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

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

[1]Department of Biology, University of Washington, Seattle, WA
[2]Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA
[3]National Center for Atmospheric Research, Boulder, CO
[4]Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique (CERFACS), Toulouse, France
[5]Department of Atmospheric Sciences, University of Washington, Seattle, WA

Key Points:

- Including the observed response of leaf traits to higher CO_2 results in lower competitive ability for modeled tropical trees
- Concurrent changes in multiple leaf traits could help maintain per-area photosynthetic rates and confer a competitive advantage
- Resulting ecosystem-scale carbon uptake depends on the magnitude of trait plasticity coupled with changes in plant type abundance

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Corresponding author: Abigail L.S. Swann, `aswann@uw.edu`

Abstract

The response of tropical ecosystems to elevated carbon dioxide (CO_2) remains a critical uncertainty in projections of future climate. Here we investigate how leaf trait plasticity in response to elevated 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 CO_2 in a tropical forest. Observationally constrained leaf trait plasticity in response to CO_2 fertilization reduces the degree to which tropical tree carbon uptake is affected by a doubling of 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 CO_2 lowers tropical ecosystem carbon uptake and evapotranspirative cooling in the absence of changes in plant type abundance. However, 'plastic' responses to high 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 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 (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 environmental 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_2 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_2 are increases in leaf mass per area (LMA, g leaf carbon m^{-2} leaf area) and the ratio of carbon to nitrogen within leaves (C: N_{leaf}, g leaf carbon g^{-1} leaf nitrogen). Observations suggest that each of these leaf traits could increase by as much as one-third under doubled CO_2 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_2 enrichment experiments suggests that accurately representing these two leaf traits is critical to predicting ecosystem responses to elevated CO_2 (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_{leaf} and LMA increase with elevated CO_2 is that CO_2 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_2 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_{leaf} 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_2. It is possible that even if plastic responses of LMA and C:N_{leaf} 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_{leaf} 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_{leaf} and LMA directly influence tropical forest functioning by altering area-based photosynthetic rates. C:N_{leaf} is the amount of nitrogen present in a given unit of leaf mass, with higher C:N_{leaf} 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_{area}, g nitrogen m^{-2} leaf area) as follows:

$$N_{area} = \frac{LMA}{C\colon N_{leaf}} \tag{1}$$

Given that nitrogen is an essential component of photosynthetic enzymes, particularly rubisco, N_{area} is an important determinant of maximum photosynthetic rates per leaf area (Drake & Gonzàlez-Meler, 1997; Kattge et al., 2009, 2011; Walker et al., 2014; Norby et al., 2017). N_{area} is therefore used in many terrestrial biosphere models to estimate photosynthetic parameters, which in turn exert strong influence over modeled carbon uptake (Verheijen et al., 2013; Bonan et al., 2011; Walker et al., 2017; Rogers et al., 2017). Changes in maximum photosynthetic rates due to altered N_{area} can also influence rates of evapotranspirative cooling, as transpiration is coupled to photosynthesis in all commonly used stomatal conductance algorithms (Ball et al., 1987; Medlyn et al., 2011).

Experimental manipulation of CO_2 in tropical forest systems has been observed to modify both LMA and $C{:}N_{leaf}$ in a wide range of tropical tree species across successional classes (Lovelock et al., 1998). These observations suggest that co-occurring changes in LMA and $C{:}N_{leaf}$ in response to a doubling of CO_2 most often caused N_{area} to decrease (Fig. 1 below diagonal line) or, in fewer cases, to be maintained (Fig. 1 on diagonal line; Lovelock et al., 1998). Thus, in the absence of other changes (such as adjusted partitioning of nitrogen between different photosynthetic processes; e.g., Xu et al., 2012; Leakey, Ainsworth, et al., 2012; Smith et al., 2019) the observed leaf trait plasticity in response to elevated CO_2 has the potential to lower projections of tropical ecosystem carbon uptake and evapotranspirative cooling by reducing photosynthetic rates and stomatal conductance.

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

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

1.2 Indirect effects of trait plasticity

Competition for light is recognized to be a dominant driver of community composition in tropical forests (e.g., Sterck et al., 2011). In addition to the direct influences described above, tropical tree responses to increasing CO_2 could also indirectly change ecosystem functioning by altering plant competition for light and the relative abundance of different plant types (reviewed by Cusack et al., 2016). The magnitude of leaf trait responses to elevated CO_2 has been observed to differ among tropical tree species (Lovelock et al., 1998; Reekie & Bazzaz, 1989; Winter et al., 2000; Winter & Lovelock, 1999). Variation in leaf trait plasticity across tropical tree types could lead to differential changes in the competitive ability for light in response to elevated CO_2 and thus alter the abundance of competing plant types. LMA and C:N$_{leaf}$ act to modify both leaf area index and biomass through their influence on per leaf area photosynthetic rates as well as total leaf area. Leaf area index and biomass in turn can influence plant competitive ability. In general, trees which accumulate less biomass may not be able to grow as tall as their neighbors and may therefore become more heavily shaded; while trees with lower leaf area index may not be able to capture as much light or shade their neighbors in competition for light. Thus changes in these traits are likely to differentially alter the competitive ability of individual trees depending on their magnitude of plasticity.

1.3 Results from previous studies

Observational manipulation experiments have shown that tropical tree trait responses to CO$_2$ are species-specific (Lovelock et al., 1998; Reekie & Bazzaz, 1989; Winter et al., 2000; Winter & Lovelock, 1999) and suggest that differences in CO$_2$ responses across species could lead to changes in community structure (reviewed by Cusack et al., 2016). Investigating the relationship between individual traits and community outcomes is challenging in empirical studies due to multiple, confounding changes in plants treated with elevated CO$_2$ (Lovelock et al., 1998; Reekie & Bazzaz, 1989). While increases in C:N$_{leaf}$ and increases in LMA both appear to have negative impacts on plants at first consideration each has the potential to confer advantage. Despite first-order reductions in nitrogen per unit plant area, increasing C:N$_{leaf}$ may benefit plants as an adaptation to N limited conditions. McMurtrie et al. (2008) showed that a temperate monoculture was able to maximize productivity under limited nitrogen availability and elevated CO$_2$ by increasing C:N$_{leaf}$ which enabled increased leaf area. Increasing LMA could also be beneficial despite the higher cost of leaf area. Previous modeling studies have used observations of LMA and C:N$_{leaf}$ change to simulate changes in assimilation and individual plant growth and found that increasing LMA helps to offset negative effects of higher C:N$_{leaf}$ on N$_{area}$ and photosynthetic rates per leaf area under elevated CO$_2$ (Luo et al., 1994; Ishizaki et al., 2003).

