Soil nutrient competitive traits of plants, microbes, and mineral surfaces explain nutrient acquisition in tropical experimental manipulations

Qing Zhu[1*], William J. Riley[1], Jinyun Tang[1], Charles D. Koven[1]

[1] Climate Sciences Department, Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA 94720

[*] Correspondence to: Q. Zhu (qzhu@lbl.gov)

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 (NH_4^+, NO_3^-, and PO_x (representing the sum of PO_4^{3-}, HPO_4^{2-}, and $H_2PO_4^-$)) 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, N_2O emissions, free phosphorus, sorbed phosphorus, and NH_4^+ pools at a tropical forest site (Tapajos). The overall model posterior 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 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 different 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 CO_2 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 CO_2 trend by absorbing roughly a quarter of anthropogenic CO_2 emissions [*Le Quéré et al.*, 2009]. However, it is still an open question whether the terrestrial CO_2 sink can be sustained [*Sokolov et al.*, 2008; *Zaehle et al.*, 2010], given that plant productivity is generally limited by soil nutrients [*Elser 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 CO_2 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 C^4MIP (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 CO_2 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 N_2 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

82 weathering has been depleted through long-term pedogenesis processes [*Vitousek and*
83 *Farrington*, 1997; *Walker and Syers*, 1976]. In natural ecosystems without external
84 nutrients inputs (*e.g.*, N deposition), soil nitrogen or phosphorus (or both) are likely
85 insufficient to satisfy both plant and microorganism demands [*Vitousek and Farrington*,
86 1997]. Plants have to compete with microorganisms and mineral surfaces [*Kaye and*
87 *Hart*, 1997; *Schimel et al.*, 1989] to obtain sufficient nutrients to sustain their biological
88 processes (*e.g.*, photosynthesis, respiration). Therefore, it is critical to improve the
89 representation of nutrient competition to accurately model how terrestrial ecosystems will
90 respond to perturbations in soil nutrient dynamics (*e.g.*, from elevated nitrogen deposition
91 or CO_2 fertilization-induced nutrient requirements).
92 Intense competition between plants and microorganisms is a well-observed
93 phenomenon in nutrient-limited systems [*Hodge et al.*, 2000a; *Johnson*, 1992; *Kaye and*
94 *Hart*, 1997]. Previously, plants were thought to be initial losers in nutrient competition,
95 due to the fact that microbes are more intimately associated with substrates [*Woodmansee*
96 *et al.*, 1981]. However, increasing observational evidence indicates that plants compete
97 effectively with soil microorganisms [*Schimel and Bennett*, 2004] under certain
98 circumstances; sometime even outcompeting them and suppressing microbial growth [*Hu*
99 *et al.*, 2001; *J Wang and Lars*, 1997]. ^{15}N isotope studies have also demonstrated that
100 plants can capture a large fraction of added nitrogen [*Hodge et al.*, 2000b; *Marion et al.*,
101 1982]. In the short term (days to months), plants maintain their competitiveness mainly
102 through (1) establishing mycorrhizal fungi associations [*Drake et al.*, 2011; *Rillig et al.*,
103 1998], which help plants acquire organic and inorganic forms of nitrogen [*Hobbie and*
104 *Hobbie*, 2006; *Hodge and Fitter*, 2010] and (2) root exudation of extracellular enzymes

105 that decompose rhizosphere soil organic matter [*Phillips et al.*, 2011]. In the relatively
106 longer term (months to years), morphological adjustment occurs; for example, plants
107 allocate more carbon to fine roots to explore deeper and larger soil volume [*Iversen et al.*,
108 2011; *Jackson et al.*, 2009]. Finally, over the course of years to decades, plant succession
109 can occur [*Medvigy et al.*, 2009; *Moorcroft et al.*, 2001] and the new plant demography
110 will need to be considered to represent nutrient controls on this time scale.

111 Given these patterns from the observational literature, nutrient competition is
112 either absent or over-simplified in existing Earth System Models (ESMs). One common
113 representation of plant-microbe competition is that plants compete poorly against
114 microbes in resource acquisition. For example, the O-CN land model [*Zaehle and Friend*,
115 2010] assumes that soil decomposing microbes have the priority to immobilize soil
116 mineral nitrogen. After microbes meet their demands, the remaining nitrogen is then
117 available for plant uptake.

118 Another treatment in ESM land models is that microbial and plant nutrient
119 acquisition competitiveness is based on their relative demands. For example, CLM4CN
120 [*Thornton et al.*, 2007] assumes that the plant and microbial nitrogen demands are
121 satisfied simultaneously. Under nitrogen infertile conditions, all nitrogen demands in the
122 system are down-regulated proportional to the individual demands and subject to
123 available soil mineral nitrogen. This approach led to unrealistic diurnal cycles of gross
124 primary production (GPP), with midday depressions in GPP occurring because of
125 predicted diurnal depletion of the soil mineral nitrogen pool. Emergent impacts of this
126 conceptualization of nutrient constraints on GPP resulted in poor predictions compared to
127 observations, with smaller than observed plant C growth responses to N deposition

[*Thomas et al.*, 2013a] 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.*, NH_4^+, NO_3^-, and PO_x (represented as the sum of PO_4^{3-}, HPO_4^{2-}, and $H_2PO_4^-$)) and multiple nutrient consumers (*i.e.*, decomposing microbes, plants, nitrifiers, denitrifiers, and mineral surfaces); (2) represent nutrient competition with ECA kinetics [*Tang and Riley*, 2013; *Zhu and Riley*, 2015], accounting for substrate (multiple substrates for one consumer) and consumer (multiple consumers competing for one substrate) effects; (3) constrain the model with *in situ* observational datasets of soil carbon, nitrogen, and phosphorus dynamics using a Markov Chain Monte Carlo (MCMC) approach; and (4) 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*, *KM*) 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 ($F_{C,j}^{dec}$, $F_{N,j}^{dec}$, $F_{P,j}^{dec}$) follow first-order decay:

$$F_{C,j}^{dec} = k_j C_j r_\theta r_T \quad (1)$$

$$F_{N,j}^{dec} = k_j N_j r_\theta r_T \quad (2)$$

$$F_{P,j}^{dec} = k_j P_j r_\theta r_T \quad (3)$$

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_θ (dimensionless) are soil temperature and moisture environmental regulators.

Decomposed carbon ($F_{C,i}^{dec}$) (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:

$$\frac{dC_j}{dt} = -F_{C,j}^{dec} + \sum_{i=1}^{N} F_{C,ij}^{move} \quad (4)$$

where $\sum_{i=1}^{N} F_{C,ij}^{move}$ 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, ..., 7*), the fractions integrated into downstream pools (j = *1, 2, ..., 7*) is summarized in a 7 by 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:

$$\frac{dN_j}{dt} = -F_{N,j}^{dec} + \sum_{i=1}^{N} F_{N,ij}^{move} + \sum_{i=1}^{N} F_{NH4,ij}^{immob} + \sum_{i=1}^{N} F_{NO3,ij}^{immob} \quad (5)$$

$$\frac{dP_j}{dt} = -F_{P,j}^{dec} + \sum_{i=1}^{N} F_{P,ij}^{move} + \sum_{i=1}^{N} F_{P,ij}^{immob} \quad (6)$$

where $F_{N,ij}^{move}$ and $F_{P,ij}^{move}$ are fluxes of nitrogen and phosphorus moving from the upstream (i) to downstream (j) pools. $F_{NH4,ij}^{immob}$, $F_{NO3,ij}^{immob}$, and $F_{P.ij}^{immob}$ are immobilization fluxes of soil mineral nitrogen and phosphorus. $F_{N,j}^{dec}$ and $F_{P,j}^{dec}$ represent soil organic matter decomposition loss.

