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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 (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 free NH_4^+ 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 the competitiveness (from most to least competitive) followed this order: (1) for NH_4^+, nitrifiers ~ decomposing microbes > plant roots, (2) for NO_3^-, denitrifiers ~ decomposing microbes > plant roots, (3) for PO_x, mineral surfaces > decomposing microbes ~ plant roots. Although smaller, plant relative competitiveness is of the same order of magnitude as microbes. 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; Thornton et al., 2009; 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 is 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[4]MIP (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, 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 resource competition in order to accurately model soil nutrient dynamics, plant nutrient uptake, and plant productivity.

5   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

10 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; Wang and Lars, 1997). [15]N 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 compet-

15 itiveness 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 longer term (months – years), morphological adjustment occurs;

20 for example, plants allocate more carbon to fine roots to explore deeper and further horizontal soil volume (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.

25 Given this understanding 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 widely adopted treatment in ESM land models is that microbes are evenly competitive with plants for nutrient acquisition. For example, CLM4CN (Thornton et al., 2007; Thornton and Zimmermann, 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 (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, ecosys (Grant et al., 2012, 2010) assume equal competitiveness of plants and microbes. 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 Chemistry 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

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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; our ultimate goal is to integrate this approach in CLM4.5 (Koven et al., 2013; Tang et al., 2013). 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, 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 (Fig. 1) to simulate soil carbon decomposition, nitrogen and phosphorus transformations, abiotic interactions, and plant demands. Although, our ultimate goal is to incor-

porate 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, slow SOM pool, and passive SOM pool. Litter is further divided into three sub-groups: metabolic, cellulose, and lignin. The soil organic C, N, and P dynamics follow first-order decay:

$$\frac{\Delta C_j}{\Delta t} = k_j C_j r_\theta r_T \tag{1}$$

$$\frac{\Delta N_j}{\Delta t} = k_j N_j r_\theta r_T \tag{2}$$

$$\frac{\Delta P_j}{\Delta t} = k_j P_j r_\theta r_T \tag{3}$$

where k_j is the rate constant of soil organic matter decay (s^{-1}); C_j, N_j, and P_j are pool sizes ($g\,m^{-3}$) 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, passive SOC); r_T and r_θ (dimensionless) are soil temperature and moisture environmental regulators.

Carbon (C, $g\,C\,m^{-3}$) either (1) enters from an upstream pool into a downstream pool or (2) is lost as CO_2. Soil organic carbon temporal changes in each pool are calculated

as:

$$\frac{dC_j}{dt} = -\frac{\Delta C_j}{\Delta t} + \sum_{i=1}^{N} F_{C,ij}^{\text{move}} \tag{4}$$

where $F_{C,ij}^{\text{move}}$ is the flux of carbon moving from the upstream pool (i) to the downstream pool (j) due to upstream pool SOC decomposition. $\frac{\Delta C_j}{\Delta t}$ represents first order decay of downstream (j) soil organic carbon. Simultaneously, soil organic N and P follow C decomposition:

$$\frac{dN_j}{dt} = -\frac{\Delta N_j}{\Delta t} + \sum_{i=1}^{N} F_{N,ij}^{\text{move}} + \sum_{i=1}^{N} F_{NH_4,ij}^{\text{immob}} + \sum_{i=1}^{N} F_{NO_3,ij}^{\text{immob}} \tag{5}$$

$$\frac{dP_j}{dt} = -\frac{\Delta P_j}{\Delta t} + \sum_{i=1}^{N} F_{P,ij}^{\text{move}} + \sum_{i=1}^{N} F_{P,ij}^{\text{immob}} \tag{6}$$

where $F_{N,ij}^{\text{move}}$ and $F_{P,ij}^{\text{move}}$ are fluxes of nitrogen and phosphorus moving from the upstream (i) to downstream (j) pools. $F_{NH_4,ij}^{\text{immob}}$, $F_{NO_3,ij}^{\text{immob}}$, and $F_{P,ij}^{\text{immob}}$ are immobilization fluxes of soil mineral nitrogen and phosphorus. $\frac{\Delta N_j}{\Delta t}$ and $\frac{\Delta P_j}{\Delta t}$ represent soil organic matter mineralization.

Equations (5) and (6) state that changes in the jth organic N or P pool are the summation of three terms: (1) organic N and P lost during soil organic matter mineralization ($-\frac{\Delta N_j}{\Delta t}$ and $-\frac{\Delta P_j}{\Delta t}$), (2) a fraction of the ith organic N or P pool (upstream) enters into the jth pool (downstream) ($F_{N,ij}^{\text{move}}$ and $F_{P,ij}^{\text{move}}$); and (3) soil microbial immobilization ($F_{NH_4,ij}^{\text{immob}}$, $F_{NO_3,ij}^{\text{immob}}$, and $F_{P,ij}^{\text{immob}}$). 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).

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The inorganic nitrogen pools (currently considered to be NH_4^+ and NO_3^-, Eqs. 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 (Eq. 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.

$$\frac{d[NH_4^+]}{dt} = \sum_{j=1}^{N} \sum_{i=1}^{N} F_{NH_4,ij}^{mob} - F_{NH_4}^{nit} - F_{NH_4}^{plant} - F_{NH_4}^{immob} + F^{BNF} + F_{NH_4}^{dep} \tag{7}$$

$$\frac{d[NO_3^-]}{dt} = -F_{NO_3}^{den} + (1 - f^{N_2O})F_{NH_4}^{nit} - F_{NO_3}^{plant} - F_{NO_3}^{immob} - F_{NO_3}^{leach} + F_{NO_3}^{dep} \tag{8}$$

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

where $F_{NH_4,ij}^{mob}$ and $F_{P,ij}^{mob}$ are gross mineralization rates for nitrogen and phosphorus. $F_{NH_4}^{nit}$ is the nitrification flux, part of which is lost through a gaseous pathway (f^{N_2O}) and the rest is incorporated into the NO_3^- pool. $F_{NO_3}^{den}$ 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 $F_{NH_4}^{plant}$, $F_{NO_3}^{plant}$, and F_{P}^{plant}, respectively. Soil decomposing microbial immobilization of soil NH_4^+, NO_3^-, and PO_x are represented as $F_{NH_4}^{immob}$, $F_{NO_3}^{immob}$, and F_{P}^{immob}, $F_{NO_3}^{leach}$, and F_{P}^{leach} are leaching losses of soil NO_3^- and PO_x, respectively. External inputs into soil inorganic N pools include atmospheric ammonia deposition ($F_{NH_4}^{dep}$), atmospheric nitrate deposition ($F_{NO_3}^{dep}$), 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:

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

$$\frac{d(P_O)}{dt} = F_P^{occl} \tag{11}$$

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

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 Sect. 2.1 has multiple potential nutrient consumers (plants, SOM decomposing microbes, nitrifiers, denitrifiers, mineral surfaces) as well as 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 Eq. 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).
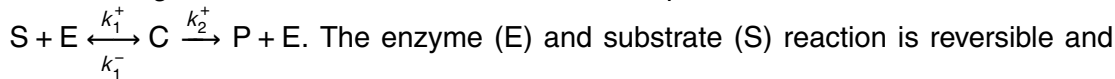
Competition between different consumers in acquiring different resources (Table 1) is formularized in N-COM with the Equilibrium Chemistry Approximation (Tang and Riley, 2013):

$$\text{ECA}_{NH_4}^{plant} = \frac{[NH_4^+]}{KM_{NH_4}^{plant} \left(1 + \overset{(1)}{\frac{[NH_4^+]}{KM_{NH_4}^{plant}}} + \overset{(2)}{\frac{[NO_3^-]}{KM_{NO_3}^{plant}}} + \overset{(3)}{\frac{[E_{NH_4}^{plant}]}{KM_{NH_4}^{plant}}} + \overset{(4)}{\frac{[E_{NH_4}^{mic}]}{KM_{NH_4}^{mic}}} + \overset{(5)}{\frac{[E_{NH_4}^{nit}]}{KM_{NH_4}^{nit}}} \right)} \qquad (13)$$

$$\text{ECA}_{NH_4}^{mic} = \frac{[NH_4^+]}{KM_{NH_4}^{mic} \left(1 + \frac{[NH_4^+]}{KM_{NH_4}^{mic}} + \frac{[NO_3^-]}{KM_{NO_3}^{mic}} + \frac{[E_{NH_4}^{plant}]}{KM_{NH_4}^{plant}} + \frac{[E_{NH_4}^{mic}]}{KM_{NH_4}^{mic}} + \frac{[E_{NH_4}^{nit}]}{KM_{NH_4}^{nit}} \right)} \qquad (14)$$

$$\text{ECA}_{NH_4}^{nit} = \frac{[NH_4^+]}{KM_{NH_4}^{nit} \left(1 + \frac{[NH_4^+]}{KM_{NH_4}^{nit}} + \frac{[E_{NH_4}^{plant}]}{KM_{NH_4}^{plant}} + \frac{[E_{NH_4}^{mic}]}{KM_{NH_4}^{mic}} + \frac{[E_{NH_4}^{nit}]}{KM_{NH_4}^{nit}} \right)} \qquad (15)$$

where the ECA defines relative competitiveness KM are half-saturation constants for different consumer-resource pairs. $[E_{NH_4}^{plant}]$, $[E_{NH_4}^{mic}]$, and $[E_{NH_4}^{nit}]$ are effective abundances of enzymes from plants, decomposing microbes, and nitrifiers to compete with binding sites. Each consumer-substrate competition reaction is formulated as: $S + E \overset{k_1^+}{\underset{k_1^-}{\rightleftharpoons}} C \overset{k_2^+}{\longrightarrow} P + E$. The enzyme (E) and substrate (S) reaction is reversible and forms complex (C). The irreversible reaction releases product (P) and enzyme (E). The enzyme concentration (E) determines the effectiveness of a consumer to bind a substrate and therefore its competitiveness. For simplicity, we assumed that enzyme abundances of all consumers were equal to a baseline value ($0.00075\,\text{g\,m}^{-2}$, Wang et al., 2012). Considering enzyme abundances in Eqs. (13)–(15) and Eqs. (A6), (A9), (A12) offer an opportunity for consumers to alter their competitiveness through exudation of enzymes. Please note that in Eqs. (A6), (A9), and (A12), VMAX is a product

of enzyme abundance and reaction rate (derivation is in Appendix B). An example is when plants exude extracellular enzymes (e.g., nitrogenases) through mycorrhizal fungi ($E_{NH_4}^{plant}$, $E_{NO_3}^{plant}$), thereby enhancing their competitiveness relative to microbes in nitrogen acquisition. Changes in enzyme abundances under different conditions and the subsequent impacts on nutrient competition are worthy of further investigation, which we leave for later work.

These equations (Eqs. 13–15) 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 Eq. 13) and (2) multiple consumers (e.g., plants, decomposing microbes, and nitrifers) 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 Eq. 13). Likewise, plants, decomposing microbes, and denitrifers compete for NO_3^- and plants, decomposing microbes, and mineral surfaces compete for PO_x as follows:

$$ECA_{NO_3}^{plant} = \frac{[NO_3^-]}{KM_{NO_3}^{plant}\left(1 + \frac{[NH_4^+]}{KM_{NH_4}^{plant}} + \frac{[NO_3^-]}{KM_{NO_3}^{plant}} + \frac{[E_{NO_3}^{plant}]}{KM_{NO_3}^{plant}} + \frac{[E_{NO_3}^{mic}]}{KM_{NO_3}^{mic}} + \frac{[E_{NO_3}^{den}]}{KM_{NO_3}^{den}}\right)} \tag{16}$$

$$ECA_{NO_3}^{mic} = \frac{[NO_3^-]}{KM_{NO_3}^{mic}\left(1 + \frac{[NH_4^+]}{KM_{NH_4}^{mic}} + \frac{[NO_3^-]}{KM_{NO_3}^{mic}} + \frac{[E_{NO_3}^{plant}]}{KM_{NO_3}^{plant}} + \frac{[E_{NO_3}^{mic}]}{KM_{NO_3}^{mic}} + \frac{[E_{NO_3}^{den}]}{KM_{NO_3}^{den}}\right)} \tag{17}$$

