

# Lawrence Berkeley National Laboratory

## LBL Publications

### Title

Leaf Trait Plasticity Alters Competitive Ability and Functioning of Simulated Tropical Trees in Response to Elevated Carbon Dioxide

### Permalink

<https://escholarship.org/uc/item/3n1623nm>

### Journal

Global Biogeochemical Cycles, 35(2)

### ISSN

0886-6236

### Authors

Kovenock, Marlies  
Koven, Charles D  
Knox, Ryan G  
et al.

### Publication Date

2021-02-01

### DOI

10.1029/2020gb006807

Peer reviewed

1           **Leaf trait plasticity alters competitive ability and**  
2           **functioning of simulated tropical trees in response to**  
3           **elevated carbon dioxide**

4           **Marlies Kovenock<sup>1</sup>, Charles D. Koven<sup>2</sup>, Ryan G. Knox<sup>2</sup>, Rosie A. Fisher<sup>3,4</sup>, &**  
5           **Abigail L.S. Swann<sup>5,1</sup>**

6   <sup>1</sup>Department of Biology, University of Washington, Seattle, WA

7   <sup>2</sup>Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA

8   <sup>3</sup>National Center for Atmospheric Research, Boulder, CO

9   <sup>4</sup>Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique (CERFACS), Toulouse,

10   France

11   <sup>5</sup>Department of Atmospheric Sciences, University of Washington, Seattle, WA

12           **Key Points:**

- 13           • Including the observed response of leaf traits to higher CO<sub>2</sub> results in lower com-  
14           petitive ability for modeled tropical trees
- 15           • Concurrent changes in multiple leaf traits could help maintain per-area photosyn-  
16           thetic rates and confer a competitive advantage
- 17           • Resulting ecosystem-scale carbon uptake depends on the magnitude of trait plas-  
18           ticity coupled with changes in plant type abundance

---

Corresponding author: Abigail L.S. Swann, [aswann@uw.edu](mailto:aswann@uw.edu)

**Abstract**

The response of tropical ecosystems to elevated carbon dioxide ( $\text{CO}_2$ ) remains a critical uncertainty in projections of future climate. Here we investigate how leaf trait plasticity in response to elevated  $\text{CO}_2$  alters projections of tropical forest competitive dynamics and functioning. We use vegetation demographic model simulations to quantify how plasticity in leaf mass per area and leaf carbon to nitrogen ratio alter the responses of carbon uptake, evapotranspiration, and competitive ability to a doubling of  $\text{CO}_2$  in a tropical forest. Observationally constrained leaf trait plasticity in response to  $\text{CO}_2$  fertilization reduces the degree to which tropical tree carbon uptake is affected by a doubling of  $\text{CO}_2$  (up to -14.7% as compared to a case with no plasticity; 95% confidence interval  $CI_{95\%}$  -14.4 to -15.0). It also diminishes evapotranspiration (up to -7.0%,  $CI_{95\%}$  -6.4 to -7.7), and lowers competitive ability in comparison to a tree with no plasticity. Consideration of leaf trait plasticity to elevated  $\text{CO}_2$  lowers tropical ecosystem carbon uptake and evapotranspirative cooling in the absence of changes in plant type abundance. However, ‘plastic’ responses to high  $\text{CO}_2$  which maintain higher levels of plant productivity are potentially more competitively advantageous, thus, including changes in plant type abundance may mitigate these decreases in ecosystem functioning. Models that explicitly represent competition between plants with alternative leaf trait plasticity in response to elevated  $\text{CO}_2$  are needed to capture these influences on tropical forest functioning and large-scale climate.

**Plain Language Summary**

When tropical trees grown in air with a high concentrations of carbon dioxide it has been observed that they grow leaves and change aspects of how leaves work, called leaf traits. We used computer simulations to look at how changes in two particular leaf traits, leaf thickness and the concentration of nitrogen in leaves, alter how much tropical trees grow when carbon dioxide concentrations are high. We find that trees grow less when they have lower concentrations of nitrogen in leaves, but that if they can simultaneously make their leaves thicker this alleviates the negative effects. This holds true both when plants are growing without any competition, and also corresponds to how likely they are to grow better than a neighbor with a different combination of leaf traits. Our findings suggest that if tropical trees change only the concentration of nitrogen in their leaves then tree growth and the related transfer of carbon into the land and water back to the atmosphere will be reduced. However if the two trait changes occur simultaneously tropical forests could maintain exchanges of carbon and water close to the rates at which they currently occur.

**1 Introduction**

Tropical forests currently exert strong control over large-scale carbon, water, and energy fluxes and thus strongly influence global climate (Bonan, 2008; Davin & de Noblet-Ducoudré, 2010; Cusack et al., 2016; Cox et al., 2000). Yet, the poorly understood response of tropical ecosystems to elevated carbon dioxide ( $\text{CO}_2$ ) over the coming decades and centuries remains a key uncertainty in projections of future climate (e.g., Ciais et al., 2013; Zhang et al., 2015; Lloyd & Farquhar, 2008; Schimel et al., 2015; Brienen et al., 2015; Hickler et al., 2008; Fisher et al., 2010; Cernusak et al., 2013; Leakey, Bishop, & Ainsworth, 2012; van der Sleen et al., 2015; Cusack et al., 2016). Predictive models of the carbon cycle are predicated on using observable plant properties (traits) as inputs to mechanistic models that project the functioning of ecosystems under unobserved future conditions. Typically, most plant traits are fixed in these models for a given plant functional type, irrespective of environmental conditions, although some newer approaches allow traits to vary based on optimality arguments (e.g. Caldararu et al., 2020). In reality, leaf traits vary both across plant types as well as within plant types across envi-

ronmental gradients. Further, under experimental conditions, a number of leaf traits have demonstrated plasticity, in that the leaves of existing trees are altered in response to, for example, elevated CO<sub>2</sub> concentrations (e.g., Garbutt et al., 1990; Yin, 2002; Verheijen et al., 2015). Alterations in leaf traits can modify plant photosynthesis and evapotranspiration rates. Thus this leaf trait plasticity could alter ecosystem functioning, with potential implications for large-scale climate. We use the term ‘plasticity’, rather than ‘acclimation’ to allow for the fact that these changes might occur as a result of nutrient scarcity, rather than a specific ‘acclimation’ to altered conditions. The capacity for leaf trait plasticity to alter ecosystem functioning could act directly, without changes in plant type abundance, as well as indirectly, through changes in plant competitive dynamics and thus the relative abundance of different plant types.

Among the most commonly observed plant trait responses to experimentally elevated CO<sub>2</sub> are increases in leaf mass per area (LMA, *g* leaf carbon *m*<sup>-2</sup> leaf area) and the ratio of carbon to nitrogen within leaves (C:N<sub>leaf</sub>, *g* leaf carbon *g*<sup>-1</sup> leaf nitrogen). Observations suggest that each of these leaf traits could increase by as much as one-third under doubled CO<sub>2</sub> in a wide range of tropical tree species spanning successional classes (Fig. 1; Lovelock et al., 1998; Reekie & Bazzaz, 1989; Winter et al., 2000; Winter & Lovelock, 1999) implying thicker leaves with lower mass-based nitrogen concentrations. Comparison of Earth system model simulations to observations at ecosystem-scale CO<sub>2</sub> enrichment experiments suggests that accurately representing these two leaf traits is critical to predicting ecosystem responses to elevated CO<sub>2</sub> (Zaehle et al., 2014; De Kauwe et al., 2014; Medlyn et al., 2015). Fisher et al. (2019) also found that LMA was a critical control over the responsiveness of ecosystems in the CLM5 land surface model.

The leading hypothesis for why C:N<sub>leaf</sub> and LMA increase with elevated CO<sub>2</sub> is that CO<sub>2</sub> fertilization leads to nitrogen limitation of plant growth and the accumulation of nonstructural carbohydrates in leaves (Winter et al., 2001; Poorter et al., 2009, 1997; Pritchard et al., 1999; Roumet et al., 1999; Meyerholt & Zaehle, 2015). This is also consistent with the prediction from optimality approaches which suggest that higher CO<sub>2</sub> should lead to lower allocation to rubisco in favor of allocating the nitrogen to other parts of the plant (Xu et al., 2012; Quebbeman & Ramirez, 2016; Smith et al., 2019). While both LMA and C:N<sub>leaf</sub> trait changes have potential benefits (discussed below), it is possible that these changes are forced upon plants as there is not enough nitrogen to retain default leaf traits under high CO<sub>2</sub>. It is possible that even if plastic responses of LMA and C:N<sub>leaf</sub> do not lead to increased assimilation they could still benefit plants, i.e. by allowing for more efficient use of N across the plant. Here we impose a range of C:N<sub>leaf</sub> and LMA plasticity levels and quantify the total canopy nitrogen required to support each leaf trait plasticity level.

### 1.1 Direct effects of trait plasticity

Plasticity in C:N<sub>leaf</sub> and LMA directly influence tropical forest functioning by altering area-based photosynthetic rates. C:N<sub>leaf</sub> is the amount of nitrogen present in a given unit of leaf mass, with higher C:N<sub>leaf</sub> indicating a lower amount of nitrogen per unit leaf mass. LMA describes the mass used to construct a unit of leaf area. Together these two traits control the nitrogen per leaf area (N<sub>area</sub>, *g* nitrogen *m*<sup>-2</sup> leaf area) as follows:

$$N_{area} = \frac{LMA}{C:N_{leaf}} \quad (1)$$

Given that nitrogen is an essential component of photosynthetic enzymes, particularly rubisco, N<sub>area</sub> is an important determinant of maximum photosynthetic rates per leaf area (Drake & González-Meler, 1997; Kattge et al., 2009, 2011; Walker et al., 2014; Norby et al., 2017). N<sub>area</sub> is therefore used in many terrestrial biosphere models to es-

117 timate photosynthetic parameters, which in turn exert strong influence over modeled car-  
 118 bon uptake (Verheijen et al., 2013; Bonan et al., 2011; Walker et al., 2017; Rogers et al.,  
 119 2017). Changes in maximum photosynthetic rates due to altered  $N_{area}$  can also influ-  
 120 ence rates of evapotranspirative cooling, as transpiration is coupled to photosynthesis  
 121 in all commonly used stomatal conductance algorithms (Ball et al., 1987; Medlyn et al.,  
 122 2011).

123 Experimental manipulation of  $CO_2$  in tropical forest systems has been observed  
 124 to modify both LMA and  $C:N_{leaf}$  in a wide range of tropical tree species across succes-  
 125 sional classes (Lovelock et al., 1998). These observations suggest that co-occurring changes  
 126 in LMA and  $C:N_{leaf}$  in response to a doubling of  $CO_2$  most often caused  $N_{area}$  to de-  
 127 crease (Fig. 1 below diagonal line) or, in fewer cases, to be maintained (Fig. 1 on diag-  
 128 onal line; Lovelock et al., 1998). Thus, in the absence of other changes (such as adjusted  
 129 partitioning of nitrogen between different photosynthetic processes; e.g., Xu et al., 2012;  
 130 Leakey, Ainsworth, et al., 2012; Smith et al., 2019) the observed leaf trait plasticity in  
 131 response to elevated  $CO_2$  has the potential to lower projections of tropical ecosystem car-  
 132 bon uptake and evapotranspirative cooling by reducing photosynthetic rates and stom-  
 133 atal conductance.

134 Leaf trait plasticity could also directly influence ecosystem functioning by modi-  
 135 fying leaf area index (LAI,  $m^2$  leaf area  $m^{-2}$  ground), which provides the surface area  
 136 over which photosynthesis and transpiration are scaled to the ecosystem level. Increas-  
 137 ing LMA increases the carbon cost of building leaf area, as thicker leaves require more  
 138 carbon to build a given unit of leaf area. For a given unit mass of carbon allocation to  
 139 leaves, LMA is, by definition, used to calculate plant leaf area. In terms of nutrient bud-  
 140 gets, for a constant  $C:N_{leaf}$ , increasing LMA also increases nitrogen requirements, while  
 141 increasing  $C:N_{leaf}$  makes leaf area less expensive in terms of nitrogen. In models, these  
 142 dynamics are of course only applicable when active nitrogen cycling is represented.

143 There are direct trade-offs between the influences of leaf plasticity on  $C:N_{leaf}$  and  
 144 LMA on photosynthetic rates and leaf area under elevated  $CO_2$ . Increases in  $C:N_{leaf}$   
 145 could reduce maximum photosynthetic rates but do not alter the carbon cost of build-  
 146 ing leaf area while increases in LMA could offset reductions in maximum photosynthetic  
 147 rates due to higher  $C:N_{leaf}$  but increase the cost of building leaf area. Thus, given both  
 148 the conflicting impacts of increasing  $C:N_{leaf}$  and LMA on  $N_{area}$ , and the secondary im-  
 149 pacts on leaf area itself, the likely net response of ecosystems to elevated  $CO_2$  taking into  
 150 account this type of leaf trait plasticity is not immediately apparent. While some nitrogen-  
 151 enabled models allow for flexible C:N stoichiometry (Zaehle & Friend, 2010; Ghimire et  
 152 al., 2016; Fisher et al., 2019; Caldararu et al., 2020), we are unaware of studies that have  
 153 specifically included these direct and indirect effects of plasticity in response to forcing  
 154 for LMA. Further, changes in leaf area and leaf functioning incur changes in respiratory  
 155 costs as well. The resulting trade-offs of changes in leaf traits for both per leaf area and  
 156 total canopy rates of functioning thus depend on assumptions about how respiratory costs  
 157 scale with either total leaf mass or total mass of nitrogen.