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 ($-F_{N,j}^{dec}$ and $-F_{P,j}^{dec}$); (2) a fraction of the i^{th} organic N or P pool (upstream) enters into the j^{th} pool (downstream) ($F_{N,ij}^{move}$ and $F_{P,ij}^{move}$); and (3) soil microbial immobilization ($F_{NH4,ij}^{immob}$, $F_{NO3,ij}^{immob}$, and $F_{P,ij}^{immob}$). 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_x) 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 $H_2PO_4^-$), but for simplicity we use the symbol PO_x to represent the sum of all possible phosphate forms throughout the paper.

$$\frac{d[NH4]}{dt} = \sum_{j=1}^{N}\sum_{i=1}^{N} F_{NH4,ij}^{mob} - F_{NH4}^{nit} - F_{NH4}^{plant} - F_{NH4}^{immob} + F^{BNF} + F_{NH4}^{dep} \quad (7)$$

$$\frac{d[NO3]}{dt} = -F_{NO3}^{den} + (1 - f^{N2O})F_{NH4}^{nit} - F_{NO3}^{plant} - F_{NO3}^{immob} - F_{NO3}^{leach} + F_{NO3}^{dep} \quad (8)$$

$$\frac{d[PO_x]}{dt} = \sum_{j=1}^{N}\sum_{i=1}^{N} F_{P,ij}^{mob} - F_P^{plant} - F_P^{immob} - F_P^{surf} - F_P^{leach} + F^{weather} \quad (9)$$

where $F_{NH4,ij}^{mob}$ and $F_{P,ij}^{mob}$ are gross mineralization rates for nitrogen and phosphorus. F_{NH4}^{nit} 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}^{den} is the denitrification flux, which transforms nitrate to N_2O and N_2 which then leave the soil system. Plant uptake of soil NH_4^+, NO_3^-,

and PO_x are represented as F_{NH4}^{plant}, F_{NO3}^{plant}, and F_P^{plant}, respectively. Soil decomposing microbial immobilization of soil NH_4^+, NO_3^-, and PO_x are represented as F_{NH4}^{immob}, F_{NO3}^{immob}, and F_P^{immob}, F_{NO3}^{leach}, and F_P^{leach} are leaching losses of soil NO_3^- and PO_x. External inputs into soil inorganic N pools include atmospheric ammonia deposition (F_{NH4}^{dep}), atmospheric nitrate deposition (F_{NO3}^{dep}), and biological nitrogen fixation (F^{BNF}). External sources of phosphate come from parent material weathering ($F^{weather}$).

Finally, the dynamics of sorbed P (P_S), occluded P (P_O), and parent material P (P_P) are modeled as:

$$\frac{d[P_S]}{dt} = F_P^{surf} - F_P^{occl} \quad (10)$$

$$\frac{d[P_O]}{dt} = F_P^{occl} \quad (11)$$

$$\frac{d[P_P]}{dt} = -F^{weather} + F_P^{dep} \quad (12)$$

where the pool of sorbed P is balanced by the adsorption flux (F_P^{surf}) and occlusion flux (F_P^{occl}). Parent material is lost by weathering ($F^{weather}$) and is slowly replenished by external atmospheric phosphorus inputs (F_P^{dep}, 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 (NH_4^+, NO_3^-, PO_x). 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 NH_4^+ and NO_3^-, 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:

$$S + E \underset{k_1^-}{\overset{k_1^+}{\rightleftharpoons}} C \xrightarrow{k_2^+} P + E \tag{13}$$

The enzyme (*E: e.g., nutrient carrier enzyme produced by plants and microbes*) and substrate (*S: e.g., NH_4^+, NO_3^-*) reaction (reversible reaction) forms a substrate-enzyme complex (*SE*). 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:

$$F_{NH4}^{plant} = k_{NH4}^{plant} \cdot \frac{[NH4] \cdot [E_N^{plant}]}{KM_{NH4}^{plant}\left(1 + \underbrace{\frac{[NH4]}{KM_{NH4}^{plant}}}_{(1)} + \underbrace{\frac{[NO3]}{KM_{NO3}^{plant}}}_{(2)} + \underbrace{\frac{[E_N^{plant}]}{KM_{NH4}^{plant}}}_{(3)} + \underbrace{\frac{[E_N^{mic}]}{KM_{NH4}^{mic}}}_{(4)} + \underbrace{\frac{[E_N^{nit}]}{KM_{NH4}^{nit}}}_{(5)}\right)} \tag{14}$$

$$F_{NH4}^{immob} = k_{NH4}^{immob} \cdot \frac{[NH4] \cdot [E_N^{mic}]}{KM_{NH4}^{mic}\left(1 + \frac{[NH4]}{KM_{NH4}^{mic}} + \frac{[NO3]}{KM_{NO3}^{mic}} + \frac{[E_N^{plant}]}{KM_{NH4}^{plant}} + \frac{[E_N^{mic}]}{KM_{NH4}^{mic}} + \frac{[E_N^{nit}]}{KM_{NH4}^{nit}}\right)} \tag{15}$$

$$F_{NH4}^{nit} = k_{NH4}^{nit} \cdot \frac{[NH4] \cdot [E_{NH4}^{nit}]}{KM_{NH4}^{nit}\left(1 + \frac{[NH4]}{KM_{NH4}^{nit}} + \frac{[E_N^{plant}]}{KM_{NH4}^{plant}} + \frac{[E_N^{mic}]}{KM_{NH4}^{mic}} + \frac{[E_N^{nit}]}{KM_{NH4}^{nit}}\right)} \tag{16}$$

$$F_{NO3}^{plant} = k_{NO3}^{plant} \cdot \frac{[NO3] \cdot [E_N^{plant}]}{KM_{NO3}^{plant}(1 + \frac{[NH4]}{KM_{NH4}^{plant}} + \frac{[NO3]}{KM_{NO3}^{plant}} + \frac{[E_N^{plant}]}{KM_{NO3}^{plant}} + \frac{[E_N^{mic}]}{KM_{NO3}^{mic}} + \frac{[E_N^{den}]}{KM_{NO3}^{den}})} \quad (17)$$