$$ECA_{NO_3}^{den} = \frac{[NO_3^-]}{KM_{NO_3}^{den}\left(1 + \frac{[NO_3^-]}{KM_{NO_3}^{den}} + \frac{[E_{NO_3}^{plant}]}{KM_{NO_3}^{plant}} + \frac{[E_{NO_3}^{mic}]}{KM_{NO_3}^{mic}} + \frac{[E_{NO_3}^{den}]}{KM_{NO_3}^{den}}\right)} \tag{18}$$

$$ECA_P^{plant} = \frac{[PO_x]}{KM_P^{plant}\left(1 + \frac{[PO_x]}{KM_P^{plant}} + \frac{[E_P^{plant}]}{KM_P^{plant}} + \frac{[E_P^{mic}]}{KM_P^{mic}} + \frac{[E_P^{surf}]}{KM_P^{surf}}\right)} \tag{19}$$

$$ECA_P^{mic} = \frac{[PO_x]}{KM_P^{mic}\left(1 + \frac{[PO_x]}{KM_P^{mic}} + \frac{[E_{PO_4}^{plant}]}{KM_P^{plant}} + \frac{[E_{PO_4}^{mic}]}{KM_P^{mic}} + \frac{[E_{PO_4}^{surf}]}{KM_P^{surf}}\right)} \tag{20}$$

$$ECA_P^{surf} = \frac{[PO_x]}{KM_P^{surf}\left(1 + \frac{[PO_x]}{KM_P^{surf}} + \frac{[E_P^{plant}]}{KM_P^{plant}} + \frac{[E_P^{mic}]}{KM_P^{mic}} + \frac{[E_P^{surf}]}{KM_P^{surf}}\right)} \tag{21}$$

where $[NO_3^-]$ and $[PO_x]$ are concentrations of nitrate and phosphate. KM is the half-saturation constants for each consumer-resource pair. $[E_{NO_3}^{plant}]$, $[E_{NO_3}^{mic}]$, and $[E_{NO_3}^{den}]$ are effective abundances of enzymes from plants, decomposing microbes, and denitrifiers to compete binding sites in nitrate acquisition. Similarly, $[E_P^{plant}]$, $[E_P^{mic}]$, and $[E_P^{surf}]$ are effective abundances of enzymes from plants, decomposing microbes, and mineral surfaces to compete binding sites in phosphate acquisition.

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 Land Model (CLM), 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 Eq. A13), (4) annual NPP (NPP_{annual} in Appendix Eq. A15), (5) NH_4^+ deposition ($F_{NH_4}^{dep}$), (6) NO_3^- deposition ($F_{NO_3}^{dep}$); and (7) hydrologic discharge (Q_{dis} in Appendix Eqn. A16). External input of mineral phosphorus is 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 the 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 biogeochemical dynamics. A set of model parameters is selected for calibration (Table 4), which comprise all nutrient competition kinetics parameters (VMAX 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. Priors of the model parameters come from either previously published values or site-level observations. Parameters related to nitrogen dynamics, (e.g., $VMAX_{NH_4}^{nit}$: maximum nitrification rate and $KM_{NH_4}^{nit}$: half-saturation constant for nitrifier NH_4^+ consumption) are obtained by fitting model predictions to observed soil free NH_4^+ and N_2O effluxes. Datasets of soil free phosphate and sorbed phosphate are employed to improve the parameters associated with phosphorus dynamics, such as $VMAX_P^{surf}$ (maximum rate of mineral surface P sorption) and KM_P^{surf} (half-saturation constant for mineral surface sorbed P). We focus only on those parameters that are most relevant to nutrient competition processes in N-COM. A subset of model parameters (e.g., soil organic matter CN and CP ratios) are not calibrated in this study, since they

either have already been well constrained by previous studies or do not substantially affect our modeling results.

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 calculates the likelihood between model simulations and observations. The Bayesian inference framework estimates the posterior probability of the sampled parameters as:

$$p(\boldsymbol{\theta}|\boldsymbol{D}) = \frac{p(\boldsymbol{D}|\boldsymbol{\theta})p(\boldsymbol{\theta})}{p(\boldsymbol{D})} \tag{22}$$

where $\boldsymbol{D}$ is a vector of observations ($\boldsymbol{D}_{ij}$); i from 1 to 5 denotes categories of data (e.g., soil CO_2 and N_2O effluxes and soil concentrations of NH_4^+, free PO_x, and sorbed PO_x); j from 1 to n denotes time series of each specific dataset of length n; $\boldsymbol{\theta}$ is a vector of model parameters ($\boldsymbol{\theta}_i$); and i from 1 to 23 represents the parameters that are calibrated (Table 4).

We assumed that the prior parameter is uniformly distributed within (10 and 500 %) of its initial value (Table 4). Then we ran MCMC to sample 50 000 parameter pairs, which in our simulations was sufficient to ensure thorough convergence. The last 1000 samples were used to calculate the posterior parameter space by fitting to a Gaussian distribution. The posterior model parameters are reported in term of means and SD. The Uncertainty Reduction (UR) is defined as:

$$UR = \left(1 - \frac{\sigma_{\text{posterior}}}{\sigma_{\text{prior}}}\right) \cdot 100\% \tag{23}$$

where σ_{prior} is prior parameter uncertainty, which we take to be 40 % of the parameter range (Zhu and Zhuang, 2014) and $\sigma_{\text{posterior}}$ is posterior parameter uncertainty, which is calculated by fitting the posterior model parameters to a Gaussian distribution. Uncertainty Reduction is a useful metric, because it quantitatively reveals the reduction in the range of a particular parameter after calibration with MCMC. It does not indicate

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that the parameter itself is more consistent with observed values of the parameter. UR is sensitive to the assumption of prior uncertainty range. For example, if σ_{prior} were 20 % of prior parameter range, UR would be much smaller than we obtained in this study. 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:

$$S_i = \frac{\text{VAR}_{p_i}(E_{p_{\sim i}}(Y|p_i))}{\text{VAR}(Y)} \tag{24}$$

where S_i is the first order sensitivity index of the ith 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) 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, 20 000, and 4 100 000 year old soils) that were fertilized with $10\,\mu g\,g^{-1}$ $^{32}PO_4^{3-}$, respectively, and microbial demand vs. 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, 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, $4.6\,\mu g\,g^{-1}$ $^{15}NH_4^+$ 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, $0.92\,\mu g\,g^{-1}$ $^{15}NO_3^-$ was added to the soil and the plant uptake and microbial immobilization was measured. The measurements were made 24 or 48 h 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 h 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.

