

We appreciate the reviewer's thoughtful and careful read of the revision of our manuscript. Below we have addressed the comments and additional issues that the reviewer has raised. Our responses will be indicated by **ERB et al.** followed by our response in *italics*. All line numbers referenced below refer to the manuscript version that includes the track changed markup.

**Second review of Shi et al., 2018, "Plant-microbe symbioses reveal underestimation of modeled climate impacts", Biogeosciences.**

In general I find that the revised manuscript is a substantial improvement on the original submission, and I consider that it is suitable for publication after minor corrections. In particular the "Material and Methods" section has had material added to better describe the series of model simulations. The revised title is also clearer.

Although the authors have introduced various caveats about the limited nature of their climate model runs (2 runs starting from the same initial conditions are compared over a 10 year period), some of the discussion is still rather limited in this respect (e.g. no explicit mention of internal variability of the model, nor of possible trends related to a common initial state). This might be a deliberate attempt to suit the intended audience, or might possibly reflect the authors' backgrounds and interests. Given the intended audience and the stated aim being to provide a first estimate of the implications of neglecting the C costs, I consider that the level of detail provided is probably sufficient. Although we need to be wary of the details of the 10yr (climate) changes described (wary of the precise quantification) I have no reason to doubt that the effects are real (possibly with different magnitude).

**ERB et al.:** *As highlighted by the reviewer, we have focused this manuscript primarily on meeting our objective to provide a first estimate on the impacts of neglecting the C costs of N acquisition by symbionts on climate. In the previous round of revisions, we have added text that addresses the uncertainties and caveats in our model estimates that we feel address the reviewer's concerns about the absolute magnitude of the changes in climate we present.*

**Minor comments**

L89-91 "we imposed a simplification" – this sounds like you actively modified CAM but I think what is meant is that you did not use interactive ocean or sea ice models (rather you prescribed SSTs and ice amounts). Rephrase along the lines of: "we used CAM with prescribed sea surface temperatures and sea ice, and introduced symbiotic processes..."

**ERB et al.:** *We have rephrased this sentence in the introduction in lines 88-91 following the reviewer's suggestion.*

L146 – Ideally we might also get more details of the experimental setup for these early simulations of CLM-FUN, though I suspect they followed the configuration used later in section 2.2. As a minimum I suggest adding something to indicate that the downregulation of NPP referred to contemporary or recent conditions, or 1995-2004, or whatever. Or if both sets of CLM simulations shared common details, move them to here.

**ERB et al.:** *We have added text to clarify the time period as well as the initial model state and spin-up in lines 138-142: "This parameter adjustment also resulted in small increase in the downregulation of NPP by FUN in CLM by 1.5 Pg C yr<sup>-1</sup> or ~3% for the last ten years of the model simulations from 1995-2004 (Figure S1). For this parameter adjustment, the spin-up, meteorological conditions, and time period are the same as outlined for CLM in Section 2.2*

below.” *We have chosen to leave the detailed model description in Section 2.2 as those model simulations represent the model simulations that were performed to meet the objectives of this study.*

L209 and following – Again, I assume that the CAM runs were for 1980-2004, as was used for CLM – but this should be stated. And so all later averages from CAM refer to the years 1995-2004?

**ERB et al.:** *To address this comment, we have added text in lines 188-190 that explicitly states the 10-year period from 1995-2004 that was analyzed for differences in climate. In addition, we have added text to the figure captions to clarify the time period over which we analyzed differences.*

L262 – What are the bounds (latitudes?) of the various areas used to calculate averages, e.g. high-latitude, mid-latitude, tropical low latitude? Add these after each, e.g. high-latitude ecosystems (60-85N). Otherwise we have these rather vague descriptions of areas next to precise statistics of changes.

**ERB et al.:** *We have added a new figure to the SI material that provides maps of the three key biome classes over which we analyzed the model results for regional changes in climate. In addition, we have added text in the results in lines 224-226 that point the reader to this figure.*

L305 and others – I don’t find these statistics of regional changes in precipitation convincing, or useful, given that they are based on only two 10-yr simulations. Personally I would consider removing much of L300-305. However, as the aim of this paper is to provide first estimates, not a detailed account of atmospheric changes, it is probably acceptable to leave the statistics in the manuscript.

