

Response Letter

CEDAR-GPP: spatiotemporally upscaled estimates of gross primary productivity incorporating CO₂ fertilization

Reviewer #1

Dear reviewer,

Thank you very much for your review and feedback of our revised manuscript! We appreciate the opportunity to further clarify these issues and address any remaining concerns. Please find our detailed point-to-point response below.

Sincerely,
Yanghui Kang
On behalf of all authors

[Reviewer Comment 1] I felt disappointed that the authors didn't run their model again since the GPP is wrong as I mentioned at the last round of comments.

Response: We regret that our previous revisions did not fully resolve your concerns regarding the GPP model. In our last revision, we aimed to address concerns related to GPP modeling, on the incorporation of direct CO₂ fertilization effect (CFE) and the capacity of VIs to represent the indirect CFE. We clarified potential misunderstandings about these aspects and improved the clarity of the related text in our manuscript and responses. We also performed additional validation to demonstrate the robustness of our models in quantifying GPP and particularly its long-term trends. We are sorry to hear that you felt disappointed that we did not run our model again to address the concerns raised, but we did not feel that was necessary.

Additionally, we would also like to emphasize that we demonstrated the robustness of our GPP models through rigorous validation and evaluation (Section 3.1, Figure 3-5, Figure S1-4, Table S3, also see responses below). Our models' performance in cross-validation with the eddy covariance data aligns well with previous datasets. Moreover, intercomparisons with other RS-based datasets, including FLUXCOM, FLUXSAT, and MODIS, confirm strong consistency in global patterns of annual mean GPP, interannual variability, and mean seasonal cycles (Section 3.2, Figure 6-9, Figure S5-8).

Our estimates of long-term trends agree with eddy covariance data across global sites. Notably, the Baseline model, which does not consider the direct CFE, underestimates GPP trends at flux towers. In contrast, the CFE-ML and CFE-Hybrid models show significant improvements, underscoring the need to consider both direct and indirect CFE. In our last revision, we performed additional validation of GPP trend by climate zones and plant functional types (Figure 5b, 5c). We also provided comparisons of estimated and observed trends at long-term sites (Figure S4).

We recognize the limitations in validation within tropical areas, which is due to data scarcity. In our response to your next comment (see Page 5-9 of this document), we show that CEDAR-GPP exhibits higher consistency with TRENDY models after incorporating the direct CFE.

Below we provide further clarifications and additional analyses to address previous comments concerning GPP modeling. We hope that these assuage your concerns but would welcome further suggestions for improvement.

[Previous comment: Main point #6]: *The water stress effect should be considered. Line 718 to L720, “Yet the model assumed a fixed ratio of leaf-internal to ambient CO₂, and thus did not include any responses to vapor pressure deficit.”. So is the CEDAR-GPP consider VPD effect for GPP? Although CFE is one of the most significant effects to the GPP trend. However, the VPD trend cannot be omitted. Li et al. 2023 reported that the VPD significantly affects the GPP at different vegetation types, so the CEDAR-GPP consider this or some setups reproduce such condition? If the CEDAR-GPP cannot reproduce the VPD effect, so under what condition can I use this product? The soil moisture is also coupled with VPD, so is the CEDAR-GPP consider the soil moisture stress, and can it reproduce the stress from soil moisture? These are needed to be mentioned.*

Response: We would like to highlight that water stress factors, such as atmospheric dryness (VPD), precipitation, and soil water availability (soil moisture) were indeed considered in our GPP predictions. We include these factors as explanatory variables in our machine learning models. The sentence highlighted by the reviewer here relates to our approach of simulating the CO₂ sensitivity of LUE (i.e. the direct CFE) in the CFE-Hybrid approach. This is not directly relevant to water stresses.

