

# **Attributing past carbon fluxes to CO<sub>2</sub> and climate change: respiration response to CO<sub>2</sub> fertilization shifts regional distribution of the carbon sink**

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## **Key Points:**

- A Bayesian data-fusion system was used to assimilate global observations to constrain centennial carbon cycle model dynamics
- The spatial variation of the carbon sink is shaped by how strongly increased plant growth leads to increased plant and soil respiration
- Higher respiration losses in wet tropics offsets stronger plant growth there, resulting in a stronger carbon sink in the temperate regions

## Abstract

Over the past century, increased atmospheric CO<sub>2</sub> concentrations have enhanced photosynthesis through CO<sub>2</sub> fertilization across the globe. However, the increased growth has also led to greater respiration rates – both from vegetation (autotrophic respiration) and through the breakdown of plant litter and soil organic matter (heterotrophic respiration). The resulting change in carbon flux – and its spatial distribution – that can be attributed to increasing CO<sub>2</sub> and climate change remain unknown. We used the Carbon Data Model Framework (CARDAMOM), a model-data fusion system that assimilates global observations from satellites and other sources to create an ensemble of observationally-constrained carbon cycle representations, to determine the photosynthesis and respiration fluxes that can be attributed to increased atmospheric CO<sub>2</sub> and associated climate change from 1920-2015. Across the globe, the response of photosynthesis and respiration to atmospheric CO<sub>2</sub> dominates their response to climate alone. The regional distribution of the carbon sink attributable to climate change and CO<sub>2</sub> is strongly influenced by the ‘loss ratio of carbon gained’ – the fraction of enhanced photosynthesis that is lost to respiration. While the wet tropics’ attributable photosynthesis flux is 1.4 times larger than that of the temperate region, the attributable flux of net carbon uptake is actually 1.25 larger in the temperate region, due to the wet tropics’ greater heterotrophic respiration response to enhanced plant growth. At global scale, the loss ratio of carbon gained is  $83 \pm 0.6\%$ . Our results highlight the importance of the respiration responses to enhanced plant growth in regulating the land carbon sink.

## Plain Language Summary

Earth's land areas have taken up a large amount of carbon from the atmosphere over the last century. However, exactly where, why, and by how much carbon uptake has increased is uncertain. We used a modeling system informed by global observations from satellites and elsewhere to quantify how the flows of carbon changed in response to the last century of increasing atmospheric CO<sub>2</sub>. We found that increased photosynthesis stimulates greater ecosystem respiration, decreasing CO<sub>2</sub>'s effect on net land carbon uptake. The fraction of increased photosynthesis that goes to respiration (rather than land carbon storage) varies by region and determines the location of the largest net land carbon uptake. Although it acts indirectly through changes in plant and soil carbon stocks, the respiration response to CO<sub>2</sub> was a dominant component of the land carbon cycle response to human-caused emissions of CO<sub>2</sub> and associated climate change.

## 1 Introduction

Human activity affects the global carbon cycle both directly (e.g., through land use change) and indirectly (primarily through changes in climate caused by greenhouse gas emissions). The resulting changes in climate affect the rate at which ecosystems grow and decompose. Increased atmospheric CO<sub>2</sub> concentrations associated with emissions also directly stimulate photosynthesis through so-called CO<sub>2</sub> fertilization (Walker et al., 2020). Taken together, CO<sub>2</sub> fertilization and climate change affect the net land carbon sink, which is the balance of photosynthesis (gross primary productivity, GPP), respiration, and disturbance fluxes (e.g. fire, land use change). This land sink in turn affects the amount of CO<sub>2</sub> remaining in the

atmosphere and thus the magnitude of associated future climate change. That is, a strong set of interacting feedbacks exists between climate, CO<sub>2</sub> concentrations, and the carbon cycle (Friedlingstein & Prentice, 2010). However, the magnitude of these feedbacks is uncertain, contributing to the large spread in predicted atmospheric CO<sub>2</sub> concentrations by 2100 for a given emissions scenario (Friedlingstein et al., 2014; Lovenduski & Bonan, 2017). A necessary starting point for constraining this uncertainty is understanding how climate change and CO<sub>2</sub> fertilization have each changed the historical carbon uptake.

Previous studies attributing historical changes in GPP have found that the effect of CO<sub>2</sub> fertilization dominates other processes such as climate change or land use change over the last century (Melnikova & Sasai, 2020; Piao et al., 2013; Schwalm et al., 2020). Accordingly, the effect of CO<sub>2</sub> fertilization on GPP, including its magnitude and spatial distribution, has been intensively studied, although the roles of tropical ecosystems, stand age, and nutrient limitations remain controversial (Chi et al., 2022; Ellsworth et al., 2017; Norby & Zak, 2011). How much the historical net terrestrial carbon uptake increased in response to the past rise in atmospheric CO<sub>2</sub> (or past climate change) is not just dependent on GPP but also depends on the response of respiration. Although there is little to no direct effect of atmospheric CO<sub>2</sub> concentrations on respiration rates, there is potential for an indirect effect (Kuzakov et al., 2019): first, increased GPP due to CO<sub>2</sub> fertilization leads to increased plant growth, then the eventual decomposition of that increased plant matter increases litter and soil organic matter pools, thus enhancing heterotrophic respiration ( $R_h$ ). That is, CO<sub>2</sub> used for photosynthesis has two possible fates: a) being respired back to the atmosphere, or b) being stored in the ecosystem's soil and carbon pools.

To understand carbon-climate feedbacks, we must understand how any enhanced carbon uptake is partitioned between respiration to the atmosphere and storage in the ecosystem. A single metric captures this partitioning: the proportion of enhanced GPP lost to respiration, instead of being stored in the ecosystem (hereafter, referred to as “the loss ratio of carbon gained”). At a single mature forest site in Australia, Jiang et al (2020) found a loss ratio value of 87%. It is unclear how this ratio varies across the globe, and if it has been as large across the history of anthropogenic CO<sub>2</sub> enhancement as it was in the Jiang et al (2020) study. It is also unclear how historical changes in respiration (and, relatedly GPP) in response to CO<sub>2</sub> enhancement have changed in the presence of climate change.

At global scales and over century-scale time periods, land surface models are one of the only tools for understanding how complex changes in climate and CO<sub>2</sub> fertilization affect the carbon balance of the terrestrial ecosystem. Yet several factors limit the utility of widely-used land surface model ensembles. First, in the absence of any information about the magnitude and distribution of carbon pools in the distant past, model ensembles generally use spin-up procedures to start long-term simulations with carbon pools in steady state (i.e. defined to have zero net carbon flux). This is unrealistic, because even pre-industrial era carbon fluxes were not at equilibrium (Bauska et al., 2015). The steady state starting conditions explain the overwhelming majority of inter-model variation in present-day net ecosystem production (Huntzinger et al., 2020; Schwalm et al., 2019). Second, model uncertainty (in either model structure or parameter choices) is a dominant source of variation in carbon cycle forecasts (Bonan & Doney, 2018) and hindcasts (Bonan et al., 2019) of net carbon fluxes. In particular, soil and carbon turnover times – which are intimately tied to respiration rates – are poorly constrained (Pugh et al., 2020; Shi et al., 2020; Wieder et al., 2018).

To address these challenges, we used a Bayesian carbon cycle model data-fusion system called the Carbon Data Model Framework (CARDAMOM). For each grid cell across the globe, CARDAMOM estimates the initial conditions, ecosystem parameters, and carbon pool histories that best match a suite of observations (Bloom et al., 2016; Bloom & Williams, 2015). These assimilated observations (and observationally constrained products) include global maps of solar-induced fluorescence (SIF), net biosphere exchange (NBE), leaf area index (LAI), soil organic matter, and biomass. In addition to determining optimal carbon cycle parameters at each grid cell that best match observations, the CARDAMOM framework systematically quantifies parameter uncertainty, a methodological step that is absent in the majority of global carbon cycle models. A key innovation between the CARDAMOM runs performed here and other prognostic modelling efforts (e.g. Chen et al., (2019)) is that CARDAMOM is constrained by estimates of the net biome exchange derived from atmospheric inversions. Combined with the model structure and other observations related to photosynthesis (e.g. LAI, SIF), the time series of this integrated flux can help to constrain the spatio-temporal variations in respiration fluxes that are otherwise relatively unknown. The use of NBE data has been shown to be particularly critical in constraining models, especially as model structural complexity increases (Famiglietti et al., 2021). These dynamic fluxes, combined with information about the amount of carbon in the ecosystem (biomass and soil organic carbon), provide a constraint on the carbon turnover times and their sensitivity to changes in temperature at each grid cell.

Although CARDAMOM contains only a single set of equations describing the carbon cycle, its flexibility to optimize parameters based on observations allows it to simulate a large range of possible flux dynamics with differing climatic sensitivities and growth patterns representative of variations within and across biomes globally. The flexibility in parameters

allows for similar carbon flux dynamics between CARDAMOM and more complex conventional land surface models (Quetin et al., 2020). This suggests that some of the uncertainty in CARDAMOM's model structure (i.e., carbon cycle equations) is accounted for through its explicit determination of parameter uncertainty, which is not accounted for in conventional land surface model ensembles. Thus, CARDAMOM systematically accounts for a range of carbon cycle uncertainty at each grid point while also balancing a large range of data from observations there in contrast to more complex models where spatial variation is more determined by broad categories of land cover types.

In this study, we used CARDAMOM to attribute what fraction of photosynthesis and respiration fluxes over the last century are due to climate change and to CO<sub>2</sub> fertilization, and constrain what proportion of enhanced GPP is lost to respiration instead of being stored in the terrestrial biosphere. We demonstrate that, across the globe, the loss ratio of carbon gained is large, significantly modulating the response of the net carbon balance to climate change and enhanced CO<sub>2</sub>. We further demonstrate that variations in the loss ratio of carbon gained – rather than variations in carbon gain alone – significantly shift where the net land carbon sink has increased over the past century.

## 2 Methods

To study changes to the carbon cycle from 1920 – 2015, we combined contemporary (between 2000 – 2015) atmospheric and land surface observations with historical (1920 – 2015) climate forcing to constrain a mechanistic carbon cycle model through data assimilation. This data assimilation is described in Section 2.1. We then ran model experiments that isolate climate

change and rising CO<sub>2</sub> effects to attribute the carbon cycles response to each change individually and together (Section 2.2).

## ***2.1 Retrieving carbon cycle parameters for the last century using model-data fusion***

We used the CARDAMOM data assimilation framework and present-day global observations (between the years 2000 and 2015) to create a 1000 member ensemble of observationally constrained carbon cycle parameters and initial conditions (Bloom et al., 2016; Quetin et al., 2020). CARDAMOM was used to optimize the initial conditions of six carbon pools and one water pool, as well as 29 parameters that control the turnover rate, allocation, and environmental response of carbon and water in the Data Assimilation Linked Ecosystem Carbon v2.1.6





estimation of parameter uncertainty (Butler et al., 2017). In particular, the Carbon Monitoring System Flux (CMS-Flux) – an atmospheric inversion estimate of net biosphere exchange using satellite observations of atmospheric concentrations of CO<sub>2</sub> – provided information on the carbon balance of the terrestrial ecosystem and constrained multiple aspects of the model (Liu et al., 2017, 2021).

