

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<sup>-1</sup>”.

**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<sup>-2</sup> should be -0.52 W m<sup>-2</sup>.

**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.*

1  
2 **Neglecting Plant-microbe Symbioses Leads to Underestimation**  
3 **of Modeled Climate Impacts**  
4

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23  
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26 **Keywords:** Mycorrhizal Fungi; Nitrogen limitation Climate Change; Community  
27 Atmosphere Model; Community Land Model, Fixation and Uptake of Nitrogen  
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33

34 **Abstract**

35 The extent to which terrestrial ecosystems slow climate change by sequestering  
36 carbon hinges in part on nutrient limitation. We used a coupled carbon–climate model that  
37 accounts for the carbon cost to plants of supporting nitrogen-acquiring microbial symbionts  
38 to explore how nitrogen limitation affects global climate. To do this, we first calculated the  
39 reduction in net primary production due to the C cost of N acquisition. We then used a  
40 climate model to estimate the impacts of the resulting increase in atmospheric CO<sub>2</sub> on  
41 temperature and precipitation regimes. The carbon costs of supporting symbiotic nitrogen  
42 uptake reduced net primary production by 8.1 Pg C yr<sup>-1</sup>, with the largest absolute effects  
43 occurring in tropical forest biomes and the largest relative changes occurring in boreal and  
44 alpine biomes. Globally, our model predicted relatively small changes in climate due to the  
45 C cost of N acquisition with temperature increasing by 0.1°C and precipitation decreasing  
46 by 6mm yr<sup>-1</sup>. However, there were strong regional impacts with the largest impact  
47 occurring in boreal and alpine ecosystems, where such costs were estimated to increase  
48 temperature by 1.0 °C and precipitation by 9 mm yr<sup>-1</sup>; as such, our results suggest that  
49 carbon expenditures to support nitrogen-acquiring microbial symbionts have critical  
50 consequences for Earth’s climate, and that carbon–climate models that omit these  
51 processes will over-predict the land carbon sink and under-predict climate change.  
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58 **1. Introduction**

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

70 Nearly all land plants have evolved symbiotic strategies for coping with nutrient  
71 limitation. Plant associations with mycorrhizal fungi such as arbuscular mycorrhizae (AM)  
72 and ectomycorrhizae (ECM), or with N-fixers, are critical for the uptake of soil nutrients  
73 and as such, impact C and nutrient cycling (Phillips *et al.* 2013; Wurzbürger *et al.* 2017).  
74 Recent data syntheses have shown that ECM and AM ecosystems have divergent C-  
75 nutrient economies that respond differently to elevated CO<sub>2</sub> and N deposition (Canham &  
76 Murphy, 2017; Terrer *et al.* 2016; Terrer *et al.* 2017). Despite this, the C cost for nutrient  
77 acquisition remains largely absent in most C-climate models which assume that plants do  
78 not expend C to take up N and that NPP is only downregulated if there is not enough N to  
79 support biomass synthesis. As such, there have been few first order estimates of the extent  
80 to which variable plant investment in strategies that facilitate N uptake can impact rates of  
81 climate change. Shi *et al.* (2016) showed that dynamically predicting and accounting for  
82 the C cost of N acquisition reduced global NPP by 13%, and thus, models that assume N  
83 uptake requires no C expenditures potentially underestimate the rate of atmospheric CO<sub>2</sub>  
84 rise. These results not only underscore the importance of including the C cost of symbiotic  
85 microbes in ESMs but also highlight the critical role that plant-microbe interactions play  
86 in mediating rates of climate change.

87 Global C-climate models represent the scientific community’s integrated  
88 hypotheses on how climate responds to anthropogenic forcing. In addition to forecasting  
89 climate, ESMs can be used to perform “experiments” at spatial and temporal scales that are  
90 logistically unfeasible to identify important feedbacks and processes in the Earth’s climate  
91 system (Fisher *et al.* 2014). Accordingly, our objective was to explore the potential  
92 feedbacks between the C cost of supporting symbiotic N acquisition ~~with~~ climate by  
93 performing model experiments with and without these costs in ~~a~~ C-climate model. To  
94 streamline the complexity of the Earth-scale computations, we ~~used the~~ Community  
95 Atmosphere Model (CAM) ~~with prescribed sea surface temperatures and sea ice and a~~  
96 ~~version of the~~ Community Land Model (CLM) which predicts ~~the impacts of symbiotic~~  
97 ~~processes on~~ coupled C and N dynamics. We are focusing on the dynamic processes  
98 between the land and atmosphere, and this C-climate model assessment represents the first  
99 effort to determine the sensitivity of the Earth’s climate system to plant-microbe symbiotic  
100 interactions.

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106 **2. Material and Methods**

107 **2.1 Models**

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

120 We used the Community Land Model version 4 (CLM) (Lawrence *et al.* 2011;  
121 Oleson *et al.* 2010). CLM is a terrestrial biosphere model that predicts the impacts of  
122 greenhouse gases and meteorological conditions on the land surface's energy, carbon, and  
123 water budgets. Importantly, CLM includes coupled C and N cycles whereby the internal  
124 recycling, loss, and inputs of N in the soil pool are dynamically modeled to predict the  
125 availability of N to support plant biomass synthesis (Lawrence *et al.* 2011; Oleson *et al.*  
126 2010).