None of these studies, however, considered communities of plants or the effects of competition between different plant types, nor did they focus on tropical tree species. Other modeling studies have found variability in plant traits, such as LMA, to have strong influences on plant competition for resources and ecosystem functioning under elevated CO$_2$ (Ali et al., 2015; Verheijen et al., 2015; Fisher et al., 2010). For example, Ali et al. (2015) found that decreasing LMA (the opposite of the observed change) was beneficial to competitive success under elevated CO$_2$, but did not consider the observed concomitant changes in C:N$_{leaf}$. Thus it remains unclear how the combination of observed trait responses to CO$_2$ will influence plant competitive dynamics, the survival of responsive trees, and tropical ecosystem structure and functioning in the future. Additionally, Verheijen et al. (2015) allowed LMA to vary with CO$_2$ (along with other environmental drivers and traits) globally in a dynamic global vegetation model, however they didn't allow LMA influence leaf area index, nor, did they focus on tropical trees.

1.4 Modeling Objectives

In this study we explore how plasticity in two key leaf traits mediates tropical ecosystem carbon uptake and evapotranspirative cooling responses to a doubling of CO$_2$ using an ensemble of simulations of the Functionally Assembled Terrestrial Ecosystem Simulator (FATES; Fisher et al., 2015; Koven et al., 2020) vegetation demographic model at a tropical forest test site, Barro Colorado Island, Panama. We investigate how different levels of plasticity in C:N$_{leaf}$ and LMA (gray squares in Fig. 1) in response to a doubling of CO$_2$: 1) modify ecosystem level carbon uptake and evapotranspirative cooling in the absence of competition; 2) alter biomass and leaf area index; and 3) alter competitive outcomes when two plant types with different leaf trait plasticity responses compete.

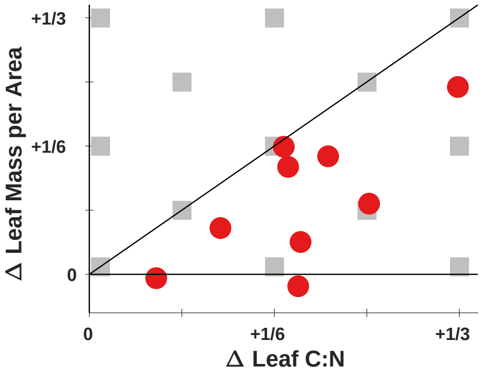

Figure 1. Leaf trait plasticity in response to a doubling of CO_2 in tropical trees for leaf C:N (leaf $gC\ gN^{-1}$) and leaf mass per area ($gC\ m^{-2}$ leaf area). Observed changes across nine tropical tree species (red circles) from Lovelock et al. (1998). Leaf trait plasticity levels sampled for 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 ($-N_{area}$).

We test leaf trait plasticity levels that increase ($+N_{area}$), decrease ($-N_{area}$), and maintain N_{area} ($=N_{area}$). Our simulations do not explicitly represent growth limitation by or competition for nitrogen. Instead, we are able to quantify the change in total canopy nitrogen (g nitrogen m^{-2} ground) required to support an ecosystem with each level of leaf trait plasticity (under doubled CO_2). We find that leaf trait plasticity levels that decrease N_{area}, - consistent with observed responses of LMA and $C{:}N_{leaf}$, could reduce projections of future carbon uptake and evapotranspiration in the absence of competition. However, trees that are able to maintain or increase N_{area} under high CO_2 would likely have a competitive advantage and could therefore maintain higher levels of ecosystem carbon uptake and evapotranspirative cooling.

2 Methods

2.1 Model Overview

We use an ensemble of simulations of the Functionally Assembled Terrestrial Ecosystem Simulator (FATES; Fisher et al., 2015; Massoud et al., 2019; Koven et al., 2020) embedded within the Community Land Model version 5 (Lawrence et al., 2018) to test the influence of leaf trait plasticity on tropical ecosystem functioning and competitive dynamics. CLM(FATES) is a cohort-based vegetation demographic model (Fisher et al., 2018; Koven et al., 2020), that mechanistically simulates plant ecological dynamics and ecosystem assembly via processes including plant growth, competition for light, recovery from disturbance, reproduction, mortality, and recruitment. A key feature of the model, based on the ecosystem demography concept (Moorcroft et al., 2001), is that it resolves distributions of vegetation height and time since disturbance, which allows it to simulate competition for light. In the model, disturbance, from tree mortality, fire, or logging, occurs at some rate across patches of the simulated ecosystem. Plants grow upon ground area within these “patches”, which are tracked by an age that represents the time since the last disturbance that that area of ground experienced. Within a patch, individual plants are grouped into “cohorts”, which can differ in height and functional type. Thus, cohorts represent individual plants of the same plant type and height as a representative average individual. The height structure of cohorts within a patch determines the light profile experienced by each cohort. The leaf area of taller cohorts in the canopy can shade cohorts deeper in the canopy, which is further depicted as discrete canopy layers using the perfect plasticity approximation (Purves et al., 2008). Photosynthesis, respiration, turnover, and mortality, as well as the interaction of these processes with the abiotic environment, control the amount of carbon each cohort can use for growth. Growth and size-dependent allometric equations then determine the height, biomass, and target leaf area of each cohort. Thus, carbon uptake is dynamic and influences plant growth, leaf area, and size, which in turn influence competition for light. Radiation streams for direct and diffuse light are calculated at the leaf layer level for each plant type, patch and canopy layer. This incoming energy drives photosynthesis and the surface energy budget, and thus rates of carbon uptake and transpiration. In sum, the model tracks fluxes of carbon, water, and energy throughout the ecosystem. This version of CLM(FATES) does not explicitly represent growth limitation by or competition for nutrients, thus, we implement C:N$_{leaf}$ and LMA plasticity levels that represent the potential influences of nutrient limitation and quantify the total canopy nitrogen required to support each leaf trait plasticity level.

