Title:

A constraint on historic growth in global photosynthesis due to rising CO_2

Authors: Keenan, T.F.[1,2*], Luo, X.[1,2], De Kauwe, M. G. [3,4,5], Medlyn, B.E.[6], Prentice, I.C.[7,8,9], Stocker, B. D.[10, 11], Smith, N.G.[12], Terrer, C.[13], Wang, H.[9], Zhang, Y. [1,2,14], Zhou, S.[1,2,15,16,17,18]

Affiliations:

[1] Department of Environmental Science, Policy and Management, UC Berkeley, Berkeley, CA, 94720 USA

[2] Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, 1 Cyclotron Road, Berkeley, CA 94720, USA

[3] ARC Centre of Excellence for Climate Extremes, Sydney, NSW 2052, Australia

[4] Climate Change Research Centre, University of New South Wales, Sydney, NSW 2052, Australia

[5] School of Biological Sciences, University of Bristol, Bristol, BS8 1TQ, UK

[6] Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW 2753, Australia

[7] Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, UK

[8] Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

[9] Department of Earth System Science, Tsinghua University, Haidian, Beijing, 100084, China

[10] Department of Environmental Systems Science, ETH, Universitätsstrasse 2, 8092 Zürich, Switzerland.

[11] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

[12] Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA

[13] Physical and Life Sciences Directorate, Lawrence Livermore National Laboratory, Livermore, CA, USA

[14] Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing, China

[15] Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY, USA

[16] Earth Institute, Columbia University, New York, NY, USA

[17] Department of Earth and Environmental Engineering, Columbia University, New York, NY, USA

[18] State Key Laboratory of Earth Surface Processes and Resources Ecology, Faculty of Geographical Science, Beijing Normal University, Beijing, China

[*] Corresponding author: trevorkeenan@berkeley.edu

Abstract

The global terrestrial carbon sink is increasing[1–3], offsetting roughly a third of anthropogenic CO_2 released into the atmosphere each decade[1], and thus serving to slow the growth rate of atmospheric CO_2[4]. It has been suggested that a CO_2-induced long-term increase in global photosynthesis, a process known as CO_2 fertilization, is responsible for a large proportion of the current terrestrial carbon sink[4–7]. The estimated magnitude of the historic increase in photosynthesis as result of rising atmospheric CO_2 concentrations, however, differs by an order of magnitude between long-term proxies and terrestrial biosphere models[7–13]. Here, we quantify the historic effect of CO_2 on global photosynthesis, by identifying an emergent constraint[14–16] that combines terrestrial biosphere models with global carbon budget estimates. Our analysis suggests that CO_2 fertilization increased global annual photosynthesis by 11.85±1.4%, or 13.98±1.63 Pg C (mean ± 95% confidence interval) between 1981 and 2020. Our results help resolve conflicting estimates of the historic sensitivity of global photosynthesis to CO_2, and highlight the large impact anthropogenic emissions have had on ecosystems worldwide.

Main

Globally, photosynthesis results in the single largest flux of carbon dioxide (CO_2) between the atmosphere and the biosphere[17,18]. Long-term changes in photosynthesis, for example in response to rising atmospheric CO_2, could therefore provide an important feedback to climate change[7]. Global photosynthesis cannot be observed directly, however, and must instead be either predicted by terrestrial biosphere models (TBMs) or inferred from proxies[18]. The multiple long-term proxies from which changes in global photosynthesis are derived include satellite-based estimates[8,9], ice-core records of carbonyl sulfide[13], and herbarium samples of deuterium isotopomers[12], along with information gleaned from the seasonal cycle of atmospheric CO_2[11]. Despite the importance of photosynthesis, however, and the multiple proxies that exist, there is no consensus regarding the expected historic global change due to rising CO_2[7–13].

Satellite-based estimates of global photosynthesis are derived from observations of surface reflectance, and are therefore often regarded as a benchmark to which TBMs should be compared[10]. Such comparisons suggest that TBMs overestimate the sensitivity of global photosynthesis to CO_2[9,10] (but see ref.[19]). However, satellite-TBM comparisons are mired by the fact that most satellite-based estimates do not incorporate the universally observed direct effect of increasing CO_2 on the light use efficiency of leaves of C_3 vegetation[20], which is not observable from space[21]. In contrast, observation-based proxies, based on ice-core records of carbonyl sulfide (COS)[13,22] and herbarium and field-based deuterium isotopomers[12], suggest that TBMs may underestimate the sensitivity of global photosynthesis to CO_2. TBMs themselves exhibit a large range of sensitivities of global photosynthesis to CO_2[11,23,24], though few demonstrate sensitivities as low as the average satellite-inferred values[9,21], or as high as those derived from the COS or deuterium proxies[12,13,24]. The spread in estimates of the sensitivity of global photosynthesis to CO_2, and the lack of a global constraint, constitutes a large source of uncertainty in future projections of the Earth system[25], and hinders attribution of the various processes responsible for long-term changes in the global carbon cycle.

Here, we combine terrestrial biosphere models and estimates of the terrestrial carbon cycle to constrain the historic response of photosynthesis to rising CO_2, and use the constraint in combination with biophysical theory to assess and reconcile differences in previous reports. Our analysis uses a variance normalization approach (see methods), which quantifies underlying relationships in multi-variate space, to identify an emergent multi-model relationship[14–16] between the modeled sensitivity of photosynthesis to CO_2 and the terrestrial carbon sink from an ensemble of terrestrial biosphere models (TBMs). When combined with independent estimates of the global terrestrial carbon sink, this relationship provides an emergent constraint[14–16], which we use to derive an observationally-inferred estimate of the historic effect of increasing CO_2 on global gross primary photosynthesis (GPP). Combined with biophysical theory, the inferred constraint helps to reconcile the large apparent difference between satellite- and TBM-inferred sensitivities of GPP to CO_2, and to examine previously published estimates from global GPP proxies.

To identify the emergent multi-model relationship[14–16] between the modeled terrestrial carbon sink and the sensitivity of photosynthesis to CO_2, we use output from an ensemble of TBMs from the Trends in Net Land Atmosphere Carbon Exchanges project (TRENDY, Extended Data Table 1[3]). We first described the magnitude of the mean TBM modeled global terrestrial residual carbon sink (S_{LAND}) over the period 1982-2012 as a function of the sensitivity of both GPP and total global ecosystem respiration (Reco) to CO_2 ($\beta_{\mathrm{R}}^{\mathrm{GPP}}$, $\beta_{\mathrm{R}}^{\mathrm{Reco}}$, Eq. 1), and an interaction term between $\beta_{\mathrm{R}}^{\mathrm{Reco}}$ and the magnitude of modeled global ecosystem carbon losses that are not respired (i.e., the non-respired flux, γ). Note that we focus on S_{LAND} in order to exclude land carbon sinks or sources directly resulting from land use and land-use change (e.g., regrowth of vegetation, deforestation). A positive univariate relationship between $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ and S_{LAND} explained 36% of the between-model variability in TBM estimates of mean annual S_{LAND} ($p = 0.03$; Extended Data Fig. 1). A linear model that also includes $\beta_{\mathrm{R}}^{\mathrm{Reco}}$ and γ, however, explained 94% of the between-model variability in TBM estimates of mean annual S_{LAND} ($p < 0.01$, Extended Data Fig. 2, Extended Data Table 2). TBM sensitivities of photosynthesis and respiration to CO_2 thus directly relate to the magnitude of the modeled terrestrial sink on a multi-decadal scale (as a stronger CO_2 fertilization effect leads to a larger modeled sink), suggesting a comparatively smaller influence of non-CO_2 changes (e.g., climate, N deposition) on S_{LAND} at the global and multi-decadal scale over the period[6,26]. The linear model (Extended Data Table 2) can be used to remove variance in the $\beta_{\mathrm{R}}^{\mathrm{GPP}} \sim S_{\mathrm{LAND}}$ relationship (Extended Data Fig. 1) that is associated with other factors, allowing us to focus on the underlying partial relationship between $\beta_R^{GPP} \sim S_{LAND}$. The resulting emergent relationship[14–16] therefore provides an opportunity to constrain the wide range in estimates of the sensitivity of GPP to CO_2 using the magnitude of S_{LAND} inferred from the global carbon budget[1].

We use the identified relationship between β_R^{GPP}, β_R^{Reco} and γ with S_{LAND} (Extended Data Fig. 2) to examine the underlying relationship between β_R^{GPP} and S_{LAND}. First, we used the linear model (Extended Data Table 2) to remove variance in the univariate $\beta_R^{GPP} \sim S_{LAND}$ relationship contributed by β_R^{Reco} and γ. Following this variance normalization, which adjusts the TBM modeled S_{LAND} to account for variance introduced by modeled β_R^{Reco} and γ (see Methods), S_{LAND} estimated from the Global Carbon Project (v6[27]) provides an emergent constraint on β_R^{GPP} of 0.54±0.03 (mean, standard dev.; Fig. 1a). The constrained CO_2 sensitivity of photosynthesis is 33.58% lower than the maximum TBM ensemble member, and 7.63% lower than the TBM ensemble mean. The associated uncertainty of the estimate is reduced by 73.90% compared to the unconstrained TBM model distribution (Fig. 1b). Considering present atmospheric CO_2 concentrations (416 ppm, 2020 A.D.), the constrained β_R^{GPP} translates to an increase of 11.85±0.71% in annual GPP between 1982 and 2020, equivalent to a 13.98±0.83 Pg C increase from 1982 to 2020 (using as reference the mean 1982 model GPP of 118 Pg C yr^{-1} from TRENDY-v6 S3). Note that although the magnitude of S_{LAND} is higher for more recent than earlier decades, the constrained β_R^{GPP} is robust to such changes and relatively independent of the period examined (Extended Data Fig. 4).

Although the linear model does not provide a direct constraint on β_R^{Reco}, due to the interaction term with γ, there is a strong correlation ($r^2 = 0.96$, Fig. 1c) between β_R^{GPP} and β_R^{Reco}, as photosynthesis and respiration are highly coupled across ecosystems. This coupling can therefore provide an indirect constraint on β_R^{Reco} (Fig. 1c). The resulting joint probability distribution of β_R^{Reco} of 0.49±0.04 is 39.44% lower than the maximum TBM ensemble member and 4.57% lower than the ensemble mean. The associated uncertainty of the estimate represents a 68.35% reduction compared to the unconstrained model distribution (Fig. 1d). Note that the resulting constraint on $\beta_{\mathrm{R}}^{\mathrm{Reco}}$ is subject to higher uncertainty due to the propagation of the uncertainty of the constrained $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ through to the joint probability distribution of $\beta_{\mathrm{R}}^{\mathrm{Reco}}$ (Fig. 1d).