### *2.1.1 Carbon cycle representation*

The carbon cycle representation in DALEC is as described in Quetin et al. (2020) and Bloom et al., (2016), except for an alteration to the calculation of GPP and stomatal conductance. To improve the representation of the effect of CO<sub>2</sub> on stomatal conductance, we calculated leaf-level GPP and stomatal conductance using the coupled leaf photosynthesis-stomatal conductance models developed by Farquhar-Ball-Berry (Ball et al., 1987; Farquhar et al., 1980) and its analytical solution (Baldocchi, 1994) (see Supporting Information). This was a key update for representing centennial GPP and water use efficiency responses to climate change and the large rise in atmospheric CO<sub>2</sub> concentrations. As is common in land surface models incorporated in Earth system models, we scaled the leaf level results of GPP and stomatal conductance to the canopy as a single ‘big leaf’ with an exponential decay function of LAI (Sellers et al., 1992) (see Supporting Information). With this new model formulation, we also added an additional ecological dynamical constraint to those already contained in CARDAMOM (Bloom & Williams, 2015), that constrained the ratio of maximum carboxylation ( $V_{\text{cmax}25}$ ) to the maximum

rate of whole chain electron transport at saturated light ( $J_{\max 25}$ ) (see Supplementary Text S1) to limit combinations that are not observed (Walker et al., 2014).

**Table 1:** Optimized parameters and initial conditions in CARDAMOM, corresponding flat prior ranges, and resulting state variables. Reproduced with modifications in bold in the “Ball Berry GPP” section from (Bloom et al., 2020; Quetin et al., 2020). Mean Temperature and Precipitation are represented by  $\bar{T}$  and  $\bar{P}$  respectively.

|                              | Parameter                | Description                                                              | Prior range                                                                                     |
|------------------------------|--------------------------|--------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------|
| Allocation fractions         | Fauto                    | Autotrophic respiration                                                  | 0.2 – 0.8                                                                                       |
|                              | Flab                     | NPP fraction to labile C                                                 | 0.01 – 0.5*                                                                                     |
|                              | Ffol                     | NPP fraction to foliar C                                                 | 0.01 – 0.5*                                                                                     |
|                              | froo                     | NPP fraction to fine root C                                              | 0.01 – 0.5*                                                                                     |
|                              | fwoo <sup>1</sup>        | NPP fraction to stem C                                                   | 0.01 – 0.5*                                                                                     |
| Turnover rates               | $\theta_{\text{woo}}$    | Stem C turnover rate                                                     | $2.5 \times 10^{-5} - 10^{-3} \text{ day}^{-1}$                                                 |
|                              | $\theta_{\text{roo}}$    | Fine root C turnover rate                                                | $10^{-4} - 10^{-2} \text{ day}^{-1}$                                                            |
|                              | $\Theta_{\text{lit}}$    | Litter C turnover rate at $\bar{T}$ , $\bar{P}$                          | $10^{-4} - 10^{-2} \text{ day}^{-1}$                                                            |
|                              | $\theta_{\text{som}}$    | Soil organic matter (SOM) turnover rate at $\bar{T}$ , $\bar{P}$         | $10^{-7} - 10^{-3} \text{ day}^{-1}$                                                            |
|                              | $\theta_{\text{min}}$    | Mineralization of litter to SOM at $\bar{T}$ , $\bar{P}$                 | $10^{-5} - 10^{-2} \text{ day}^{-1}$                                                            |
|                              | $\Theta$                 | Heterotrophic temperature dependence factor                              | 0.018 – 0.08                                                                                    |
|                              | $S_p$                    | Heterotrophic precipitation dependence factor                            | 0.01 - 1                                                                                        |
| Canopy                       | $d_{\text{onset}}$       | Leaf onset day                                                           | 0 – 365.25                                                                                      |
|                              | $d_{\text{fall}}$        | Leaf fall day                                                            | 0 – 365.25                                                                                      |
|                              | $c_{\text{LMA}}$         | Leaf C mass per area                                                     | 5 – 200 g C m <sup>-2</sup>                                                                     |
|                              | $c_{\text{ll}}$          | Leaf loss fraction                                                       | 1/8 - 1                                                                                         |
|                              | $c_{\text{lr}}$          | Annual labile C release fraction                                         | 1/8 - 1                                                                                         |
|                              | $c_{\text{ronset}}$      | Labile release period                                                    | 10 – 100 days                                                                                   |
|                              | $c_{\text{rfall}}$       | Leaf fall period                                                         | 20 – 150 days                                                                                   |
| Fire                         | $\pi_{\text{foliar}}^3$  | Combustion factors of foliar C                                           | 0.01 – 1                                                                                        |
|                              | $\pi_{\text{biomass}}^3$ | Combustion factors of non-foliar biomass C                               | 0.01 – 1                                                                                        |
|                              | $\pi_{\text{SOM}}^3$     | Combustion factor of soil C                                              | 0.01 – 1                                                                                        |
|                              | R                        | Resilience factor                                                        | 0.01 – 1                                                                                        |
| Water                        | $\omega$                 | Water stress threshold                                                   | $1 - 10^4 \text{ Kg H}_2\text{O m}^{-2}$                                                        |
|                              | $\alpha$                 | <sup>3</sup> Second order runoff decay constant                          | $3 \times 10^{-7} - 0.03 \text{ mm}^{-1} \text{ day}^{-1}$                                      |
| State variables <sup>2</sup> | $C_{\text{lab}}^{(t)}$   | Labile C at time $t$                                                     | 1 – 2000 gC m <sup>-2</sup>                                                                     |
|                              | $C_{\text{fol}}^{(t)}$   | Foliar C at time $t$                                                     | 1 – 2000 gC m <sup>-2</sup>                                                                     |
|                              | $C_{\text{roo}}^{(t)}$   | Fine root C at time $t$                                                  | 1 – 2000 gC m <sup>-2</sup>                                                                     |
|                              | $C_{\text{woo}}^{(t)}$   | Above- and below-ground woody C at time $t$                              | 1 – 10 <sup>5</sup> gC m <sup>-2</sup>                                                          |
|                              | $C_{\text{lit}}^{(t)}$   | Litter C at time $t$                                                     | 1 – 2000 gC m <sup>-2</sup>                                                                     |
|                              | $C_{\text{som}}^{(t)}$   | Soil organic C at time $t$                                               | 1 – 2×10 <sup>5</sup> gC m <sup>-2</sup>                                                        |
|                              | $W^{(t)}$                | Plant-available water at time $t$                                        | 1 – 10 <sup>4</sup> mm                                                                          |
| Ball Berry GPP               | $V_{\text{cmax}25}$      | <b>maximum carboxylation rate</b>                                        | <b>10 – 400 <math>\mu\text{mol m}^{-2} \text{s}^{-1}</math></b><br><b>(Walker et al., 2014)</b> |
|                              | $J_{\text{max}}$         | <b>Maximum rate of whole chain electron transport at saturated light</b> | <b>20 – 400 <math>\mu\text{mol m}^{-2} \text{s}^{-1}</math></b><br><b>(Walker et al., 2014)</b> |
|                              | $m_{\text{stomata}}$     | <b>Stomatal conductance slope</b>                                        | <b>2 – 30 (Oleson et al., 2010)</b>                                                             |

|                            |                                                          |                                                                                    |
|----------------------------|----------------------------------------------------------|------------------------------------------------------------------------------------|
| <b>b<sub>stomata</sub></b> | <b>Stomatal conductance intercept</b>                    | <b>.001 - .1 mol m<sup>-2</sup> s<sup>-1</sup></b><br><b>(Oleson et al., 2010)</b> |
| <b>g<sub>b</sub></b>       | <b>Leaf boundary layer conductance to CO<sub>2</sub></b> | <b>.4 – 10 mol m<sup>-2</sup> s<sup>-1</sup> (Martin</b><br><b>et al., 1999)</b>   |

<sup>1</sup> *f<sub>woo</sub>* is equivalent to  $1 - f_{\text{auto}} - f_{\text{fol}} - f_{\text{lab}}$

\*Prior ranges are conservative approximations, see Fox et al., (2009) and CARDAMOM sample code for details on sequential allocation fraction sampling in DALEC models.

<sup>2</sup>Only initial conditions (at time t=0) are optimized in DALECV2.1.6.

<sup>3</sup>Using the ecological and dynamical constraint approach (Bloom & Williams, 2015) we ensure that that  $\pi_{\text{foliar}} > \pi_{\text{biomass}}$  and  $\pi_{\text{foliar}} > \pi_{\text{SOM}}$

### 2.1.2 Assimilated Carbon Cycle Observations

Our whole assimilation run spanned 1920 – 2015, with assimilated observations from 2000 – 2015. All variables in Table 1 were optimized. The suite of observations (summarized in Table 1) was chosen to leverage new remote sensing observations of the global carbon cycle. A key set of assimilated observations is CMS-Flux net biome exchange (NBE), which was determined through atmospheric inversion (Bey et al., 2001; Liu et al., 2017, 2021). These NBE estimates had previously been used to better constrain global respiration fluxes (Konings et al., 2019), as well as the balance of photosynthesis and respiration across the tropics (Liu et al., 2017), and as emergent constraints on carbon-climate feedbacks (Barkhordarian et al., 2021), among others. Additional observations were derived from the following gridded datasets: remotely sensed solar induced fluorescence (SIF) as a proportional constraint for GPP (Bloom et al., 2020; Frankenberg et al., 2011), remotely sensed leaf area index (LAI) (Bi et al., 2015), remotely sensed carbon monoxide (CO) to constrain the fraction of carbon lost from pools due to fire (Bowman et al., 2017; Worden et al., 2017), remotely sensed total biomass (Carreiras et al.,

2017; Saatchi et al., 2011), and soil organic matter from the Harmonized World Soil Database (HWSD) (Hiederer & Köchy, 2011).

The biomass and soil organic material observations were both drawn from a static map and assimilated in the year and/or month most representative of their observation (June of 2015 for biomass and the year 2000 for soil organic material) as in (Bloom et al., 2016; Quetin et al., 2020). By contrast, NBE and SIF were assimilated as monthly time series from 2010 – 2015 and LAI as the long term mean from 2010 – 2015. The CO observations constrain biomass burning emissions fractions (see Table 1). Each dataset was re-gridded to 4°x5° latitude/longitude on the Goddard Earth Observing System - Chem (GEOS-Chem) for consistency with the CMS-Flux estimates (see Table 2, Supporting Information Section S3). All CARDAMOM assimilation and forward runs (i.e., DALEC model runs with the retrieved optimal parameters) were also performed at this resolution.

**Table 2.** Observation-based datasets assimilated into the 4°x5° CARDAMOM simulation. Adapted with modification from (Bloom et al., 2020; Quetin et al., 2020).

| Observation                               | Years       | Dataset description                                                                     | Uncertainty <sup>4</sup>                                                               |
|-------------------------------------------|-------------|-----------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------|
| Leaf area index (LAI)                     | 2010 – 2015 | MODIS LAI retrievals <sup>1</sup> .                                                     | $\pm \log(1.2)$                                                                        |
| Soil organic matter (SOM)                 | 2000        | Soil C from harmonized world soils database (HWSD) (Hiederer & Köchy, 2011)             | $\pm \log(1.5)$                                                                        |
| Above- and below-ground biomass (ABGB)    | 2015        | GLAS-informed biomass map (Carreiras et al., 2017; Saatchi et al., 2011)                | $\geq \pm \log(1.5)$ <sup>see 3</sup>                                                  |
| Solar-induced Fluorescence (SIF)          | 2010 – 2015 | GOSAT retrievals of fluorescence (Frankenberg et al., 2011) <sup>2</sup>                | $\pm \log(2)$ <sup>see 2</sup>                                                         |
| Fire C emissions (BB)                     | 2010 – 2015 | 4°x5° inverse estimates of fire C emissions (Bowman et al., 2017; Worden et al., 2017). | $\pm 20\%$                                                                             |
| Net Biosphere exchange (NBE) <sup>5</sup> | 2010 – 2015 | GOSAT CO <sub>2</sub> and OCO <sub>2</sub> CO <sub>2</sub> derived 4°x5° inverse        | Seasonal= $\pm 0.05$ g C/m <sup>2</sup> /d<br>Annual= $\pm 0.02$ g C/m <sup>2</sup> /d |

estimates of terrestrial NBE  
(Liu et al., 2017, 2021).

