where biotic (e.g., plant roots, micro-organisms) and abiotic (e.g., mineral surfaces) consumers compete for resources necessary for life (e.g., nitrogen, phosphorus). This competition is ecologically significant, since it regulates the dynamics of soil nutrients and controls aboveground plant productivity. Here we develop, calibrate, and test a nutrient competition model that accounts for multiple soil nutrients interacting with multiple biotic and abiotic consumers. As applied here for tropical forests, the Nutrient COMpetition model (N-COM) includes three primary soil nutrients (NH₄⁺, NO₃⁻, and PO₄ (representing the sum of PO₄³⁻, HPO₄²⁻, and H₂PO₄⁻)) and five potential competitors (plant roots, decomposing microbes, nitrifiers, denitrifiers, and mineral surfaces). The competition is formulated with a quasi-steady-state chemical equilibrium approximation to account for substrate (multiple substrates share one consumer) and consumer (multiple consumers compete for one substrate) effects. N-COM successfully reproduced observed soil heterotrophic respiration, N₂O emissions, free phosphorus, sorbed phosphorus, and NH₄⁺ pools at a tropical forest site (Tapajos). The overall model uncertainty was moderately well constrained. Our sensitivity analysis
revealed that soil nutrient competition was primarily regulated by consumer-substrate affinity rather than environmental factors such as soil temperature or soil moisture. Our results also imply that under strong nutrient limitation, relative competitiveness depends strongly on the competitor functional traits (affinity and nutrient carrier enzyme abundance). We then applied the N-COM model to analyze field nitrogen and phosphorus perturbation experiments in two tropical forest sites (in Hawaii and Puerto Rico) not used in model development or calibration. Under soil inorganic nitrogen and phosphorus elevated conditions, the model accurately replicated the experimentally observed competition among nutrient consumers. Although we used as many observations as we could obtain, more nutrient addition experiments in tropical systems would greatly benefit model testing and calibration. In summary, the N-COM model provides an ecologically consistent representation of nutrient competition appropriate for land BGC models integrated in Earth System Models.
1 Introduction

Atmospheric CO₂ concentrations have risen sharply since the pre-industrial era, primarily due to anthropogenic fossil fuel combustion and land use and land cover change [Houghton, 2003; Le Quéré et al., 2013; Marland et al., 2003]. Terrestrial ecosystems mitigate the increasing atmospheric CO₂ trend by absorbing roughly a quarter of anthropogenic CO₂ emissions [Le Quéré et al., 2009]. However, it is still an open question whether the terrestrial CO₂ sink can be sustained [Sokolov et al., 2008; Zaehle et al., 2007; LeBauer and Treseder, 2008; Vitousek and Howarth, 1991] and soil nutrients could be quickly depleted through biogeochemical [Chauhan et al., 1981; Nordin et al., 2001; Shen et al., 2011] and hydrological [Dise and Wright, 1995; Perakis and Hedin, 2002] processes. Therefore, a holistic representation of soil nutrient dynamics is critically important to model the responses of terrestrial ecosystem CO₂ uptake to climate change.

Until recently, land models integrated in Earth System Models (ESMs) have largely ignored the close coupling between soil nutrient dynamics and the carbon cycle, although the impacts of soil nutrients (primarily Nitrogen and Phosphorus) regulating carbon-climate feedback are clearly required in ecosystem biogeochemistry and land models [Zaehle and Dalmonech, 2011; Zhang et al., 2011]. For example, none of the land models in C₄MIP (Coupled Climate Carbon Cycle Model Intercomparison Project phase 4) had coupled Carbon and Nitrogen dynamics [Friedlingstein et al., 2006]. The current generation of CMIP5 [Anav et al., 2013] models used for the recent IPCC (Intergovernmental Panel on Climate Change) assessment had only two members (CLM4CN: Thornton et al. [2007]; and BNU-ESM: Ji et al., 2014) that considered
nitrogen regulation of terrestrial carbon dynamics. However, as discussed below, several
recent studies have shown that these models had large biases in most of the individual
processes important for simulating nutrient dynamics. We therefore believe that, at the
global scale, no credible representation of nutrient constraints on terrestrial carbon
cycling yet exists in ESMs.

Further, none of the CMIP5 ESMs included a phosphorus cycle, which is likely
important for tropical forest carbon budgets [Vitousek and Sanford, 1986]. The recent
IPCC report highlights the importance of nitrogen and phosphorus availability on land
carbon storage, even though the phosphorus limitation effect is uncertain [Stocker et al.,
2013]. Since the next generation of ESMs participating in the CMIP6 synthesis will
continue to focus on the impacts of a changing climate on terrestrial CO2 and abiotic
exchanges with the atmosphere [Provides, 2014], developing ecologically realistic and
observationally-constrained representations of soil nutrient dynamics and carbon-nutrient
interactions in ESMs is critical.

The importance of nutrient limitations in terrestrial ecosystems has been widely
demonstrated by nitrogen and phosphorus fertilization experiments [Elser et al., 2007].
For instance, plant Net Primary Production (NPP) is enhanced in plots with nutrient
addition [LeBauer and Treseder, 2008]. Similarly, plant growth can be stimulated due to
atmospheric nitrogen deposition [Matson et al., 2002]. Boreal forests are strongly limited
by nitrogen availability [Vitousek and Howarth, 1991], because low temperatures reduce
nitrogen mineralization [Bonan and Cleve, 1992] and N2 fixation [DeLuca et al., 2008;
DeLuca et al., 2002]. In contrast, tropical forests are often phosphorus limited [Vitousek
et al., 2010], since tropical soils are old and phosphorus derived from parent material
weathering has been depleted through long-term pedogenesis processes [Vitousek and Farrington, 1997; Walker and Syers, 1976]. In natural ecosystems without external nutrients inputs (e.g., N deposition), soil nitrogen or phosphorus (or both) are likely insufficient to satisfy both plant and microorganism demands [Vitousek and Farrington, 1997]. Plants have to compete with microorganisms and mineral surfaces [Kaye and Hart, 1997; Schimel et al., 1989] to obtain sufficient nutrients to sustain their biological processes (e.g., photosynthesis, respiration). Therefore, it is critical to improve the representation of nutrient competition to accurately model how terrestrial ecosystems will respond to perturbations in soil nutrient dynamics (e.g., from elevated nitrogen deposition or CO₂ fertilization-induced nutrient requirements).

Intense competition between plants and microorganisms is a well-observed phenomenon in nutrient-limited systems [Hodge et al., 2000a; Johnson, 1992; Kaye and Hart, 1997]. Previously, plants were thought to be initial losers in nutrient competition, due to the fact that microbes are more intimately associated with substrates [Woodmansee et al., 1981]. However, increasing observational evidence indicates that plants compete effectively with soil microorganisms [Schimel and Bennett, 2004] under certain circumstances; sometime even outcompeting them and suppressing microbial growth [Hu et al., 2001; J Wang and Lars, 1997]. ¹⁵N isotope studies have also demonstrated that plants can capture a large fraction of added nitrogen [Hodge et al., 2000b; Marion et al., 1982]. In the short term (days to months), plants maintain their competitiveness mainly through (1) establishing mycorrhizal fungi associations [Drake et al., 2011; Rillig et al., 1998], which help plants acquire organic and inorganic forms of nitrogen [Hobbie and Hobbie, 2006; Hodge and Fitter, 2010] and (2) root exudation of extracellular enzymes.
that decompose rhizosphere soil organic matter [Phillips et al., 2011]. In the relatively
ger longer term (months to years), morphological adjustment occurs; for example, plants
allocate more carbon to fine roots to explore laterally and deeper [Iversen et al., 2011;
Jackson et al., 2009]. Finally, over the course of years to decades, plant succession can
occur [Medvigy et al., 2009; Moorcroft et al., 2001] and the new plant demography will
need to be considered to represent nutrient controls on this time scale.

Given these patterns from the observational literature, nutrient competition is
either absent or over-simplified in existing Earth System Models (ESMs). One common
representation of plant-microbe competition is that plants compete poorly against
microbes in resource acquisition. For example, the O-CN land model [Zaehle and Friend,
2010] assumes that soil decomposing microbes have the priority to immobilize soil
mineral nitrogen. After microbes meet their demands, the remaining nitrogen is then
available for plant uptake.

Another treatment in ESM land models is that microbial and plant nutrient
acquisition competitiveness is based on their relative demands. For example, CLM4CN
[Thornton et al., 2007] assumes that the plant and microbial nitrogen demands are
satisfied simultaneously. Under nitrogen infertile conditions, all nitrogen demands in the
system are down-regulated proportional to the individual demands and subject to
available soil mineral nitrogen. This approach led to unrealistic diurnal cycles of gross
primary production (GPP), with midday depressions in GPP occurring because of
predicted diurnal depletion of the soil mineral nitrogen pool. Emergent impacts of this
conceptualization of nutrient constraints on GPP resulted in poor predictions compared to
observations, with smaller than observed plant C growth responses to N deposition
and larger than observed responses to N fertilization [Thomas et al., 2013b]. Further, most biogeochemistry models not integrated in ESMs also adopt one of these approaches. For instance, Biome-BGC [Running and Coughlan, 1988], CENTURY [Parton et al., 1988], CASA (Carnegie-Ames-Stanford Approach; [Potter et al., 1993]) and the Terrestrial Ecosystem Model - TEM [McGuire et al., 1992] assume that available nutrients preferentially satisfy the soil microbial immobilization demand.

