Neglecting Plant-microbe Symbioses Leads to Underestimation of Modeled Climate Impacts

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Abstract

The extent to which terrestrial ecosystems slow climate change by sequestering carbon hinges in part on nutrient limitation. We used a coupled carbon–climate model that accounts for the carbon cost to plants of supporting nitrogen-acquiring microbial symbionts to explore how nitrogen limitation affects global climate. To do this, we first calculated the reduction in net primary production due to the C cost of N acquisition. We then used a climate model to estimate the impacts of the resulting increase in atmospheric CO_2 on temperature and precipitation regimes. The carbon costs of supporting symbiotic nitrogen uptake reduced net primary production by 8.1 Pg C yr^{-1}, with the largest absolute effects occurring at low-latitudes and the largest relative changes occurring at high-latitudes. Globally, our model predicted relatively small changes in climate due to the C cost of N acquisition with temperature increasing by 0.1°C and precipitation decreasing by 6mm yr^{-1}. However, there were strong regional impacts with the largest impact occurring in high-latitude ecosystems, where such costs were estimated to increase temperature by 1.0 °C and precipitation by 9 mm yr^{-1}; as such, our results suggest that carbon expenditures to support nitrogen-acquiring microbial symbionts have critical consequences for Earth's climate, and that carbon–climate models that omit these processes will over-predict the land carbon sink and under-predict climate change.

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1. Introduction

The magnitude of carbon (C) uptake by the terrestrial biosphere strongly depends on the availability of nutrients to support net primary production (NPP) (Zaehle *et al.* 2015; Wieder *et al.* 2015; Wang *et al.* 2015). Most soil nutrients exist in unavailable forms and consequently plants must expend a portion of their assimilated C on nutrient acquisition (Johnson, 2010; Mohan *et al*. 2014). Many plants allocate up to 20% of their C to support symbiotic mycorrhizal fungi, which can be responsible for almost half of plant nitrogen (N) uptake in ecosystems (Hobbie, 2006; Högberg & Högberg, 2002; Parniske, 2008) or to support symbiotic N-fixing bacteria (Shi *et al*. 2016). Given the magnitude of these C expenditures, Earth System Models (ESMs) that do not account for the costs of supporting symbiotic microbes may overestimate NPP and the ability of terrestrial ecosystems to slow climate change.

Nearly all land plants have evolved symbiotic strategies for coping with nutrient limitation. Plant associations with mycorrhizal fungi such as arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM), or with N-fixers, are critical for the uptake of soil nutrients and as such, impact C and nutrient cycling (Phillips *et al*. 2013; Wurzburger *et al*. 2017). Recent data syntheses have shown that ECM and AM ecosystems have divergent C-nutrient economies that respond differently to elevated CO_2 and N deposition (Canham & Murphy, 2017; Terrer *et al*. 2016; Terrer *et al*. 2017). Despite this, the C cost for nutrient acquisition remains largely absent in most C–climate models which assume that plants do not expend C to take up N and that NPP is only downregulated if there is not enough N to support biomass synthesis. As such, there have been few first order estimates of the extent to which variable plant investment in strategies that facilitate N uptake can impact rates of climate change. Shi *et al*. (2016) showed that dynamically predicting and accounting for the C cost of N acquisition reduced global NPP by 13%, and thus, models that assume N uptake requires no C expenditures potentially underestimate the rate of atmospheric CO_2 rise. These results not only underscore the importance of including the C cost of symbiotic microbes in ESMs but also highlight the critical role that plant-microbe interactions play in mediating rates of climate change.

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Global C-climate models represent the scientific community's integrated hypotheses on how climate responds to anthropogenic forcing. In addition to forecasting climate, ESMs can be used to perform "experiments" at spatial and temporal scales that are logistically unfeasible to identify important feedbacks and processes in the Earth's climate system (Fisher *et al*. 2014). Accordingly, our objective was to explore the potential feedbacks between the C cost of supporting symbiotic N acquisition and climate by performing model experiments with and without these costs in an C-climate model. To streamline the complexity of the Earth-scale computations, we imposed a simplification of the ocean and ice components in the Community Atmosphere Model (CAM) along with symbiotic processes included in the Community Land Model (CLM) which predicts coupled C and N dynamics. We are focusing on the dynamic processes between the land and atmosphere, and this C-climate model assessment represents the first effort to determine the sensitivity of the Earth's climate system to plant-microbe symbiotic interactions.

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2. Material and Methods

2.1 Models

We used the Fixation and Uptake of Nitrogen (FUN) sub-model to dynamically compute the C cost and N benefit of AM fungi, ECM fungi, and N-fixers. FUN optimally allocates the C gained from NPP to N acquisition through the following pathways: uptake from soil (via AM or ECM roots, or non-mycorrhizal roots), retranslocation from senescing leaves, and symbiotic biological N fixation (Brzostek *et al*. 2014; Fisher *et al*. 2010). FUN then down-regulates NPP based upon the integrated C cost across each pathway and how much N was acquired to fix C into biomass. The C cost of each pathway is calculated using functions that relate costs to drivers with soil uptake a function of soil N concentration and root biomass, retranslocation a function of leaf N, and fixation a function of temperature (Brzostek *et al*. 2014; Shi *et al*. 2016). In FUN, AM plants benefit when N is relatively abundant, ECM plants benefit when N is strongly limiting, and N-fixers thrive in high energy environments with high N demand (Brzostek *et al*. 2014).

We used the Community Land Model version 4 (CLM) (Lawrence *et al*. 2011; Oleson *et al*. 2010). CLM is a terrestrial biosphere model that predicts the impacts of greenhouse gases and meterological conditions on the land surface's energy, carbon, and water budgets. Importantly, CLM includes coupled C and N cycles whereby the internal recycling, loss, and inputs of N in the soil pool are dynamically modeled to predict the avaialbility of N to support plant biomass synthesis (Lawrence *et al*. 2011; Oleson *et al*. 2010).

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FUN was recently coupled into CLM (CLM-FUN) with model simulations showing that the C cost of N acquisition reduces the C sink strength of the terrestrial biosphere (Shi *et al*. 2016). CLM-FUN predicts the C cost of N acquisition from the soil by ectomycorrhizal, arbuscular mycorrhizal, and nonmycorrhizal roots based upon root biomass (a proxy for access) and soil nitrogen concentrations (a measure of availability of N for plants to take up). Previously, the parameter controlling the sensitivity of the C cost of N acquisition to root biomass was low. As such the C cost of N acquisition showed little to no sensitivity to variability in root biomass across grid cells and the ECM cost of N acquisition was always lower than the AM cost of N acquisition even in high N biomes. We have updated this parameter so that the updated CLM-FUN is equally sensitive to both availability and access, and can better capture latitudinal gradients in the benefit of ECM uptake or AM uptake as N becomes more limiting. This adjustment also ensures that while ECM plants invest more C belowground, they get a greater return on this investment relative to AM-associated plants when the ratio of N needed to support NPP to available soil N increases (e.g., enhanced N limitation under elevated CO_2) (Terrer *et al.* 2017). Specifically, we modified an AM-related uptake parameter and an ECM-related uptake parameter from 2.7×10^{-4} (g C m^{-2}) to 6.2 (g C m^{-2}) and from 1.6×10^{-3} (g C m^{-2}) to 34.1 (g C m^{-2}), respectively (see Table S1 for original and updated parameters). This parameter adjustment also resulted in small increase in the downregulation of NPP by FUN in CLM by 1.5 Pg C yr^{-1} or ~3% (Figure S1).