The identified emergent constraint provides a point of comparison for satellite-based estimates of the sensitivity of global photosynthesis to CO_2, the analysis of which has led to reports that TBMs greatly overestimate the effect of increasing CO_2 on global photosynthesis[9,10]. When examined as a function of CO_2, satellite-based estimates of $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) GPP algorithm (MA)[28] and a widely used machine learning upscaling approach (ML)[29], are 68.95% and 69.82% lower than that inferred from the emergent constraint, respectively (Fig. 2). These commonly used GPP estimates however only account for the indirect effect of increasing CO_2 on the fraction of absorbed photosynthetically active radiation (fAPAR)[21].

We reconciled the apparent difference between the emergent constraint and satellite-based estimates of the sensitivity of GPP to CO_2 (Fig. 2) by modifying the satellite-based estimates to account for the direct effect of increasing CO_2 on C_3 light use efficiency (LUE). This direct effect reflects the competition between CO_2 and O_2 at the active sites of the RuBisCO enzyme, and the increasing competitiveness of CO_2 as atmospheric CO_2 rises (see methods). The direct effect of CO_2-induced increases in LUE was roughly twice as large as the indirect effect of increases in fAPAR (Fig. 2a,b). The long-term sensitivity of the remote sensing-based estimates of GPP modified to account for both the direct (β_{R}^{LUE}) and indirect ($\beta_{\mathrm{R}}^{fAPAR}$) effect of increasing CO_2 ($\beta_{\mathrm{R}}^{\mathrm{GPP}}$) was 0.50±0.09 and 0.46±0.13 for the ML and MA approaches, respectively, (Fig. 2b), which more closely approximated that of the TBM ensemble mean ($\beta_{\mathrm{R}}^{\mathrm{GPP}}$= 0.59±0.15, mean, std.) (Fig. 2b). The modified RS-based methods predict a 7.27±0.69% (ML) and 6.72±0.91% (MODIS) increase in global annual GPP for a 14.49% increase in atmospheric CO_2 between 1982 and 2012, similar to that predicted by the constrained $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ (7.8±0.41% mean, std.).

The identified emergent constraint also provides a point of comparison for other reported estimates of the sensitivity of global photosynthesis to CO_2. A long-term COS proxy has been proposed[13], which simulates photosynthetic change based on a mass balance of global COS sources and sinks from 1900 to 2013, and suggests an increase in photosynthesis equivalent to an effective β_R^{GPP} of 0.94 (Extended Data Table 3). This is comparable to the highest sensitivity of the TBM models used here[24]. The COS estimate however integrates over a longer time-period, and therefore potentially captures changes in the land surface unrelated to CO_2 such as reforestation and the agricultural green revolution[30] and is thus not directly comparable to the emergent constraint and updated remote sensing estimates presented here. Another proxy, based on deuterium isotopomers gathered from herbarium specimens and field trials[12], suggests a historic change equivalent to a β_R^{GPP} of 1.03. Although higher than that derived from COS, the deuterium isotopomer estimate reflects the effect of increasing CO_2 on photosynthesis in the absence of light limitation, and is thus expected to be much higher than the canopy integrated sensitivity. The emergent constraint identified here and the updated satellite methods suggest that such larger implied sensitivities are overestimates, as they would necessitate a larger residual terrestrial sink (Fig. 1a) than current evidence supports[1].

The closer agreement between the updated remote sensing approaches and the TBMs (Fig. 2) allows for their response to CO_2 to be probed more deeply. The sensitivity of C_3 photosynthesis to CO_2 is a strong function of temperature[31] (Fig. 3a; Eq. 2-7), due to the fact that the suppression of oxygenation by ribulose-1,5-bisphosphate carboxylase-oxygenase (RuBisCO) with increasing CO_2 is greater at higher temperatures. Reduced RuBisCo oxygenation reduces photorespiration at high temperatures, as represented by the temperature dependence of the photosynthetic CO_2 compensation point (Γ^*, Eq. 3). The resulting latitudinal gradient is reproduced by both the TBMs examined (Fig. 3b) and the updated remote sensing approaches (Fig. 3c,d,e). The results suggest that the influence of CO_2 on photosynthesis at high latitudes is limited due to low temperatures. Estimates of the long-term change in GPP from the updated remote sensing approaches show large changes particularly in areas of intensive agriculture such as the midwestern US corn belt, central and northern Europe, and India (Fig. 3c, d). Compared to the remote sensing approaches (Fig. 3d), the TBMs predict smaller increases in arid mid- and low-latitude regions, particularly in Australia and South Africa, but larger increases in tropical forests (Fig. 3d). The lower TBM sensitivity, in particular of shrublands (Fig. 3f), is potentially due to poorly represented TBM processes such as the positive relationship between CO_2 and woody shrub expansion[32]. The relatively higher TBM sensitivity regions, particularly tropical forests (Extended Data Fig. 5), may be due to insufficient TBM representation of nutrient constraints[33], or the saturation of remote sensing vegetation indices at high leaf area[34], reflecting large uncertainty regarding the response of tropical forest photosynthesis to CO_2[35].

The magnitude of the constrained TBM and updated satellite $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ suggests that the global photosynthetic response to CO_2 is consistent with the response of the light-limited photosynthetic rate which has also been suggested by observations of photosynthesis and biomass changes at the ecosystem scale[36–38], theoretical models[39,40], and by model results showing that electron transport-limited leaves are responsible for the majority of global carbon assimilated through photosynthesis[41]. That said, there are multiple processes inadequately represented in both TBMs and the satellite approaches that could lead to biases in the derived $\beta_{\mathrm{R}}^{\mathrm{GPP}}$. For example, models have been shown to poorly reproduce changes in the seasonal cycle of atmospheric CO_2[42], and demonstrate a range of responses when compared to Free Air CO_2 Enrichment observations[43]. Nutrient limitation, woody encroachment, soil moisture feedbacks, disturbances and leaf area dynamics are all poorly represented in TBMs[43,44], while remote sensing-based estimates of GPP are known to have biased responses to drought[45]. Such issues and differences in process representations lead to the spread in models. However, this spread is essential for developing an emergent constraint[16].

A strong emergent relationship between the unknown and the observable (in this case photosynthesis and the recent land carbon sink) would not be apparent if ignored and varying model factors affect the relationship. It is important to highlight, however, as with any application of the emergent constraint technique, multiple factors could lead to biases and undermine the robustness of the derived constraint. Of primary concern is the potential for emergent constraints to rely on spurious cross-model correlations that are not based on a clear physical relationship[46]. The constraint we identify is based on the known relationship between CO_2 and the land-sink[7], and tests suggest it is temporally robust (Extended Data Fig. 4). An additional source of uncertainty relates to the degree of structural similarity between models and the potential for systematic cross-model biases. For example, if all models in the ensemble had the same missing or biased process representation, which led to systematic bias in the modeled relationship between the sensitivity of photosynthesis to CO_2 and the land sink across models, that could bias the emergent constraint reported here. Systematic cross-model biases with shared structural similarity could also lead to an underestimation of the uncertainty associated with the values derived from the emergent constraint[46,47]. The models we examine represent the state-of-the-science for land surface modeling, and have substantial diversity of process representations and responses to forcings[48], even for well-studied processes such as photosynthesis. Our analysis is also designed to reduce the influence of structural diversity on the results through variance normalization. That said, future implementations of new process representations or model structures may lead to updated inference on the response of photosynthesis to CO_2.

Global photosynthesis is the largest flux of carbon dioxide in the global carbon cycle, and small changes over time can lead to large changes in the net carbon sink. The resulting feedback from the effect of increasing CO_2 on photosynthesis (the carbon-concentration feedback) has been estimated to be over four times larger, and more uncertain, than the direct carbon-climate feedback[49]. The large differences between estimates of historic changes in GPP[8,9,11–13,22] is therefore disconcerting, and could potentially lead to incorrect inference regarding biases in current terrestrial biosphere models[9,21], and long-term changes in related components of the global carbon cycle such as soil respiration[10,50]. The emergent constraint we identify bounds the plausible range of the historic effect of CO_2 on global photosynthesis to a $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ of 0.54±0.03 (mean, standard dev.; Fig. 1a), and helps reconcile differences in previous estimates. The results also show that widely used remote sensing-based estimates of global photosynthesis need to incorporate the effect of increasing CO_2 on photosynthetic light use efficiency, and provide a globally applicable approach that is consistent with the emergent constraint. Together, our results suggest that increases in atmospheric CO_2 have led to a large increase in global photosynthesis since 1982, representing a carbon-concentration feedback that is underestimated by standard satellite-based methods[9], but overestimated by terrestrial biosphere models and other proxies[12,13].

References

1 Friedlingstein P, Jones MW, O'Sullivan M, Andrew RM, Hauck J, Peters GP *et al.* Global carbon budget 2019. *Earth Syst Sci Data* 2019; **11**: 1783–1838.

2 Ballantyne AP, Alden CB, Miller JB, Tans PP, White JWC. Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* 2012; **488**: 70–72.

3 Sitch S, Friedlingstein P, Gruber N, Jones SD, Murray-Tortarolo G, Ahlström A *et al.* Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences* 2015; **12**: 653–679.

4 Keenan TF, Prentice IC, Canadell JG, Williams CA, Wang H, Raupach M *et al.* Recent pause in the growth rate of atmospheric CO2 due to enhanced terrestrial carbon uptake. *Nat Commun* 2016; **7**: 13428.

5 Schimel D, Stephens BB, Fisher JB. Effect of increasing CO_2 on the terrestrial carbon cycle. *Proc Natl Acad Sci* 2015; **112**: 436–441.

6 Huntzinger DN, Michalak AM, Schwalm C, Ciais P, King AW, Fang Y *et al.* Uncertainty in the response of terrestrial carbon sink to environmental drivers undermines carbon-climate feedback predictions. *Sci Rep* 2017; **7**: 1–8.

7 Walker AP, De Kauwe MG, Bastos A, Belmecheri S, Georgiou K, Keeling RF *et al.* Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO2. *New Phytol* 2020; : nph.16866.