We believe the two conceptualizations of competition used in ESMs substantially over-simplify competitive interactions between plants and microbes and lead to biases in carbon cycle predictions. To begin to address the problems with these simplified approaches, Tang and Riley (2013) showed that complex consumer-substrate networks can be represented with an approach (called Equilibrium Chemical Approximation (ECA) kinetics) that simultaneously resolves multiple demands for multiple substrates, and demonstrated that the approach was consistent with observed litter decomposition observations. ECA kinetics has also recently been applied to analyze the emergent temperature response of SOM decomposition, considering equilibrium, non-equilibrium, and enzyme temperature sensitivities and abiotic interactions with mineral surfaces [Tang and Riley, 2014]. We extend on that work here by presenting an implementation of ECA kinetics to represent competition for multiple soil nutrients in a multiple consumer environment. We note that this paper demonstrates a method to handle instantaneous competition in the complex soil-plant network, but a robust competition representation for climate-scale models will require representation of dynamic changes in plant allocation and plant composition.
The aim of this study is to provide a reliable nutrient competition approach applicable for land models integrated in ESMs. However, before integration into an ESM, the competition model needs to be carefully calibrated and independently tested against observational data. This paper will therefore focus on model development and evaluation at several tropical forest sites where observations are available. Our objectives are to: (1) develop a soil biogeochemistry model with multiple nutrients (i.e., \( \text{NH}_4^+ \), \( \text{NO}_3^- \), and \( \text{PO}_x \) (represented as the sum of \( \text{PO}_4^{3-} \), \( \text{HPO}_4^{2-} \), and \( \text{H}_2\text{PO}_4^- \)) and multiple nutrient consumers (i.e., decomposing microbes, plants, nitrifiers, denitrifiers, and mineral surfaces) competition using ECA kinetics [Tang and Riley, 2013; Zhu and Riley, 2015]; (2) constrain the model with in situ observational datasets of soil carbon, nitrogen, and phosphorus dynamics using a Markov Chain Monte Carlo (MCMC) approach; and (3) test model performance against nitrogen and phosphorus fertilization studies.
2 Method

2.1 Model development

The Nutrient COMpetition model (N-COM) is designed as a soil biogeochemistry model (Figure 1) to simulate soil carbon decomposition, nitrogen and phosphorus transformations, abiotic interactions, and plant demands. Although our ultimate goal is to incorporate N-COM into a decomposition model that represents active microbial activity as the primary driver of decomposition, we start here by presenting the N-COM approach using a Century-like [Koven et al., 2013; Parton et al., 1988] structure, with additions to account for phosphorus dynamics. In our approach, we calculate potential immobilization using literature-derived parameters (e.g., \( VMAX, K_M \)) in a Michaelis-Menten (MM) kinetics framework. The potential immobilization is subsequently modified using the ECA competition method.

Five pools of soil organic Carbon (C), Nitrogen (N), and Phosphorus (P) are considered: Coarse Wood Debris (CWD), litter, fast Soil Organic Matter (SOM) pool, medium SOM pool, and slow SOM pool. Litter is further divided into three sub-groups: metabolic, cellulose, and lignin. The soil organic C, N, and P decomposition (\( F^{dec}_{C,j}, F^{dec}_{N,j}, F^{dec}_{P,j} \)) follow first-order decay:

\[
F^{dec}_{C,j} = k_j C_j r_T \\
F^{dec}_{N,j} = k_j N_j r_T \\
F^{dec}_{P,j} = k_j P_j r_T
\]

where \( k_j \) is the rate constant of soil organic matter decay (s\(^{-1}\)); \( C_j, N_j, \) and \( P_j \) are pool sizes (g m\(^{-2}\)) of carbon, nitrogen, and phosphorus, respectively (\( j \) from 1 to 7 represents the soil organic matter pools: CWD, metabolic litter, cellulose litter, lignin litter, fast...
SOC, median SOC, slow SOC; \( r_t \) and \( r_s \) (dimensionless) are soil temperature and moisture environmental regulators.

Decomposed carbon \( (F_{C, i}^{\text{dec}}) \) (upstream \( i^{th} \) pool) either (1) enters a downstream pool \( j^{th} \) or (2) is lost as CO\(_2\). Soil organic carbon (downstream \( j^{th} \) pool) temporal change is calculated as:

\[
\frac{dC_j}{dt} = -F_{C,j}^{\text{dec}} + \sum_{i=1}^{N} F_{C,j}^{\text{move}}
\]  

(4)

where \( \sum_{i=1}^{N} F_{C,j}^{\text{move}} \) is the summation of carbon fluxes that move from the upstream pool \( i \) to the downstream pool \( j \) due to the decomposition of upstream SOC. For each upstream carbon pool \( (i = 1, 2, \ldots, 7) \), the fractions integrated into downstream pools \( (j = 1, 2, \ldots, 7) \) is summarized in a \( 7 \times 7 \) matrix \( f_{ij} \) (Table 2). The percentage of decomposed carbon that is respired as CO\(_2\) is represented by \( g_i \) (Table 2). Simultaneously, soil organic N and P changes follow C decomposition:

\[
\frac{dN_j}{dt} = -F_{N,j}^{\text{dec}} + \sum_{i=1}^{N} F_{N,j}^{\text{move}} + \sum_{i=1}^{N} F_{N,j}^{\text{immob}} + \sum_{i=1}^{N} F_{N,j}^{\text{immob}} + \sum_{i=1}^{N} F_{N,j}^{\text{immob}}
\]  

(5)

\[
\frac{dP_j}{dt} = -F_{P,j}^{\text{dec}} + \sum_{i=1}^{N} F_{P,j}^{\text{move}} + \sum_{i=1}^{N} F_{P,j}^{\text{immob}} + \sum_{i=1}^{N} F_{P,j}^{\text{immob}}
\]  

(6)

where \( F_{N,j}^{\text{move}} \) and \( F_{P,j}^{\text{move}} \) are fluxes of nitrogen and phosphorus moving from the upstream \( (i) \) to downstream \( (j) \) pools. \( F_{N,j}^{\text{immob}} \), \( F_{N,j}^{\text{immob}} \), and \( F_{P,j}^{\text{immob}} \) are immobilization fluxes of soil mineral nitrogen and phosphorus. \( F_{C,j}^{\text{dec}} \) and \( F_{C,j}^{\text{dec}} \) represent soil organic matter decomposition losses.
Equations (5) and (6) state that changes in the $j^{th}$ organic N or P pool are the summation of three terms: (1) organic N and P lost during soil organic matter mineralization ($-F_{N,j}^{\text{dec}}$ and $-F_{P,j}^{\text{dec}}$); (2) a fraction of the $j^{th}$ organic N or P pool (upstream) enters into the $j^{th}$ pool (downstream) ($F_{N,j}^{\text{move}}$ and $F_{P,j}^{\text{move}}$); and (3) soil microbial immobilization ($F_{NH4,j}^{\text{immob}}$, $F_{NO3,j}^{\text{immob}}$, and $F_{P,j}^{\text{immob}}$). Immobilization occurs only when the newly entering organic N is insufficient to sustain the soil C:N (or C:P) ratio (more details described in Appendix A).

The inorganic nitrogen pools (NH$_4^+$ and NO$_3^-$ (Eqn. 7-8)) are altered by production (organic N mobilized by microbes), consumption (uptake by plants and microbes, gaseous or aqueous losses), and transformation (nitrification and denitrification). Inorganic P ($PO_4^{3-}$) is assumed to be either taken up by plants and decomposing microbes or adsorbed to mineral surfaces (Eqn. 9). Plants utilize all forms of phosphate (e.g., PO$_4^{3-}$, HPO$_4^{2-}$, and H$_2$PO$_4^-$), but for simplicity we use the symbol $PO_4^{3-}$ to represent the sum of all possible phosphate forms throughout the paper.

$$\frac{d[NH4]}{dt} = \sum_{j=1}^{N} \sum_{i=1}^{N} F_{NH4,j}^{\text{mob}} - F_{NH4}^{\text{loss}} - F_{NH4}^{\text{plant}} - F_{NH4}^{\text{immob}} + F_{\text{BSF}} + F_{\text{dep}}$$ (7)

$$\frac{d[NO3]}{dt} = -F_{NO3}^{\text{den}} + (1 - f^{N2O})F_{NO3}^{\text{ni}} - F_{NO3}^{\text{plant}} - F_{NO3}^{\text{immob}} - F_{NO3}^{\text{weather}} + F_{NO3}^{\text{dep}}$$ (8)

$$\frac{d[PO4]}{dt} = \sum_{j=1}^{N} \sum_{i=1}^{N} F_{P,j}^{\text{mob}} - F_{P}^{\text{plant}} - F_{P}^{\text{immob}} - F_{P}^{\text{weather}} + F_{P}^{\text{dep}}$$ (9)

where $F_{NH4,j}^{\text{mob}}$ and $F_{P,j}^{\text{mob}}$ are gross mineralization rates for nitrogen and phosphorus. $F_{NH4}^{\text{ni}}$ is the nitrification flux, part of which is lost through a gaseous pathway ($f^{N2O}$) and the rest is incorporated into the NO$_3^-$ pool. $F_{NO3}^{\text{den}}$ is the denitrification flux, which transforms nitrate to N$_2$O and N$_2$ which then leave the soil system. Plant uptake of soil NH$_4^+$, NO$_3^-$,
and PO₄ are represented as $F^{\text{plant}}_{\text{NH}_4}$, $F^{\text{plant}}_{\text{NO}_3}$, and $F^{\text{plant}}_{\text{PO}_4}$, respectively. Soil decomposing microbial immobilization of soil NH₄⁺, NO₃⁻, and PO₄ are represented as $F^{\text{immob}}_{\text{NH}_4}$, $F^{\text{immob}}_{\text{NO}_3}$, and $F^{\text{immob}}_{\text{PO}_4}$. External inputs into soil inorganic N pools include atmospheric ammonia deposition ($F^{\text{dep}}_{\text{NH}_4}$), atmospheric nitrate deposition ($F^{\text{dep}}_{\text{NO}_3}$), and biological nitrogen fixation ($F^{\text{NF}}_{\text{B}}$). External sources of phosphate come from parent material weathering ($F^{\text{weather}}_{\text{P}}$).

Finally, the dynamics of sorbed P ($P_s$), occluded P ($P_o$), and parent material P ($P_{\text{P}}$) are modeled as:

$$\frac{d[P_s]}{dt} = F^{\text{sof}}_{sp} - F^{\text{occl}}_{sp}$$

$$\frac{d[P_o]}{dt} = F^{\text{occl}}_{sp}$$

$$\frac{d[P_{\text{P}}]}{dt} = -F^{\text{weather}}_{sp} + F^{\text{dep}}_{sp}$$

where the pool of sorbed P is balanced by the adsorption flux ($F^{\text{sof}}_{sp}$) and occlusion flux ($F^{\text{occl}}_{sp}$). Parent material is lost by weathering ($F^{\text{weather}}_{sp}$) and is slowly replenished by external atmospheric phosphorus inputs ($F^{\text{dep}}_{sp}$, such as dust). More detailed information on the modeled C, N, and P fluxes is documented in Appendix A.