In the CFE-Hybrid model, we prescribed the direct CFE onto GPP estimated by machine learning models at a reference CO₂ level, which already accounts for water stress. The direct CFE was quantified by a CO₂ sensitivity function of LUE based on the optimal coordination theory. Our CO₂ sensitivity function of LUE uses a fixed leaf-internal to ambient CO₂ concentration ratio (c_i/c_a) based on the global long-term average, without considering potential responses to air temperature or VPD.

In this round of revision, we provided additional analyses to demonstrate that the fixed c_i/c_a approach provided consistent results compared to a more dynamic approach, justifying our choice of using the simplest model with equivalent performance. We applied a dynamic c_i/c_a model based on temperature and VPD to estimate the direct CFE at monthly intervals across the global flux towers. Results show that the direct CFE and GPP trends from CFE-Hybrid model are highly consistent between the fixed and dynamic c_i/c_a approaches. The dynamic model predicted c_i/c_a has a mean of 0.7, consistent with the global long-term mean value used in our fixed c_i/c_a approach. The standard deviation is only 0.04 suggesting that c_i/c_a is relatively stable. We have incorporated this analysis and relevant figures in the newly revised manuscript. Here we provide the relevant figure. Additionally, we also revised the description of the CO₂ sensitivity function of LUE for clarity.

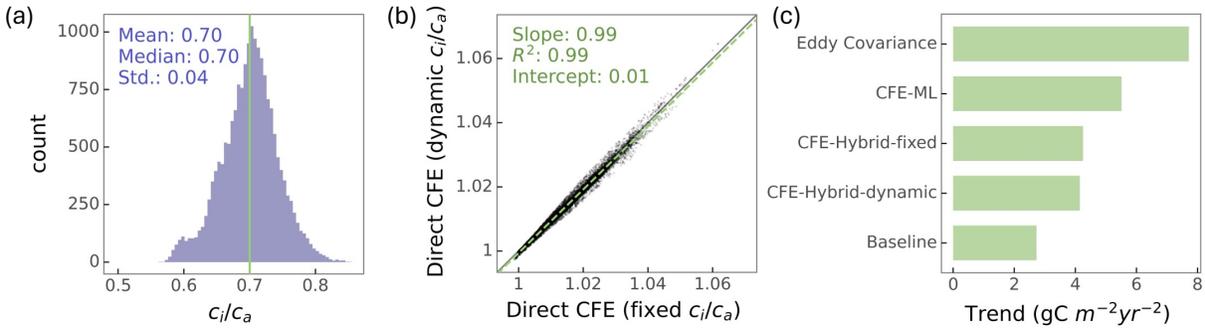


Figure S11. Comparison of CO₂ sensitivity of LUE with dynamic vs. fixed values of χ , i.e. the leaf internal to atmospheric CO₂ concentration ratio (c_i/c_a). The dynamic model simulates χ as a function of air temperature and VPD, whereas the other approach has a fixed χ at the global long-term average ($\chi=0.7$). (a) Statistical distribution of c_i/c_a (monthly values) across global eddy covariance tower. (b) Comparison of the direct CO₂ fertilization effect (CFE) between the two models. The direct CFE is quantified as the ratio between LUE under ambient CO₂ levels and LUE at a reference CO₂ level (the value of year 2001). This corresponds to the $(\phi_{CO_2}^t / \phi_{CO_2}^{t_0})$ term in eq. A8. (c) Aggregated GPP trends across global flux towers over 2002 to 2019 from eddy covariance data and model estimates. The CFE-Hybrid-fixed model assumes a constant c_i/c_a and the CFE-Hybrid-dynamic model computes c_i/c_a as a function of air temperature and VPD based on an eco-evolutionary optimality theory.