**ERB et al.:** *We have chosen to leave this text in the manuscript as we added text in the previous round of revisions that clearly states the uncertainty in these estimates in lines 243-245: “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”.*

L312 – I think this is the first mention of using 10yr statistics from CAM (see earlier request for clarity on this). Also rephrase along the lines of “temperature increased by 1degC over 10 years and precipitation increased by 9 mm yr-1”.

**ERB et al.:** *We have revised the text in lines 259-262 to make it explicit that this is referring to the differences in the last ten years of the model simulations.*

L341 – -5.2 W m-2 should be -0.52 W m-2.

**ERB et al.:** *We have corrected this error.*

Figures – captions should say that they refer to 10 year averages (or whatever).

**ERB et al.:** *We have added this information to all the figure captions in the main manuscript and SI material where this is applicable.*

Table S1 – I can’t see where footnote a is referenced. I suspect it applies to (at least) the middle column.

**ERB et al.:** *We have corrected this error so that the footnote a refers to the middle column in the table.*

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2 **Neglecting Plant-microbe Symbioses Leads to Underestimation**  
3 **of Modeled Climate Impacts**  
4

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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<sub>2</sub> on temperature and precipitation regimes. The carbon costs of supporting symbiotic nitrogen uptake reduced net primary production by 8.1 Pg C yr<sup>-1</sup>, with the largest absolute effects occurring in tropical forest biomes and the largest relative changes occurring in boreal and alpine biomes. 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<sup>-1</sup>. However, there were strong regional impacts with the largest impact occurring in boreal and alpine ecosystems, where such costs were estimated to increase temperature by 1.0 °C and precipitation by 9 mm yr<sup>-1</sup>; 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; Wurzbürger *et al.* 2017). Recent data syntheses have shown that ECM and AM ecosystems have divergent C-nutrient economies that respond differently to elevated CO<sub>2</sub> 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<sub>2</sub> 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.

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 ~~with~~ climate by performing model experiments with and without these costs in ~~a~~ C-climate model. To streamline the complexity of the Earth-scale computations, we ~~used the~~ Community Atmosphere Model (CAM) ~~with prescribed sea surface temperatures and sea ice and a version of~~ the Community Land Model (CLM) which predicts ~~the impacts of symbiotic processes on~~ 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 meteorological 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 availability of N to support plant biomass synthesis (Lawrence *et al.* 2011; Oleson *et al.* 2010).

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<sub>2</sub>) (Terrer *et al.* 2017). Specifically, we modified an AM-related uptake parameter and an ECM-related uptake parameter from  $2.7 \times 10^{-4}$  (g C m<sup>-3</sup>) to  $6.2$  (g C m<sup>-3</sup>) and from  $1.6 \times 10^{-3}$  (g C m<sup>-3</sup>) to  $34.1$  (g C m<sup>-3</sup>), 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<sup>-1</sup> or ~3% for the last ten years of the model simulations from 1995-2004 (Figure S1). For this parameter adjustment, the spin-up, meteorological conditions, and time period are the same as outlined for CLM in Section 2.2 below.

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) (Neale *et al.* 2010). CAM dynamically predicts

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the impacts of external forcing factors such as anthropogenic CO<sub>2</sub> emissions on global and regional climate (i.e., temperature and 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 meteorological 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<sub>2</sub> concentration was fixed to 338 ppm, the atmospheric CO<sub>2</sub> 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<sup>-1</sup>. 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<sub>2</sub> (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<sup>-1</sup> of C released to the atmosphere at a 3.8 ppm of CO<sub>2</sub> 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<sub>2</sub> or surface energy budgets (herein CAM), and (2) a simulation that included mycorrhizal impacts on atmospheric CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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 from 1980-2004. In CAM, the ambient CO<sub>2</sub> 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<sub>2</sub> started increasing from 338 ppm at the 3.8 ppm of CO<sub>2</sub> annual rate, and all the respired CO<sub>2</sub> is mixed into the atmosphere homogenously. We also present the means of the CAM-based results for the last 10 simulation years from 1995-2004. We evaluated the climate impacts resulting from

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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 did this in order to identify which factor, ET vs. LAI vs. enhanced atmospheric CO<sub>2</sub>, led to our observed shifts in climate. It also allowed us to identify if the 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<sub>2</sub> increase was calculated with an empirical equation (Myhre *et al.* 1998):