## 158 1.2 Indirect effects of trait plasticity

159 Competition for light is recognized to be a dominant driver of community compo-  
 160 sition in tropical forests (e.g., Sterck et al., 2011). In addition to the direct influences  
 161 described above, tropical tree responses to increasing  $CO_2$  could also indirectly change  
 162 ecosystem functioning by altering plant competition for light and the relative abundance  
 163 of different plant types (reviewed by Cusack et al., 2016). The magnitude of leaf trait  
 164 responses to elevated  $CO_2$  has been observed to differ among tropical tree species (Lovelock  
 165 et al., 1998; Reekie & Bazzaz, 1989; Winter et al., 2000; Winter & Lovelock, 1999). Vari-  
 166 ation in leaf trait plasticity across tropical tree types could lead to differential changes  
 167 in the competitive ability for light in response to elevated  $CO_2$  and thus alter the abun-

168 dance of competing plant types. LMA and  $C:N_{leaf}$  act to modify both leaf area index  
 169 and biomass through their influence on per leaf area photosynthetic rates as well as to-  
 170 tal leaf area. Leaf area index and biomass in turn can influence plant competitive abil-  
 171 ity. In general, trees which accumulate less biomass may not be able to grow as tall as  
 172 their neighbors and may therefore become more heavily shaded; while trees with lower  
 173 leaf area index may not be able to capture as much light or shade their neighbors in com-  
 174 petition for light. Thus changes in these traits are likely to differentially alter the com-  
 175 petitive ability of individual trees depending on their magnitude of plasticity.

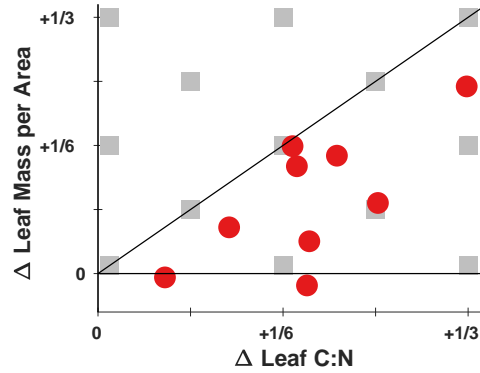
### 176 1.3 Results from previous studies

177 Observational manipulation experiments have shown that tropical tree trait responses  
 178 to  $CO_2$  are species-specific (Lovell et al., 1998; Reekie & Bazzaz, 1989; Winter et al.,  
 179 2000; Winter & Lovell, 1999) and suggest that differences in  $CO_2$  responses across species  
 180 could lead to changes in community structure (reviewed by Cusack et al., 2016). Invest-  
 181 igating the relationship between individual traits and community outcomes is challeng-  
 182 ing in empirical studies due to multiple, confounding changes in plants treated with el-  
 183 evated  $CO_2$  (Lovell et al., 1998; Reekie & Bazzaz, 1989). While increases in  $C:N_{leaf}$   
 184 and increases in LMA both appear to have negative impacts on plants at first consid-  
 185 eration each has the potential to confer advantage. Despite first-order reductions in ni-  
 186 trogen per unit plant area, increasing  $C:N_{leaf}$  may benefit plants as an adaptation to  
 187 N limited conditions. McMurtrie et al. (2008) showed that a temperate monoculture was  
 188 able to maximize productivity under limited nitrogen availability and elevated  $CO_2$  by  
 189 increasing  $C:N_{leaf}$  which enabled increased leaf area. Increasing LMA could also be ben-  
 190 efitial despite the higher cost of leaf area. Previous modeling studies have used obser-  
 191 vations of LMA and  $C:N_{leaf}$  change to simulate changes in assimilation and individual  
 192 plant growth and found that increasing LMA helps to offset negative effects of higher  
 193  $C:N_{leaf}$  on  $N_{area}$  and photosynthetic rates per leaf area under elevated  $CO_2$  (Luo et al.,  
 194 1994; Ishizaki et al., 2003).

195 None of these studies, however, considered communities of plants or the effects of  
 196 competition between different plant types, nor did they focus on tropical tree species.  
 197 Other modeling studies have found variability in plant traits, such as LMA, to have strong  
 198 influences on plant competition for resources and ecosystem functioning under elevated  
 199  $CO_2$  (Ali et al., 2015; Verheijen et al., 2015; Fisher et al., 2010). For example, Ali et al.  
 200 (2015) found that decreasing LMA (the opposite of the observed change) was beneficial  
 201 to competitive success under elevated  $CO_2$ , but did not consider the observed concomi-  
 202 tant changes in  $C:N_{leaf}$ . Thus it remains unclear how the combination of observed trait  
 203 responses to  $CO_2$  will influence plant competitive dynamics, the survival of responsive  
 204 trees, and tropical ecosystem structure and functioning in the future. Additionally, Verheijen  
 205 et al. (2015) allowed LMA to vary with  $CO_2$  (along with other environmental drivers and  
 206 traits) globally in a dynamic global vegetation model, however they didn't allow LMA  
 207 influence leaf area index, nor, did they focus on tropical trees.

### 208 1.4 Modeling Objectives

209 In this study we explore how plasticity in two key leaf traits mediates tropical ecosys-  
 210 tem carbon uptake and evapotranspirative cooling responses to a doubling of  $CO_2$  us-  
 211 ing an ensemble of simulations of the Functionally Assembled Terrestrial Ecosystem Sim-  
 212 ulator (FATES; Fisher et al., 2015; Koven et al., 2020) vegetation demographic model  
 213 at a tropical forest test site, Barro Colorado Island, Panama. We investigate how dif-  
 214 ferent levels of plasticity in  $C:N_{leaf}$  and LMA (gray squares in Fig. 1) in response to a  
 215 doubling of  $CO_2$ : 1) modify ecosystem level carbon uptake and evapotranspirative cool-  
 216 ing in the absence of competition; 2) alter biomass and leaf area index; and 3) alter com-  
 217 petitive outcomes when two plant types with different leaf trait plasticity responses com-  
 218 pete.



**Figure 1.** Leaf trait plasticity in response to a doubling of  $\text{CO}_2$  in tropical trees for leaf C:N (leaf  $gC\ gN^{-1}$ ) and leaf mass per area ( $gC\ m^{-2}$  leaf area). Observed changes across nine tropical tree species (red circles) from Lovelock et al. (1998). Leaf trait plasticity levels sampled for our experiments (gray squares). Diagonal black line indicates where nitrogen per area ( $N_{area}$ ,  $gN\ m^{-2}$  leaf area) remains at control levels. Above the diagonal line nitrogen per area increases ( $+N_{area}$ ) compared to the control; below the diagonal line it decreases ( $-N_{area}$ ).

219 We test leaf trait plasticity levels that increase ( $+N_{area}$ ), decrease ( $-N_{area}$ ), and  
 220 maintain  $N_{area}$  ( $=N_{area}$ ). Our simulations do not explicitly represent growth limitation  
 221 by or competition for nitrogen. Instead, we are able to quantify the change in total canopy  
 222 nitrogen ( $g$  nitrogen  $m^{-2}$  ground) required to support an ecosystem with each level of  
 223 leaf trait plasticity (under doubled  $\text{CO}_2$ ). We find that leaf trait plasticity levels that  
 224 decrease  $N_{area}$ , - consistent with observed responses of LMA and  $C:N_{leaf}$ , could reduce  
 225 projections of future carbon uptake and evapotranspiration in the absence of competi-  
 226 tion. However, trees that are able to maintain or increase  $N_{area}$  under high  $\text{CO}_2$  would  
 227 likely have a competitive advantage and could therefore maintain higher levels of ecosys-  
 228 tem carbon uptake and evapotranspirative cooling.

## 229 2 Methods

### 230 2.1 Model Overview

231 We use an ensemble of simulations of the Functionally Assembled Terrestrial Ecosystem  
 232 Simulator (FATES; Fisher et al., 2015; Massoud et al., 2019; Koven et al., 2020) em-  
 233 bedded within the Community Land Model version 5 (Lawrence et al., 2018) to test the  
 234 influence of leaf trait plasticity on tropical ecosystem functioning and competitive dy-  
 235 namics. CLM(FATES) is a cohort-based vegetation demographic model (Fisher et al.,  
 236 2018; Koven et al., 2020), that mechanistically simulates plant ecological dynamics and  
 237 ecosystem assembly via processes including plant growth, competition for light, recov-  
 238 ery from disturbance, reproduction, mortality, and recruitment. A key feature of the model,  
 239 based on the ecosystem demography concept (Moorcroft et al., 2001), is that it resolves  
 240 distributions of vegetation height and time since disturbance, which allows it to simu-  
 241 late competition for light. In the model, disturbance, from tree mortality, fire, or log-  
 242 ging, occurs at some rate across patches of the simulated ecosystem. Plants grow upon  
 243 ground area within these “patches”, which are tracked by an age that represents the time  
 244 since the last disturbance that that area of ground experienced. Within a patch, indi-  
 245 vidual plants are grouped into “cohorts”, which can differ in height and functional type.  
 246 Thus, cohorts represent individual plants of the same plant type and height as a repre-  
 247 sentative average individual. The height structure of cohorts within a patch determines



248 the light profile experienced by each cohort. The leaf area of taller cohorts in the canopy  
 249 can shade cohorts deeper in the canopy, which is further depicted as discrete canopy lay-  
 250 ers using the perfect plasticity approximation (Purves et al., 2008). Photosynthesis, res-  
 251 piration, turnover, and mortality, as well as the interaction of these processes with the  
 252 abiotic environment, control the amount of carbon each cohort can use for growth. Growth  
 253 and size-dependent allometric equations then determine the height, biomass, and tar-  
 254 get leaf area of each cohort. Thus, carbon uptake is dynamic and influences plant growth,  
 255 leaf area, and size, which in turn influence competition for light. Radiation streams for  
 256 direct and diffuse light are calculated at the leaf layer level for each plant type, patch  
 257 and canopy layer. This incoming energy drives photosynthesis and the surface energy  
 258 budget, and thus rates of carbon uptake and transpiration. In sum, the model tracks fluxes  
 259 of carbon, water, and energy throughout the ecosystem. This version of CLM(FATES)  
 260 does not explicitly represent growth limitation by or competition for nutrients, thus, we  
 261 implement  $C:N_{leaf}$  and LMA plasticity levels that represent the potential influences of  
 262 nutrient limitation and quantify the total canopy nitrogen required to support each leaf  
 263 trait plasticity level.

264 Baseline parameters for the model (Table S1) were chosen from a parameter en-  
 265 semble that sampled plant parameters from observations when possible following the meth-  
 266 ods of Koven et al. (2020) and described in Kovenock (2019). In brief, Kovenock (2019)  
 267 sampled 287 plausible parameterizations from the tropical tree trait space for 12 param-  
 268 eters, 6 of which were based on observations (see further discussion in Supporting In-  
 269 formation Text S1.1 and Kovenock, 2019). Our primary results used the parameteriza-  
 270 tion that allowed the simulated ecosystem to best match present day measurements of  
 271 leaf area index, above-ground biomass, basal area, net primary productivity, latent heat  
 272 fluxes, and sensible heat fluxes at our test site, Barro Colorado Island, Panama (also used  
 273 in Koven et al., 2020). We further test the sensitivity of our results to the next two best  
 274 performing parameter sets. (See Supporting Information Text S1.1 and S2.1 for details.)

## 275 2.2 Leaf trait plasticity estimation and implementation

276 Our experiments test 13 levels of leaf plasticity in  $C:N_{leaf}$  and LMA sampled from  
 277 the two-dimensional leaf trait plasticity space in Fig. 1 (gray squares). We test the equi-  
 278 librium response to elevated  $CO_2$  rather than representing dynamic changes in time. The  
 279 leaf trait plasticity space represents both observed (at or below diagonal line in Fig. 1)  
 280 and hypothetical (above the diagonal line in Fig. 1) levels of leaf trait plasticity. The  
 281 observed leaf trait plasticity space is estimated from observations of leaf responses to a  
 282 doubling of  $CO_2$  in nine tropical tree species, including early, mid- and late successional  
 283 classes (Lovelock et al., 1998, Fig. 1 red circles), and supported by additional studies in  
 284 tropical trees and many other C3 plant types (e.g., Lovelock et al., 1998; Reekie & Baz-  
 285 zaz, 1989; Winter et al., 2000; Winter & Lovelock, 1999). These observations suggest that  
 286 both  $C:N_{leaf}$  and LMA could increase by as much as one-third in response to a doubling  
 287 of  $CO_2$  while  $N_{area}$  (Eqn 1) decreases or remains constant. Thus, we define observed leaf  
 288 trait plasticity levels as those that maintain  $N_{area}$  at ( $=N_{area}$ ) or below ( $-N_{area}$ ) con-  
 289 trol (CTRL and CC) levels. We also test leaf trait plasticity levels that increase  $N_{area}$   
 290 ( $+N_{area}$ ), to determine if such a response could help tropical trees enhance their pro-  
 291 ductivity and competitive ability. Given the wide diversity of tropical tree species it is  
 292 possible that some tropical tree species, (e.g. those with traits that enhance nutrient for-  
 293 aging or fixing capabilities), could in principle increase  $N_{area}$  (Fig. 1 above diagonal line)  
 294 in response to higher  $CO_2$ .

295 Changes in  $C:N_{leaf}$  and LMA in our simulations drive changes in  $N_{area}$ , maximum  
 296 photosynthetic and respiration rates, and leaf area index. Plasticity in  $C:N_{leaf}$  and LMA  
 297 drives changes in  $N_{area}$  (as described above) and this in turn alters maximum rates of  
 298 photosynthesis (e. g.  $V_{cmax}$ ,  $J_{max}$ ,  $T_{pmax}$ ) and leaf respiration, following Eqn 1. We di-  
 299 rectly implement changes in  $V_{cmax25}$  to vary in proportion to  $N_{area}$  (which was allowed



to change with changes to  $C:N_{leaf}$  and LMA). Changes in the other maximum photosynthetic rates,  $J_{max25}$  and  $T_{pmax25}$ , are thus also altered as they are calculated by the model in proportion to  $V_{cmax25}$ . Changes in maximum rates of photosynthesis and leaf respiration assume no changes in nitrogen partitioning among photosynthetic enzymes (c.f. Xu et al., 2012). We assume that LMA decreases with canopy depth following the observations of Lloyd et al. (2010) as previously implemented in FATES by Kovenock (2019). In FATES, leaf area index responds dynamically to carbon available for leaf growth, reducing canopy depth until no leaf layers are in negative annual carbon balance (Fisher et al., 2015). See further discussion in Supporting Information Text S1.2 for details.

