



# The impacts of elevated CO<sub>2</sub> on forest growth, mortality and recovery in the Amazon rainforest

Yitong Yao<sup>1,2</sup>, Philippe Ciais<sup>1</sup>, Emilie Joetzjer<sup>3</sup>, Wei Li<sup>4</sup>, Lei Zhu<sup>1,4</sup>, Yujie Wang<sup>2</sup>, Christian Frankenberg<sup>2,5</sup>, Nicolas Viovy<sup>1</sup>

5 <sup>1</sup>Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS-UVSQ, Université Paris-Saclay, Gif-sur-Yvette, 91191, France

<sup>2</sup>Division of Geological and Planetary Sciences, California Institute of Technology, Pasadena, CA 91125, USA

<sup>3</sup>INRAE, Université de Lorraine, AgroParisTech, UMR Silva, Nancy, 54280, France

10 <sup>4</sup>Department of Earth System Science, Ministry of Education Key Laboratory for Earth System Modeling, Institute for Global Change Studies, Tsinghua University, Beijing, 100084, China

<sup>5</sup>Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109, USA

*Correspondence to:* Yitong Yao (yyao2@caltech.edu)

**Abstract.** The Amazon rainforest plays a crucial role in global carbon storage, but a minor destabilization of these forests could result in considerable carbon loss. Among the external factors affecting vegetation, elevated CO<sub>2</sub> (eCO<sub>2</sub>) levels have long been anticipated to have positive impacts on vegetation, including direct photosynthesis / productivity enhancement and increasing water use efficiency. However, the overall impact of eCO<sub>2</sub> on the net carbon balance, especially concerning tree mortality-induced carbon loss and recovery following extreme drought events, has remained elusive. Here, we use a process-based model that couples physiological CO<sub>2</sub> effects with demography and drought mortality / resistance processes. The model was previously calibrated to reproduce observed drought responses of Amazon forest sites. The model results, based on factorial simulations with and without eCO<sub>2</sub>, reveal that eCO<sub>2</sub> enhances forest growth and promotes competition between trees, leading to more natural self-thinning of the forest stands, following a growth-mortality trade-off response although the growth outweighs the tree loss. Additionally, eCO<sub>2</sub> provides water-saving benefits, reducing the risk of tree mortality during drought episodes, although extra carbon losses still could occur due to eCO<sub>2</sub> induced increase in background biomass density, thus 'more carbon available to lose' when severe droughts happen. Furthermore, we found that eCO<sub>2</sub> accelerates the drought recovery and enhances drought resistance and resilience. These findings illuminate the intricate ways in which increasing CO<sub>2</sub> concentrations shape forest carbon dynamics, offering valuable insights into the evolution of the Amazon rainforest.

## 1 Introduction

The intact Amazon rainforest influences present and future global carbon dynamics, accounting for a current carbon sink of 0.42-0.65 PgC yr<sup>-1</sup> for 1990-2007 (Pan et al., 2011), and containing 40% of the tropical forest aboveground biomass (Liu et al., 2015), a large carbon stock that is projected to be vulnerable to climate change (Boulton et al., 2022). Preserving



35 this carbon stock is essential for regulating global CO<sub>2</sub> levels and stabilizing the Earth's climate. As climate change progresses and CO<sub>2</sub> levels rise, tropical rainforests can both increase carbon sequestration and become destabilized by climate risks. The impact of elevated CO<sub>2</sub> (eCO<sub>2</sub>) on carbon sequestration separates into direct effect related to higher leaf carboxylation rates, that may translate into higher leaf area index, tree productivity and biomass, known as CO<sub>2</sub> fertilization as well as indirect effects of partial stomatal closure and subsequently increased water use efficiency (WUE, CO<sub>2</sub> physiological forcing) (Smith et al., 2020). In turn, higher leaf area increases transpiration and can increase water stress. However, the potential translation of increased individual tree growth rates into biomass accumulation at ecosystem level remains uncertain, given that eCO<sub>2</sub> not only enhances carbon inputs at ecosystem level, but also amplifies carbon loss, 40 through growth-mortality trade-offs with higher growth possibly leading to more competition between trees and higher mortality rates. Such 'high gain high loss' patterns reflecting a coupling between growth and mortality have been identified across spatial gradients (Needham et al., 2020; Stephenson & van Mantgem, 2005; Walker et al., 2021) and also seem to emerge in terms of temporal trajectories, with a parallel increase of growth and mortality, observed e.g. in the Amazon (Lewis et al., 2004) and other rainforests from long term inventories (Hubau et al., 2020). For example, repeated census of 45 forest inventory plots within intact tropical forests in Amazonia have found a faster increase in carbon losses from tree mortality, which surpasses the increase in carbon gains attributed to both tree growth and new tree recruitment, resulting in a decline in the net forest carbon sink (Hubau et al., 2020). Although a positive effect of eCO<sub>2</sub> on increased tree loss has been hypothesized by McDowell et al (2022), establishing a significant correlation between carbon loss and eCO<sub>2</sub> has proven to be elusive (Hubau et al., 2020).

50

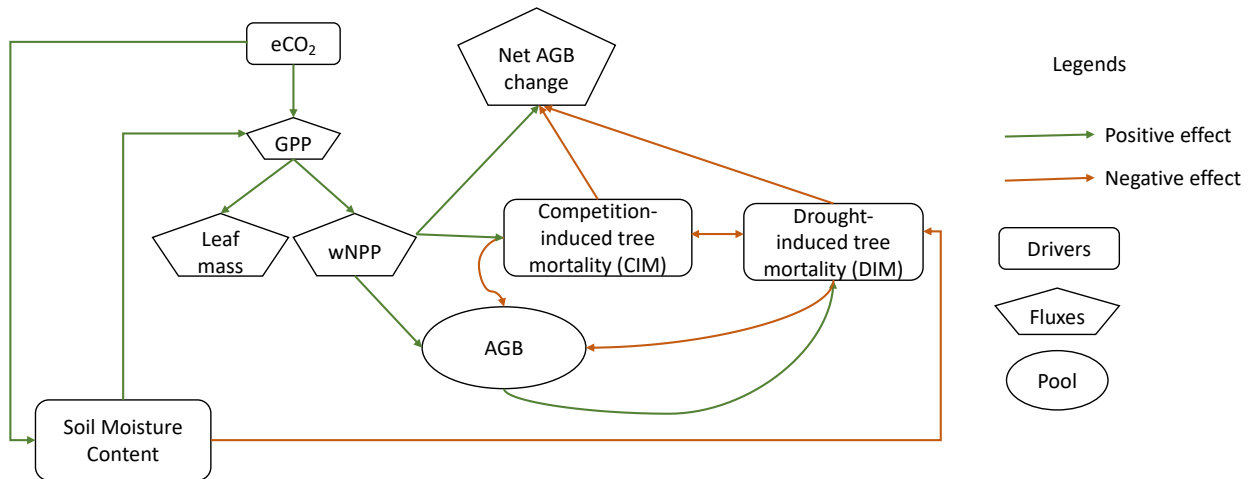
Compared to the research concentrating on vegetation productivity in response to eCO<sub>2</sub>, less attention has been directed toward the response of carbon loss, although minor disruptions of mortality rates in high-biomass systems like the Amazon intact rainforests could trigger substantial carbon loss. An increase in tree mortality can reduce the plant carbon residence time and consequently counteract the enhanced productivity (Friend et al., 2014). A comprehensive understanding 55 of the response of tree mortality to eCO<sub>2</sub> is thus crucial for unravelling the forest biomass carbon dynamics. Carbon loss can arise from internal ecosystem processes like competition-induced self-thinning and death of demoted trees, death of individual large trees forming gaps, as well as from external drivers such as extreme climate events, insects, and pathogens (Fig. 1). McDowell et al (2018) outlined two potential mechanisms underlying the connection between eCO<sub>2</sub> and an increased tree mortality rate. First, enhanced individual tree growth rates could accelerate self-thinning due to increased competition. Second, eCO<sub>2</sub> makes trees larger and more vulnerable to external environmental conditions of wind damage, 60 drought, and heat (Gora & Esquivel-Muelbert, 2021; Maia et al., 2020). These two mechanisms correspond to competition-induced carbon loss and drought-induced carbon loss, and they pose threats on smaller trees and larger trees, separately. But eCO<sub>2</sub> also has the potential to promote tree survival by improving water use efficiency during drought (Brienen et al., 2017a, 2017b; Van der Sleen et al., 2015). Liu et al (2017) demonstrated, through simulations with a detailed soil-plant hydraulic 65 model, that eCO<sub>2</sub> mitigates drought risks by decreasing the fraction of days when the daily minimum xylem water potential



70

is below a critical threshold. Findings from a global model simulating hydraulics and demography conducted by Yao et al (2023) also indicated that drought exposure could be alleviated under eCO<sub>2</sub> in the Amazon. Besides, eCO<sub>2</sub> effects are also regulated by hydro-climatic conditions. Fatichi et al (2016) revealed that indirect effects on productivity from eCO<sub>2</sub> tend to be more pronounced in water-limited ecosystems although severe water stress can offset the expected CO<sub>2</sub> fertilization effects (Kolby Smith et al., 2015). The magnitude of the water saving effect is also modulated by the intensity and duration of water stress events (Birami et al., 2020). Therefore, given the interplay of enhanced photosynthesis, heightened competition, vulnerability due to larger size, and mitigating effect from water saving benefits, the impact of eCO<sub>2</sub> on carbon balance is not a straightforward monotonic relationship. The relative rates at which gross carbon fluxes change with eCO<sub>2</sub> play a crucial role in determining the net changes in AGB (Fig. 1).