3 Results and discussion

3.1 Posterior model parameters

Our best estimates (1000 posterior samples) of the twenty-four selected model parameters based on the observations in the Tapajos National Forest, Para, Brazil are shown in Fig. 2. Although some parameter posterior distributions roughly followed a Gaussian distribution, such as the half-saturation constant for decomposing microbe NH_4^+ immobilization ($KM_{NH_4}^{mic}$), and maximum rate of decomposing microbe PO_x uptake ($VMAX_P^{mic}$), most posterior parameters were irregularly distributed. Even though the parameters' probability distributions were hard to generalize, we found that the probability distribution of 1000 posterior samples is not heavily tailed. Therefore, we conclude that (1) a value near the center of that numerical range is a reasonable estimate of the parameter posterior mean and (2) the parameter posterior uncertainty was well constrained since the spread of the posterior parameters in the 1000 samples was small. In order to quantitatively compare the posterior parameter distributions with prior distributions, we fit all parameter distributions to a Gaussian distribution and estimated their means and SD (Table 4).

The posterior parameter means were mostly different than their initial values. For example, the turnover rate of coarse woody debris was changed from 4.1 to 6.3 ± 0.5 years (i.e., an increase of 50 %). 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 on average parameter uncertainty was reduced by 94 %. We note that UR is highly sensitive to the prior uncertainty (σ_{prior} in this study is assumed to be 40 % of prior parameter range; when σ_{prior} is assumed to be 20 % of the prior parameter range, the average parameter un-

certainty reduction was roughly 60 %). Using $\sigma_{prior} = 40\,\%$, all parameter uncertainties were improved by at least 80 %. 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 1000 posterior samples were not widely spread across the potential parameter space (Fig. 2). There were two nitrification parameters that were not as well constrained as the others: (1) maximum nitrification rate ($VMAX_{NH_4}^{nit}$) and (2) half-saturation constant for nitrifiers ($KM_{NH_4}^{nit}$). The wide posterior distribution for these two parameters probably occurred because of a lack of N_2O efflux data from the observations used to constrain the posterior distributions. The N-COM model produces gaseous N_2O losses from both nitrification and denitrification, so assimilating datasets into N-COM that differentiate N_2O emissions between nitrification and denitrification processes (e.g., using isotope labels: Bateman and Baggs, 2005; Riley and Matson, 2000) would improve these two nitrification-associated parameters). However, these types of dataset were not available for the site observations we applied in this study.

Using the posterior model, and under a nutrient abundant situation, the relative competitiveness of each consumer (ECA terms defined by Eqs. 13–21) is dominated by the concentration of nutrients: $[NH_4^+]$, $[NO_3^-]$, or $[PO_x]$. Therefore, the relative competitiveness is close to 1 : 1, implying that different competitors are evenly competitive. However, under nutrient limited conditions, the ECA terms are controlled by the inverse of consumer-substrate affinity (KM^{-1}). For instance, our posterior model implied that the relative competitiveness of plants and decomposing microbes in acquiring (1) NH_4^+ was about 2.5 : 10 ($\frac{1/KM_{NH_4}^{plant}}{1/KM_{NH_4}^{mic}}$), (2) NO_3^- was around 3 : 10 ($\frac{1/KM_{NO_3}^{plant}}{1/KM_{NO_3}^{mic}}$); and (3) PO_x was 1 : 1 ($\frac{1/KM_P^{plant}}{1/KM_P^{mic}}$). These results showed that the competitiveness of plants was smaller but of the same order of magnitude as decomposing microbes. We therefore conclude that it is inappropriate to assume that microbes completely win the initial nutrient competition (as assumed by many ecosystem biogeochemistry models). Although consumers

tend to be evenly competitive under nutrient abundant conditions, such conditions are unlikely to be representative of natural ecosystems, since they are often limited by nitrogen or phosphorus or both (Elser et al., 2007; Vitousek and Farrington, 1997; Vitousek et al., 2010). Therefore, we conclude that it is also problematic to impose an "even competitiveness assumption" for all soil nutrients in the ecosystem biogeochemistry models. Our model offers an approach to realistically simulate the relative competitiveness of different consumers for different soil nutrients.

In addition, our posterior model affinity parameters (KM) indicated that tropical ecosystem plant had relatively higher phosphorus competitiveness (similar to decomposing microbes) than nitrogen competitiveness (smaller than decomposing microbes). In tropical ecosystems, plants are thought to be strongly phosphorus-limited (Alvarez-Clare et al., 2014; Vitousek et al., 2010). They attempt to reduce this limitation by establishing Arbuscular Mycorrhizal Fungi associations, which are effective in competing for free phosphorus against soil microbes (Hodge et al., 2000a). Therefore, it is reasonable to find that tropical ecosystem plants have high phosphorus competitiveness.

3.2 Model sensitivity analysis

Through sensitivity analysis, we separately investigated the factors controlling NH_4^+, NO_3^-, and PO_x competition, (Fig. 3). Each sensitivity analysis consisted of three scenarios: (1) normal conditions (control), (2) elevated soil T ($+T_s$); and (3) elevated soil moisture ($+\theta$). We found that the plant NH_4^+ half-saturation parameter ($KM_{NH_4}^{plant}$) and maximum NH_4^+ uptake rate ($VMAX_{NH_4}^{plant}$) were the most sensitive factors. Together, they explained more than 50 % of the variance of plant NH_4^+ uptake. Plant NO_3^- uptake and plant PO_x uptake were also mostly regulated by their ECA half-saturation parameters $KM_{NO_3}^{plant}$ and KM_P^{plant}; the first order sensitivity values (S_i) for half-saturation coefficients were relatively consistent and large across the sensitivity scenarios. For example, sen-

sitivity of plant PO_x uptake with respect to KM_P^{plant} was 0.39 (control), 0.38 ($+T_s$), and 0.38 ($+\theta$). Enhanced soil temperature and soil moisture accelerated soil organic carbon turnover, thereby releasing more free phosphorus into the soil. Under relatively fertile conditions, plant P uptake would be less sensitive to its relative competitiveness with other consumers. Initial conditions of soil nutrients were also important in controlling plant nutrient competition, at least for short-term competition (one day). We found that initial conditions of nutrients were ranked as the third (for Nitrogen uptake) and fourth (for Phosphorus uptake) most sensitive parameters. Our sensitivity indicates that the nutrient competition is mostly regulated by the internal consumer-substrate affinity (KM) rather than external environmental conditions (e.g., T_s, θ). The environment affects the nutrient competition primarily through altering the nutrient abundance.