<sup>1</sup>Only mean 2010-2015 LAI is assimilated into CARDAMOM, in order to mitigate the influence of seasonal LAI retrieval biases (Bi et al., 2015).

<sup>2</sup>Time-resolved SIF is assimilated as a relative constraint on the temporal variability of GPP when temperatures are greater than 5°C and LAI is greater than 0.2.

<sup>3</sup>see ref (Bloom et al., 2016) for details on the uncertainty on ABGB.

<sup>4</sup>Uncertainties denoted as  $\pm \log()$  indicates log-transformed model and observed quantities.

<sup>5</sup>The CMS-Flux NBE is spatially smoothed using a 3x3 gaussian smoother to reduce noise.

### 2.1.3 Data assimilation methodology

CARDAMOM parameter optimization was performed with Bayesian inference in which observations  $O$  are paired to model parameters, states, and fluxes ( $y$ ) to form the likelihood function (Bloom et al., 2016, 2020; Bloom & Williams, 2015; Quetin et al., 2020). The likelihood probability function was calculated as the product of individual likelihoods:

$$P(\mathbf{O}|\mathbf{y}) = P_{LAI} P_{SOM} P_{ABGB} P_{SIF} P_{NBE} P_{CO} \quad (1)$$

where  $P(O|y)$  was the likelihood of  $y$  given observations ( $O$ ) and  $P_X$  was the probability of variable  $X$  given the observations of that variable (Table 2). This formulation assumes that the error between observations was independent. The  $P_{LAI}$ ,  $P_{SOM}$  and  $P_{ABGB}$ , and  $P_{CO}$  were derived as (Bloom et al., 2020; Quetin et al., 2020):

$$P \propto e^{-\frac{1}{2} \sum_i \left( \frac{m_i - o_i}{\sigma_i} \right)^2} \quad (2)$$

where  $m_i$  and  $o_i$  corresponds to the  $i^{th}$  observation of the corresponding DALEC-modeled quantity and  $\sigma_i$  accounts for the combined effects of DALEC model structural error, model inputs, and observation errors. To better capture the interannual variability,  $P_{NBE}$  included

separate probability calculations with different uncertainty estimates for monthly and annual likelihoods and the units of SIF and GPP in  $P_{SIF}$  were normalized by the mean, such that GPP dynamics were constrained by SIF even though the units are not the same. Consistent with previous CARDAMOM runs (e.g. (Bloom et al., 2016, 2020; Quetin et al., 2020)), uncertainties were ultimately chosen manually based on expert experience of the underlying dataset and the impact on CARDAMOM's match to the observations. For example, the seasonal uncertainty of NBE is held within a reasonable range of observed uncertainty but small enough to induce a seasonal cycle in NBE. See Quetin et al. (2020) and included references for further details. Additionally, CARDAMOM applied 'ecological and dynamical constraints' that reduce equifinality (Huntzinger et al., 2017) by eliminating parameter combinations that may match observations despite limited ecological plausibility (Bloom & Williams, 2015).

Finally, we replaced the Adaptive Metropolis-Hastings Markov Chain Monte Carlo (MHMCMC) algorithm which was previously used in CARDAMOM (described in Bloom et al. (2020)) with a Differential Evolution Markov Chain Monte Carlo (DEMCMC) to sample  $P(y|O)$  (Braak, 2006) (Levine et al. 2022, in prep). The DEMCMC allowed for an order of magnitude increase in random starting points to avoid local minima and path dependency, while it also provided modest improvement in computation time. The DEMCMC produced similar results to

the MHMCMC algorithm in minimizing the mismatch between carbon cycle observations and model values.

#### *2.1.4 Model inputs for assimilation and attribution*

CARDAMOM requires external inputs for climate variables (insolation, precipitation, temperature, and vapor pressure deficit), atmospheric concentration of CO<sub>2</sub>, and burned area. For the assimilation runs, the climate inputs were taken from monthly CRUNCEP v7 reanalysis, which was chosen primarily for being available for most of the past century. CRUNCEP v7 is a combined datasets of the Climate Research Unit (CRU) and reanalysis data from National Centers for Environmental Prediction (NCEP) (Viovy, 2018). The atmospheric concentrations of CO<sub>2</sub> were taken from the historical values of the globally-averaged annual means used by the Intergovernmental Panel on Climate Change with values for 2006 – 2015 taken from RCP8.5 scenario which include a rise in CO<sub>2</sub> of 98.6 ppm between 1920 and 2015 (Pachauri & Reisinger, 2008; Taylor et al., 2012).

CARDAMOM simulates fire fluxes based on burned area inputs and optimized emissions factors relating burned area to emission rates of CO and CO<sub>2</sub>. These simulations are necessary to relate simulated net ecosystem productivity with observed net biome exchange (since the latter also accounts for fire fluxes). We used the Global Fire Emissions Database (GFED) V4.1s burned area to drive CARDAMOM during the observational period (1997 – 2015) (Randerson et al., 2017). Prior to the observational period, we synthesized burned area at each point for the last century by randomly resampling from the distribution of observed GFED V4.1s observations for a given month. This synthesized burned area contained the same variance as the observations and



309 did not have a long-term trend. We also investigated an empirical linkage between burned area  
310 and climate inputs but found the burned area synthesized from observations had less error  
311 relative to observed burned area in recent decades (not shown). Although we did not investigate  
312 fire specifically in this study, fire is accounted for implicitly in the carbon cycle data assimilation  
313 in CARDAMOM (Exbrayat et al., 2018).

## 315 ***2.2 Attributing Change in the Carbon Cycle***

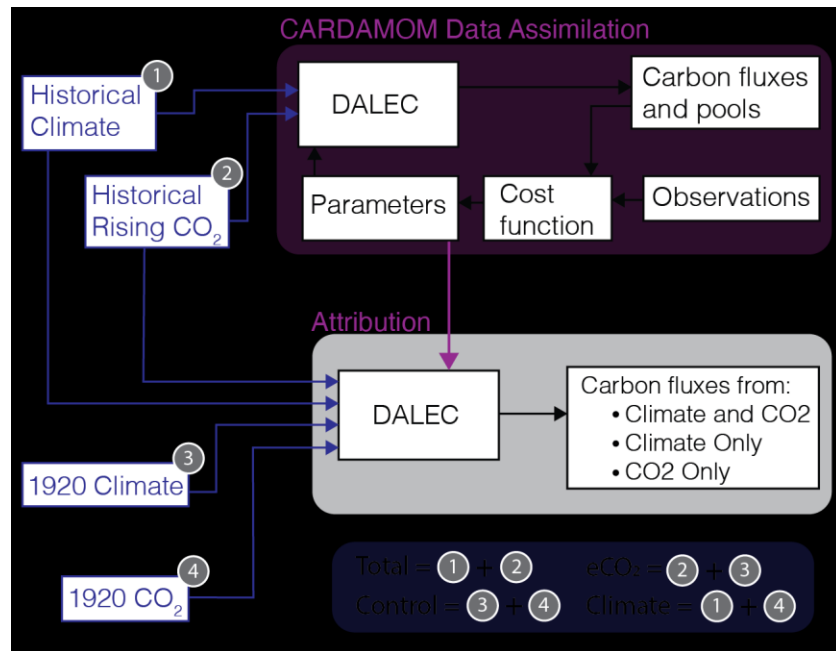
316 Our overall approach for attributing the carbon cycle response to different past  
317 environmental changes is illustrated in Figure 2. We ran factorial forcing scenarios that included  
318 different combinations of climate change and historically rising CO<sub>2</sub>: i) historical climate change  
319 and increased atmospheric CO<sub>2</sub> concentrations, as during the assimilation stage (referred to as the  
320 ‘Total’ scenario); ii) a control climate – repeating 1920 CRUNCEP meteorology – and steady  
321 atmospheric concentrations of CO<sub>2</sub> equal to those in the 1920s (‘Control’ scenario); iii) a  
322 historically rising (enhanced) atmospheric concentration of CO<sub>2</sub> with a control climate (‘eCO<sub>2</sub>’  
323 scenario); and iv) a scenario with historical climate changes but constant CO<sub>2</sub> at 1920 levels  
324 (‘Climate’ scenario, i.e. without CO<sub>2</sub> fertilization). The burned area was left the same as the  
325 assimilation runs across experiments. These combined Total, Control, eCO<sub>2</sub>, and Climate  
326 experiments are similar to the approach used in previous studies to diagnose climate-carbon  
327 feedbacks in C4MIP (Arora et al., 2020; Friedlingstein et al., 2014; Jones et al., 2016), thus

isolating the effect of CO<sub>2</sub> on plant physiology from the effect of climate change on the carbon cycle.

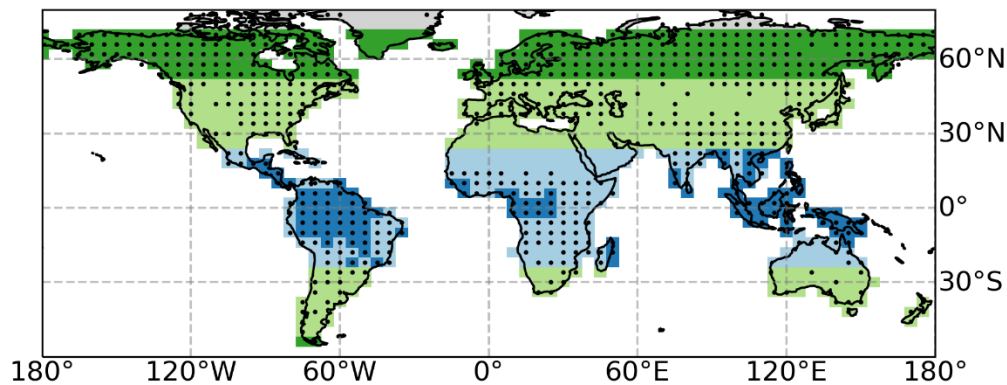
Attribution of change in carbon fluxes was then determined as the difference between the respective carbon fluxes of the forced scenarios ('Total', 'eCO<sub>2</sub>', and 'Climate') minus the control run ('Control'). Throughout this manuscript, we denote the attributed change in a flux due to enhanced CO<sub>2</sub> as  $\Delta X^{eCO_2}$ , the attributed change in a flux to climate as  $\Delta X^{climate}$ , and the attributed change when they both are combined as  $\Delta X^{total}$ . In each of the above cases, X denotes the carbon flux variable, such as GPP or  $R_h$ . For example, net ecosystem productivity due to enhanced CO<sub>2</sub> ( $\Delta NEP^{eCO_2}$ ) is calculated as in Equation 3:

$$\begin{aligned} \Delta NEP^{eCO_2} &= NEP^{eCO_2} - NEP^{Control} \\ &= NEP(control\ climate, historical\ CO_2) - NEP(control\ climate, control\ CO_2) \end{aligned} \quad (3)$$

Attribution was performed at each grid point on the cumulative sums from 1920 – 2015 and then spatially aggregated to calculate global and regional attribution, with regions defined as in Figure 3. The spatial aggregation method is discussed in Supplementary Text S2.