### 2.2 Multiple-consumer-multiple-resource competition network

The soil biogeochemistry model presented in section 2.1 has multiple potential nutrient consumers (plants, SOM decomposing microbes, nitrifiers, denitrifiers, mineral surfaces) and multiple soil nutrients (NH₄⁺, NO₃⁻, PO₄). The consumer-resource network is summarized in Table 1. As in many land BGC models (CLM, Century, etc.), we have
not explicitly included the mineral surface adsorptions of NH₄⁺ and NO₃⁻, since we assume ammonia is quickly protected by mineral surfaces from leaching (no leaching term in Eqn. 7) but then released for plant and microbial uptake when the biotic demand arises. An improved treatment of these dynamics would necessitate a prognostic model for pH, which is beyond the scope of this analysis. Unlike sorbed P (which can be occluded), there is no further abiotic loss of sorbed ammonia. Therefore, the free ammonia pool is interpreted in the current model structure as a potential free ammonia pool (free + sorbed).

Competition between different consumers in acquiring different resources is summarized in Table 1. Each consumer-substrate competition reaction is represented by:

\[ S + E \xrightarrow{k_s} C \xrightarrow{k_i} P + E \]  

(13)

The enzyme (E: e.g., nutrient carrier enzyme produced by plants and microbes) and substrate (S: e.g., NH₄⁺, NO₃⁻) reaction (reversible reaction) forms a substrate-enzyme complex (C). The following irreversible reaction leads to product (P: meaning the nutrients has been taken up) and releases enzyme (E) back into soil media. For the whole complex reaction network, nutrient uptakes are formulated as:

\[ F_{\text{NH}_4}^{\text{plant}} = k_{\text{NH}_4}^{\text{plant}} \frac{[\text{NH}_4] \cdot [E_N]}{K_{\text{NH}_4}^{\text{plant}} (1 + \frac{[\text{NH}_4]}{K_{\text{NH}_4}^{\text{plant}}} + \frac{[\text{NO}_3]}{K_{\text{NO}_3}^{\text{plant}}} + \frac{E_N}{K_{E_N}^{\text{plant}}} + \frac{E_N}{K_{E_N}^{\text{plant}}} + \frac{E_N}{K_{E_N}^{\text{plant}}})} \]  

(14)

\[ F_{\text{NH}_4}^{\text{mineral}} = k_{\text{NH}_4}^{\text{mineral}} \frac{[\text{NH}_4] \cdot [E_N]}{K_{\text{NH}_4}^{\text{mineral}} (1 + \frac{[\text{NH}_4]}{K_{\text{NH}_4}^{\text{mineral}}} + \frac{[\text{NO}_3]}{K_{\text{NO}_3}^{\text{mineral}}} + \frac{E_N}{K_{E_N}^{\text{mineral}}} + \frac{E_N}{K_{E_N}^{\text{mineral}}} + \frac{E_N}{K_{E_N}^{\text{mineral}}})} \]  

(15)

\[ F_{\text{NH}_4}^{\text{total}} = k_{\text{NH}_4}^{\text{total}} \frac{[\text{NH}_4] \cdot [E_N]}{K_{\text{NH}_4}^{\text{total}} (1 + \frac{[\text{NH}_4]}{K_{\text{NH}_4}^{\text{total}}} + \frac{[\text{NO}_3]}{K_{\text{NO}_3}^{\text{total}}} + \frac{E_N}{K_{E_N}^{\text{total}}} + \frac{E_N}{K_{E_N}^{\text{total}}} + \frac{E_N}{K_{E_N}^{\text{total}}})} \]  

(16)
\[ F_{\text{plant}}^{\text{NO}_3} = k_{\text{NO}_3}^{\text{plant}} \frac{[\text{NO}_3] \cdot [E_{\text{plant}}^p]}{K_M^{\text{plant,NO}_3} (1 + \frac{[\text{NH}_4]}{K_M^{\text{plant,NH}_4}} + \frac{[\text{NO}_3]}{K_M^{\text{plant,NO}_3}} + \frac{[E_{\text{plant}}^p]}{K_M^{E_{\text{plant}}^p}} + \frac{[E_{\text{mic}}^p]}{K_M^{E_{\text{mic}}^p}} + \frac{[E_{\text{den}}^p]}{K_M^{E_{\text{den}}^p}})} \]  

\[ F_{\text{inmob}}^{\text{NO}_3} = k_{\text{inmob}}^{\text{mic}} \frac{[\text{NO}_3] \cdot [E_{\text{mic}}^p]}{K_M^{\text{mic,NO}_3} (1 + \frac{[\text{NH}_4]}{K_M^{\text{mic,NH}_4}} + \frac{[\text{NO}_3]}{K_M^{\text{mic,NO}_3}} + \frac{[E_{\text{plant}}^p]}{K_M^{E_{\text{plant}}^p}} + \frac{[E_{\text{mic}}^p]}{K_M^{E_{\text{mic}}^p}} + \frac{[E_{\text{den}}^p]}{K_M^{E_{\text{den}}^p}})} \]  

\[ F_{\text{den}}^{\text{NO}_3} = k_{\text{den}}^{\text{mic}} \frac{[\text{NO}_3] \cdot [E_{\text{den}}^p]}{K_M^{\text{den,NO}_3} (1 + \frac{[\text{NH}_4]}{K_M^{\text{den,NH}_4}} + \frac{[\text{NO}_3]}{K_M^{\text{den,NO}_3}} + \frac{[E_{\text{plant}}^p]}{K_M^{E_{\text{plant}}^p}} + \frac{[E_{\text{mic}}^p]}{K_M^{E_{\text{mic}}^p}} + \frac{[E_{\text{den}}^p]}{K_M^{E_{\text{den}}^p}})} \]  

\[ F_{\text{plant}}^p = k_{\text{plant}}^p \frac{[\text{PO}_4] \cdot [E_{\text{plant}}^p]}{K_M^{\text{plant,PO}_4} (1 + \frac{[\text{PO}_4]}{K_M^{\text{plant,PO}_4}} + \frac{[E_{\text{plant}}^p]}{K_M^{E_{\text{plant}}^p}} + \frac{[E_{\text{mic}}^p]}{K_M^{E_{\text{mic}}^p}} + \frac{[E_{\text{den}}^p]}{K_M^{E_{\text{den}}^p}})} \]  

\[ F_{\text{mic}}^p = k_{\text{mic}}^p \frac{[\text{PO}_4] \cdot [E_{\text{mic}}^p]}{K_M^{\text{mic,PO}_4} (1 + \frac{[\text{PO}_4]}{K_M^{\text{mic,PO}_4}} + \frac{[E_{\text{plant}}^p]}{K_M^{E_{\text{plant}}^p}} + \frac{[E_{\text{mic}}^p]}{K_M^{E_{\text{mic}}^p}} + \frac{[E_{\text{den}}^p]}{K_M^{E_{\text{den}}^p}})} \]  

\[ F_{\text{den}}^p = k_{\text{den}}^p \frac{[\text{PO}_4] \cdot [E_{\text{den}}^p]}{K_M^{\text{den,PO}_4} (1 + \frac{[\text{PO}_4]}{K_M^{\text{den,PO}_4}} + \frac{[E_{\text{plant}}^p]}{K_M^{E_{\text{plant}}^p}} + \frac{[E_{\text{mic}}^p]}{K_M^{E_{\text{mic}}^p}} + \frac{[E_{\text{den}}^p]}{K_M^{E_{\text{den}}^p}})} \]  

where \( F \) represent the nutrient uptake fluxes and \( k \) is the base reaction rate that enzyme-substrate complex forms product (\( k^*_e \) in Eqn. 13). \([E]\) and \(K_M\) denote enzyme abundance and half saturation constants (substrate-enzyme affinity). Superscripts and subscripts refer to consumers and substrates, respectively. These equations account for the effect of (1) multiple substrates (e.g., NH\(_4^+\) and NO\(_3^-\)) sharing one consumer, which inhibits the effective binding between any specific substrate and the consumer (terms (1) and (2) in Eqn. 14) and (2) multiple consumers (e.g., plants, decomposing microbes, and nitrifiers).
sharing one substrate (e.g., NH$_4^+$), which lowers the probability of effective binding
between any consumer and NH$_4^+$ (terms $^3$, $^4$, and $^5$ in Eqn. 14).

For our reaction network (Eqn. 13 – 22), we assume that: (1) plant roots and
decomposing microbes possess two types of nutrient carrier enzymes (nutrient
transporters). One is for nitrogen (NH$_4^+$ and NO$_3^-$; $E^\text{plant}_N$, $E^\text{mic}_N$), and the other is for
phosphorus, including different forms of phosphate ( $E^\text{plant}_P$, $E^\text{mic}_P$). (2) Nutrient carrier
enzyme abundance is scaled with biomass (fine root or microbial biomass). Scaling
factors are 0.0000125 (for plants) and 0.05 (for decomposing microbes) (Table 2). (3)
Mineral surface “effective enzyme” abundance ( $E^\text{surf}_N$) is approximated by the available
sorption surface area ($V^\text{MAX}_N - [SP]$). (4) Nitrifiers and denitrifiers are not explicitly
simulated, therefore we assume that their biomass and associated nutrient transporter
abundance are fixed ( $E^\text{nit}_N$, $E^\text{den}_N$).