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

2.2 Leaf trait plasticity estimation and implementation

Our experiments test 13 levels of leaf plasticity in C:N$_{leaf}$ and LMA sampled from the two-dimensional leaf trait plasticity space in Fig. 1 (gray squares). We test the equilibrium response to elevated CO$_2$ rather than representing dynamic changes in time. The leaf trait plasticity space represents both observed (at or below diagonal line in Fig. 1) and hypothetical (above the diagonal line in Fig. 1) levels of leaf trait plasticity. The observed leaf trait plasticity space is estimated from observations of leaf responses to a doubling of CO$_2$ in nine tropical tree species, including early, mid- and late successional classes (Lovelock et al., 1998, Fig. 1 red circles), and supported by additional studies in tropical trees and many other C3 plant types (e.g., Lovelock et al., 1998; Reekie & Bazzaz, 1989; Winter et al., 2000; Winter & Lovelock, 1999). These observations suggest that both C:N$_{leaf}$ and LMA could increase by as much as one-third in response to a doubling of CO$_2$ while N$_{area}$ (Eqn 1) decreases or remains constant. Thus, we define observed leaf trait plasticity levels as those that maintain N$_{area}$ at (=N$_{area}$) or below (-N$_{area}$) control (CTRL and CC) levels. We also test leaf trait plasticity levels that increase N$_{area}$ (+N$_{area}$), to determine if such a response could help tropical trees enhance their productivity and competitive ability. Given the wide diversity of tropical tree species it is possible that some tropical tree species, (e.g. those with traits that enhance nutrient foraging or fixing capabilities), could in principle increase N$_{area}$ (Fig. 1 above diagonal line) in response to higher CO$_2$.

Changes in C:N$_{leaf}$ and LMA in our simulations drive changes in N$_{area}$, maximum photosynthetic and respiration rates, and leaf area index. Plasticity in C:N$_{leaf}$ and LMA drives changes in N$_{area}$ (as described above) and this in turn alters maximum rates of photosynthesis (e. g. V$_{cmax}$, J$_{max}$, T$_{pmax}$) and leaf respiration, following Eqn 1. We directly 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 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; 1xCO_2). The second control is identical to the first except that the ecosystem experiences a fixed atmospheric CO_2 concentration of 800 ppm (CC; 2xCO_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 2xCO_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 2xCO_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 coexistence in the FATES model see Koven et al. (2020). We define one plant type as "winning" the competition when it overtakes at least two-thirds of the total ecosystem biomass (see below for further details). We quantify differences in competitive ability due to leaf trait plasticity using a measure called percent wins (% wins), which is the percent of all pairwise competitions a plant type with a given leaf trait plasticity level wins across competition with the other plant types in the ensemble.

The 1xCO_2 control simulation (CTRL) was started from near-bare ground and integrated for 700 years. All variables came into equilibrium within 450 years, the time required to grow a mature forest with our model set up. The 2xCO_2 control simulation (CC) and all experiments were branched from the 1xCO_2 control simulation (mature forest) at year 500 and experienced an abrupt doubling of CO_2 to a time-invariant concentration of 800 ppm CO_2. The 2xCO_2 control and experiment simulations were run to the point that the community was dominated by one plant type considered the "winner". Specifically, every simulation was run for 3,500 years, at which point 99% of competitions between plant types with different trait changes were complete (one plant type reached at least 95% of the ecosystem biomass). In the remaining 1% of competitions one plant type had become dominant (taken over at least 67% of ecosystem biomass and trending towards overtaking all ecosystem biomass). We analyze the last 100 years of each simulation as our equilibrium ecosystem.

2.4 Statistical Analysis

We quantify the influence of leaf trait plasticity in the absence of competition (i.e. simulations with only one plant type) using 1) differences in annual mean ecosystem properties and 2) relationships between leaf trait plasticity levels and annual mean ecosystem properties across simulations. We use bootstrap methods with model years as the unit of replication (n = 50,000) to construct confidence intervals for annual mean leaf area index, biomass, net primary productivity, evapotranspiration, and total canopy nitrogen and test for differences between simulations. We use bootstrapping methods because some variables have time series that are non-normally distributed, have unequal variances, and temporal autocorrelation. The 100 model years we analyze for each variable are unique despite repeating the 14 years of meteorological forcing, as ecological dynamics also influence the environment (e.g., light availability) and ecosystem structure and functioning in our simulations. We use simple, multiple, and stepwise linear regression methods to test for relationships between leaf trait plasticity levels ($C\!:N_{leaf}$, LMA, N_{area}) and annual mean ecosystem properties across simulations. Correlations between percent wins and annual mean net primary productivity and evapotranspiration across simulations were tested using Pearson's linear correlation coefficient. Differences, relationships, and correlations were considered statistically significant at the 95% confidence level. (See Supporting Information Text S1.4 for details.)

