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Plant-microbe Symbioses Reveal 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. The carbon costs of supporting symbiotic nitrogen uptake reduced net primary production, with the largest absolute effects occurring at low-latitudes and the largest relative changes occurring at high-latitudes. The largest impact occurred in high-latitude ecosystems, where such costs were estimated to increase temperature by 1.0 °C and precipitation by 9 mm yr^{-1}. Globally, our model predicted that nitrogen limitation enhances temperature and decreases precipitation; 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, and 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) reported that models that do not account for the C cost of N uptake can overestimate global NPP by 13%, and thus, 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.

ESMs 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 ESM. To streamline the complexity of the Earth-scale computations, we imposed a simplification of the ocean and ice components in the Community Earth System Model (CESM) with symbiotic processes included. We are focusing on the dynamic processes between the land and atmosphere, and this ESM 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 (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 with coupled C and N dynamics (CLM) (Lawrence *et al*. 2011; Oleson *et al*. 2010). FUN was coupled into CLM (CLM-FUN) (Shi *et al*. 2016). The previous CLM-FUN version was more sensitive to variability in N availability than root biomass (proxy for access); thus, we updated the parameters that control the cost functions for mycorrhizal uptake. Consequently, 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. We also used CAM version 4 (CAM), an atmospheric general circulation model that includes CLM (or CLM-FUN), an optional slab mixed-layer ocean model, and a thermodynamic sea ice model (Neale *et al*. 2010), to investigate the root symbiont associated C–climate feedback. CLM and CAM are the land and atmospheric components of the Community Earth System Model version 1.2 (CESM1.2), respectively.

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 forcing data (Qian *et al.* 2006). We ran both CLM and CLM-FUN at the 0.9°×1.25° and half-hourly spatio-temporal resolution for 25 years (1980–2004) with the meteorological forcing data from Qian *et al.* (2006). 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 is 8.2 Pg C yr^{-1}. This additionally respired C from CLM-FUN represents the C amount that plants expend to take up N and was not considered in CLM. With this calculation, we assume that without integrating the C costs for N acquisition will underestimate an 8.2 Pg C yr^{-1} of C released to the atmosphere at a 3.8 ppm of CO_2 annual rate.

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Second, we ran two simulations of the land–atmosphere model, CAM4.0-CLM 4.0: (1) A control simulation with coupled C and N dynamics but without mycorrhizal impacts on atmospheric CO_2 or surface energy budgets (herein CAM), and (2) a simulation that included both the coupled C and N dynamics and mycorrhizal impacts on atmospheric CO_2 as well as surface energy budgets, which was ramped up based on the down regulation of NPP in the first step (herein CAM-FUN). 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 *spatiotemporal* resolution for 25 years. In CAM, the ambient CO_2 concentration was 338 ppm. 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.

In this study, we also estimated the radiative forcing variations causing the climate impacts. We use the reflected solar radiation difference between CAM and CAM-FUN to estimate the radiative forcing variations from surface albedo change. 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).

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

where α is estimated as 5.35 (g C 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.

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).

The global NPP reduction (8.2 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. Overall, 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 leaf area due to modifications of ET and surface albedo of the vegetated land surface, leading to an overall net cooling effect

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of -0.52 W m^{-2} (Figure 2). 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.

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). 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). 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

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enzyme model at the ecosystem scale has shown that the ability of ECM fungi to prime soil organic matter allowed them to mine N 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 CESM. In addition, 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 this bias impacting the model's ability to predict absolute numbers, our modeling experiments allowed us to test 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.

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.