3.3 Posterior model performance

The prior and posterior models were compared against observational datasets of soil free phosphate, sorbed phosphate, soil free NH_4^+, CO_2 efflux, and N_2O efflux (Fig. 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. Both prior and posterior models captured the seasonal dynamics of soil free PO_x reasonably well: relatively high in the dry season (lasting from August to November), and low in the wet season. However, both models underestimated the magnitude of free phosphate during the wet season and overestimated it during the dry season. The posterior model did not substantially improve PO_x predictions, probably because the available data were too scarce (only three data points). A similar problem occurred for sorbed phosphate and soil free NH_4^+. We had only four and five data points for sorbed P and free NH_4^+, respectively; further, one of the observed sorbed P ($3.7\,g\,P\,m^{-2}$) values was likely an outlier. The CO_2 and N_2O effluxes were more frequently observed at Tapajos National Forest during 1999 to 2001. Most of the measurements were collected during the wet season. Therefore the mod-

eled CO_2 and N_2O emissions were largely improved by assimilating these datasets. For example, in June 2000 the observed N_2O emission ($\sim 0.005\,\mathrm{g\,N\,m^{-2}\,day^{-1}}$) was more than twice the prior model simulated N_2O emission ($\sim 0.002\,\mathrm{g\,N\,m^{-2}\,day^{-1}}$). The posterior model was able to capture the magnitude of peak emissions during the wet
5 season as well as the seasonal variation between wet and dry seasons.

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
10 to acquire more datasets that had the full suite of measurements required. Datasets of soil nutrient pool sizes and CO_2 and N_2O effluxes with high 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
15 experiments (24 or 48 h simulations) by manually imposing an input flux into nutri-ent 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 manip-ulations.

In the P addition experiments across the Hawaiian chronosequence, the partitioning
20 of phosphate between microbes and mineral surfaces was well represented by the N-COM model in the intermediate (20 Ky) and old (4.1 My) sites (Fig. 5b and c), with no significant differences between model predictions and observations. In the youngest Hawaiian site (300 y; Fig. 5a), the relative partitioning was correctly simulated, but the predicted PO_4^{3-} magnitudes were lower than observations. Our simulations indi-
25 cated 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 pos-sible 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 Microbial-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 (Fig. 5d). However, the model underestimated nitrifier NH_4^+ uptake. NO_3^- competition in this site was also relatively accurately predicted (Fig. 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 means, 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/P ratio also limited microbial 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 P fertilization. From observations, the 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.

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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, 1999), and atmospheric composition (e.g., CO_2 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 CO_2 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 NH_4^+ 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 com-

petition. Some other large-scale terrestrial biogeochemistry models (e.g., CLM4CN, ecosys), 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 and the relative demands. As a result, plant
5 and soil microbes are assumed equally competitive for nutrients.

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
10 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
15 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,
20 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; Bouskill et al., 2012; Lambers et al., 2009; Maggi et al., 2008; Maggi and Riley, 2009; Moorhead and Sinsabaugh, 2006; Reynolds and Pacala, 1993)
25 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). Our sensitivity analysis confirmed that the consumer-substrate affinity

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was an important factor regulating relatively short-term competitive interactions (Fig. 3). 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. Our model simulation at Luquillo tropical forest site in Puerto Rico confirmed that plant nitrogen (NH_4^+ and NO_3^-) competiveness is of the same order of magnitude (although lower) as microbe competiveness (Fig. 5d and e).

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 model CLM. We described the multiple-consumer and multiple-nutrient competition network with the Equilibrium Chemistry Approximation (ECA) (Tang and Riley, 2013) considering two inhibitive effects: (1) multiple substrates (e.g., NH_4^+ and NO_3^-) sharing one consumer inhibits the effective binding between any specific substrate and the consumer and (2) multiple consumers (e.g., plants, decomposing microbes, nitrifers) sharing one substrate (e.g., NH_4^+) 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 model parameters were well constrained compared with their prior distributions (Table 4). The posterior parameter uncertainties were greatly reduced (on average by 94 %, assuming a prior parameter uncertainty of 40 %). The posterior model compared to multiple categories of observational data was substantially improved over the prior model (Fig. 4). The seasonal dynamics of soil carbon, nitrogen, and phosphorus were

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moderately well captured. However, our results would likely be more robust if more temporally resolved observations of carbon, nitrogen, and phosphorous were available in the individual consumer pools.

To test the resulting model using the posterior 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 NH_4^+ uptake by nitrifiers, probably due to the loosely constrained nitrification parameters that were the result of data paucity during calibration at the Brazil site (Table 4). Datasets of soil nutrient pool sizes and CO_2 and N_2O effluxes with high frequency sampling would significantly benefit the model uncertainty reduction.

To date, many terrestrial ecosystem biogeochemistry models assume microbes out-compete plants and immobilize nutrients first (Wang et al., 2007; Zaehle and Friend, 2010; Zhu and Zhuang, 2013), although CLM currently assumes constant and equal 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 out-competing 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 (microbes always win or at least equally competitive to plants). We showed that (in Sect. 3.1) the "evenly competitiveness assumption" is only valid when soil nutrients are relatively abundant and that under nutrient limited conditions the relative competitiveness is comparable with soil decomposing microbes. As a result, traditional models might underestimate or overestimate the availability of plant accessible soil nutrients, misleading the estimates of plants gross primary production.

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This study is a crucial 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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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

Table 2. Model initialization and baseline parameter values.