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To investigate the root symbiont associated C–climate feedback, we also used Community Atmosphere Model version 4 (CAM), an atmospheric general circulation model that includes CLM (or CLM-FUN) and a thermodynamic sea ice model (Neale *et al*. 2010). CAM dynamically predicts the impacts of external forcing factors such as anthropogenic CO2 emissions on global and regional climate (i.e., temperature and

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precipitation) by dynamically representing key atmospheric process including cloud formation, aerosol impacts, radiative processes, and mixing (Neale *et al*. 2010).

2.2 Experimental Design

In the first step of our model experiment, we leveraged the ability of FUN to downregulate NPP in order to calculate the extent to which mycorrhizal fungi impact the balance of C in the atmosphere vs. plant biomass. We estimated this by calculating the difference in NPP between CLM runs with FUN turned on or off using the same meterological forcing data (Qian *et al.* 2006). The surface condition and plant functional type (PFT) data are from the standard release of CLM4.0. The surface spin-up conditions, in which the plant and soil C pools are at a quasi-equilibrium state, are provided with CLM4.0 by the National Center for Atmospheric Research (NCAR). As such, both models started from the same baseline values. We ran both CLM and CLM-FUN at the 0.9°×1.25° and half-hourly spatio-temporal resolution for 25 years (1980–2004). The ambient CO_2 concentration was fixed to 338 ppm, the atmospheric CO_2 level in 1980. We calculated the mean annual NPP difference between CLM and CLM-FUN in 1995–2004, and the value was 8.1 Pg C yr^{-1}. This additionally respired C from CLM-FUN represents the C amount that plants expend to take up N and we assumed that the all of this C went into the atmospheric pool. We then converted this mass of extra C going into the atmosphere into concentration units by dividing our mass (8.1Pg C) by the mass of C in 1ppm of CO_2 (2.135 Pg C). As such, we assume that integrating the C costs for N acquisition leads to an additional 8.1 Pg C $yr^{-1}$of C released to the atmosphere at a 3.8 ppm of CO_2 annual rate.

Second, we ran two simulations of the land–atmosphere model, CAM4.0-CLM 4.0: (1) A control simulation without mycorrhizal impacts on atmospheric CO_2 or surface energy budgets (herein CAM), and (2) a simulation that included mycorrhizal impacts on atmospheric CO_2 as well as surface energy budgets (herein CAM-FUN). Due to the complexity and computational cost of running the fully coupled C-climate model, it was necessary to prescribe the increase in CO_2 concentrations in CAM-FUN at a 3.8ppm increase per year to reflect the transfer of C from NPP to the atmosphere. The CAM runs did have dynamic representations of how the C cost of N acquisition impacted leaf area index (LAI), evapotranspiration (ET), and resulting energy budgets. We acknowledge that this assumption simplifies many of the interactions between the land, atmosphere and ocean C pools. However, given that our objective was to provide a first approximation of how the C cost of N acquisition could impact climate, the prescribed CO_2 increase provides a balance between meeting that objective and minimizing computational costs. We used the specified modern climatological sea surface temperatures and sea ice distributions and ran the models at the 0.9°×1.25° and half-hourly spatio-temporal resolution for 25 years. In CAM, the ambient CO_2 concentration was 338 ppm. For all other model inputs, we used the default input files that are automatically loaded during each model run, such that both CAM and CAM-FUN start off with the same initial conditions. In CAM-FUN, we assumed that atmospheric CO_2 started increasing from 338 ppm at the 3.8 ppm of CO_2 annual rate, and all the respired CO_2 is mixed into the atmosphere homogenously. We also analyzed the CAM-based results in the last 10 simulation years. We evaluated the climate impacts resulting from including the mycorrhizal dynamics into CAM by calculating the surface air temperature and precipitation differences between CAM and CAM-FUN in different regions.

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In this study, we also estimated the radiative forcing variations causing the climate impacts. We did this in order to identify which factor, ET vs. LAI vs. enhanced atmospheric CO_2, led to our observed shifts in climate. It also allowed us to identify if three different forcing factors had a cooling or warming effect on the climate. We use the reflected solar radiation difference between CAM and CAM-FUN to estimate the radiative forcing variations from surface albedo change due to shifts in LAI. The evapotranspiration (ET) difference between these two model runs was used to estimate the radiative forcing from ET variation. The radiative forcing from CO_2 increase was calculated with an empirical equation as (Myhre *et al*. 1998).

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$$\Delta F = \alpha \ln\left(\frac{C}{C_0}\right) \qquad (1)$$

where α is estimated as 5.35 (W m^{-2}), *C* is CO_2 in parts per million by volume, and C_0 is the reference concentration, which is 338 ppm, the atmospheric CO_2 level in 1980.

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3. Results

Compared to the CAM runs where N was obtained at no cost, when we included the C cost of symbiont-mediated N acquisition (i.e., CAM-FUN), C uptake by the terrestrial biosphere was more strongly constrained by N availability. Consequently, N limitation reduced global NPP by 2.4 g C m^{-2} yr^{-1}, leading to alterations in atmospheric CO_2, global leaf area index (LAI; Figures 1a and 1b), and surface energy budgets (Figure 2). Globally, NPP and LAI were affected similarly, with the strongest relative effects occurring at the poles and the strongest absolute effects occurring near the equator. In high-latitude ecosystems, LAI was reduced by 34% (a decrease of 0.05 m^{2} m^{-2}) while NPP was reduced by 42% (a decrease of 12 g C m^{-2} yr^{-1}). In mid-latitude temperate ecosystems, LAI was reduced by 17% (a decrease of 0.16 m^{2} m^{-2}) while NPP was reduced by 33% (a decrease of 30 g C m^{-2} yr^{-1}). Tropical low latitude ecosystems had the largest absolute reductions in LAI (0.24 m^{2} m^{-2}; 10% decrease) and NPP (53 g C m^{-2} yr^{-1}; 22% decrease). Compared to NPP and LAI, ET had a more heterogeneous spatial pattern with a global mean ET reduction 7.3 mm yr^{-1}, which represents a ~3% decrease across high, mid, and low latitude ecosystems (Figure 1c). While we present differences between model runs in LAI, ET and NPP in Figure 1, global maps of the absolute values are presented in Figures S2 & S3.

Elevated CO_2 due to the reduction in NPP was the strongest driver of climate shifts. The global NPP reduction (8.1 Pg C yr^{-1}) from the land model simulations resulted in an increase in atmospheric CO_2 concentrations of 3.8 ppm yr^{-1}, and ~95 ppm over a 25-year simulation. Accounting for the C cost of N acquisition in CAM's representation of N limitation led to a net warming effect of 1.11 W m^{-2} (Figure 2). By contrast, there was an opposing effect of differences in LAI due to modifications of ET and surface albedo of the vegetated land surface, leading to an overall net cooling effect of -0.52 W m^{-2} (Figure 2). The reduction in ET led to a cooling effect because it resulted in less water vapor in the atmosphere which is a potent greenhouse gas. Integrated globally, these two opposing effects led to a net warming effect of 0.59 W m^{-2}(Figure 2), which resulted in a net increase in surface air temperature by 0.1 °C and a net decrease in precipitation by 6 mm yr^{-1}, globally.