75



80

**Figure 1.** A schematic plot illustrating the influence of eCO<sub>2</sub> on forest biomass carbon balance. A positive effect means that the impacted variable is expected to increase from eCO<sub>2</sub> as compared to pre-industrial CO<sub>2</sub>. A positive effect on net AGB change means that eCO<sub>2</sub> leads to a higher AGB net carbon gain. When CO<sub>2</sub> concentration rises, water use efficiency increases due to partial closure of stomata. Consequently, soil water consumption decreases, leading to an increase in soil moisture content (positive effect on soil moisture content, SMC). This increase in SMC offers a degree of mitigation against drought exposure, referred to as water-saving benefits (negative effect on drought induced mortality, DIM). Simultaneously, eCO<sub>2</sub> enhances photosynthesis, resulting in greater carbon gains (positive effect on canopy leaf mass and woody NPP, wNPP). This enhanced tree growth also intensifies competition, leading to natural self-thinning (positive effect on competition induced mortality, CIM). While the reduction in drought exposure through higher SMC offers a reduction of DIM, the availability of ‘more carbon available to lose’ under eCO<sub>2</sub> contributes to increased drought-induced biomass carbon loss by drought mortality (negative effect of DIM on AGB). The combined effects of enhanced carbon gain, reduced drought exposure, and higher biomass density influence positively or negatively net biomass carbon change.

85



90

Given the unavailability of Free Air CO<sub>2</sub> Enrichment (FACE) experiments and the scarcity of in-situ measurements within the complex Amazon rainforest, employing process-based modelling emerges as a promising approach for investigating how eCO<sub>2</sub> influences the accumulation and loss of biomass. Koch et al (2021) demonstrated that models participating in Coupled Model Intercomparison Project 5 (CMIP5) and CMIP6 can reproduce the response of carbon gains attributed to tree growth in response to environmental drivers but were rather unable to reproduce the carbon losses observed in inventory data. This model shortcoming primarily results from the fact that CMIP5 and CMIP6 models do not include processes related to tree competition and that (most of them) ignore climate induced mortality processes, although a new generation of global models is under development to address these research gaps (Eller et al., 2020; Koven et al., 2020; Yao et al., 2022). Yu et al (2022) underscored this issue and showed that biomass loss due to tree mortality was overestimated in Dynamic Global Vegetation Models (DGVMs) when compared to historical forest inventory measurements, and that incorporating observation-based constraints into these models would lead to a reduction in carbon sink predictions by the end of the century. Therefore, conducting modelling studies with realistic representation of tree mortality and incorporating observation-based constraints are crucial steps toward achieving a more reliable projection of the evolution of the Amazon intact forests carbon stocks.

105

As the representation of mortality in most process-based models is based on prescribing a fixed loss fraction of standing biomass stocks (Adams et al., 2013), there is a clear need for a more realistic simulation of tree mortality-induced carbon loss. In Yao et al (2023), an empirical hydraulic failure and a light competition tree mortality module in the ORCHIDEE land surface model were tested over the Amazon rainforest. This model has been calibrated to reproduce tree-size dependent mortality rates at Caxiuana (a long term throughfall exclusion experiment) and proven effective in reproducing the increasing carbon loss due to tree mortality rate and the resulting basin-scale deceleration in the net carbon sink observed by inventories from Hubau et al. (2020).

In this study, we explore the impact of eCO<sub>2</sub> on forest growth, tree mortality, and drought recovery in the Amazon rainforest. Our analysis leverages the newly-upgraded process-based model ORCHIDEE-CAN-NHA (r7236) with competition and drought induced mortalities, following the methodology outlined in Yao et al (2023). We conducted two factorial simulations, one with rising CO<sub>2</sub> levels since 1901, and one without, respectively. The three key specific questions we address here are as follows: (i) does eCO<sub>2</sub> lead to a greater increase in tree mortality compared to productivity? (ii) does eCO<sub>2</sub> promote carbon loss more during wet years compared to dry years? (iii) does eCO<sub>2</sub> alleviate the impact of drought on net AGB carbon balance and benefit drought recovery? Our hypothesis is that eCO<sub>2</sub> leads to a lesser increase in tree mortality compared to carbon gain, and this net benefit for AGB changes is greater during dry years, contributing to accelerated drought recovery. The process-based model ORCHIDEE-CAN-NHA has been well-calibrated. In brief, this model incorporates a mechanistic plant hydraulic architecture simulating water potentials at half-hour intervals within the



soil-root-stem-leaf continuum. It also includes a drought exposure-related tree mortality scheme and accounts for size-  
125 dependent tree mortality rates under exposure conditions. For detailed model description, calibration information and  
validation against observed datasets, please refer to Yao et al (2022) and section 2.

## 2 Materials and methods

### 2.1 Model description

ORCHIDEE-CAN-NHA incorporates a plant hydraulic architecture that enables the modelling of water potential  
130 and hydraulic conductance along the vertical profile of plants. This module considers both vertical water flow driven by  
water potential gradients and the movement of water into or out of water storage pools, regulated by water capacitance. By  
simulating the plant hydrodynamics, we derive a critical indicator of plant water stress: the percentage loss of conductance  
(PLC). PLC has been demonstrated to correlate with tree mortality (Choat et al., 2012), like  $\psi_{50}$ , which represents the water  
potential at which 50% of conductance is lost. Building on the simulation of  $\psi_{50}$ , we have integrated an empirical tree  
135 mortality module that is based on drought exposure, which can help reproduce the size-dependent tree mortality pattern of  
higher tree mortality rate in cohorts with larger circumference class. Within this framework, two crucial empirical  
parameters have been introduced: the drought exposure threshold and the fraction of tree mortality once this threshold is  
reached. These two parameters were calibrated using observed water potentials, sap flux transpiration and stem mortality  
rates from long-term throughfall exclusion experiment conducted at the Caxiuana site located in northeastern Amazon (Yao  
140 et al., 2022). The calibrated model has proven accurate for capturing the sensitivity of carbon fluxes to drought and the long-  
term trends in net carbon sink dynamics, in comparisons of the simulated sensitivity of biomass loss rates and growth rates to  
water deficit against plot observations for the droughts of 2015 and 2010 (Yao et al., 2023). Besides such a drought-induced  
tree mortality, ORCHIDEE also parametrizes the light competition-induced self-thinning process (Joetzjer et al., 2022),  
which offers competition-induced tree mortality. The self-thinning process in ORCHIDEE is regulated by the quadratic  
145 mean diameter, where smaller trees are killed in priority.

Our analysis only focuses on carbon gains (CG) and carbon losses (CL) from trees with diameter at breast height  
exceeding 10 cm to facilitate the comparison with periodic forest inventory results. Observational time series of carbon  
gains, losses, and the net carbon balance for Amazonian forests are obtained from Brienen et al (2015). To gain a deeper  
insight into how eCO<sub>2</sub> impacts carbon loss, we examined both changes in competition-induced (self-thinning, CIM) and  
150 drought-induced tree mortality (DIM) as distinct components. For drought mortality, we compared the drought exposure  
under constant and eCO<sub>2</sub>, for assessing how eCO<sub>2</sub> alleviates the risk of tree mortality from hydraulic failure.

Following a TRENDY-type protocol (Seiler et al., 2022), we have implemented two distinct scenarios in our study.  
The first scenario maintains a constant CO<sub>2</sub> concentration at the 1901 level but varying climate forcing (A1), while the  
second scenario permits variations in both CO<sub>2</sub> concentration and climate forcing (A2). Here A2 is similar to S2 in  
155 TRENDY protocol despite that we did not consider land cover change.



## 2.2 Climate forcing data

The gridded climate forcing dataset employed is CRUJRA v2.1 (Harris, 2020) used in the TRENDY simulations. CRUJRA v2.1 was created by re-gridding data from the Japanese Reanalysis Data (JRA), a product of the Japanese Meteorological Agency. This re-gridded dataset was adjusted to align with the monthly observation-based Climatic Research Unit (CRU) TS4.04 data (Harris et al., 2020). CRUJRA v2.1 provides 6-hourly meteorological variables spanning from January 1901 to December 2019, at a spatial resolution of 0.5°.

## 2.3 Drought characteristics

Following Papastefanou et al (2022), for the evaluation of drought area and severity, the maximum climatological water deficit (MCWD) was used to compare droughts, as given by Equations (1) and (2) with a fixed value for evapotranspiration (ET) of ~100 mm per month being used (Phillips et al., 2009). When monthly rainfall ( $P_m$ ) is below 100 mm, the forest undergoes water deficit. Water deficit accumulates over the hydrological year from October in the previous year to September in the current one. MCWD is the most negative value of the water deficit among all 12 months.

$$CWD_m = CWD_{m-1} + (P_m - 100) \text{ if } P_m < 100, \text{ else } CWD_m = 0 \quad (1)$$

with  $m$  being the month from October to September.

$$MCWD = \min(CWD_m), m=1, \dots, 12 \quad (2)$$

Then the decadal mean of MCWD over the whole period ( $\mu_{MCWD}$ ) was subtracted from MCWD of a year with drought ( $MCWD_i$ ), giving a MCWD anomaly (Eq. 3).

$$MCWD \text{ anomaly} = MCWD_i - \mu_{MCWD} \quad i=1980-2019. \quad (3)$$

We derived Z-scores of MCWD time series at annual scale following Equation (4) as in Feldpausch et al (2016), according to:

$$Z_{MCWD} = \frac{MCWD_i - \mu_{MCWD}}{\sigma_{MCWD}} \quad i=1980-2019 \quad (4)$$

$\sigma_{MCWD}$  is the inter-annual standard deviation of MCWD.