Variables	Definition	Unit	Value	Reference
States				
C	Soil organic C	$\mathrm{g\,C\,m^{-2}}$	(0, 0, 0, 0, 20, 300, 13500)	Parton et al. (1988)
N	Soil organic N	$\mathrm{g\,N\,m^{-2}}$	(0, 0, 0, 0, 1.53, 18.75, 1708.86)	Parton et al. (1988)
P	Soil organic P	$\mathrm{g\,P\,m^{-2}}$	(0, 0, 0, 0, 0.18, 0.94, 118.42)	Parton et al. (1988)
$[\mathrm{NH_4^+}]$	Soil $\mathrm{NH_4^+}$	$\mathrm{g\,N\,m^{-2}}$	1.2	Hedin et al. (2003)
$[\mathrm{NO_3^-}]$	Soil $\mathrm{NO_3^-}$	$\mathrm{g\,N\,m^{-2}}$	1.2	Hedin et al. (2003)
$(\mathrm{PO_x})$	Soil $\mathrm{PO_4^{3-}}$, $\mathrm{HPO_4^{2-}}$, $\mathrm{H_2PO_4^-}$	$\mathrm{g\,P\,m^{-2}}$	0.64	McGroddy et al. (2008)
$\mathrm{P_S}$	Loosely sorb P	$\mathrm{g\,P\,m^{-2}}$	4.81	McGroddy et al. (2008)
$\mathrm{P_O}$	Occluded P	$\mathrm{g\,P\,m^{-2}}$	5.46	McGroddy et al. (2008)
$\mathrm{P_P}$	Parent material P	$\mathrm{g\,P\,m^{-2}}$	0.84	Yang et al. (2014a)
Parameters				
C associated				
g_i	Percentage of carbon remains in the soil after decomposition of ith 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 ith pool and enter into jth 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, 0.995, 0.005; 0, 0, 0, 0, 0.93, 0, 0.07; 0, 0, 0, 1, 0, 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)
$\mathrm{TURN_{SOM}}$	Soil organic matter turnover (CWD, metabolic lit, cellulose lit, lignin lit, fast SOM, slow SOM, passive SOM)	year	(4.1, 0.066, 0.25, 0.25, 0.17, 5, 270)	Koven et al. (2013)
N associated				
$\mathrm{VMAX_{NH_4}^{plant}}$	Maximum rate of plant $\mathrm{NH_4^+}$ uptake	$\mathrm{g\,m^{-2}\,day^{-1}}$	5.43	Jackson et al. (1997), Kuzyakov and Xu (2013)
$\mathrm{KM_{NH_4}^{plant}}$	Half-saturation constant for plant $\mathrm{NH_4^+}$ uptake	$\mathrm{g\,m^{-2}}$	0.09	Kuzyakov and Xu (2013)
$\mathrm{VMAX_{NH_4}^{mic}}$	Maximum rate of decomposing microbe $\mathrm{NH_4^+}$ uptake	$\mathrm{g\,m^{-2}\,day^{-1}}$	5.32	Kuzyakov and Xu (2013)
$\mathrm{KM_{NH_4}^{mic}}$	Half-saturation constant for decomposing microbe $\mathrm{NH_4^+}$ immobilization	$\mathrm{g\,m^{-2}}$	0.02	Kuzyakov and Xu (2013)
$\mathrm{VMAX_{NH_4}^{nit}}$	Maximum nitrification rate	$\mathrm{day^{-1}}$	10 %	Parton et al. (2001)
$\mathrm{KM_{NH_4}^{nit}}$	Half-saturation constant for nitrifier $\mathrm{NH_4^+}$ consumption	$\mathrm{g\,m^{-2}}$	0.076	Drtil et al. (1993)
$f^{\mathrm{N_2O}}$	Fraction of nitrification flux lost as $\mathrm{N_2O}$	–	6×10^{-4}	Li et al. (2000)

Table 2. Continued.

Variables	Definition	Unit	Value	Reference
$VMAX_{NO_3}^{plant}$	Maximum rate of plant NO_3^- uptake	$g\,m^{-2}\,day^{-1}$	0.91	Jackson et al. (1997), Kuzyakov and Xu (2013)
$KM_{NO_3}^{plant}$	Half-saturation constant for plant NO_3^- uptake	$g\,m^{-2}$	0.07	Kuzyakov and Xu (2013)
$VMAX_{NO_3}^{mic}$	Maximum rate of decomposing microbe NO_3^- uptake	$g\,m^{-2}\,day^{-1}$	4.32	Kuzyakov and Xu (2013)
$KM_{NO_3}^{mic}$	Half-saturation constant for decomposing microbe NO_3^- immobilization	$g\,m^{-2}$	0.04	Kuzyakov and Xu (2013)
$KMAX_{NO_3}^{den}$	Half-saturation constant for denitrifier NO_3^- consumption	$g\,m^{-2}$	0.011	Murray et al. (1989)
P associated				
$k_{weather}$	Parent material P weathering rate	$g\,P\,m^{-2}\,year^{-1}$	0.004	Wang et al. (2010)
k_{occl}	P occlude rate	$month^{-1}$	1.0×10^{-6}	Yang et al. (2014b)
$VMAX_P^{plant}$	Maximum rate of plant PO_x uptake	$g\,m^{-2}\,day^{-1}$	0.24	Cogliatti and Clarkson (1983)
KM_P^{plant}	Half-saturation constant for plant PO_x uptake	$g\,m^{-2}$	0.067	Cogliatti and Clarkson (1983)
$VMAX_P^{mic}$	Maximum rate of decomposing microbe PO_x uptake	$g\,m^{-2}\,day^{-1}$	2.1	Chen (1974)
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	$g\,m^{-2}$	0.21	Özacar (2003)
KM_P^{surf}	Half-saturation constant for mineral surface PO_x adsorption	$g\,m^{-2}$	0.00155	Özacar (2003)

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Table 3. Observational datasets used for calibration.

Processes	Datasets		Location	References
C associated	Soil CO_2 efflux		Tapajos National Forest, Para, Brazil	Silver et al. (2012)
N associated	Soil free 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)

Table 4. Model parameters calibrated, prior values, posterior means and variance, and uncertainty reduction from assimilating the observational datasets.