For simplicity, we group the “decomposing microbes/nitrifier/denitrifier/mineral
surface nutrient carrier enzyme [E]” and their “base reaction rate k” into one single
variable “$V^\text{MAX}$” (see Appendix B for full derivation). Furthermore, we defined
“potential rates (potential immobilizaiton, nitrification, denitrification, adsorption rates)”
and used them as proxies of “$V^\text{MAX}$”. Therefore, Eqn. 15, 16, 18, 19, 21, 22 become:

\[
F^\text{immob}_{\text{NH}_4} = F^\text{immob, pot}_{\text{NH}_4} \cdot \frac{[\text{NH}_4]}{K^\text{min, NH}_4(1 + \frac{[\text{NH}_4]}{K^\text{min, NH}_4} + \frac{[\text{NO}_3]}{K^\text{min, NO}_3} + \frac{E^\text{plant}_N}{K^\text{min, NH}_4} + \frac{E^\text{mic}_N}{K^\text{min, NH}_4} + \frac{E^\text{nit}_N}{K^\text{min, NH}_4})}
\]

(23)

\[
F^\text{pot}_{\text{NH}_4} = F^\text{pot, pot}_{\text{NH}_4} \cdot \frac{[\text{NH}_4]}{K^\text{min, NH}_4(1 + \frac{[\text{NH}_4]}{K^\text{min, NH}_4} + \frac{E^\text{nit}_N}{K^\text{min, NH}_4})}
\]

(24)
The model is design to be a component of the
Community and ACME Land Models (CLM, ALM; which are essentially currently equivalent), we used CLM4.5 site-level simulations to acquire temporally-resolved: (1) soil temperature factors on decomposition \( r_T \); (2) soil moisture factors on decomposition \( r_\theta \); (3) the anoxic fraction of soil pores \( f_{anox} \) in Appendix Eqn. A10-11; (4) annual NPP \( NPP_{annual} \) in Appendix Eqn. A13; (5) \( NH_4^+ \) deposition \( F_{NH4dep} \); (6) \( NO_3^- \) deposition \( F_{NO3dep} \); and (7) hydrologic discharge \( Q_{dis} \) in Appendix Eqn. A14).

External inputs of mineral phosphorus are derived from Mahowald et al., [2005, 2008].

2.3 Model parameterization and sensitivity analysis

We constrained model parameters and performed sensitivity analyses using a suite of observations distinct from the observations we used subsequently to test the model against the N and P manipulation experiments. Because tropical systems can be either nitrogen or phosphorous limited (or both) [Elser et al., 2007; Vitousek et al., 2010], we chose observations from a tropical forest site to constrain the N and P competition in our model (Tapajos National Forest, Para, Brazil (Table 3)).

In the parameter estimation procedure, several data streams are assimilated into the N-COM model, including measurements of soil \( NH_4^+ \) concentrations, soil free phosphate concentrations, sorbed phosphate concentrations, and \( N_2O \) and \( CO_2 \) flux measurements. The datasets are summarized in Table 3 and cover a wide range of N and P biogeochemistry dynamics. A set of model parameters is selected for calibration (Table 4), which comprise nutrient competition kinetics parameters \((k\ and\ K_M)\) as well as the fast soil carbon turnover time \( TURN_{SOM} \). Because we had only a short-term \( CO_2 \) respiration flux record, we were unable to calibrate the longer turnover time parameters. However, since we test the calibrated model against short-term fertilization responses, this omission
will not affect our evaluation. Longer records from eddy covariance flux towers and $^{14}$C
soil measurements are required to constrain the longer turnover time pool values.

We employed the Markov Chain Monte Carlo (MCMC) approach [Ricciuto et al., 2008] to assimilate the observations into N-COM. MCMC directly draws samples from a
pre-defined parameter space and tries to minimize a pre-defined cost function:

$$J = (M(\theta) - D)^T R^{-1}(M(\theta) - D)$$  \hspace{2cm} (29)

where $M(\theta)$ and $D$ are vectors of model outputs and observations including time series of
different simulated variables (e.g., soil CO$_2$ and N$_2$O effluxes and soil concentrations of
NH$_4^+$, free PO$_x$, and sorbed PO$_x$); $\theta$ is a vector of model parameters ($\theta_i$); and $i$ from 1 to
20 represents the parameters that are calibrated (Table 4). $R^{-1}$ is the inverse of data error
covariance matrix. We assumed that diagonal elements are 40% of observed values and
off-diagonal elements are zeros. We further assumed that the prior parameter follows a
lognormal distribution. $\mu$ and $\sigma$ were 0.91 and 0.95 of their initial values, respectively
(Table 4). We then ran MCMC to sample 50,000 parameter pairs (Fig. A1). The second
half of the samples was fit to a Gaussian distribution. We also employed the Gelman-
Rubin criterion to quantitatively show whether or not the MCMC chain converged. The
calibrated model parameters are reported in term of means and standard deviations.

Uncertainty Reduction ($UR$) is calculated based on (1) variance (Eqn. 30a) and (2) 25%
and 75% quantile (Eqn. 30b):

$$UR_\sigma = (1 - \frac{\sigma_{\text{posterior}}}{\sigma_{\text{prior}}}) \cdot 100\%$$  \hspace{2cm} (30a)

$$UR_Q = (1 - \frac{Q_{\text{posterior}}^{25}}{Q_{\text{prior}}^{25}} \cdot \frac{Q_{\text{prior}}^{75} - Q_{\text{prior}}^{25}}{Q_{\text{posterior}}^{75} - Q_{\text{posterior}}^{25}}) \cdot 100\%$$  \hspace{2cm} (30b)
where $\sigma_{\text{prior}}$ is prior parameter uncertainty, which is 95% of the parameter initial value.

$\sigma_{\text{posterior}}$ is calibrated parameter uncertainty, which is calculated by fitting the calibrated model parameters to a Gaussian distribution. $Q^{25}$ and $Q^{75}$ are 75% and 25% percentage quantile of each parameter. Uncertainty Reduction is a useful metric [Zhu and Zhuang, 2014], because it quantitatively reveals the reduction in the range of a particular parameter after calibration with MCMC. It does not, however, indicate that the parameter itself is more consistent with observed values of the parameter. A large value of $UR$ implies a more robust model.

In addition, we conducted a sensitivity study to identify the dominant controlling factors regulating nutrient competition in N-COM. Three scenarios were considered: (1) baseline climate and soil conditions; (2) elevated soil temperature (by 5 °C); and (3) elevated soil moisture (by 50%). SOBOL sampling [Pappas et al., 2013], a global sensitivity technique, is employed to calculate the sensitivities of output variables with respect to various inputs:

$$ S_i = \frac{VAR_{p_i} (E_{p_i} (Y | p_i))}{VAR(Y)} $$

where $S_i$ is the first order sensitivity index of the $i^{th}$ parameter and ranges from 0 to 1. By comparing the values of $S_i$, we were able to evaluate which processes affect the pattern of nutrient competition. $Y$ represents the model outputs of plant $\text{NH}_4^+$, $\text{NO}_3^-$, or $\text{PO}_4$ uptake; $p_i$ is the target parameter; $p_{\text{adj}}$ denotes all parameters that are associated with nutrient competition except the target parameter; and $VAR(.)$ and $E(.)$ represent variance and mean, respectively.

### 2.4 Model application
After calibration, we applied the N-COM model to several tropical forest nutrient fertilization studies not included in the calibration dataset, where isotopically labeled nitrogen or phosphorous fertilizer was injected into the soil. The fertilization experiments measured the fate of added nutrients; for example, identifying the fraction of added N or P that goes into the plant, is immobilized by microbes, or is stabilized by mineral surfaces. These measurements offer an effective baseline to test whether the N-COM model captures short-term nutrient competition.

Because we have focused in this paper on applications in tropical forests, we choose three tropical forest fertilization experiments with (1) PO$_4^{3-}$, (2) NH$_4^+$, and (3) NO$_3^-$ additions (Table 5). The PO$_4^{3-}$ fertilization experiment [Olander and Vitousek, 2005] was conducted in three Hawaiian tropical forests along a soil chronosequence (300, 20000, and 410000 year old soils) that were fertilized with 10 µg g$^{-1}$ $^{32}$PO$_4^{3-}$, respectively, and microbial demand versus soil sorption was measured. We did not evaluate the role of plants in phosphorus competition for the Hawaii sites, since plant phosphorus uptake was not measured in those field studies. Our model discriminates the Hawaii sites along the chronosequence by setting distinct initial pool sizes (derived from [Olander and Vitousek, 2004; Olander and Vitousek, 2005]) of soil organic carbon, nitrogen and phosphorus, and soil parent material phosphorus.

We also used measurements from NH$_4^+$ and NO$_3^-$ fertilization studies located at the Luquillo tropical forest in Puerto Rico [Templer et al., 2008]. In that study, 4.6 µg g$^{-1}$ $^{15}$NH$_4^+$ was added into the highly weathered tropical forest soil and the consumption of $^{15}$NH$_4^+$ by plant roots, decomposing microbes, and nitrifiers were measured. In the same study, 0.92 µg g$^{-1}$ $^{15}$NO$_3^-$ was added to the soil and the plant uptake and microbial...
immobilization was measured. The measurements were made 24 or 48 hours after the fertilizers were added.

For the model scenarios, we (1) spun up the N-COM model for 100 years; (2) perturbed the soil nutrient pool by the same amount as the fertilization; (3) ran the model for 24 or 48 hours and calculated how much of the added nutrients were absorbed by plants, microbes, or mineral surfaces; and (4) compared our model simulations with the observed data to assess model predictability. The 100-year spin up simulation aimed at eliminating the effects of imposed initial inorganic pool sizes on fertilization experiments, rather than accumulating soil organic matter in the system, since we initialized the soil organic carbon pools from CLM4.5 steady state predictions.

3. Results and discussion

3.1 Calibrated model parameters

Our best estimates (second half of the MCMC chain) of the selected model parameters based on the observations at the Tapajos National Forest, Para, Brazil are shown in Figure 2. We found that calibrated parameter samples were not heavily tailed and they generally follow Gaussian distributions (Figure A3). In order to quantitatively compare the calibrated parameter distributions with prior distributions, we fit parameter samples to a Gaussian distribution and estimated its means and standard deviations (Table 4).

Even though the parameter mean was improved, the uncertainty may still be relatively large. In other words, a prognostic prediction based on these calibrated parameters could be relatively uncertain [Scholze et al., 2007], due to large uncertainty
associated with the calibrated parameters. Therefore, we calculated the variance-based Uncertainty Reduction ($UR_\sigma$) (Eqn. 30a) to evaluate model improvement in terms of parameter uncertainty. We found that parameters’ uncertainties were reduced by 13%–98%. This calculation might either overestimate or underestimate the $UR_\sigma$, due to the fact that the calibrated parameters did not strictly follow Gaussian distributions. But the actual $UR_\sigma$ should not be far from our estimates, because these samples were not widely spread across the potential parameter space (Figure 2). The least constrained parameter was $k_{\text{plant}}^{\text{NO}_3}$ (reaction rate of plant nitrogen carrier enzyme with NO$_3^-$ substrate).