3 Results

3.1 Elevated CO_2 response in the control simulation

Previous observations, simulations, and theory show that elevated atmospheric CO_2 concentration enhances photosynthesis and reduces stomatal conductance, which has the potential to enhance productivity and reduce evapotranspiration at the ecosystem scale (e.g, Cernusak et al., 2013; Cusack et al., 2016; Lloyd & Farquhar, 2008; Zhu et al., 2016; Lloyd & Farquhar, 2008; Swann et al., 2016; De Kauwe et al., 2013, and references therein). In our control simulation (no leaf trait plasticity) a doubling of atmospheric CO_2 concentration from 400 ppm to 800 ppm (CC-CTRL) increases annual mean net primary productivity (+74.2%), leaf area index (+7.0%), and biomass (+102.6%), and reduces evapotranspiration (-9.2%) (Table 1, Fig. 2). As noted in the methods section, the FATES model we use here does not explicitly represent nutrient limitation, thus we directly im-

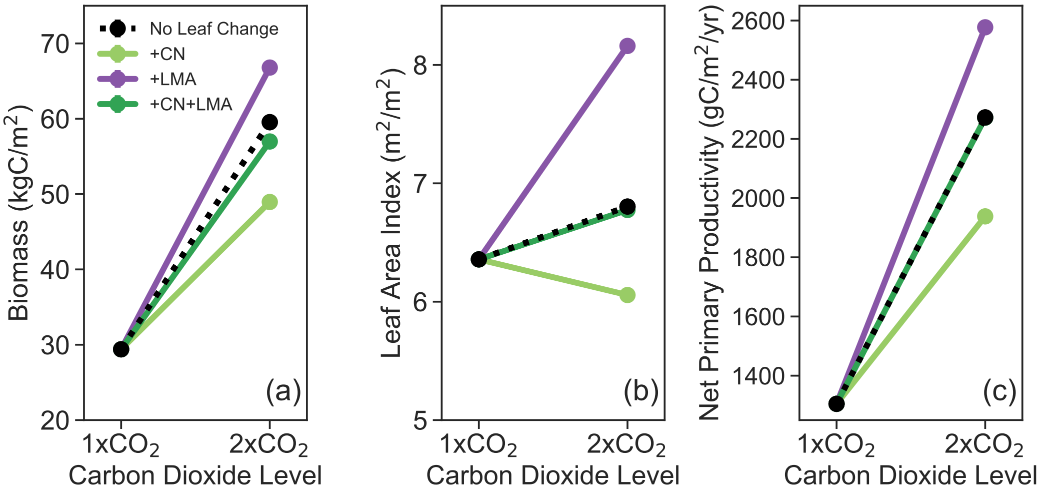

Figure 2. Annual mean (a) biomass ($kgC\ m^{-2}$) and (b) leaf area index ($m^2\ m^{-2}$) and (c) net primary productivity ($gC\ m^{-2}\ s^{-1}$) for the 1xCO$_2$ control, 2xCO$_2$ control (black), and the following leaf trait plasticity levels in the absence of competition: a one-third increase in leaf 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.

plement leaf trait changes in our experiments that represent potential influences of nutrient limitation and quantify the total canopy nitrogen required to support each leaf trait plasticity level.

The actual expected magnitude of tropical forest responses to elevated CO$_2$ is highly uncertain and little experimental data exists, particularly at the ecosystem scale (Lloyd & Farquhar, 2008; Hickler et al., 2008; Mahowald et al., 2016; Cusack et al., 2016; Norby et al., 2016; Fleischer et al., 2019; Holm et al., 2020). However, our control simulation response to elevated CO$_2$ shows reasonable agreement with observations from temperate forest FACE experiments (De Kauwe et al., 2013, 2014) if one assumes a linear scaling with increasing CO$_2$ (Cernusak et al., 2019). For example, a +200ppm CO$_2$ increase at Duke Forest enhanced net primary productivity by approximately 30% (De Kauwe et al., 2013), which when scaled to +400pm results in a +60% increase in net primary productivity (we find +74.2%, in the absence of N limitation). Similarly, when scaled to +400ppm these FACE experiments saw changes equivalent to approximately +6% and +30% in leaf area index at Oak Ridge and Duke, respectively (we find +7%) ; -40% in transpiration at Oak Ridge (no significant change at Duke Forest) (we find +9.2%); and +100% in biomass increment at Duke (we find total biomass changes, which are not directly equivalent, of +102%). Thus our modeled changes are all roughly comparable with these ranges, with slightly higher modeled increases in net primary productivity in our tropical simulations compared to these observational estimates from temperate forests. Lastly, changes in each of these ecosystem properties in our control simulation also fall within the simulated ranges from 11 Earth system models at these two temperate forest FACE sites after linearly scaling for CO$_2$ concentration (De Kauwe et al., 2013, 2014). While our control simulation response to elevated CO$_2$ is comparable to those estimated from observations in temperate forests, tropical forest responses may of course be subject to different constraints (e.g., De Graaff et al., 2006; Luo et al., 2006; Hickler et al., 2008; Zaehle et al., 2014; Fleischer et al., 2019). Davies-Barnard et al. (2020) illustrate that for five CMIP6 class models with active nitrogen cycles, the fertilization impact of

+200ppm CO_2 had a mean net primary productivity response of 16-18% for models other than CLM4.5 (which has an anomalously strong N limitation) which is about half the size of what we find (37% for +200ppm). These models, however, are all subject to N limitation, and also show strong spatial variation, with tropical forests showing higher than average simulated CO_2 fertilization rates.

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

We find that imposed leaf trait plasticity alters net primary productivity, biomass, and leaf area index responses to a doubling of CO_2 in the absence of competition (Fig. 2). Under elevated CO_2, increasing C:N_{leaf} by one-third (the upper bound of our observed range) diminishes the increase in net primary productivity (-334 $gCm^{-2}s^{-1}$) and biomass (-10.6 $kgCm^{-2}$), as well as decreasing leaf area index (-0.7 m^2m^{-2}) compared to the control plant type (CN - CC). In contrast, increasing LMA by one-third enhances the increases in both simulated biomass (+7.2 $kgCm^{-2}$) and leaf area index (+1.4 m^2m^{-2}) compared to the control plant type (LMA - CC), via increases in net primary productivity (+304 $gCm^{-2}s^{-1}$) from increasing N_{area} that has a larger effect than the more costly leaf construction. Increasing both C:N_{leaf} and LMA simultaneously by one-third under a doubling of CO_2 (CNLMA) results in only a slightly reduced increase in biomass (-2.6 $kgCm^{-2}$) and no change in leaf area index (0.0 m^2m^{-2}) or net primary productivity (-0.8 $gCm^{-2}s^{-1}$) compared to the control plant type (CNLMA - CC).