Parameters	Definition	Unit	Prior	Posterior	Uncertainty Reduction
$TURN_{SOM}$	Soil organic matter turn over (CWD, metabolic lit, cellulose lit, lignin lit, fast SOM, slow SOM)	year	(4.1, 0.066, 0.25, 0.25, 0.17, 5)	(6.3 ± 0.5, 0.072 ± 0.006, 0.21 ± 0.015, 0.15 ± 0.027, 0.24 ± 0.022, 3.7 ± 0.24)	(94 %, 95 %, 97 %, 94 %, 93 %, 97 %)
$KM_{NH_4}^{plant}$	Half-saturation constant for plant NH_4^+ uptake	$g\,m^{-2}$	0.09	0.12 ± 0.009	94 %
$KM_{NH_4}^{mic}$	Half-saturation constant for decomposing microbe NH_4^+ immobilization	$g\,m^{-2}$	0.02	0.029 ± 0.0023	94 %
$KM_{NH_4}^{nit}$	Half-saturation constant for nitrifier NH_4^+ consumption	$g\,m^{-2}$	0.076	0.031 ± 0.019	86 %
$KM_{NO_3}^{plant}$	Half-saturation constant for plant NO_3^- uptake	$g\,m^{-2}$	0.07	0.076 ± 0.0036	97 %
$KM_{NO_3}^{mic}$	Half-saturation constant for decomposing microbe NO_3^- immobilization	$g\,m^{-2}$	0.04	0.023 ± 0.0037	95 %
$KM_{NO_3}^{den}$	Half-saturation constant for denitrifier NO_3^- consumption	$g\,m^{-2}$	0.011	0.015 ± 0.0020	90 %
KM_P^{plant}	Half-saturation constant for plant PO_x uptake	$g\,m^{-2}$	0.067	0.025 ± 0.012	90 %
KM_P^{mic}	Half-saturation constant for decomposing microbe PO_x immobilization	$g\,m^{-2}$	0.02	0.027 ± 0.0024	94 %
KM_P^{surf}	Half-saturation constant for mineral surface PO_x adsorption	$g\,m^{-2}$	0.00155	0.0013 ± 0.00007	98 %
$VMAX_{NH_4}^{plant}$	Maximum rate of plant NH_4^+ uptake	$g\,m^{-2}\,day^{-1}$	5.43	6.51 ± 0.35	97 %
$VMAX_{NH_4}^{mic}$	Maximum rate of decomposing microbe NH_4^+ uptake	$g\,m^{-2}\,day^{-1}$	5.32	8.55 ± 0.78	92 %
$VMAX_{NH_4}^{nit}$	Maximum nitrification rate	day^{-1}	0.1	0. 17 ± 0.033	83 %
$VMAX_{NO_3}^{plant}$	Maximum rate of plant NO_3^- uptake	$g\,m^{-2}\,day^{-1}$	0.91	0.58 ± 0.073	96 %
$VMAX_{NO_3}^{mic}$	Maximum rate of decomposing microbe NO_3^- uptake	$g\,m^{-2}\,day^{-1}$	4.32	6.21 ± 0.78	91 %
$VMAX_P^{plant}$	Maximum rate of plant PO_x uptake	$g\,m^{-2}\,day^{-1}$	0.24	0.33 ± 0.046	90 %
$VMAX_P^{mic}$	Maximum rate of decomposing microbe PO_x uptake	$g\,m^{-2}\,day^{-1}$	2.1	1.8 ± 0.11	98 %
$VMAX_P^{surf}$	Maximum mineral surface PO_x adsorption	$g\,m^{-2}$	0.21	0.24 ± 0.017	96 %

Table 5. Short-term (24 or 48 h) 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	$10\,\mu g\,g^{-1}$	i. Mineral surface	ii. Decomposing microbe		48	Olander and Vitousek (2005)
NH_4^+ fertilization	$4.6\,\mu g\,g^{-1}$	i. Plant	ii. Decomposing microbe	iii. Nitrifier	24	Templer et al. (2008)
NO_3^- fertilization	$0.92\,\mu g\,g^{-1}$	i. Plant	ii. Decomposing microbe		24	Templer et al. (2008)