$$F_{NO3}^{immob} = k_{NO3}^{immob} \cdot \frac{[NO3] \cdot [E_N^{mic}]}{KM_{NO3}^{mic}(1 + \frac{[NH4]}{KM_{NH4}^{mic}} + \frac{[NO3]}{KM_{NO3}^{mic}} + \frac{[E_N^{plant}]}{KM_{NO3}^{plant}} + \frac{[E_N^{mic}]}{KM_{NO3}^{mic}} + \frac{[E_N^{den}]}{KM_{NO3}^{den}})} \quad (18)$$

$$F_{NO3}^{den} = k_{NO3}^{den} \cdot \frac{[NO3] \cdot [E_{NO3}^{den}]}{KM_{NL3}^{den}(1 + \frac{[NO3]}{KM_{NO3}^{den}} + \frac{[E_N^{plant}]}{KM_{NO3}^{plant}} + \frac{[E_N^{mic}]}{KM_{NO3}^{mic}} + \frac{[E_N^{den}]}{KM_{NO3}^{den}})} \quad (19)$$

$$F_P^{plant} = k_P^{plant} \cdot \frac{[PO_x] \cdot [E_P^{plant}]}{KM_P^{plant}(1 + \frac{[PO_x]}{KM_P^{plant}} + \frac{[E_P^{plant}]}{KM_P^{plant}} + \frac{[E_P^{mic}]}{KM_P^{mic}} + \frac{[E_P^{surf}]}{KM_P^{surf}})} \quad (20)$$

$$F_P^{mic} = k_P^{mic} \cdot \frac{[PO_x] \cdot [E_P^{mic}]}{KM_P^{mic}(1 + \frac{[PO_x]}{KM_P^{mic}} + \frac{[E_P^{plant}]}{KM_P^{plant}} + \frac{[E_P^{mic}]}{KM_P^{mic}} + \frac{[E_P^{surf}]}{KM_P^{surf}})} \quad (21)$$

$$F_P^{surf} = k_P^{surf} \cdot \frac{[PO_x] \cdot [E_P^{mic}]}{KM_P^{surf}(1 + \frac{[PO_x]}{KM_P^{surf}} + \frac{[E_P^{plant}]}{KM_P^{plant}} + \frac{[E_P^{mic}]}{KM_P^{mic}} + \frac{[E_P^{surf}]}{KM_P^{surf}})} \quad (22)$$

where F represent the nutrient uptake fluxes and k is the base reaction rate that enzyme-substrate complex forms product (k_2^+ in Eqn. 13). $[E]$ and KM denote enzyme abundance and half saturation constants (substrate-enzyme affinity). Superscripts and subscripts refer to consumers and substrates. 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_N^{plant}, E_N^{mic}), and the other is for phosphorus, including different forms of phosphate (E_P^{plant}, E_P^{mic}). (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_P^{surf}) is approximated by $VMAX_P^{surf} - [SP]$. (4) Nitrifiers and denitrifiers are not explicitly simulated, therefore we assume that their biomass and associated nutrient transporter abundance are fixed (E_N^{nit}, E_N^{denit}).

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 "*VMAX*" (see Appendix B for full derivation). Furthermore, we defined "potential rates (potential immoblizaiton, nitrification, denitrification, adsorption rates)" and used them as proxies of "*VMAX*". Therefore, Eqn. 15, 16, 18, 19, 21, 22 become:

$$F_{NH4}^{immob} = F_{NH4}^{immob,pot} \cdot \frac{[NH4]}{KM_{NH4}^{mic}(1+\frac{[NH4]}{KM_{NH4}^{mic}}+\frac{[NO3]}{KM_{NO3}^{mic}}+\frac{[E_N^{plant}]}{KM_{NH4}^{plant}}+\frac{[E_N^{mic}]}{KM_{NH4}^{mic}}+\frac{[E_N^{nit}]}{KM_{NH4}^{nit}})} \quad (23)$$

$$F_{NH4}^{nit} = F_{NH4}^{nit,pot} \cdot \frac{[NH4]}{KM_{NH4}^{nit}(1+\frac{[NH4]}{KM_{NH4}^{nit}}+\frac{[E_N^{plant}]}{KM_{NH4}^{plant}}+\frac{[E_N^{mic}]}{KM_{NH4}^{mic}}+\frac{[E_N^{nit}]}{KM_{NH4}^{nit}})} \quad (24)$$

$$F_{NO3}^{immob} = F_{NO3}^{immob,pot} \cdot \frac{[NO3]}{KM_{NO3}^{mic}(1+\frac{[NH4]}{KM_{NH4}^{mic}}+\frac{[NO3]}{KM_{NO3}^{mic}}+\frac{[E_N^{plant}]}{KM_{NO3}^{plant}}+\frac{[E_N^{mic}]}{KM_{NO3}^{mic}}+\frac{[E_N^{den}]}{KM_{NO3}^{den}})} \quad (25)$$

$$F_{NO3}^{den} = F_{NO3}^{den,pot} \cdot \frac{[NO3]}{KM_{NL3}^{den}(1+\frac{[NO3]}{KM_{NO3}^{den}}+\frac{[E_N^{plant}]}{KM_{NO3}^{plant}}+\frac{[E_N^{mic}]}{KM_{NO3}^{mic}}+\frac{[E_N^{den}]}{KM_{NO3}^{den}})} \quad (26)$$

$$F_P^{mic} = F_P^{immob,pot} \cdot \frac{[PO_x]}{KM_P^{mic}(1+\frac{[PO_x]}{KM_P^{mic}}+\frac{[E_P^{plant}]}{KM_P^{plant}}+\frac{[E_P^{mic}]}{KM_P^{mic}}+\frac{[E_P^{surf}]}{KM_P^{surf}})} \quad (27)$$

$$F_P^{surf} = F_P^{surf,pot} \cdot \frac{[PO_x]}{KM_P^{surf}(1+\frac{[PO_x]}{KM_P^{surf}}+\frac{[E_P^{plant}]}{KM_P^{plant}}+\frac{[E_P^{mic}]}{KM_P^{mic}}+\frac{[E_P^{surf}]}{KM_P^{surf}})} \quad (28)$$

In this case, the potential rates are treated as maximum reaction rates (*VMAX*), because they are calculated without nutrient constraints or biotic and abiotic interactions. For example, potential P immobilization rate ($F_P^{immob,pot}$) is based on the total phosphorus demand that can perfectly maintain the soil CP stoichiometry during soil organic matter decomposition (Eqn. A9). This potential immobilization rate represents the maximum phosphorus influx that the soil could take up at that moment. The maximum adsorption rate ($F_P^{surf,pot}$) is the time derivative of the Langmuir equation (Eqn. A12), which is a theoretically maximal adsorption rate excluding all other biotic and abiotic interactions. The potential rates (*VMAX*) are updated by the model rather than calibrated, except for $VMAX_P^{surf}$. $VMAX_P^{surf}$ denotes the maximum adsorption capacity (not maximum adsorption rate), which affects the potential adsorption rate ($F_P^{surf,pot}$).