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While the averaged global impact of the C cost of microbial symbionts on climate was minor (i.e., 0.1 °C surface air temperature increase and 6 mm yr^{-1} precipitation decrease), there were strong regional impacts in key biomes, particularly in forested regions with

ECM fungi (Figure 3). Moreover, the regional shifts in temperature were stronger those of precipitation with shifts in precipitation being much more variable and patchier than those of temperature (Figure 3). Given difficulties in predicting regional precipitation as well as the high variability in our estimates, we present the data but acknowledge that these regional estimates are uncertain. The ECM-dominated boreal forest of Russia became warmer (increases in surface air temperature by 1.0 °C) and wetter (increases in precipitation by 9 mm yr^{-1}). Temperate forest ecosystems, which include plants that possess all three nutrient acquisition strategies, were also impacted. The eastern part of North America, Europe, and China had surface air temperature increases of 0.5 °C, and precipitation shifted by 11, -37, and 2 mm yr^{-1} in these three regions, respectively. Tropical forests, which are dominated by AM fungi, were impacted less with temperature; Amazon and Congo basin both had temperature increase by ~0.3 °C. However, precipitation changes in tropical forests varied, with the Amazon and Congo basin drying by 4 mm yr^{-1} and 49 mm yr^{-1}, respectively.

4. Discussion and Conclusions

Here, we demonstrate that integrating the C cost of N acquisition into the formulation of N limitation in CAM reduced global NPP, LAI, and ET, with the greatest percentage decreases in high-latitude ecosystems (Figure 1). These reductions led to substantial impacts on climate, particularly in high-latitude ecosystems where temperature increased by 1°C and precipitation increased by 9 mm yr^{-1} in 10 years (Figure 3). It is important to note, that the regional impacts of the C cost of N acquisition on temperature were much stronger than those on precipitation. These results suggest that by reducing C stored in woody biomass (Figure not shown), the C transferred to symbionts leads to more atmospheric CO_2 that would otherwise be locked up in vegetation (Figure 2). This reduction in terrestrial productivity (Figure 1a) and decrease of terrestrial C sink in CAM-FUN appears to alter the partitioning of energy fluxes at the land surface into sensible heat flux as well, which accelerates land-surface warming and intensified regional land–atmosphere feedback (Jung *et al*. 2010). Collectively, these results suggest that the C cost of symbiont-mediated N acquisition are an important component of the Earth's climate system that has the potential to alter future climate trajectories.

The C expended by plants to support symbiont-mediated N uptake reduced the amount of C available to support leaf growth and thus, reduced LAI. This global reduction in LAI (Figure 1b) indirectly influenced climate through energy balance (i.e., albedo and ET) feedbacks (Buermann *et al*. 2001). It has been suggested that changes in the atmospheric heating pattern in the tropics as a result of the variations in latent heat flux may modify the Hadley circulation, which then can change the generation of waves along the polar front (Chase *et al*. 1996). As such, tropical LAI shifts (Figure 1b) can potentially affect mid- and high-latitude climates and nearby ocean conditions through atmospheric teleconnections (Feddema *et al*. 2005), a possible explanation for the greater climate alterations we observed at high-latitudes.

We found greater spatial heterogeneity in ET shifts than NPP or LAI shifts when we included the C cost of microbial symbionts in the model (Figure 1). Some of this spatial variability may reflect the high sensitivity of ET to increases in atmospheric CO_2 concentrations (Shi *et al*. 2013). Moreover, this variability likely reflects the large uncertainties and challenges associated with simulating regional scale ET in coupled climate–atmosphere models (Boé & Terray, 2008; Pan *et al.* 2015). However, on the global scale, the reduction of ET, which decreased the atmospheric concentration of water vapor, a potent greenhouse gas, led to a -5.2 W m^{-2} radiative forcing change (Figure 2). This result is consistent with the Institut Pierre Simon Laplace climate model (IPSL-CM4) (Davin *et al.* 2007), where ET was also reduced globally and had a net cooling effect on global temperatures. Nevertheless, this cooling effect was outweighed by the warming effect of increasing atmospheric CO_2 concentrations in CAM-FUN.

Our results suggest that models that do not account for plant-microbe symbiotic interactions and the C cost of N acquisition may underestimate both N limitation to NPP and rates of climate change. Nutrient limitation remains a key area of uncertainty for ESMs with the CMIP5 comparison highlighting the limited representations of N limitation as a primary reason for mismatch between the models and the observed C sink (Anav *et al.* 2013). Additionally, CAM-FUN identifies an important underestimation of nutrient limitation and climate shifts in high latitudes that has the potential to enhance other climate feedbacks. Boreal forests, which dominate high-latitude regions, are characterized by low rates of soil decomposition and low N availability (Read *et al.* 2004). This leads to CAM-FUN predicting that boreal forests expend nearly 18% of NPP to gain N through symbionts, a result that is supported by a recent empirical synthesis which found that boreal forests have a 13-fold greater C cost of soil resource acquisition than tropical forests (Gill & Finzi, 2016). However, to the extent that the greater C cost to ECM plants (relative to AM plants) provides a greater return on investment of N under elevated CO_2 (Terrer *et al.* 2017), some of the predicted warming may be attenuated over time. Nevertheless, predicted acceleration of warming in boreal forests is likely to be consequential given feedbacks between surface warming with sea ice cover loss, sea surface temperature increase, and permafrost thaw (Parmentier *et al.* 2013).

While CAM-FUN identifies an important interaction between the C cost of N limitation and climate, there still remain key uncertainties in the model on the extent to which other processes that govern the C cost of acquiring soil resources impacts C-climate feedbacks. First, not all ecosystems are predominantly N limited (Wang *et al.* 2010). Nearly 30% of terrestrial ecosystems are limited by phosphorus (P) or water (Elser *et al.*, 2007, Fisher *et al.*, 2010, Wieder *et al.*, 2015) two key limitations that are currently absent from the model that may alter the climate trajectories shown here, particularly for strongly P-limited ecosystems like tropical forests or water-limited ecosystems like Mediterranean forests. However, FUN utilizes a modular structure based on optimal allocation theory that could incorporate the C costs of P or water acquisition on NPP and hence climate. As such, the optimal allocation parameterization in FUN could be modified to include other resource costs and thus provides a framework for ESMs to assess how multiple resource limitation impacts climate.

Second, the climate impacts we identify are sensitive to factors that alter N availability. Across many ecosystems, increasing soil temperatures that enhance decomposition (Melillo *et al.* 2011) or rising rates of N deposition in developing countries (Liu *et al.* 2013) could increase N availability and lower the C cost of N acquisition. Moreover, as currently formulated, the model omits important feedbacks between C allocation to mycorrhizal symbionts and their ability to upregulate soil enzyme production, prime soil organic matter decomposition and increase N availability (Brzostek *et al.* 2015, Cheng *et al.* 2014, Finzi *et al.* 2015). A recent effort to couple FUN to a microbial soil enzyme model at the ecosystem scale has shown that the ability of ECM fungi to prime soil organic matter allowed them to mine N at the expense of soil C stocks to a greater extent under elevated CO$_2$ than AM fungi (Sulman *et al*. 2017). This result is consistent with recent meta-analyses that show that even though ECM plants invest more C belowground than AM plants, they receive a greater N return on their investment under elevated CO$_2$ (Terrer *et al*. 2017). As such, integrating C and N feedbacks between plant and symbiotic microbes at the global scale represents a critical area for future model development.