**Figure 2:** Summary of experimental design. We combine (pink) contemporary (2001-2016) atmospheric and land surface carbon cycle observations and historical climate forcing datasets (1920-2015) to constrain mechanistic carbon cycle responses to climate and atmospheric CO<sub>2</sub>. Model runs (grey) forced by combinations of historical or control climate and CO<sub>2</sub> concentrations to create the ‘Total’, ‘Control’, ‘eCO<sub>2</sub>’, and ‘Climate’ scenarios.



**Figure 3:** Regional divisions used for analysis. boreal (dark green), temperate (light green), wet tropics (blue), dry tropics (light blue). Black dots show points where CARDAMOM was able to complete the inversion (i.e. find a solution) in the simulated number of iterations.

### 3 Results and Discussion

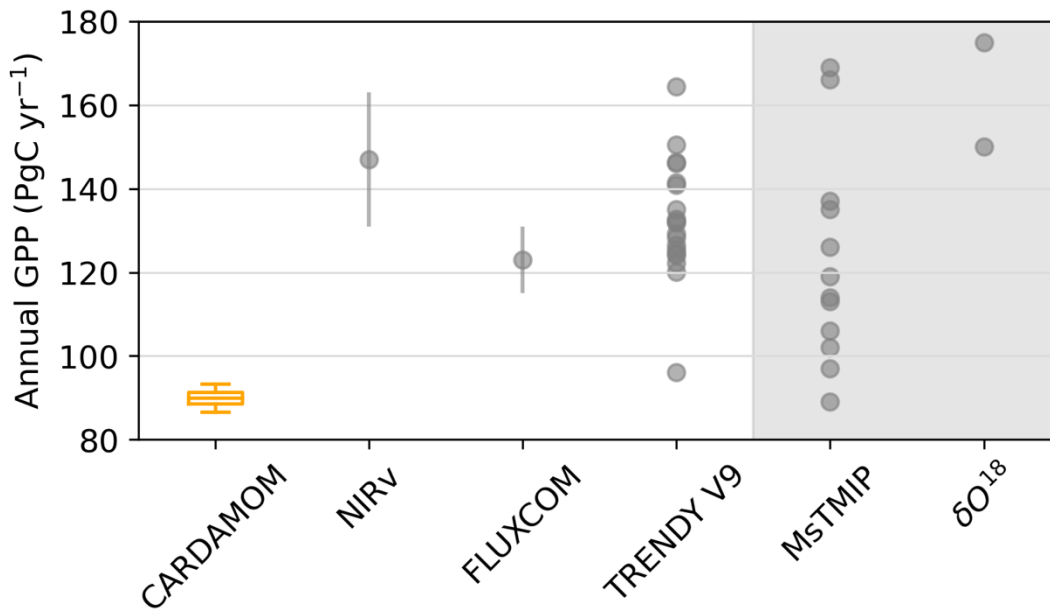
#### 3.1 Comparison of CARDAMOM simulations to assimilated estimates

We compared CARDAMOM to assimilated observations for verification, as well as to alternate independent modeled and observed estimates of the carbon cycle. Compared to assimilated observations, CARDAMOM has a strong match of the seasonal cycle of net biosphere exchange for all regions and a slightly muted interannual variation (Figure S1). Across space, the observations generally fall within CARDAMOM's uncertainty, although simulated leaf area is high and net biosphere exchange is somewhat lower than observations (that is, simulated uptake is higher than observed) around the equator. In the Sahel region, biomass is low and soil organic matter high relative to observations (Figure S2, Text S3). For the majority of

land points, CARDAMOM was able to retrieve a solution (Figure 3, black dots). Failed points primarily fell within the highly arid regions of the globe where there is relatively little carbon cycle activity. Some failed points may encompass regions important to the interannual variation of the carbon cycle (Poulter et al., 2014).

### ***3.2 Comparison of CARDAMOM simulations to independent estimates***

CARDAMOM's simulated carbon cycle dynamics are within range of several independent constraints that were not directly assimilated. The average global GPP from CARDAMOM ( $90 \pm 1.3$  Pg C/yr, 25-75<sup>th</sup> percentile uncertainty for the period 2003 – 2015) is at the low end – but within the range of – several alternative estimates (Figure 4). CARDAMOM GPP are generally on the low end of other estimates in the tropical regions, while CARDAMOM GPP is more similar in both the seasonal cycle and mean annual value in the Boreal and Temperate regions (Figure S4). These alternative estimates include observations (i.e. optical retrievals from NIRv and  $\delta O^{18}$  ratios), an observationally-informed machine learning model (FLUXCOM), or model ensembles (i.e. the Multi-scale synthesis and Terrestrial Model Intercomparison Project (MsTMIP) and Trends in Net Land-Atmosphere Carbon Exchange (TRENDY V9), see Table S1 for list of models used) (Badgley et al., 2019; Friedlingstein et al., 2020; Huntzinger et al., 2013; Sitch et al., 2008; Welp et al., 2011).

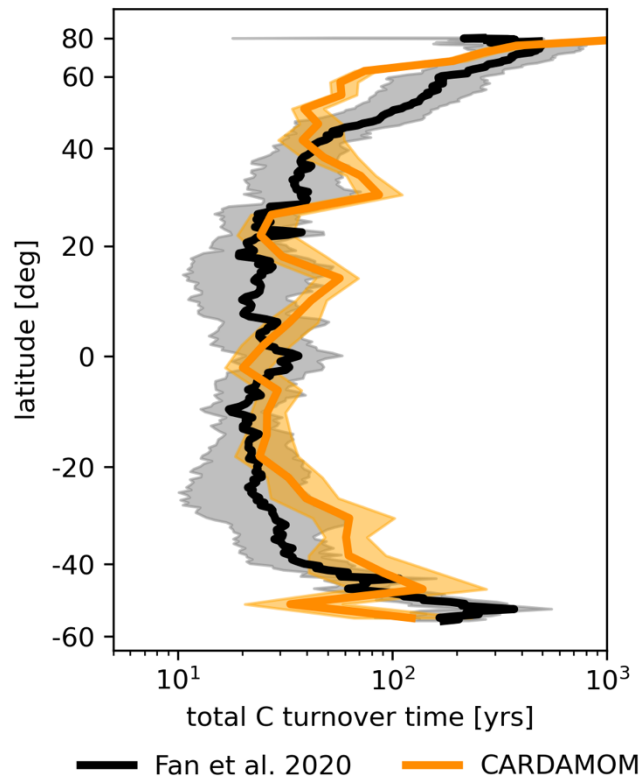


**Figure 4:** CARDAMOM mean annual Gross Primary Productivity (GPP, Pg C/yr) parameter ensemble spread with CRUNCEP climate 2003 – 2015 (Orange). Compared with observation-based estimates of global GPP from NIRv (2003 – 2015), FLUXCOM (2003 – 2015), and  $\delta O^{18}$  (1980 – 2010), and terrestrial biosphere estimates from TRENDY V9 (2003 – 2015), MsTMIP (2003 – 2010) (all in grey). Figure structure and data for NIRv, FLUXCOM, MsTMIP, and  $\delta O^{18}$  adapted from (Badgley et al., 2019). Whiskers of boxplot show 5<sup>th</sup> – 95<sup>th</sup> percentiles. Grey shading demarks literature values that do not directly overlap in time.

The zonal pattern of the apparent turnover time of the total ecosystem carbon for CARDAMOM (calculated using the total summed soil and vegetation carbon stocks, as in Fan et al. (2020)) is broadly similar to that of a recent observation-derived estimate of global turnover times for the same time span (Fan et al., (2020), which is an updated version of the estimate in Carvalhais et al. (2014)), at least between the latitudes of 46° S and 46° N (Figure 5). This is

reflected in the average values – 41 years for CARDAMOM and 30 years for that of Fan et al. (2020) (Figure 5). At high latitudes, however, the two estimates in Figure 5 diverge significantly, with CARDAMOM predicting a shorter turnover time. This divergence may relate to an under-prediction of the size of soil carbon pools in CARDAMOM in regions with complex permafrost dynamics, since CARDAMOM does not have an explicit representation of the dynamics for permafrost and frozen soils. In addition, the soil organic matter estimates at high latitudes are highly uncertain because of the limited number of measurements. The HWSD soil organic matter dataset assimilated in CARDAMOM was shown to be on the low end of estimates in Fan et al. (2020), which would tend to drive CARDAMOM towards a shorter turnover time as well. Resolving this divergence and others illustrated above is likely to improve the accuracy and precision of carbon cycle analyses derived from CARDAMOM.

The difficulty in acquiring observations of soil carbon dynamics and their complexity makes the parameterization of turnover times in land surface models highly uncertain (Carvalhais et al., 2014; Friend et al., 2014; Koven et al., 2015), including at high latitudes (Koven et al., 2017). By contrast, the soil carbon turnover rates and initial carbon pool sizes in CARDAMOM are informed by observations of carbon fluxes and carbon states through data assimilation. The close match between the turnover times estimated by CARDAMOM and those estimated by observationally-driven and quasi-independent (some datasets included in Fan et al. (2020) are assimilated in CARDAMOM, some are not) values hints at the success of CARDAMOM's ability to accurately infer carbon cycle dynamics based on the assimilated observations.

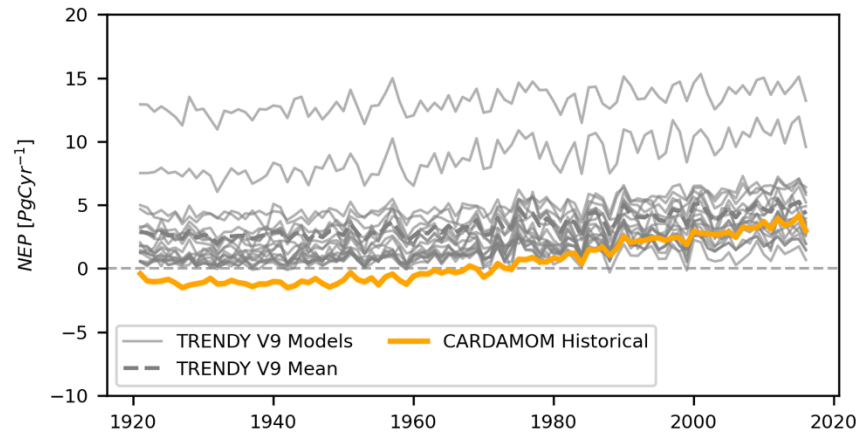


**Figure 5:** The zonally averaged turnover time for total ecosystem C in CARDAMOM (orange) compared to the quasi-independent estimates of Fan et al. 2020 (black), calculated between 2001 – 2014. Shading demarks 5<sup>th</sup> – 95<sup>th</sup> range of ensembles, solid line is median.