Two other NO$_3^-$ dynamics related parameters were also not well constrained: $UR_\sigma$ of $K_m^{\text{mic,NO}_3}$ (half-saturation constant for decomposing microbe NO$_3^-$ immobilization) and $K_m^{\text{den,NO}_3}$ (half-saturation constant for denitrifier NO$_3^-$ consumption) were only 63% and 68%, respectively. Compared with NH$_4^+$ or PO$_4$ competition related parameters, we concluded that parameters associated with NO$_3^-$ competition were the least constrained in the model. This result was primarily due to the lack of NO$_3^-$ pool size data, and secondarily due to the fact that NO$_3^-$ was not the major nitrogen source for plant or decomposing microbes. We also provide quantile-based Uncertainty Reduction for reference (Table 4). The above-mentioned conclusions still hold with quantile-based $UR_Q$, although the quantile-based $UR_Q$ is generally higher than variance-based $UR_\sigma$. One parameter was calibrated to be at the upper boundary of its prior ranges ($k_{\text{plant}}^{\text{NO}_3}$), implying that this tropical plant is highly efficient in phosphorus uptake. Although we do not have direct kinetic parameter observations for the specific tropical species involved in our study, an inferred high phosphorus uptake efficiency is reasonable for tropical species
that have adapted to these phosphorus deficient environments [Begum and Islam, 2005; FÖHse et al., 1988].

Convergence of model parameters is reported with the Gelman-Rubin criterion (univariate potential scale reduction factor) (Table 4 and Figure A2). Using this criterion, seven (out of twenty) parameters are found to converge (Gelman-Rubin < 1.1). The lack of convergence (in addition, 20-dimensional multivariate potential scale reduction factor is 12.04) of the remaining parameters is partly due to data paucity. In particular, starting from different initial values, MCMC calibrations may result in different models that give rise to similar model-data misfit (i.e., “equifinality” [Tang and Zhuang, 2008]). In this regard, high frequency measurements may improve model calibration (see more discussion in section 3.3). The non-convergence of model parameters implies an imperfect model. Therefore, for large-scale model application, more work on data collection, parameter tuning, and uncertainty analysis is needed. However, even with these caveats, the model predictability is reasonably good when applied to the tropical forest fertilization experiments described in Section 3.4.

We re-organize the right hand sides of Eqns. 14 – 22 to be the product of potential nutrient uptake rate and an ECA limitation term; for example for plant NH$_4^+$ uptake:

$$ F_{NH_4}^{\text{amo}} = k_{NH_4}^{\text{amo}} \cdot ECA_{NH_4}^{\text{amo}} $$

(32)

$$ ECA_{NH_4}^{\text{amo}} = \frac{[NH_4]}{K_M^{NH_4} + [NH_4]} \cdot \frac{[E_N]}{K_M^{EN} + [E_N]} \cdot \frac{[E_{Ni}]}{K_M^{EN} + [E_{Ni}]} \cdot \frac{[E_{Mc}]}{K_M^{EN} + [E_{Mc}]} $$

(33)

Other “consumer-substrate reactions” have similar forms. Under a nutrient abundant situation (e.g., fertilized agriculture ecosystem), the relative competitiveness of each consumer (ECA) is dominated by its specific enzyme abundance ([E]). Under such
conditions, substrate affinity is no longer a controlling factor. In contrast, under nutrient limited conditions (e.g., many natural ecosystems), ECA is dominated by the specific enzyme abundance as well as the substrate affinity ([E]/K_m). Therefore, consumers could either enable an alternative high affinity nutrient transporter system (low K_m) or exude more enzyme to enhance competitiveness. For example, at the whole-soil scale it has been shown that root spatial occupation (C_{root}) determines a plant’s competitiveness when low soil nutrient diffusivity is limiting nutrient supply [Raynaud and Leadley, 2004]. Consistently, our results highlighted the dominant role of nutrient carrier enzyme abundance (E proportional to C_{root}) in controlling competition. If we further assumed that plants, decomposing microbes, and nitrifiers enzyme abundances were approximately equal, we will have that the relative their competitiveness in acquiring NH_4^+ was about 4:10:9 (1/K_M^{plant,NH_4}:1/K_M^{mic,NH_4}:1/K_M^{nit,NH_4}). However, such results could not be easily generalized to other ecosystems, because they heavily relied on the traits (affinity) of specific competitors. For a different ecosystem, those traits would be drastically different due to the change of, e.g., plant species composition and microbial community structure. Even for the same ecosystem, those traits could be highly heterogeneous. For example, the community structure of decomposing microbes could be different in rhizosphere and bulk soil (with different K_m). However, in this work we assumed a well-mixed environment (one soil column), in order to be consistent with large-scale ecosystem models. Although beyond the scope of the current study, the consequences of ignoring the rhizosphere versus bulk soil heterogeneity warrants further investigation. Large-scale models aim to quantify ecosystem level dynamics, although they are usually driven by parameters inferred from in situ field observations.
absence of a model that explicitly represents this spatial heterogeneity, it is difficult to quantify the impacts of using inferred rhizosphere decomposer affinities on model predictions of the whole soil [Schimel et al., 1989]. Furthermore, the assumption of well-mixed environment in large-scale model is an inevitable flaw, because of large computational demands and a lack of scale-aware parameters and model structures for large-scale models to run fine scale simulations.

Although in this study ECA was applied to a large-scale model, the competition framework is readily applicable to fine scale models that consider soil heterogeneity. In fine-scale models, bulk soil nutrient competition can occur only among different microbes because they are ubiquitous in the soil (e.g., nitrifier versus microbial decomposer), while rhizosphere nutrient competition occurs among plants and microbes (e.g., nitrifier versus microbial decomposer versus roots). This distinction implies that the competitiveness parameters we infer here for N-COM, which does not currently explicitly represent bulk versus rhizosphere processes, subsume the range of fine scale processes controlling nutrient uptake. More research is required to link these different model spatial scales, theory, and parameterizations.

Our modeling framework highlights the important concept that “competitiveness” is a dynamic property of the competition network, and more importantly that it is linked to competitor functional traits (affinity and nutrient carrier enzyme abundance). This concept is in contrast to the prevailing assumption underlying all major large-scale ecosystem models, which either assume “relative demand competitiveness for different nutrient consumers” [Thornton et al., 2007] or “soil microbes outcompete plants” [McGuire et al., 1992; Parton et al., 1988]. Imposing such pre-defined orders of
competitiveness neglects the diversity of nutrient competitors (plants and microbes) and their differences in nutrient uptake capacity expressed by relevant functional traits. Our model framework offers a theoretically consistent approach to account for the diversity of nutrient competition in different competitor networks.

3.2 Model sensitivity analysis

Through sensitivity analysis, we separately investigated the factors controlling plant NH$_4^+$, NO$_3^-$, and PO$_4^{3-}$ competition (Figure 3). Each sensitivity analysis consisted of three scenarios: (1) normal conditions (control); (2) elevated soil temperature (+$T_s$); and (3) elevated soil moisture (+$\theta$). The sensitivity analysis indicates that the model is highly sensitive to kinetics parameters (e.g., $K_M$). Furthermore, the model is consistently sensitive to the same parameters across all temperature and moisture conditions. The environment affects the nutrient competition primarily through altering the nutrient abundance. Enhanced soil temperature and soil moisture accelerated soil organic carbon turnover, thereby releasing more inorganic nutrient into the soil (gross mineralization). However, the impacts on plant nutrient uptake are limited (Figure 3) because the enhanced soil organic matter decay also requires higher immobilization fluxes to sustain the soil organic matter CNP stoichiometry. The enhancement of net mineralization would be limited, and therefore would not change soil nutrient status dramatically.

3.3 Model performance

The prior and calibrated models were compared against observational datasets of pool sizes of soil free phosphate, sorbed phosphate, and NH$_4^+$, CO$_2$ efflux, and N$_2$O efflux (Figure 4). We note that although we attempted to acquire as many datasets that contained these five observations as possible, more observations in tropical ecosystems
would clearly improve the parameter estimates. For example, in the experiment we analyzed, only three measurements of soil free phosphate were made during 1999. Many detailed dynamics are therefore missing and could impact our parameter estimates. The prior model predicted an increasing trend of soil free PO₄, which resulted from underestimates of plant P uptake (by underestimating \( k_{p}^{\text{plant}} \)) and soil microbial P immobilization (by overestimating \( K_{M}^{\text{mic,P}} \)). The calibrated model captured the seasonal dynamics of soil free PO₄ reasonably well: increases during the wet season and gradual decreasing during the dry season (August to November). The prior model also largely underestimated the seasonal variability of nitrogen dynamics and underestimated the NH₄⁺ pool size due to overestimation of plant NH₄⁺ uptake (\( k_{NH₄}^{\text{plant}} \)). In addition, it also underestimated the denitrification N₂O emissions, because of an underestimation of NH₄⁺ to NO₃⁻ transformation rate (\( k_{\text{nit}} \)). Consequently, there was not enough NO₃⁻ substrate to react with denitrifiers and release N₂O. The calibrated model, however, accurately reproduced the seasonal dynamics of both NH₄⁺ pool sizes and soil N₂O emissions. There were small differences between the prior and calibrated model predictions of soil CO₂ emissions. The CO₂ and N₂O effluxes were more frequently observed at Tapajos National Forest during 1999 to 2001, compared with phosphorus data. Most of the measurements were collected during the wet season. Therefore the modeled CO₂ and N₂O emissions were largely improved by assimilating these datasets.

The model performance implies that after assimilating multiple datasets, our model predictions were improved over the prior model. However, it is clear that more observations of the metrics applied in our MCMC approach would benefit the model calibration. Unfortunately, because of our focus on tropical sites, we were unable to
acquire more datasets that had the full suite of measurements required. Datasets of soil nutrient pool sizes (e.g., NO$_3^-$) and higher frequency sampling of those sparse measurements (e.g., POx) would significantly benefit the model uncertainty reduction.

3.4 Model testing against nitrogen and phosphorus fertilization studies

To test the calibrated N-COM model, we conducted short-term numerical competition experiments (24-hour or 48-hour simulations) by manually imposing an input flux into nutrient pools equivalent to the N and P fertilization experiments described above and in Table 5. The simulated results were compared with observations from the field manipulations.