127 FUN was recently coupled into CLM (CLM-FUN) with model simulations showing  
128 that the C cost of N acquisition reduces the C sink strength of the terrestrial biosphere (Shi  
129 *et al.* 2016). CLM-FUN predicts the C cost of N acquisition from the soil by  
130 ectomycorrhizal, arbuscular mycorrhizal, and nonmycorrhizal roots based upon root  
131 biomass (a proxy for access) and soil nitrogen concentrations (a measure of availability of  
132 N for plants to take up). Previously, the parameter controlling the sensitivity of the C cost  
133 of N acquisition to root biomass was low. As such the C cost of N acquisition showed little  
134 to no sensitivity to variability in root biomass across grid cells and the ECM cost of N  
135 acquisition was always lower than the AM cost of N acquisition even in high N biomes.  
136 We have updated this parameter so that the updated CLM-FUN is equally sensitive to both  
137 availability and access, and can better capture latitudinal gradients in the benefit of ECM  
138 uptake or AM uptake as N becomes more limiting. This adjustment also ensures that while  
139 ECM plants invest more C belowground, they get a greater return on this investment  
140 relative to AM-associated plants when the ratio of N needed to support NPP to available  
141 soil N increases (e.g., enhanced N limitation under elevated CO<sub>2</sub>) (Terrer *et al.* 2017).  
142 Specifically, we modified an AM-related uptake parameter and an ECM-related uptake  
143 parameter from  $2.7 \times 10^{-2}$  (g C m<sup>-2</sup>) to 6.2 (g C m<sup>-2</sup>) and from  $1.6 \times 10^{-3}$  (g C m<sup>-2</sup>) to 34.1 (g C m<sup>-2</sup>),  
144 respectively (see Table S1 for original and updated parameters). This parameter  
145 adjustment also resulted in small increase in the downregulation of NPP by FUN in CLM  
146 by 1.5 Pg C yr<sup>-1</sup> or ~3% for the last ten years of the model simulations from 1995-2004  
147 (Figure S1). For this parameter adjustment, the spin-up, meteorological conditions, and  
148 time period are the same as outlined for CLM in Section 2.2 below.

149 To investigate the root symbiont associated C–climate feedback, we also used  
150 Community Atmosphere Model version 4 (CAM), an atmospheric general circulation  
151 model that includes CLM (or CLM-FUN) (Neale *et al.* 2010). CAM dynamically predicts

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154 the impacts of external forcing factors such as anthropogenic CO<sub>2</sub> emissions on global and  
155 regional climate (i.e., temperature and precipitation) by dynamically representing key  
156 atmospheric process including cloud formation, aerosol impacts, radiative processes, and  
157 mixing (Neale *et al.* 2010).  
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## 159 2.2 Experimental Design

160 In the first step of our model experiment, we leveraged the ability of FUN to  
161 downregulate NPP in order to calculate the extent to which mycorrhizal fungi impact the  
162 balance of C in the atmosphere vs. plant biomass. We estimated this by calculating the  
163 difference in NPP between CLM runs with FUN turned on or off using the same  
164 ~~meteorological~~ forcing data (Qian *et al.* 2006). The surface condition and plant functional  
165 type (PFT) data are from the standard release of CLM4.0. The surface spin-up conditions,  
166 in which the plant and soil C pools are at a quasi-equilibrium state, are provided with  
167 CLM4.0 by the National Center for Atmospheric Research (NCAR). As such, both models  
168 started from the same baseline values. We ran both CLM and CLM-FUN at the 0.9°×1.25°  
169 and half-hourly spatio-temporal resolution for 25 years (1980–2004). The ambient CO<sub>2</sub>  
170 concentration was fixed to 338 ppm, the atmospheric CO<sub>2</sub> level in 1980. We calculated the  
171 mean annual NPP difference between CLM and CLM-FUN in 1995–2004, and the value  
172 was 8.1 Pg C yr<sup>-1</sup>. This additionally respired C from CLM-FUN represents the C amount  
173 that plants expend to take up N and we assumed that the all of this C went into the  
174 atmospheric pool. We then converted this mass of extra C going into the atmosphere into  
175 concentration units by dividing our mass (8.1Pg C) by the mass of C in 1ppm of CO<sub>2</sub> (2.135  
176 Pg C). As such, we assume that integrating the C costs for N acquisition leads to an  
177 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.