For more complete insight into the full historical dynamics simulated by CARDAMOM, we further compared it to independent model estimates of carbon flux timeseries from TRENDY V9 scenario 2 (change in climate and CO<sub>2</sub> but not land use change) (Figure 6, S3) and estimates of the sensitivity of GPP and NEP to increased CO<sub>2</sub> (Figure 7) (Friedlingstein et al., 2020). We find that the net primary productivity in the CARDAMOM ‘Total’ (Historical) run falls just below the TRENDY V9 set of models between 1920 and about 1980 (Figure 6). Up until 1960, CARDAMOM is a weak source to the atmosphere, while TRENDY V9 is neutral to a sink



throughout. These early differences highlight the difference in initial conditions between CARDAMOM and the models contained in TRENDY. While TRENDY models are run to equilibrium in 1700, CARDAMOM retrieves the initial carbon and water pools that serve to best match the observations assimilated. After 1980, the CARDAMOM Historical runs fall within the spread of models contained in TRENDY, ending in 2015 very close to the mean of the TRENDY models (Figure 6). This convergence in modern times may be due to the influence of similar observations on both models, which are systematically assimilated in CARDAMOM and assert influence over TRENDY as they are often used as validation. Like for NEP, the growth in CARDAMOM GPP since 1960 is much faster in CARDAMOM than in the TRENDY simulations (Figure S3), possibly due to analogous differences in initial condition parameterization and the influence of modern measurements. The relatively rapid CARDAMOM GPP growth compared to TRENDY is consistent with the results of Campbell et al. (2017), who used carbonyl sulfide records to show that historical GPP growth is higher than simulated by earth system models. During the period 1900 - 2013, GPP was estimated to grow by  $31 \pm 5\%$ , consistent with the  $39 \pm 7\%$ , simulated here during the slightly later period 1920 – 2015. As also shown in Fig. 4, the historical GPP simulated by CARDAMOM is lower than that simulated by the TRENDY models. Consistent with this pattern, autotrophic respiration is also lower than in the TRENDY models, while the heterotrophic respiration and LAI simulated by CARDAMOM are lower than most TRENDY models, but still fall within the low end of their range (Figure S3).



**Figure 6:** The annual timeseries of Net Ecosystem Productivity (NEP) from 1920 – 2015 from the CARDAMOM Historical run (orange, shading 5<sup>th</sup> – 95<sup>th</sup> percentile of ensemble), the individual TRENDY v9 models (grey solid) (Friedlingstein et al., 2020), and their multi-model mean (grey dashed). For a fair comparison, the global aggregation was performed only where there was a successful CARDAMOM run (black dots in Figure 3).

Lastly, because our study focused in part on the effect of historical atmospheric CO<sub>2</sub> increases on terrestrial carbon fluxes, we investigated whether the GPP and NEP CO<sub>2</sub> sensitivity calculated by CARDAMOM was in line with that of alternative estimates. Specifically, we calculated the CARDAMOM sensitivity of gross primary productivity as a percentage ( $\beta_{\text{GPP}}$ ) and net ecosystem production ( $\beta_{\text{NEP}}$ ) to enhanced CO<sub>2</sub>. The  $\beta_{\text{GPP}}$  and  $\beta_{\text{NEP}}$  were calculated by dividing the fractional gain of GPP or the carbon gained through NEP from 1920 – 2015 that was attributed to enhanced CO<sub>2</sub> by the change in atmospheric concentration of CO<sub>2</sub> over this period. Note that when calculating  $\beta_{\text{GPP}}$ , unlike when calculating  $\beta_{\text{NEP}}$ , the numerator was calculated as a percentage gain over 1920-2015 to facilitate comparison with literature values. Experimental manipulations in Free Air CO<sub>2</sub> Enrichment (FACE) studies provided observation-based but site-

specific estimates of relative GPP sensitivity to increased CO<sub>2</sub> (Hickler et al., 2008, p. 200), which cannot be directly compared to CARDAMOM because of its coarse resolution. Some differences in results between FACE studies and CARDAMOM would also be expected because of differences in the absolute atmospheric CO<sub>2</sub> levels between the two. Nevertheless, when considering CARDAMOM's relative GPP sensitivity to CO<sub>2</sub> across pixels, many pixels within the 5-95<sup>th</sup> percentile CARDAMOM range show the same sensitivity as observationally observed at four FACE experiments, which fall slightly below the 25<sup>th</sup> CARDAMOM percentile (Figure 7). Across the globe, model ensembles provide a further point of comparison. The GPP sensitivity to CO<sub>2</sub> simulated by TRENDY V9 models and sampled at the CARDAMOM simulation points for 1920 - 2015 is generally considerably lower than that of CARDAMOM (Figure 7b). Like CARDAMOM's, the TRENDY GPP CO<sub>2</sub> sensitivity is also uncertain, both because of imperfect modelling assumptions and because no data are assimilated into TRENDY. It is thus difficult to ascertain whether or by how much CARDAMOM's GPP CO<sub>2</sub> sensitivity is too high or TRENDY's is too low.

The relatively high CARDAMOM GPP sensitivity to CO<sub>2</sub> relative to that of conventional models is also reflected in the comparison between CARDAMOM NEP sensitivity to CO<sub>2</sub> and that of model intercomparisons, including estimates from TRENDY V9, which were regridded to CARDAMOM resolution and sampled where CARDAMOM provided a solution (black dots Figure 3), the Coupled Climate Carbon Cycle Model Intercomparison Project (C4MIP), and MsTMIP (Arora et al., 2013; Friedlingstein et al., 2006, 2020; Huntzinger et al., 2017) (Figure 7c). CARDAMOM's NEP sensitivity is on the high end of estimates from TRENDY and C4MIP, but in the middle of the range for MsTMIP. The different sensitivities exhibited by models from different intercomparison systems is reflective of their uncertainty. Nevertheless,

the differences between conventional model ensembles and CARDAMOM add a note of caution to the results described in the manuscript.

Taken together, the reasonable – though imperfect – match between the CARDAMOM-simulated historical carbon cycle (Figures 4-7, S3-S4) and independent estimates demonstrates CARDAMOM's utility for process attribution of historical fluxes, as performed below.

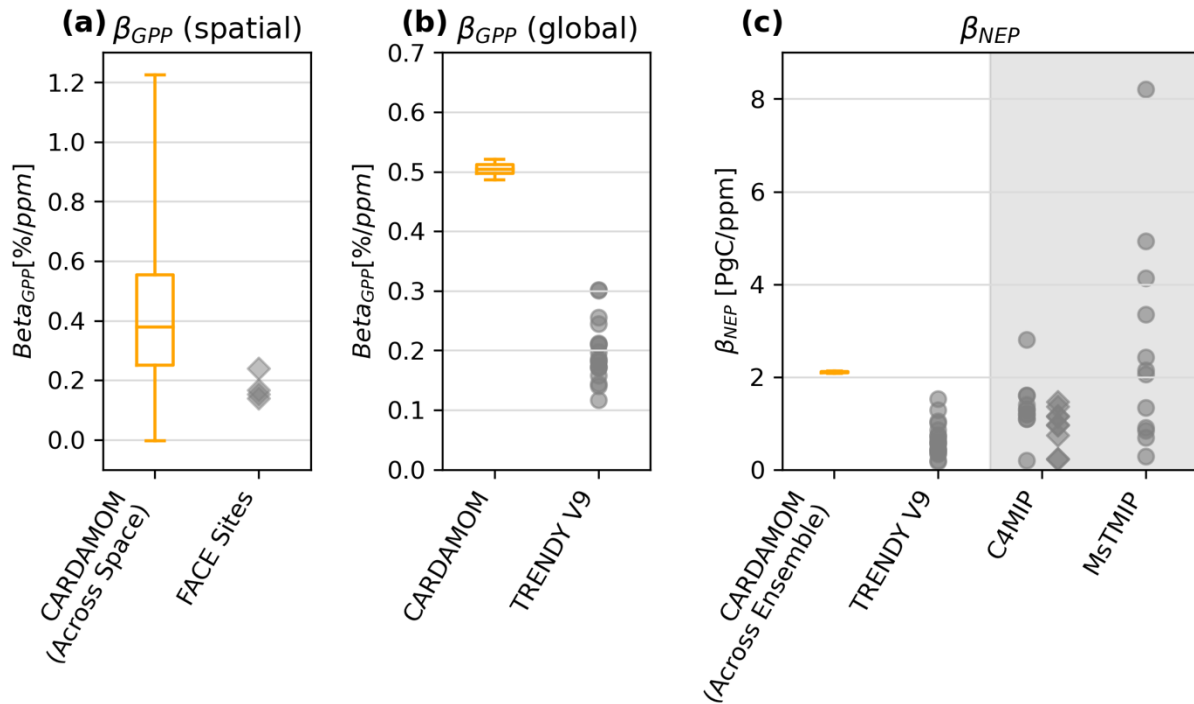


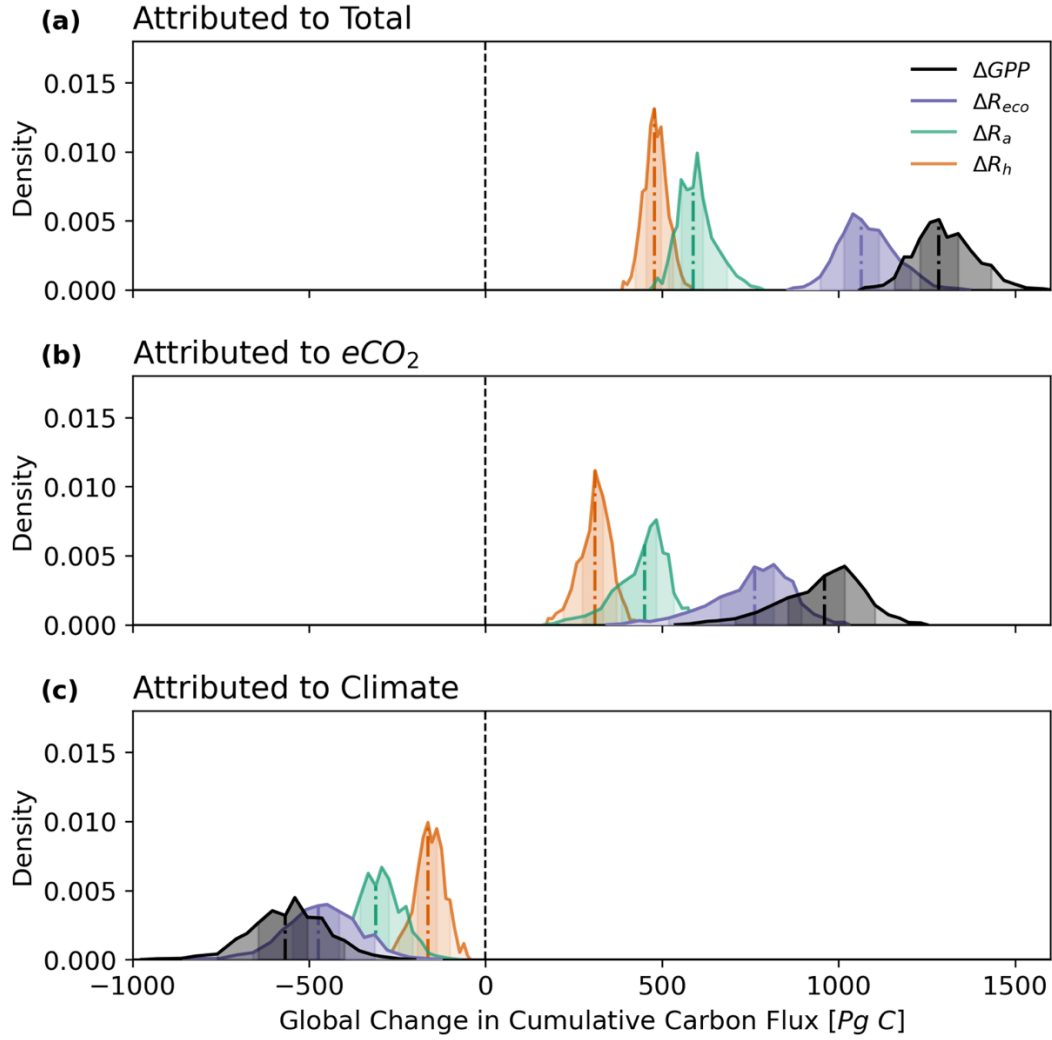
Figure 7: Comparison of the CARDAMOM mean sensitivity of carbon to  $eCO_2$  for percent change in GPP with a) the CARDAMOM spread across space with FACE sites, b) CARDAMOM parameter spread of global mean with TRENDY V9 model spread. In c) the absolute change in NEP per change in ppm  $CO_2$  for CARDAMOM simulations (orange, 1920 – 2015) including the ensemble uncertainty of the global mean and TRENDY V9 (1920 – 2015) models (Friedlingstein et al., 2020) and values drawn from literature for C4MIP (1901 – 2015) circles for (Friedlingstein et al., 2006, p. 20) and diamonds for (Arora et al., 2013) estimates, MsTMIP (1959 – 2010) from (Huntzinger et al., 2017) (all in grey). All CARDAMOM values are for 1920 – 2015. For a fair comparison, the global aggregation was performed only where there was a successful CARDAMOM run (black dots in Figure 3). Whiskers of boxplot show 5<sup>th</sup> – 95<sup>th</sup> percentiles. Grey shading demarks literature values that do not directly overlap in time.