### 2.3 Simulations

We ran simulations for a tropical forest test site at Barro Colorado Island in Panama. All simulations were forced with repeating meteorological data from this site from the years 2003-2016 (Faybishenko et al., 2018). All of our simulations used one or two broadleaf evergreen tropical trees, characteristic of our tropical forest test site. This plant functional type represents an average of many species within the evergreen tropical tree plant type, and thus here is not meant to resolve trait distinctions between species or successional classes. Two control simulations represent a baseline tropical forest ecosystem without leaf trait plasticity. The first control simulates the ecosystem with  $CO_2$  concentration fixed at 400 ppm  $CO_2$  (CTRL;  $1 \times CO_2$ ). The second control is identical to the first except that the ecosystem experiences a fixed atmospheric  $CO_2$  concentration of 800 ppm ( $CC$ ;  $2 \times CO_2$ ). Plants in these control simulations do not experience leaf trait plasticity in response to elevated  $CO_2$  (gray square at origin in Fig. 1). The difference between the control simulations ( $CC - CTRL$ ) quantifies the influence of  $CO_2$  fertilization on the baseline simulated tropical ecosystem. Meteorological air temperature does not change in response to elevated  $CO_2$  in our simulations to reflect the experimental conditions under which the leaf plasticity was observed. We chose these two levels of  $CO_2$  concentration to represent a doubling of  $CO_2$  from current conditions which results in a similar change but slightly higher baseline values compared to the conditions imposed in (Lovelock et al., 1998) from which we draw empirical inference for the magnitude of trait response of tropical trees.

We quantify the direct influence of different degrees of leaf trait plasticity, in the absence of competition, using an ensemble of simulations that are identical to the  $2 \times CO_2$  control ( $CC$ ). Each ensemble member imposes a different level of leaf trait plasticity (gray squares sampled from leaf trait plasticity space in Fig. 1) on all plants in the simulation. We call these simulations of the ecosystem “in absence of competition” because different plant types that compete against each other are not present. We further group leaf trait plasticity experiments by whether they decrease ( $-N_{area}$ , below diagonal line in Fig. 1), maintain ( $=N_{area}$ , on diagonal line in Fig. 1), or enhance  $N_{area}$  ( $+N_{area}$ , above diagonal line in Fig. 1). We calculate the total canopy nitrogen required for each “in absence of competition” simulation as total canopy leaf carbon ( $g$  leaf  $C m^{-2}$  ground) divided by  $C:N_{leaf}$  ( $g C g N^{-1}$ ).

We test the influence of leaf trait plasticity level on competitive ability using a second ensemble of simulations, which we refer to as “pairwise competition” simulations. These simulations are identical to the  $2 \times CO_2$  control ( $CC$ ) except that each experiment includes two different plant types with identical initial conditions, which are identical in all traits except in their level of leaf trait plasticity. The two plant types are allowed to compete for light within the ecosystem. We repeat these pairwise competition experiments for all factorial combinations of two levels of leaf trait plasticity sampled from the species-specific points in leaf trait plasticity space (gray squares in Fig. 1), including the control “no leaf trait plasticity” plant type (gray square at origin in Fig. 1). We find that in each competition simulation, one plant type (i.e. one level of leaf trait plasticity) always eventually out-competes the other. For an analysis of the dynamics of co-

352 existence in the FATES model see Koven et al. (2020). We define one plant type as “win-  
 353 ning” the competition when it overtakes at least two-thirds of the total ecosystem biomass  
 354 (see below for further details). We quantify differences in competitive ability due to leaf  
 355 trait plasticity using a measure called percent wins (% wins), which is the percent of all  
 356 pairwise competitions a plant type with a given leaf trait plasticity level wins across com-  
 357 petition with the other plant types in the ensemble.

358 The 1xCO<sub>2</sub> control simulation (CTRL) was started from near-bare ground and in-  
 359 tegrated for 700 years. All variables came into equilibrium within 450 years, the time  
 360 required to grow a mature forest with our model set up. The 2xCO<sub>2</sub> control simulation  
 361 (CC) and all experiments were branched from the 1xCO<sub>2</sub> control simulation (mature for-  
 362 est) at year 500 and experienced an abrupt doubling of CO<sub>2</sub> to a time-invariant concen-  
 363 tration of 800 ppm CO<sub>2</sub>. The 2xCO<sub>2</sub> control and experiment simulations were run to  
 364 the point that the community was dominated by one plant type considered the “winner”.  
 365 Specifically, every simulation was run for 3,500 years, at which point 99% of competi-  
 366 tions between plant types with different trait changes were complete (one plant type reached  
 367 at least 95% of the ecosystem biomass). In the remaining 1% of competitions one plant  
 368 type had become dominant (taken over at least 67% of ecosystem biomass and trend-  
 369 ing towards overtaking all ecosystem biomass). We analyze the last 100 years of each sim-  
 370 ulation as our equilibrium ecosystem.

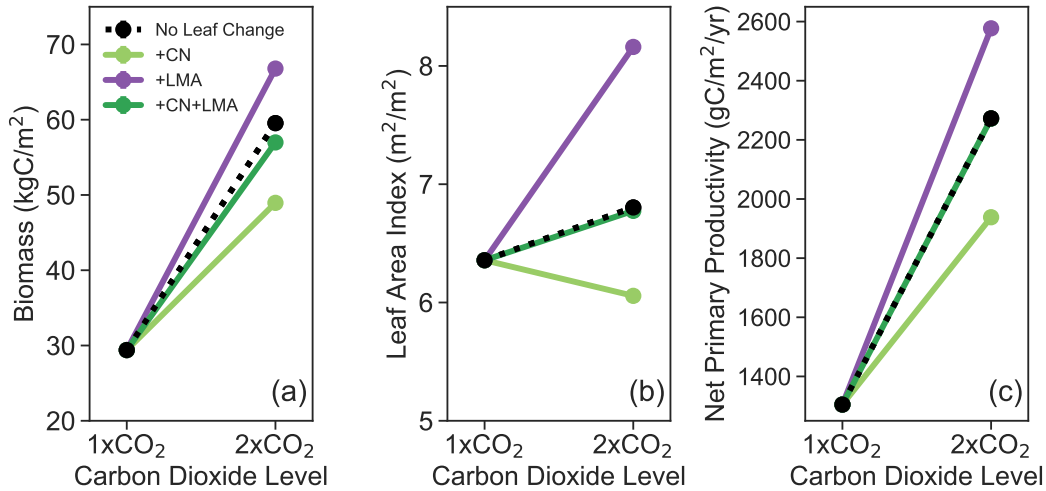
## 371 2.4 Statistical Analysis

372 We quantify the influence of leaf trait plasticity in the absence of competition (i.e.  
 373 simulations with only one plant type) using 1) differences in annual mean ecosystem prop-  
 374 erties and 2) relationships between leaf trait plasticity levels and annual mean ecosys-  
 375 tem properties across simulations. We use bootstrap methods with model years as the  
 376 unit of replication ( $n = 50,000$ ) to construct confidence intervals for annual mean leaf  
 377 area index, biomass, net primary productivity, evapotranspiration, and total canopy ni-  
 378 trogen and test for differences between simulations. We use bootstrapping methods be-  
 379 cause some variables have time series that are non-normally distributed, have unequal  
 380 variances, and temporal autocorrelation. The 100 model years we analyze for each vari-  
 381 able are unique despite repeating the 14 years of meteorological forcing, as ecological dy-  
 382 namics also influence the environment (e.g., light availability) and ecosystem structure  
 383 and functioning in our simulations. We use simple, multiple, and stepwise linear regres-  
 384 sion methods to test for relationships between leaf trait plasticity levels ( $C:N_{leaf}$ , LMA,  
 385  $N_{area}$ ) and annual mean ecosystem properties across simulations. Correlations between  
 386 percent wins and annual mean net primary productivity and evapotranspiration across  
 387 simulations were tested using Pearson’s linear correlation coefficient. Differences, rela-  
 388 tionships, and correlations were considered statistically significant at the 95% confidence  
 389 level. (See Supporting Information Text S1.4 for details.)

## 390 3 Results

### 391 3.1 Elevated CO<sub>2</sub> response in the control simulation

392 Previous observations, simulations, and theory show that elevated atmospheric CO<sub>2</sub>  
 393 concentration enhances photosynthesis and reduces stomatal conductance, which has the  
 394 potential to enhance productivity and reduce evapotranspiration at the ecosystem scale  
 395 (e.g. Cernusak et al., 2013; Cusack et al., 2016; Lloyd & Farquhar, 2008; Zhu et al., 2016;  
 396 Lloyd & Farquhar, 2008; Swann et al., 2016; De Kauwe et al., 2013, and references therein).  
 397 In our control simulation (no leaf trait plasticity) a doubling of atmospheric CO<sub>2</sub> con-  
 398 centration from 400 ppm to 800 ppm (CC-CTRL) increases annual mean net primary  
 399 productivity (+74.2%), leaf area index (+7.0%), and biomass (+102.6%), and reduces  
 400 evapotranspiration (-9.2%) (Table 1, Fig. 2). As noted in the methods section, the FATES  
 401 model we use here does not explicitly represent nutrient limitation, thus we directly im-



**Figure 2.** Annual mean (a) biomass ( $kgC\ m^{-2}$ ) and (b) leaf area index ( $m^2\ m^{-2}$ ) and (c) net primary productivity ( $gC\ m^{-2}\ s^{-1}$ ) for the  $1xCO_2$  control,  $2xCO_2$  control (black), and the following leaf trait plasticity levels in the absence of competition: a one-third increase in leaf C:N alone (+CN, light green), a one-third increase in leaf mass per area alone (+LMA, purple), and a one-third increase in both leaf C:N and leaf mass per area (+CN+LMA, dark green). A bootstrap 95% confidence interval for the mean value all fall within the size of the markers.

402 supplement leaf trait changes in our experiments that represent potential influences of nu-  
 403 trient limitation and quantify the total canopy nitrogen required to support each leaf trait  
 404 plasticity level.

405 The actual expected magnitude of tropical forest responses to elevated  $CO_2$  is highly  
 406 uncertain and little experimental data exists, particularly at the ecosystem scale (Lloyd  
 407 & Farquhar, 2008; Hickler et al., 2008; Mahowald et al., 2016; Cusack et al., 2016; Norby  
 408 et al., 2016; Fleischer et al., 2019; Holm et al., 2020). However, our control simulation  
 409 response to elevated  $CO_2$  shows reasonable agreement with observations from temper-  
 410 ate forest FACE experiments (De Kauwe et al., 2013, 2014) if one assumes a linear scal-  
 411 ing with increasing  $CO_2$  (Cernusak et al., 2019). For example, a +200ppm  $CO_2$  increase  
 412 at Duke Forest enhanced net primary productivity by approximately 30% (De Kauwe  
 413 et al., 2013), which when scaled to +400ppm results in a +60% increase in net primary  
 414 productivity (we find +74.2%, in the absence of N limitation). Similarly, when scaled  
 415 to +400ppm these FACE experiments saw changes equivalent to approximately +6% and  
 416 +30% in leaf area index at Oak Ridge and Duke, respectively (we find +7%); -40% in  
 417 transpiration at Oak Ridge (no significant change at Duke Forest) (we find +9.2%); and  
 418 +100% in biomass increment at Duke (we find total biomass changes, which are not di-  
 419 rectly equivalent, of +102%). Thus our modeled changes are all roughly comparable with  
 420 these ranges, with slightly higher modeled increases in net primary productivity in our  
 421 tropical simulations compared to these observational estimates from temperate forests.  
 422 Lastly, changes in each of these ecosystem properties in our control simulation also fall  
 423 within the simulated ranges from 11 Earth system models at these two temperate for-  
 424 est FACE sites after linearly scaling for  $CO_2$  concentration (De Kauwe et al., 2013, 2014).  
 425 While our control simulation response to elevated  $CO_2$  is comparable to those estimated  
 426 from observations in temperate forests, tropical forest responses may of course be sub-  
 427 ject to different constraints (e.g., De Graaff et al., 2006; Luo et al., 2006; Hickler et al.,  
 428 2008; Zaehle et al., 2014; Fleischer et al., 2019). Davies-Barnard et al. (2020) illustrate  
 429 that for five CMIP6 class models with active nitrogen cycles, the fertilization impact of

430 +200ppm CO<sub>2</sub> had a mean net primary productivity response of 16-18% for models other  
 431 than CLM4.5 (which has an anomalously strong N limitation) which is about half the  
 432 size of what we find (37% for +200ppm). These models, however, are all subject to N  
 433 limitation, and also show strong spatial variation, with tropical forests showing higher  
 434 than average simulated CO<sub>2</sub> fertilization rates.

### 435 3.2 Influence of leaf trait plasticity on canopy structure in absence of 436 competition

437 We find that imposed leaf trait plasticity alters net primary productivity, biomass,  
 438 and leaf area index responses to a doubling of CO<sub>2</sub> in the absence of competition (Fig.  
 439 2). Under elevated CO<sub>2</sub>, increasing C:N<sub>leaf</sub> by one-third (the upper bound of our ob-  
 440 served range) diminishes the increase in net primary productivity ( $-334 \text{ gCm}^{-2}\text{s}^{-1}$ ) and  
 441 biomass ( $-10.6 \text{ kgCm}^{-2}$ ), as well as decreasing leaf area index ( $-0.7 \text{ m}^2\text{m}^{-2}$ ) compared  
 442 to the control plant type (CN - CC). In contrast, increasing LMA by one-third enhances  
 443 the increases in both simulated biomass ( $+7.2 \text{ kgCm}^{-2}$ ) and leaf area index ( $+1.4 \text{ m}^2\text{m}^{-2}$ )  
 444 compared to the control plant type (LMA - CC), via increases in net primary produc-  
 445 tivity ( $+304 \text{ gCm}^{-2}\text{s}^{-1}$ ) from increasing N<sub>area</sub> that has a larger effect than the more  
 446 costly leaf construction. Increasing both C:N<sub>leaf</sub> and LMA simultaneously by one-third  
 447 under a doubling of CO<sub>2</sub> (CNLMA) results in only a slightly reduced increase in biomass  
 448 ( $-2.6 \text{ kgCm}^{-2}$ ) and no change in leaf area index ( $0.0 \text{ m}^2\text{m}^{-2}$ ) or net primary produc-  
 449 tivity ( $-0.8 \text{ gCm}^{-2}\text{s}^{-1}$ ) compared to the control plant type (CNLMA - CC).