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178 Second, we ran two simulations of the land–atmosphere model, CAM4.0-CLM 4.0:  
179 (1) A control simulation without mycorrhizal impacts on atmospheric CO<sub>2</sub> or surface  
180 energy budgets (herein CAM), and (2) a simulation that included mycorrhizal impacts on  
181 atmospheric CO<sub>2</sub> as well as surface energy budgets (herein CAM-FUN). Due to the  
182 complexity and computational cost of running the fully coupled C-climate model, it was  
183 necessary to prescribe the increase in CO<sub>2</sub> concentrations in CAM-FUN at a 3.8ppm  
184 increase per year to reflect the transfer of C from NPP to the atmosphere. The CAM runs  
185 did have dynamic representations of how the C cost of N acquisition impacted leaf area  
186 index (LAI), evapotranspiration (ET), and resulting energy budgets. We acknowledge that  
187 this assumption simplifies many of the interactions between the land, atmosphere and  
188 ocean C pools. However, given that our objective was to provide a first approximation of  
189 how the C cost of N acquisition could impact climate, the prescribed CO<sub>2</sub> increase provides  
190 a balance between meeting that objective and minimizing computational costs. We used  
191 the specified modern climatological sea surface temperatures and sea ice distributions and  
192 ran the models at the 0.9°×1.25° and half-hourly spatio-temporal resolution for 25 years  
193 ~~from 1980-2004~~. In CAM, the ambient CO<sub>2</sub> concentration was 338 ppm. For all other  
194 model inputs, we used the default input files that are automatically loaded during each  
195 model run, such that both CAM and CAM-FUN start off with the same initial conditions.  
196 In CAM-FUN, we assumed that atmospheric CO<sub>2</sub> started increasing from 338 ppm at the  
197 3.8 ppm of CO<sub>2</sub> annual rate, and all the respired CO<sub>2</sub> is mixed into the atmosphere  
198 homogenously. We also ~~present the means of~~ the CAM-based results ~~for~~ the last 10  
199 simulation years ~~from 1995-2004~~. We evaluated the climate impacts resulting from

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203 including the mycorrhizal dynamics into CAM by calculating the surface air temperature  
204 and precipitation differences between CAM and CAM-FUN in different regions.

205 In this study, we also estimated the radiative forcing variations causing the climate  
206 impacts. We did this in order to identify which factor, ET vs. LAI vs. enhanced atmospheric  
207 CO<sub>2</sub>, led to our observed shifts in climate. It also allowed us to identify if the three different  
208 forcing factors had a cooling or warming effect on the climate. We use the reflected solar  
209 radiation difference between CAM and CAM-FUN to estimate the radiative forcing  
210 variations from surface albedo change due to shifts in LAI. The evapotranspiration (ET)  
211 difference between these two model runs was used to estimate the radiative forcing from  
212 ET variation. The radiative forcing from CO<sub>2</sub> increase was calculated with an empirical  
213 equation (Myhre *et al.* 1998):

$$214 \Delta F = \alpha \ln\left(\frac{C}{C_0}\right) \quad (1)$$

215 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  
216 reference concentration, which is 338 ppm, the atmospheric CO<sub>2</sub> level in 1980.

### 217 218 3. Results

219 Compared to the CAM runs where N was obtained at no cost, when we included  
220 the C cost of symbiont-mediated N acquisition (i.e., CAM-FUN), C uptake by the terrestrial  
221 biosphere was more strongly constrained by N availability. Consequently, N limitation  
222 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  
223 area index (LAI; Figures 1a and 1b), and surface energy budgets (Figure 2). Globally, NPP  
224 and LAI were affected similarly, with the strongest relative effects occurring at the poles  
225 and the strongest absolute effects occurring near the equator. In addition, we analyzed  
226 temperature and precipitation shifts across three key biome classes that are delineated in  
227 Figure S4. In boreal and alpine ecosystems, LAI was reduced by 34% (a decrease of 0.05  
228 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  
229 temperate ecosystems, LAI was reduced by 17% (a decrease of 0.16 m<sup>2</sup> m<sup>-2</sup>) while NPP was  
230 reduced by 33% (a decrease of 30 g C m<sup>-2</sup>yr<sup>-1</sup>). Tropical forest ecosystems had the largest  
231 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%  
232 decrease). Compared to NPP and LAI, ET had a more heterogeneous spatial pattern with a  
233 global mean ET reduction 7.3 mm yr<sup>-1</sup>, which represents a ~3% decrease across all of the  
234 ecosystems (Figure 1c). While we present differences between model runs in LAI, ET and  
235 NPP in Figure 1, global maps of the absolute values are presented in Figures S2 & S3.

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

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253 While the averaged global impact of the C cost of microbial symbionts on climate  
254 was minor (i.e., 0.1 °C surface air temperature increase and 6 mm yr<sup>-1</sup> precipitation decrease),  
255 there were strong regional impacts in key biomes, particularly in forested regions with  
256 ECM fungi (Figure 3). Moreover, the regional shifts in temperature were stronger those of  
257 precipitation with shifts in precipitation being much more variable and patchier than those  
258 of temperature (Figure 3). Given difficulties in predicting regional precipitation as well as  
259 the high variability in our estimates, we present the data but acknowledge that these  
260 regional estimates are uncertain. ECM-dominated areas in boreal and alpine biomes,  
261 became warmer (increases in surface air temperature by 1.0 °C) and wetter (increases in  
262 precipitation by 9 mm yr<sup>-1</sup>). Temperate forest ecosystems, which include plants that possess  
263 all three nutrient acquisition strategies, were also impacted. The eastern part of North  
264 America, Europe, and China had surface air temperature increases of 0.5 °C, and  
265 precipitation shifted by 11, -37, and 2 mm yr<sup>-1</sup> in these three regions, respectively. Tropical  
266 forests, which are dominated by AM fungi, were impacted less with temperature; Amazon  
267 and Congo basin both had temperature increase by ~0.3 °C. However, precipitation  
268 changes in tropical forests varied, with the Amazon and Congo basins drying by 4 mm yr<sup>-1</sup>  
269 and 49 mm yr<sup>-1</sup>, respectively.