### 3.3 Large gains in GPP under rising CO<sub>2</sub> are largely offset by the response of respiration to increased plant growth

Over the past century, the CARDAMOM simulations attribute large increases in global GPP to the combination of the historical enhanced atmospheric concentrations of CO<sub>2</sub> and climate change ( $\Delta GPP^{total} = 1294 \pm 57$  Pg C, where the uncertainty is  $\pm$  the 25<sup>th</sup> – 75<sup>th</sup> range divided by two) (Figure 8). This modeled increase in global GPP is consistent with increasing GPP driving the satellite-observed greening of the Earth (Zhu et al., 2016). The increase in global GPP is primarily attributed to the GPP response to enhanced atmospheric concentrations of CO<sub>2</sub> ( $\Delta GPP^{eCO_2} = 974 \pm 76$  Pg C), which accounts for 75% of the total GPP change. The larger response to CO<sub>2</sub> than the response to climate is consistent with past studies using traditional model ensembles (Arora et al., 2013; Melnikova & Sasai, 2020; Piao et al., 2013; Schwalm et al., 2020), although this study is the first to quantify this effect using a data-constrained methodology.

Changes in climate over the past century have also impacted the carbon cycle. When only climate change is simulated, GPP decreases globally relative to the control experiment ( $\Delta GPP^{Climate} = -551 \pm 72$  Pg C). The negative response of GPP to the Climate only scenario is broadly consistent with negative responses of NPP seen in C4MIP experiments (Friedlingstein et al., 2006). Except under particularly hot conditions in the wet tropics, increased temperatures generally increase GPP by increasing chemical activity, but increased vapor pressure deficit reduces GPP by causing stomatal closure and reducing stomatal conductance (Fu et al., 2022). Overall, the potential benefits from warming due to climate change are offset by the effects of vapor pressure deficit-driven stomatal closure. (Note that changes in sunlight and precipitation were relatively small between 1920 – 2015, such that direct temperature and VPD effects were

the dominant climate drivers). This explains the global decrease in GPP in the climate change-only scenario. By contrast, the fact that  $\Delta GPP$  is larger in the total scenario ( $\Delta GPP^{total} = 1294 \pm 57$  Pg C) than in the enhanced CO<sub>2</sub>-only scenario ( $\Delta GPP^{eCO_2} = 974 \pm 76$  Pg C) suggests that when CO<sub>2</sub> and climate changes interact, climate has a positive (rather than negative as in  $\Delta GPP^{Climate}$ ) influence on the Total scenario. Under the increased CO<sub>2</sub> scenario, CO<sub>2</sub>-induced stomatal closure limits the impact of vapor pressure deficit-induced stomatal closure. This is consistent with observations (Dusenge et al., 2019) and with the recognition that stomatal closure in response to enhanced CO<sub>2</sub> reduces evaporation (Lemordant et al., 2018; Swann et al., 2016). As a result, the direct positive effects of increasing temperature on GPP dominate, and the effect of climate change on GPP is positive. This coupling between the carbon-concentration and carbon-climate feedbacks allows climate changes to have a positive impact on GPP when increases in atmospheric CO<sub>2</sub> are present.



**Figure 8:** Magnitude of global cumulative sum of terrestrial carbon fluxes from 1920 - 2015 attributed to a) combined climate change and enhanced  $\text{CO}_2$  ('Total' minus 'Control'), b) enhanced  $\text{CO}_2$  alone ('e $\text{CO}_2$ ' minus 'Control'), and c) climate change alone ('Climate' minus 'Control'). Distributions for gross primary productivity ( $\Delta\text{GPP}$ ), ecosystem respiration ( $\Delta R_{\text{eco}}$ ), autotrophic respiration ( $\Delta R_a$ ), and heterotrophic respiration from litter and soils ( $\Delta R_h$ ) ( $\text{Pg C}$ ). Colors per legend. The median of the whole distribution is shown as a colored dot-dashed line, while the percentiles of 5<sup>th</sup> – 95<sup>th</sup> and 25<sup>th</sup> – 75<sup>th</sup> percentile are shown as gradually darker shading.  $R_{\text{eco}}$  is equal to  $R_h + R_a$ .

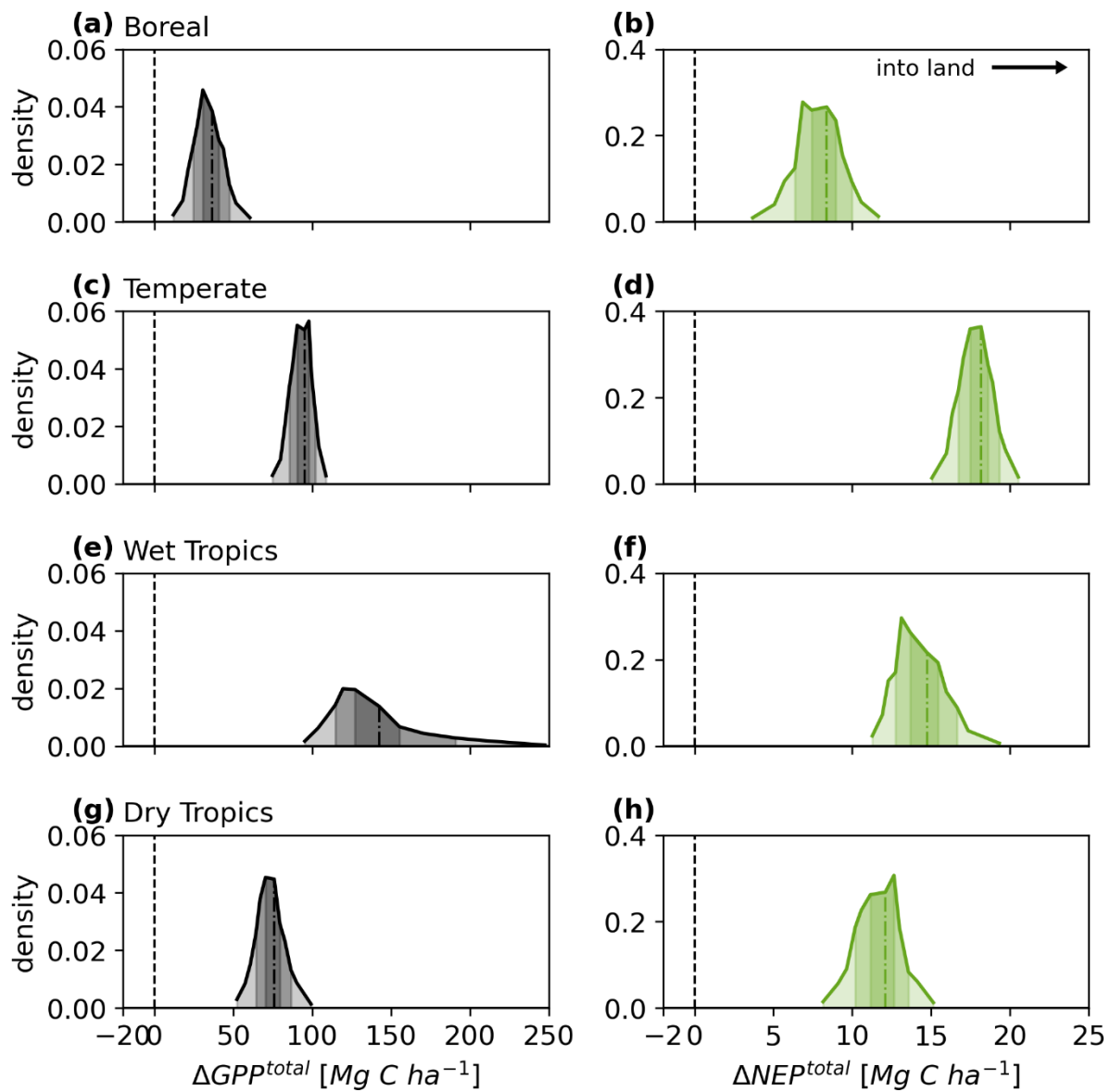


The majority of the enhanced ecosystem respiration over the last century is due to a change in plant growth (i.e., input of additional carbon into the ecosystem), rather than an acceleration in the turnover of carbon due to the sensitivity to increasing temperature. Our analysis attributes a large increase of ecosystem respiration in response to the increased plant growth that occurs due to CO<sub>2</sub> fertilization. The majority of  $\Delta GPP^{eCO_2}$  is lost to respiration ( $\Delta R_{eco}^{eCO_2} = 774 \pm 72$  Pg C out of  $\Delta GPP^{eCO_2} = 974 \pm 76$  Pg C) (Figure 8). This increase in respiration is due to both autotrophic respiration ( $\Delta R_a^{eCO_2} = 460 \pm 46$  Pg C) and heterotrophic respiration ( $\Delta R_h^{eCO_2} = 315 \pm 28$  Pg C) rising significantly. This large respiration response to CO<sub>2</sub>-fertilization-driven increases in photosynthesis is consistent with observations at site-scale free-air carbon dioxide enrichment (FACE) studies, which have found that elevated atmospheric CO<sub>2</sub> concentrations lead to increases in soil respiration (King et al., 2004). By contrast, FACE studies find only mixed evidence for significant increases in soil organic matter (Hungate et al., 2009; Norby & Zak, 2011), which is consistent with our result that a large portion of stimulated photosynthesis is ultimately respired rather than stored in carbon pools.