450 The first-order impacts are that, for any given increase in C:N<sub>leaf</sub>, a simultane-  
 451 ous increase in LMA allows plants to maintain biomass and leaf area index that are closer  
 452 to the control plant type. It is worth noting additionally that the simultaneous change  
 453 is not a perfect cancellation between the two factors. When LMA increases in isolation  
 454 leaves get thicker and more productive per area with increased N<sub>area</sub>. When C:N<sub>leaf</sub> is  
 455 increased, N<sub>area</sub> and net primary productivity decrease. When both factors occur simul-  
 456 taneously, thicker leaves compensate for a lower mass density of nitrogen. The two fac-  
 457 tors cancel one another out in terms of net primary productivity, as N<sub>area</sub> is conserved,  
 458 however biomass is reduced slightly relative to the case with no leaf change. We hypoth-  
 459 esize that this happens because thicker leaves require more carbon allocated to leaves  
 460 relative to wood and thus the overall whole plant turnover of carbon is faster resulting  
 461 in a smaller total biomass. Consistent with this hypothesis, we find that the fractional  
 462 allocation of net primary productivity to leaves goes up even for the case where N<sub>area</sub>  
 463 is conserved (by +0.023, see Table S2), and the lifetime of total biomass decreases (by  
 464 -0.72 years, see Table S2).

### 465 3.3 Influence of leaf trait plasticity on competitive ability

466 We find that the control plant type, with no leaf trait plasticity (and thus no change  
 467 in N<sub>area</sub>), is more competitively advantageous than all leaf trait plasticity levels sam-  
 468 pled where N<sub>area</sub> either decreases or remains constant under a doubling of CO<sub>2</sub> (Fig. 3).  
 469 The control plant type (origin in Fig. 3) wins all of pairwise competitions against plant  
 470 types with leaf trait plasticity levels sampled from the trait changes that maintain N<sub>area</sub>  
 471 (=N<sub>area</sub>, along black dashed diagonal line in Fig. 3) or reduce N<sub>area</sub> (-N<sub>area</sub>, below black  
 472 dashed diagonal line in Fig. 3).

473 Increasing C:N<sub>leaf</sub> strongly diminished competitive ability, as evidenced by the de-  
 474 creasing percentage of competitions a plant type wins as C:N<sub>leaf</sub> increases (left to right,  
 475 Fig. 3). At a given C:N<sub>leaf</sub>, increasing LMA typically enhances competitive ability. At  
 476 very high C:N<sub>leaf</sub> there is little change, (bottom to top, Fig. 3) however, reflecting the  
 477 trade-off between the impacts on N<sub>area</sub> (reduced productivity) and leaf area index (in-  
 478 creased productivity). This results from decreased net primary productivity, biomass,  
 479 and leaf area index, as N<sub>area</sub> is reduced (Fig. 4).

480 These results from our competition experiments are consistent with our findings  
 481 in the absence of competition—higher C:N<sub>leaf</sub> leads to lower net primary productivity,  
 482 biomass, and leaf area index and increasing LMA results in net primary productivity,  
 483 biomass, and leaf area index gains (Fig. 2). However, LMA increases sampled from plas-  
 484 ticity levels that maintain or decrease N<sub>area</sub> do not, in this model, fully compensate for  
 485 the negative influence of higher C:N<sub>leaf</sub> on competitive ability at any level. Furthermore,  
 486 the competitive benefit of increasing LMA diminishes at higher C:N<sub>leaf</sub>, as evidenced  
 487 by the sinusoidal shape of the 50% wins shading (white) in Fig. 3. In sum, we find that  
 488 plant types that can maintain higher N<sub>area</sub> in high CO<sub>2</sub>, have greater competitive abil-  
 489 ity.

490 Leaf trait plasticity levels that enhance N<sub>area</sub> (+N<sub>area</sub>, above diagonal line in Fig.  
 491 3) enhance competitive ability compared to the control leaf type, as well as all leaf trait  
 492 plasticity levels sampled from the =N<sub>area</sub> and -N<sub>area</sub> space (Fig. 3). This is consistent  
 493 with our finding that increasing LMA in isolation enhances biomass and leaf area index  
 494 beyond the control case in the absence of competition (Fig. 2).

### 495 3.4 Changes in carbon uptake and evapotranspirative cooling

496 Ecosystem carbon uptake is tightly coupled to changes in LMA and C:N<sub>leaf</sub>, both  
 497 directly via their impacts on photosynthetic rate, and indirectly via impacts on leaf area  
 498 index. In our experiments we impose changes in leaf traits, which result in emergent rates  
 499 of carbon uptake, while in a fully evolving system we expect that the carbon uptake rates  
 500 and nutrient availability are likely involved in setting the leaf traits to begin with (see  
 501 further discussion in section 4.3). Evapotranspiration is additionally a downstream re-  
 502 sult of stomatal conductance and leaf area index. Given that the meteorological condi-  
 503 tions are the same in our experiments and our control, the changes in ET that we found  
 504 result from changes to plant traits and functioning only, and tend to change in concert  
 505 with carbon fluxes. Leaf trait plasticity levels sampled from the -N<sub>area</sub> space are asso-  
 506 ciated with lower carbon uptake and evapotranspiration compared to the control response  
 507 to a doubling of CO<sub>2</sub> (CC) in our experiments reflecting the influence of reduced pho-  
 508 tosynthetic capacity (Fig. 5, Table 1). On average the observed changes in C:N<sub>leaf</sub> and  
 509 LMA reduce the increase in annual mean net primary productivity by -9.2% and further  
 510 reduce annual mean ET by -4.4% compared to the 2xCO<sub>2</sub> control (-N<sub>area</sub> - CC). The  
 511 largest reduction in net primary productivity (-14.7%) and evapotranspiration (-7.0%)  
 512 results from the leaf trait plasticity level that increases C:N<sub>leaf</sub> by one-third without a  
 513 co-occurring increase in LMA (CN - CC), a response which was not specifically observed  
 514 by Lovelock et al. (1998).

515 Leaf trait plasticity levels that maintain N<sub>area</sub> equal to the control (=N<sub>area</sub>) also  
 516 maintain carbon uptake and evapotranspiration at control levels (Fig. 5, Table 1). An-  
 517 nual mean net primary productivity and evapotranspiration do not differ significantly  
 518 between =N<sub>area</sub> simulations and the control simulation under a doubling of CO<sub>2</sub> (=N<sub>area</sub>  
 519 - CC). Leaf changes that enhance N<sub>area</sub> (+N<sub>area</sub>) increase carbon uptake and moder-  
 520 ate the reduction in evapotranspiration compared to the control response to a doubling  
 521 of CO<sub>2</sub> (Fig. 5, Table 1). On average +N<sub>area</sub> leaf trait plasticity levels increase annual  
 522 mean net primary productivity by +8.4% and lessen the reduction in evapotranspira-  
 523 tion by +4.8% (+N<sub>area</sub> - CC). The largest enhancement of net primary productivity (+13.4%)  
 524 and evapotranspiration (+7.9%) results from the leaf trait plasticity level that increases  
 525 LMA by one-third but does not alter C:N<sub>leaf</sub> (LMA - CC).

526 Leaf trait plasticity levels that confer a higher competitive advantage also have a  
 527 higher carbon uptake (Fig. 5). We expect that more N<sub>area</sub> generally leads to higher pro-  
 528 ductivity and thus higher associated evapotranspiration. The competitive ability of a plant  
 529 type with a given level of leaf trait plasticity, as measured by the percent of competi-



tions won against plant types with other levels of plasticity (percent wins), is significantly correlated with net primary productivity ( $r = 0.91$ ) and evapotranspiration ( $r = 0.91$ ).

### 3.5 Total canopy nitrogen

Progressive nitrogen limitation is hypothesized to limit plant growth in response to elevated  $\text{CO}_2$  (Luo et al., 2004) and may be a cause of  $\text{C:N}_{leaf}$  and LMA plasticity in response to elevated  $\text{CO}_2$  (Poorter et al., 2009, 1997; Pritchard et al., 1999; Roumet et al., 1999; Meyerholt & Zaehle, 2015). Here we report the total amounts of canopy nitrogen required for ecosystems with differing levels of leaf trait plasticity, and compare them to the  $1\times\text{CO}_2$  control simulation (CTRL), which provides a reference for the amount of nitrogen used by canopies in the simulated current day ecosystem. Variation in total canopy nitrogen across simulations results from the leaf trait plasticity changes we imposed and changes in overall leaf carbon, which is an emergent property of each simulation.

Under  $1\times\text{CO}_2$  conditions, our control simulation (CTRL) had a total canopy nitrogen content of  $8.3 \text{ gNm}^{-2}$  ground. Doubling  $\text{CO}_2$  increased the control ecosystems total canopy nitrogen content by  $+0.3 \text{ gNm}^{-2}$  or  $+3.2\%$  (Fig. 3 red contours). This increase is only due to the increase in leaf biomass, which at the canopy level in FATES is governed by a combination of within-plant optimization of leaf biomass to maximize canopy carbon export combined with the ability of plants to survive in the understory, both of which are expected to promote slightly higher leaf carbon under the elevated  $\text{CO}_2$  conditions. Leaf trait plasticity levels that maintain  $\text{N}_{area}$  at control levels ( $=\text{N}_{area}$ ) but have increases in both  $\text{C:N}_{leaf}$  and LMA also increase the total amount of canopy nitrogen required beyond the  $1\times\text{CO}_2$  control level, although by slightly less than the  $2\times\text{CO}_2$  control, with the mean change across  $=\text{N}_{area}$  simulations ranging from 2.1% to 3.0% ( $=\text{N}_{area}$  - CTRL; Fig. 3). The  $-\text{N}_{area}$  scenarios all maintain canopy N content at or below the  $1\times\text{CO}_2$  control level ( $-\text{N}_{area}$ ; Fig. 3). Simulation with high C:N and unchanged LMA lowered canopy N content by as much as -23.2%.

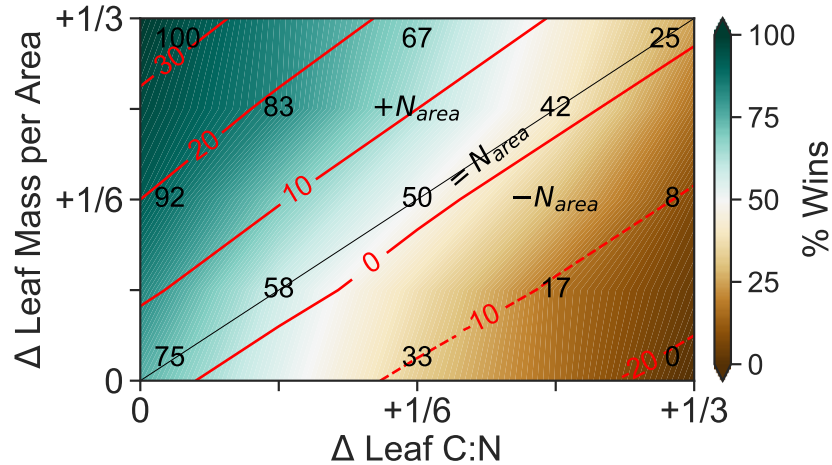
## 4 Discussion

### 4.1 Large-scale climate implications

We find that observed changes in leaf C:N ratios and LMA reduce model predictions of tropical tree productivity, evapotranspiration, and competitive ability under high  $\text{CO}_2$  and alter carbon and water fluxes, with implications for projections of future large-scale climate. We expect that reductions in evapotranspirative cooling over tropical forests would lead directly to local warming (Kovenock & Swann, 2018). Reductions in carbon uptake leave more  $\text{CO}_2$  in the atmosphere thus if such reductions were to be widespread over tropical forests there might be global scale implications for warming through the greenhouse effect of  $\text{CO}_2$  (Kovenock & Swann, 2018). We find that, as is intuitive, tropical trees which are more able to maintain their leaf nitrogen per unit area near present day levels have the highest competitive abilities and also show the smallest changes in carbon and water fluxes (Fig. 5), suggesting that if changes in plant type abundance shift to reflect the most competitive members of the community this will allow maintenance of higher gas exchange rates, leaf area index, and biomass.