## 2.4 Drought resistance and resilience

For each drought event, we defined drought resistance as the relative rate of net biomass carbon change during and before drought disturbance, and drought resilience as the ability of net biomass carbon change to recover to the pre-drought state. The calculation of drought resistance and resilience of net biomass carbon change followed Tao et al (2022). We also used the net biomass carbon balance 2 years before and 2 years after the drought event to represent forest pre- and post-drought conditions, respectively (Tao et al., 2022). Resistance and resilience were calculated for each pixel and for all the drought events during the past four decades following Equations (5) and (6) and were reported at the basin scale by taking the median value across drought-affected pixels ( $Z_{MCWD}$  below -1).



$$Drought\ resistance = \frac{Y_e - Y_{pre}}{Y_{pre}} \quad (5)$$

$$Drought\ resilience = \frac{Y_{post} - Y_{pre}}{Y_{pre}} \quad (6)$$

$Y_{pre}$  as the pre-drought value of net biomass carbon change (CG minus CL)

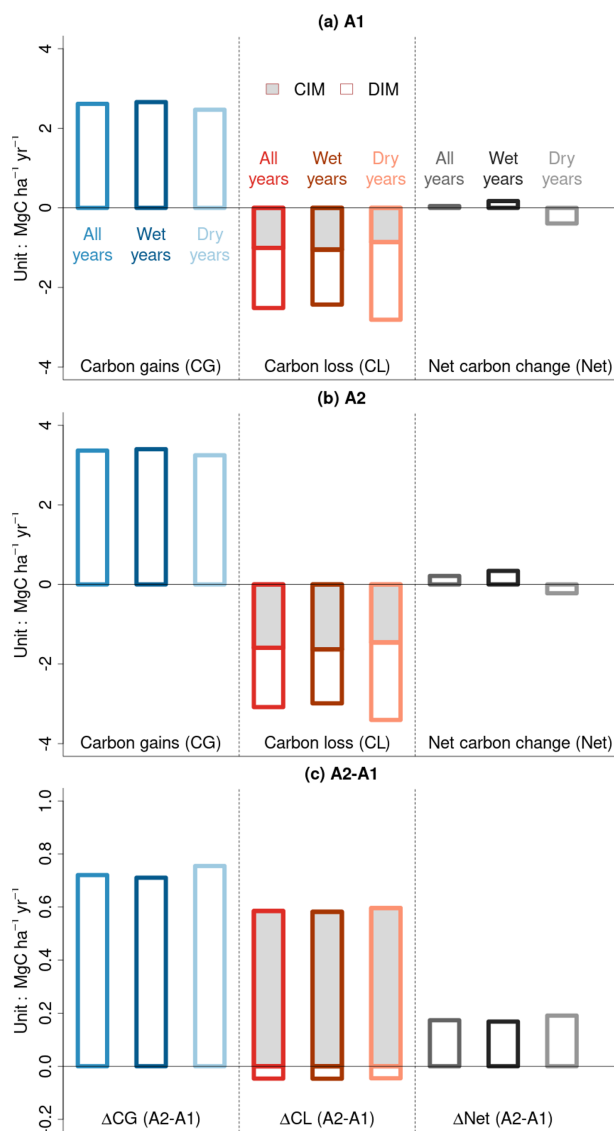
$Y_{post}$  as the post-drought value of net biomass carbon change

190  $Y_e$  as the signal during the drought event of net biomass carbon change

### 3 Results

#### 3.1 The mean carbon gains and carbon losses over the Amazon rainforest

Our model simulations over the past four decades, driven by varying CO<sub>2</sub> and climate forcing, reveal that carbon gain (CG) slightly surpasses carbon loss (CL) at the basin scale, resulting in a positive net carbon balance ('Net' in Fig. 2a).  
195 When we separate years into wet and dry categories based on the basin-scale median of Z-transformed MCWD ( $Z_{MCWD} > 0$  as wet years,  $Z_{MCWD} < 0$  as dry years), we find a net carbon sink during wet years and a net carbon source during dry years. The pattern arises because CG is lower and CL is higher during dry years compared to wet years and vice versa. During dry years, competition-induced carbon loss (CIM) is a bit lower compared to wet years and increased drought-induced tree mortality (DIM) leads to higher CL. Under constant CO<sub>2</sub> concentration conditions (A1), both CG and CL decrease compared  
200 to A2, with the reduction in CG being more pronounced, resulting in a much smaller net carbon sink than under eCO<sub>2</sub> conditions (Fig. 2b). Carbon loss from CIM decreases as well during dry years compared to wet years, and its fraction in the total carbon loss becomes lower, as drought-induced tree dieback increases can suppress self-thinning. Comparing the model simulations with and without eCO<sub>2</sub>, higher  $\Delta CG$  during dry years compared to wet years suggests the CO<sub>2</sub> fertilization effect is more efficient during dry years (Fig. 2c).  $\Delta CL$  is primarily affected by CIM, even though  $\Delta CIM$  and  $\Delta DIM$  have opposing  
205 effects on it (Fig. 2c). Our model simulation thus implies that the CO<sub>2</sub> fertilization effect plays a dominant role in augmenting forest aboveground productivity (carbon gains) and to a lesser extent biomass loss rates from mortality.



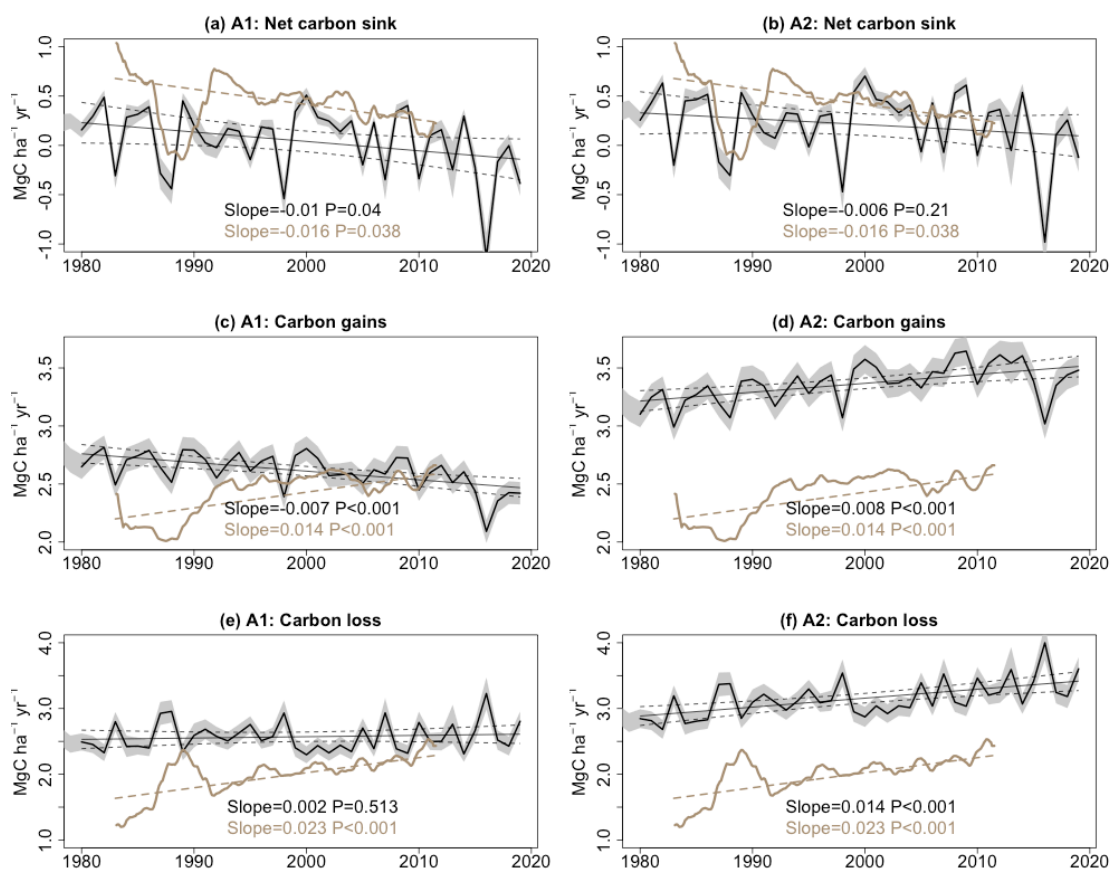
**Figure 2.** Basin-scale average of forest biomass carbon gains (CG), carbon losses (CL) and the net balance of gains minus losses (Net) over the last four decades. (a) eCO<sub>2</sub>, (b) constant CO<sub>2</sub> at pre-industrial level, (c) difference between eCO<sub>2</sub> and constant CO<sub>2</sub> ( $\Delta$ ). By convention gains are positive and losses are negative in (a) and (b). In panel (c),  $\Delta\text{CL}$  is calculated by the difference between absolute values of CL in panels (a) and (b). Dry years are defined as those in which the median of Z-transformed cumulative water deficit ( $Z_{\text{MCWD}}$ ) at the basin scale fails below 0. For biomass carbon loss, CIM represents competition-induced self-thinning processes, and DIM represents drought-induced tree mortality processes.