The first-order impacts are that, for any given increase in C: N_{leaf}, a simultaneous increase in LMA allows plants to maintain biomass and leaf area index that are closer to the control plant type. It is worth noting additionally that the simultaneous change is not a perfect cancellation between the two factors. When LMA increases in isolation leaves get thicker and more productive per area with increased N_{area}. When C:N_{leaf} is increased, N_{area} and net primary productivity decrease. When both factors occur simultaneously, thicker leaves compensate for a lower mass density of nitrogen. The two factors cancel one another out in terms of net primary productivity, as N_{area} is conserved, however biomass is reduced slightly relative to the case with no leaf change. We hypothesize that this happens because thicker leaves require more carbon allocated to leaves relative to wood and thus the overall whole plant turnover of carbon is faster resulting in a smaller total biomass. Consistent with this hypothesis, we find that the fractional allocation of net primary productivity to leaves goes up even for the case where N_{area} is conserved (by +0.023, see Table S2), and the lifetime of total biomass decreases (by -0.72 years, see Table S2).

3.3 Influence of leaf trait plasticity on competitive ability

We find that the control plant type, with no leaf trait plasticity (and thus no change in N_{area}), is more competitively advantageous than all leaf trait plasticity levels sampled where N_{area} either decreases or remains constant under a doubling of CO_2 (Fig. 3). The control plant type (origin in Fig. 3) wins all of pairwise competitions against plant types with leaf trait plasticity levels sampled from the trait changes that maintain N_{area} (=N_{area}, along black dashed diagonal line in Fig. 3) or reduce N_{area} (-N_{area}, below black dashed diagonal line in Fig. 3).

Increasing C:N_{leaf} strongly diminished competitive ability, as evidenced by the decreasing percentage of competitions a plant type wins as C:N_{leaf} increases (left to right, Fig. 3). At a given C:N_{leaf}, increasing LMA typically enhances competitive ability. At very high C:N_{leaf} there is little change, (bottom to top, Fig. 3) however, reflecting the trade-off between the impacts on N_{area} (reduced productivity) and leaf area index (increased productivity). This results from decreased net primary productivity, biomass, and leaf area index, as N_{area} is reduced (Fig. 4).

These results from our competition experiments are consistent with our findings in the absence of competition–higher C:N_{leaf} leads to lower net primary productivity, biomass, and leaf area index and increasing LMA results in net primary productivity, biomass, and leaf area index gains (Fig. 2). However, LMA increases sampled from plasticity levels that maintain or decrease N_{area} do not, in this model, fully compensate for the negative influence of higher C:N_{leaf} on competitive ability at any level. Furthermore, the competitive benefit of increasing LMA diminishes at higher C: N_{leaf}, as evidenced by the sinusoidal shape of the 50% wins shading (white) in Fig. 3. In sum, we find that plant types that can maintain higher N_{area} in high CO_2, have greater competitive ability.

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

3.4 Changes in carbon uptake and evapotranspirative cooling

Ecosystem carbon uptake is tightly coupled to changes in LMA and C: N_{leaf}, both directly via their impacts on photosynthetic rate, and indirectly via impacts on leaf area index. In our experiments we impose changes in leaf traits, which result in emergent rates of carbon uptake, while in a fully evolving system we expect that the carbon uptake rates and nutrient availability are likely involved in setting the leaf traits to begin with (see further discussion in section 4.3). Evapotranspiration is additionally a downstream result of stomatal conductance and leaf area index. Given that the meteorological conditions are the same in our experiments and our control, the changes in ET that we found result from changes to plant traits and functioning only, and tend to change in concert with carbon fluxes. Leaf trait plasticity levels sampled from the -N_{area} space are associated with lower carbon uptake and evapotranspiration compared to the control response to a doubling of CO_2 (CC) in our experiments reflecting the influence of reduced photosynthetic capacity (Fig. 5, Table 1). On average the observed changes in C:N_{leaf} and LMA reduce the increase in annual mean net primary productivity by -9.2% and further reduce annual mean ET by -4.4% compared to the 2xCO_2 control (-N_{area} - CC). The largest reduction in net primary productivity (-14.7%) and evapotranspiration (-7.0%) results from the leaf trait plasticity level that increases C:N_{leaf} by one-third without a co-occurring increase in LMA (CN - CC), a response which was not specifically observed by Lovelock et al. (1998).

Leaf trait plasticity levels that maintain N_{area} equal to the control (=N_{area}) also maintain carbon uptake and evapotranspiration at control levels (Fig. 5, Table 1). Annual mean net primary productivity and evapotranspiration do not differ significantly between =N_{area} simulations and the control simulation under a doubling of CO_2 (=N_{area} - CC). Leaf changes that enhance N_{area} (+N_{area}) increase carbon uptake and moderate the reduction in evapotranspiration compared to the control response to a doubling of CO_2 (Fig. 5, Table 1). On average +N_{area} leaf trait plasticity levels increase annual mean net primary productivity by +8.4% and lessen the reduction in evapotranspiration by +4.8% (+N_{area} - CC). The largest enhancement of net primary productivity (+13.4%) and evapotranspiration (+7.9%) results from the leaf trait plasticity level that increases LMA by one-third but does not alter C:N_{leaf} (LMA - CC).