8 Sun Z, Wang X, Zhang X, Tani H, Guo E, Yin S *et al.* Evaluating and comparing remote sensing terrestrial GPP models for their response to climate variability and CO 2 trends. *Sci Total Environ* 2019; **668**: 696–713.

9 Smith WK, Reed SC, Cleveland CC, Ballantyne AP, Anderegg WRL, Wieder WR *et al.* Large divergence of satellite and Earth system model estimates of global terrestrial CO2 fertilization. *Nat Clim Chang* 2016; **6**: 306–310.

10 Li W, Ciais P, Wang Y, Yin Y, Peng S, Zhu Z *et al.* Recent Changes in Global Photosynthesis and Terrestrial Ecosystem Respiration Constrained From Multiple Observations. *Geophys Res Lett* 2018; **45**: 1058–1068.

11 Wenzel S, Cox PM, Eyring V, Friedlingstein P. Projected land photosynthesis constrained by changes in the seasonal cycle of atmospheric CO2. *Nature* 2016; **538**: 499–501.

12 Ehlers I, Augusti A, Betson TR, Nilsson MB, Marshall JD, Schleucher J. Detecting long-term metabolic shifts using isotopomers: CO_2 -driven suppression of photorespiration in C_3 plants over the 20th century. *Proc Natl Acad Sci* 2015; : 201504493.

13 Campbell JE, Berry JA, Seibt U, Smith SJ, Montzka SA, Launois T *et al.* Large historical growth in global terrestrial gross primary production. *Nature* 2017; **544**: 84–87.

14 Eyring V, Cox PM, Flato GM, Gleckler PJ, Abramowitz G, Caldwell P *et al.* Taking climate model evaluation to the next level. *Nat Clim Chang* 2019; **9**: 102–110.

15 Winkler AJ, Myneni RB, Brovkin V. Investigating the applicability of emergent constraints. *Earth Syst Dyn* 2019; **10**: 501–523.

16 Hall A, Cox P, Huntingford C, Klein S. Progressing emergent constraints on future climate change. *Nat Clim Chang* 2019; **9**: 269–278.

17 Keenan TF, Williams CA. The Terrestrial Carbon Sink. *Annu Rev Environ Resour* 2018; **43**: 219–243.

18 Ryu Y, Berry JA, Baldocchi DD. What is global photosynthesis? History, uncertainties

and opportunities. *Remote Sens Environ* 2019; **223**: 95–114.
19 Winkler AJ, Myneni RB, Alexandrov GA, Brovkin V. Earth system models underestimate carbon fixation by plants in the high latitudes. *Nat Commun* 2019; **10**. doi:10.1038/s41467-019-08633-z.
20 Ainsworth EA, Long SP. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. *New Phytol* 2005; **165**: 351–372.
21 De Kauwe MG, Keenan TF, Medlyn BE, Prentice IC, Terrer C. Satellite based estimates underestimate the effect of CO2 fertilization on net primary productivity. *Nat Clim Chang* 2016; **6**: 892–893.
22 Cernusak LA, Haverd V, Brendel O, Le Thiec D, Guehl J-M, Cuntz M. Robust Response of Terrestrial Plants to Rising CO2. *Trends Plant Sci* 2019; **24**: 578–586.
23 Piao S, Sitch S, Ciais P, Friedlingstein P, Peylin P, Wang X *et al.* Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO 2 trends. *Glob Chang Biol* 2013; **19**: 2117–2132.
24 Haverd V, Smith B, Canadell JG, Cuntz M, Mikaloff-Fletcher S, Farquhar G *et al.* Higher than expected CO2 fertilization inferred from leaf to global observations. *Glob Chang Biol* 2020; **26**: 2390–2402.
25 Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, Liddicoat SK *et al.* Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *J Clim* 2014; **27**: 511–526.
26 Zhao F, Zeng N, Asrar G, Friedlingstein P, Ito A, Jain A *et al.* Role of CO2, climate and land use in regulating the seasonal amplitude increase of carbon fluxes in terrestrial ecosystems: a multimodel analysis. *Biogeosciences* 2016; **13**: 5121–5137.
27 Le Quéré C, Andrew RM, Friedlingstein P, Sitch S, Pongratz J, Manning AC *et al.* Global Carbon Budget 2017. *Earth Syst Sci Data* 2018; **10**: 405–448.
28 Running SW, Zhao M. Daily GPP and Annual NPP (MOD17A2/A3) products NASA Earth Observing System MODIS Land Algorithm - User's guide V3. 2015; : 28.
29 Jung M, Reichstein M, Margolis H a., Cescatti A, Richardson AD, Arain MA *et al.* Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. *J Geophys Res* 2011; **116**: 1–16.
30 Zeng N, Zhao F, Collatz GJ, Kalnay E, Salawitch RJ, West TO *et al.* Agricultural Green Revolution as a driver of increasing atmospheric CO2 seasonal amplitude. *Nature* 2014; **515**: 394–397.
31 Long SP. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO2 concentrations: Has its importance been underestimated? *Plant Cell Environ* 1991; **14**: 729–739.
32 Stevens N, Lehmann CER, Murphy BP, Durigan G. Savanna woody encroachment is widespread across three continents. *Glob Chang Biol* 2017; **23**: 235–244.
33 Fleischer K, Rammig A, De Kauwe MG, Walker AP, Domingues TF, Fuchslueger L *et al.* Amazon forest response to CO2 fertilization dependent on plant phosphorus acquisition. *Nat Geosci* 2019; **12**: 736–741.
34 Myneni RB, Hoffman S, Knyazikhin Y, Privette JL, Glassy J, Tian Y *et al.* Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sens Environ* 2002; **83**: 214–231.

35 Cernusak LA, Winter K, Dalling JW, Holtum JAM, Jaramillo C, Körner C *et al.* Tropical forest responses to increasing atmospheric CO2: Current knowledge and opportunities for future research. *Funct Plant Biol* 2013; **40**: 531–551.
36 Ainsworth EA, Rogers A. The response of photosynthesis and stomatal conductance to rising [CO2]: mechanisms and environmental interactions. *Plant Cell Environ* 2007; **30**: 258–70.
37 Baig S, Medlyn BE, Mercado LM, Zaehle S. Does the growth response of woody plants to elevated CO2 increase with temperature? A model-oriented meta-analysis. *Glob Chang Biol* 2015; **21**: 4303–4319.
38 Yang J, Medlyn BE, De Kauwe MG, Duursma RA, Jiang M, Kumarathunge D *et al.* Low sensitivity of gross primary production to elevated CO2 in a mature eucalypt woodland. *Biogeosciences* 2020; **17**: 265–279.
39 McMurtrie RE, Comins HN, Kirschbaum MUF, Wang YP. Modifying existing forest growth models to take account of effects of elevated CO2. *Aust J Bot* 1992; **40**: 657–677.
40 Luo Y, Sims DA, Thomas RB, Tissue DT, Ball JT. Sensitivity of leaf photosynthesis to CO2 concentration is an invariant function for C3 plants: A test with experimental data and global applications. *Global Biogeochem Cycles* 1996; **10**: 209–222.
41 Li Q, Lu X, Wang Y, Huang X, Cox PM, Luo Y. Leaf area index identified as a major source of variability in modeled CO2 fertilization. *Biogeosciences* 2018; **15**: 6909–6925.
42 Graven HD, Keeling RF, Piper SC, Patra PK, Stephens BB, Wofsy SC *et al.* Enhanced seasonal exchange of CO2by Northern ecosystems since 1960. *Science (80-)* 2013; **341**: 1085–1089.
43 Zaehle S, Medlyn BE, De Kauwe MG, Walker AP, Dietze MC, Hickler T *et al.* Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO2 Enrichment studies. *New Phytol* 2014; **202**: 803–822.
44 De Kauwe MG, Medlyn BE, Zaehle S, Walker AP, Dietze MC, Wang YP *et al.* Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO2 enrichment sites. *New Phytol* 2014; **203**: 883–899.
45 Stocker BD, Zscheischler J, Keenan TF, Prentice IC, Seneviratne SI, Peñuelas J. Drought impacts on terrestrial primary production underestimated by satellite monitoring. *Nat Geosci* 2019; **12**: 264–270.
46 Williamson MS, Thackeray CW, Cox PM, Hall A, Huntingford C, Nijsse FJMM. Emergent constraints on climate sensitivities. *Rev Mod Phys* 2021; **93**: 025004.
47 Sanderson B, Pendergrass A, Koven C, Brient F, Booth B, Fisher R *et al.* On structural errors in emergent constraints. *Earth Syst Dyn Discuss* 2021; : 1–30.
48 Fisher JB, Huntzinger DN, Schwalm CR, Sitch S. Modeling the Terrestrial Biosphere. *Annu Rev Environ Resour* 2014; **39**: 91–123.
49 Arora VK, Boer GJ, Friedlingstein P, Eby M, Jones CD, Christian JR *et al.* Carbon-concentration and carbon-climate feedbacks in CMIP5 earth system models. *J Clim* 2013; **26**: 5289–5314.
50 Ballantyne A, Smith W, Anderegg W, Kauppi P, Sarmiento J, Tans P *et al.* Accelerating net terrestrial carbon uptake during the warming hiatus due to reduced respiration. *Nat Clim Chang* 2017; **7**: 148–152.

Figure Legends

Figure 1 | A constraint on the sensitivity of global photosynthesis to CO_2. *a*, the relationship between the modelled sensitivity of global primary photosynthesis (GPP) to CO_2 ($\beta_{\mathrm{R}}^{\mathrm{GPP}}$, TRENDY experiment S1: dynamic CO_2 only) and the modelled normalized terrestrial carbon sink (PgC y^{-1}, TRENDY experiment S3: dynamic CO_2, climate and land-use). Individual TRENDY model (A-N) details are listed in Extended Table 1. The vertical dashed line and gray shading show the mean and standard error of the decadal residual terrestrial carbon sink between 1982 and 2012 as estimated by the Global Carbon Project [27]. The red line and shaded area show the best linear fit across models, and the associated 95% prediction intervals. The horizontal dashed line shows the implied constraint on the sensitivity of GPP to CO_2. ***b***, The unconstrained probability density function (PDF) distribution of $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ across models (black line, gray bars), which assumes that all of the TRENDY models are equally likely to be correct and that they come from a Gaussian distribution. The orange area represents the conditional probability distribution derived by applying the constraint from (***a***) to the across-model relationship. **c**, the relationship between $\beta_{\mathrm{R}}^{\mathrm{GPP}}$and the sensitivity of ecosystem respiration to CO_2 ($\beta_{\mathrm{R}}^{\mathrm{Reco}}$, TRENDY experiment S1). The vertical dashed line identifies the $\beta_{\mathrm{R}}^{\mathrm{Reco}}$ value that corresponds to the $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ identified by the relationship in (***a***), and the dashed red line is the 1:1 line. ***d***, The unconstrained probability density function (PDF) of $\beta_{\mathrm{R}}^{\mathrm{Reco}}$ across models (black line, gray bars). The orange area represents the conditional probability distribution derived by applying the constraint from (***c***) to the across-model relationship. See Extended Data Fig. 3 and Extended Data Table 1 for attribution to individual models. Note that the figure presents the partial relationship with the terrestrial carbon sink, excluding the influence of other factors through normalization. See Extended Data Fig. 1 for the underlying relationship between $\beta_{\mathrm{R}}^{\mathrm{GPP}}$and the terrestrial carbon sink. The constrained distributions presented in Fig. 1b,d account for multiple sources of uncertainty in addition to the uncertainty of the regressions presented in Fig. 1a,b (see Extended Data Fig. 3b).