### 215 3.2 Effect of eCO<sub>2</sub> on the trends of biomass net carbon sink, carbon gains and carbon losses

Our simulation that accounts for varying climate and CO<sub>2</sub> concentration (A2) produces a decline in the net biomass carbon sink since 1980, declining at a rate of 0.006 MgC ha<sup>-1</sup> yr<sup>-2</sup> (6 kgC ha<sup>-1</sup> yr<sup>-2</sup>). This decelerating trend can be predominantly attributed to the increase in carbon loss resulting from tree mortality, which amounts to 0.014 MgC ha<sup>-1</sup> yr<sup>-2</sup>, surpassing the enhanced carbon gain trend of 0.008 MgC ha<sup>-1</sup> yr<sup>-2</sup>. The trend of the biomass sink in A2 has the same sign as  
 220 in forest inventory records, but it is 60% smaller in magnitude (see Fig. 3). When CO<sub>2</sub> concentration is held constant, the A1 scenario indicates a larger decline in the net carbon sink. This more negative trend is primarily driven by reduced carbon gains, while carbon loss increases less.



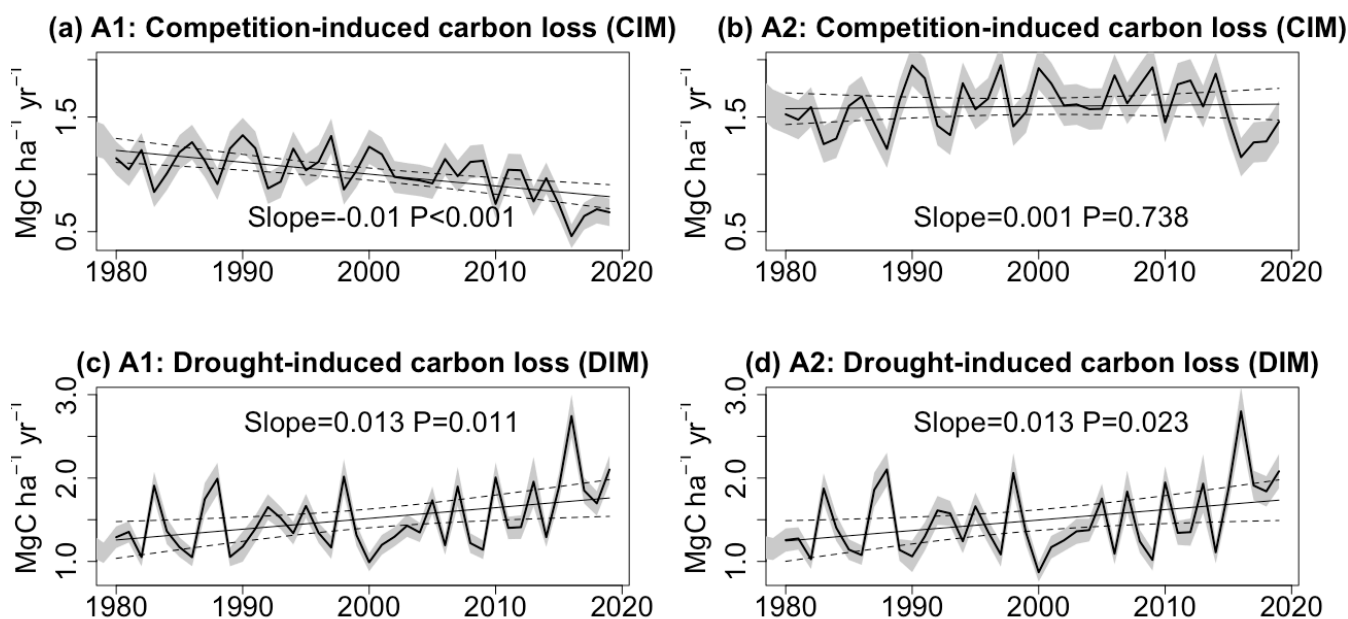
225 **Figure 3.** Trends in (a, b) net aboveground live biomass carbon sink, (c, d) carbon gains, and (e, f) carbon losses from tree mortality, obtained from ORCHIDEE model simulations (black lines) and forest inventory data (brown lines). Shading represents the 95% confidence interval. The slopes and associated P values are from linear regression models. It should be noted that the number of measurements for each year in inventory varies and ‘linear mixed-effects model’ was used to



230 account for the weight associated with different sampling plot areas and their monitoring time length. Therefore, in inventory pooling results, the trend for net carbon sink is not equal to the difference between trends in carbon gain and carbon loss.

### 3.3 Effect of eCO<sub>2</sub> on competition-induced and drought-induced carbon losses

As described in Section 3.1, carbon loss resulting from tree mortality can be categorized into two distinct processes: competition-induced (CIM) and drought-induced (DIM). Figure 4 illustrates the trends in carbon loss attributed to these two processes. In the A2 scenario, the simulated CIM displays no significant trend (slope=0.001 MgC ha<sup>-1</sup> yr<sup>-2</sup>, P=0.738). However, when CO<sub>2</sub> remains constant in A1, this term exhibits a notable decrease (slope=-0.01 MgC ha<sup>-1</sup> yr<sup>-2</sup>, P<0.001). In contrast, both A1 and A2 exhibit significant increasing trends in DIM (slope=0.013 MgC ha<sup>-1</sup> yr<sup>-2</sup>, P<0.05). Consequently, the lack of a significant overall trend in total carbon loss in A1 can be attributed to the opposing effects of CIM and DIM. Our model simulations reaffirm that the increasing carbon loss in the A2 scenario is primarily a result of a higher drought-induced tree mortality. Without the sustained increase in CO<sub>2</sub>, the net carbon sink would have diminished at a faster pace (slope=-0.01 MgC ha<sup>-1</sup> yr<sup>-2</sup> in A1 vs. slope=-0.006 MgC ha<sup>-1</sup> yr<sup>-2</sup> in A2).

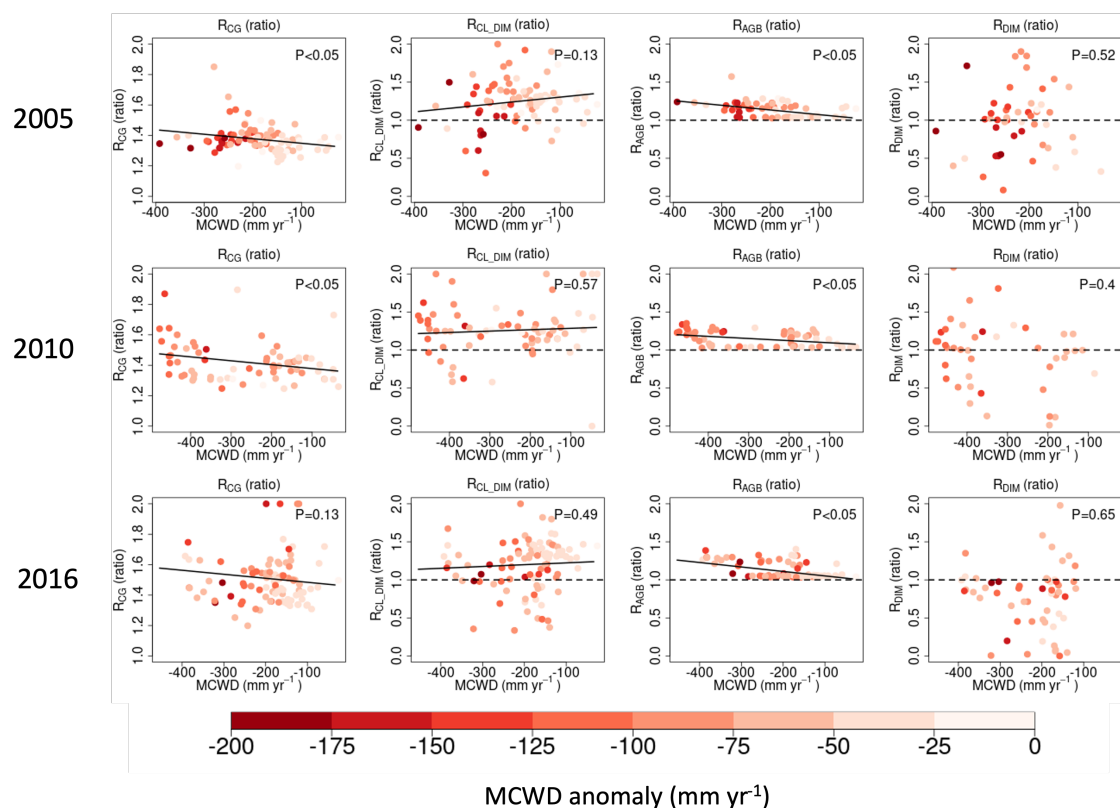


245 **Figure 4.** Trends in carbon losses due to (a,b) competition-induced (CIM) and (c,d) drought-induced tree mortality (DIM) with and without eCO<sub>2</sub>.



### 3.4 Water conditions mediate biomass carbon fluxes responses to eCO<sub>2</sub>

The impact of eCO<sub>2</sub> on biomass carbon sinks is influenced by prevailing water conditions. To explore how hydro-climate conditions regulate the impact of eCO<sub>2</sub> on carbon gain and carbon loss, we focused on three recent mega-drought events (2005, 2010, 2015/2016). In line with the methodology applied by Pan et al (2022) to eCO<sub>2</sub> vs. control experiments, we used the ratio between enhanced CO<sub>2</sub> (A2) and the constant CO<sub>2</sub> scenario (A1) to assess the relative response (R) of ecosystems for carbon gain (R<sub>CG</sub>) and carbon loss (R<sub>CL</sub>). During these three drought events, we found that forests in drier climate zones (more negative MCWD) exhibited greater R<sub>CG</sub> compared to their wetter counterparts (Fig. 5), and this model response prevails across all cohorts, with larger-sized cohorts showing lower R<sub>CG</sub> and less negative sensitivity of R<sub>CG</sub> to water deficit of MCWD due to more carbon allocation to smaller cohorts (Fig. S1). Interestingly, R<sub>CL</sub> does not show monotonic change from small to large cohorts even though the average over the drought epicenter indicates higher R<sub>CL</sub> in smaller cohorts (Fig. S2). Self-thinning may not always occur due to the suppression by DIM. Therefore, even though higher R<sub>CG</sub> is found under eCO<sub>2</sub> along the water stress gradient, self-thinning does not always change coordinately. Here, R<sub>CL</sub> is mainly contributed by drought-induced carbon loss (R<sub>CL\_DIM</sub>), where the self-thinning is suppressed. However, R<sub>CL\_DIM</sub> does not exhibit a significant correlation with MCWD (Fig. 5). It's worth noting that DIM-induced carbon loss is influenced by two key factors: background biomass density and tree mortality rate. The former one is boosted by eCO<sub>2</sub>, indicating 'more carbon available to lose' (Fig. 5), while the response of the latter is the opposite because eCO<sub>2</sub> leads to a reduction in stomatal conductance and transpiration, alleviating water stress, shown by less drought exposure days (Fig. S3) and lower fraction of trees killed due to DIM in the A2 scenario compared to the A1 scenario across most regions within the epicenter of drought events ( $Z_{MCWD} < -1$ , Fig. 5). This suggests that eCO<sub>2</sub> has a positive impact on mitigating the effects of drought on biomass loss driven by DIM.