Leaf trait plasticity levels that confer a higher competitive advantage also have a higher carbon uptake (Fig. 5). We expect that more N_{area} generally leads to higher productivity and thus higher associated evapotranspiration. The competitive ability of a plant type with a given level of leaf trait plasticity, as measured by the percent of competitions 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 CO_2 (Luo et al., 2004) and may be a cause of C:N$_{leaf}$ and LMA plasticity in response to elevated 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 1xCO_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 1xCO_2 conditions, our control simulation (CTRL) had a total canopy nitrogen content of 8.3 gNm^{-2} ground. Doubling CO_2 increased the control ecosystems total canopy nitrogen content by +0.3 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 CO_2 conditions. Leaf trait plasticity levels that maintain N$_{area}$ at control levels (=N$_{area}$) but have increases in both C:N$_{leaf}$ and LMA also increase the total amount of canopy nitrogen required beyond the 1xCO_2 control level, although by slightly less than the 2xCO_2 control, with the mean change across =N$_{area}$ simulations ranging from 2.1% to 3.0% (=N$_{area}$ - CTRL; Fig. 3). The -N$_{area}$ scenarios all maintain canopy N content at or below the 1xCO_2 control level (-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 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 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 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 N$_{area}$ with a doubling of 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 N$_{area}$, this limits the possible leaf trait plasticity space by excluding the control and central diagonal band along with the en-

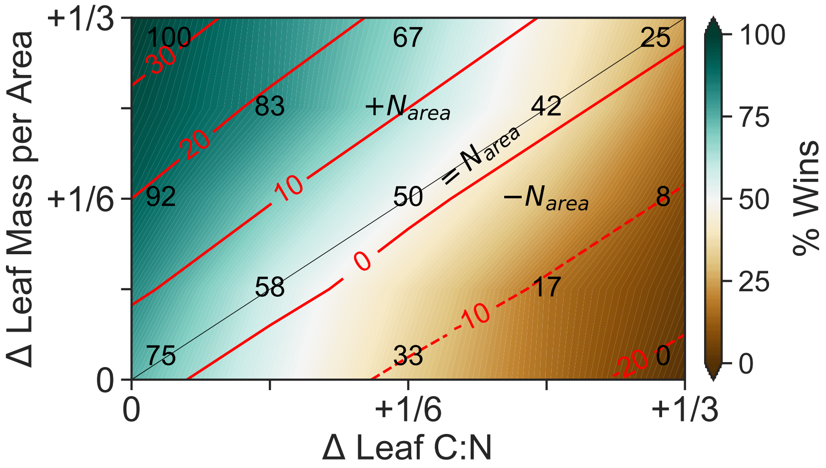

Figure 3. The percent of pairwise competitions won (% Wins, color shading and black numbers) and percent change in total canopy nitrogen compared to the $1xCO_2$ control (red contours) for each leaf trait plasticity level of leaf C:N and leaf mass per area. Percent wins for sampled trait changes (black 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.

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

4.3 Why do leaf changes occur?

Our model results suggest that, in the context of the FATES parameterization used here, observed increases in $C{:}N_{leaf}$ in response to elevated CO_2 do not confer a competitive advantage. We find that plant types in which $C{:}N_{leaf}$ increases in response to elevated CO_2 suffer in several metrics of plant fitness, including biomass, leaf area index, net primary productivity, and competitive ability. Thus our results suggest that changes in $C{:}N_{leaf}$ are likely forced upon plants by changes in elevated CO_2, rather than occurring as a beneficial acclimation. This is consistent with the leading hypothesis for the mechanism underlying $C{:}N_{leaf}$ increases with elevated CO_2. Nitrogen limitation has been proposed as a cause for lower mass-based nitrogen concentrations in leaves (e.g., Poorter et al., 1997; Winter et al., 2001; Fyllas et al., 2009; Cusack et al., 2016). As carbon dioxide fertilizes plant growth the demand for nutrients is likely to increase and eventually result in the depletion of nitrogen available for growth (Luo et al., 2004; Hungate et al., 2003). The limited availability of nitrogen, as well as accumulation of nonstructural car-

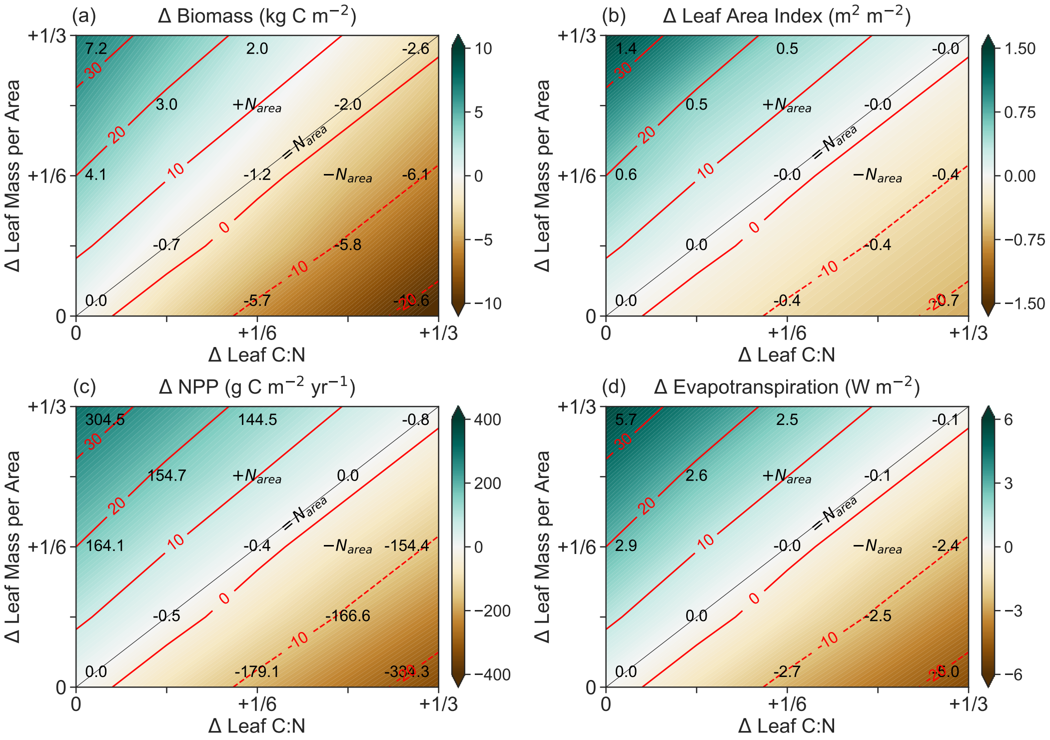

Figure 4. Changes in (a) biomass ($kgC\ m^{-2}$), (b) leaf area index ($m^2\ m^{-2}$), (c) net primary productivity ($gC\ m^{-2}\ yr^{-1}$), and (d) evapotranspiration ($W\ m^{-2}$) compared to the 2xCO$_2$ control (color shading and black numbers) and percent change in total canopy nitrogen compared to the 1xCO$_2$ 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.