The model is run on an hourly time step, initialized with state variables and critical parameters (Table 2). Since the model is designed to be a component of the

Community and ACME Land Models (CLM, ALM; which are essentially equivalent at this time), 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_θ); (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_{NH4}^{dep}); (6) NO_3^- deposition (F_{NO3}^{dep}); 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 *KM*) 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 posterior 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:

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

where $\boldsymbol{M(\theta)}$ and $\boldsymbol{D}$ are vectors of model outputs and observations including time series of different simulated variables (*e.g.*, soil CO_2 and N_2O effluxes and soil concentrations of NH_4^+, free PO_x, and sorbed PO_x); $\boldsymbol{\theta}$ is a vector of model parameters ($\boldsymbol{\theta_i}$); and $\boldsymbol{i}$ 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 value and off-diagonal elements are zeros. We further assumed that the prior parameter follows a lognormal distribution. μ and σ were 0.91 and 0.95 of their initial values, respectively (Table 4). We then ran MCMC to sample 50,000 parameter pairs, which in our simulations was sufficient to ensure thorough convergence (Fig. A1). The second half of the samples was used to calculate the posterior parameter space by fitting to a Gaussian distribution. The posterior model parameters are reported in term of means and standard deviations. The Uncertainty Reduction (*UR*) is defined as:

$$UR = (1 - \frac{\sigma_{posteiror}}{\sigma_{prior}}) \cdot 100\% \quad (30)$$

where σ_{prior} is prior parameter uncertainty, which is 95% of the parameter initial value. $\sigma_{posterior}$ is posterior parameter uncertainty, which is calculated by fitting the posterior model parameters to a Gaussian distribution. 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 indicate that the parameter itself is more consistent with observed values of the parameter. UR is sensitive to the assumption of prior uncertainty range. A large value of *UR* implies a more robust posterior 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:

$$S_i = \frac{VAR_{p_i}(E_{p_{\sim i}}(Y \mid p_i))}{VAR(Y)} \tag{31}$$

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 were relatively more important in affecting nutrient competition. Y represents the model outputs of plant NH_4^+, NO_3^-, or PO_x uptake; p_i is the target parameter; $p_{\sim i}$ 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) $PO4^{3-}$; (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 4100000 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 Posterior 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 posterior parameter samples were not heavily tailed and they generally follow Gaussian distributions (Figure A2). In order to quantitatively compare the posterior 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 posterior mean was improved, the uncertainty of the posterior model may still be relatively large. In other words, a prognostic prediction based on these posterior parameters could be relatively uncertain [*Scholze et al.*, 2007], due to large uncertainty associated with the posterior parameters. Therefore, we calculated the Uncertainty Reduction (*UR*) to evaluate model improvement in terms of posterior

uncertainty. We found that parameters' uncertainties were reduced by 13%~98%. This calculation might either overestimate or underestimate the *UR*, due to the fact that the posterior parameters did not strictly follow Gaussian distributions. But the actual *UR* should not be far from our estimates, because the posterior samples were not widely spread across the potential parameter space (Figure 2). The least constrained parameter was k_{NO3}^{plant} (reaction rate of plant nitrogen carrier enzyme with NO_3^- substrate). Two other NO_3^- dynamics related parameters were also not well constrained: *UR* of KM_{NO3}^{mic} (half-saturation constant for decomposing microbe NO_3^- immobilization) and KM_{NO3}^{den} (half-saturation constant for denitrifier NO_3^- consumption) were only 64% and 67%, respectively. Compared with NH_4^+ or PO_x competition related parameters, we concluded that parameters associated with NO_3^- competition were the least constrained in the model. This 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 re-organize the right hand sides of Eqns. 14 – 22 and define those fraction terms as relative competitiveness parameter (*ECA*); for example for plant NH_4^+ uptake:

$$F_{NH4}^{plant} = k_{NH4}^{plant} \cdot ECA_{NH4}^{plant} \tag{32}$$

$$ECA_{NH4}^{plant} = \frac{[NH4]\cdot[E_N^{plant}]}{KM_{NH4}^{plant}(1+\frac{[NH4]}{KM_{NH4}^{plant}}+\frac{[NO3]}{KM_{NO3}^{plant}}+\frac{[E_N^{plant}]}{KM_{NH4}^{plant}}+\frac{[E_N^{mic}]}{KM_{NH4}^{mic}}+\frac{[E_N^{nit}]}{KM_{NH4}^{nit}})} \tag{33}$$

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.*, natural ecosystem), ECA is dominated by the specific enzyme abundance as well as the substrate affinity ([*E*]/*KM*). Therefore, consumers could either enable an alternative high affinity nutrient transporter system (low *KM*) or exudate more enzyme to enhance competitiveness. For example, it has been shown that root spatial occupation (C_{froot}) determines 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_{froot}) 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 ($1/KM_{NH4}^{plant} : 1/KM_{NH4}^{mic} : 1/KM_{NH4}^{nit}$). 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 *KM*). However, in this work we assumed a well-mixed environment (one soil column), in order to be consistent with large-scale ecosystem models.

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_x competition (Figure 3). Each sensitivity analysis consisted of three scenarios: (1) normal conditions (control); (2) elevated soil T ($+T_s$); and (3) elevated soil moisture ($+\theta$). The sensitivity indicates that nutrient competition is mostly regulated by internal competitor kinetics rather than external environmental conditions (*e.g.*, T_s, θ). 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 Posterior model performance

The prior and posterior models were compared against observational datasets of pool sizes of soil free phosphate, sorbed phosphate, and NH_4^+, CO_2 efflux, and N_2O

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 posterior parameter estimates. The prior model predicted an increasing trend of soil free PO_x, which resulted from underestimates of plant P uptake (by underestimating of k_P^{plant}) and soil microbial P immobilization (by overestimating KM_P^{mic}). The posterior model captured the seasonal dynamics of soil free PO_x 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 NH_4^+ pool size due to overestimation of plant NH_4^+ uptake (k_{NH4}^{plant}). In addition, it also underestimated the denitrification N_2O emissions, because of an underestimation of NH_4^+ to NO_3^- transformation rate (k_{nit}). Consequently, there was not enough NO_3^- substrate to react with denitrifiers and release N_2O. The posterior model, however, accurately reproduced the seasonal dynamics of both NH_4^+ pool sizes and soil N_2O emissions. There were small differences between the prior and posterior model predictions of soil CO_2 emissions. The CO_2 and N_2O 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 CO_2 and N_2O emissions were largely improved by assimilating these datasets.

The posterior 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 posterior model. 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 CO_2 and N_2O effluxes with higher frequency sampling would significantly benefit the model uncertainty reduction.