**Figure 5.** The effect of eCO<sub>2</sub> on carbon gain ( $R_{CG}$ ), carbon loss due to drought induced tree mortality ( $R_{CL\_DIM}$ ), AGB ( $R_{AGB}$ ), and the proportion of trees affected by DIM ( $R_{DIM}$ ) in relation to water conditions and drought intensity in the years 2005, 2010 and 2016. Water conditions are characterized by MCWD during the drought year on the horizontal axis, where negative values indicate drier climate. Dots are color-coded to reflect the drought intensity characterized by MCWD anomaly, with darker colors indicating more severe water deficits. The dots shown in the panel correspond to pixels located in the epicenter of the drought, featuring  $Z_{MCWD}$  values below -1. This threshold is set to ensure an adequate number of pixels for our analysis.

275

### 3.5 Effect of eCO<sub>2</sub> on drought recovery

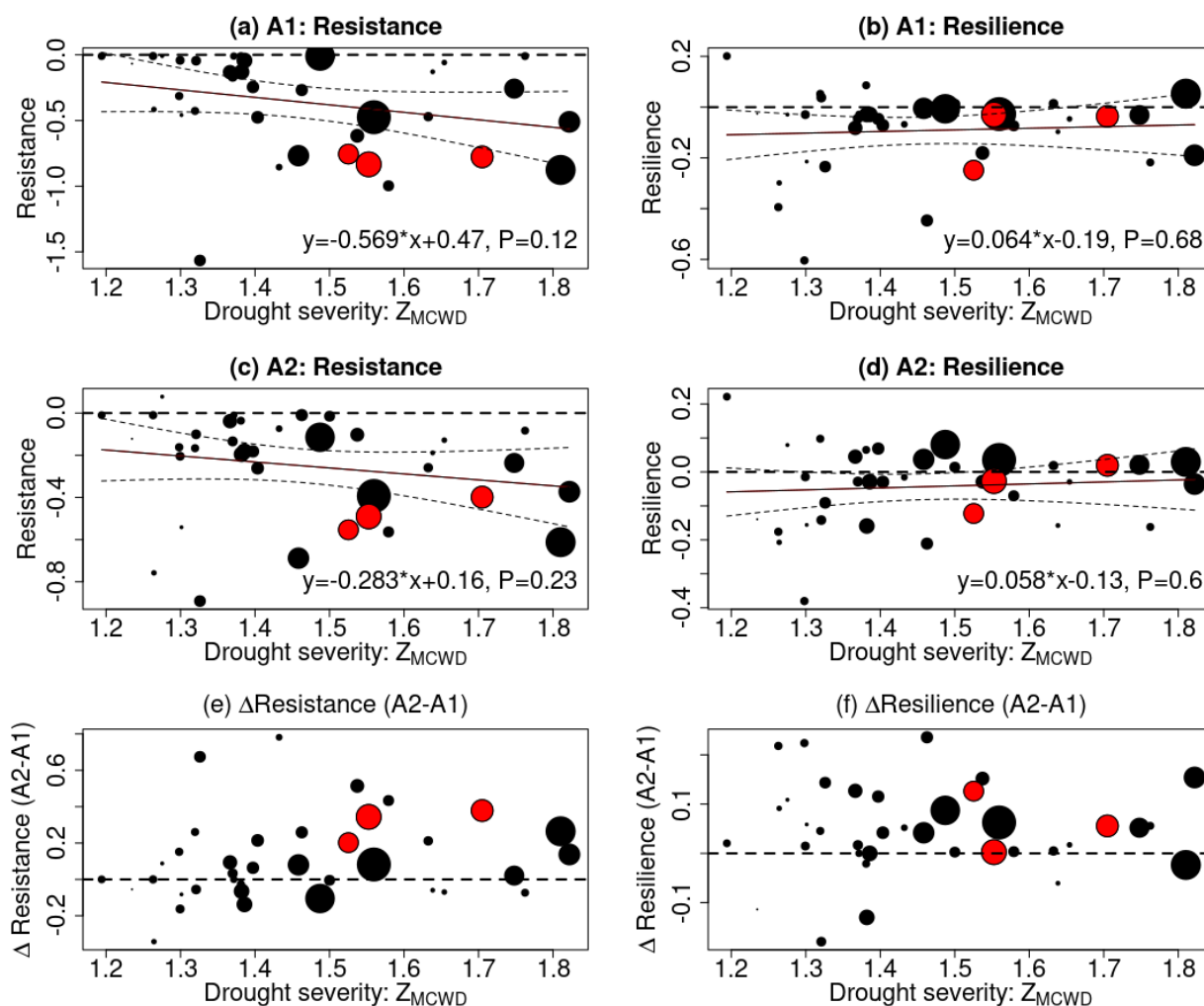
After a drought, eCO<sub>2</sub> supports faster or more complete recovery due to growth enhancement (De Kauwe et al., 2021). eCO<sub>2</sub> can also enable deeper root depth, thus a better access to deeper soil moisture (Iversen, 2010). In addition to investigating the impact of eCO<sub>2</sub> on carbon loss during droughts, our study delved into whether eCO<sub>2</sub> confers benefits to drought recovery considering the likely promoted growth and two different tree mortality regimes of CIM and DIM. To identify past drought events, we calculated the MCWD for each year and each pixel. Droughts were defined as pixels in a year with a Z score of MCWD falling below -1 since 1980. This threshold, while not extremely severe, was chosen to ensure

280



285 enough pixels for analysis. Following the methodology outlined by Tao et al (2022), we aggregated the pixel-level results to the basin scale by calculating the median value across all pixels. Considering the findings of Tao et al (2022), which indicated increased drought resistance across a gradient of drought severity using C-band radar signals, we would see if the process-based model can reproduce this drought response. Figure 6 illustrates the relationship between drought resistance and resilience of net biomass carbon change in relation to drought severity expressed as  $Z_{MCWD}$ . In both the A1 and A2 scenarios, we observed a well-expected declining trend in resistance as drought severity increased. When drought severity was defined using absolute value of MCWD anomaly, a similar declining trend of resistance for net carbon change was found (Fig. S4). Notably, the rainforests did not fully recover to their pre-drought conditions following drought events of higher severity (A1:  $62 \pm 12\%$  vs. A2:  $59 \pm 16\%$  of the area located in drought epicenter showing resilience below 0). When examining the differences in drought resistance and resilience between the A1 and A2 scenarios, our findings indicate that  $eCO_2$  enhances both drought resistance and resilience. For drought sensitive areas where the tree mortality regime shifts from CIM to DIM, their drought resistance and resilience are lower than that of insensitive areas due to higher carbon loss.

290  
295 This suggests that elevated  $CO_2$  levels contribute to improved forest resilience and their ability to withstand and recover from drought events.



**Figure 6.** The effect of eCO<sub>2</sub> on drought recovery in aspects of resistance and resilience of net biomass carbon change. For each drought event, the median resistance, resilience and drought severity of the drought-affected pixels ( $Z_{MCWD}$  below -1) were calculated, shown as dots in each panel. Drought severity was defined by the  $Z_{MCWD}$ . The size of the dots indicates the area situated within the drought epicenter. The dots for 2005, 2010, and 2016 were color-coded in red. A trend fitting was applied to panels a-d, with its equation labelled and 95% confidence bound shaded. Resistance was computed, where lower values mean a more pronounced reduction in net biomass carbon sink during a drought. Resilience was computed, where positive values indicate complete recovery of the forest to pre-drought conditions, while negative values signify incomplete recovery. In panels a-d, a horizontal dashed line indicates a resistance and resilience value of zero. In panels e-f, a horizontal dashed line was drawn as well to denote no change in resistance or resilience under eCO<sub>2</sub> conditions.