Figure 2 | Long-term changes in global annual photosynthesis from terrestrial biosphere models and multiple satellite observations. ***a***, Relative changes in global photosynthesis (ΔGPP, %) from 1982 (CO_2 = 341ppm) to 2012 (CO_2 = 391ppm) based on simulations from process-based models in the TRENDY project model ensemble (orange, mean±std), and two different satellite approaches (empirical MODIS algorithm (MA, solid lines); a machine learning method (ML, dashed lines)). Estimates from the satellite approaches were obtained allowing for an effect of increasing CO_2 on either: the fraction of absorbed photosynthetically active radiation (fAPAR, red lines, dots), the light use efficiency (LUE) of photosynthesis (blue line), or both fAPAR and LUE (black lines, dots). ***b***, Inferred CO_2 sensitivities ($\beta_{\mathrm{R}}^{\mathrm{GPP}}$, see methods) from the data presented in (a), for the standard satellite-based approaches using machine learning (ML) and the MODIS algorithm (MA) with the CO_2 effect on GPP manifest through changes in fAPAR, the modified MA approach with a CO_2 effect only on light use efficiency (MA, only LUE), and both ML and MA satellite remote sensing based approaches with an effect of increasing CO_2 on both LUE and fAPAR. Black error bars represent the standard error of $\beta_{\mathrm{R}}^{\mathrm{GPP}}$. The horizontal orange area and dashed line indicate the $\beta_{\mathrm{R}}^{\mathrm{GPP}}$constraint inferred from Fig. 1b (mean±std).

Figure 3 | Spatial differences in the estimated long-term changes in global photosynthesis from light use efficiency theory, terrestrial biosphere models and satellite observations combined with theory. The global distribution of: ***a***, the sensitivity of photosynthesis on a leaf area basis to CO_2 ($\beta_{\mathrm{R}}^{\mathrm{LUE}}$) due to changes in light use efficiency; ***b***, CO_2 induced changes in photosynthesis (ΔGPP, gC m^{-2} yr^{-1}) from 1982 to 2012 from an ensemble of terrestrial biosphere models (TBMs; TRENDY-S1); ***c***, mean CO_2-induced changes in GPP from the two updated satellite methods, which includes both a modelled direct ($\beta_{\mathrm{R}}^{\mathrm{LUE}}$)

and measured indirect ($\beta_{\mathrm{R}}^{\mathrm{fAPAR}}$) effect of increasing CO_2 on GPP; ***d***, the difference between the data presented in panels ***b*** and ***c***; ***e***, The latitudinal distribution of long-term changes in gross primary photosynthesis (ΔGPP, PgC) from 1982 to 2012, from the TBM ensemble (orange shaded area, mean, standard deviation across models), and ΔGPP predicted from remote sensing (RS) approaches with (black, mean, standard deviation between MODIS and machine learning approaches) and without (red) a direct effect of CO_2 on light use efficiency (see methods); ***f***, Long-term changes in ΔGPP, separated by plant functional types (EBF, Evergreen broadleaved forest; SAV, savanna; DBF, deciduous broadleaved forests; CRO, croplands; SH, shrublands; GRA, grasslands; ENF, evergreen needleleaf forests; WET, wetlands).

Methods

Deriving an emergent constraint on the effect of increasing CO_2 on global photosynthesis

Emergent constraints have gained prominence in recent years as a means by which to infer unobserved quantities of interest in land surface and climate models[14–16]. The underlying core concept is that although there is a large spread in the model estimates of an observed variable X and an unobserved variable Y across models, the relationship linking the two is sometimes tightly constrained across models. Given the existence of a strong and robust relationship across models between X and Y, observations of X can be used to generate a probabilistic inference, or constraint, on Y. This approach has been termed 'emergent' because the functional relationship cannot be diagnosed from a single model, but rather emerges from examining the model spread[14–16].

The emergent constraint identified in this study links the sensitivity of gross primary photosynthesis to CO_2 (β_{R}^{GPP}, see definition below) to the magnitude of the residual terrestrial sink (S_{LAND}). It is derived from a multiple linear regression across an ensemble of terrestrial biosphere models (TBMs) between the modelled S_{LAND}, the sensitivity of gross primary photosynthesis to CO_2, the sensitivity of total ecosystem respiration (calculated as the sum of autotrophic and heterotrophic respiration (R_{a}, R_{h})) to CO_2 ($\beta_{\mathrm{R}}^{Reco}$), and an interaction term between $\beta_{\mathrm{R}}^{Reco}$ and the magnitude of the non-respired flux (γ). The non-respired flux, γ (Pg C y^{-1}), represents all ecosystem CO_2 losses that are not a result of respiration or land use change. The interaction term reflects the fact that the relationship between $\beta_{\mathrm{R}}^{Reco}$ and S_{LAND} is expected to be smaller if ecosystem respiration constitutes a smaller portion of total ecosystem carbon losses. The use of a multiple linear regression allows for variance normalization, which removes explainable variance imposed on the $\beta_{\mathrm{R}}^{GPP} \sim S_{\mathrm{LAND}}$ relationship, and provides a stronger emergent constraint than could be derived from the simple univariate relationship β_{R}^{GPP} and S_{LAND}.

We use global simulations from 14 TBMs (Extended Data Table 1) run as part of the Trends in Net Land-Atmosphere Exchange (TRENDY-v6) initiative (https://sites.exeter.ac.uk/trendy) (v6 data are reported in Le Quere et al., 2018[27]). In TRENDY, common input forcing data was prescribed for a series of model experiments from 1901 to 2015. Here we use both the results of the TRENDY-v6 scenario S3 simulations (temporally dynamic climate, CO_2, land use) as reported in the Global Carbon Project (GCP[27]), and the TRENDY-v6 scenario S1 simulations (CO_2-only: temporally dynamic CO_2, time-invariant climate; pre-industrial land use mask). For more details on the TRENDY project see Sitch et al. (2015)[3] and for details of the TRENDY-v6 simulations used here see Le Quere et al. (2018)[27].

We estimated β_{R}^{GPP} and $\beta_{\mathrm{R}}^{Reco}$ for each TRENDY-v6 TBM from annual GPP and Reco from the S1 (CO_2-only) simulations, performed by 14 models (Extended Data Table 1), using Eq. 1 over the 1982-2012 period (in order to maintain consistency with the remote sensing methods assessed). γ is calculated for each TRENDY-v6 TBM from the S3 simulations as the annual difference between Net Biome Production plus land use change emissions and (GPP-Reco), averaged over the 1982-2012 period. Note that processes included in this category (e.g, fire, volatile organic compounds, dissolved organic carbon fluxes) differ by TBM. S_{LAND} (Pg C y^{-1}) is calculated for each TRENDY-v6 TBM from the S3 simulations reported by the GCP[27], as the annual mean net biome productivity plus emissions from land use change, averaged over the same 1982-2012 period.

We related the modeled GPP CO_2 sensitivity (derived from S1 simulations) to the magnitude of the modeled terrestrial sink[27] (Fig. 2) using a multiple linear regression. The regression model used ($S_{\mathrm{LAND}} \sim \beta_{\mathrm{R}}^{GPP} + \beta_{\mathrm{R}}^{Reco} + \beta_{\mathrm{R}}^{Reco}\!:\gamma$) explained 94% of variation in between-model differences in the projected magnitude of S_{LAND} (Extended Data Table 2, Extended Data Fig. 2).

In order to extract the partial relationship between S_{LAND} and β_{R}^{GPP}(Fig. 1a), we normalized the S_{LAND} from each TBM to remove variance contributed by $\beta_{\mathrm{R}}^{Reco}$ and γ. Specifically, normalized S_{LAND} (S'_{LAND}) was calculated as $S'_{\mathrm{LAND}} = S_{\mathrm{LAND}} - (\varepsilon - \bar{\varepsilon})$, where $\varepsilon = (b\beta_{\mathrm{R}}^{Reco} + c\beta_{\mathrm{R}}^{Reco}\!:\gamma)$, $\bar{\varepsilon}$ is the mean across models, and b and c are the corresponding regression coefficients of the terms in the linear model of S_{LAND} (Extended Data Table 2). Using variance normalization to remove the influence of $\beta_{\mathrm{R}}^{Reco}$and the interaction between $\beta_{\mathrm{R}}^{Reco}$ and γ led to improved inference of β_{R}^{GPP} compared to the unnormalized relationship between S_{LAND} and β_{R}^{GPP} (Extended Data Fig. 1).

The emergent constraint approach relies on a tight relationship between a model predicted variable for which an observational constraint exists, and one for which there is no observational constraint available[14–16]. In the case of the relationship between β_{R}^{GPP} and S_{LAND}, estimates of S_{LAND} are made annually by the Global Carbon Project, along with the associated uncertainties[1]. The observed S_{LAND} values we use are the mean reported annual values from the Global Carbon Project[1] over the satellite era we study here (1982-2012). Note that the time period we used was chosen to both coincide with the satellite observations we use and to be sufficiently long so as to minimize the effect of macroclimatic events such as strong El Nino periods and volcanic eruptions, but our results were not highly dependent on the choice of period (Extended Data Fig. 4). The Global Carbon Project does not report uncertainties on annual values, but quantifies S_{LAND} uncertainty on a decadal basis, with an average uncertainty value of 0.9 PgC for each of the four decades including in this study[1]. This uncertainty reflects uncertainties from the component terms used to estimate S_{LAND} (emissions from fossil fuel use and cement production; emissions from land use change; the growth rate of atmospheric CO_2; the ocean sink), which the Global Carbon Project sums in quadrature to estimate the associated decadal S_{LAND} uncertainty.