#### 271 4. Discussion and Conclusions

272 Here, we demonstrate that integrating the C cost of N acquisition into the  
273 formulation of N limitation in CAM reduced global NPP, LAI, and ET, with the greatest  
274 percentage decreases in boreal and alpine ecosystems (Figure 1). These reductions led to  
275 substantial impacts on climate, particularly in boreal and alpine ecosystems where  
276 temperature increased by 1°C and precipitation increased by 9 mm yr<sup>-1</sup> over the last ten  
277 years of the simulations (1995-2004) (Figure 3). It is important to note, that the regional  
278 impacts of the C cost of N acquisition on temperature were much stronger than those on  
279 precipitation. These results suggest that by reducing C stored in woody biomass, the C  
280 transferred to symbionts leads to more atmospheric CO<sub>2</sub> that would otherwise be locked up  
281 in vegetation (Figure 2). This reduction in terrestrial productivity (Figure 1a) and decrease  
282 of terrestrial C sink in CAM-FUN appears to alter the partitioning of energy fluxes at the  
283 land surface into sensible heat flux as well, which accelerates land-surface warming and  
284 intensified regional land-atmosphere feedback (Jung *et al.* 2010). Collectively, these  
285 results suggest that the C cost of symbiont-mediated N acquisition is an important  
286 component of the Earth's climate system that has the potential to alter future climate  
287 trajectories.

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

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305 We found greater spatial heterogeneity in ET shifts than NPP or LAI shifts when  
306 we included the C cost of microbial symbionts in the model (Figure 1). Some of this spatial  
307 variability may reflect the high sensitivity of ET to increases in atmospheric CO<sub>2</sub>  
308 concentrations (Shi *et al.* 2013). Moreover, this variability likely reflects the large  
309 uncertainties and challenges associated with simulating regional scale ET in coupled  
310 climate–atmosphere models (Boé & Terray, 2008; Pan *et al.* 2015). However, on the global  
311 scale, the reduction of ET, which decreased the atmospheric concentration of water vapor,  
312 a potent greenhouse gas, led to a  $-0.52 \text{ W m}^{-2}$  radiative forcing change (Figure 2). This  
313 result is consistent with the Institut Pierre Simon Laplace climate model (IPSL-CM4)  
314 (Davin *et al.* 2007), where ET was also reduced globally and had a net cooling effect on  
315 global temperatures. Nevertheless, this cooling effect was outweighed by the warming  
316 effect of increasing atmospheric CO<sub>2</sub> concentrations in CAM-FUN.

317 Our results suggest that models that do not account for plant-microbe symbiotic  
318 interactions and the C cost of N acquisition may underestimate both N limitation to NPP  
319 and rates of climate change. Nutrient limitation remains a key area of uncertainty for ESMs  
320 with the CMIP5 comparison highlighting the limited representations of N limitation as a  
321 primary reason for mismatch between the models and the observed C sink (Anav *et al.*  
322 2013). Additionally, CAM-FUN identifies an important underestimation of nutrient  
323 limitation and climate shifts in **boreal and alpine ecosystems** that has the potential to  
324 enhance other climate feedbacks. Boreal forests, which dominate high-latitude regions, are  
325 characterized by low rates of soil decomposition and low N availability (Read *et al.* 2004).  
326 This leads to CAM-FUN predicting that boreal forests expend nearly 18% of NPP to gain  
327 N through symbionts, a result that is supported by a recent empirical synthesis which found  
328 that boreal forests have a 13-fold greater C cost of soil resource acquisition than tropical  
329 forests (Gill & Finzi, 2016). However, to the extent that the greater C cost to ECM plants  
330 (relative to AM plants) provides a greater return on investment of N under elevated CO<sub>2</sub>  
331 (Terrer *et al.* 2017), some of the predicted warming may be attenuated over time.  
332 Nevertheless, predicted acceleration of warming in boreal forests is likely to be  
333 consequential given feedbacks between surface warming with sea ice cover loss, sea  
334 surface temperature increase, and permafrost thaw (Parmentier *et al.* 2013).

335 While CAM-FUN identifies an important interaction between the C cost of N  
336 limitation and climate, there still remain key uncertainties in the model on the extent to  
337 which other processes that govern the C cost of acquiring soil resources impacts C-climate  
338 feedbacks. First, not all ecosystems are predominantly N limited (Wang *et al.* 2010). Nearly  
339 30% of terrestrial ecosystems are limited by phosphorus (P) or water (Elser *et al.*, 2007,  
340 Fisher *et al.*, 2010, Wieder *et al.*, 2015). **These are** two key limitations that are currently  
341 absent from the model that may alter the climate trajectories shown here, particularly for  
342 strongly P-limited ecosystems like tropical forests or water-limited ecosystems like  
343 Mediterranean forests. However, FUN utilizes a modular structure based on optimal  
344 allocation theory that could incorporate the C costs of P or water acquisition on NPP and  
345 hence climate. As such, the optimal allocation parameterization in FUN could be modified  
346 to include other resource costs and thus provides a framework for ESMs to assess how  
347 multiple resource limitation impacts climate.