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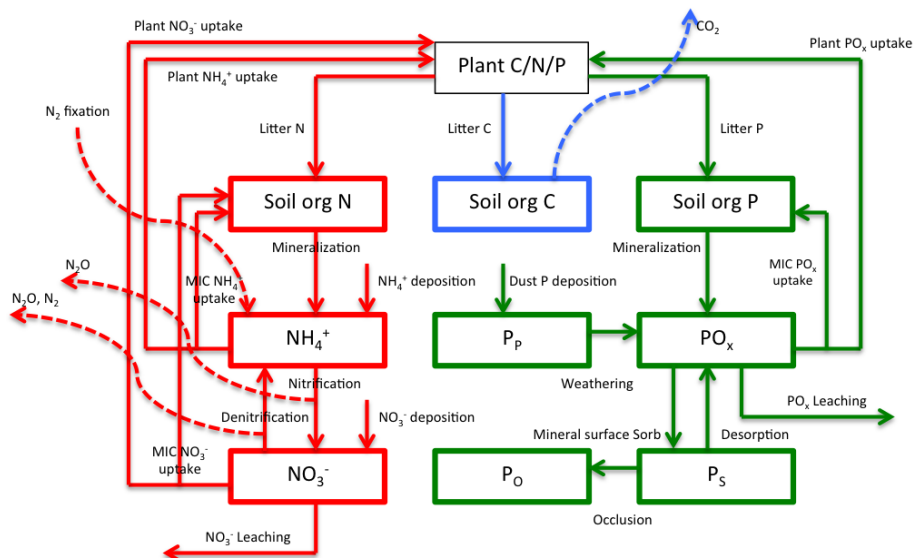
Figure 1. Model structure. Boxes represent pools, solid arrows represent aqueous fluxes, and dashed arrows represent gaseous pathways out or into the system. Three essential chemical elements (Carbon (C), Nitrogen (N) and Phosphorus (P)) are simulated in N-COM (blue, red, and green represent C, N, and P pools and processes, respectively).
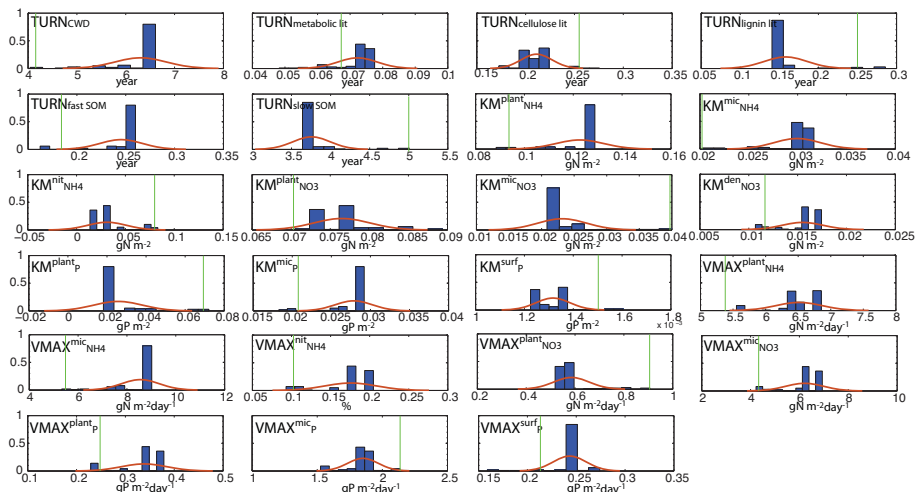
Figure 2. Probability density of posterior model parameters. Only a few parameters roughly follow a Gaussian distribution, while the probability distributions of others are highly irregular. However, to compare the posterior parameters with our prior knowledge, we fit all of the twenty-three parameters to Gaussian distribution (red lines). The green lines indicate prior parameters' value.
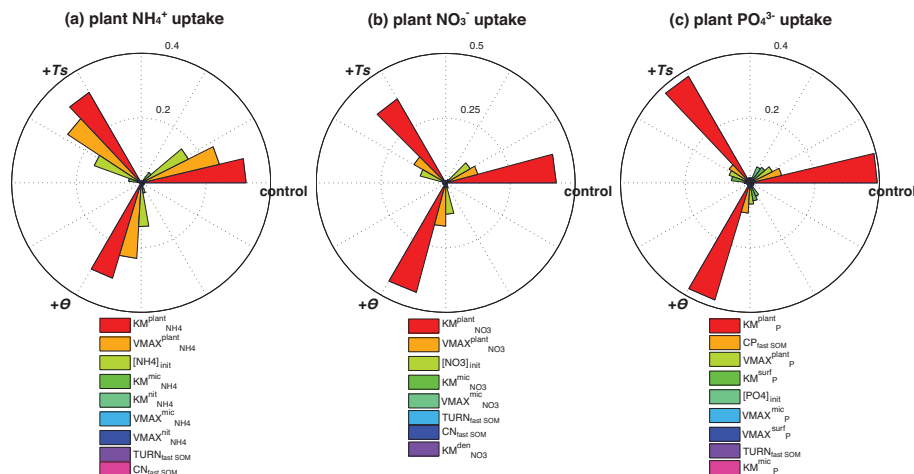
Figure 3. Model sensitivity analysis with SOBOL sampling. For each metric, three scenarios are shown: baseline (Control), elevated soil temperature by 5 °C ($+T_s$), and elevated soil moisture by 50 % ($+\theta$), respectively. The length of bar (plot in polar coordinate) is the sensitivity (unitless) of model output with respect to model input variables. Our results showed that the plant nutrient uptake was mostly regulated by internal consumer-substrate affinity (KM) rather than the external environmental conditions (e.g., T_s, θ).
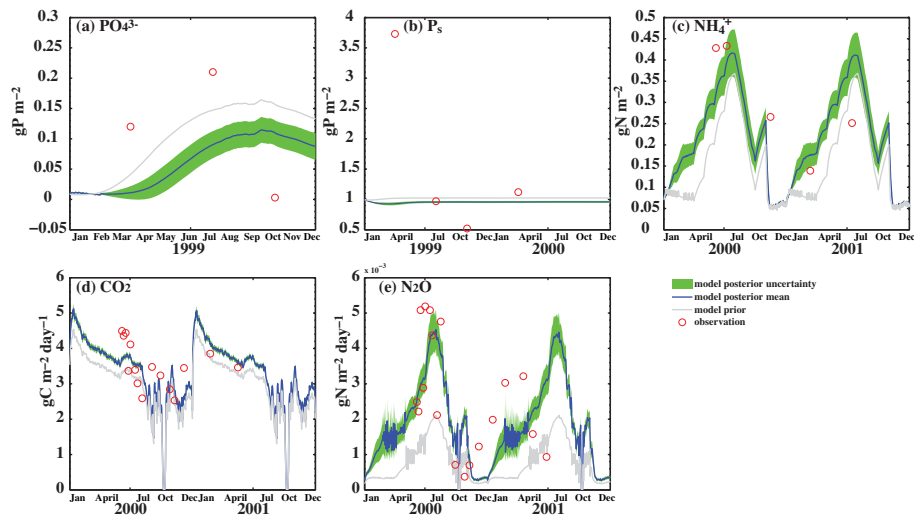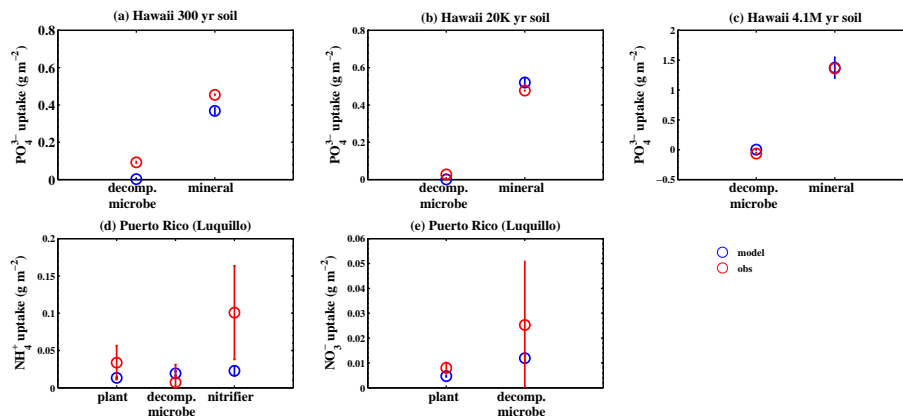
Figure 4. Model performance at Tapajos National Forest, Para, Brazil. Overall, the posterior model (blue line) improved predictions over the prior model (grey line) when compared to observations. Green areas indicate the posterior model uncertainties.

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 did not include the plants in the perturbation study.