The probability distribution of the constrained β_{R}^{GPP} (Fig. 2c) accounts for four sources of uncertainty. The first and second represent uncertainty in the Global Carbon Project S_{LAND} estimate, used as a constraint, and uncertainty in the relationship between β_{R}^{GPP} and the normalized S_{LAND}. These two sources of uncertainty are propagated to the joint probability distribution of β_{R}^{GPP} through bootstrapping with 10,000 bootstrapped samples, where each bootstrapped sample quantifies the β_{R}^{GPP} inferred from random sample of TBMs, with replacement, and a random sample from the distribution of Global Carbon Project S_{LAND} estimates. The resulting joint probability uncertainty is the largest of the uncertainties considered (Extended Data Fig. 3b). The third and fourth sources of uncertainty reflect uncertainty in the normalization of S_{LAND} due to the influence of individual models on the coefficients of the normalizing regression (Extended Data Table 2), and uncertainty regarding the true size of the non-respired flux contribution to S_{LAND}. To quantify the uncertainty associated with the influence of individual models, we performed S_{LAND} normalization and quantified β_{R}^{GPP} by using coefficients from 10,000 regression models estimated from model subsets. To quantify and propagate uncertainty regarding the true size of the non-respired flux contribution to S_{LAND}, we also bootstrapped the S_{LAND} normalization and quantified β_{R}^{GPP} assuming that the model estimates of the non-respired flux are equally likely to be correct and that they come from a Gaussian distribution. These two sources of uncertainty represent the second and third largest sources of the uncertainties considered (Extended Data Fig. 3b). The total uncertainty associated with the constrained β_{R}^{GPP} was then calculated by summing the individual uncertainties in quadrature, and was then propagated through to the uncertainty associated with the constrained $\beta_{\mathrm{R}}^{Reco}$.

Other factors, in particular turnover times of vegetation and soil, and model-dependent climate sensitivities, are also expected to lead to between-model differences in S_{LAND}. We included both vegetation and soil carbon turnover times, and three estimates of the sensitivity of GPP to climate (calculated as the slope of the relationship between annual S_{LAND} and annual global temperature, annual tropical temperature, and the annual Multivariate ENSO Index (MEIv2; https://psl.noaa.gov/enso/mei/) individually in the regression model to assess their importance. None were significant terms in the multiple linear regression and the best predictor (MEIv2 sensitivity) only explained an additional 3% of between-model variance (see Extended Data Table 2). Specifically, when added individually as predictors to our baseline linear model, MEIv2 proved the best predictor (CS-MEI, $p = 0.22$), followed by tropical and global temperatures (CS-tropicalT and CS-globalT, $p = 0.45$, 0.90 respectively; Extended Data Table 2). Each led to a reduction in the predicted R-squared (0.86, 0.85, 0.82 vs 0.89 for the baseline linear model), suggesting that the additional term in the model increased overfitting. We conclude from this analysis that differences in model sensitivities to climate are not responsible for differences in modeled S_{LAND}, which are effectively predicted by $S_{\mathrm{LAND}} \sim \beta_{\mathrm{R}}^{\mathrm{GPP}} + \beta_{\mathrm{R}}^{\mathrm{Reco}} + \beta_{\mathrm{R}}^{\mathrm{Reco}}{:}\gamma$ (Extended Data Table 2). Although sensitivities to climate are known to vary between models, and climate change is known to have had a large impact on the carbon sink in some regions, especially high-latitudes[51] (Extended Data Fig. 7), the lack of an influence of differences in model sensitivities to climate suggests that climate change has had a smaller effect on the land sink at a global scale, compared to that of rising CO_2, during our study period. This could be because climate change has both positive (e.g., growing season extensions) and negative (e.g., increased respiration) regional impacts on the land sink, which counterbalance each other at the global scale. This is supported by recent reports of a negligible influence of climate on the cumulative global land sink over the past few decades[6], and projections from the models examined here (Extended Data Fig. 7).

The β metric of CO_2 sensitivity

We quantified the apparent sensitivity of GPP to CO_2 in the remote sensing, terrestrial biosphere model and independent proxy estimates using two approaches: (1) the percent change in GPP with respect to GPP at the start of the time period (i.e. the $f(CO_2)$ introduced above), and (2) a β metric defined as the response ratio (R) of GPP with respect to CO_2:

$$\beta_R = \frac{[GPP(t) - GPP(t_0)]/GPP(t_0)}{[Ca(t) - Ca(t_0)]/Ca(t_0)} \qquad \text{Eq. 1}$$

where GPP(t) is the value of gross primary photosynthesis (GPP) at time t, and Ca(t) is the value of atmospheric [CO_2] at time t. Although other methods to calculate the β-factor have been proposed (e.g. [52]), we use Eq. 1 for ease of interpretation. A β of 1 represents direct proportionality between the GPP CO_2 response and the change in CO_2. Note that to avoid undue influence of year-to-year variability in GPP, we estimated GPP(t) and GPP(t_0) based on a linear regression fit to the GPP timeseries.

Assessing the CO_2-sensitivity of satellite-based estimates of GPP

Recent reports have highlighted that the most commonly used satellite-based estimates of GPP have a much lower CO_2-sensitivity than that derived from TBMs[9,10]. However, most satellite-based estimates do not incorporate the universally observed direct effect of increasing CO_2 on the light use efficiency of leaves of C_3 vegetation[20], which is not observable from space[21]. The effect of increasing CO_2 on global C_3 photosynthesis that we examine here manifests through two primary pathways: though increasing the biochemical rate of photosynthesis on a leaf area basis[53], which we refer to as the direct effect, and through increases in leaf area on a ground area basis, allowing for the interception of greater amounts of light[54,55], which we refer to as the indirect effect. The former, direct response, is due to the fact that CO_2 is a substrate for the photosynthetic enzyme, Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO). Both CO_2 and O_2 compete at the active site of RuBisCO, so changes in the concentration of either affect the rate at which CO_2 is assimilated, effectively changing the light use efficiency (LUE) of photosynthesis on a leaf area basis at a given light level. The latter, indirect response of increasing leaf area index (LAI[55]) and the resulting increase in the fraction of absorbed photosynthetically active radiation (fAPAR), reflects both the increased carbon available to invest in structural growth under elevated CO_2, and potential changes in the hydrological equilibrium due to elevated CO_2-induced increases in water use efficiency, which can lead to increased leaf area in water-limited ecosystems[56–58]. Both response pathways are incorporated in terrestrial biosphere models[3], and long-term proxies account for each to differing degrees. The majority of satellite-based estimates, however, do not account for the direct effect of increasing CO_2 on the biochemical rate of photosynthesis[21,59].

We assessed whether incorporating a CO_2 sensitivity of LUE in remote sensing-based approaches for estimating GPP reconciled the difference between the sensitivity of remote sensing-based GPP to increasing CO_2 and that implied by the emergent constraint. To do so, we develop a CO_2 sensitivity function for incorporating the effect of increasing CO_2 on the LUE of photosynthesis into satellite GPP estimates, based on the conservative assumption that the ecosystem-scale CO_2 sensitivity is consistent with that of the electron-transport-limited rate of photosynthesis (Aj). This is supported by reports that the observed CO_2 response of photosynthesis and biomass closely corresponds to the CO_2-sensitivity of Aj[37]. In addition, it has been suggested that shaded, and thus primarily electron-transport limited, leaves contribute the majority of canopy[38,60] and global photosynthesis [41]. The assumption is further supported by optimal coordination theory, which posits that photosynthesis under typical daytime field conditions is close to the point where Rubisco-limited (Ac) and Aj are colimiting. The colimitation of Ac and Aj has been shown to hold across a range of ecosystems[61], as has the downregulation of the maximum velocity of carboxylation (Vcmax) under elevated CO_2 in order to maintain coordination[62]. Given the fact that the sensitivity of Aj to CO_2 is much smaller than that of Ac[63], the sensitivity of Aj to CO_2 therefore represents a conservative approach to incorporate a CO_2 sensitivity of light use efficiency[39] in remote sensing estimates of photosynthesis. Note that we also make the conservative assumption that C_4 plants operate at or near CO_2 saturation[64].

The mechanistic photosynthesis model proposed by Farquhar et al. (1980)[53] captures the biochemical controls of leaf photosynthesis and responses to variations in temperature, light and CO_2 concentration. According to the model, the gross photosynthesis rate, A, is limited by either the capacity of the RuBisCO enzyme for the carboxylation of RuBP (Ribulose-1,5-bisphosphate), the electron transport capacity for RuBP regeneration. In the case of the limitation by the electron transport capacity for RuBP regeneration, the photosynthetic rate (A_j, µmol m^{-2} s^{-1}) is given by:

$$A_j = \varphi_0 I \frac{c_i - \Gamma^*}{c_i + 2\Gamma^*} \qquad \text{Eq. 2}$$

where φ_0 is the intrinsic quantum efficiency, I is the absorbed light (µmol m^{-2} s^{-1}), c_i (Pa) is the leaf internal CO_2 concentration, and Γ^* (Pa) is the CO_2 compensation point. Γ^* depends on temperature, as estimated through a biochemical rate parameter (r)[65]:

$$\Gamma^* = r_{25} e^{\frac{\Delta H (T - 298.15)}{298.15 RT}} \qquad \text{Eq. 3}$$

where R is the molar gas constant (8.314 J mol^{-1} K^{-1}), r_{25} = 4.22 Pa, is the photorespiratory point at 25 ˚C. ΔH is the activation energy for Γ^* (37.83 kJ mol^{-1}), and T is the temperature in K. Assuming the CO_2 sensitivity of light-limited photosynthesis allows for the development of an index of the effect of CO_2 on photosynthetic LUE[39] which can be incorporated in any remote sensing-based LUE model or empirical upscaling estimate of gross primary photosynthesis (GPP).