348 Second, the climate impacts we identify are sensitive to factors that alter N  
349 availability. Across many ecosystems, increasing soil temperatures that enhance  
350 decomposition (Melillo *et al.* 2011) or rising rates of N deposition in developing countries

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354 (Liu *et al.* 2013) could increase N availability and lower the C cost of N acquisition.  
355 Moreover, as currently formulated, the model omits important feedbacks between C  
356 allocation to mycorrhizal symbionts and their ability to upregulate soil enzyme production,  
357 prime soil organic matter decomposition and increase N availability (Brzostek *et al.* 2015,  
358 Cheng *et al.* 2014, Finzi *et al.* 2015). A recent effort to couple FUN to a microbial soil  
359 enzyme model at the ecosystem scale has shown that the ability of ECM fungi to prime  
360 soil organic matter allowed them to mine N at the expense of soil C stocks to a greater  
361 extent under elevated CO<sub>2</sub> than AM fungi (Sulman *et al.* 2017). This result is consistent  
362 with recent meta-analyses that show that even though ECM plants invest more C  
363 belowground than AM plants, they receive a greater N return on their investment under  
364 elevated CO<sub>2</sub> (Terrer *et al.* 2017). As such, integrating C and N feedbacks between plant  
365 and symbiotic microbes at the global scale represents a critical area for future model  
366 development.

367 Finally, we acknowledge that the simplification of land-atmosphere interactions in  
368 our model experiment may have precluded our ability to examine fully coupled feedbacks  
369 that may have stimulated the land or ocean C sink. This simplification was needed owing  
370 to the complexity and computational resources needed to run the fully coupled model. As  
371 such, our estimates of the sensitivity of climate to the C cost of N acquisition likely  
372 represents an upper bound. This is due to two reasons. First, we assumed that all of the  
373 carbon not sequestered as NPP was released into the atmosphere as CO<sub>2</sub>. In a fully coupled  
374 model, it is likely that a portion of this CO<sub>2</sub> would have been sequestered by the ocean.  
375 Second, the reduction of NPP due to the C cost of N acquisition also reduced heterotrophic  
376 respiration by 3.3 Pg C yr<sup>-1</sup>. However, both empirical and modeling evidence suggests that  
377 C expended belowground to gain N leads to greater soil organic matter decomposition and  
378 respiration due to priming effects (Brzostek *et al.* 2015; Sulman *et al.* 2017). Lastly,  
379 compared to other ESMs included in the Fifth Phase of the Coupled Model Intercomparison  
380 Project (CMIP5), the land C pool in CESM/CLM4 is underestimated (Hoffman *et al.* 2014),  
381 associated with a high-biased N downregulation and short turnover times for decomposing  
382 C (Koven *et al.* 2014). This low-biased land C pool indicates an overestimation of the  
383 atmospheric CO<sub>2</sub> burden over the 20th century (Hoffman *et al.* 2014). Despite our  
384 assumptions, experimental design, and bias impacting the model's ability to predict  
385 absolute numbers, our modeling experiments allowed us to make the first test of the  
386 sensitivity of the Earth's climate system to plant-microbial interactions.

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

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

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406 **6. Acknowledgments.** Funding was provided by the US Department of Energy (Office of  
407 Biological and Environmental Research, Terrestrial Ecosystem Science Program) and the  
408 US National Science Foundation (Division of Environmental Biology, Ecosystem Studies  
409 Program. The computations were performed at the Jet Propulsion Laboratory and at the  
410 National Aeronautics and Space Administration (NASA) Ames Research Center. Junjie  
411 Liu assisted with the computational resources. MS and JBF carried out the research at the  
412 Jet Propulsion Laboratory, California Institute of Technology, under a contract with NASA,  
413 and at the Joint Institute for Regional Earth System Science and Engineering, University  
414 of California at Los Angeles. Government sponsorship acknowledged. Copyright 2018. All  
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417 **7. Author contributions**