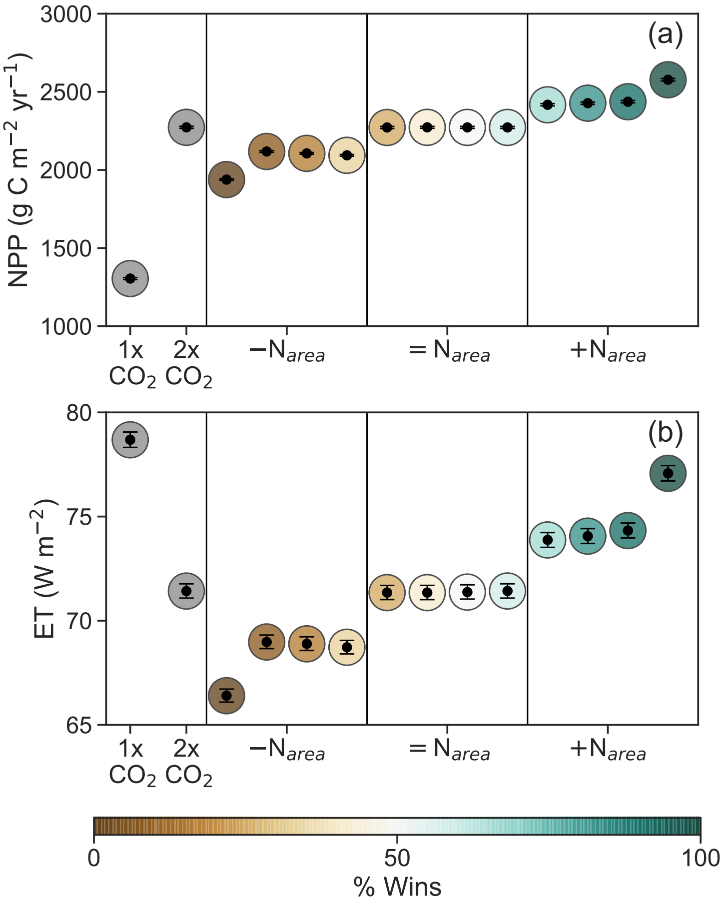

Figure 5. Annual mean (a) net primary productivity (NPP, $gC\ m^{-2}\ yr^{-1}$) and (b) evapotranspiration (ET, $W\ m^{-2}$) for the 1xCO$_2$ control, 2xCO$_2$ control (no leaf trait plasticity), and 12 ecosystems each consisting entirely of one plant type with a different level of leaf trait plasticity sampled from the -N$_{area}$, =N$_{area}$, and +N$_{area}$ 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.

bohydrates due to sink limitation of growth, could lower mass-based leaf nitrogen concentrations and result in higher C:N$_{leaf}$ (e.g., Poorter et al., 1997; Winter et al., 2001). Manipulation experiments in which tropical tree seedlings are treated with elevated CO$_2$ provide evidence that CO$_2$ stimulation of growth is enhanced by the addition of soil nutrients, suggesting that nutrient limitation does indeed impact leaf trait responses (Winter et al., 2001). Plants in which C:N$_{leaf}$ increases more in response to elevated CO$_2$ may be those that are unable to adjust to lower nitrogen availability or higher competition for nitrogen. Tropical trees with traits that allow them to better acquire nitrogen, for example associations with nitrogen fixing bacteria or fungi, may be better able to maintain C:N$_{leaf}$ levels under elevated CO$_2$ with advantages for growth and competitive success (Lovelock et al., 1998; Cusack et al., 2016; Cernusak et al., 2013).

Further, it has been suggested that the increase in LMA with elevated CO$_2$ is mediated by nitrogen (or other resource limitation of plant growth causing nonstructural carbohydrates accumulation in leaves; Poorter et al., 2009, 1997; Pritchard et al., 1999; Roumet et al., 1999). We find that coordinated responses of both LMA and C:N$_{leaf}$ are beneficial: plants that are able to increase LMA most for a given level of C:N$_{leaf}$ change are those that are best able to maintain high biomass, leaf area index, productivity, and competitive ability. Concurrently increasing LMA along with C:N$_{leaf}$ leads to maintenance of equal N$_{area}$ by counteracting decreases in mass-based nitrogen concentration (Luo et al., 1994; Ishizaki et al., 2003). Indeed, we found that even when limited to control levels of total canopy nitrogen, plants could maintain close to equal amounts of N$_{area}$. As nitrogen is an essential component of photosynthetic enzymes, maintaining N$_{area}$ can maintain area-based maximum photosynthetic rates (Kattge et al., 2009, 2011; Walker et al., 2014; Norby et al., 2017), and we find that net primary productivity closely follows the amount of N$_{area}$ in our simulations. Observations by Lovelock et al. (1998) of tropical tree leaf trait responses to a doubling of CO$_2$ (Fig. 1) suggest that increases in LMA are generally higher for larger increases in C:N$_{leaf}$, helping to maintain N$_{area}$ – and thus functioning – closer to control levels (Fig. 5). While it is logical that increasing LMA concurrently with C:N$_{leaf}$ is advantageous to plants, this leaves open the question of why these two factors would change in the first place if canopy nitrogen is the limiting constraint.