Revisions:

Line 943 – 951: We fixed χ to the global long-term average value 0.7 typical to C3 plants (Prentice et al., 2014; Wang et al., 2017). We further tested a dynamic model that quantified χ as a function of air temperature and vapor pressure deficit following an eco-evolutionary theory across global flux sites (Keenan et al., 2023). The estimated χ had a mean and median of 0.7 and a standard deviation of 0.04 (Figure S11a). Differences in the direct CO₂ effect between the dynamic and fixed χ approaches were minimal, with an R² of 0.99 and a slope of 0.99 from a least squares linear regression line (Figure S11b). GPP trends across flux towers were also highly consistent between the two approaches (Figure S11b, c). Since these results indicated that χ is relatively stable, we used the fixed χ approach to produce the CEDAR-GPP dataset.

Line 900 – 905: Appendix A: CO₂ sensitivity function of Light Use Efficiency. In the CFE-Hybrid model, the direct CO₂ fertilization effect was prescribed onto machine learning estimated GPP at a reference CO₂ level using a theoretical CO₂ sensitivity function of LUE. The sensitivity function, which describes the fractional change in LUE due to CO₂ relative to the reference period, is described below.

Line 785 - 790: Robust modeling of LUE responses to rising CO₂ under various environmental conditions remains challenging (Wang et al., 2017). Future work is needed to better understand how these factors affect the quantification of GPP and its long-term temporal variations.

[Previous comment]: L249 'do not consider the direct effect of CO2 on light use efficiency', this is inaccurate, the VI sometimes can capture the LUE change from direct CFE.

Response: As clarified in our last response, VIs used in our analysis, such NDVI, EVI, and NIRv, primarily capture changes in vegetation structures (or LAI), thus the ability to intercept

light. These VIs are designed to highlight the strong NIR reflectivity caused by leaf internal mesophyll structures in vegetation. These VIs are not sensitive to direct CO₂ impacts on LUE, which are associated with photochemical processes. Therefore, our baseline model, without considering CO₂, does not capture the direct CFE.

[Previous comment]: Function A2 $A = AC = A_j$? I cannot agree with this! There are just one condition $Ac = A_j$ is the photosynthesis transfer from lighted-limited to nutrient limited.