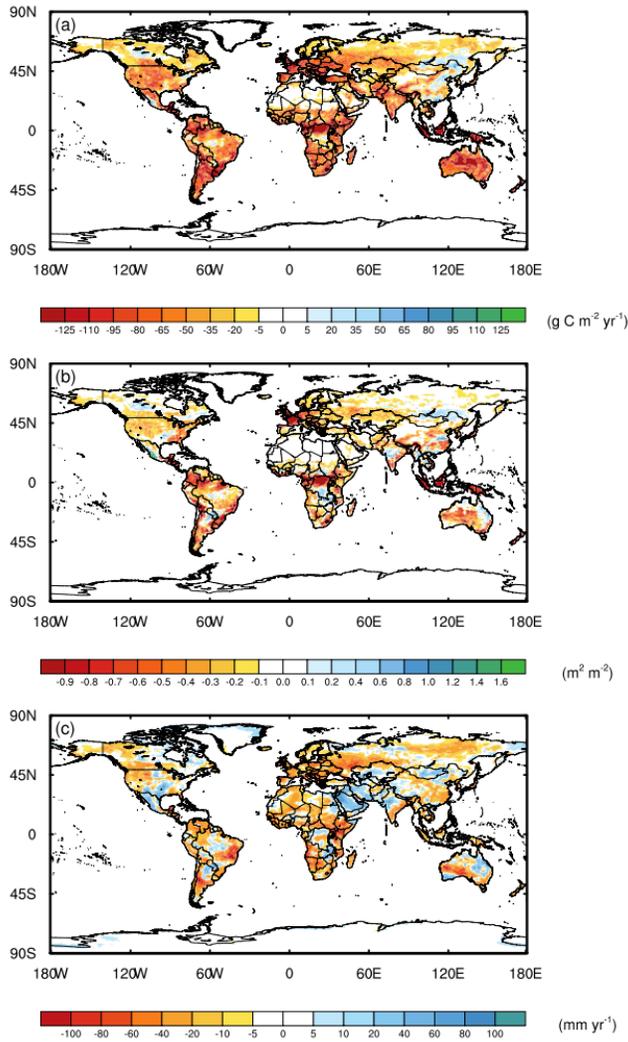
418 M.S. and E.R.B designed the research; M.S. conducted the model simulations and  
419 performed the analyses; E.R.B and J.B.F contributed essential ideas of analyzing the  
420 results; E.R.B and M.S wrote the manuscript with contributions from J.B.F. and R.P.P.

421

422 **8. Competing interests**

423 The authors declare no competing financial interests.

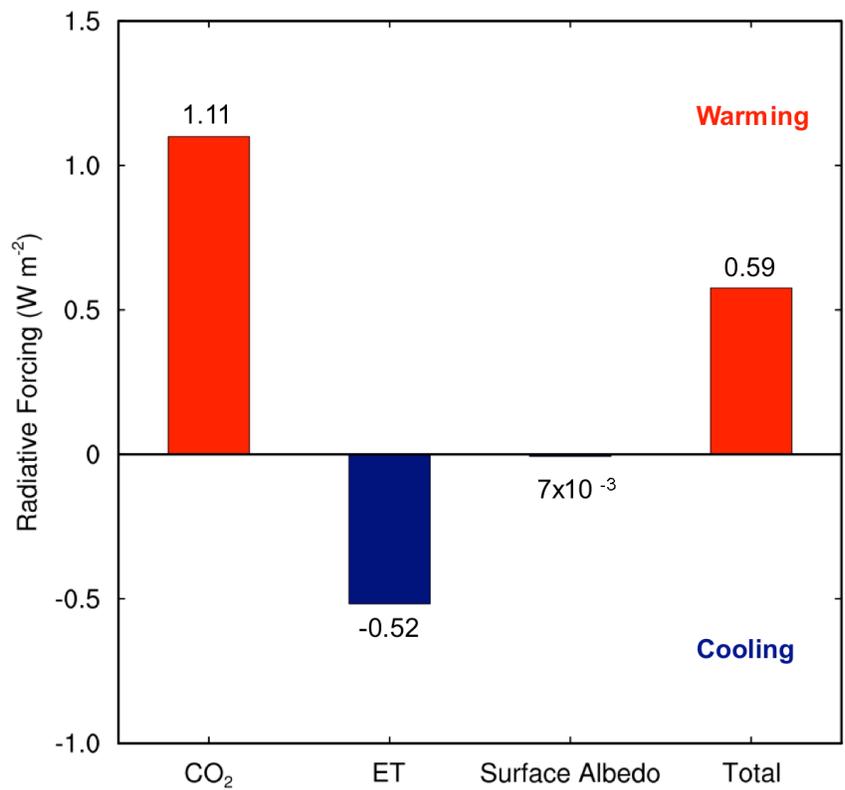
424 9. Figures



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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.