4.4 Other potential leaf trait plasticity trade-offs

Other coordinated plant plasticity responses to elevated CO$_2$ and nutrient limitation could further influence the impacts of leaf trait plasticity on competitive ability and tropical forest functioning. Observations show that many trees, including tropical trees, enhance carbon and nitrogen allocation to root growth at the expense of leaf growth in response to elevated CO$_2$ (e.g., Luo et al., 2006, Körner and Arnone, 1992; reviewed in Cusack et al., 2016; Cernusak et al., 2013). Such partitioning of nitrogen away from leaves could increase C:N$_{leaf}$ but benefit plants if they use the nitrogen to build other structures that help alleviate resource limitation, such as roots that can access further nutrients (reviewed in Cusack et al., 2016; Cernusak et al., 2013) although, in some cases, this growth strategy has been found to be ineffective (Norby et al., 2010). Our primary results isolate the influence of leaf trait plasticity changes and do not include changes in the target ratio of root mass to leaf area. However, we test the sensitivity of our results to increasing target root mass in coordination with leaf trait plasticity using additional simulations (Supporting Information Text S1.3.2 and S2.1). In these additional experiments, trees increase target root mass in proportion with increases in LMA. This accounts for the additional carbon cost of growing more roots to support the additional nutrient requirements for greater leaf mass. This makes it even more costly to increase LMA, which we expect should reduce the competitive advantage of doing so. In this case, we find that the control plant type is always at competitive advantage, and the benefit 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_2 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_2, 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 gradients 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_2 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_2 we test here. However, warming and CO_2 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_2 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_2, nutrient availability, and temperature - and how these responses differ by tree type (e.g. successional class or species) and developmental stage (e.g. Cusack et al., 2016). Our ability to characterize leaf trait plasticity in response to environmental change may ultimately require a better understanding of whole plant carbon and nutrient dynamics, as leaf carbon and nitrogen can depend on supply and demand from other plant organs (e.g. Luo et al., 1994; Pritchard et al., 1999; Norby et al., 2010; Xu et al., 2012; Winter et al., 2001; Zaehle et al., 2014).

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

4.8 Implications

Here we show that leaf trait plasticity in response to elevated CO_2 could alter tropical forest influences on climate directly, by altering the functioning of tropical trees, and indirectly, by modifying plant competitive dynamics and the abundance of different plant types. As such, including the effects of leaf trait plasticity could have a significant influence on projections of future climate. These results further support the need for more observations of tropical tree responses to environmental change and the use of plant competition models within earth system models used to predict future climate change.

Acknowledgments

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	Biomass ($kgC\ m^{-2}$)		LAI ($m^2\ m^{-2}$)		NPP ($gC\ m^{-2}\ yr^{-1}$)	
	Mean (CI$_{95}$)	% (CI$_{95}$)	Mean (CI$_{95}$)	% (CI$_{95}$)	Mean (CI$_{95}$)	% (CI$_{95}$)
double CO$_2$	30.1	102.6	0.45	7	967.8	74.2
	(30,30.2)	(102.1,103)	(0.43,0.46)	(6.8,7.2)	(958.8,976.8)	(73.2,75.1)
-N$_{area}$	-7.1	-11.9	-0.5	-7.4	-208.6	-9.2
	(-7.1,-7)	(-12,-11.7)	(-0.51,-0.49)	(-7.5,-7.2)	(-215.7,-201.6)	(-9.5,-8.9)
=N$_{area}$	-1.6	-2.7	-0.02	-0.3	-0.4	0
	(-1.7,-1.5)	(-2.9,-2.6)	(-0.03,-0.01)	(-0.4,-0.1)	(-7.7,6.8)	(-0.3,0.3)
+N$_{area}$	4.1	6.9	0.76	11.1	191.9	8.4
	(4,4.2)	(6.7,7)	(0.75,0.77)	(10.9,11.3)	(184.4,199.6)	(8.1,8.8)
+CN	-10.6	-17.8	-0.75	-11	-334.3	-14.7
	(-10.7,-10.5)	(-18,-17.6)	(-0.76,-0.74)	(-11.1,-10.8)	(-342.4,-326.3)	(-15,-14.4)
+LMA	7.2	12.2	1.36	20	304.5	13.4
	(7.1,7.4)	(11.9,12.4)	(1.34,1.38)	(19.7,20.2)	(294.2,314.9)	(12.9,13.9)
+CN+LMA	-2.6	-4.3	-0.03	-0.4	-0.8	0
	(-2.7,-2.4)	(-4.5,-4.1)	(-0.04,-0.02)	(-0.6,-0.3)	(-9.9,8.4)	(-0.4,0.4)

	ET ($W\ m^{-2}$)		Total Canopy N ($gN\ m^{-2}$)	
	Mean (CI$_{95}$)	% (CI$_{95}$)	Mean (CI$_{95}$)	% (CI$_{95}$)
double CO$_2$	-7.3	-9.2	0.26	3.2
	(-7.8,-6.8)	(-9.8,-8.6)	(0.26,0.27)	(3.1,3.3)
-N$_{area}$	-3.2	-4.4	-	-
	(-3.6,-2.8)	(-5,-3.9)		
=N$_{area}$	0	-0.1	-	-
	(-0.4,0.3)	(-0.6,0.5)		
+N$_{area}$	3.4	4.8	-	-
	(3,3.8)	(4.2,5.3)		
+CN	-5	-7	-1.93	-23.2
	(-5.5,-4.6)	(-7.7,-6.4)	(-1.93,-1.92)	(-23.3,-23.2)
+LMA	5.7	7.9	3.02	36.3
	(5.1,6.2)	(7.2,8.6)	(3,3.03)	(36.2,36.5)
+CN+LMA	-0.1	-0.1	0.18	2.1
	(-0.6,0.4)	(-0.8,0.6)	(0.17,0.18)	(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$_2$” 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$_2$, 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$_2$ and Experiment refers to experiments with different leaf trait plasticity levels. Bootstrap 95% confidence intervals (CI$_{95}$%) in parentheses. -N$_{area}$, = N$_{area}$, and +N$_{area}$ average across experiments with leaf trait plasticity levels that decrease, maintain, and enhance leaf nitrogen per area, respectively. +CN experiment increases C:N$_{leaf}$ by one-third; +LMA increases LMA by one-third; and +CN+LMA, simultaneously increases C:N$_{leaf}$ 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`.

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