3.4 Model testing against nitrogen and phosphorus fertilization studies

To test the posterior 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/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/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

562 Terrestrial ecosystem growth and function are continuously altered by climate
563 (*e.g.*, warming, drought; [*Chaves et al.*, 2003; *Springate and Kover*, 2014]), external
564 nutrient inputs (*e.g.*, N deposition; [*Matson et al.*, 2002; *Matson et al.*, 1999]), and
565 atmospheric composition (*e.g.*, CO_2 concentration; [*Norby et al.*, 2010; *Oren et al.*, 2001;
566 *Reich et al.*, 2006]). Improved understanding of the underlying mechanisms regulating
567 ecosystem responses to environmental changes has been obtained through *in situ* level to
568 large-scale and long-term manipulation experiments. For example, decade-long Free-Air
569 Carbon Dioxide Enrichment (FACE) experiments have revealed that nitrogen limitation
570 diminished the CO_2 fertilization effect of forests [*Norby et al.*, 2010] and grasslands
571 [*Reich and Hobbie*, 2013] ecosystems. However, fewer efforts have been made towards
572 incorporating the observed process-level knowledge into Earth System Models (ESMs).
573 Therefore, a major uncertainty that has limited the predictability of ESMs has been the
574 incomplete representation of soil nutrient dynamics [*Zaehle et al.*, 2014]. Even though
575 new soil nutrient cycle paradigms were proposed during recent decades [*Korsaeth et al.*,
576 2001; *Schimel and Bennett*, 2004], they were restricted to either conceptual models or
577 only applied to explain laboratory experiments.
578 Many large-scale terrestrial biogeochemistry models (*e.g.*, O-CN, CASA, TEM)
579 have adopted the classical paradigm that microbes decompose soil organic matter and
580 release NH_4^+ as a "waste" product [*Waksman*, 1931]. The rate of this process is defined
581 as "net N mineralization", and is adopted as a "measure" of plant available inorganic N
582 [*Schimel and Bennett*, 2004]. This classical paradigm overlooked the fact that "net N
583 mineralization" actually comprised two individual processes - gross N mineralization and
584 microbial N immobilization. Implicitly, the classical paradigm assumes that the microbes

585 have priority to assimilate as much of the available nutrient pool as possible. Soil
586 nutrients were only available for plant uptake if there were not enough free energy
587 materials (*e.g.*, dissolved soil organic carbon) to support microbial metabolism. As a
588 result, soil microbes were considered "victors" in the short-term nutrient competition.
589 Some other large-scale terrestrial biogeochemistry models (*e.g.*, CLM4CN), simplify the
590 concept of nutrient competition differently. They calculate the plant N uptake and soil N
591 immobilization separately; and then down-regulate the two fluxes according to the soil
592 mineral N availability. As a result, plant and soil microbe competitiveness for nutrients is
593 determined by their relative demand.

594 Climate-scale land models have over-simplified or ignored competition between
595 plants, microbes, and abiotic mechanisms. In reality, under high nutrient stress
596 conditions, plants can exude nutrient carrier enzymes or facilitate mycorrhizal fungi
597 associations to enhance competitiveness for nutrient acquisition [*Drake et al.*, 2011;
598 *Hobbie and Hobbie*, 2006; *Treseder and Vitousek*, 2001]. In addition, plants can adjust C
599 allocation to construct more fine roots, which scavenge nutrients over larger soil volumes
600 [*Iversen et al.*, 2011; *Jackson et al.*, 2009; *Norby et al.*, 2004]. Soil spatial heterogeneity
601 might also contribute to the success of plant nutrient competition [*Korsaeth et al.*, 2001].
602 Therefore, most ecosystem biogeochemistry models with traditional treatments of
603 nutrient competition likely underestimate plant nutrient uptake.

604 Nutrient competition should be treated as a complex consumer-substrate reaction
605 network: multiple 'consumers', including plant roots, soil heterotrophic microbes,
606 nitrifiers, denitrifiers, and mineral surfaces, each competing for substrates of organic and
607 inorganic nitrogen and phosphorus as nutrient supply. In such a model structure, the

608 success of any consumer in substrate acquisition is affected by its consumer-substrate
609 affinity [*Nedwell*, 1999]. Such competitive interactions have been successfully applied to
610 microbe-microbe and plant-microbe substrate competition modeling [*Bonachela et al.*,
611 2011; *Lambers et al.*, 2009; *Maggi et al.*, 2008; *Maggi and Riley*, 2009; *Moorhead and*
612 *Sinsabaugh*, 2006; *Reynolds and Pacala*, 1993] for many years.

613 Here, we applied the consumer-substrate network in a broader context of plant,
614 microorganism, and abiotic mineral interactions. We analyzed the consumer-substrate
615 network using a first-order accurate equilibrium chemistry approximation (ECA) [*Tang*
616 *and Riley*, 2013; *Zhu and Riley*, 2015]. Our sensitivity analysis confirmed that the
617 consumer-substrate affinity and nutrient carrier enzyme abundance were the most
618 important factors regulating relatively short-term competitive interactions. The ECA
619 competition treatment represents ecosystem responses to environmental changes and has
620 the potential to be linked to a microbe-explicit land biogeochemistry model. The
621 approach allows competition between plants, microbes, and mineral surfaces to be
622 prognostically determined based on nutrient status and capabilities of each consumer.
623

624 **4. Conclusions**

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

631 considering two inhibitive effects: (1) multiple substrates (*e.g.*, NH_4^+ and NO_3^-) sharing
632 one consumer inhibits the effective binding between any specific substrate and the
633 consumer and (2) multiple consumers (*e.g.*, plants, decomposing microbes, nitrifers)
634 sharing one substrate (*e.g.*, NH_4^+) lowers the probability of effective binding between any
635 consumer and that substrate. We calibrated the model at a tropical forest site with highly
636 weathered soil (Tapajos National Forest, Para, Brazil), using multiple observational
637 datasets with the Markov Chain Monte Carlo (MCMC) approach. The model parameters
638 were well constrained compared with their prior distributions (Table 4). The posterior
639 parameter uncertainties were greatly reduced (on average by 75%). The posterior model
640 compared to multiple categories of observational data was substantially improved over
641 the prior model (Figure 4). The seasonal dynamics of soil carbon, nitrogen, and
642 phosphorus were moderately well captured. However, our results would likely be more
643 robust if more temporally resolved observations of carbon, nitrogen, and phosphorous
644 were available in the individual consumer pools.
645 To test the resulting model using the posterior parameters, we applied N-COM to
646 two other tropical forests (Hawaii tropical forest and Luquillo tropical forest) not used in
647 the calibration process and conducted nutrient perturbation studies consistent with
648 fertilization experiments at these sites. The results showed that N-COM simulated the
649 nitrogen and phosphorus competition well for the majority of the observational metrics.
650 However, the model underestimated NH_4^+ uptake by nitrifiers, probably due to the
651 loosely constrained nitrification parameters that were the result of NO_3^- pool size data
652 paucity during calibration at the Brazil site (Table 4). Datasets of soil nutrient pool sizes