The increase in respiration in the eCO<sub>2</sub> scenario ( $\Delta R_{eco}^{eCO_2} = 774 \pm 72$  Pg C) is large relative to that of the Total scenario ( $\Delta R_{eco}^{total} = 1074 \pm 52$  Pg C), suggesting that most of the attributable respiration increase is due to increases in the magnitude of respiring carbon pools, rather than climate-driven increases in respiration rates. The importance of plant growth to changes in respiration over long periods of time in our experiments is consistent with observations of both a tight coupling between GPP and respiration across space and a strong relationship between interannual variations in GPP and respiration in flux tower observations (Baldocchi, 2008; Dusenke et al., 2019; Fernández-Martínez et al., 2014). The high respiration

response to plant growth is driven by both autotrophic ( $\Delta R_a^{total} = 595 \pm 33$  Pg C) and heterotrophic respiration ( $\Delta R_h^{total} = 481 \pm 21$  Pg C) in both the total and eCO<sub>2</sub> scenarios.

The dominance of the respiration response to carbon inputs alone, rather than to soil warming for example, highlights how the baseline (unmodified by climate) turnover times of different carbon pools play a large role in determining how much of the increased plant growth will stay in the ecosystem and the ultimate net carbon sink. These baseline turnover rates are set by many processes, including allocation of carbon between different plant pools with different respiration rates and microbial effects on heterotrophic respiration. This emphasizes the need for global carbon cycle studies to consider how the base turnover rates of different respiration pools are calibrated across the globe, not just their extensively-studied climatic sensitivities e.g. (Mahecha et al., 2010; Nottingham et al., 2020).



**Figure 9:** Distribution of cumulative per area change in  $\Delta GPP^{total}$  (a, c, e, g) and  $\Delta NEP^{total}$  (b, d, f, h). Note:  $NEP = - NEE$ . Carbon flux change by region attributed to the Total forcing (i.e., Total – Control) which includes both increasing  $CO_2$  and changing climate. Darker shading corresponds to 5<sup>th</sup> – 95<sup>th</sup> percentile and 25<sup>th</sup> – 75<sup>th</sup> percentile of distributions due to both parameter and climate spread. Note that the y-axis is the same scale for all subplots in each column.

### 3.4 Respiration response to CO<sub>2</sub> shapes regional balance of the net carbon flux

The changes in carbon sinks from rising CO<sub>2</sub> concentrations and changing climate vary across regions due to both spatial variation in enhanced carbon input (GPP) (Figure 9) and the respiration response. It is not surprising that the wet tropics, the region with the highest GPP on Earth (Badgley et al., 2019), also has the largest GPP increase due to enhanced CO<sub>2</sub>. However, even though the greatest increase in ecosystem carbon input (GPP) is in the wet tropics, the total attributed  $\Delta NEP^{total}$  is largest in the temperate region ( $17.8 \pm 0.7$  Mg C/ha). This increase in the temperate carbon sink per unit area is larger than that in the wet tropics ( $14.2 \pm 1.1$  Mg C/ha), about twice as large as in the boreal ( $7.9 \pm 1.0$  Mg C/ha) and in the dry tropics ( $11.6 \pm 0.9$  Mg C/ha) (Figure 9). Thus, the net carbon sink in the temperate region has increased more than the net carbon sink in the wet tropics, despite GPP increasing more in the wet tropics ( $\Delta GPP^{total} = 133.5 \pm 15.5$  Mg C/ha for wet tropics and  $\Delta GPP^{total} = 92.8 \pm 4.6$  Mg C/ha for temperate). Independent atmospheric inversions for net carbon flux also find a strong carbon sink in the present-day temperate region compared to the nearly neutral tropics (Byrne et al., 2020; Gaubert et al., 2019). This geographic mismatch between the largest increase in GPP and largest increase in the carbon sink demonstrates the importance of respiration dynamics in determining the carbon balance of an ecosystem.

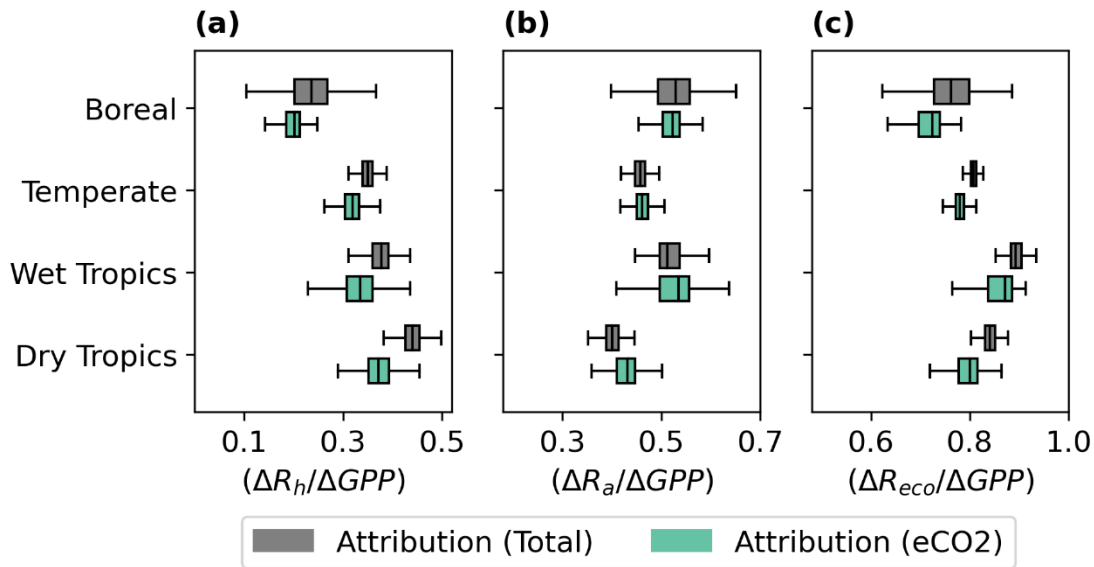
We can quantitatively summarize the response of the ecosystem to increased carbon input as the amount of new carbon lost compared to the increased carbon input, or the “loss ratio of carbon gained” ( $\Delta R / \Delta GPP$ ). Note that the loss ratio of carbon gained is a distinct quantity from the ratio between total  $R_{eco}$  and GPP in historical fluxes (Baldocchi, 2008), as it reflects the response to added carbon input, rather than to total carbon input. As future ecosystem dynamics respond to climate change and increasing atmospheric CO<sub>2</sub> concentrations, the loss ratio of

carbon gained tracks how well they will serve as a sink in comparison to changes in carbon input. The  $(\Delta R_{eco}/\Delta GPP)^{total}$  changes significantly across regions (Figure 10). It is highest in the wet tropics ( $89 \pm 1\%$ ), where the highest portion of increased GPP is lost to respiration. It is lowest in the boreal region ( $76 \pm 4\%$ ), such that more of the increased GPP remains stored in boreal ecosystems than in other regions. Both the temperate ( $81 \pm 0.5\%$ ) and dry tropics ( $84 \pm 1\%$ ) regions have values between the boreal and wet tropics. Across regions, the loss ratios of carbon gained in the Total scenarios are only a few percentage points larger than the equivalent values in the eCO<sub>2</sub> scenario, which does not experience climate change (Figure 10). The small change due to climate change shows that the loss ratio of carbon gained is primarily set by the base turnover rates in different regions, rather than changes in the turnover rates due to their climatic sensitivities.

The loss ratio of carbon gained due to heterotrophic respiration varies more between regions (e.g., from  $44 \pm 1.5\%$  in the dry tropics to  $24 \pm 3.4\%$  in the boreal) than that due to autotrophic respiration, which varies no more than 12 percentage points across regions (Figure 10). Thus, spatial variations in the loss ratio of carbon gained are primarily driven by spatial patterns of the heterotrophic respiration's loss ratio of carbon gained (i.e.  $(\Delta R_h/\Delta GPP)^{total}$ ), rather than by that for autotrophic respiration (Figure 10). The higher heterotrophic respiration responses to enhanced CO<sub>2</sub> in tropical regions offsets the much larger response of GPP to CO<sub>2</sub> fertilization in the (wet) tropics, dropping the attributable net carbon flux below that of other regions. Note that our finding that the relatively large enhancements of CO<sub>2</sub> in the wet tropics translate to greater heterotrophic respiration fluxes is consistent with isotopic evidence from the flanks of two Costa Rican volcanoes, which are exposed to higher CO<sub>2</sub> concentrations. In these areas a strong relationship was found between trees with high xylem concentrations of CO<sub>2</sub> –

suggesting higher CO<sub>2</sub> fertilization – and higher nearby soil respiration fluxes (Bogue et al., 2019).

This study is the first to explicitly compare the amount of additional carbon fluxes across regions. The pattern of spatial variability in the loss ratio of carbon gained has significant consequences for the land carbon sink. While the increase in wet tropical GPP attributable to climate change and CO<sub>2</sub> is 1.4 – 4.0 times higher than in other regions, the high loss ratio of carbon gained causes the wet tropical gain in NEP to be only 0.8 – 1.8 times higher than that of other regions. This suggests a more limited regional importance for the wet tropics than would be apparent if only photosynthesis CO<sub>2</sub> fertilization rates were considered. Additionally, if it can be further supported, the finding of a particularly high respiration response to CO<sub>2</sub> fertilization in the wet tropics, driven by both soil and plant respiration rates, could be a useful constraint for understanding the net carbon flux of undisturbed tropical forests, particularly since they are under-represented in most in situ observational networks (Bond-Lamberty & Thomson, 2018; Jian et al., 2020; Schimel et al., 2015).



**Figure 10:** Ranges for the loss ratio of carbon gained ( $\Delta R/\Delta GPP$ ) for a) heterotrophic respiration, b) autotrophic respiration, and c) ecosystem respiration. Larger values mean more carbon lost to the atmosphere. Gray denotes Total run minus Control and green denotes elevated  $CO_2$  run minus Control. Vertical line is the median, colored box is the 25<sup>th</sup> – 75<sup>th</sup> range, and whiskers are the 5<sup>th</sup> to 95<sup>th</sup> range. Note that the x-axis is not the same scale for all subplots.