Finally, we acknowledge that the simplification of land-atmosphere interactions in our model experiment may have precluded our ability to examine fully coupled feedbacks that may have stimulated the land or ocean C sink. This simplification was needed owing to the complexity and computational resources needed to run the fully coupled model. As such, our estimates of the sensitivity of climate to the C cost of N acquisition likely represents an upper bound. This is due to two reasons. First, we assumed that all of the carbon not sequestered as NPP was released into the atmosphere as CO$_2$. In a fully coupled model, it is likely that a portion of this CO$_2$ would have been sequestered by the ocean. Second, the reduction of NPP due to the C cost of N acquisition also reduced heterotrophic respiration by 3.3 Pg C yr^{-1}. However, both empirical and modeling evidence suggests that C expended belowground to gain N leads to greater soil organic matter decomposition and respiration due to priming effects (Brzostek *et al*. 2015; Sulman *et al*. 2017). Lastly, compared to other ESMs included in the Fifth Phase of the Coupled Model Intercomparison Project (CMIP5), the land C pool in CESM/CLM4 is underestimated (Hoffman *et al*. 2014), associated with a high-biased N downregulation and short turnover times for decomposing C (Koven *et al*. 2014). This low-biased land C pool indicates an overestimation of the atmospheric CO$_2$ burden over the 20th century (Hoffman *et al*. 2014). Despite our assumptions, experimental design, and bias impacting the model's ability to predict absolute numbers, our modeling experiments allowed us to make the first test of the sensitivity of the Earth's climate system to plant-microbial interactions.

To fully integrate the C cost of multiple soil resource acquisition into ESMs, there are key empirical gaps that still need to be addressed including advancing observational datasets of the distribution of nutrient acquisition strategies at the global scale and expanding the spatial coverage and enhancing the temporal resolutions of both *in-situ* and remote sensing data that can better parameterize the C cost of nutrient acquisition as well as the N benefit of microbial symbionts (Fisher *et al*. 2016). This study shows that high-latitude regions with low N available are more impacted by C cost of N acquisition. However, remote sensing observations are limited in high-latitudes regions as a result of the long snow-cover season and cloud contamination, Thus, *in-situ* and aircraft data can potentially provide more accurate information in high-latitude regions. Given that the next version of CESM will include the optimal allocation theory of FUN, addressing these empirical and modeling gaps will aid in reducing uncertainty in the extent to which nutrient limitation drives C–climate feedbacks.

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5. Data and Code Availability: The data for all three figures as well as the model code are available at: https://github.com/coffeesmj/Biogeosciences-Submission.git

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7. Author contributions

M.S. and E.R.B designed the research; M.S. conducted the model simulations and performed the analyses; E.R.B and J.B.F contributed essential ideas of analyzing the results; E.R.B and M.S wrote the manuscript with contributions from J.B.F. and R.P.P.

8. Competing interests

The authors declare no competing financial interests.

9. Figures

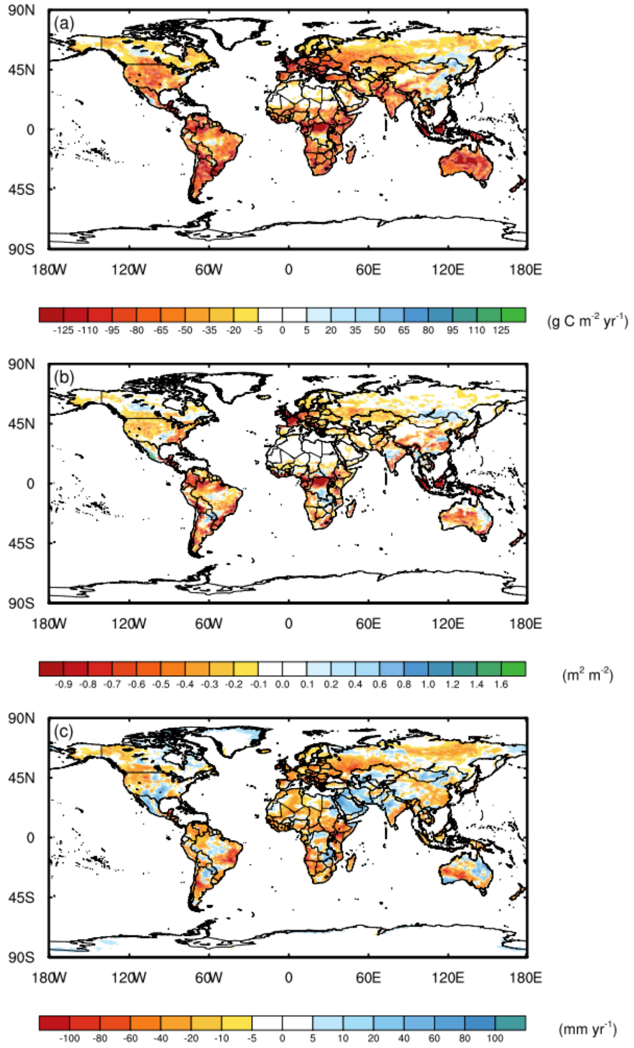

Figure 1. The C expended on symbiont-mediated N acquisition altered the spatial patterns of (a) NPP, (b) LAI and (c) ET. These results were obtained from CAM runs with and without the symbiont sub-module (CLM-FUN).

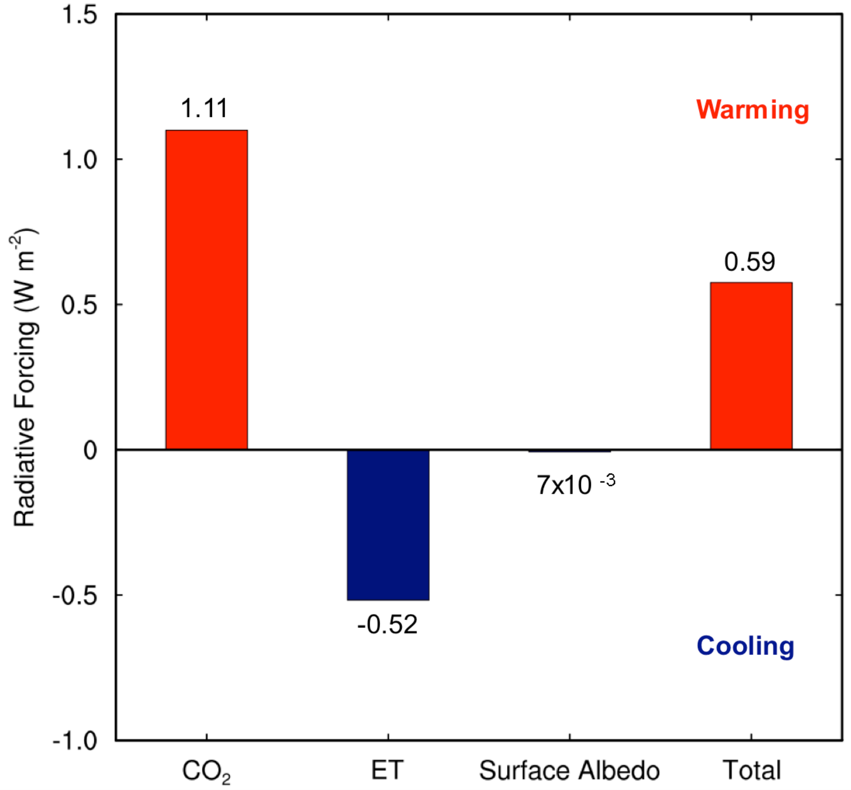

Figure 2. The impacts of the C cost of symbiont-mediated N acquisition led to a net increase in global radiative forcing. The warming due to increasing atmospheric CO_2 was offset partially by cooling due to reduced evapotranspiration (ET) and surface albedo. These results were obtained from CAM runs with and without the symbiont sub-module (CLM-FUN).