### 4.2 Constraints from canopy nitrogen budgets

Maintaining present-day leaf  $\text{N}_{area}$  with a doubling of  $\text{CO}_2$  requires an increase in canopy nitrogen for the control case (CC; red contour lines in Fig. 3) to support the increase in leaf area index (Fig. 2). Thus if we assume that ecosystem N limitation imposes a requirement for conservation of canopy  $\text{N}_{area}$ , this limits the possible leaf trait plasticity space by excluding the control and central diagonal band along with the en-



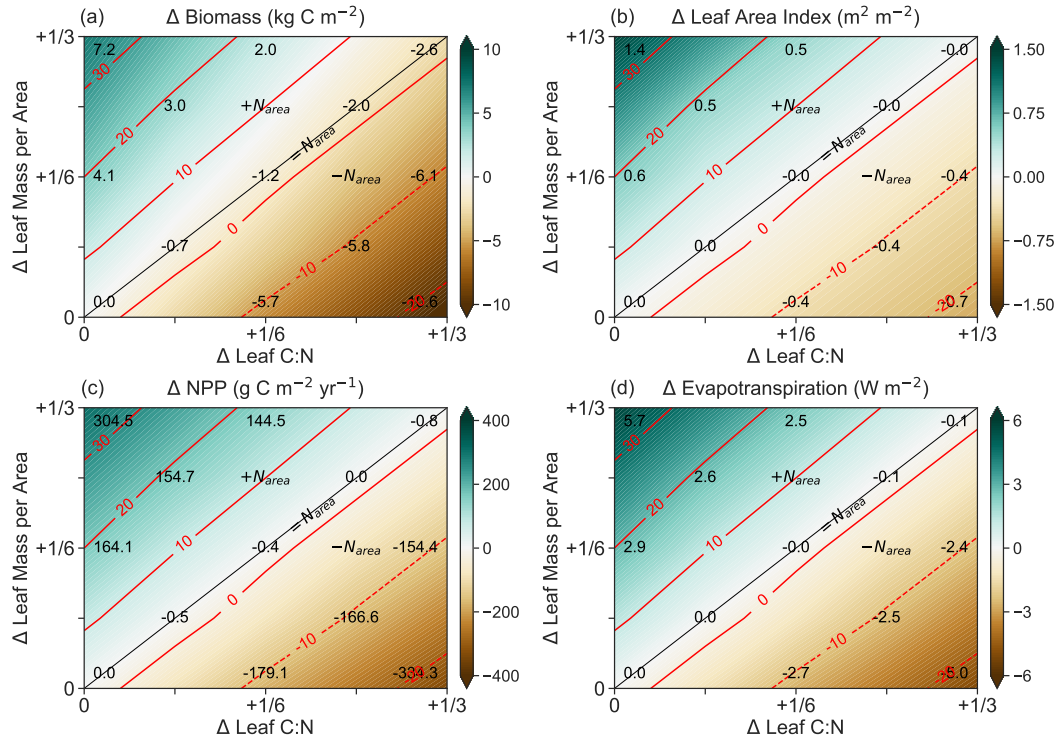
**Figure 3.** The percent of pairwise competitions won (% Wins, color shading and black numbers) and percent change in total canopy nitrogen compared to the 1xCO<sub>2</sub> control (red contours) for each leaf trait plasticity level of leaf C:N and leaf mass per area. Percent wins for sampled trait changes (black numbers). Diagonal line (dashed black) indicates where nitrogen per area ( $N_{area}$ ,  $gN\ m^{-2}$  leaf area) remains at control levels ( $=N_{area}$ ). Leaf trait plasticity levels below the diagonal line reduce  $N_{area}$  ( $-N_{area}$ ) compared to the control plant type. Leaf trait plasticity levels above the diagonal line enhance  $N_{area}$  ( $+N_{area}$ ) compared to the control plant type. Linear interpolation used to estimate percent wins and change in total canopy nitrogen between sampled trait changes.

578 tire upper-left triangle in Fig. 3. This limitation of nitrogen may thus partially explain  
 579 why the control case, where LMA and  $C:N_{leaf}$  are simultaneously conserved, is not ob-  
 580 served in the real world. Although phosphorus limitation is thought to be the primary  
 581 nutrient constraint on plant growth in the tropics, evidence from empirical studies and  
 582 manipulation experiments suggests that tree growth is also limited by nitrogen in the  
 583 tropics (e.g. Winter et al., 2001; reviewed in Cernusak et al., 2013). Most of the changes  
 584 in leaf traits observed by Lovelock et al. (1998) show reduced  $N_{area}$ , which in our sim-  
 585 ulations leads to a reduction in total canopy nitrogen. This could be due to a change in  
 586 nitrogen allocation. For example, nitrogen allocation to roots could increase or increases  
 587 in woody biomass could require greater total amounts of nitrogen (see discussion below).

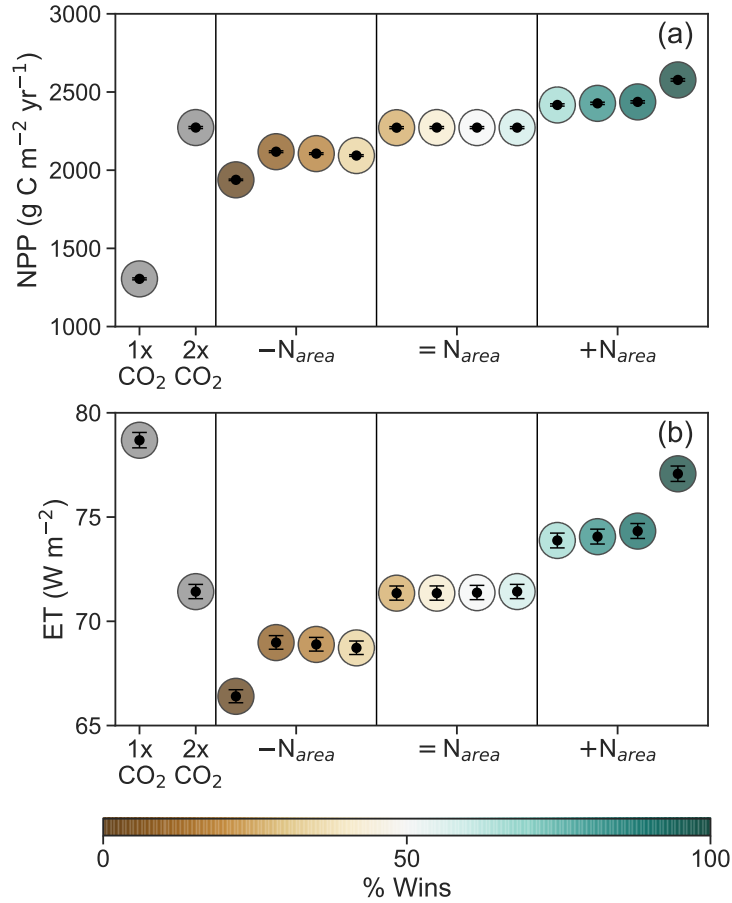
### 588 4.3 Why do leaf changes occur?

589 Our model results suggest that, in the context of the FATES parameterization used  
 590 here, observed increases in  $C:N_{leaf}$  in response to elevated CO<sub>2</sub> do not confer a compet-  
 591 itive advantage. We find that plant types in which  $C:N_{leaf}$  increases in response to el-  
 592 evated CO<sub>2</sub> suffer in several metrics of plant fitness, including biomass, leaf area index,  
 593 net primary productivity, and competitive ability. Thus our results suggest that changes  
 594 in  $C:N_{leaf}$  are likely forced upon plants by changes in elevated CO<sub>2</sub>, rather than occur-  
 595 ring as a beneficial acclimation. This is consistent with the leading hypothesis for the  
 596 mechanism underlying  $C:N_{leaf}$  increases with elevated CO<sub>2</sub>. Nitrogen limitation has been  
 597 proposed as a cause for lower mass-based nitrogen concentrations in leaves (e.g., Poorter  
 598 et al., 1997; Winter et al., 2001; Fyllas et al., 2009; Cusack et al., 2016). As carbon diox-  
 599 ide fertilizes plant growth the demand for nutrients is likely to increase and eventually  
 600 result in the depletion of nitrogen available for growth (Luo et al., 2004; Hungate et al.,  
 601 2003). The limited availability of nitrogen, as well as accumulation of nonstructural car-





**Figure 4.** Changes in (a) biomass ( $kgC\ m^{-2}$ ), (b) leaf area index ( $m^2\ m^{-2}$ ), (c) net primary productivity ( $gC\ m^{-2}\ yr^{-1}$ ), and (d) evapotranspiration ( $W\ m^{-2}$ ) compared to the 2xCO<sub>2</sub> control (color shading and black numbers) and percent change in total canopy nitrogen compared to the 1xCO<sub>2</sub> control (red contours, identical on all plots) for each leaf trait plasticity level of leaf C:N and leaf mass per area. Diagonal line (dashed black) indicates where nitrogen per area ( $N_{area}$ ,  $gN\ m^{-2}$  leaf area) remains at control levels. Leaf trait plasticity levels at or below the diagonal line reduce  $N_{area}$  ( $-N_{area}$ ) compared to the control plant type. Leaf trait plasticity levels above the diagonal line enhance  $N_{area}$  ( $+N_{area}$ ) compared to the control plant type. Changes were measured for sampled trait changes (black numbers). Linear interpolation used to estimate changes between sampled trait changes.



**Figure 5.** Annual mean (a) net primary productivity (NPP,  $gC m^{-2} yr^{-1}$ ) and (b) evapotranspiration (ET,  $W m^{-2}$ ) for the 1xCO<sub>2</sub> control, 2xCO<sub>2</sub> control (no leaf trait plasticity), and 12 ecosystems each consisting entirely of one plant type with a different level of leaf trait plasticity sampled from the -N<sub>area</sub>, =N<sub>area</sub>, and +N<sub>area</sub> trait plasticity spaces. Color indicates the percentage of all pairwise competitions won by each level of leaf trait plasticity (% Wins). Error bars show bootstrap 95% confidence intervals for the mean value.

602 carbohydrates due to sink limitation of growth, could lower mass-based leaf nitrogen con-  
 603 centrations and result in higher C:N<sub>leaf</sub> (e.g., Poorter et al., 1997; Winter et al., 2001).  
 604 Manipulation experiments in which tropical tree seedlings are treated with elevated CO<sub>2</sub>  
 605 provide evidence that CO<sub>2</sub> stimulation of growth is enhanced by the addition of soil nu-  
 606 trients, suggesting that nutrient limitation does indeed impact leaf trait responses (Winter  
 607 et al., 2001). Plants in which C:N<sub>leaf</sub> increases more in response to elevated CO<sub>2</sub> may  
 608 be those that are unable to adjust to lower nitrogen availability or higher competition  
 609 for nitrogen. Tropical trees with traits that allow them to better acquire nitrogen, for  
 610 example associations with nitrogen fixing bacteria or fungi, may be better able to main-  
 611 tain C:N<sub>leaf</sub> levels under elevated CO<sub>2</sub> with advantages for growth and competitive suc-  
 612 cess (Lovelock et al., 1998; Cusack et al., 2016; Cernusak et al., 2013).

613 Further, it has been suggested that the increase in LMA with elevated CO<sub>2</sub> is medi-  
 614 ated by nitrogen (or other resource limitation of plant growth causing nonstructural  
 615 carbohydrates accumulation in leaves; Poorter et al., 2009, 1997; Pritchard et al., 1999;  
 616 Roumet et al., 1999). We find that coordinated responses of both LMA and C:N<sub>leaf</sub> are  
 617 beneficial: plants that are able to increase LMA most for a given level of C:N<sub>leaf</sub> change  
 618 are those that are best able to maintain high biomass, leaf area index, productivity, and  
 619 competitive ability. Concurrently increasing LMA along with C:N<sub>leaf</sub> leads to mainte-  
 620 nance of equal N<sub>area</sub> by counteracting decreases in mass-based nitrogen concentration  
 621 (Luo et al., 1994; Ishizaki et al., 2003). Indeed, we found that even when limited to control  
 622 levels of total canopy nitrogen, plants could maintain close to equal amounts of N<sub>area</sub>.  
 623 As nitrogen is an essential component of photosynthetic enzymes, maintaining N<sub>area</sub> can  
 624 maintain area-based maximum photosynthetic rates (Kattge et al., 2009, 2011; Walker  
 625 et al., 2014; Norby et al., 2017), and we find that net primary productivity closely fol-  
 626 lows the amount of N<sub>area</sub> in our simulations. Observations by Lovelock et al. (1998) of  
 627 tropical tree leaf trait responses to a doubling of CO<sub>2</sub> (Fig. 1) suggest that increases in  
 628 LMA are generally higher for larger increases in C:N<sub>leaf</sub>, helping to maintain N<sub>area</sub> –  
 629 and thus functioning – closer to control levels (Fig. 5). While it is logical that increas-  
 630 ing LMA concurrently with C:N<sub>leaf</sub> is advantageous to plants, this leaves open the ques-  
 631 tion of why these two factors would change in the first place if canopy nitrogen is the  
 632 limiting constraint.

#### 633 4.4 Other potential leaf trait plasticity trade-offs

634 Other coordinated plant plasticity responses to elevated CO<sub>2</sub> and nutrient limita-  
 635 tion could further influence the impacts of leaf trait plasticity on competitive ability and  
 636 tropical forest functioning. Observations show that many trees, including tropical trees,  
 637 enhance carbon and nitrogen allocation to root growth at the expense of leaf growth in  
 638 response to elevated CO<sub>2</sub> (e.g., Luo et al., 2006, Körner and Arnone, 1992; reviewed in  
 639 Cusack et al., 2016; Cernusak et al., 2013). Such partitioning of nitrogen away from leaves  
 640 could increase C:N<sub>leaf</sub> but benefit plants if they use the nitrogen to build other struc-  
 641 tures that help alleviate resource limitation, such as roots that can access further nu-  
 642 trients (reviewed in Cusack et al., 2016; Cernusak et al., 2013) although, in some cases,  
 643 this growth strategy has been found to be ineffective (Norby et al., 2010). Our primary  
 644 results isolate the influence of leaf trait plasticity changes and do not include changes  
 645 in the target ratio of root mass to leaf area. However, we test the sensitivity of our re-  
 646 sults to increasing target root mass in coordination with leaf trait plasticity using ad-  
 647 ditional simulations (Supporting Information Text S1.3.2 and S2.1). In these additional  
 648 experiments, trees increase target root mass in proportion with increases in LMA. This  
 649 accounts for the additional carbon cost of growing more roots to support the additional  
 650 nutrient requirements for greater leaf mass. This makes it even more costly to increase  
 651 LMA, which we expect should reduce the competitive advantage of doing so. In this case,  
 652 we find that the control plant type is always at competitive advantage, and the bene-  
 653 fit of increasing LMA that we saw in our primary results no longer consistently occurs

(Fig. S3). This result highlights the importance of considering the whole plant system and coordinated trade-offs that might occur under modified environmental conditions.

Other potential trade-offs for leaf trait plasticity responses could be thought to alter their influence on tropical forest ecosystem dynamics and functioning. For example, enhanced leaf lifespan is associated with greater LMA across species (Wright et al., 2004) and could be expected to further enhance productivity and competitive outcomes. However, this relationship across species does not necessarily hold within species (Anderegg et al., 2018; Fisher et al., 2015; Lusk et al., 2008) and varies in response to elevated carbon dioxide (Norby et al., 2003, 2010; Taylor et al., 2008; Lovelock et al., 1998), thus we chose not to couple increases in leaf lifespan with increases in LMA in our experiments. Higher carbon to nitrogen ratios are also associated with defense against herbivory (reviewed in Cusack et al., 2016), which could increase with climate change (e.g. Deutsch et al., 2018) but are not considered in our simulations.