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

where  $\alpha$  is estimated as 5.35 (W m<sup>-2</sup>),  $C$  is CO<sub>2</sub> in parts per million by volume, and  $C_0$  is the reference concentration, which is 338 ppm, the atmospheric CO<sub>2</sub> 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<sup>-2</sup> yr<sup>-1</sup>, leading to alterations in atmospheric CO<sub>2</sub>, 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 addition, we analyzed temperature and precipitation shifts across three key biome classes that are delineated in Figure S4. In boreal and alpine ecosystems, LAI was reduced by 34% (a decrease of 0.05 m<sup>2</sup> m<sup>-2</sup>) while NPP was reduced by 42% (a decrease of 12 g C m<sup>-2</sup> yr<sup>-1</sup>). In mid-latitude temperate ecosystems, LAI was reduced by 17% (a decrease of 0.16 m<sup>2</sup> m<sup>-2</sup>) while NPP was reduced by 33% (a decrease of 30 g C m<sup>-2</sup> yr<sup>-1</sup>). Tropical forest ecosystems had the largest absolute reductions in LAI (0.24 m<sup>2</sup> m<sup>-2</sup>; 10% decrease) and NPP (53 g C m<sup>-2</sup> yr<sup>-1</sup>; 22% decrease). Compared to NPP and LAI, ET had a more heterogeneous spatial pattern with a global mean ET reduction 7.3 mm yr<sup>-1</sup>, which represents a ~3% decrease across all of the 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<sub>2</sub> due to the reduction in NPP was the strongest driver of climate shifts. The global NPP reduction (8.1 Pg C yr<sup>-1</sup>) from the land model simulations resulted in an increase in atmospheric CO<sub>2</sub> concentrations of 3.8 ppm yr<sup>-1</sup>, 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<sup>-2</sup> (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<sup>-2</sup> (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<sup>-2</sup> (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<sup>-1</sup>, 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<sup>-1</sup> 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 than 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. ECM-dominated ~~areas in boreal and alpine biomes~~ became warmer (increases in surface air temperature by 1.0 °C) and wetter (increases in precipitation by 9 mm yr<sup>-1</sup>). 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<sup>-1</sup> 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 basins drying by 4 mm yr<sup>-1</sup> and 49 mm yr<sup>-1</sup>, 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 ~~boreal and alpine~~ ecosystems (Figure 1). These reductions led to substantial impacts on climate, particularly in ~~boreal and alpine~~ ecosystems where temperature increased by 1°C and precipitation increased by 9 mm yr<sup>-1</sup> ~~over the last ten years of the simulations (1995-2004)~~ (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, the C transferred to symbionts leads to more atmospheric CO<sub>2</sub> 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 ~~is~~ 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.

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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<sub>2</sub> 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  $-0.52 \text{ W m}^{-2}$  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<sub>2</sub> 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 **boreal and alpine ecosystems** 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<sub>2</sub> (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). **These are** 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