In the P addition experiments across the Hawaiian chronosequence, the partitioning of phosphate between microbes and mineral surfaces was well represented by the N-COM model in the intermediate (20K yr) and old (4.1M yr) sites (Figures 5b and 5c), with no significant differences between model predictions and observations. In the youngest Hawaiian site (300 yr; Figure 5a), the relative partitioning was correctly simulated, but the predicted PO$_4^{3-}$ magnitudes were lower than observations. Our simulations indicated that at the young soil site the added P exceeded microbial demand, resulting in lower predicted microbial P uptake than observed. This discrepancy reflected a possible deficiency of first-order SOC decay models (as we used here), which implicitly treat microbes as a part of soil organic matter. Since microbial nutrient immobilization is strictly regulated by the SOC turnover rate in this type of model, external nutrient inputs will no longer affect microbial nutrient uptake if the inputs exceed potential microbial demand. We therefore believe that explicit Microbe-Enzyme models might be able to better explain the strong microbe PO$_4^{3-}$ uptake signal observed at the young Hawaii
fertilization experiment site. Microbial models explicitly simulate the dynamics of microbial biomass, which might be able to capture the expected rapid growth of microbial communities under conditions of improved substrate quality [Kaspari et al., 2008; Wieder et al., 2009].

In the Puerto Rican Luquillo forest nitrogen addition experiments, partitioning of added ammonium between plants and heterotrophic bacteria was well captured by the N-COM model, with no significant differences between model predictions and observations (Figure 5d). However, the model underestimated nitrifier NH$_4^+$ uptake. NO$_3^-$ competition in this site was also relatively accurately predicted (Figure 5e), although the measurements did not include denitrification. Model estimates of plant NO$_3^-$ uptake and microbial NO$_3^-$ immobilization were consistent with the observed ranges, but we highlight the large observational uncertainties, particularly for microbial NO$_3^-$ uptake.

In the pseudo-first-order decomposition model we applied here to demonstrate the ECA competition methodology, the soil organic matter C:N:P ratio also limited microbial N and P uptake. For this type of decomposition model, stoichiometric differences between soil organic matter and microbes are not dynamically simulated. Such a simplification of soil and microbial stoichiometry favors large spatial scale model structures over long temporal periods, but hampers prediction of microbial short-term responses to N and P fertilization. For example, 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 a fixed soil organic matter C:P ratio could be only 17% of that based on microbial C:P ratio.
3.5 Implications of ECA competition treatment

Terrestrial ecosystem growth and function are continuously altered by climate (e.g., warming, drought; [Chaves et al., 2003; Springate and Kover, 2014]), external nutrient inputs (e.g., N deposition; [Matson et al., 2002; Matson et al., 1999]), and atmospheric composition (e.g., CO₂ concentration; [Norby et al., 2010; Oren et al., 2001; Reich et al., 2006]). Improved understanding of the underlying mechanisms regulating ecosystem responses to environmental changes has been obtained through in situ level to large-scale and long-term manipulation experiments. For example, decade-long Free-Air Carbon Dioxide Enrichment (FACE) experiments have revealed that nitrogen limitation diminished the CO₂ fertilization effect of forests [Norby et al., 2010] and grasslands [Reich and Hobbie, 2013] ecosystems. However, fewer efforts have been made towards incorporating the observed process-level knowledge into Earth System Models (ESMs). Therefore, a major uncertainty that has limited the predictability of ESMs has been the incomplete representation of soil nutrient dynamics [Zaehle et al., 2014]. Even though new soil nutrient cycle paradigms were proposed during recent decades [Korsaeth et al., 2001; Schimel and Bennett, 2004], they were restricted to either conceptual models or only applied to explain laboratory experiments.

Many large-scale terrestrial biogeochemistry models (e.g., O-CN, CASA, TEM) have adopted the classical paradigm that microbes decompose soil organic matter and release NH₄⁺ as a “waste” product [Waksman, 1931]. The rate of this process is defined as “net N mineralization”, and is adopted as a “measure” of plant available inorganic N [Schimel and Bennett, 2004]. This classical paradigm overlooked the fact that “net N mineralization” actually comprised two individual processes - gross N mineralization and...
microbial N immobilization. Implicitly, the classical paradigm assumes that the microbes
have priority to assimilate as much of the available nutrient pool as possible. Soil
nutrients were only available for plant uptake if there were not enough free energy
materials (e.g., dissolved soil organic carbon) to support microbial metabolism. As a
result, soil microbes were considered “victors” in the short-term nutrient competition.
Some other large-scale terrestrial biogeochemistry models (e.g., CLM4CN), simplify the
concept of nutrient competition differently. They calculate the plant N uptake and soil N
immobilization separately; and then down-regulate the two fluxes according to the soil
mineral N availability. As a result, plant and soil microbe competitiveness for nutrients is
determined by their relative demand.
Climate-scale land models have over-simplified or ignored competition between
plants, microbes, and abiotic mechanisms. In reality, under high nutrient stress
conditions, plants can exude nutrient carrier enzymes or facilitate mycorrhizal fungi
associations to enhance competitiveness for nutrient acquisition [Drake et al., 2011;
Hobbie and Hobbie, 2006; Treseder and Vitousek, 2001]. In addition, plants can adjust C
allocation to construct more fine roots, which scavenge nutrients over larger soil volumes
[Iversen et al., 2011; Jackson et al., 2009; Norby et al., 2004]. Soil spatial heterogeneity
might also contribute to the success of plant nutrient competition [Korsaeth et al., 2001].
Therefore, most ecosystem biogeochemistry models with traditional treatments of
nutrient competition likely underestimate plant nutrient uptake.
Nutrient competition should be treated as a complex consumer-substrate reaction
network: multiple ‘consumers’, including plant roots, soil heterotrophic microbes,
nitrifiers, denitrifiers, and mineral surfaces, each competing for substrates of organic and
inorganic nitrogen and phosphorus as nutrient supply. In such a model structure, the success of any consumer in substrate acquisition is affected by its consumer-substrate affinity [Nedwell, 1999]. Such competitive interactions have been successfully applied to microbe-microbe and plant-microbe substrate competition modeling [Bonachela et al., 2011; Lambers et al., 2009; Maggi et al., 2008; Maggi and Riley, 2009; Moorhead and Sinsabaugh, 2006; Reynolds and Pacala, 1993] for many years. Here, we applied the consumer-substrate network in a broader context of plant, microorganism, and abiotic mineral interactions. We analyzed the consumer-substrate network using a first-order accurate equilibrium chemistry approximation (ECA) [Tang and Riley, 2013; Zhu and Riley, 2015]. Our sensitivity analysis confirmed that the consumer-substrate affinity and nutrient carrier enzyme abundance were the most important factors regulating relatively short-term competitive interactions. The ECA competition treatment represents ecosystem responses to environmental changes and has the potential to be linked to a microbe-explicit land biogeochemistry model. The approach allows competition between plants, microbes, and mineral surfaces to be prognostically determined based on nutrient status and capabilities of each consumer.

4. Conclusions

In this study, we developed a soil biogeochemistry model (N-COM) that resolves the dynamics of soil nitrogen and phosphorus, plant uptake of nutrients, microbial uptake, and abiotic interactions. We focused on the implementation, parameterization, and testing of the nutrient competition scheme that we plan to incorporate into the ESM land models CLM and ALM. We described the multiple-consumer and multiple-nutrient competition
network with the Equilibrium Chemical Approximation (ECA) [Tang and Riley, 2013]

considering two inhibitive effects: (1) multiple substrates (e.g., NH4+ and NO3-) sharing
one consumer inhibits the effective binding between any specific substrate and the
consumer and (2) multiple consumers (e.g., plants, decomposing microbes, nitrifiers)
sharing one substrate (e.g., NH4+) lowers the probability of effective binding between any
consumer and that substrate. We calibrated the model at a tropical forest site with highly
weathered soil (Tapajos National Forest, Para, Brazil), using multiple observational
datasets with the Markov Chain Monte Carlo (MCMC) approach. The calibrated model
compared to multiple categories of observational data was substantially improved over
the prior model (Figure 4). The seasonal dynamics of soil carbon, nitrogen, and
phosphorus were moderately well captured. However, our results would likely be more
robust if more temporally resolved observations of carbon, nitrogen, and phosphorous
were available. Although the calibrated model is the best one we can derive based on
limited data, several model parameters were not well converged. We therefore conclude
that more work on data collection, parameter tuning, and uncertainty analysis is needed.

To test the resulting model using the calibrated parameters, we applied N-COM to
two other tropical forests (Hawaii tropical forest and Luquillo tropical forest) not used in
the calibration process and conducted nutrient perturbation studies consistent with
fertilization experiments at these sites. The results showed that N-COM simulated the
nitrogen and phosphorus competition well for the majority of the observational metrics.
However, the model underestimated NH4+ uptake by nitrifiers, probably due to the
loosely constrained nitrification parameters that were the result of NO3- pool size data
paucity during calibration at the Brazil site (Table 4). Datasets of soil nutrient pool sizes
and CO\textsubscript{2} and N\textsubscript{2}O effluxes with high frequency sampling would significantly benefit the model uncertainty reduction.

To date, many terrestrial ecosystem biogeochemistry models assume microbes outcompete plants and immobilize nutrients first [Y P Wang et al., 2007; Zaehle and Friend, 2010; Zhu and Zhuang, 2013], although CLM currently assumes constant and relative demand competitiveness of plants and microbes. Few models, to our knowledge, consider the role of abiotic interactions in the competitive interactions. In the case of microbes outcompeting plants, the plant is only able to utilize the nutrients that exceed microbial demands during that time step. The leftover nutrients are defined as net mineralization, which is a widely adopted concept in soil biogeochemistry modeling [Schimel and Bennett, 2004]. These models oversimplify plant-microbe interactions by imposing dubious assumptions (e.g., microbes always win against plants). We showed that (in section 3.1) “competitiveness” is a dynamic rather than fixed property of the competition network, and more importantly, it should be linked to competitor functional traits (affinity and nutrient carrier enzyme abundance).

This study is an important step towards implementing more realistic nutrient competition schemes in complex climate-scale land models. Traditional ESMs generally lack realistic soil nutrient competition, which likely biases the estimates of terrestrial ecosystem carbon productivity and biosphere-climate feedbacks. This study showed the effectiveness of ECA kinetics in representing soil multiple-consumer and multiple-nutrient competition networks. Offline calibration and independent site-level testing is critically important to ensuring the newly incorporated model will perform reasonably when integrated in a complex ESM. To this end, we provide a universal calibration
approach using MCMC, which could in the future be used to further constrain N-COM across plant functional types, climate, and soil types.