#### 4.5 Indirect effects of plant type abundance

With limited changes in spatial distributions of plant types, the observed plastic response of plants under high CO<sub>2</sub> is likely to lead to decreases in  $N_{area}$  and thus to overall decreases in carbon uptake and evapotranspirative cooling. On the other hand, if the distribution of plants in an ecosystem changes due to differences in competitive ability, plant types that can maintain higher  $N_{area}$  and thus confer greater competitive advantage could, in the longer term, increase in abundance and bring carbon uptake and evapotranspirative cooling more in line with projections that assume leaf traits remain as in the control.

#### 4.6 Potential role of rising temperatures

Warming temperatures could be expected to alter the response of leaf traits to CO<sub>2</sub>, with implications for the influence of leaf trait plasticity on ecosystem functioning and composition. For example, warmer temperatures have been found to be associated with lower leaf nitrogen content across a spatial gradient in present-day tropical forests (Cusack et al., 2016; Fyllas et al., 2009; Tully & Lawrence, 2010), plausibly via the negative impacts of plant respiration with high nitrogen content (Cernusak et al., 2013). Such decreases in leaf nutrient concentration could amplify the leaf responses to elevated CO<sub>2</sub> we test here (unless there were accompanying changes in the allocation of N to different plant processes). Higher temperatures have been associated with lower LMA in manipulation experiments (Poorter et al., 2009), as well as across an elevational gradient in present-day tropical forests (Doughty et al., 2018). This influence could be expected to offset the LMA increase in response to CO<sub>2</sub> we test here. However, warming and CO<sub>2</sub> are hypothesized to influence LMA through different mechanisms (leaf expansion vs. accumulation of carbohydrates, respectively), making it difficult to predict the combined influence of these two environmental factors on LMA. Thus, the combined influence of elevated CO<sub>2</sub> and temperature on tropical tree traits remains poorly constrained (Cusack et al., 2016; Cernusak et al., 2013).

#### 4.7 Recommendations for including leaf trait plasticity in projections of future climate

We illustrate here that a better understanding of tropical tree responses to environmental change, as well as the use of plant competition models, will be needed to accurately include the effects of leaf trait plasticity in projections of future climate.

First, more observations are required to constrain tropical tree leaf responses to multiple environmental factors - including CO<sub>2</sub>, nutrient availability, and temperature - and how these responses differ by tree type (e.g. successional class or species) and develop-

702 mental stage (e.g. Cusack et al., 2016). Our ability to characterize leaf trait plasticity  
703 in response to environmental change may ultimately require a better understanding of  
704 whole plant carbon and nutrient dynamics, as leaf carbon and nitrogen can depend on  
705 supply and demand from other plant organs (e.g. Luo et al., 1994; Pritchard et al., 1999;  
706 Norby et al., 2010; Xu et al., 2012; Winter et al., 2001; Zaehle et al., 2014).

707 Second, numerous models of the terrestrial biosphere represent the cycling of nu-  
708 trients, and a subset of these represent flexibility in tissue C:N ratios in response to N  
709 availability (Zaehle & Friend, 2010; Zaehle et al., 2014). Here we show that simulation  
710 of changes in C:N ratio in isolation of apparently coordinated changes in LMA may over-  
711 estimate the impact of changing stoichiometry on future gas exchange. Complex as it  
712 is, models should thus strive to represent the temporal dynamics of important plant traits  
713 themselves—including LMA—under changing environmental conditions. Here we test  
714 the impacts of modifying plant traits as observed, but many studies aim to predict such  
715 plant properties from principles of evolutionary optimality theory (McMurtrie & Dewar,  
716 2011; Prentice et al., 2014; Dewar et al., 2012; Thomas & Williams, 2014; Xu et al., 2012),  
717 for example, to maximize leaf or canopy carbon export per unit N investment, or sim-  
718 ilar metrics. Optimality models typically predict single optimal solutions for a given set  
719 of conditions, without consideration of demographic time lags or genetic limitations on  
720 trait plasticity. Vegetation demographic models, wherein competing plants might move  
721 the community mean towards an optimum, provide an alternative means of predicting  
722 plant trait dynamics in time (Weng et al., 2015; Falster et al., 2017; Fisher et al., 2018).  
723 Using a model of plant competition, we show here that changes in leaf traits can alter  
724 plant competitive dynamics and the abundance of different plant types with implications  
725 for ecosystem functioning. Ideally, some consideration of the degree to which traits are  
726 plastic within existing species would provide the best means to combining these two ap-  
727 proaches (Fisher & Koven, 2020), but would require detailed studies of limits to plas-  
728 ticity (e.g. Geange et al., 2017; Power et al., 2019). Consideration of alternative opti-  
729 mal approaches to trait prediction will be investigated in future versions of FATES.

#### 730 4.8 Implications

731 Here we show that leaf trait plasticity in response to elevated CO<sub>2</sub> could alter trop-  
732 ical forest influences on climate directly, by altering the functioning of tropical trees, and  
733 indirectly, by modifying plant competitive dynamics and the abundance of different plant  
734 types. As such, including the effects of leaf trait plasticity could have a significant in-  
735 fluence on projections of future climate. These results further support the need for more  
736 observations of tropical tree responses to environmental change and the use of plant com-  
737 petition models within earth system models used to predict future climate change.

#### 738 Acknowledgments

739 MK, ALSS, CDK, RAF designed the study, all authors contributed to model develop-  
740 ment, MK completed the simulations, MK analyzed the output, all authors contributed  
741 to interpretations of the results, and MK, ALSS wrote the paper with input from all au-  
742 thors. We thank Janneke Hille Ris Lambers and Elizabeth Van Volkenburgh for their in-  
743 sightful suggestions on an earlier version of this manuscript. We acknowledge support  
744 from the National Science Foundation AGS-1553715 to the University of Washington.  
745 RAF acknowledges the support of the National Center for Atmospheric Research, which  
746 is a major facility sponsored by the National Science Foundation under Cooperative Agree-  
747 ment 1852977. CDK acknowledges support by the Director, Office of Science, Office of  
748 Biological and Environmental Research of the U.S. Department of Energy (DOE BER)  
749 under Contract DE-AC02-05CH11231 through the Early Career Research Program, the  
750 Regional and Global Model Analysis Program (RUBISCO SFA). CDK, RAF, and RGK  
751 acknowledge support from the DOE-BER Next Generation Ecosystem Experiment-Tropics  
752 (NGEE-Tropics) project. All simulations were run on the National Center for Atmospheric

	Biomass ( $kgC\ m^{-2}$ )		LAI ( $m^2\ m^{-2}$ )		NPP ( $gC\ m^{-2}\ yr^{-1}$ )		
	Mean (CI <sub>95</sub> )	% (CI <sub>95</sub> )	Mean (CI <sub>95</sub> )	% (CI <sub>95</sub> )	Mean (CI <sub>95</sub> )	% (CI <sub>95</sub> )	
double CO <sub>2</sub>	30.1 (30,30.2)	102.6 (102.1,103)	0.45 (0.43,0.46)		7 (6.8,7.2)	967.8 (958.8,976.8)	74.2 (73.2,75.1)
-N <sub>area</sub>	-7.1 (-7.1,-7)	-11.9 (-12,-11.7)	-0.5 (-0.51,-0.49)		-7.4 (-7.5,-7.2)	-208.6 (-215.7,-201.6)	-9.2 (-9.5,-8.9)
=N <sub>area</sub>	-1.6 (-1.7,-1.5)	-2.7 (-2.9,-2.6)	-0.02 (-0.03,-0.01)		-0.3 (-0.4,-0.1)	-0.4 (-7.7,6.8)	0 (-0.3,0.3)
+N <sub>area</sub>	4.1 (4,4.2)	6.9 (6.7,7)	0.76 (0.75,0.77)		11.1 (10.9,11.3)	191.9 (184.4,199.6)	8.4 (8.1,8.8)
+CN	-10.6 (-10.7,-10.5)	-17.8 (-18,-17.6)	-0.75 (-0.76,-0.74)		-11 (-11.1,-10.8)	-334.3 (-342.4,-326.3)	-14.7 (-15,-14.4)
+LMA	7.2 (7.1,7.4)	12.2 (11.9,12.4)	1.36 (1.34,1.38)		20 (19.7,20.2)	304.5 (294.2,314.9)	13.4 (12.9,13.9)
+CN+LMA	-2.6 (-2.7,-2.4)	-4.3 (-4.5,-4.1)	-0.03 (-0.04,-0.02)		-0.4 (-0.6,-0.3)	-0.8 (-9.9,8.4)	0 (-0.4,0.4)
	ET ( $W\ m^{-2}$ )		Total Canopy N ( $gN\ m^{-2}$ )				
	Mean (CI <sub>95</sub> )	% (CI <sub>95</sub> )	Mean (CI <sub>95</sub> )	% (CI <sub>95</sub> )			
double CO <sub>2</sub>	-7.3 (-7.8,-6.8)	-9.2 (-9.8,-8.6)	0.26 (0.26,0.27)		3.2 (3.1,3.3)		
-N <sub>area</sub>	-3.2 (-3.6,-2.8)	-4.4 (-5,-3.9)	-		-		
=N <sub>area</sub>	0 (-0.4,0.3)	-0.1 (-0.6,0.5)	-		-		
+N <sub>area</sub>	3.4 (3,3.8)	4.8 (4.2,5.3)	-		-		
+CN	-5 (-5.5,-4.6)	-7 (-7.7,-6.4)	-1.93 (-1.93,-1.92)		-23.2 (-23.3,-23.2)		
+LMA	5.7 (5.1,6.2)	7.9 (7.2,8.6)	3.02 (3,3.03)		36.3 (36.2,36.5)		
+CN+LMA	-0.1 (-0.6,0.4)	-0.1 (-0.8,0.6)	0.18 (0.17,0.18)		2.1 (2.1,2.2)		

Biomass, Leaf area index (LAI), net primary productivity (NPP), evapotranspiration (ET), and total canopy nitrogen (total canopy N) mean and percent (%) changes. “Double CO<sub>2</sub>” mean and percent changes are calculated as (CC - CTRL) and (CC - CTRL)/CTRL, respectively, where CTRL and CC are the control simulations at 400 ppm and 800 ppm CO<sub>2</sub>, respectively. All other mean and percent changes are calculated as (Experiment - CC) and (Experiment - CC)/CC, where CC is the control simulation at 800 ppm CO<sub>2</sub> and Experiment refers to experiments with different leaf trait plasticity levels. Bootstrap 95% confidence intervals (CI<sub>95</sub>%) in parentheses. -N<sub>area</sub>, = N<sub>area</sub>, and +N<sub>area</sub> average across experiments with leaf trait plasticity levels that decrease, maintain, and enhance leaf nitrogen per area, respectively. +CN experiment increases C:N<sub>leaf</sub> by one-third; +LMA increases LMA by one-third; and +CN+LMA, simultaneously increases C:N<sub>leaf</sub> and LMA by one-third.

Table 1.



Research's Cheyenne system. High-performance computing support from Cheyenne (doi:10.5065/D6RX99HX) was provided by NCAR's Computational and Information Systems Laboratory, sponsored by the National Science Foundation. Model output used in this study is available through the University of Washington Libraries ResearchWorks digital repository at <http://hdl.handle.net/1773/46218>.

## References

- Ali, A. A., Medlyn, B. E., Aubier, T. G., Crous, K. Y., & Reich, P. B. (2015, October). Elevated carbon dioxide is predicted to promote coexistence among competing species in a trait-based model. *Ecology and Evolution*, *5*(20), 4717–4733. doi: 10.1002/ece3.1733
- Anderegg, L. D., Berner, L. T., Badgley, G., Sethi, M. L., Law, B. E., & HilleRis-Lambers, J. (2018). Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecology Letters*, *21*(5), 734–744. doi: 10.1111/ele.12945
- Ball, J. T., Woodrow, I. E., & Berry, J. A. (1987, January). A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. *Progress in Photosynthesis Research*, *4*, 221–224. doi: 10.1007/978-94-017-0519-6\_48
- Bonan, G. B. (2008, June). Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, *320*, 1444–1449. doi: 10.1126/science.1155121
- Bonan, G. B., Lawrence, P. J., Oleson, K. W., Levis, S., Jung, M., Reichstein, M., ... Swenson, S. C. (2011, May). Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data. *Journal of Geophysical Research*, *116*(G2), G02014. doi: 10.1029/2010JG001593
- Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., BAKER, T. R., Lloyd, J., ... Zagt, R. J. (2015). Long-term decline of the Amazon carbon sink. *Nature*, *519*(7543), 344–+. doi: 10.1038/nature14283
- Caldararu, S., Thum, T., Yu, L., & Zaehle, S. (2020, 2020/08/27). Whole-plant optimality predicts changes in leaf nitrogen under variable co2 and nutrient availability. *New Phytologist*, *225*(6), 2331–2346. doi: 10.1111/nph.16327
- Cernusak, L. A., Haverd, V., Brendel, O., Le Thiec, D., Guehl, J.-M., & Cuntz, M. (2019). Robust response of terrestrial plants to rising co2. *Trends in plant science*, *24*(7), 578–586.
- Cernusak, L. A., Winter, K., Dalling, J. W., Holtum, J. A. M., Jaramillo, C., Körner, C., ... Wright, S. J. (2013). Tropical forest responses to increasing atmospheric CO2: current knowledge and opportunities for future research. *Functional Plant Biology*, *40*(6), 531–551. doi: 10.1071/FP12309
- Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., ... others (2013). Carbon and Other Biogeochemical Cycles. In *Climate change 2013: the physical science basis. contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change* (pp. 465–570). Cambridge University Press.
- Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., & Totterdell, I. J. (2000). Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model (vol 408, pg 184, 2000). *Nature*, *408*(6813), 750–750.
- Cusack, D. F., Karpman, J., Ashdown, D., Cao, Q., Ciochina, M., Halterman, S., ... Neupane, A. (2016). Global change effects on humid tropical forests: Evidence for biogeochemical and biodiversity shifts at an ecosystem scale. *Reviews of Geophysics*, *54*(3), 523–610.
- Davies-Barnard, T., Meyerholt, J., Zaehle, S., Friedlingstein, P., Brovkin, V., Fan, Y., ... Wiltshire, A. (2020). Nitrogen cycling in cmip6 land surface mod-