#### 4 Discussion

310 The CO<sub>2</sub> fertilization effect has gained widespread recognition as a primary driver of vegetation greening observed  
as an increase of LAI in most regions around the world (Zhu et al., 2016). Our model forced by eCO<sub>2</sub> also captures the LAI  
greening in most areas over the basin, while a constant CO<sub>2</sub> setup results in browning (Fig. S5). However, it is important to  
clarify that this greening phenomenon doesn't necessarily translate into increased biomass accumulation because the carbon  
allocation shift and processes that control biomass loss can be decoupled from the increasing trend of LAI and productivity  
315 (Fan et al., 2022). The dynamics of the net carbon sink are fundamentally shaped by the balance between productivity and  
carbon loss. The concept of a growth-mortality trade-off or "high gain high loss" has been observed across spatial gradients  
(Wright et al., 2010), but it remains more difficult to prove in terms of temporal changes expressed as "faster gains imply  
higher losses" because one can observe an acceleration of both gains and losses like Hubau et al (2020) but a causal relation  
between the two can't be empirically proven. A demography model including more detailed stand dynamics can help test  
320 this hypothesis. eCO<sub>2</sub> enhancing on tree competition in wet tropical forest has the potential to couple a faster gain to a higher  
loss, and thus may not universally lead to a boost in the net carbon sink due to an accelerated carbon turnover rate (Walker et  
al., 2021). Future CO<sub>2</sub> fertilization could potentially increase not only recruitment and growth, but also tree mortality  
(McDowell et al., 2020). In our study, we conducted model experiments to disentangle the effect of eCO<sub>2</sub> on forest biomass  
carbon fluxes, including carbon gain, carbon loss, and net carbon balance. Our model simulations revealed a compelling  
325 insight. When we deactivated the CO<sub>2</sub> fertilization effect, the model simulated a LAI browning trend (Fig. S5) and a  
declining trend in carbon gain compared to forest inventory observations (Fig. 2). This finding aligns with a similar  
compensatory effect on LAI from rising CO<sub>2</sub> in TRENDY models in the tropical forests, as noted in Winkler et al (2021).  
Our results also underscored that eCO<sub>2</sub> doesn't solely drive enhanced biomass carbon gains; it also plays a pivotal role in  
shaping carbon losses (Figs. 3, 4). Specifically, turning off the eCO<sub>2</sub> effect leads to a dampened increase in carbon loss. This  
330 attenuation is primarily attributable to the muted response of natural self-thinning related tree mortality, determined by less  
growth, that is the deceleration of carbon gain. Meanwhile, the more negative net carbon sink trend derived in scenario A1 is  
primarily driven by the deceleration of carbon gain. Basin-scale average shows that CL\_DIM is lower under eCO<sub>2</sub> but  
CL\_ST is highly promoted under eCO<sub>2</sub>. Thus  $\Delta CL\_DIM$  and  $\Delta CL\_ST$  oppose each other, although  $\Delta CL\_ST$  dominates the  
magnitude of  $\Delta CL$  (Fig. 1c). Such net forest biomass carbon loss in the absence of eCO<sub>2</sub> was similar to the finding in de  
335 Almeida Castanho et al (2016) using multiple model simulations. They showed a decline in biomass over the last several  
decades when not considering eCO<sub>2</sub> effects, although the tree mortality has not been incorporated yet. In total, our work  
steps further to separate the contributions of competition-induced and drought-induced tree carbon loss and provides  
evidence that eCO<sub>2</sub> benefits the forest biomass net carbon sink over the Amazon rainforest, although such benefit still may  
not be sufficient to offset the carbon loss caused by prolonged external climate stressors, like the long-term temperature  
340 induced carbon loss (Sullivan et al., 2020).



The response of biomass carbon flux dynamics to eCO<sub>2</sub> is intricately linked to water availability. Taking the years 2005, 2010, and 2016 as examples, the enhancement ratio of carbon gain (R<sub>CG</sub>) exhibits a negative correlation with the water deficit metric of MCWD, indicating that the eCO<sub>2</sub> effect is more pronounced in drier regions. Pan et al (2022) demonstrated that extra-tropical woody ecosystems characterized by drier baseline climates tend to exhibit a higher average enhancement in aboveground carbon gain in response to eCO<sub>2</sub>. Our model simulations suggest that a similar pattern may persist in wet tropical forests within the Amazon as well. The negative interactions found between eCO<sub>2</sub> and water deficit suggests that vegetation in drier climates can benefit more from the combination of enhanced photosynthesis, reduced photorespiration, and higher WUE. Alongside potential growth advantages, the tree-ring width data analysis by Zuidema et al (2020) reveals that eCO<sub>2</sub>-induced partial stomata closure and reduced transpiration may attenuate the cooling effect on leaf surfaces, potentially pushing leaf surface temperatures beyond the optimal range for photosynthesis. Our modelling results, showing enhanced carbon gain over the Amazon rainforest, suggest the temperature may not have exceeded the optimal range in this case given the mean annual land surface temperature under eCO<sub>2</sub> increases almost 0.26°C at most during 2015-16 El Niño (Fig. S6). Nonetheless, the potential shift in sensitivity within the carbon flux response of tropical forests to eCO<sub>2</sub> depending on the balance between benefits and potential temperature-related challenges, emphasizes the necessity for optimizing and refining the process-based representation of climate-growth relationships. For instance, employing various sensitivity scenarios involving temperature intervals and CO<sub>2</sub> concentrations can offer valuable insights for identifying the critical threshold beyond which the benefits of eCO<sub>2</sub> cannot outweigh the adverse high temperature effects.

While self-thinning induced carbon loss is heightened in the eCO<sub>2</sub> scenario because of increased competition, drought-induced carbon loss might not always be exacerbated under eCO<sub>2</sub> although there is more biomass built up over time that is available for carbon loss, revealing the influence of water saving conditions on carbon loss. An important indicator we employed in our model, the cumulative drought exposure, reveals a reduction over most areas when accounting for the water-saving effects driven by eCO<sub>2</sub> (Fig. S3). Regarding tree mortality triggered by drought events, our modelling work confirms the alleviated drought exposure, consistent with previous modelling findings that eCO<sub>2</sub> will bring about water saving due to increased WUE, thus enhance vegetation productivity and decrease the probability of forest dieback in the eastern Amazon basin threatened by drier and warmer climate scenarios (Huntingford et al., 2013; Lapola et al., 2009; Zhang et al., 2015), although these studies mainly considered the enhanced productivity in sustaining the biomass rather than carbon loss changes. The strength of this mitigation effect depends on the intensity and duration of stress (Lapola et al., 2009) and could postpone the point at which forests shift from being a carbon sink to a carbon source (Feng et al., 2017). The decreased frequency of tree mortality risk, combined with an increase in background biomass stock facilitated by eCO<sub>2</sub>, however, contribute to uncertainty regarding the fate of carbon loss.

In our modelling study, we found an increase in both WUE and tree growth (Figs. 1, S7). While van der Sleen et al (2014) reported no growth stimulation of tropical trees by CO<sub>2</sub> fertilization, they did find an increase in WUE in their tree





ring width analysis, focusing on a fixed tree size class. However, it has been argued by Brienen et al (2017b) that this approach, aimed to remove the effect of tree size, might lead to biased interpretation of growth trends, particularly when there is a clustered age distribution with the coexistence of fast-growing and slow-growing trees. Concerning the less controversial increase in WUE, Brienen et al (2017a) suggested that the observed trends could be related to developmental effects rather than being solely the result of climate and CO<sub>2</sub> effects on WUE. It is crucial to investigate and distinguish these factors, as WUE varies with tree developmental stages, especially in broadleaf forests. The partial stomatal closure, driven by increasing constraints in water transport with tree height and increasing photosynthesis due to greater light availability with tree height, can lead to changes in intrinsic WUE (McDowell et al., 2011). To better isolate the effects of external factors like eCO<sub>2</sub> through size-stratified sampling and account for varying tree gas regulation strategies throughout a tree's lifespan, it is essential to incorporate a stratified simulation of stomatal conductance, as well as corresponding photosynthesis. While our ORCHIDEE model features a stratified LAI pattern, it does not yet include stratified simulation of stomatal conductance. Implementing a more detailed water budget per canopy layer would provide a more comprehensive understanding of tree height-related shifts in WUE.

Regarding drought resistance and resilience, C-band radar data has demonstrated a decrease in resistance to drought over the Amazon rainforest during the past three decades, while forest resilience did not decline significantly (Tao et al., 2022). Our model simulation also detected a well-expected phenomenon of decreased resistance with increasing drought severity. The resistance and resilience of net biomass carbon balance were found to benefit from eCO<sub>2</sub>, which is broadly consistent with the enhanced resistance to drought due to restricted stomatal conductance and improved WUE in Feng et al (2017). This suggests that eCO<sub>2</sub> can enhance the recovery of ecosystem carbon uptake after short-term drought events.

Several uncertainties warrant in-depth investigations. Whether eCO<sub>2</sub> would lead to biomass growth also depends on the carbon allocation strategies subsequently the carbon turnover rate (Friend et al., 2014; Hofhansl et al., 2016), which has been found to be governed by hydraulic constraints, such as the hydraulic adjustment of the ratio between leaf area and sapwood area (Trugman et al., 2019). Given that both tree productivity and mortality responses during drought are sensitive to hydraulic traits (Anderegg et al., 2016; 2018), incorporating varying hydraulic traits adaptive to the environment will be highly important (Madani et al., 2018). For example, tree mortality risk is intricately linked to plant water use strategies, with isohydric tree species exhibiting a lower xylem embolism risk due to their tendency to close stomata earlier to conserve water. In contrast, anisohydric tree species, characterized by less conservative water use strategies, may derive more significant benefits from eCO<sub>2</sub>-induced partial stomatal closure. Additionally, the analysis of water deficit affiliation has indicated that genera affiliated with wetter climate regimes exhibit a higher risk of drought-induced tree mortality (Esquivel-Muelbert et al., 2017). Exploring the interactions between eCO<sub>2</sub> and varying hydraulic vulnerabilities would be a potential avenue for further examining the effects of eCO<sub>2</sub> on biomass carbon dynamics. Besides the hydraulic failure induced tree mortality, other possible sources including carbon starvation should be included as more carbon gain enhanced by eCO<sub>2</sub>