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9. Figures

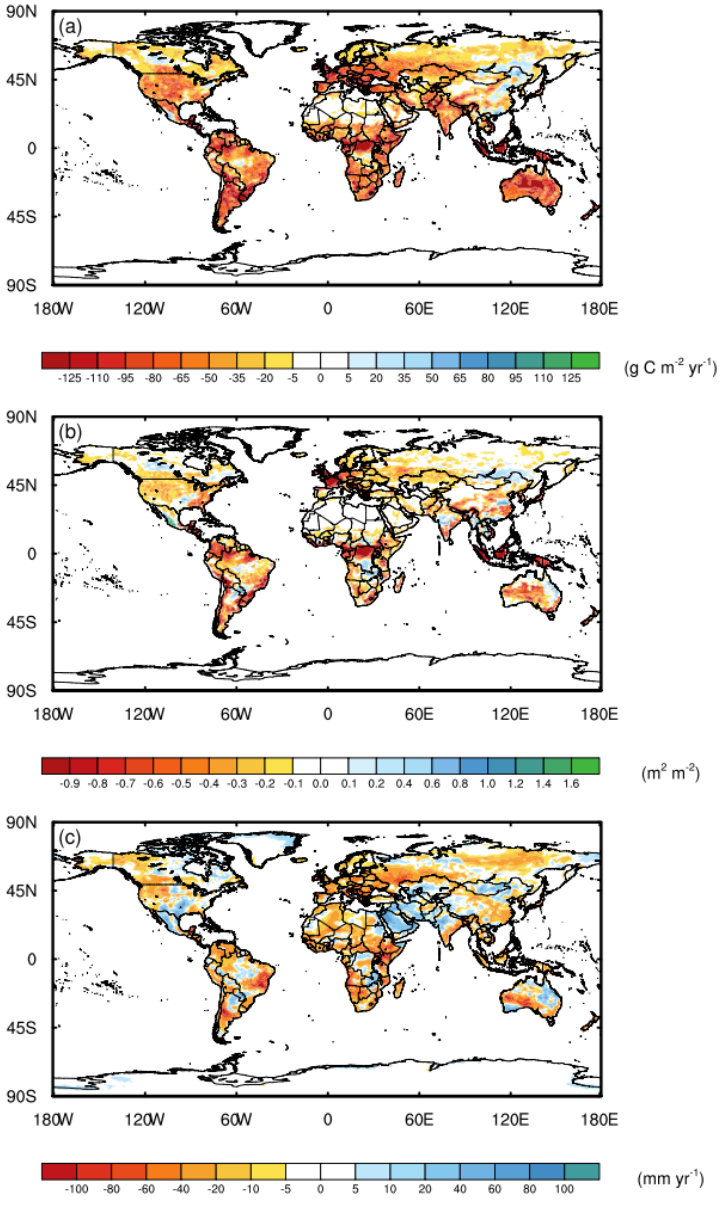

Figure 1. The C expended on symbiont-mediated N acquisition altered the spatial patterns of (a) NPP, (b) LAI and (c) ET. These results were obtained from CAM runs with and without the symbiont sub-module (CLM-FUN).

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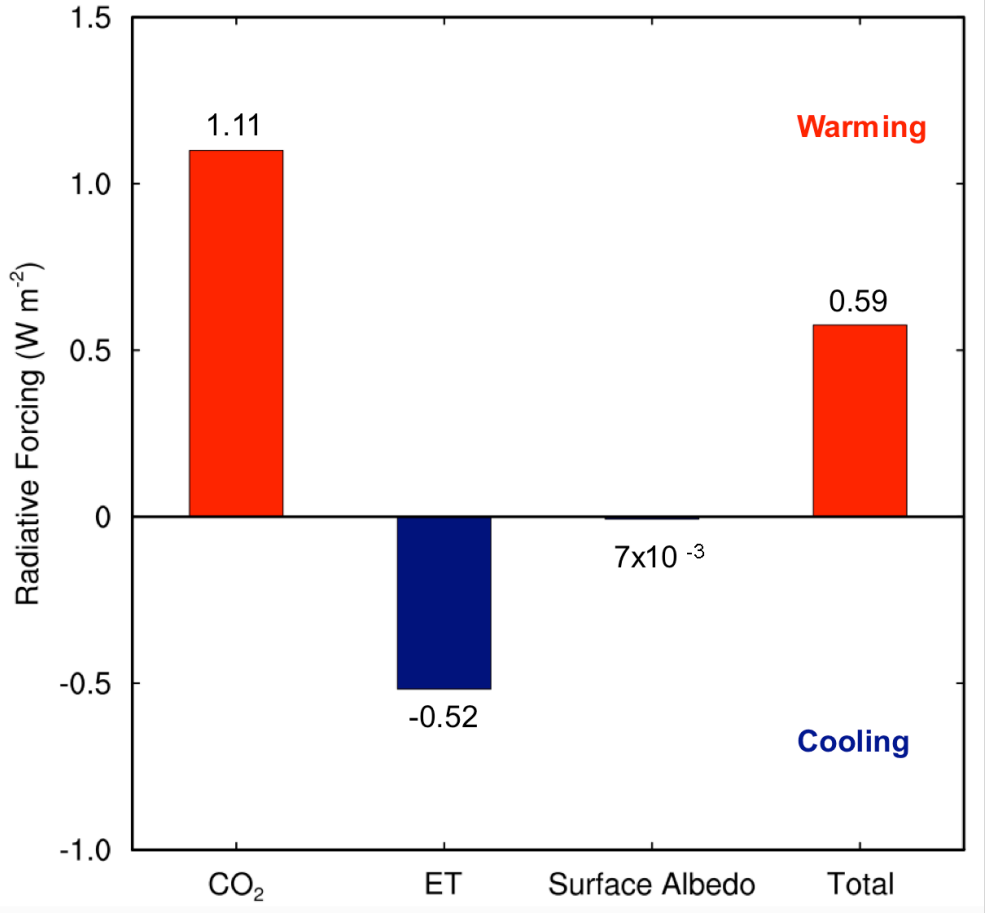