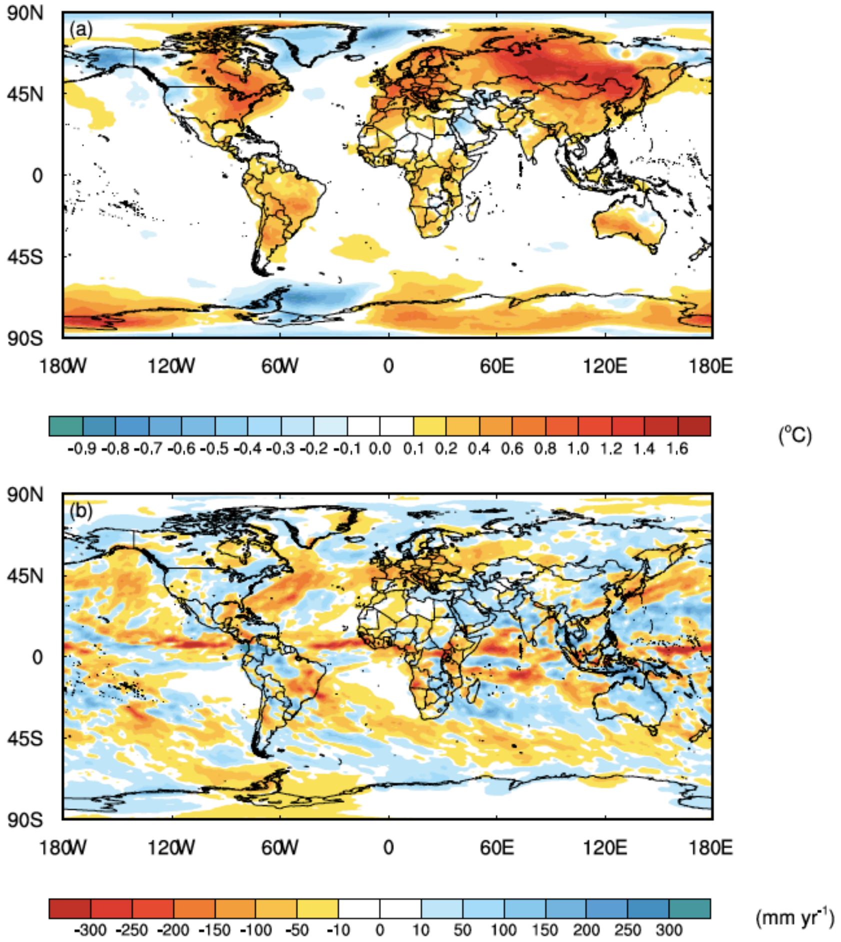

Figure 3. Feedbacks between symbiont-mediated N acquisition and C have a direct impact on global climate. (a) Surface air temperatures increase across much of the land surface; whereas (b) precipitation patterns are more variable. The values represent the differences for each grid cell between CAM-FUN with ramping CO$_2$ and the baseline CAM.

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11. Supplementary Materials

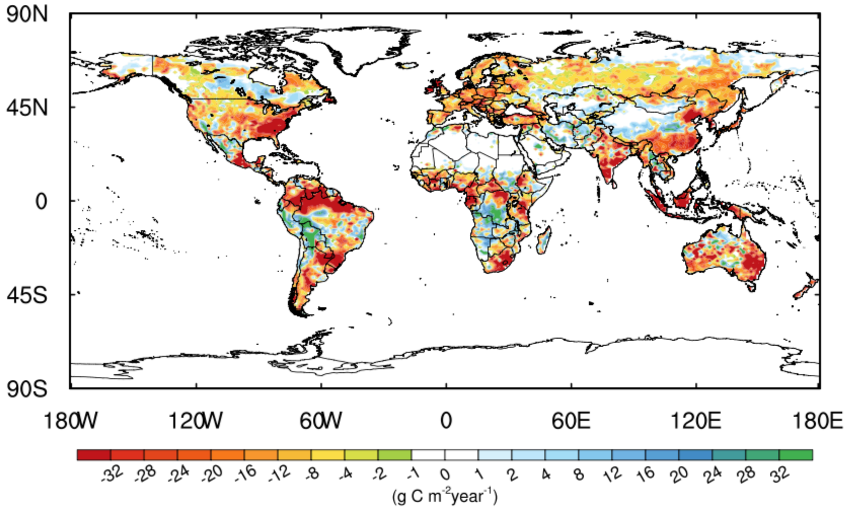

Figure S1. Impacts of parameter adjustments in FUN on predicted global NPP in CLM. Values represent the difference between the original parameterization and the new parameterization. On a global scale, the new parameterization reduced NPP from 50.8 Pg C yr^{-1} to 49.3 Pg C yr^{-1}.

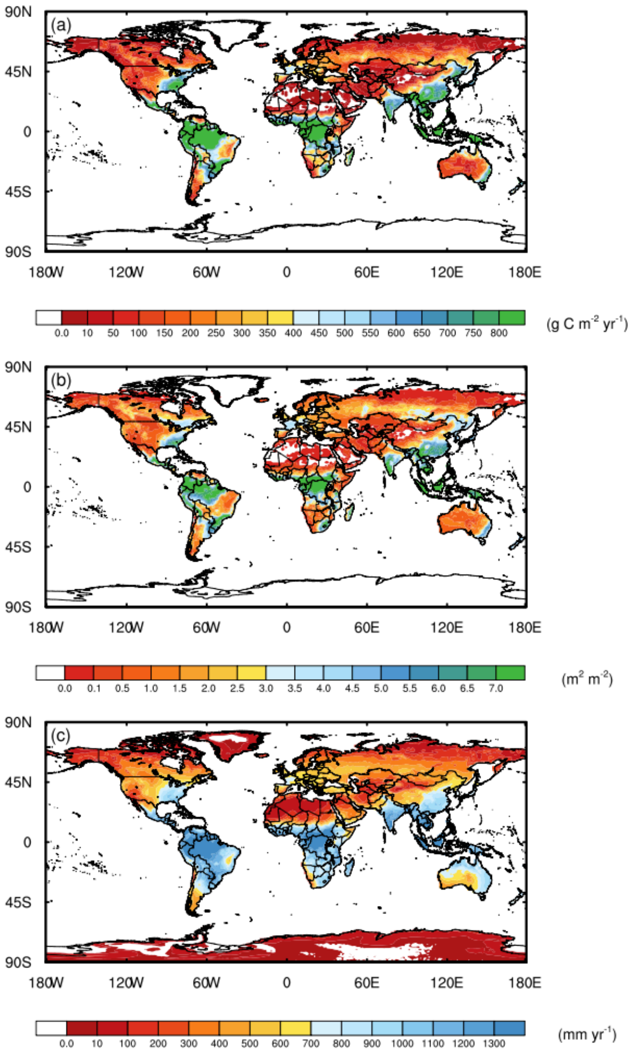

Figure S2. Absolute values of (a) NPP, (b) LAI, and (c) ET in CAM without CLM-FUN.