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(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<sub>2</sub> 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<sub>2</sub> (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<sub>2</sub>. In a fully coupled model, it is likely that a portion of this CO<sub>2</sub> 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<sup>-1</sup>. 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<sub>2</sub> 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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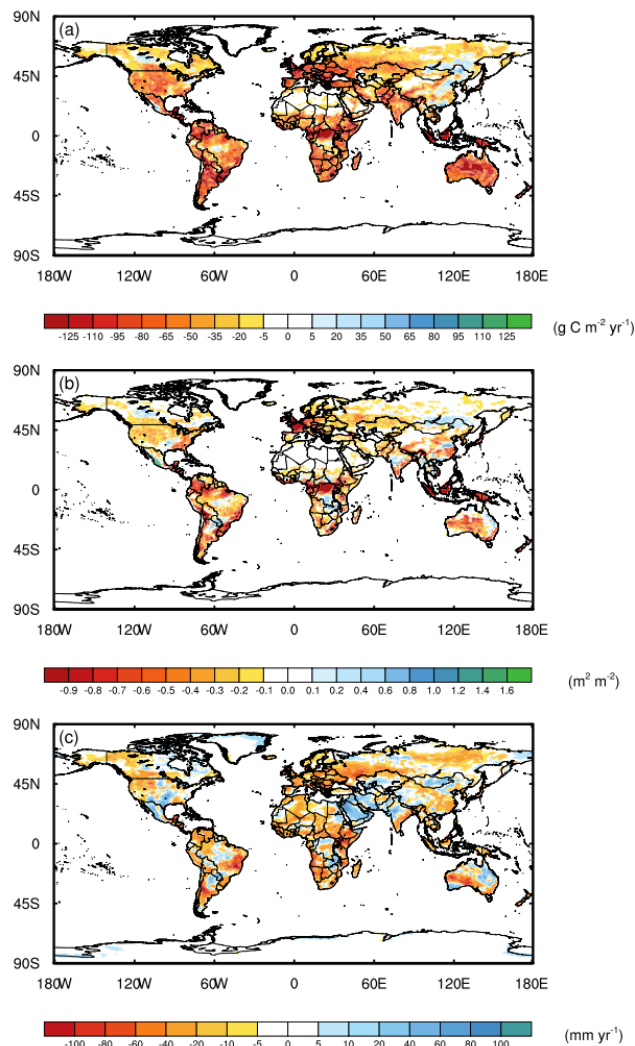
#### **7. Author contributions**

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**

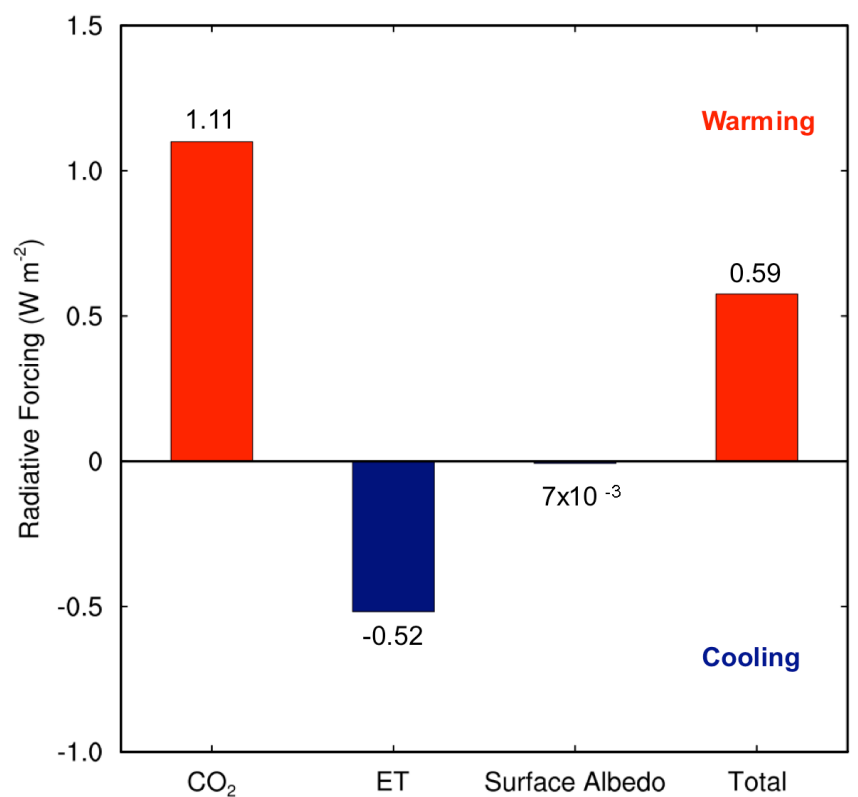
The authors declare no competing financial interests.