### 3.5 Strong relationship between respiration and GPP constrained by observations

CARDAMOM-derived loss ratios of carbon gained show reasonably high overlap with those from land surface models included in the TRENDY V9 S2 experiment. This holds true for each of the cases where either the total, heterotrophic, or autotrophic respiration is considered – though TRENDY generally has a higher loss ratio of carbon gained for autotrophic respiration and thus total respiration (Figure 11). This similarity occurs despite the disagreement between CARDAMOM and TRENDY in the mean GPP magnitude and the sensitivity of GPP to increasing  $CO_2$  (Figures 4, 7), and despite the very different inputs used to parameterize

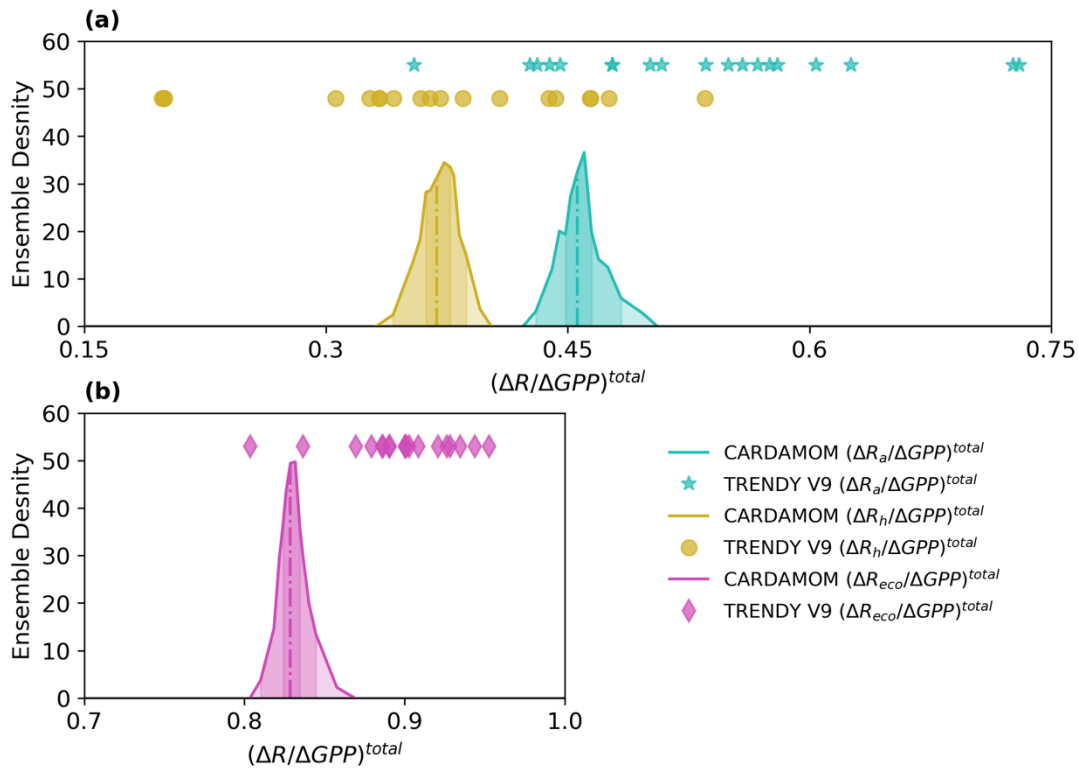
CARDAMOM and TRENDY (i.e. parameters derived from observations in CARDAMOM, using plant functional types in TRENDY). This similarity is likely due to the similar process representations of carbon allocation and respiration in the two ensembles. However, the uncertainty across the TRENDY models is considerably larger than that of the observationally-constrained CARDAMOM ensemble.

The CARDAMOM loss ratio of carbon gained varies within a few percentage points at regional and global scales (Figures 10, 11). Put another way, there is a strong proportional relationship between the  $\Delta GPP^{total}$  and the  $\Delta R_{eco}^{total}$ ,  $\Delta R_a^{total}$ , and  $\Delta R_h^{total}$  (as well as in the eCO<sub>2</sub> and Climate scenarios, not shown). This strong relationship echoes a previous finding by Hajima et al. (2014), who found a tightly constrained ratio of changes in heterotrophic respiration to net primary productivity in response to climate change and enhanced atmospheric concentrations of CO<sub>2</sub> in Earth System Models. Overall, the loss ratio of carbon gained may be a useful additional constraint on model representations of carbon cycle responses to global change, particularly given the large remaining uncertainties in the magnitude of global fluxes of respiration (Bond-Lamberty, 2018; Jian et al., 2022) and GPP (Badgley et al., 2019; Welp et al., 2011),.

Nevertheless, the tightly constrained nature and value of the loss ratio of carbon gained are subject to the uncertainties in the CARDAMOM system (as further discussed in Sec. 3.6 below) that will require further validation, ideally across different assimilation systems driven by observational data. These could include, e.g. other data assimilation systems (Fox et al., 2018; Peylin et al., 2016; Smith et al., 2020), or CARDAMOM runs with alternative observational constraints. For example, studies using radiocarbon have found that most carbon cycle models simulate unrealistically young median ages of soil C (Shi et al., 2020), suggesting our simulation and related studies would benefit from the explicit assimilation of radiocarbon observations.



Overall, as more and longer time series of observations become available, CARDAMOM and other data assimilation systems have the potential to further constrain the loss ratio of carbon gained.



**Figure 11:** The global distributions of loss ratio of carbon gained ( $\Delta R^{total} / \Delta GPP^{total}$ ) for a) heterotrophic respiration ( $R_h$ ) and autotrophic respiration ( $R_a$ ), and b) the ecosystem respiration ( $R_{eco}$ ) over GPP. Points are the same ratio for individual TRENDY V9 models (Friedlingstein et al., 2020). Darker shading in the histograms for CARDAMOM distributions is for the 5<sup>th</sup> – 95<sup>th</sup> and 25<sup>th</sup> – 75<sup>th</sup> range. Note that the y-axis is the same scale for both subplots.

### 3.6 Uncertainties in *CARDAMOM* flux estimates

A number of relevant terrestrial carbon cycle processes are not explicitly represented in *CARDAMOM*, adding uncertainty to the above results. These include soil priming (van Groenigen et al., 2014), changes in microbial biomass (Wieder et al., 2013), lateral carbon flux (Regnier et al., 2013) and vegetation demography (Fisher et al., 2018). *CARDAMOM* uses relatively simplistic treatments of autotrophic respiration (proportional to photosynthesis with spatially variable carbon use efficiency) and heterotrophic respiration (using just two pools, litter and soil organic matter). Temporally variable nutrient limitations are also not represented, though spatial variability in nutrient limitations can be partially accounted for through reduced  $V_{\text{cmax25}}$  values. Past attribution studies using conventional model ensembles have found a significant effect from including the nitrogen cycle by lowering the carbon gained due to increased atmospheric concentrations of  $\text{CO}_2$  (Huntzinger et al., 2017), lowering accumulation of soil carbon (Huntingford et al., 2022), and nutrient deposition impacts on photosynthesis (Schwalm et al., 2020). However, note that Chen et al. (2019) found that accounting for nitrogen deposition only mildly enhanced the simulated NEP since 1981 (Chen et al., 2019).

Another key source of uncertainty in this study is the fact that *CARDAMOM* does not explicitly represent land use and land cover change (LULCC). Because a model without an explicit LULCC representation is assimilating observations that are influenced by the true historical LULCC, the *CARDAMOM*-retrieved parameters (and the associated carbon pools and fluxes) are likely to partially reflect historical LULCC. The lack of sub-grid scale heterogeneity in vegetation type in *CARDAMOM* makes it difficult to simulate LULCC. However, a sensitivity analysis can be performed by altering simulated burned area patterns to mimic land cover changes due to LULCC. When tested for several representative locations, this sensitivity

analysis did not lead to any systematic change in the loss ratio of carbon gained, nor any other significant qualitative changes to the results discussed above (not shown). This suggests that the key qualitative conclusions of this manuscript are robust to LULCC effects, consistent with Schwalm et al. (2020), who found LULCC to be a relatively minor factor affecting GPP over the last century, and much smaller than CO<sub>2</sub> fertilization. Nevertheless, our sensitivity analyses were performed only on a small number of representative pixels and do not fully capture the potential effects of LULCC, which adds some uncertainty to our results.

CARDAMOM's advantage relative to conventional terrestrial biosphere model ensembles is not that it has an inherently more accurate ecosystem respiration representation, but that the observational constraints allow an exploration of the dynamics of carbon fluxes that is not dependent on *a priori* assumptions of the magnitude of the climatic sensitivities or base turnover times of various respiring carbon pools. Because dynamic net biome exchange and a snapshot of carbon stocks are assimilated into CARDAMOM (along with other observations such as SIF and LAI, and uncertainty accounting), turnover and respiration parameters can be explicitly constrained. This constraint is dependent in part on the observational uncertainty assumed. Although data assimilation systems can suffer from equifinality issues that can limit the utility of the assimilation outside the observational period, CARDAMOM's ecological and dynamic constraints (Bloom & Williams, 2015) and intermediate structural complexity (Famiglietti et al., 2021) help to reduce such equifinality. Thus, turnover should be more accurately constrained (see Figure 5) than in past prognostic models that use only information about vegetation states (e.g. Chen et al., (2019), Melnikova & Sesai, (2020)).

Despite the above limitations, previous research has shown that CARDAMOM is capable of representing ecosystem temporal dynamics similar to those of more structurally complex

conventional carbon cycle models (See Figure 6, 7 and 8 in Quetin et al. (2020)). In effect, CARDAMOM's explicit treatment of parameter uncertainty allows it to partially compensate for the added structural uncertainty compared to more complex models. As such, and based on the reasonable match to observations discussed in Text S3 and Sec 3.1, we expect the qualitative conclusions of our attribution calculations above to be robust.

#### **4. Conclusions**

We used data assimilation in CARDAMOM to attribute change in the terrestrial carbon cycle in response to enhanced atmospheric concentrations of CO<sub>2</sub> and climate change over the past century. Our analysis allowed for the retrieval of a parameters, including initial conditions, that are consistent with present-day observations of the carbon cycle at each grid point. This approach avoids the assumed spin-up to equilibrium that is common in other modeled projections of the carbon cycle, and estimates carbon cycle dynamics based on ecosystem observations rather than broad distributions of plant functional types.

The response of the carbon cycle is dominated by increased plant growth due to CO<sub>2</sub> fertilization across the globe and all regions. We identify the largest per area increase of GPP to be in the wet tropics, and the largest per area carbon sink to be in the temperate region. The location of the largest net carbon sink region per area is due the combination of large increases in plant growth with a relatively low 'loss ratio of carbon gained' in the temperate region compared to the more productive wet tropics. While the increase in wet tropical GPP is 1.4 – 4.0 times higher than in other regions, the wet tropical gain in NEP is only 0.8 – 1.8 times higher, because respiration fluxes are so much more responsive than in other regions even without considering changes in soil temperature.

The global loss ratio of carbon gained (globally,  $83 \pm 0.6\%$ ) across the CARDAMOM ensemble's range of parameters is much less uncertain than the range of GPP increase, and accounts for the majority of increased productivity respired to the atmosphere. A significant portion of the loss ratio of carbon gained is due to heterotrophic respiration as a response to increased plant growth. This suggests that the base turnover rates of an ecosystem – rather than the sensitivity of those turnover rates to climate change – is the dominant driver of how much of and where the carbon fixed by enhanced CO<sub>2</sub> is stored in ecosystems under past and near-term climate change.

## **Acknowledgments, Samples, and Data**

GRQ, KWB, AAB and AGK were supported by NASA NNH16ZDA001N-IDS. GRQ and AGK were also supported by NSF DEB-1942133. GRQ was also supported by NSF Grant 2003205. NSD acknowledges support from Stanford University. Part of this work was carried out at the Jet Propulsion Laboratory, California Institute of Technology, under a contract with the National Aeronautics and Space Administration.

ATT acknowledges funding from the NSF Grants 2003205 and 2017949, the USDA National Institute of Food and Agriculture, Agricultural and Food Research Initiative Competitive Programme Grant No. 2018-67012-31496 and the University of California Laboratory Fees Research Program Award No. LFR-20-652467. All CARDAMOM datasets presented in this analysis are available on figshare ([10.6084/m9.figshare.19952315](https://figshare.com/10.6084/m9.figshare.19952315), [10.6084/m9.figshare.19952246](https://figshare.com/10.6084/m9.figshare.19952246), [10.6084/m9.figshare.19951928](https://figshare.com/10.6084/m9.figshare.19951928)), as well as the analysis script ([10.6084/m9.figshare.21545547](https://figshare.com/10.6084/m9.figshare.21545547)) and CARDAMOM code ([10.6084/m9.figshare.21834501](https://figshare.com/10.6084/m9.figshare.21834501)). All other datasets used are publicly available (see Methods).

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