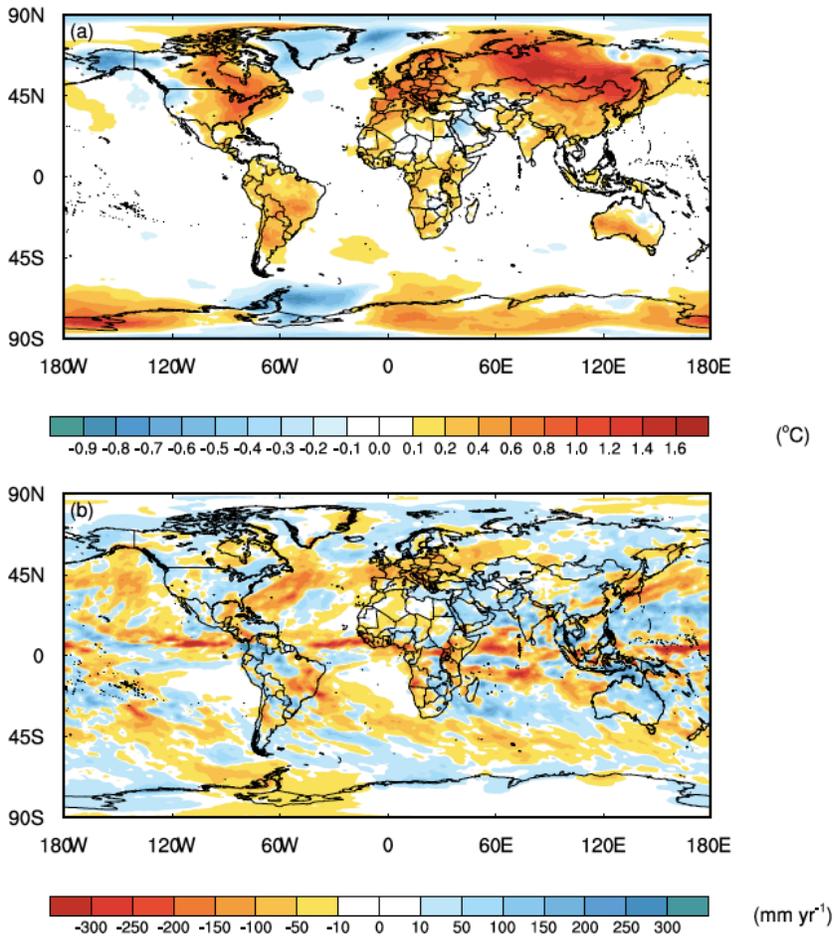
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**Figure 2.** The impacts of the C cost of symbiont-mediated N acquisition led to a net increase in global radiative forcing. The warming due to increasing atmospheric CO<sub>2</sub> was offset partially by cooling due to reduced evapotranspiration (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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 444 **Figure 3.** Feedbacks between symbiont-mediated N acquisition and C have a direct impact  
 445 on global climate. (a) Surface air temperatures increase across much of the land surface;  
 446 whereas (b) precipitation patterns are more variable. The values represent the mean  
 447 differences for each grid cell between CAM-FUN with ramping CO<sub>2</sub> and the baseline CAM  
 448 for the last 10 years of the simulations from 1995-2004.  
 449