653 and CO_2 and N_2O effluxes with high frequency sampling would significantly benefit the
654 model uncertainty reduction.
655 To date, many terrestrial ecosystem biogeochemistry models assume microbes
656 outcompete plants and immobilize nutrients first [*Y P Wang et al.*, 2007; *Zaehle and*
657 *Friend*, 2010; *Zhu and Zhuang*, 2013], although CLM currently assumes constant and
658 relative demand competitiveness of plants and microbes. Few models, to our knowledge,
659 consider the role of abiotic interactions in the competitive interactions. In the case of
660 microbes outcompeting plants, the plant is only able to utilize the nutrients that exceed
661 microbial demands during that time step. The leftover nutrients are defined as net
662 mineralization, which is a widely adopted concept in soil biogeochemistry modeling
663 [*Schimel and Bennett*, 2004]. These models oversimplify plant-microbe interactions by
664 imposing dubious assumptions (*e.g.*, microbes always win against plants). We showed
665 that (in section 3.1) "competitiveness" is a dynamic rather than fixed property of the
666 competition network, and more importantly, it should be linked to competitor functional
667 traits (affinity and nutrient carrier enzyme abundance).
668 This study is a crucial step towards implementing more realistic nutrient
669 competition schemes in complex climate-scale land models. Traditional ESMs generally
670 lack realistic soil nutrient competition, which likely biases the estimates of terrestrial
671 ecosystem carbon productivity and biosphere-climate feedbacks. This study showed the
672 effectiveness of ECA kinetics in representing soil multiple-consumer and multiple-
673 nutrient competition networks. Offline calibration and independent site-level testing is
674 critically important to ensuring the newly incorporated model will perform reasonably
675 when integrated in a complex ESM. To this end, we provide a universal calibration

676 approach using MCMC, which could in the future be used to further constrain N-COM
677 across plant functional types, climate, and soil types.
678
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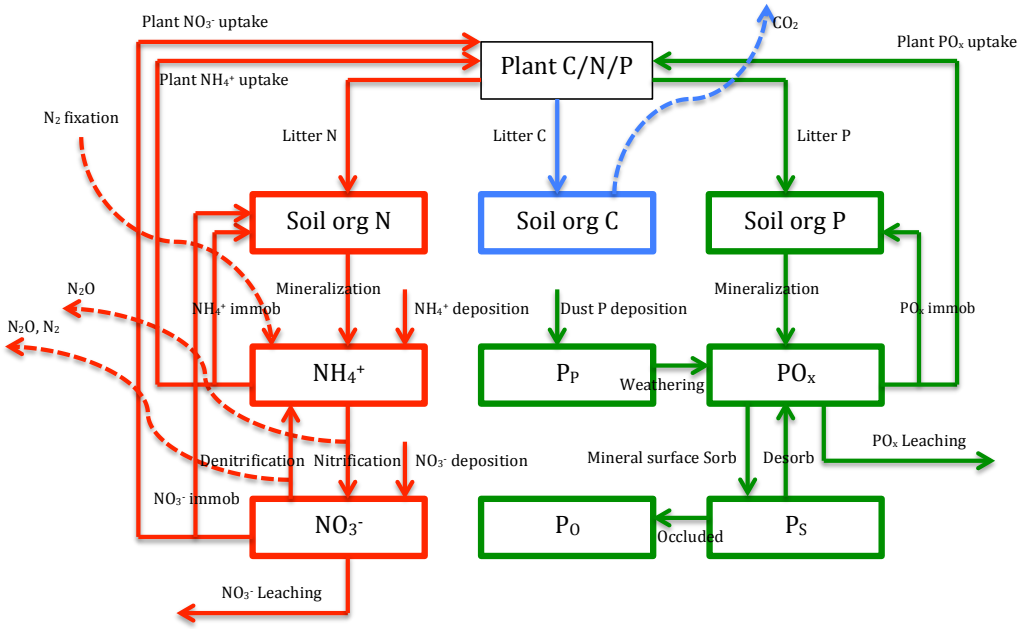
682 Modeling (RGCM) and ACME programs.

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).



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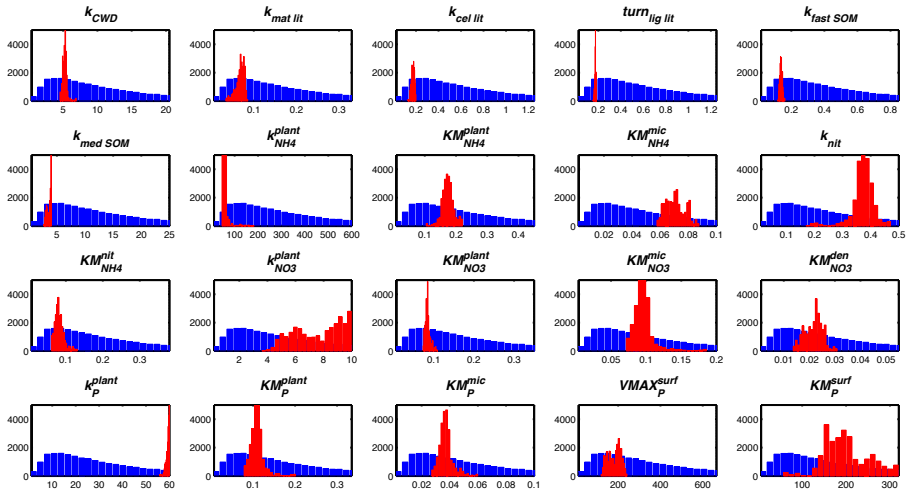
Comment [1]: Figure is updated. "MIC NH4 uptake", "MIC NO3 uptake", "MIC POx" uptake are changed to "NH4 immob", "NO3 immob", and "POx immob"

688 **Figure 2.** Distribution of prior and posterior model parameters.



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Comment [2]: Figure is updated. Please note that prior and posterior distribution of parameters are plotted together for comparison.

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% ($+\theta$), 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).

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Comment [3]: Figure is updated

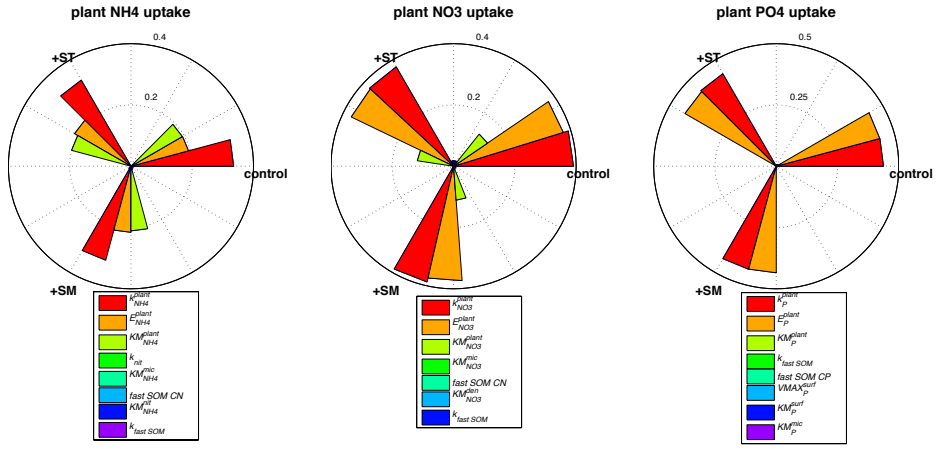

Figure 4. Model performance at Tapajos National Forest, Para, Brazil. Overall, the posterior model (blue line) improved predictions over the prior model (grey line) when compared to observations. Green areas indicate the posterior model uncertainties.