424 9. Figures



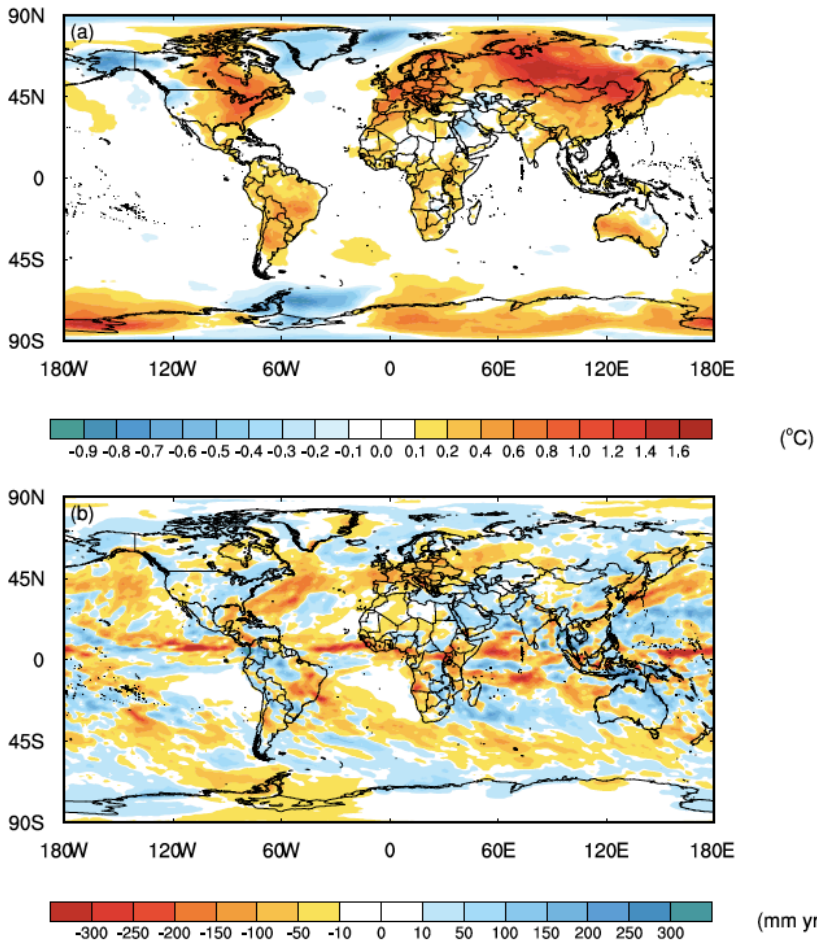
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426  
427 **Figure 1.** The C expended on symbiont-mediated N acquisition altered the spatial patterns  
428 of (a) NPP, (b) LAI and (c) ET. These results were obtained from CAM runs with and  
429 without the symbiont sub-module (CLM-FUN) and represent the mean of the last 10 years  
430 of the simulation from 1995-2004.

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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<sub>2</sub> 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) and represent the mean of the last 10 years of the simulation from 1995-2004.

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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 mean differences for each grid cell between CAM-FUN with ramping CO<sub>2</sub> and the baseline CAM for the last 10 years of the simulations from 1995-2004.

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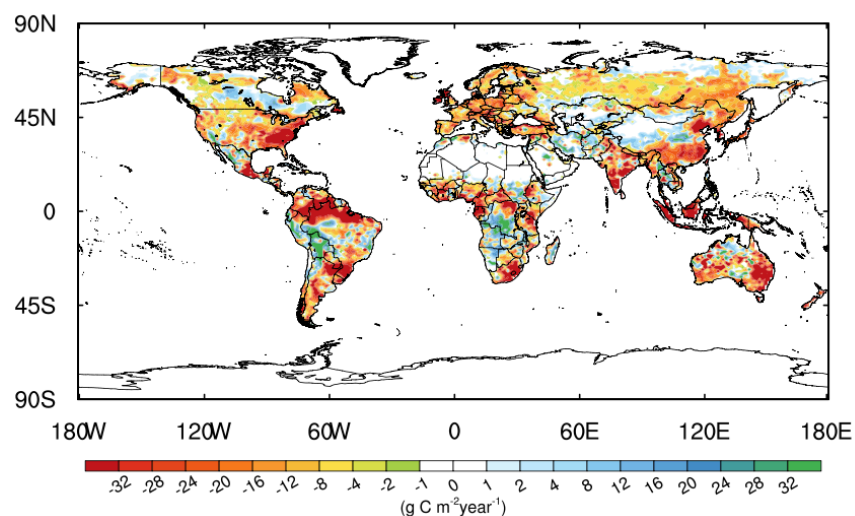
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# 11. Supplementary Materials



**Figure S1.** Impacts of parameter adjustments in FUN on predicted global NPP in CLM. Values represent the mean difference between the original parameterization and the new parameterization for the last ten years of the simulation from 1995-2004. On a global scale, the new parameterization reduced NPP from 50.8 Pg C yr<sup>-1</sup> to 49.3 Pg C yr<sup>-1</sup>.