Figure 2. The impacts of the C cost of symbiont-mediated N acquisition led to a net increase in global radiative forcing. The warming due to increasing atmospheric CO_2 was offset partially by cooling due to reduced evapotranspiration (ET) and surface albedo. These results were obtained from CAM runs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

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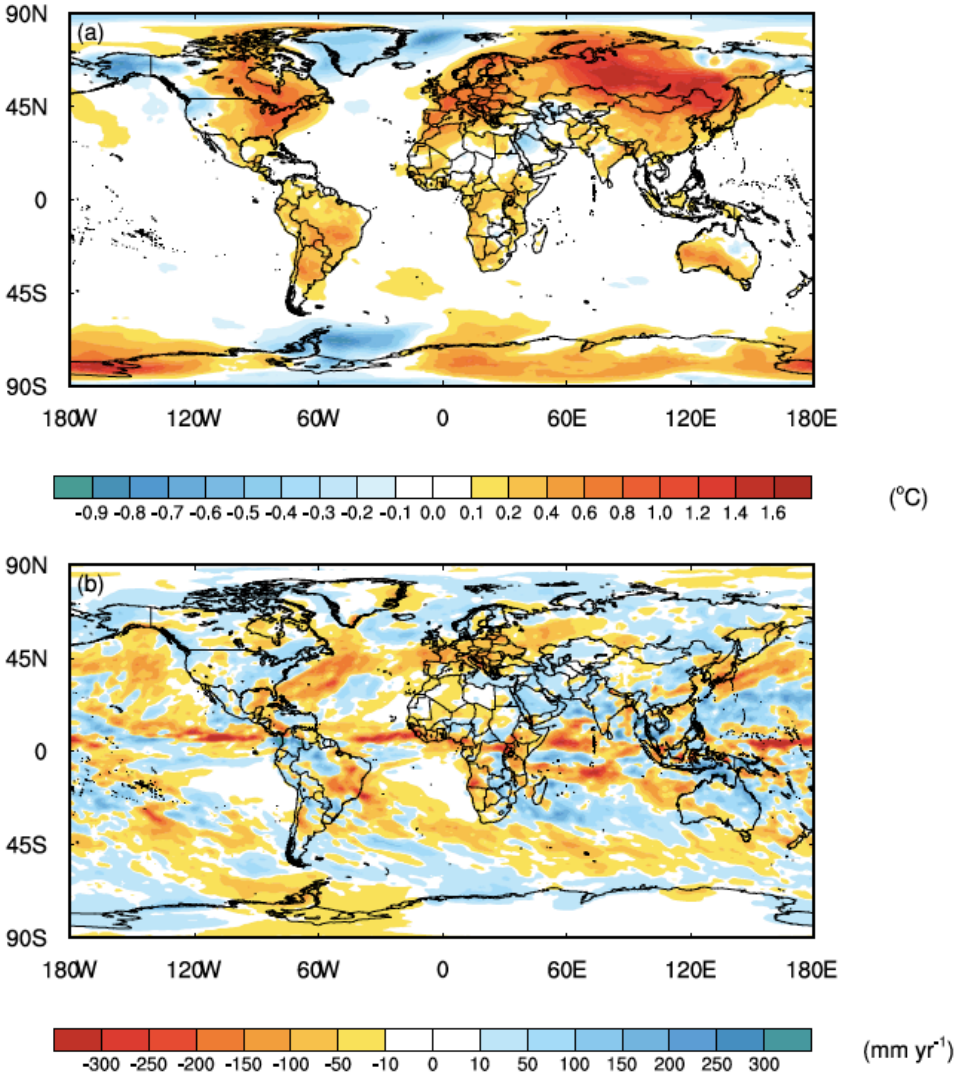

Figure 3. Feedbacks between symbiont-mediated N acquisition and C have a direct impact on global climate. (a) Surface air temperatures increase across much of the land surface; whereas (b) precipitation patterns are more variable. The values represent the differences for each grid cell between CAM-FUN with ramping CO_2 and the baseline CAM.

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