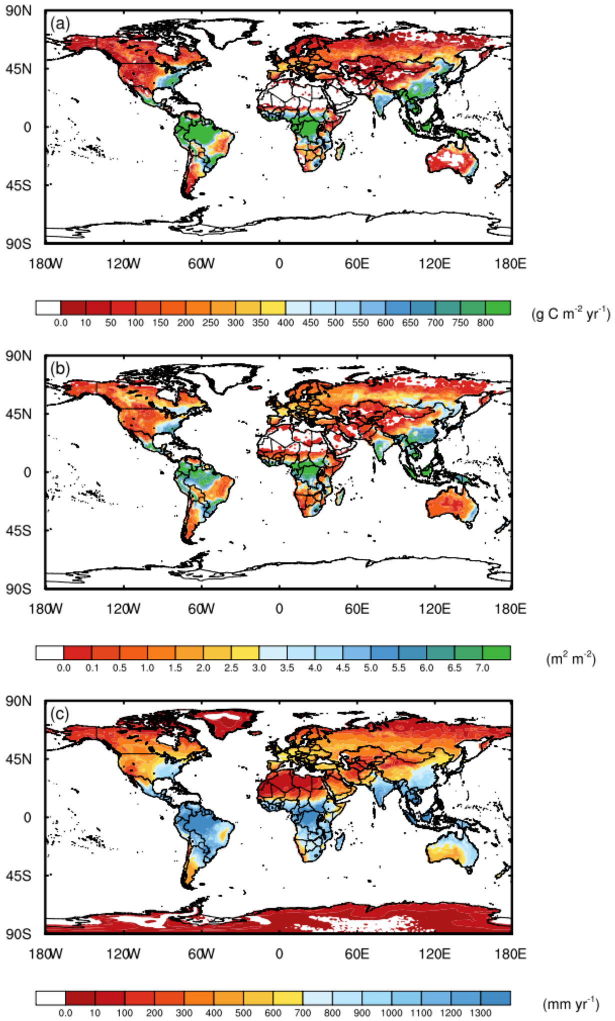

Figure S3. Absolute values of (a) NPP, (b) LAI, and (c) ET in CAM with CLM-FUN.

Table S1. The adjusted parameters in CLM-FUN

Cost Parameter	Original	Updated
AK_C	2.7×10^{-4}	6.2
AK_N	5.5×10^{-5}	5.5×10^{-5}
EK_C	1.6×10^{-3}	34.1
EK_N	2.7×10^{-4}	2.7×10^{-4}
K_C	5.5×10^{-5}	5.5×10^{-5}
K_N	3.3×10^{-3}	3.3×10^{-3}
K_R	$8.0/4.4\times10^{-4}$ [b]	$8.0/4.4\times10^{-4}$ [b]

[a] The parameter values used in Shi *et al*. [2016].

[b] 8.0 was used for deciduous plant functional types (PFTs) and 4.4×10^{-4} was used for evergreen PFTs.

Anonymous Referee #1

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General Comments

Shi et al. address the effect of nitrogen (N) limitation on the land carbon (C) uptake and climate change by estimating C costs for N acquisition. They coupled the Fixation and Uptake of Nitrogen (FUN) sub-model, which directly calculates C costs for different N acquisition strategies, to the Community Land Model (CLM) and run CLM, and CLM- FUN respectively, to estimate the reduction of net primary production (NPP) under N limitation, firstly. Secondly they used CAM, an atmospheric circulation model that includes CLM (or CLM-FUN), to take impacts on climate change into account. They show that C costs for N acquisition lower NPP and the Leaf Area Index globally, what has implications for the global C budget as well as for evapotranspiration and surface albedo. This influences the global radiative forcing and water balance and leads to changes in surface temperature and precipitation. Shi et al. summarize that Earth System Models that do not take C costs for N acquisition into account might over- estimate the land C sink and following under-predict climate change, but they also emphasize that P and water limitations play a role as well.

Overall, I think this is an interesting study and fits thematically the scope of BG quite well, but I have some major issues regarding the built and implementation of the study that make the evaluation impossible.

Specific Comments

I think, the 'Material and Methods' section is to short. Based on the given information it is impossible to reproduce the study, because it is unclear, what the authors have actually done and under which conditions the simulations run. The 'Results' part is very short, too, and does not show any base values, but only absolute and relative changes between model simulations. These short preparations of the following discussion make it impossible to fully understand the study and evaluate the paper.

ERB: *In the materials and methods section, we have added significant detail on the model simulations, the initial conditions, and the assumptions that we made. This includes both a better introduction into what each model does, more detailed information on the coupled CAM-CLM and CAM-CLM-FUN runs, and the initial conditions and forcing data for the models.*

In the results section, we have included two new global map figures in the supplemental information that show the absolute values of NPP, LAI, and ET in CAM-CLM and CAM-CLM-FUN.

Comments on FUN model

I miss more information about the modified parameters for N uptake by ECM / AM infected roots. Changes in orders of magnitudes require some more information. Not only, why the parameters were changed, but also how this effects the results compared to previous studies and/or a sensitivity analysis.

ERB: *The FUN model predicts the C cost of N acquisition from the soil by ectomycorrhizal, arbuscular mycorrhizal, and nonmycorrhizal roots based upon root biomass (a proxy for access) and soil nitrogen concentrations (a measure of availability of N for plants to take up). Previously, the parameter controlling the sensitivity of the C cost of N acquisition to root biomass was low. As such the C cost of N acquisition showed little to no sensitivity to variability in root biomass across grid cells and the ECM cost of N acquisition was always lower than the AM cost of N acquisition even in high N biomes. We have included a figure in the supplementary material that shows how modeled NPP changes with the new parameters as well as a table that shows the parameter changes. The parameter adjustment reduces global NPP by 1.5Pg or ~3%. Finally, we include text above in the material and methods in lines 130-149 that discusses this figure and the rationale behind the parameter adjustment.*

Comments on CLM vs CLM-FUN simulations

Regarding CLM-FUN vs CLM a proper set-up description is missing. If the reader wants to reproduce the study, he needs to know, if there is a spin-up done and how, how the models are initialized etc. From given information it is impossible to know for example, whether both models (CLM and CLM-FUN) start with the same biomass, or if they already differ in the beginning of the analyzed period, because of different spin-up results.

ERB: *We have added text in lines 178-182 that states the model spinup and configuration files are the default inputs that NCAR provides with the model. Both model configurations thus start from the same initial conditions and then diverge as FUN downregulates NPP in CLM based upon the C cost of acquisition.*

Secondly, the models calculate a global NPP difference of 8.2 PgC/yr. As consequence biomass in CLM-FUN should be lower as in CLM and thus also heterotrophic respira- tion should change. Do the authors consider that? If not, they might over-estimate the effect of N acquisition costs. Same for just looking at the land surface. As soon as the global land C sink is lowered, the ocean will take up more C, and not all additional C will remain in the atmosphere to force climate change. Over all it is completely unclear, how the authors derive the yearly CO2 increase of 3.8 ppm from the calculated NPP difference. Moreover the increase of 3.8 ppm per year just because of taking C costs for N acquisition into account seems very high compared to the actually measured at- mospheric CO2 growth rate, which is around 2 ppm per year. Hence the derivation of the yearly atmospheric CO2 increase should be described very detailed.