By rewriting Eq. 2, substituting c_i by the product of atmospheric CO_2 (c_a) and the ratio of leaf-internal to -ambient CO_2 ($\chi = c_i/c_a$), the sensitivity of GPP and LUE to CO_2 can be described as:

$$\frac{\partial GPP}{\partial CO_2} = \frac{\partial\, \varphi_0 I \frac{c_a \chi - \Gamma^*}{c_a \chi + 2\Gamma^*}}{\partial CO_2},$$

$$= \varphi_0 I \frac{\partial\, \phi_{CO2}}{\partial CO_2},$$

$$\Rightarrow \quad \frac{\partial LUE}{\partial CO_2} = \frac{\partial\, \phi_{CO2}}{\partial CO_2} \qquad \text{Eq. 4}$$

where $\phi_{CO2} = \frac{c_a \chi - \Gamma^*}{c_a \chi + 2\Gamma^*}$, and LUE = GPP/$\varphi_0 I$. Note that the indirect effect of CO_2 on GPP through

$\varphi_0 I$, is explicitly accounted for in satellite-based methods through changes in the fraction of absorbed photosynthetically active radiation (fAPAR), and considered here as an independent effect. However, the direct effect, through changes in LUE, (ϕ_{CO2}), is not. We used Eq. 4 to derive a scalar, $f(CO_2)$, to account for the direct effect of CO_2 in any LUE based estimate of GPP (e.g., satellite or empirical upscaling approaches). To do so, we calculated ΔGPP in year *t* due to the effect of CO_2 on LUE as $\mathrm{GPP}(\mathrm{t}=0) * f(CO_2)$, where:

$$f(CO_2) = \frac{(\phi_{CO2}^{t} - \phi_{CO2}^{1982})}{\phi_{CO2}^{1982}} \qquad \text{Eq. 5}$$

$f(CO_2)$ thus represents the fractional increase in LUE due to the direct effect of CO_2 relative to a baseline period (here 1982, the start of the timeseries for the satellite-based methods considered here).

The sensitivity of LUE to CO_2 thus depends on both Γ^*, which is calculated via Eq. 3, and χ. We estimated χ using the least-cost hypothesis[66,67]. This states that an optimal long-term effective value of χ can be predicted as a result of plants minimizing their total carbon costs associated with photosynthetic carbon gain, and explicitly expressed with the following model:

$$\chi \approx \frac{\xi}{\xi + \sqrt{D}}, where\ \xi = \sqrt{\frac{bK}{1.6\eta^*}} \qquad \text{Eq. 6}$$

where D is vapor pressure deficit, and η^* is the viscosity of water relative to its value at 25 °C [68], and b is the ratio of the cost of maintaining carboxylation relative to that of maintaining transpiration[66]. The Michaelis-Menten coefficient of Rubisco (K) is given by:

$$K = K_c \left(1 + \frac{P_o}{K_o}\right) \qquad \text{Eq. 7}$$

where K_c and K_o are the Michaelis-Menten coefficient of Rubisco for carboxylation and oxygenation, respectively, expressed in partial pressure units, and P_o is the partial pressure of O_2. K responds to temperature via K_c and K_o, the temperature responses for which are described using a temperature response function described by Eq. 3 with specific parameters: ΔH is 79.43 kJ mol^{-1} for K_c and 36.38 kJ mol^{-1} for K_o, r_{25} is 39.97 kPa for K_c and 27.48 kPa for K_o [65]. We applied this derived sensitivity to the remote sensing approaches detailed below, on a per pixel basis in proportion to the percentage of C_3 plants in a given pixel[69], as C_4 plants operate at or near CO_2 saturation[64]. We thus make the conservative assumption of no direct CO_2 effect on LUE in the C_4 proportion of each pixel.

Incorporating a CO_2 sensitivity of light-use efficiency into satellite-based estimates of GPP

The approach for incorporating a CO_2 sensitivity we outline above (Eq. 5) can be incorporated into any satellite-based photosynthesis product. Here, we test it on two broadly used approaches. The first, the MODIS MOD17 algorithm ($\mathrm{GPP_{MODIS}}$[28]) and the second an empirical upscaling method based on a model tree ensemble ($\mathrm{GPP_{MTE}}$[29]). We applied the MODIS MOD17 GPP algorithm driven by 30-year (1982–2012) Global Inventory Modeling and Mapping Studies (GIMMS3g) fAPAR data[70], to calculate a new 30-year global monthly gridded (0.5°) dataset of MODIS-derived GPP:

$$
\begin{aligned}
\mathrm{GPP'_{MODIS}} &= \mathrm{GPP_{MODIS}} \times (1 + f(CO_2)) \\
&= \mathrm{fAPAR} \times \mathrm{PAR} \times \mathrm{LUEmax} \times f(D) \times f(T_{min}) \times (1 + f(CO_2)) \\
&= \mathrm{fAPAR} \times \mathrm{PAR} \times \mathrm{LUE} \qquad \text{Eq. 8}
\end{aligned}
$$

where LUEmax represents biome-specific maximum light use efficiency, $f(D)$ represents a water stress reduction scalar based on the atmospheric vapor pressure deficit, and $f(T_{min})$ represents a low-temperature stress reduction scalar. LUEmax, $f(D)$, and $f(T_{min})$ are parameterized according to Zhao and Running (2010)[71]. $f(CO_2)$ is estimated on a per-pixel based using Eq. 5. We used global monthly gridded (0.5°) weather data, provided by the Climate Research Unit at East Anglia University (CRU TS4.01). The total available photosynthetically active radiation (PAR), and vapor pressure deficit (D) were calculated from insolation and CRU climate data using a simple process-based bioclimatic model (STASH[72]).

To incorporate a CO_2 sensitivity in a global empirical upscaling dataset based on a model tree ensemble machine learning technique ($\mathrm{GPP_{MTE}}$, 1982–2012[29]), which does not account for the direct effect of CO_2 on LUE, we followed the approach outlined for the MODIS GPP product. Specifically, we applied the CO_2 function (Eq. 5) to spatially distributed $\mathrm{GPP_{MTE}}$, as:

$$\mathrm{GPP}'_{\mathrm{MTE}} = \mathrm{GPP}_{\mathrm{MTE}}(1 + f(CO_2)) \qquad \text{Eq. 9}$$

Early remote sensing GPP models[39,73] advocated for including a CO_2 effect on LUE, though primarily used the larger, light-saturated, sensitivity. A recent review[8] found that the most widely used modern remote sensing GPP approaches[28,29] do not include a CO_2 effect on LUE, and of the 3 that did (out of 14 assessed) two are enzyme kinetics, not LUE, models (BESS[74], BEPS[75]). The third (cFix[73]) assumes the light-saturated CO_2 sensitivity, which is not suitable for global application given the large contribution of RuBP regeneration limited leaves[38,76]. A recent study[77] incorporated a CO_2 effect on LUE using the light-limited sensitivity, as we do here, but the approach taken requires the reparameterization of the LUE model and is thus not easily applicable to other remote sensing GPP products. The approach proposed here provides a generic and conservative method for incorporating CO_2 effects on LUE in any remote sensing GPP product, which allows us to quantify the relative importance of incorporating a CO_2 effect in remote sensing GPP products and reconciles the large difference between remote sensing and TBM-derived sensitivities to CO_2. Note that although many remote sensing GPP products are calibrated to observations from eddy-covariance networks, our implementation does not require recalibration, in particular as it only affects the CO_2 sensitivity, and eddy-covariance observations are not known to contain information on the effect of CO_2 on photosynthesis (Extended Data Fig. 6).

Methods References

51 Forkel M, Carvalhais N, Roedenbeck C, Keeling RF, Heimann M, Thornicke K et al. Enhanced seasonal CO2 exchange caused by amplified plant productivity in northern ecosystems. Science (80-) 2016; 351: 696–699.

52 Friedlingstein P, Fung I, Holland E, John J, Brasseur G, Erickson D et al. On the contribution of CO2 fertilization to the missing biospheric sink. Global Biogeochem Cycles 1995; 9: 541–556.

53 Farquhar GD, von Caemmerer S, Berry JA. A biochemical model of photosynthetic CO2 assimilation in leaves of C 3 species. Planta 1980; 149: 78–90.

54 Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 1997; 386: 698–702.

55 Zhu Z, Piao S, Myneni RB, Huang M, Zeng Z, Canadell JG et al. Greening of the Earth and its drivers. Nat Clim Chang 2016; 6: 791–795.

56 Keenan TF, Hollinger DY, Bohrer G, Dragoni D, Munger JW, Schmid HP et al. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 2013; 499: 324–327.
57 Ukkola AM, Keenan TF, Kelley DI, Prentice IC. Vegetation plays an important role in mediating future water resources. Environ Res Lett 2016; 11: 094022.
58 Donohue RJ, Roderick ML, McVicar TR, Farquhar GD. Impact of CO2 fertilization on maximum foliage cover across the globe's warm, arid environments. Geophys Res Lett 2013; 40: 3031–3035.
59 Smith NG, Dukes JS. Plant respiration and photosynthesis in global-scale models: Incorporating acclimation to temperature and CO2. Glob Chang Biol 2013; 19: 45–63.
60 De Kauwe MG, Lin YS, Wright IJ, Medlyn BE, Crous KY, Ellsworth DS et al. A test of the 'one-point method' for estimating maximum carboxylation capacity from field-measured, light-saturated photosynthesis. New Phytol 2016; 210: 1130–1144.
61 Maire V, Martre P, Kattge J, Gastal F, Esser G, Fontaine S et al. The coordination of leaf photosynthesis links C and N fluxes in C3 plant species. PLoS One 2012; 7: 1–15.
62 Smith NG, Keenan TF. Mechanisms underlying leaf photosynthetic acclimation to warming and elevated CO2 as inferred from least-cost optimality theory. Glob Chang Biol 2020; : 806–834.
63 Lloyd J, Farquhar G. The CO2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO2 concentrations and their interaction with soil nutrient status. I. General principles and forest ecosystems. Funct Ecol 1996; 10: 4–32.
64 Ehleringer J, Björkman O. Quantum Yields for CO(2) Uptake in C(3) and C(4) Plants: Dependence on Temperature, CO(2), and O(2) Concentration. Plant Physiol 1977; 59: 86–90.
65 Bernacchi CJ, Singsaas EL, Pimentel C, Portis Jr a. R, Long SP. Improved temperature response functions for models of Rubisco-limited photosynthesis. Plant, Cell Environ 2001; 24: 253–259.
66 Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ. Balancing the costs of carbon gain and water transport: Testing a new theoretical framework for plant functional ecology. Ecol Lett 2014; 17: 82–91.
67 Wang H, Prentice IC, Keenan TF, Davis TW, Wright IJ, Cornwell WK et al. Towards a universal model for carbon dioxide uptake by plants. Nat Plants 2017; 3: 734–741.
68 Huber ML, Perkins RA, Laesecke A, Friend DG, Sengers J V., Assael MJ et al. New international formulation for the viscosity of H2 O. J Phys Chem Ref Data 2009; 38: 101–125.
69 Still CJ, Berry JA, Collatz GJ, DeFries RS. Global distribution of C_3 and C_4 vegetation: Carbon cycle implications. Global Biogeochem Cycles 2003; 17: 6-1-6–14.
70 Zhu Z, Bi J, Pan Y, Ganguly S, Anav A, Xu L et al. Global Data Sets of Vegetation Leaf Area Index (LAI)3g and Fraction of Photosynthetically Active Radiation (FPAR)3g Derived from Global Inventory Modeling and Mapping Studies (GIMMS) Normalized Difference Vegetation Index (NDVI3g) for the Period 1981 to 2. Remote Sens 2013; 5: 927–948.
71 Zhao M, Running SW. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science 2010; 329: 940–3.
72 Gallego-Sala A, Clark J, House J, Orr H, Prentice I, Smith P et al. Bioclimatic envelope model of climate change impacts on blanket peatland distribution in Great Britain. Clim Res 2010; 45: 151–162.