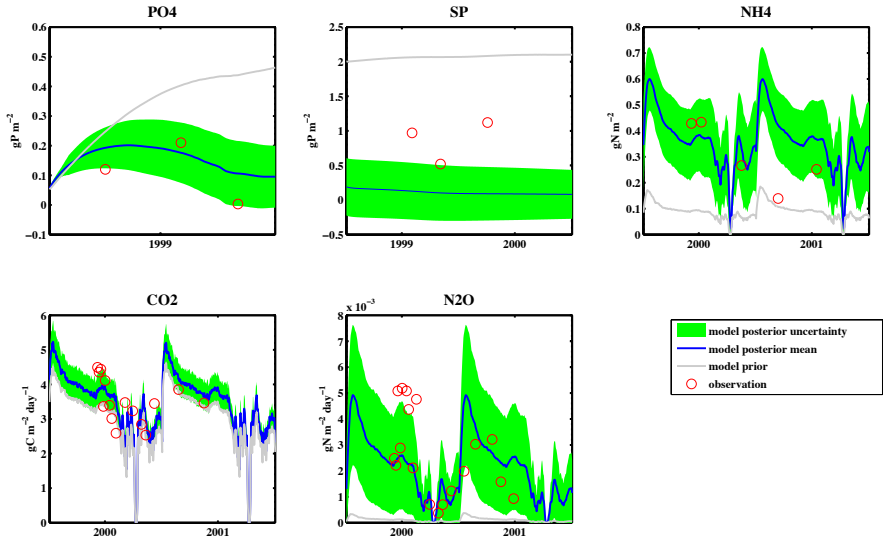

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Figure 5. Model perturbation experiments compared with nitrogen and phosphorus fertilization field experimental data. The blue dots show the difference between control and perturbed simulations, which mean how much newly added nutrient each consumer 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.

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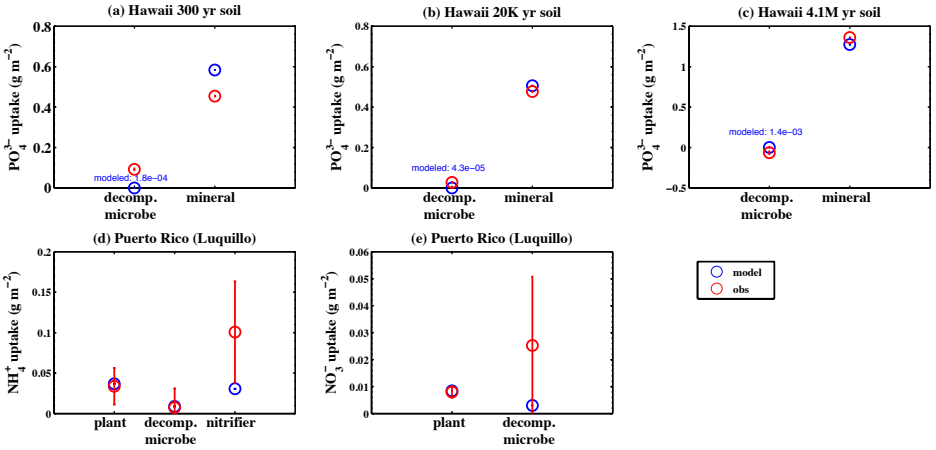

709 **Table 1.** A summary of the modeled consumer-resource competition network.

Resources	**Consumers**		
NH_4^+	Plant	Decomposing Microbe	Nitrifier
NO_3^-	Plant	Decomposing Microbe	Denitrifier
PO_x	Plant	Decomposing Microbe	Mineral surface

710

711 **Table 2.** Model parameters and baseline values.

C associated				
g_i	Percentage of carbon remains in the soil after decomposition of i^{th} SOM	-	[1.0; 0.45; 0.5; 0.5; 0.83; 0.45; 0.45]	[*Koven et al.*, 2013]
f_{ij}	fraction of SOM leave from i^{th} pool and enter into j^{th} pool	-	[0, 0, 0.76, 0.24, 0, 0, 0; 0, 0, 0, 0, 1, 0, 0; 0, 0, 0, 0, 1, 0, 0; 0, 0, 0, 0, 0, 1, 0; 0, 0, 0, 0, 0, 0.995, 0.005; 0, 0, 0, 0, 0.93, 0, 0.07; 0, 0, 0, 0, 1, 0, 0]	[*Koven et al.*, 2013]
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 turn over [CWD, metabolic lit, cellulose lit, lignin lit, fast SOM, medium SOM, slow SOM]	year	[4.1, 0.066, 0.25, 0.25, 0.17, 5, 270]	[*Koven et al.*, 2013]
N associated				
k_{NH4}^{plant}	Reaction rate of plant NH_4^+ carrier enzyme	day^{-1}	120 [(a)]	[*Jackson et al.*, 1997; *Min et al.*, 2000]
KM_{NH4}^{plant}	Half-saturation constant for plant NH_4^+ uptake	$g\ m^{-2}$	0.09	[*Kuzyakov and Xu*, 2013]
KM_{NH4}^{mic}	Half-saturation constant for decomposing microbe NH_4^+ immobilization	$g\ m^{-2}$	0.02	[*Kuzyakov and Xu*, 2013]
k_{nit}	Maximum fraction of NH_4^+ pool that could be utilized by nitrifiers	day^{-1}	10%	[*Parton et al.*, 2001]
KM_{NH4}^{nit}	Half-saturation constant for nitrifier NH_4^+ consumption	$g\ m^{-2}$	0.076	[*Drtil et al.*, 1993]
k_{NO3}^{plant}	Reaction rate of plant NO_3^- carrier enzyme	day^{-1}	2 [(a)]	[*Jackson et al.*, 1997; *Min et al.*, 2000]
KM_{NO3}^{plant}	Half-saturation constant for plant NO_3^- uptake	$g\ m^{-2}$	0.07	[*Kuzyakov and Xu*, 2013]
KM_{NO3}^{mic}	Half-saturation constant for decomposing microbe NO_3^- immobilization	$g\ m^{-2}$	0.04	[*Kuzyakov and Xu*, 2013]
KM_{NO3}^{den}	Half-saturation constant for denitrifier NO_3^- consumption	$g\ m^{-2}$	0.011	[*Murray et al.*, 1989]
$[E_N^{plant}]$	Plant nitrogen carrier enzyme abundance for nitrogen uptake	$g\ m^{-2}$	$C_{froot} \cdot 0.0000125$ [(a)]	[*Tang and Riley*, 2013; *Trumbore et al.*, 2006]
$[E_N^{mic}]$	Decomposing microbes nitrogen carrier enzyme abundance for nitrogen immobilization	$g\ m^{-2}$	$\frac{E_N^{immob,pot}}{1000}$ [(b)]	[*Tang and Riley*, 2013]
$[E_N^{nit}]$	Nitrifier nitrogen carrier enzyme abundance for NH_4^+ assimilation	$g\ m^{-2}$	$1.2E^{-3}$	[*Raynaud et al.*, 2006]