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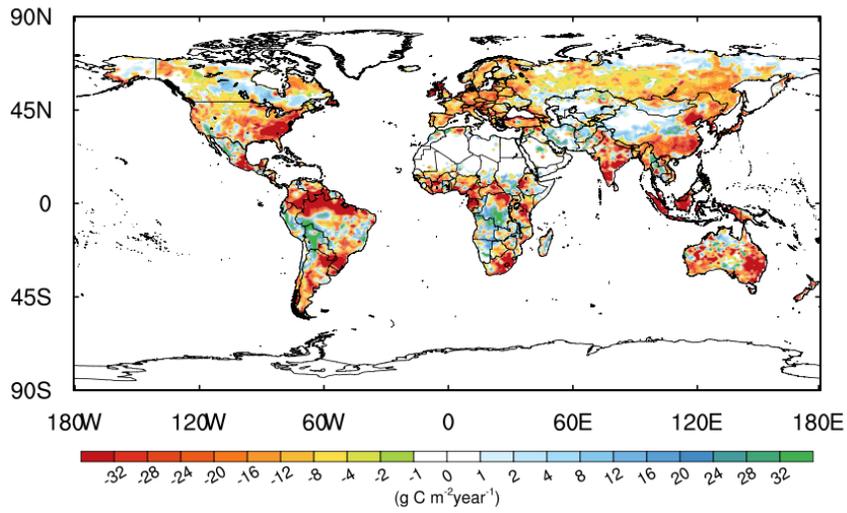
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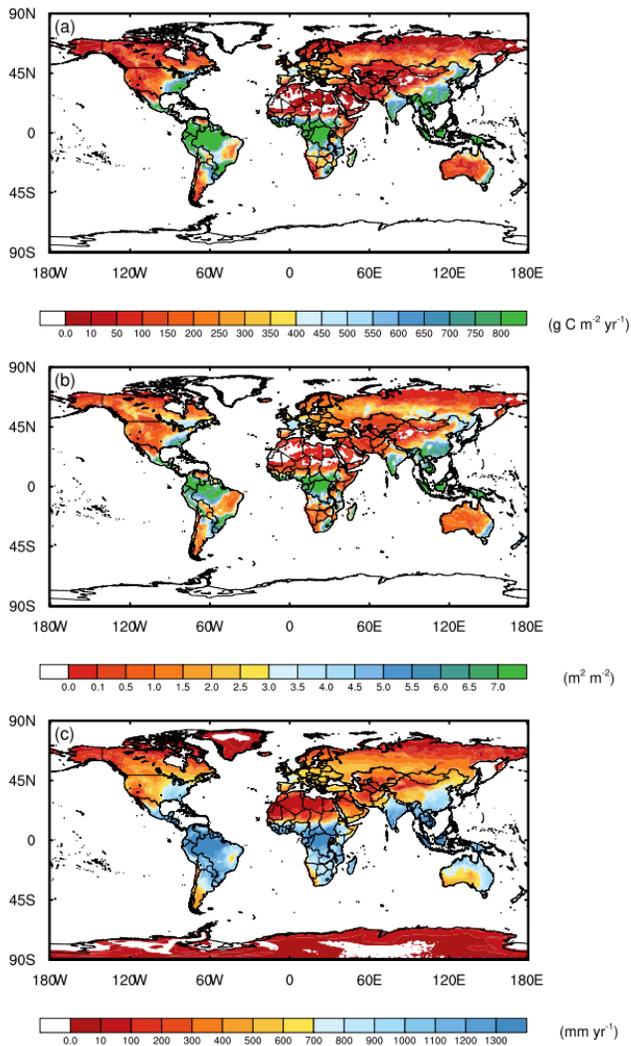
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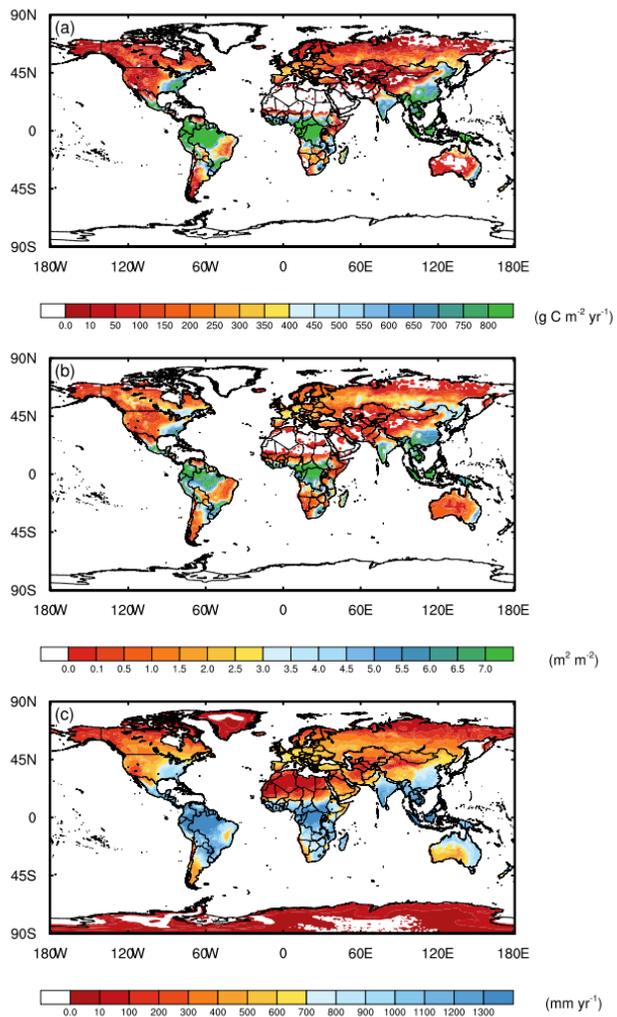
613 11. Supplementary Materials  
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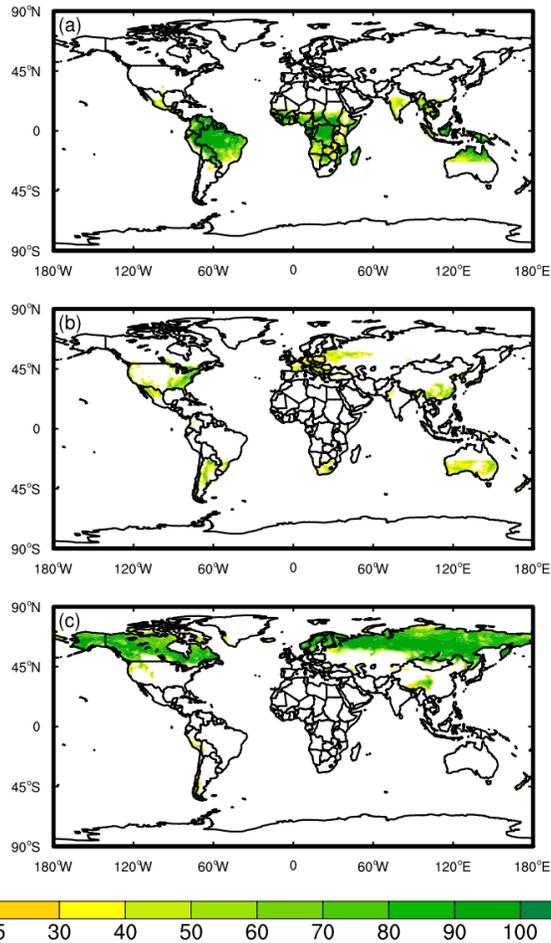
615 **Figure S1.** Impacts of parameter adjustments in FUN on predicted global NPP in CLM.  
616 Values represent the mean difference between the original parameterization and the new  
617 parameterization for the last ten years of the simulation from 1995-2004. On a global scale,  
618 the new parameterization reduced NPP from 50.8 Pg C yr<sup>-1</sup> to 49.3 Pg C yr<sup>-1</sup>.  
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 622 Figure S2. Absolute values of (a) NPP, (b) LAI, and (c) ET in CAM without CLM-FUN.  
 623 These values represent the mean of the last ten years of the simulation from 1995-2004.  
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 627 Figure S3. Absolute values of (a) NPP, (b) LAI, and (c) ET in CAM with CLM-FUN.  
 628 These values represent the mean of the last ten years of the simulation from 1995-2004.  
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630  
 631 Figure S4. Global maps of three key biome classes that were analyzed for regional shifts  
 632 in temperature and precipitation: (a) tropical forests, (b) temperate forests, and (c) boreal  
 633 and alpine forests. Areas were delineated by grid cells that contained greater than 25% of  
 634 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>

636

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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