- 806 els: Progress and limitations. *Biogeosciences Discussions*, 2020, 1–32. doi:  
807 10.5194/bg-2019-513
- 808 Davin, E. L., & de Noblet-Ducoudré, N. (2010, January). Climatic Impact of Global-  
809 Scale Deforestation: Radiative versus Nonradiative Processes. *Journal of Cli-*  
810 *mate*, 23(1), 97–112. doi: 10.1175/2009JCLI3102.1
- 811 De Graaff, M.-A., Van Groenigen, K.-J., Six, J., Hungate, B., & Van Kessel, C.  
812 (2006, 2020/08/04). Interactions between plant growth and soil nutrient cy-  
813 cling under elevated co<sub>2</sub>: a meta-analysis. *Global Change Biology*, 12(11),  
814 2077–2091. doi: 10.1111/j.1365-2486.2006.01240.x
- 815 De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Hick-  
816 ler, T., . . . Norby, R. J. (2013, March). Forest water use and water use  
817 efficiency at elevated CO<sub>2</sub>: a model-data intercomparison at two contrasting  
818 temperate forest FACE sites. *Global Change Biology*, 19(6), 1759–1779. doi:  
819 10.1111/gcb.12164
- 820 De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang,  
821 Y.-P., . . . Norby, R. J. (2014, May). Where does the carbon go? A model-  
822 data intercomparison of vegetation carbon allocation and turnover processes at  
823 two temperate forest free-air CO<sub>2</sub> enrichment sites. *New Phytologist*, 203(3),  
824 883–899. doi: 10.1111/nph.12847
- 825 Deutsch, C. A., Tewksbury, J. J., Tigchelaar, M., Battisti, D. S., Merrill, S. C.,  
826 Huey, R. B., & Naylor, R. L. (2018). Increase in crop losses to insect pests in a  
827 warming climate. *Science*, 361(6405), 916–919.
- 828 Dewar, R. C., Tarvainen, L., Parker, K., Wallin, G., & McMurtrie, R. E. (2012).  
829 Why does leaf nitrogen decline within tree canopies less rapidly than light? an  
830 explanation from optimization subject to a lower bound on leaf mass per area.  
831 *Tree Physiology*, 32(5), 520–534.
- 832 Doughty, C. E., Santos-Andrade, P. E., Shenkin, A., Goldsmith, G. R., Bentley,  
833 L. P., Blonder, B., . . . others (2018). Tropical forest leaves may darken in  
834 response to climate change. *Nature ecology & evolution*, 2(12), 1918–1924.
- 835 Drake, B. G., & González-Meler, M. A. (1997). More efficient plants: a consequence  
836 of rising atmospheric CO<sub>2</sub>? *Annual Review of Plant Physiology*, 48(1), 609–  
837 639. doi: 10.1146/annurev.arplant.48.1.609
- 838 Falster, D. S., Brännström, Å., Westoby, M., & Dieckmann, U. (2017). Multitrait  
839 successional forest dynamics enable diverse competitive coexistence. *Proceed-*  
840 *ings of the National Academy of Sciences*, 114(13), E2719–E2728.
- 841 Faybishenko, B., Paton, S., Powell, T., Knox, R., Pastorello, G., Varadharajan, C.,  
842 . . . Agarwal, D. (2018). *QA/QC-ed BCI meteorological drivers* (Tech. Rep.).  
843 United States. doi: doi:10.15486/ngt/1423307
- 844 Fisher, R. A., & Koven, C. D. (2020, 2020/05/12). Perspectives on the future of  
845 land surface models and the challenges of representing complex terrestrial sys-  
846 tems. *Journal of Advances in Modeling Earth Systems*, 12(4), e2018MS001453.  
847 doi: 10.1029/2018MS001453
- 848 Fisher, R. A., Koven, C. D., Anderegg, W. R., Christoffersen, B. O., Dietze, M. C.,  
849 Farrior, C. E., . . . others (2018). Vegetation demographics in Earth System  
850 Models: A review of progress and priorities. *Global Change Biology*, 24(1),  
851 35–54.
- 852 Fisher, R. A., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., . . .  
853 Ian Woodward, F. (2010). Assessing uncertainties in a second-generation  
854 dynamic vegetation model caused by ecological scale limitations. *New Phytolo-*  
855 *gist*, 187(3), 666–681.
- 856 Fisher, R. A., Muszala, S., Versteinstein, M., Lawrence, P., Xu, C., McDowell, N. G.,  
857 . . . Bonan, G. (2015). Taking off the training wheels: the properties of a  
858 dynamic vegetation model without climate envelopes. *Geoscientific Model*  
859 *Development Discussions*, 8(4), 3293–3357. doi: 10.5194/gmdd-8-3293-2015
- 860 Fisher, R. A., Wieder, W. R., Sanderson, B. M., Koven, C. D., Oleson, K. W., Xu,

- 861 C., ... Lawrence, D. M. (2019). Parametric controls on vegetation responses  
862 to biogeochemical forcing in the clm5. *Journal of Advances in Modeling Earth*  
863 *Systems*, 11(9), 2879–2895.
- 864 Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F.,  
865 Fuchslueger, L., ... others (2019). Amazon forest response to co<sub>2</sub> fertiliza-  
866 tion dependent on plant phosphorus acquisition. *Nature Geoscience*, 12(9),  
867 736–741.
- 868 Fyllas, N. M., Patiño, S., Baker, T. R., Bielefeld Nardoto, G., Martinelli, L. A.,  
869 Quesada, C. A., ... Lloyd, J. (2009). Basin-wide variations in foliar proper-  
870 ties of amazonian forest: phylogeny, soils and climate. *Biogeosciences*, 6(11),  
871 2677–2708. doi: 10.5194/bg-6-2677-2009
- 872 Garbutt, K., Williams, W. E., & Bazzaz, F. A. (1990, 2020/07/17). Analysis of  
873 the differential response of five annuals to elevated co<sub>2</sub> during growth. *Ecology*,  
874 71(3), 1185–1194. doi: 10.2307/1937386
- 875 Geange, S. R., Briceño, V. F., Aitken, N. C., Ramirez-Valiente, J. A., Holloway-  
876 Phillips, M.-M., & Nicotra, A. B. (2017). Phenotypic plasticity and water  
877 availability: responses of alpine herb species along an elevation gradient. *Cli-*  
878 *mate Change Responses*, 4(1), 5.
- 879 Ghimire, B., Riley, W. J., Koven, C. D., Mu, M., & Randerson, J. T. (2016, March).  
880 Representing leaf and root physiological traits in CLM improves global car-  
881 bon and nitrogen cycling predictions. *Journal of Advances in Modeling Earth*  
882 *Systems*. doi: 10.1002/2015MS000538
- 883 Hickler, T., Smith, B., Prentice, I. C., Mjöfors, K., Miller, P., Arneth, A., & Sykes,  
884 M. T. (2008, July). CO<sub>2</sub> fertilization in temperate FACE experiments not  
885 representative of boreal and tropical forests. *Global Change Biology*, 14(7),  
886 1531–1542. doi: 10.1111/j.1365-2486.2008.01598.x
- 887 Holm, J. A., Knox, R. G., Zhu, Q., Fisher, R. A., Koven, C. D., Nogueira Lima,  
888 A. J., ... others (2020). The central amazon biomass sink under current  
889 and future atmospheric co<sub>2</sub>: Predictions from big-leaf and demographic veg-  
890 etation models. *Journal of Geophysical Research: Biogeosciences*, 125(3),  
891 e2019JG005500.
- 892 Hungate, B. A., Dukes, J. S., Shaw, M. R., Luo, Y., & Field, C. B. (2003, Novem-  
893 ber). Nitrogen and climate change. *Science*, 302, 1512–1513. doi: 10.1126/  
894 science.1091390
- 895 Ishizaki, S., Hikosaka, K., & Hirose, T. (2003). Increase in leaf mass per area ben-  
896 efits plant growth at elevated CO<sub>2</sub> concentration. *Annals of Botany*, 91(7),  
897 905–914. doi: 10.1093/aob/mcg097
- 898 Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bonisch, G., ... al, e.  
899 (2011). TRY—a global database of plant traits. *Global Change Biology*, 17,  
900 2905–2935. doi: 10.1111/j.1365-2486.2011.02451.x
- 901 Kattge, J., Knorr, W., Raddatz, T., & Wirth, C. (2009, April). Quantifying photo-  
902 synthetic capacity and its relationship to leaf nitrogen content for global-scale  
903 terrestrial biosphere models. *Global Change Biology*, 15(4), 976–991. doi:  
904 10.1111/j.1365-2486.2008.01744.x
- 905 Körner, C., & Arnone, J. A. (1992). Responses to elevated carbon dioxide in artifi-  
906 cial tropical ecosystems. *Science*, 257(5077), 1672–1675.
- 907 Koven, C. D., Knox, R. G., Fisher, R. A., Chambers, J. Q., Christoffersen, B. O.,  
908 Davies, S. J., ... Xu, C. (2020). Benchmarking and parameter sensitivity  
909 of physiological and vegetation dynamics using the functionally assembled  
910 terrestrial ecosystem simulator (fates) at barro colorado island, panama. *Bio-*  
911 *geosciences*, 17(11), 3017–3044. doi: 10.5194/bg-17-3017-2020
- 912 Kovenock, M. (2019). *Ecosystem and large-scale climate impacts of plant leaf dy-*  
913 *namics* (Unpublished doctoral dissertation). University of Washington.
- 914 Kovenock, M., & Swann, A. L. S. (2018, October). Leaf Trait Acclimation Amplifies  
915 Simulated Climate Warming in Response to Elevated Carbon Dioxide. *Global*

- 916 *Biogeochemical Cycles*, 32. doi: 10.1029/2018GB005883
- 917 Lawrence, D., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Verten-
- 918 stein, M., . . . Xu, C. (2018, May). Technical Description of version 5.0 of the
- 919 Community Land Model (CLM).
- 920 Leakey, A. D. B., Ainsworth, E. A., Bernacchi, C. J., Zhu, X., Long, S. P., &
- 921 Ort, D. R. (2012). Photosynthesis in a CO<sub>2</sub>-Rich Atmosphere. In *Pho-*
- 922 *tosynthesis in silico* (pp. 733–768). Dordrecht: Springer Netherlands. doi:
- 923 10.1007/978-94-007-1579-0\_29
- 924 Leakey, A. D. B., Bishop, K. A., & Ainsworth, E. A. (2012, June). A multi-biome
- 925 gap in understanding of crop and ecosystem responses to elevated CO<sub>2</sub>. *Cur-*
- 926 *rent Opinion in Plant Biology*, 15(3), 228–236. doi: 10.1016/j.pbi.2012.01.009
- 927 Lloyd, J., & Farquhar, G. D. (2008, May). Effects of rising temperatures and
- 928 [CO<sub>2</sub>] on the physiology of tropical forest trees. *Philosophical Transactions*
- 929 *of the Royal Society B: Biological Sciences*, 363(1498), 1811–1817. doi:
- 930 10.1098/rstb.2007.0032
- 931 Lloyd, J., Patiño, S., Paiva, R. Q., Quesada, C. A. N., Nardoto, G. B., Santos,
- 932 A. J. B., . . . Mercado, L. M. (2010). Optimisation of photosynthetic carbon
- 933 gain and within-canopy gradients of associated foliar traits for Amazon forest
- 934 trees. *Biogeosciences*, 7(6), 1833–1859. doi: 10.5194/bg-7-1833-2010
- 935 Lovelock, C. E., Winter, K., Mersits, R., & Popp, M. (1998). Responses of com-
- 936 munities of tropical tree species to elevated CO<sub>2</sub> in a forest clearing. *Oecologia*,
- 937 116(1), 207–218.
- 938 Luo, Y., Field, C. B., & Mooney, H. A. (1994, November). Predicting responses of
- 939 photosynthesis and root fraction to elevated [CO<sub>2</sub>]: interactions among car-
- 940 bon, nitrogen, and growth. *Plant, Cell and Environment*, 17(11), 1195–1204.
- 941 doi: 10.1111/j.1365-3040.1994.tb02017.x
- 942 Luo, Y., Hui, D., & Zhang, D. (2006, January). Elevated CO<sub>2</sub> stimulates net ac-
- 943 cumulations of carbon and nitrogen in land ecosystems: A meta-analysis. *Ecol-*
- 944 *ogy*, 87(1), 53–63.
- 945 Luo, Y., Su, B., Currie, W. S., Dukes, J. S., Finzi, A. C., Hartwig, U., . . . Field,
- 946 C. B. (2004, August). Progressive nitrogen limitation of ecosystem re-
- 947 sponses to rising atmospheric carbon dioxide. *BioScience*, 54(8), 731–739.
- 948 doi: 10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2
- 949 Lusk, C. H., Reich, P. B., Montgomery, R. A., Ackerly, D. D., & Cavender-Bares, J.
- 950 (2008). Why are evergreen leaves so contrary about shade? *Trends in Ecology*
- 951 *& Evolution*, 23(6), 299–303. doi: 10.1016/j.tree.2008.02.006
- 952 Mahowald, N., Lo, F., Zheng, Y., Harrison, L., Funk, C., Lombardozzi, D., &
- 953 Goodale, C. (2016). Projections of leaf area index in earth system models.
- 954 *Earth System Dynamics*, 7(1), 211–229. doi: 10.5194/esd-7-211-2016
- 955 Massoud, E. C., Xu, C., Fisher, R. A., Knox, R. G., Walker, A. P., Serbin, S. P.,
- 956 . . . others (2019). Identification of key parameters controlling demographi-
- 957 cally structured vegetation dynamics in a land surface model: Clm4. 5 (fates).
- 958 *Geoscientific Model Development*, 12(9), 4133–4164.
- 959 McMurtrie, R. E., & Dewar, R. C. (2011). Leaf-trait variation explained by the
- 960 hypothesis that plants maximize their canopy carbon export over the lifespan
- 961 of leaves. *Tree physiology*, 31(9), 1007–1023.
- 962 McMurtrie, R. E., Norby, R. J., Medlyn, B. E., Dewar, R. C., Pepper, D. A., Reich,
- 963 P. B., & Barton, C. V. (2008). Why is plant-growth response to elevated CO<sub>2</sub>
- 964 amplified when water is limiting, but reduced when nitrogen is limiting? A
- 965 growth-optimisation hypothesis. *Functional Plant Biology*, 35(6), 521–534.
- 966 Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton,
- 967 C. V. M., . . . Wingate, L. (2011, January). Reconciling the optimal and em-
- 968 pirical approaches to modelling stomatal conductance. *Global Change Biology*,
- 969 17(6), 2134–2144. doi: 10.1111/j.1365-2486.2010.02375.x
- 970 Medlyn, B. E., Zaehle, S., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Han-