ERB: *In CLM-FUN heterotrophic respiration was 3.3 Pg C yr^{-1} less than in CLM without FUN. This represents about 40% of the reduction we observed in NPP. While not including this reduction in heterotrophic respiration may impact the results we present, empirical and modeling evidence suggests that including the C cost of N acquisition likely enhances heterotrophic respiration. This would occur through C being sent belowground to rhizosphere microbes which enhances their ability to prime soil organic matter decomposition. This is why we highlighted the coupling of FUN with a microbial decomposition model in lines 368-370. We have also added text in the* *discussion to highlight this assumption as well as the lack of ocean uptake of* CO_2 *in the model in lines 383-391. We also acknowledge that our estimate of climate impacts represents an upper boundary condition that may be mediated by heterotrophic respiration and ocean processes. Also note that there was a rounding error in the NPP reduction and we have revised it down to 8.1 Pg C* yr^{-1}.

In addition, we assume that all of the C from the reduction of NPP is transferred to the atmosphere. We have included more detail on this calculation in lines 195-204. We have added text to the discussion to describe how these assumptions influence our results.

Comments on CAM vs CAM-FUN simulations

First of all, it is unclear, whether FUN is actually coupled to CAM (and the abbreviation CAM-FUN indicates that somehow), or if only the additional C release to the atmo- sphere (3.8 ppm/yr), which is calculated be CLM-FUN, is added to the atmosphere of CAM.

If FUN is coupled to CAM, the reader needs again a proper set-up description as required already for CLM-FUN. For a fully coupled CAM-FUN model, I don't understand the reason for the atmospheric CO2 increase, because that should evolve internally by itself.

ERB: *Due to complexity of running the fully coupled model of CAM with CLM in which the terrestrial biosphere impacts on C cycling dynamically interact with the atmosphere, we instead used an offline CLM-FUN run to calculate in experiment 1 the down regulation in NPP and assumed that this carbon that did not go into biomass instead went into the atmosphere. In experiment 2, we then run CAM with CLM or CLM-FUN. We then prescribe a* CO_2 *increase in CAM-FUN and compare it to CAM with CLM only. Despite the lack of C cycling coupling, the resulting impacts of LAI or ET on energy budgets does influence radiative forcing. We have added text to clarify and justify this approach in lines 192-215 as well as text to state that CAM and CAM-FUN start off with the same initial conditions.*

If only the atmospheric CO2 concentration in CAM-FUN is increased compared to CAM, the analyzed effects might rather depend on the CO2 forcing of CAM in gen- eral than on C costs for N acquisition. From the manuscript it is unclear, if any other changed values/fluxes from CLM-FUN are introduced to CAM-FUN, for example NPP to outbalance the additional C input to the atmosphere or is the total amount of C in CAM-FUN increasing. If NPP in CAM-FUN is constrained by CLM-FUN, how does that influence vegetation dynamics and development in CAM-FUN under increased atmospheric CO2?

ERB: *Due to the computational cost of running the fully coupled model, we used the prescribed* CO_2 *approach to assess the sensitivity of the climate system to the C cost of N acquisition. However, in the CAM-CLM and CAM-CLM-FUN runs we were able to assess the impacts of changing climate conditions on NPP, LAI, and ET.*

Besides all that, the introduction of the optional slab mixed-layer ocean model is misleading, since it is not used. Is it?

ERB: *We did not use the slab mixed-layer ocean model and have removed this from the text.*

Technical Corrections

L111: CAM is introduced as abbreviation of CAM version 4. Is there any other name for CAM than 'an atmospheric general circulation model that includes CLM'?

ERB: *We have clearly defined CAM as the Community Atmosphere Model and have provided text to describe its function in lines 150-171.*

L122-L125: double reference to forcing data set L124: spatio-temporal vs L139 spatiotemporal

ERB: *We have corrected these errors.*

Response to Reviewer 2

This is a study of the implications of the fact that most (or all) conventional modeling studies do not represent the expenditure of energy (C) by plants on the uptake of N. Apreviously-developed model of plant uptake (FUN) is used with the CLM land surface model to estimate the reduction in NPP as a result of N acquisition. This reduction in terrestrial uptake of C is then converted to a corresponding increase in atmospheric CO2 which is fed into the CAM atmospheric model. Simulations of CAM with and without the FUN sub-model are used to quantify the impacts of N acquisition on global climate.

Although the manuscript is well-written in terms of the language used, I have serious concerns over the methodology and the information presented. As such I suggest that it requires major revision before it would be acceptable for publication.

At the very least the manuscript needs to do a better job at explaining what has been done (and possible limitations), but it is also possible that further simulations are required (particularly to clarify if the signal is robust).

General comments

One of my main concerns is that I am not sure I understand what the authors did – there is a need for more material in the methods section. A series of complicated modeling systems has been used but few details of the configurations and simulations are provided. I am not looking for 100% reproducibility - that is very difficult to achieve unless the author's github site includes all the configuration files, which I haven't checked – but the paper should provide more details than it does. For example, what were the initial conditions, was there a spin-up phase, what additional inputs are provided?

ERB: *We have added more detail to the materials and methods section to address these concerns. We now have text in lines 170-174 and 199-201 that states that the initial conditions, spinup configuration and other necessary conditions needed to run the simulations for both CLM and CAM. All of the configuration and spinup files are the default model inputs that are provided by the National Center for Atmospheric Research. We have also clearly defined the scope of our model experiments to alleviate confusion regarding the coupling of the two models.*

The discussion of the results is also very brief with only 35 lines in the Results section.

ERB: *In response to Reviewer 1, we have added in global maps of the absolute values of NPP, ET, and LAI for CAM-CLM with and without FUN to the Supplementary Material in lines 244-256. We have also highlighted the stronger impacts of the C cost of N acquisition for temperature than precipitation and greater uncertainty in precipitation estimates in lines 270-279.*

Specific comments

Abstract - I would like this to be more quantitative and also give some indication of the nature (and limitations) of the experimental design (e.g. ramped CO_2). At present it highlights the changes in "high-latitude" temperature and precipitation, but there are no other numbers.

ERB: *We have added in more quantitative information into the Abstract. In addition, we have added a sentence that describes the experimental design.*

L67 - It might be useful to add a line or two about the approach used in most climate models, e.g. N is "free" and NPP is simply "snipped" to match the N availability, to contrast with the approach used in FUN.

ERB: *We have added text in lines 76-78 to state how typical climate models work per the reviewer's suggestion. In addition, we have added text to lines 80-82 to show how our previous work with FUN contrasts this common approach.*

Section 2.1 - I don't expect full details of CLM (those can presumably be found in the literature that is cited) but a brief overview would be useful, particularly for people who have little or no idea what a land surface model is.