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Figure 1. Model structure. Boxes represent pools, solid arrows represent aqueous fluxes, and dashed arrows represent gaseous pathways out or into the system. Three essential chemical elements (Carbon (C), Nitrogen (N) and Phosphorus (P)) are simulated in N-COM (blue, red, and green represent C, N, and P pools and processes, respectively).
Figure 2. Distribution of prior and calibrated model parameters.
Figure 3. Model sensitivity analysis with SOBOL sampling. For each metric, three scenarios are shown: baseline (Control), elevated soil temperature by 5 °C (+T_s), and elevated soil moisture by 50% (+θ), respectively. The length of bar (plot in polar coordinate) is the sensitivity (unit-less) of model output with respect to model input variables. Our results showed that the plant nutrient uptake was mostly regulated by internal consumer-substrate uptake kinetics rather than the external environmental conditions (e.g., T_s, θ).
Figure 4. Model performance at Tapajos National Forest, Para, Brazil. Overall, the calibrated model (blue line) improved predictions over the prior model (grey line) when compared to observations. Green areas indicate the calibrated model uncertainties.
Figure 5. Model perturbation experiments compared with nitrogen and phosphorus fertilization field experimental data. The blue dots show the difference between control and perturbed simulations, which mean how much newly added nutrient each consumer takes up. The red circles are recovered isotopically labeled nutrient within each consumer. Since plants phosphorus uptake was not measured at Hawaii sites, we didn’t include the plants in the perturbation study.
Table 1. A summary of the modeled consumer-resource competition network.

<table>
<thead>
<tr>
<th>Resources</th>
<th>Consumers</th>
</tr>
</thead>
<tbody>
<tr>
<td>NH$_4^+$</td>
<td>Plant, Decomposing Microbe, Nitrifier</td>
</tr>
<tr>
<td>NO$_3^-$</td>
<td>Plant, Decomposing Microbe, Denitrifier</td>
</tr>
<tr>
<td>PO$_x$</td>
<td>Plant, Decomposing Microbe, Mineral surface</td>
</tr>
</tbody>
</table>
### Table 2. Model parameters and baseline values.

<table>
<thead>
<tr>
<th><strong>C associated</strong></th>
<th>Description</th>
<th>Values</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$g_i$</td>
<td>Percentage of carbon remains in the soil after decomposition of $i$th SOM</td>
<td>1.0; 0.45; 0.5; 0.83; 0.45; 0.45</td>
<td>Koven et al., 2013</td>
</tr>
<tr>
<td>$f_{ij}$</td>
<td>Fraction of SOM leave from $i$th pool and enter into $j$th pool</td>
<td>[0, 0, 0.76, 0.24, 0, 0, 0; 0, 0, 0, 1, 0, 0, 0; 0, 0, 0, 0, 1, 0, 0; 0, 0, 0, 0, 0, 0.995, 0.005; 0, 0, 0, 0.93, 0, 0.07; 0, 0, 0, 0, 1, 0, 0]</td>
<td>Koven et al., 2013</td>
</tr>
</tbody>
</table>

| **CN** | Soil organic matter CN ratio | 13,16,7.9 | Parton et al., 1988 |
| **CP** | Soil organic matter CP ratio | [110,320,114] | Parton et al., 1988 |
| TURN$_{SOM}$ | Soil organic matter turnover [CWD, metabolic lit, cellulose lit, lignin lit, fast SOM, medium SOM, slow SOM] | [4.1, 0.066, 0.25, 0.25, 0.17, 5, 270] | Koven et al., 2013 |

<table>
<thead>
<tr>
<th><strong>N associated</strong></th>
<th>Description</th>
<th>Values</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$e_{\text{plant}}^{\text{NH}4}$</td>
<td>Reaction rate of plant NH$_4^+$ carrier enzyme</td>
<td>day$^{-1}$</td>
<td>120 $^{(a)}$</td>
</tr>
<tr>
<td>$K^{\text{NH}4}_{\text{plant}}$</td>
<td>Half-saturation constant for plant NH$_4^+$ uptake</td>
<td>g m$^{-2}$</td>
<td>0.09</td>
</tr>
<tr>
<td>$k^{\text{mic,NH}4}$</td>
<td>Maximum fraction of NH$_4^+$ pool that could be utilized by nitrifiers</td>
<td>g m$^{-2}$</td>
<td>0.02</td>
</tr>
<tr>
<td>$F^{\text{NH}4}_{\text{plant}}$</td>
<td>Reaction rate of plant NH$_4^+$ consumption</td>
<td>day$^{-1}$</td>
<td>0.076</td>
</tr>
<tr>
<td>$e_{\text{plant}}^{\text{NO}3}$</td>
<td>Reaction rate of plant NO$_3^-$ carrier enzyme</td>
<td>day$^{-1}$</td>
<td>2 $^{(a)}$</td>
</tr>
<tr>
<td>$K^{\text{NO}3}_{\text{plant}}$</td>
<td>Half-saturation constant for plant NO$_3^-$ uptake</td>
<td>g m$^{-2}$</td>
<td>0.07</td>
</tr>
<tr>
<td>$K^{\text{mic,NO}3}$</td>
<td>Half-saturation constant for decomposing microbe NO$_3^-$ immobilization</td>
<td>g m$^{-2}$</td>
<td>0.04</td>
</tr>
<tr>
<td>$e_{\text{mic,NO}3}$</td>
<td>Reaction rate of plant NO$_3^-$ consumption</td>
<td>day$^{-1}$</td>
<td>0.11</td>
</tr>
<tr>
<td>$e_{\text{den,NO}3}$</td>
<td>Reaction rate of denitrifier NO$_3^-$ consumption</td>
<td>day$^{-1}$</td>
<td>C$_{\text{fust}}$ - 0.0000125 $^{(a)}$</td>
</tr>
<tr>
<td>$[E_{\text{N}f}^{\text{mic}}]$</td>
<td>Plant nitrogen carrier enzyme abundance for nitrogen uptake</td>
<td>g m$^{-2}$</td>
<td>$^{(a)}$</td>
</tr>
<tr>
<td>$[E_{\text{N}f}^{\text{mic}}]$</td>
<td>Decomposing microbes nitrogen carrier enzyme abundance for nitrogen immobilization</td>
<td>g m$^{-2}$</td>
<td>$^{(a)}$</td>
</tr>
<tr>
<td>$[E_{\text{N}f}^{\text{mic}}]$</td>
<td>Nitrifier nitrogen carrier enzyme abundance for NH$_4^+$ assimilation</td>
<td>g m$^{-2}$</td>
<td>1.2E$^3$</td>
</tr>
</tbody>
</table>
\begin{tabular}{|c|c|c|c|}
\hline
\textbf{Parameter} & \textbf{Denitrifier nitrogen carrier enzyme abundance for NO$_3^-$ assimilation} & \textbf{g m$^{-2}$} & \textbf{1.2E$^{-3}$} & \textbf{[Raynaud et al., 2006]} \\
$P^{NO}_M$ & Fraction of nitrification flux lost as N$_2$O & - & 6E$^5$ & \textbf{[Li et al., 2000]} \\
\hline
\end{tabular}

\begin{tabular}{|c|c|c|c|}
\hline
$P^{ass}$ & Parent material $P$ weathering rate & g P m$^{-3}$ year$^{-1}$ & 0.004 & \textbf{[Yu P Wang et al., 2010]} \\
& $k_{red}$ & & & \\
$k_{occl}$ & $P$ occlude rate & month$^{-1}$ & 1.0E$^{-4}$ & \textbf{[Yang et al., 2014]} \\
$k_P$ & Reaction rate of plant PO, carrier enzyme & & & \textbf{[Colpaert et al., 1999]} \\
\hline
$P^{max}$ & Half-saturation constant for plant PO uptake & g m$^{-2}$ & 12 $^{30}$ & \\
$P^{max, P}$ & Half-saturation constant for decomposing microbe PO$_4$ immobilization & g m$^{-2}$ & 0.02 & \textbf{[Cogniatti and Clarkson, 1983]} \\
\hline
$V_{MAX}^{mef}$ & Maximum mineral surface PO$_4$ adsorption & g m$^{-2}$ & 133 & \textbf{[Yu P Wang et al., 2010]} \\
$K_{Mf}^{mef}$ & Half-saturation constant for mineral surface PO$_4$ adsorption & g m$^{-2}$ & 64 & \textbf{[Yu P Wang et al., 2010]} \\
\hline
$P^{max}$ & Plant phosphorus carrier enzyme abundance for PO$_4$ uptake & g m$^{-2}$ & & \textbf{[Tang and Riley, 2013; Trumbore et al., 2006]} \\
$E_{V_f}^{max}$ & Decomposing microbes phosphorus carrier enzyme abundance for PO$_4$, immobilization & g m$^{-2}$ & & \textbf{[Tang and Riley, 2013]} \\
$E_{V_f}^{mef}$ & Mineral surface “effective enzyme” abundance for PO$_4$ adsorption & & & \textbf{[Tang and Riley, 2013]} \\
\end{tabular}