- 971 son, P. J., . . . Norby, R. J. (2015, June). Using ecosystem experiments to  
 972 improve vegetation models. *Nature Climate Change*, 5(6), 528–534. doi:  
 973 10.1038/nclimate2621
- 974 Meyerholt, J., & Zaehle, S. (2015, July). The role of stoichiometric flexibility in  
 975 modelling forest ecosystem responses to nitrogen fertilization. *New Phytologist*,  
 976 208(4), 1042–1055. doi: 10.1111/nph.13547
- 977 Moorcroft, P. R., Hurtt, G. C., & Pacala, S. W. (2001). A method for scaling veg-  
 978 etation dynamics: the ecosystem demography model (ED). *Ecological mono-*  
 979 *graphs*, 71, 557–586.
- 980 Norby, R. J., De Kauwe, M. G., & Domingues, T. F. (2016). Model–data synthesis  
 981 for the next generation of forest free-air CO<sub>2</sub> enrichment (FACE) experiments.  
 982 *New Phytologist*, 209, 17–28.
- 983 Norby, R. J., Gu, L., Haworth, I. C., Jensen, A. M., Turner, B. L., Walker, A. P., . . .  
 984 Winter, K. (2017). Informing models through empirical relationships between  
 985 foliar phosphorus, nitrogen and photosynthesis across diverse woody species in  
 986 tropical forests of panama. *New Phytologist*, 215(4), 1425–1437.
- 987 Norby, R. J., Sholtis, J. D., Gunderson, C. A., & Jawdy, S. S. (2003, August). Leaf  
 988 dynamics of a deciduous forest canopy: no response to elevated CO<sub>2</sub>. *Oecolo-*  
 989 *gia*, 136(4), 574–584. doi: 10.1007/s00442-003-1296-2
- 990 Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., & McMurtrie, R. E.  
 991 (2010). CO<sub>2</sub> enhancement of forest productivity constrained by limited nitro-  
 992 gen availability. *Proceedings of the National Academy of Sciences of the United*  
 993 *States of America*, 107(45), 19368–19373. doi: 10.1073/pnas.1006463107
- 994 Poorter, H., Berkel, Y. v., Baxter, R., Hertog, J. d., Dijkstra, P., Gifford, R. M., . . .  
 995 Wong, S. C. (1997). The effect of elevated CO<sub>2</sub> on the chemical composition  
 996 and construction costs of leaves of 27 C<sub>3</sub> species. *Plant, Cell and Environment*,  
 997 20(4), 472–482. doi: 10.1046/j.1365-3040.1997.d01-84.x
- 998 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009, May).  
 999 Causes and consequences of variation in leaf mass per area (LMA): a meta-  
 1000 analysis. *New Phytologist*, 182, 565–588. doi: 10.1111/j.1469-8137.2009.02830  
 1001 .x
- 1002 Power, S. C., Verboom, G. A., Bond, W. J., & Cramer, M. D. (2019). Does a  
 1003 tradeoff between trait plasticity and resource conservatism contribute to the  
 1004 maintenance of alternative stable states? *New Phytologist*, 223(4), 1809–1819.
- 1005 Prentice, I. C., Dong, N., Gleason, S. M., Maire, V., & Wright, I. J. (2014). Bal-  
 1006 ancing the costs of carbon gain and water transport: testing a new theoretical  
 1007 framework for plant functional ecology. *Ecology letters*, 17(1), 82–91.
- 1008 Pritchard, S. H., Rogers, H. O., Prior, S. A., & Peterson, C. M. (1999). Elevated  
 1009 CO<sub>2</sub> and plant structure: a review. *Global Change Biology*, 5(7), 807–837. doi:  
 1010 10.1046/j.1365-2486.1999.00268.x
- 1011 Purves, D. W., Lichstein, J. W., Strigul, N., & Pacala, S. W. (2008). Predicting and  
 1012 understanding forest dynamics using a simple tractable model. *Proceedings of*  
 1013 *the National Academy of Sciences*, 105(44), 17018–17022.
- 1014 Quebbeman, J., & Ramirez, J. (2016). Optimal allocation of leaf-level nitrogen:  
 1015 Implications for covariation of v<sub>cmax</sub> and j<sub>max</sub> and photosynthetic downregu-  
 1016 lation. *Journal of Geophysical Research: Biogeosciences*, 121(9), 2464–2475.
- 1017 Reekie, E. G., & Bazzaz, F. A. (1989, January). Competition and patterns of  
 1018 resource use among seedlings of five tropical trees grown at ambient and ele-  
 1019 vated CO<sub>2</sub>. *Oecologia*, 79(2), 212–222. doi: 10.2307/4218947?ref=no-x-route:  
 1020 40f91c19f6c4e030b308b9050ce77413
- 1021 Rogers, A., Medlyn, B. E., Dukes, J. S., Bonan, G., von Caemmerer, S., Dietze,  
 1022 M. C., . . . Zaehle, S. (2017, January). A roadmap for improving the represen-  
 1023 tation of photosynthesis in Earth system models. *The New phytologist*, 213(1),  
 1024 22–42. doi: 10.1111/nph.14283
- 1025 Roumet, C., Laurent, G., & Roy, J. (1999). Leaf structure and chemical composition

- 1026 as affected by elevated CO<sub>2</sub>: genotypic responses of two perennial grasses. *New*  
 1027 *Phytologist*, *143*(1), 73–81. doi: 10.1046/j.1469-8137.1999.00437.x
- 1028 Schimel, D., Stephens, B. B., & Fisher, J. B. (2015, January). Effect of increasing  
 1029 CO<sub>2</sub> on the terrestrial carbon cycle. *Proceedings of the National Academy of*  
 1030 *Sciences of the United States of America*, *112*(2), 436–441. doi: 10.1073/pnas  
 1031 .1407302112
- 1032 Smith, N. G., Keenan, T. F., Colin Prentice, I., Wang, H., Wright, I. J., Niinemets,  
 1033 Ü., ... others (2019). Global photosynthetic capacity is optimized to the  
 1034 environment. *Ecology letters*, *22*(3), 506–517.
- 1035 Sterck, F., Markesteijn, L., Schieving, F., & Poorter, L. (2011). Functional traits de-  
 1036 termine trade-offs and niches in a tropical forest community. *Proceedings of the*  
 1037 *National Academy of Sciences*, *108*(51), 20627–20632.
- 1038 Swann, A. L. S., Hoffman, F. M., Koven, C. D., & Randerson, J. T. (2016,  
 1039 September). Plant responses to increasing CO<sub>2</sub> reduce estimates of cli-  
 1040 mate impacts on drought severity. *Proceedings of the National Academy*  
 1041 *of Sciences of the United States of America*, *113*(36), 10019–10024. doi:  
 1042 10.1073/pnas.1604581113
- 1043 Taylor, G., Tallis, M. J., Giardina, C. P., Percy, K. E., Miglietta, F., Gupta,  
 1044 P. S., ... Karnosky, D. F. (2008). Future atmospheric CO<sub>2</sub> leads to de-  
 1045 layed autumnal senescence. *Global Change Biology*, *14*(2), 264–275. doi:  
 1046 10.1111/j.1365-2486.2007.01473.x
- 1047 Thomas, R. Q., & Williams, M. (2014). A model using marginal efficiency of in-  
 1048 vestment to analyze carbon and nitrogen interactions in terrestrial ecosystems  
 1049 (aconite version 1). *Geoscientific Model Development*, *7*(5), 2015–2037.
- 1050 Tully, K., & Lawrence, D. (2010). Declines in leaf litter nitrogen linked to rising  
 1051 temperatures in a wet tropical forest. *Biotropica*, 526–530.
- 1052 van der Sleen, P., Groenendijk, P., Vlam, M., Anten, N. P. R., Boom, A., Bongers,  
 1053 F., ... Zuidema, P. A. (2015, January). No growth stimulation of tropi-  
 1054 cal trees by 150 years of CO<sub>2</sub> fertilization but water-use efficiency increased.  
 1055 *Nature*, *8*(1), 24–28. doi: 10.1038/ngeo2313
- 1056 Verheijen, L. M., Aerts, R., Brovkin, V., Cavender-Bares, J., Cornelissen, J. H. C.,  
 1057 Kattge, J., & van Bodegom, P. M. (2015, March). Inclusion of ecologically  
 1058 based trait variation in plant functional types reduces the projected land car-  
 1059 bon sink in an earth system model. *Global Change Biology*, *21*(8), 3074–3086.  
 1060 doi: 10.1111/gcb.12871
- 1061 Verheijen, L. M., Brovkin, V., Aerts, R., Bonisch, G., Cornelissen, J. H. C., Kattge,  
 1062 J., ... Van Bodegom, P. M. (2013). Impacts of trait variation through  
 1063 observed trait–climate relationships on performance of an Earth system  
 1064 model: a conceptual analysis. *Biogeosciences*, *10*(8), 5497–5515. doi:  
 1065 10.5194/bg-10-5497-2013
- 1066 Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues,  
 1067 T. F., ... Woodward, F. I. (2014). The relationship of leaf photosynthetic  
 1068 traits–V<sub>cm</sub> and J<sub>max</sub>–to leaf nitrogen, leaf phosphorus, and specific leaf  
 1069 area: a meta-analysis and modeling study. *Ecology and Evolution*, *4*(16),  
 1070 3218–3235.
- 1071 Walker, A. P., Quaipe, T., van Bodegom, P. M., De Kauwe, M. G., Keenan, T. F.,  
 1072 Joiner, J., ... others (2017). The impact of alternative trait-scaling hypotheses  
 1073 for the maximum photosynthetic carboxylation rate (v<sub>cm</sub>) on global gross  
 1074 primary production. *New Phytologist*, *215*(4), 1370–1386.
- 1075 Weng, E., Malyshev, S., Lichstein, J., Farrior, C., Dybzinski, R., Zhang, T., ...  
 1076 Pacala, S. W. (2015). Scaling from individual trees to forests in an earth  
 1077 system modeling framework using a mathematically tractable model of height-  
 1078 structured competition. *Biogeosciences*.
- 1079 Winter, K., Garcia, M., Gottsberger, R., & Popp, M. (2001). Marked growth re-  
 1080 sponse of communities of two tropical tree species to elevated co2 when soil



- 1081 nutrient limitation is removed. *Flora*, 196(1), 47–58.
- 1082 Winter, K., Garcia, M., Lovelock, C. E., Gottsberger, R., & Popp, M. (2000).  
 1083 Responses of model communities of two tropical tree species to elevated atmo-  
 1084 spheric CO<sub>2</sub>: growth on unfertilized soil. *Flora*, 195(4), 289–302.
- 1085 Winter, K., & Lovelock, C. E. (1999). Growth responses of seedlings of early and  
 1086 late successional tropical forest trees to elevated atmospheric CO<sub>2</sub>. *Flora*,  
 1087 194(2), 221–227.
- 1088 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ...  
 1089 Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985),  
 1090 821–827. doi: 10.1038/nature02403
- 1091 Xu, C., Fisher, R., Wullschleger, S. D., Wilson, C. J., Cai, M., & McDowell, N. G.  
 1092 (2012). Toward a mechanistic modeling of nitrogen limitation on vegetation  
 1093 dynamics. *PloS one*, 7(5), e37914.
- 1094 Yin, X. (2002). Responses of leaf nitrogen concentration and specific leaf area to at-  
 1095 mospheric CO<sub>2</sub> enrichment: a retrospective synthesis across 62 species. *Global*  
 1096 *Change Biology*, 8(7), 631–642.
- 1097 Zaehle, S., & Friend, A. D. (2010, February). Carbon and nitrogen cycle dynamics  
 1098 in the O-CN land surface model: 1. Model description, site-scale evaluation,  
 1099 and sensitivity to parameter estimates. *Global Biogeochemical Cycles*, 24(1).  
 1100 doi: 10.1029/2009GB003521
- 1101 Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hick-  
 1102 ler, T., ... Norby, R. J. (2014, January). Evaluation of 11 terrestrial  
 1103 carbon-nitrogen cycle models against observations from two temperate  
 1104 Free-Air CO<sub>2</sub> Enrichment studies. *New Phytologist*, 202(3), 803–822. doi:  
 1105 10.1111/nph.12697
- 1106 Zhang, K., Kimball, J. S., Nemani, R. R., Running, S. W., Hong, Y., Gourley, J. J.,  
 1107 & Yu, Z. (2015, October). Vegetation Greening and Climate Change Promote  
 1108 Multidecadal Rises of Global Land Evapotranspiration. *Nature Publishing*  
 1109 *Group*, 1–9. doi: 10.1038/srep15956
- 1110 Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., ... Zeng, N.  
 1111 (2016, April). Greening of the Earth and its drivers. *Nature Climate Change*.  
 1112 doi: 10.1038/nclimate3004