Berkeley Lab 7/31/15 2:07 PM
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$[E_N^{den}]$	Denitrifier nitrogen carrier enzyme abundance for NO_3^- assimilation	g m^{-2}	$1.2E^{-3}$	[*Raynaud et al.*, 2006]
f^{N2O}	Fraction of nitrification flux lost as N_2O	-	$6E^{-4}$	[*Li et al.*, 2000]
P associated				
$k_{weather}$	Parent material P weathering rate	g P m^{-2} $year^{-1}$	0.004	[*Y P Wang et al.*, 2010]
k_{occl}	P occlude rate	$month^{-1}$	$1.0E^{-6}$	[*Yang et al.*, 2014]
k_P^{plant}	Reaction rate of plant PO_x carrier enzyme	day^{-1}	12 (a)	[*Colpaert et al.*, 1999]
KM_P^{plant}	Half-saturation constant for plant PO_x uptake	g m^{-2}	0.067	[*Cogliatti and Clarkson*, 1983]
KM_P^{mic}	Half-saturation constant for decomposing microbe PO_x immobilization	g m^{-2}	0.02	[*Chen*, 1974]
$VMAX_P^{surf}$	Maximum mineral surface PO_x adsorption	g m^{-2}	133	[*Y P Wang et al.*, 2010]
KM_P^{surf}	Half-saturation constant for mineral surface PO_x adsorption	g m^{-2}	64	[*Y P Wang et al.*, 2010]
$[E_P^{plant}]$	Plant phosphorus carrier enzyme abundance for PO_x uptake	g m^{-2}	$C_{froot} \cdot 0.0000125$ (a)	[*Tang and Riley*, 2013; *Trumbore et al.*, 2006]
$[E_P^{mic}]$	Decomposing microbes phosphorus carrier enzyme abundance for PO_x immobilization	g m^{-2}	$\frac{F_P^{immob,pot}}{800}$ (b)	[*Tang and Riley*, 2013]
$[E_P^{surf}]$	Mineral surface "effective enzyme" abundance for PO_x adsorption	g m^{-2}	$VMAX_P^{surf} - [SP]$	[*Tang and Riley*, 2013]

(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, $C_{froot} \cdot x = C_{mic} \cdot 0.05$ or $400 \cdot x = 0.1 \cdot 0.05$. We have $x = 0.0000125$. Further, we have $k_{NH4}^{plant} \cdot [E_N^{plant}] = VMAX_{NH4}^{plant}$. We know that typical values for $VMAX_{NH4}^{plant}$ and $[E_N^{plant}]$ are 0.6 g m^{-2} day^{-1} [*Min et al.*, 2000] and 0.005 g m^{-2}. Then we have $k_{NH4}^{plant} = 120$ day^{-1}. Similarly, we have $k_{NO3}^{plant} \cdot [E_N^{plant}] = VMAX_{NO3}^{plant}$, $k_P^{plant} \cdot [E_P^{plant}] = VMAX_P^{plant}$. Knowing that typical values for $VMAX_{NO3}^{plant}$ and $VMAX_P^{plant}$ are 0.01 [*Min et al.*, 2000] and 0.06 [*Colpaert et al.*, 1999] g m^{-2} day^{-1}, we have $k_{NO3}^{plant} = 2$ and $k_P^{plant} = 12$ day^{-1}.

(b) For decomposing microbes, we have $VMAX_N^{mic} = k_N^{mic} \cdot [E^{mic}_N]$. Typical values for $VMAX_N^{immob}$ and $[E_N^{mic}]$ are 5 g m^{-2} day^{-1} [*Kuzyakov and Xu*, 2013] and 0.005 g m^{-2} [*Tang and Riley*, 2013]. Therefore, we have $k_N^{mic} = 1000$. Since our model calculates potential N immobilization rates and approximates them as $VMAX_N^{mic}$. The changes of potential N immobilization rates at each time step imply the changes of enzyme abundance through $[E_N^{mic}] = \frac{F_N^{immob,pot}}{k_N^{mic}} = \frac{F_N^{immob,pot}}{1000}$. Similarly, we have that $VMAX_P^{immob}$ and $[E_N^{mic}]$ are 2 g m^{-2} day^{-1} [*Chen*, 1974] and 0.005 g m^{-2}. Therefore, $k_P^{mic} = 800$ and $E_P^{mic} = \frac{F_P^{immob,pot}}{800}$.

712 **Table 3.** Observational datasets used for calibration.

Processes	Datasets		Location	References
C associated	Soil heterotrophic respiration		Tapajos National Forest, Para, Brazil	[*Silver et al.*, 2012]
N associated	Soil NH_4^+	N_2O efflux	Tapajos National Forest, Para, Brazil	[*Silver et al.*, 2012]
P associated	Soil free phosphate	Sorb phosphate	Tapajos National Forest, Para, Brazil	[*McGroddy et al.*, 2008]

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Table 4. Calibrated model parameters, prior mean, posterior means, and uncertainty reduction after assimilating the observational datasets.

Berkeley Lab 7/31/15 2:07 PM
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Parameters	μ_{prior}	σ_{prior}	$\mu_{posterior}$	$\sigma_{posterior}$	Uncertainty Reduction %
$TURN_{SOM}$ [CWD, metabolic lit, cellulose lit, lignin lit, fast SOM, medium SOM]	[3.7, 0.06, 0.23, 0.23,0.16, 4.6]	[3.9, 0.06, 0.24, 0.24, 0.18, 4.8]	[5.2, 0.07, 0.17, 0.17, 0.14, 3.6]	[0.33, 0.01, 0.01, 0.005, 0.008, 0.37]	[92, 83, 96, 98, 96, 92]
k_{NH4}^{plant}	109	114	58	14	88
KM_{NH4}^{plant}	0.082	0.086	0.173	0.018	79
KM_{NH4}^{mic}	0.018	0.019	0.071	0.0067	65
k_{nit}	0.091	0.095	0.37	0.038	60
KM_{NH4}^{nit}	0.069	0.072	0.082	0.012	83
k_{NO3}^{plant}	1.8	1.9	7.6	1.7	13
KM_{NO3}^{plant}	0.064	0.067	0.085	0.0064	90
KM_{NO3}^{mic}	0.036	0.038	0.096	0.014	63
KM_{NO3}^{den}	0.0101	0.0105	0.022	0.0034	68
k_{P}^{plant}	11	11.5	59	0.75	93
KM_{P}^{plant}	0.061	0.064	0.11	0.015	77
KM_{P}^{mic}	0.018	0.019	0.037	0.0047	75
$VMAX_{P}^{surf}$	121	127	182	30	76
KM_{P}^{surf}	64	58	200	50	18

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.

Datasets	Added nutrient	Competitors			Duration (hour)	References
PO_4^{3-} fertilization	10 μg g^{-1}	I. Mineral surface	II. Decomposing microbe		48	[*Olander and Vitousek*, 2005]
NH_4^+ fertilization	4.6 μg g^{-1}	I. Plant	II. Decomposing microbe	III. Nitrifier	24	[*Templer et al.*, 2008]
NO_3^- fertilization	0.92 μg g^{-1}	I. Plant	II. Decomposing microbe		24	[*Templer et al.*, 2008]

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