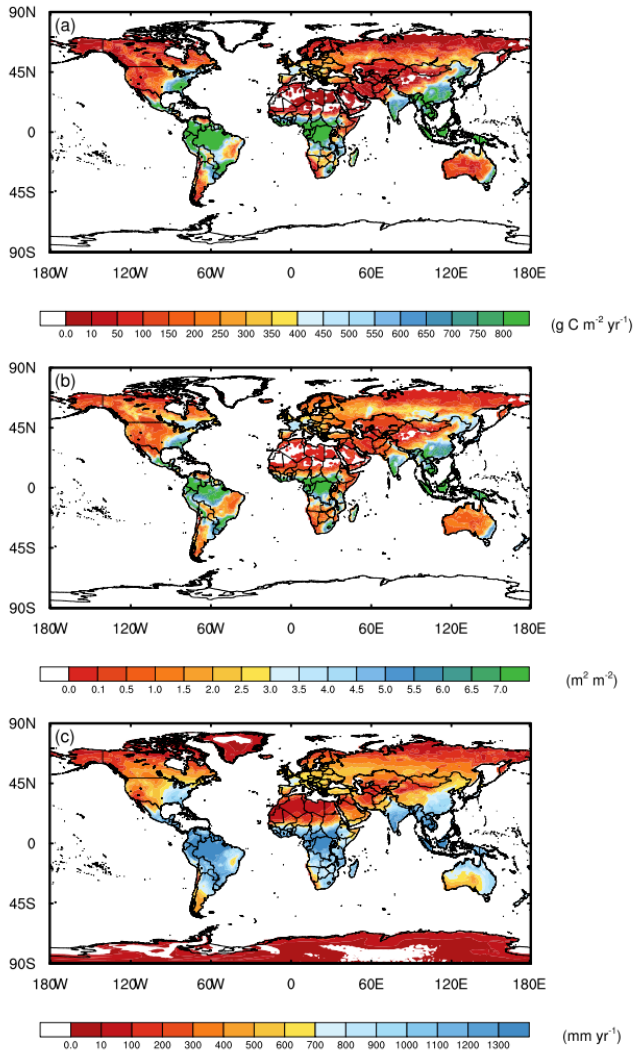


Figure S2. Absolute values of (a) NPP, (b) LAI, and (c) ET in CAM without CLM-FUN. These values represent the mean of the last ten years of the simulation from 1995-2004.