ERB: *We have added text to provide a brief overview of the CLM and CAM models in lines 124-129 and lines 150-171, respectively.*

L102 "we updated the parameters" - It appears that the values of two parameters were changed by about 4 orders of magnitude and this is justified by a description of how the new model is better, but I would like to see more detail/evidence/justification. I haven't read all the literature cited for FUN but I am left wondering why it was necessary to adjust the parameters by so much - or is it just that the results are not very sensitive to these values? In this area it might also help if the previous work with FUN was summarised - e.g. this is what has been done and found using FUN (coupled with other models?) previously. Can we see "before and after" patterns of, say, NPP, to show the improvements produced by changing the parameter values? If possible the names of the altered parameters should also be given (even if it is possibly obvious to anyone who reads the cited papers).

ERB: *The FUN model predicts the C cost of N acquisition from the soil by ectomycorrhizal, arbuscular mycorrhizal, and nonmycorrhizal roots based upon root biomass (a proxy for access) and soil nitrogen concentrations (a measure of availability of N for plants to take up). Previously, the parameter controlling the sensitivity of the C cost of N acquisition to root biomass was low. As such the C cost of N acquisition showed little to no sensitivity to variability in root biomass across gridcells and the ECM cost of N acquisition was always lower than the AM cost of N acquisition even in high N biomes. We have included a figure in the supplementary material that shows how modeled NPP changes with the new parameters as well as a table that shows the* *parameter changes. The parameter adjustment reduces global NPP by 1.5Pg or ~3%. Finally, we include text above in the material and methods in lines 130-149 that discusses this figure and the rationale behind the parameter adjustment.*

L111 CAM - I think this stands for Community Atmosphere Model, which should be explained. "optional slab mixed-layer ocean model" - I'm not so bothered that it is optional, but I do want to know if it is used here. L137 suggests prescribed SSTs were used and if that means no slab model then don't mention it. Is it relevant that CLM and CAM are part of CESM? Again, if not, don't mention it.

ERB: *We have deleted this text from the materials and methods as we used prescribed sea surface temperatures as the reviewer noted and did not use the slab ocean model.*

Experimental Design - CLM - how was the initial state of CLM prescribed? Was there a spin up? Was land use change included? Again I'm not looking for every detail so that I can definitely reproduce the results, but the reader should get a pretty good idea of what was done - which they don't at present.

ERB: *We have added text in lines 178-182 that states the model spinup and configuration files are the default inputs that NCAR provides with the model. Both model configurations thus start from the same initial conditions and then diverge as FUN downregulates NPP in CLM based upon the C cost of acquisition.*

Experimental design - CAM - I think that CAM-FUN means CAM with CLM and FUN...but I am not 100% sure. Another possibility is that it means "CAM with extra CO2 calculated from offline runs of CLM-FUN". Either way it needs to be clarified. Why is CO_2 ramped up, why not just start from a higher value? I guess the point is that N-acquistion gradually leads to enhanced atmospheric CO2...but on the other hand that is not something that started in 1980 and, ideally, one might have started both runs from a pre-industrial CO2. Why is the full 8.2 Pg C yr^{-1} added to the atmosphere? In reality only a fraction (40%) of anthropogenic emissions of CO2 remain in the atmosphere, with ocean drawdown a large part of the story, so one might expect that something similar would apply here. I'm a bit confused by the whole approach to CO_2 used here, and this is another aspect. From the description it appears that CO2 is prescribed and not interactive in CAM(-FUN) (i.e. CLM-calculated fluxes of C do not change the atmospheric CO_2) but this should be clarified. Do both CAM and CAMFUN start with the same amount of vegetation? Clarify what fluxes CLM exchanges with CAM, what is prescribed and what is interactive. All in all the design has to be better explained and justified.

ERB: *The reviewer is correct in how we configured the model runs. Due to complexity of running the fully coupled model of CAM with CLM in which the terrestrial biosphere impacts on C cycling dynamically interact with the atmosphere, we instead used an offline CLM-FUN run to calculate in experiment 1 the down regulation in NPP and assumed that this carbon that did not go into biomass instead went into the atmosphere. In experiment 2, we then run CAM with CLM or CLM-FUN. We then prescribe a CO_2 increase in CAM-FUN and compare it to CAM with CLM only. Despite the lack of C cycling coupling, the resulting impacts of LAI or ET on energy budgets does influence radiative forcing. We have added text to clarify and justify this approach in lines 195-204 as well as text in lines 207-209 to state that CAM and CAM-FUN start off with the same initial conditions.*

Results

Are the changes in modeled climate (particularly temperature and precipitation) statistically significant? It is many years since I was involved in a paper that presented changes in modeled climate, but at that time it was considered essential to use an ensemble of runs (e.g. using different initial states) to quantify internal variability, and maps of changes would indicate the statistical significance of the change at each location. The widespread areas of increased temperature in Fig.3a are consistent with the "expected" change and are likely "meaningful", but the much more patchy changes in precipitation (Fig.3b) are less obviously signal rather than noise. If there can be no estimate of significance I think the discussion of changes in atmospheric hydrology have to be couched in much less certain language, with the limitations of the method flagged up. This becomes even more important at regional level.

ERB: *Given that we did not do an ensemble of runs, we are not able to evaluate significance. As such, we have added text in the results in lines 273-282 to couch the precipitation results and to acknowledge the low signal to noise ratio in the precipitation results.*

Fig.2 and related discussion - I am not very familiar with how radiative forcing is used or calculated, but I am confused by the discussion! How is the radiative forcing from reduced evaporation calculated? Is this just the reduction in the latent heat flux (W m^{-2})? The caption "warming...was offset..by..reduced evapotranspiration" is rather confusing - with reduced evaporation one might expect increased sensible heat flux (all else being equal) which would have a warming effect. L224 suggests that the ET change resulted in reduced water vapor and implies that that is where the radiative forcing comes from. I think we need better discussion of the energy balance and clarification of the radiative forcing/mechanisms. It might be quite correct but I am sure many readers of Biogeosciences are not familiar with the ideas of radiative forcing.

ERB: *We have added text in the methods to explain why we were doing this analysis which lets us see which of these factors had the biggest impact on climate in lines 231-233 and also in the results to state that ET had a cooling effect due to reductions in water vapor in lines 267-268.*

I can see that the study represents a "first look" at the implications of the C cost of N uptake on modeled climate - but it is unclear whether the methodology used allows for a meaningful estimate of the impact. Improved description and justification of the experimental design would clarify this, and at least improve the reader's confidence in the design, but at present I am left wondering what the experiment with a relatively rapid ramping up of atmospheric CO_2 (3.8 ppm per year) from an arbitrary start year
(1980) actually tells us about the "real world". The authors conceded in L276 that there might be limitations to their method but do not properly enlarge on this. Convince me and I will be happy!

ERB: *We have increased the text describing the limitations as well as benefits of our approach in the Discussion in lines 383-391. In addition, we have made substantial changes to the methods to help clarify and justify our approach as highlighted in responses above.*

Further details

Title - I don't like this. "Plant-microbe symbioses reveal underestimation" suggests that the symbioses were somehow active or involved in the study. I would rephrase it as something like "Neglecting symbioses leads to underestimation of modeled impacts...".

ERB: *We have changed the title to: "Neglecting plant-microbe symbioses leads to underestimation of modeled climate impacts."*

L153 - if the units of dF are W m^{-2}, those of alpha should be the same (not g m^{-2}).

ERB: *We have corrected this mistake.*