73 Veroustraete F. On the use of a simple deciduous forest model for the interpretation of climate change effects at the level of carbon dynamics. Ecol Modell 1994; 75–76: 221–237.

74 Jiang C, Ryu Y. Multi-scale evaluation of global gross primary productivity and evapotranspiration products derived from Breathing Earth System Simulator (BESS). Remote Sens Environ 2016; 186: 528–547.

75 Zhang S, Zhang J, Bai Y, Koju UA, Igbawua T, Chang Q et al. Evaluation and improvement of the daily boreal ecosystem productivity simulator in simulating gross primary productivity at 41 flux sites across Europe. Ecol Modell 2018; 368: 205–232.

76 Liu Y, Hejazi M, Li H, Zhang X, Leng G. A hydrological emulator for global applications-HE v1.0.0. Geosci Model Dev 2018; 11: 1077–1092.

77 Yuan W, Zheng Y, Piao S, Ciais P, Lombardozzi D, Wang Y et al. Increased atmospheric vapor pressure deficit reduces global vegetation growth. Sci Adv 2019; 5: 1–13.

78 Haverd V, Smith B, Nieradzik L, Briggs PR, Woodgate W, Trudinger CM et al. A new version of the CABLE land surface model (Subversion revision r4601) incorporating land use and land cover change, woody vegetation demography, and a novel optimisation-based approach to plant coordination of photosynthesis. Geosci Model Dev 2018; 11: 2995–3026.

79 Melton JR, Arora VK. Competition between plant functional types in the Canadian Terrestrial Ecosystem Model (CTEM) v. 2.0. Geosci Model Dev 2016; 9: 323–361.

80 Oleson KW, Lawrence DM, Gordon B, Flanner MG, Kluzek E, Peter J et al. Technical description of version 4.0 of the Community Land Model (CLM). 2013 doi:10.5065/D6RR1W7M.

81 Tian H, Chen G, Lu C, Xu X, Hayes DJ, Ren W et al. North American terrestrial CO2 uptake largely offset by CH4 and N2O emissions: toward a full accounting of the greenhouse gas budget. Clim Change 2015; 129: 413–426.

82 Jain AK, Meiyappan P, Song Y, House JI. CO2 emissions from land-use change affected more by nitrogen cycle, than by the choice of land-cover data. Glob Chang Biol 2013; 19: 2893–2906.

83 Reick CH, Raddatz T, Brovkin V, Gayler V. Representation of natural and anthropogenic land cover change in MPI-ESM. J Adv Model Earth Syst 2013; 5: 459–482.

84 Clark DB, Mercado LM, Sitch S, Jones CD, Gedney N, Best MJ et al. The Joint UK Land Environment Simulator (JULES), model description – Part 2: Carbon fluxes and vegetation dynamics. Geosci Model Dev 2011; 4: 701–722.

85 Smith B, Wärlind D, Arneth A, Hickler T, Leadley P, Siltberg J et al. Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. Biogeosciences 2014; 11: 2027–2054.

86 Sitch S, Smith B, Prentice IC, Arneth a., Bondeau a., Cramer W et al. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Glob Chang Biol 2003; 9: 161–185.

87 Keller KM, Lienert S, Bozbiyik A, Stocker TF, Churakova Sidorova O V., Frank DC et al. 20th century changes in carbon isotopes and water-use efficiency: Tree-ring-based evaluation of the CLM4.5 and LPX-Bern models. Biogeosciences 2017; 14: 2641–2673.

88 Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P et al. A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Global Biogeochem Cycles 2005; 19: GB1015.

89 Guimberteau M, Zhu D, Maignan F, Huang Y, Yue C, Dantec-N d lec S et al. ORCHIDEE-MICT (v8.4.1), a land surface model for the high latitudes: model description and validation. Geosci Model Dev 2018; 11: 121–163.

90 Zeng N, Mariotti A, Wetzel P. Terrestrial mechanisms of interannual CO2 variability. Global Biogeochem Cycles 2005; 19: 1–15.

91 Kato E, Kinoshita T, Ito A, Kawamiya M, Yamagata Y. Evaluation of spatially explicit emission scenario of land-use change and biomass burning using a process-based biogeochemical model. J Land Use Sci 2013; 8: 104–122.

92 Fernández-Martínez M, Vicca S, Janssens IA, Ciais P, Obersteiner M, Bartrons M et al. Atmospheric deposition, CO2, and change in the land carbon sink. Sci Rep 2017; 7: 9632.

93 Ciais P, Tagliabue A, Cuntz M, Bopp L, Scholze M, Hoffmann G et al. Large inert carbon pool in the terrestrial biosphere during the Last Glacial Maximum. Nat Geosci 2012; 5: 74–79.

94 Cheng L, Zhang L, Wang YP, Canadell JG, Chiew FHS, Beringer J et al. Recent increases in terrestrial carbon uptake at little cost to the water cycle. Nat Commun 2017; 8. doi:10.1038/s41467-017-00114-5.

95 Ueyama M, Ichii K, Kobayashi H, Kumagai T, Beringer J, Merbold L et al. Inferring CO2 fertilization effect based on global monitoring land-atmosphere exchange with a theoretical model. Environ Res Lett 2020. doi:10.1088/1748-9326/ab79e5.

96 Pastorello G, Trotta C, Canfora E, Chu H, Christianson D, Cheah YW et al. The FLUXNET2015 dataset and the ONEFlux processing pipeline for eddy covariance data. Sci data 2020; 7: 225

Acknowledgements

TFK, XL and YZ acknowledge primary support from the NASA IDS Award NNH17AE86I. TFK acknowledges additional support from NASA award 80NSSC21K1705 and by the Director, Office of Science, Office of Biological and Environmental Research of the US Department of Energy (DOE) under Contract DE-AC02-05CH11231 as part of the RuBiSCo SFA and a DOE ECRP Award DE-SC0021023. MDK acknowledges support from the Australian Research Council (ARC) Centre of Excellence for Climate Extremes (CE170100023), the ARC Discovery Grant (DP190101823) and the NSW Research Attraction and Acceleration Program. ICP acknowledges the Imperial College initiative on Grand Challenges in Ecosystems and the Environment and the European Research Council (ERC) under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement no: 787203 REALM). NGS acknowledges support from Texas Tech University. BDS was funded by the Swiss National Science Foundation grant no. PCEFP2_181115. CT was supported by a Lawrence Fellow award through Lawrence Livermore National Laboratory (LLNL), the DOE LLNL contract DE-AC52-07NA27344, and the LLNL-LDRD Program project 20-ERD-055. We thank Ranga Myneni and Zaichun Zhu for the provision of the fAPAR data set, the Max Planck Institute for Biogeochemistry Department of Biogeochemical Integration for the provision of the upscaled GPP data. We thank the TRENDY team for the provision of the DGVM simulations, and the researchers of the Global Carbon Project for making their data publicly available. We thank Anthony Walker for useful discussions on interpreting the deuterium isotopomer results, and acknowledge the stimulating discussions during the Integrating CO_2 Fertilization Evidence Streams and Theory (ICOFEST) meeting September 2018, part of the FACE model Data-Synthesis project funded by the US Department of Energy, Office of Science, Office of Biological and Environmental Research.

Author Contributions

TFK designed the study, performed the analysis, and wrote the manuscript. XL aided in the regridding of the TRENDY model data. MDK, BS, ICP, WH, NS, BM, XL and SZ provided feedback on the remote sensing implementation. SZ and YZ provided feedback on the emergent constraint implementation. BS provided feedback on the TRENDY model data interpretation. All authors discussed and commented on the results and the manuscript.

Author Information

All requests for reprints and permissions should be addressed to the corresponding author, TF Keenan. The authors declare no competing interests.

Data Availability Statement

All data used to support the findings of this study are publicly available. TRENDY model simulations are available on request from TRENDY coordinator Stephen Sitch (s.a.sitch@exeter.ac.uk; https://sites.exeter.ac.uk/trendy). The Multivariate ENSO Index is available from https://psl.noaa.gov/enso/mei/. The GIMMS fAPAR data is available from http://cliveg.bu.edu/modismisr/lai3g-fpar3g.html. Climate forcings used are available from Climate Research Unit at East Anglia University (https://crudata.uea.ac.uk/cru/data/hrg/). Upscaled GPP data are available from the Max Planck Institute for Biogeochemistry (https://www.bgcjena.mpg.de/geodb/projects/Home.php). Locations for FLUXNET tower sites are available at www.fluxnet.org.

Code Availability Statement

Code used to support the findings of this study is publicly available at www.github/trevorkeenan/gpp-co2.

Extended Data Titles and Legends

Extended Data Table 1 | The terrestrial biosphere models (TBMs) used. The model ensemble used the Trends in Net Land Carbon Exchange (TRENDY) version 6, as presented in the 2017 Global Carbon Project report[27].

[Footnote:] Note that VEGAS does not report S_{LAND} in the Global Carbon Project. LPJ-GUESS does not report heterotrophic respiration in TRENDY-v6 S1. SDGVM and OCN are two additional models included in the Global Carbon Project and TRENDY-v6 that were excluded from our analysis due to data issues in the submitted simulations (SDGVM) and the lack of S1 simulations (OCN).