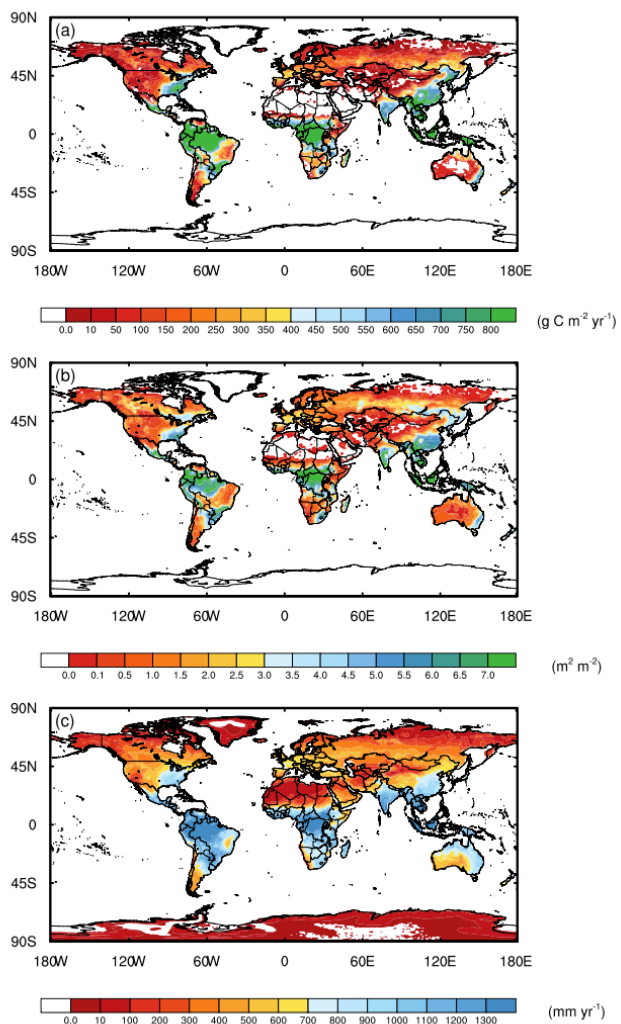


Figure S3. Absolute values of (a) NPP, (b) LAI, and (c) ET in CAM with CLM-FUN. These values represent the mean of the last ten years of the simulation from 1995-2004.

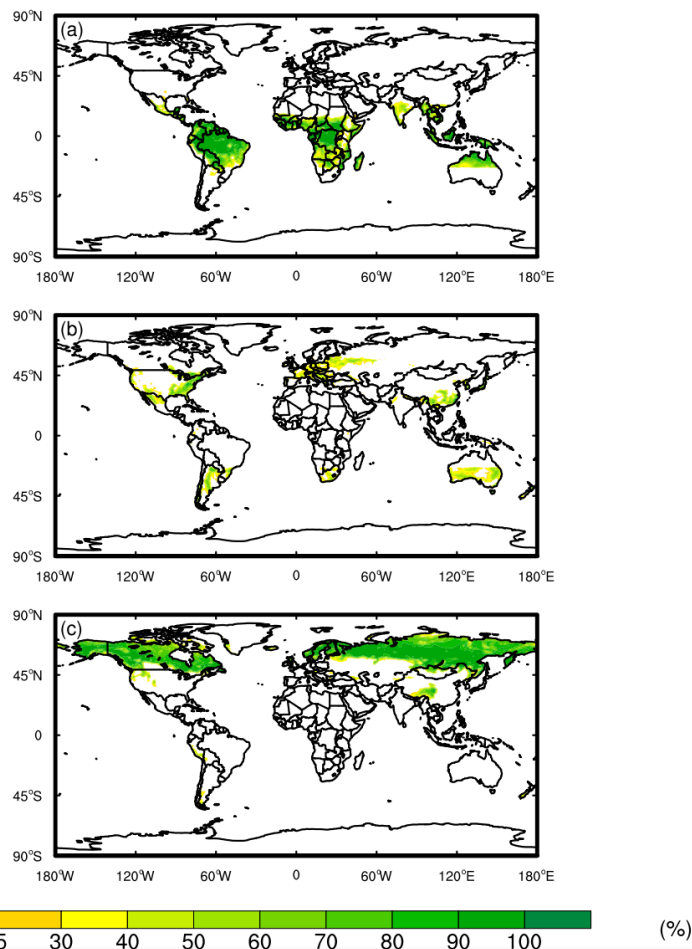


Figure S4. Global maps of three key biome classes that were analyzed for regional shifts in temperature and precipitation: (a) tropical forests, (b) temperate forests, and (c) boreal and alpine forests. Areas were delineated by grid cells that contained greater than 25% of each plant functional type.



635 **Table S1.** The adjusted parameters in CLM-FUN

Cost Parameter	Original <sup>a</sup>	Updated
AK <sub>C</sub>	2.7×10 <sup>-4</sup>	6.2
AK <sub>N</sub>	5.5×10 <sup>-5</sup>	5.5×10 <sup>-5</sup>
EK <sub>C</sub>	1.6×10 <sup>-3</sup>	34.1
EK <sub>N</sub>	2.7×10 <sup>-4</sup>	2.7×10 <sup>-4</sup>
K <sub>C</sub>	5.5×10 <sup>-5</sup>	5.5×10 <sup>-5</sup>
K <sub>N</sub>	3.3×10 <sup>-3</sup>	3.3×10 <sup>-3</sup>
K <sub>R</sub>	8.0/4.4×10 <sup>-4</sup> <sup>b</sup>	8.0/4.4×10 <sup>-4</sup> <sup>b</sup>

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637 <sup>a</sup> The parameter values used in Shi *et al.* [2016].

638 <sup>b</sup> 8.0 was used for deciduous plant functional types (PFTs) and 4.4×10<sup>-4</sup> was used for  
639 evergreen PFTs.

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