410 would delay the depletion of carbohydrate reserves. Furthermore, it's essential to consider the legacy effects of drought, a  
dimension that has not been addressed in process-based modelling. Yang et al (2023) used a first-order kinetics model to  
account for the gradual decomposition of coarse woody debris, yielding a better correspondence between net biomass carbon  
change and variability in atmospheric CO<sub>2</sub> growth rate. The legacy effects from tree mortality should be carefully revisited,  
given the evidence suggesting that external drivers can lead to increased mortality for at least two years after a climatic event  
415 (Aleixo et al., 2019). Regarding the strength and persistence of eCO<sub>2</sub>, previous studies have suggested that such fertilization  
effects could slow down (Penuelas et al., 2017), and the eCO<sub>2</sub> effect has declined in recent years, possibly due to nutrient  
limitation (Winkler et al., 2021). Wieder et al (2015) demonstrated that accounting for nitrogen and nitrogen-phosphorus  
limitation lowers projected productivity and could even turn terrestrial ecosystems into carbon sources. Fleischer et al (2019)  
highlighted the important role of phosphorus acquisition and use strategies in regulating forest response to eCO<sub>2</sub>, reducing  
420 the expected stimulation otherwise by 50% over the Amazon rainforest. The lack of downregulation on fertilization in the  
model could lead to an overestimation of eCO<sub>2</sub> effects. Therefore, estimating the strength and persistence of the CO<sub>2</sub>  
fertilization effect under future climate scenarios remains challenging (Nolte et al., 2023). Additional observations are  
imperative, and the AmazonFACE project will be a strong observational constraint on our knowledge of the rainforest  
response to eCO<sub>2</sub> (Lapola and Norby, 2014).

425

In our study, we conducted offline simulations and found that eCO<sub>2</sub> leads to an increase in WUE (Fig. S7), which  
could partially mitigate drought risk through soil-atmosphere feedback mechanisms. However, it's noteworthy that CO<sub>2</sub>-  
induced physiological effects reduce ET and subsequently precipitation in land-atmosphere coupled mode. A recent study  
using coupled climate model simulations has highlighted that the reduction of ET under eCO<sub>2</sub> and its impact on  
430 precipitation, contribute to potential water stress (Li et al., 2023; Skinner et al., 2018). Tree dieback indeed leads to reduction  
in plant transpiration, but also decreases the soil moisture consumption. We found eCO<sub>2</sub> leads to an increase of 0-0.26°C in  
land surface temperature based on the simulation during 2015-16 El Nino (Fig. S6). Therefore, given the contribution of  
moisture recycling to precipitation over the Amazon rainforest, a comprehensive investigation of the effects of eCO<sub>2</sub> on  
biomass carbon dynamics, like whether eCO<sub>2</sub> can mitigate the negative effects of water stress due to changes in  
435 precipitation, should be conducted in a coupled mode including tree mortality module to capture the intricate interactions  
among these components.

## 5 Conclusions

In summary, this work offers a comprehensive basin-scale quantitative assessment of how eCO<sub>2</sub> influences  
440 aboveground biomass carbon gain and carbon loss in a warming and increasingly water-stressed climate. We systematically  
disentangle the effect of eCO<sub>2</sub> in this complex ecosystem. Our findings not only underscore the role of eCO<sub>2</sub> in shaping the  
'high gain high loss' pattern but also highlight its water saving benefits. Additionally, we identify an enhancement in drought



resistance and resilience attributed to eCO<sub>2</sub>, as it accelerates drought recovery. Our results offer valuable insights into ecosystem response to eCO<sub>2</sub> that cannot be easily obtained through field experiments alone. These results serve as a compelling impetus for further modelling and observational work aimed at gaining a deeper understanding of the role of eCO<sub>2</sub> in predicting the forest biomass carbon budget within the Amazon rainforest.

### Code availability

The ORCHIDEE-CAN-NHA model (r7236) code used in this study is deposited at [https://forge.ipsl.jussieu.fr/orchidee/browser/branches/publications/ORCHIDEE\\_CAN\\_NHA](https://forge.ipsl.jussieu.fr/orchidee/browser/branches/publications/ORCHIDEE_CAN_NHA) (last access: 17 June 2021) and archived at <https://doi.org/10.14768/8C2D06FB-0020-4BC5-A831-C876F5FBBFE9> (Yao, 2021).

### Competing interests

The authors declare that they have no conflict of interest.

### Author contribution

PC and YY designed the study. YY ran the simulation, analyzed the outputs and drafted the manuscript. All authors contributed to the final manuscript.

### Acknowledgements

This work was financially supported by the CLAND Convergence Institute funded by ANR (16-CONV-0003). YY also acknowledges support from Make Our Planet Great Again (MOPGA) Scholarship.

### References

- Adams, H. D., Williams, A. P., Xu, C., et al. Empirical and process-based approaches to climate-induced forest mortality models. *Front. in Plant Sci.*, 4, 438, 2013.
- Aleixo, I., Norris, D., Hemerik, L., et al. Amazonian rainforest tree mortality driven by climate and functional traits. *Nat. Clim. Change*, 9(5), 384-388, 2019.
- Anderegg, W. R., Klein, T., Bartlett, M., et al. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proc. Natl. Acad. Sci.*, 113(18), 5024-5029, 2016.
- Anderegg, W. R., Konings, A. G., Trugman, A. T., et al. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, 561(7724), 538-541, 2018.
- Birami, B., Nägele, T., Gattmann, M., et al. Hot drought reduces the effects of elevated CO<sub>2</sub> on tree water-use efficiency and carbon metabolism. *New Phytol.*, 226(6), 1607-1621, 2020.



- 475 Boulton, C. A., Lenton, T. M., & Boers, N. Pronounced loss of Amazon rainforest resilience since the early 2000s. *Nat. Clim. Change*, 12(3), 271-278, 2022.
- Brienen, R. J. W., Gloor, E., Clerici, S., et al. Tree height strongly affects estimates of water-use efficiency responses to climate and CO<sub>2</sub> using isotopes. *Nat. Comm.*, 8(1), 288, 2017a.
- Brienen, R. J., Gloor, M., & Ziv, G. Tree demography dominates long-term growth trends inferred from tree rings. *Glob. Change Biol.*, 23(2), 474-484, 2017b.
- 480 Brienen, R. J., Phillips, O. L., Feldpausch, T. R., et al. Long-term decline of the Amazon carbon sink. *Nature*, 519(7543), 344-348, 2015.
- Choat, B., Jansen, S., Brodribb, T. J., et al. Global convergence in the vulnerability of forests to drought. *Nature*, 491(7426), 752-755, 2012.
- 485 de Almeida Castanho, A. D., Galbraith, D., Zhang, K., et al. Changing Amazon biomass and the role of atmospheric CO<sub>2</sub> concentration, climate, and land use. *Global Biogeochem. Cy.*, 30(1), 18-39, 2016.
- De Kauwe, M. G., Medlyn, B. E., & Tissue, D. T. To what extent can rising [CO<sub>2</sub>] ameliorate plant drought stress?. *New Phytol.*, 231(6), 2118-2124, 2021.
- Eller, C. B., Rowland, L., Mencuccini, M., et al. Stomatal optimization based on xylem hydraulics (SOX) improves land  
490 surface model simulation of vegetation responses to climate. *New Phytol.*, 226(6), 1622-1637, 2020.
- Esquivel-Muelbert, A., Galbraith, D., Dexter, K. G., et al. Biogeographic distributions of neotropical trees reflect their directly measured drought tolerances. *Sci. Rep.*, 7(1), 8334, 2017.
- Fan, L., Wigneron, J. P., Ciais, P., et al. Siberian carbon sink reduced by forest disturbances. *Nat. Geosci.*, 16(1), 56-62, 2023.
- 495 Feldpausch, T. R., Phillips, O. L., Brienen, R. J. W., et al. Amazon forest response to repeated droughts. *Global Biogeochem. Cy.*, 30(7), 964-982, 2016.
- Feng, X., Uriarte, M., González, G., et al. Improving predictions of tropical forest response to climate change through integration of field studies and ecosystem modeling. *Glob. Change Biol.*, 24(1), e213-e232, 2018.
- Fleischer, K., Rammig, A., De Kauwe, M. G., et al. Amazon forest response to CO<sub>2</sub> fertilization dependent on plant  
500 phosphorus acquisition. *Nat. Geosci.*, 12(9), 736-741, 2019.
- Friend, A. D., Lucht, W., Rademacher, T. T., et al. Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO<sub>2</sub>. *Proc. Natl. Acad. Sci.*, 111(9), 3280-3285, 2014.
- Gora, E. M., & Esquivel-Muelbert, A. Implications of size-dependent tree mortality for tropical forest carbon dynamics. *Nat. Plants*, 7(4), 384-391, 2021.
- 505 Harris, I., Osborn, T.J., Jones, P. et al. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Sci. Data*, <https://doi.org/10.1038/s41597-020-0453-3>, 2020.
- Hofhansl, F., Andersen, K. M., Fleischer, K., et al. Amazon forest ecosystem responses to elevated atmospheric CO<sub>2</sub> and alterations in nutrient availability: filling the gaps with model-experiment integration. *Front. Earth Sci.*, 4, 19, 2016.