Extended Data Table 2 | Linear models of the land sink as estimated from terrestrial biosphere models. The baseline linear model presents the model used for variance normalization presented in the main text. The other three models assessing the role of climate sensitivities (CS) in a linear model of the land sink as estimated from terrestrial biosphere models. We tested the influence of climate by calculating the sensitivity of modeled S_{LAND} to climate in three different ways, in order to assess whether between-model differences in the modeled sensitivity of S_{LAND} to climate variability translate to between-model differences in predicted S_{LAND}. Specifically, we calculated the climate sensitivity (CS) of each model as: (1) CS-globalT: The sensitivity of modeled global S_{LAND} to global temperature (T), calculated as the slope between annual anomalies in modeled global S_{LAND} and global T; (2) CS-tropicalT: The sensitivity of modeled global S_{LAND} to tropical T variations, calculated as the slope between annual anomalies in modeled global S_{LAND} and tropical T (motivated by a tight correlation between tropical T and the growth rate of atmospheric CO_2); (3) CS-MEI: The slope of the relationship between annual modeled global S_{LAND} anomalies and the Multivariate ENSO Index Version 2 (MEIv2: https://psl.noaa.gov/enso/mei/), as this integrates global interannual changes in climate.

[Footnote:] Where γ denotes the non-respired flux, quantified as S_{LAND} – (GPP - Reco), where S_{LAND} is the residual terrestrial carbon sink taken from the Global Carbon Project, and GPP (Gross Primary Photosynthesis) and Reco (total ecosystem respiration) taken from TRENDY simulation S3 of the models listed in Extended Data Table 1. $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ and $\beta_{\mathrm{R}}^{\mathrm{Reco}}$ are estimated from TRENDY-v6 S1 simulations.

Extended Data Table 3 | Calculation of $\boldsymbol{\beta_{\mathrm{R}}^{\mathrm{GPP}}}$ from existing proxies.

[Footnote:] ***Notes on published estimates of the response of global photosynthesis to CO_2*:** Wenzel et al.[11] use atmospheric observations of the seasonal cycle of CO_2 to infer a GPP increase of 32% for northern extra-tropical ecosystems under a doubling of CO_2, equivalent to a $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ of 0.32. This reflects the sensitivity of extra-tropical ecosystem photosynthesis to CO_2, and is therefore expected to be lower than the global sensitivity due to the temperature dependence of the effect of CO_2 on photosynthesis (Fig. 3a). It is also based on a doubling of CO_2, and due to the saturating response of photosynthesis to elevated CO_2 is likely an underestimate of, and not directly comparable to, the historic sensitivity.

Ehlers et al.[12] estimate the sensitivity of photosynthesis to CO_2 based on measurements of deuterium isotopomers in herbarium samples of natural C_3 vascular plant species, crops, and a Sphagnum moss species. Deuterium isotopomers provide an estimate of the photosynthesis/respiration ratio, and it's change over time. In order to translate the change in the photosynthesis/respiration ratio to a change in photosynthesis, Ehlers et al. used a model with the assumption that photosynthesis is not limited by light[12]. The resulting $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ of 1.03 therefore represents the sensitivity of photosynthesis in the absence of light limitation, which is expected to be considerably higher than that of whole-ecosystem global photosynthesis due to the large contribution of shaded leaves, as $\partial Ac/\partial CO_2 >> \partial Aj/\partial CO_2$ (see methods).

Other published estimates of the effect of CO_2 on global photosynthesis include correlative analyses based on eddy-covariance observations (Fernandez-Martinez et al., 2017[92]; $\beta_{\mathrm{R}}^{\mathrm{GPP}}$=1.2), oxygen isotope estimates (Ciais et al., 2012[93]; $\beta_{\mathrm{R}}^{\mathrm{GPP}}$=1.3±2.3), and modeled products (Cheng et al., 2017[94]; Cernusak et al., 2020[22]; Haverd et al., 2020[24]; Ueyama et al. 2020[95];Sun et al., 2019[8]; overall modeled $\beta_{\mathrm{R}}^{\mathrm{GPP}}$range 0.1-1.6). We do not discuss these estimates in the main text due to the lack of causal relationship in [92], the very large uncertainty in [93], and the variety of assumptions employed in the modeled estimates [8,22,24,94,95].

Extended Data Figure 1 | The relationship between the sensitivity of global primary photosynthesis (GPP) to CO_2 ($\beta_{\mathrm{R}}^{\mathrm{GPP}}$) and the terrestrial carbon sink (S_{LAND}, PgC y^{-1}). The emergent constraint on $\beta_{\mathrm{R}}^{\mathrm{GPP}}$is comparable to that derived using the normalized S_{LAND}, though the associated uncertainty is considerably higher due to the unexplained variance in the $\beta_{\mathrm{R}}^{\mathrm{GPP}}$~$S_{\mathrm{LAND}}$ relationship**.** The red line and shaded area show the best linear fit across models, and the associated 95% prediction intervals.

Extended Data Figure 2 | A multiple linear model of the terrestrial biosphere model predictions of the global carbon sink. ***a***, The terrestrial biosphere model (TBM) predictions of the global carbon sink are predicted as a function of the modeled sensitivity of photosynthesis to CO_2 ($\beta_{\mathrm{R}}^{\mathrm{GPP}}$), the modeled sensitivity of respiration to CO_2 ($\beta_{\mathrm{R}}^{\mathrm{Reco}}$) and the magnitude of the modeled non-respired carbon flux (γ) (Extended Data Table 2). The red line and shaded area show the best linear fit across models, and the associated 95% prediction intervals. ***b***, the effect size of each of the terms included in the model (mean, 95% CI), which estimates main effect on the response from changing each predictor value, averaging out the effects of the other predictors. TBM names and details are provided in Extended Data Table 1. Details of the linear model used are provided in Extended Data Table 2.

Extended Data Figure 3 | An emergent constraint on the sensitivity of global photosynthesis to CO_2. ***a***, The relationship between the sensitivity of global primary photosynthesis (GPP) to CO_2 and the modeled terrestrial carbon sink (PgC y^{-1}), in relative terms (ΔGPP (%)). The vertical gray shading shows the range of the observed terrestrial residual carbon sink over the period of 1982 to 2012, as estimated by the Global Carbon Project. The red line and shaded area show the best linear fit across models, and the associated 95% prediction intervals, and the horizontal dashed line shows the implied emergent constraint on the sensitivity of GPP to CO_2. This figure reproduces Fig. 1a, but includes model names, which correspond to labels given in Extended Data Table 1. See Extended Data Fig. 1 for the underlying relationship between the sensitivity of GPP to CO_2 and the terrestrial carbon sink. ***b***, Uncertainty contributions to the constrained sensitivity of global photosynthesis to CO_2. The unconstrained probability density function (PDF) distribution of $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ across models (black line, gray bars), which assumes that all of the TRENDY models are equally likely to be correct and that they come from a Gaussian distribution. The orange area represents the conditional probability distribution derived by applying the constraint from (***a***) to the across model relationship, with dashed and dotted lines in the orange area indicating the relative contribution of different sources of uncertainty (see methods).

Extended Data Figure 4 | Assessment of the effect of choice of period on the sensitivity of global primary photosynthesis (GPP) to CO_2 ($\boldsymbol{\beta_{\mathrm{R}}^{\mathrm{GPP}}}$). Estimates of the residual terrestrial sink (S_{LAND}) from the Global Carbon Project (GCP) used in this study were split into two 15-year periods (1982-1997 (***a***, ***b***) and 1998-2012 (***c***, ***d***)) and the emergent constraint approach (see methods) was applied to each independently, using GCP estimates of the land sink for those periods to estimate a constrained value of $\beta_{\mathrm{R}}^{\mathrm{GPP}}$ from the TRENDY dynamic global vegetation models (Extended Data Table 1). Estimated S_{LAND} in panel ***a*** and ***c*** is $S_{\mathrm{LAND}} \sim 1 + \beta_{\mathrm{R}}^{\mathrm{GPP}} + \beta_{\mathrm{R}}^{\mathrm{Reco}} + \beta_{\mathrm{R}}^{\mathrm{Reco}} \cdot \gamma$. The vertical dashed lines in ***a*** and ***c*** indicate the GCP estimate of the mean residual sink for that period. The red lines and shaded areas in ***a*** and ***c*** show the best linear fit across models, and the associated 95% prediction intervals.

Extended Data Figure 5 | Long-term changes in annual gross primary production (GPP) of global tropical forests. GPP estimated by terrestrial biosphere models (TBMs) in the TRENDY model ensemble considers either temporally dynamic CO_2 and fixed climate and land use (orange, experiment S1), temporally dynamic CO_2 and climate, and fixed land use (red, experiment S2), or temporally dynamic CO_2, climate, and land use (purple, experiment S3). Shaded areas represent the mean and standard error of the annual estimate across the TRENDY ensemble. Remote sensing (RS) GPP considers temporally dynamic climate and land use, and either fixed (blue) or varying (red) CO_2. Tropical forests represent the Evergreen Broadleaf Forest classification within tropical latitudes (23.5°N: 23.5°S).

Extended Data Figure 6 | Assessment of the effect of CO_2 on global primary photosynthesis (GPP) at sites included in the FLUXNET 2015 dataset. (***a***) The distribution of the length of the observational record at each of the 206 sites in the FLUXNET 2015 open access database. The vertical red line indicates the median site record length (5 years). (***b***) The expected effect of CO_2 on GPP at all sites, demonstrated by comparing the GPP predicted by the original (x-axis) and updated (y-axis) remote sensing-based methods for all site months of observations in the FLUXNET 2015 database[96]. The mean expected difference across sites is 2.39%.

Extended Data Figure 7 | Global and high latitude changes in the terrestrial carbon cycle. Both the global (a, b, c) and northern land (high latitude, > 45°N) (d, e, f) contribution of CO_2 (orange shaded area, derived from TRENDYv6 CO_2-only simulations (S1)) and climate (red shaded area, derived from the difference between TRENDYv6 CO_2-only simulations and CO_2 + Climate simulations (S2-S1)), to long term (1900-2016) changes in annual net ecosystem productivity (NEP), gross primary production (GPP) and ecosystem respiration (RECO). The shaded areas represent the annual mean and standard error across the TRENDY model ensemble. The impact of climate change is large in high latitude ecosystems, increasing both GPP (e) and RECO (f). This does not however translate to a large impact on the global carbon cycle (a, b, c).