\begin{itemize}
\item[(a)] The scaling factor for plant nutrient enzyme abundance is 0.0000125. This number is inferred by assuming that growing season plant nutrient carrier enzymes are roughly the same order of magnitude compared with decomposing microbes. Typical values for soil decomposing microbe biomass and tropical forest fine root biomass are 0.1 [Tang and Riley, 2013] and 400 [Trumbore et al., 2006] gC m$^{-2}$. A typical value of scaling factor that scales microbial biomass to enzyme abundance is 0.05 [Tang and Riley, 2013]. Therefore, $C_{MIC} = C_{mef} = 0.05$ or $400 \times 0.1 = 0.05$. We have $x = 0.0000125$. Further, we have $k^{mef}_{V_f} [E_{V_f}^{mef}] = V_{MAX}^{mef}$. We know that typical values for $V_{MAX}^{mef}$ and $[E_{V_f}^{mef}]$ are 0.6 g m$^{-2}$ day$^{-1}$ [Min et al., 2000] and 0.005 g m$^{-2}$. Then we have $k^{mef}_{V_f} = 120$ day$^{-1}$. Similarly, we have $k^{mef}_{V_f} [E_{V_f}^{mef}] = V_{MAX}^{mef}$, $k^{mef}_{V_f} [E_{V_f}^{mef}] = V_{MAX}^{mef}$. Knowing that typical values for $V_{MAX}^{mef}$ and $V_{MAX}^{mef}$ are 0.01 [Min et al., 2000] and 0.06 [Colpaert et al., 1999] g m$^{-2}$ day$^{-1}$, we have $k^{mef}_{V_f} = 2$ and $k^{mef}_{V_f} = 12$ day$^{-1}$. \\
\item[(b)] For decomposing microbes, we have $V_{MAX}^{mef} = k^{mef}_{V_f} [E_{V_f}^{mef}]$. Typical values for $V_{MAX}^{mef}$ and $[E_{V_f}^{mef}]$ are 5 g m$^{-2}$ day$^{-1}$ [Kozyakov and Xu, 2013] and 0.005 g m$^{-2}$ [Tang and Riley, 2013]. Therefore, we have $k^{mef}_{V_f} = 1000$. Since our model calculates potential N immobilization rates and approximates them as $V_{MAX}^{mef}$. The changes of potential N immobilization rates at each time step imply the changes of enzyme abundance through $[E_{V_f}^{mef}] = k^{mef}_{V_f} [E_{V_f}^{mef}]$. Similarly, we have that $V_{MAX}^{mef}$ and $[E_{V_f}^{mef}]$ are 2 g m$^{-2}$ day$^{-1}$ [Chen, 1974] and 0.005 g m$^{-2}$. Therefore, $k^{mef}_{V_f} = 800$ and $E_{V_f}^{mef} = \frac{E_{V_f}^{mef}}{800}$.
\end{itemize}
Table 3. Observational datasets used for calibration. Number of observations for each data stream is included in brackets.

<table>
<thead>
<tr>
<th>Processes</th>
<th>Datasets</th>
<th>Location</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>C associated</td>
<td>Soil heterotrophic respiration (20)</td>
<td>Tapajos National Forest, Para, Brazil</td>
<td>[Silver et al., 2012]</td>
</tr>
<tr>
<td>N associated</td>
<td>Soil NH$_4^+$ (5) N$_2$O efflux (20)</td>
<td>Tapajos National Forest, Para, Brazil</td>
<td>[Silver et al., 2012]</td>
</tr>
<tr>
<td>P associated</td>
<td>Soil free phosphate (3) Sorb phosphate (3)</td>
<td>Tapajos National Forest, Para, Brazil</td>
<td>[McGroddy et al., 2008]</td>
</tr>
</tbody>
</table>
**Table 4.** Calibrated parameters are reported in terms of (1) mean/standard deviation by fitting to a Gaussian distribution; (2) 25% and 75% quantile. Both variance-based and quantile-based parameters uncertainty reduction are provided; (3) Gelman-Rubin convergence criterion.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>(\mu_{\text{prior}})</th>
<th>(\sigma_{\text{prior}})</th>
<th>(\mu_{\text{posterior}})</th>
<th>(\sigma_{\text{posterior}})</th>
<th>(Q^{25}_{\text{prior}})</th>
<th>(Q^{75}_{\text{prior}})</th>
<th>(Q^{25}_{\text{posterior}})</th>
<th>(Q^{75}_{\text{posterior}})</th>
<th>UR</th>
<th>Gelman-Rubin criterion</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\text{TURN}^\text{Nut})</td>
<td>[3.7, 3.9]</td>
<td>[5.2, 0.33]</td>
<td>[92, 83, 5.33]</td>
<td>[19.32, 5.05, 0.64]</td>
<td>[5.05, 0.31, 1.18]</td>
<td>[5.39, 0.16, 0.14]</td>
<td>[97, 94, 97, 99, 98, 96]</td>
<td>[1.69, 1.03, 1.75]</td>
<td>1.01, 1.06, 1.55</td>
<td></td>
</tr>
<tr>
<td>[CWD, metabolic, cellulose, lignin]</td>
<td>0.23, 0.06, 0.07, 0.01, 96, 98, 0.086, 0.33, 0.31, 1.18, 0.16, 0.17, 0.13, 0.18, 0.18, 0.14, 98, 96</td>
<td>0.23, 0.24, 0.17, 0.01, 96, 92</td>
<td>0.33, 0.22, 1.18, 0.8, 3.2</td>
<td>0.23, 0.16, 0.24, 0.17, 0.005, 6.5</td>
<td>23.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(k_{\text{NH}_4}^\text{plant})</td>
<td>4.6, 0.18, 4.8, 0.14, 3.6, 0.008</td>
<td>0.37</td>
<td>109</td>
<td>114</td>
<td>58</td>
<td>14</td>
<td>88</td>
<td>156.1</td>
<td>565.4</td>
<td>52.8</td>
</tr>
<tr>
<td>(K_{M}^\text{plant, NH}_4)</td>
<td>0.082</td>
<td>0.086</td>
<td>0.173</td>
<td>0.018</td>
<td>79</td>
<td>0.12</td>
<td>0.42</td>
<td>0.16</td>
<td>0.18</td>
<td>93</td>
</tr>
<tr>
<td>(K_{M}^\text{plant, NH}_4)</td>
<td>0.018</td>
<td>0.019</td>
<td>0.071</td>
<td>0.0067</td>
<td>65</td>
<td>0.026</td>
<td>0.094</td>
<td>0.065</td>
<td>0.076</td>
<td>85</td>
</tr>
<tr>
<td>(k_{\text{Nit}}^\text{plant})</td>
<td>0.091</td>
<td>0.095</td>
<td>0.37</td>
<td>0.038</td>
<td>60</td>
<td>0.13</td>
<td>0.47</td>
<td>0.36</td>
<td>0.39</td>
<td>91</td>
</tr>
<tr>
<td>(K_{M}^\text{Nit, NH}_4)</td>
<td>0.069</td>
<td>0.072</td>
<td>0.082</td>
<td>0.012</td>
<td>83</td>
<td>0.10</td>
<td>0.36</td>
<td>0.07</td>
<td>0.09</td>
<td>94</td>
</tr>
<tr>
<td>(k_{\text{Nit}}^\text{plant})</td>
<td>1.8</td>
<td>1.9</td>
<td>7.6</td>
<td>1.7</td>
<td>13</td>
<td>2.60</td>
<td>9.42</td>
<td>6.11</td>
<td>9.14</td>
<td>56</td>
</tr>
<tr>
<td>$K_{\text{plant, NO}_3}$</td>
<td>0.064</td>
<td>0.067</td>
<td>0.085</td>
<td>0.0864</td>
<td>90</td>
<td>0.09</td>
<td>0.33</td>
<td>0.08</td>
<td>0.09</td>
<td>97</td>
</tr>
<tr>
<td>--------------------------</td>
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<td>-------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
<td>----</td>
</tr>
<tr>
<td>$K_{\text{min, NO}_3}$</td>
<td>0.036</td>
<td>0.038</td>
<td>0.096</td>
<td>0.014</td>
<td>63</td>
<td>0.05</td>
<td>0.19</td>
<td>0.09</td>
<td>0.10</td>
<td>92</td>
</tr>
<tr>
<td>$K_{\text{diss, NO}_3}$</td>
<td>0.0101</td>
<td>0.0105</td>
<td>0.022</td>
<td>0.0034</td>
<td>68</td>
<td>0.014</td>
<td>0.052</td>
<td>0.019</td>
<td>0.024</td>
<td>87</td>
</tr>
<tr>
<td>$K_{\text{plant}}$</td>
<td>11</td>
<td>11.5</td>
<td>59</td>
<td>0.75</td>
<td>93</td>
<td>15.61</td>
<td>56.54</td>
<td>58.86</td>
<td>59.81</td>
<td>98</td>
</tr>
<tr>
<td>$K_{\text{plant, P}}$</td>
<td>0.061</td>
<td>0.064</td>
<td>0.11</td>
<td>0.015</td>
<td>77</td>
<td>0.09</td>
<td>0.32</td>
<td>0.10</td>
<td>0.12</td>
<td>94</td>
</tr>
<tr>
<td>$K_{\text{min, P}}$</td>
<td>0.018</td>
<td>0.019</td>
<td>0.037</td>
<td>0.0047</td>
<td>75</td>
<td>0.026</td>
<td>0.094</td>
<td>0.034</td>
<td>0.039</td>
<td>93</td>
</tr>
<tr>
<td>$V_{\text{MAX}_p}$</td>
<td>121</td>
<td>127</td>
<td>182</td>
<td>30</td>
<td>76</td>
<td>173.0</td>
<td>626.6</td>
<td>156.5</td>
<td>206.3</td>
<td>89</td>
</tr>
<tr>
<td>$K_{\text{surf, P}}$</td>
<td>64</td>
<td>58</td>
<td>200</td>
<td>50</td>
<td>18</td>
<td>83.2</td>
<td>301.5</td>
<td>162.6</td>
<td>233.0</td>
<td>68</td>
</tr>
</tbody>
</table>
Table 5. Short-term (24 or 48 hours) fertilization experiments of NH$_4^+$, NO$_3^-$, or PO$_4^{3-}$ additions used to evaluate the performance of the N-COM competition scheme.

<table>
<thead>
<tr>
<th>Datasets</th>
<th>Added nutrient</th>
<th>Competitors</th>
<th>Duration (hour)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>PO$_4^{3-}$ fertilization</td>
<td>10 µg g$^{-1}$</td>
<td>I. Mineral surface II. Decomposing microbe</td>
<td>48</td>
<td>[Olander and Vitousek, 2005]</td>
</tr>
<tr>
<td>NH$_4^+$ fertilization</td>
<td>4.6 µg g$^{-1}$</td>
<td>I. Plant II. Decomposing microbe III. Nitrifier</td>
<td>24</td>
<td>[Templer et al., 2008]</td>
</tr>
<tr>
<td>NO$_3^-$ fertilization</td>
<td>0.92 µg g$^{-1}$</td>
<td>I. Plant II. Decomposing microbe</td>
<td>24</td>
<td>[Templer et al., 2008]</td>
</tr>
</tbody>
</table>
References:


Silver, W. L., A. W. Thompson, M. E. McGroddy, R. K. Varner, J. R. Robertson, H. S. J.D.


Tang, J. Y., and W. J. Riley (2013), A total quasi-steady-state formulation of substrate uptake kinetics in complex networks and an example application to microbial