- Hubau, W., Lewis, S. L., Phillips, O. L., et al. Asynchronous carbon sink saturation in African and Amazonian tropical  
510 forests. *Nature*, 579(7797), 80-87, 2020.
- Huntingford, C., Zelazowski, P., Galbraith, D., et al. M. Simulated resilience of tropical rainforests to CO<sub>2</sub>-induced climate  
change. *Nat. Geosci.*, 6(4), 268-273, 2013.
- Iversen, C. M. Digging deeper: fine-root responses to rising atmospheric CO<sub>2</sub> concentration in forested ecosystems. *New  
Phytol.*, 186(2), 346-357, 2010.
- 515 Joetzier, E., Maignan, F., Chave, J., et al. Effect of tree demography and flexible root water uptake for modeling the carbon  
and water cycles of Amazonia. *Ecol. Model.*, 469, 109969, 2022.
- Koch, A., Hubau, W., & Lewis, S. L. Earth system models are not capturing present-day tropical forest carbon dynamics.  
*Earth's Future*, 9(5), e2020EF001874, 2021.
- Kolby Smith, W., Reed, S. C., Cleveland, C. C., et al. Large divergence of satellite and Earth system model estimates of  
520 global terrestrial CO<sub>2</sub> fertilization. *Nat. Clim. Change*, 6(3), 306-310, 2016.
- Koven, C. D., Knox, R. G., Fisher, R. A., et al. Benchmarking and parameter sensitivity of physiological and vegetation  
dynamics using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama.  
*Biogeosciences*, 17(11), 3017-3044, 2020.
- Lapola, D. M., Oyama, M. D., & Nobre, C. A. Exploring the range of climate biome projections for tropical South America:  
525 The role of CO<sub>2</sub> fertilization and seasonality. *Global Biogeochem. Cy.*, 23(3), 2009.
- Lapola, D. M., & Norby, R. J. Amazon FACE: Assessing the effects of increased atmospheric CO<sub>2</sub> on the ecology and  
resilience of the Amazon forest – Science Plan and Implementation Strategy. Brasilia, Brazil: Ministerio de Ciencia,  
Tecnologia e Inovação – MCTI, 2014.
- Lewis, S. L., Phillips, O. L., Baker, T. R., et al. Concerted changes in tropical forest structure and dynamics: evidence from  
530 50 South American long-term plots. *Philos. T. Roy. Soc. B.*, 359(1443), 421-436, 2004.
- Li, Y., Baker, J. C., Brando, P. M., et al. Future increases in Amazonia water stress from CO<sub>2</sub> physiology and deforestation.  
*Nat. Water*, 1(9), 769-777, 2023.
- Liu, Y., Parolari, A. J., Kumar, M., et al. Increasing atmospheric humidity and CO<sub>2</sub> concentration alleviate forest mortality  
risk. *Proc. Natl. Acad. Sci.*, 114(37), 9918-9923, 2017.
- 535 Liu, Y. Y., Van Dijk, A. I., De Jeu, R. A., et al. Recent reversal in loss of global terrestrial biomass. *Nat. Clim. Change*, 5(5),  
470-474, 2015.
- Madani, N., Kimball, J. S., Ballantyne, A. P., et al. Future global productivity will be affected by plant trait response to  
climate. *Sci. Rep.*, 8(1), 2870, 2018.
- Maia, V. A., Santos, A. B. M., de Aguiar-Campos, N., et al. The carbon sink of tropical seasonal forests in southeastern  
540 Brazil can be under threat. *Sci. Adv.*, 6(51), eabd4548, 2020.
- McDowell, N. G., Bond, B. J., Dickman, L. T., et al. in *Size-and Age-Related Changes in Tree Structure and Function*. 255–  
286 (Springer, 2011)



- McDowell, N., Allen, C. D., Anderson-Teixeira, K., et al. Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol.*, 219(3), 851-869, 2018.
- 545 McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., et al. Pervasive shifts in forest dynamics in a changing world. *Science*, 368(6494), eaaz9463, 2020.
- McDowell, N. G., Sapes, G., Pivovarov, A., et al. Mechanisms of woody-plant mortality under rising drought, CO<sub>2</sub> and vapour pressure deficit. *Nat. Rev. Earth & Env.*, 3(5), 294-308, 2022.
- Needham, J. F., Chambers, J., Fisher, R., et al. Forest responses to simulated elevated CO<sub>2</sub> under alternate hypotheses of  
550 size-and age-dependent mortality. *Glob. Change Biol.*, 26(10), 5734-5753, 2020.
- Nölte, A., Yousefpour, R., Cifuentes-Jara, M., & Hanewinkel, M. Sharp decline in future productivity of tropical reforestation above 29° C mean annual temperature. *Sci. Adv.*, 9(34), eadg9175, 2023.
- Pan, Y., Birdsey, R. A., Fang, J., et al. A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988-993, 2011.
- 555 Pan, Y., Jackson, R. B., Hollinger, D. Y., et al. Contrasting responses of woody and grassland ecosystems to increased CO<sub>2</sub> as water supply varies. *Nat. Ecol. & Evol.*, 6(3), 315-323, 2022.
- Papastefanou, P., Zang, C. S., Angelov, Z., et al. Recent extreme drought events in the Amazon rainforest: assessment of different precipitation and evapotranspiration datasets and drought indicators. *Biogeosciences*, 19(16), 3843-3861, 2022.
- Peñuelas, J., Ciais, P., Canadell, J. G., et al. Shifting from a fertilization-dominated to a warming-dominated period. *Nat. Ecol. & Evol.*, 1(10), 1438-1445, 2017.
- 560 Phillips, O. L., Aragão, L. E., Lewis, S. L., et al. Drought sensitivity of the Amazon rainforest. *Science*, 323(5919), 1344-1347, 2009.
- Seiler, C., Melton, J. R., Arora, V. K., et al. Are terrestrial biosphere models fit for simulating the global land carbon sink? *J. Adv. Model Earth Sy.*, 14(5), e2021MS002946, 2022.
- 565 Skinner, C. B., Poulsen, C. J., & Mankin, J. S. Amplification of heat extremes by plant CO<sub>2</sub> physiological forcing. *Nat. Comm.*, 9(1), 1094, 2018.
- Smith, W. K., Fox, A. M., MacBean, N., et al. Constraining estimates of terrestrial carbon uptake: New opportunities using long-term satellite observations and data assimilation. *New Phytol.*, 225(1), 105-112, 2020.
- Stephenson, N. L., & van Mantgem, P. J. Forest turnover rates follow global and regional patterns of productivity. *Ecol. Lett.*, 8(5), 524-531, 2005.
- 570 Sullivan, M. J., Lewis, S. L., Affum-Baffoe, K., et al. Long-term thermal sensitivity of Earth's tropical forests. *Science*, 368(6493), 869-874, 2020.
- Tao, S., Chave, J., Frison, P. L., et al. Increasing and widespread vulnerability of intact tropical rainforests to repeated droughts. *Proc. Natl. Acad. Sci.*, 119(37), e2116626119, 2022.
- 575 Trugman, A. T., Anderegg, L. D., Wolfe, B. T., et al. Climate and plant trait strategies determine tree carbon allocation to leaves and mediate future forest productivity. *Glob. Change Biol.*, 25(10), 3395-3405, 2019.



- Van Der Sleen, P., Groenendijk, P., Vlam, M., et al. No growth stimulation of tropical trees by 150 years of CO<sub>2</sub> fertilization but water-use efficiency increased. *Nat. Geosci.*, 8(1), 24-28, 2015.
- Walker, A. P., De Kauwe, M. G., Bastos, A., et al. Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO<sub>2</sub>. *New Phytol.*, 229(5), 2413-2445, 2021.
- 580 Wieder, W. R., Cleveland, C. C., Smith, W. K., & Todd-Brown, K. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nat. Geosci.*, 8(6), 441-444, 2015.
- Winkler, A. J., Myneni, R. B., Hannart, A., et al. Slowdown of the greening trend in natural vegetation with further rise in atmospheric CO<sub>2</sub>. *Biogeosciences*, 18(17), 4985-5010, 2021.
- 585 Wright, S. J., Kitajima, K., Kraft, N. J., et al. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, 91(12), 3664-3674, 2010.
- Yang, H., Ciais, P., Frappart, F. et al. Global increase in biomass carbon stock dominated by growth of northern young forests over past decade. *Nat. Geosci.* <https://doi.org/10.1038/s41561-023-01274-4>, 2023.
- Yao, Y.: ORCHIDEE-CAN-NHA model (r7236), IPSL Data Catalog [code], <https://doi.org/10.14768/8C2D06FB-0020-4BC5-A831-C876F5FBBFE9>, 2021.
- 590 Yao, Y., Joetzjer, E., Ciais, P., et al. Forest fluxes and mortality response to drought: model description (ORCHIDEE-CAN-NHA r7236) and evaluation at the Caxiuanã drought experiment. *Geosci. Model Dev.*, 15(20), 7809-7833, 2022.
- Yao, Y., Ciais, P., Viovy, N., et al. How drought events during the last century have impacted biomass carbon in Amazonian rainforests. *Glob. Change Biol.*, 29(3), 747-762, 2023.
- 595 Yu, K., Ciais, P., Seneviratne, S. I., et al. Field-based tree mortality constraint reduces estimates of model-projected forest carbon sinks. *Nat. Comm.*, 13(1), 2094, 2022.
- Zhang, K., de Almeida Castanho, A. D., Galbraith, D. R., et al. The fate of Amazonian ecosystems over the coming century arising from changes in climate, atmospheric CO<sub>2</sub>, and land use. *Glob. Change Biol.*, 21(7), 2569-2587, 2015.
- Zhu, Z., Piao, S., Myneni, R. B., et al. Greening of the Earth and its drivers. *Nat. Clim. Change*, 6(8), 791-795, 2016.
- 600 Zuidema, P. A., Heinrich, I., Rahman, M., et al. Recent CO<sub>2</sub> rise has modified the sensitivity of tropical tree growth to rainfall and temperature. *Glob. Change Biol.*, 26(7), 4028-4041, 2020.