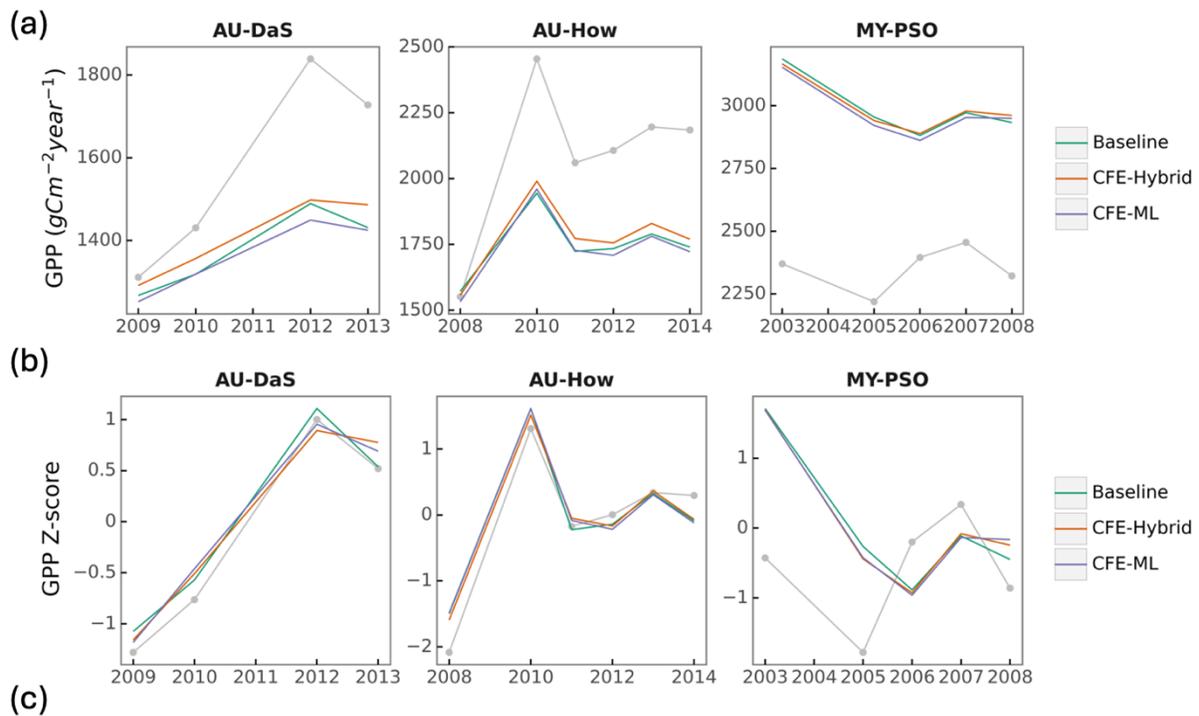
Response: This comment is associated with our CO₂ sensitivity function of LUE as part of the CFE-Hybrid model. As we clarified previously, this function is based on the eco-evolution theory, specifically the optimal coordination hypothesis, which predicts that the electron-transport (A_j) and Rubisco-limited (Ac) rates of photosynthesis converge on the time scale of physiological acclimation. This coordination hypothesis is based on the idea that resources would be wasted if overcapacity of one process is maintained over the other. Many studies have found that coordination theory is consistent with leaf to canopy level measurements (e.g. Chen et al., 1993; Haxeltine & Prentice, 1996; Maire et al., 2012; Quebbeman & Ramirez, 2016; Wang et al., 2017). Harrison et al. (2021) provides a thorough review of the eco-evolutionary optimality theory for plant and vegetation processes. Given that the coordination of A_j and Ac happens in the order of a few weeks, the coordination theory can be readily applied to our monthly GPP estimates. Additionally, this theory allows us to model LUE sensitivity to CO₂ based on A_j , which has a lower response to CO₂ than Ac . Therefore, our CFE-Hybrid model provides a conservative estimate of the direct CFE. Lastly, note that we did not use Function A2 to directly model GPP; rather these are used to derive the direct CFE. Representations of GPP response to climatic and environmental factors, including the indirect CFE and water stress, are directly estimated by the machine learning models based on global eddy covariance data.

- Chen, J.-L., Reynolds, J. F., Harley, P. C., and Tenhunen, J. D.: Coordination theory of leaf nitrogen distribution in a canopy, *Oecologia*, 93, 63–69, <https://doi.org/10.1007/BF00321192>, 1993.
- Haxeltine, A. and Prentice, I. C.: A General Model for the Light-Use Efficiency of Primary Production, *Functional Ecology*, 10, 551–561, <https://doi.org/10.2307/2390165>, 1996.
- Maire, V., Martre, P., Kattge, J., Gastal, F., Esser, G., Fontaine, S., and Soussana, J.-F.: The Coordination of Leaf Photosynthesis Links C and N Fluxes in C3 Plant Species, *PLOS ONE*, 7, e38345, <https://doi.org/10.1371/journal.pone.0038345>, 2012.
- Quebbeman, J. A. and Ramirez, J. A.: Optimal allocation of leaf-level nitrogen: Implications for covariation of V_{cmax} and J_{max} and photosynthetic downregulation, *Journal of Geophysical Research: Biogeosciences*, 121, 2464–2475, <https://doi.org/10.1002/2016JG003473>, 2016.
- Wang, H., Prentice, I. C., Keenan, T. F., Davis, T. W., Wright, I. J., Cornwell, W. K., Evans, B. J., and Peng, C.: Towards a universal model for carbon dioxide uptake by plants, *Nature Plants*, 3, 734–741, <https://doi.org/10.1038/s41477-017-0006-8>, 2017.
- Harrison, S. P., Cramer, W., Franklin, O., Prentice, I. C., Wang, H., Brännström, Å., de Boer, H., Dieckmann, U., Joshi, J., Keenan, T. F., Lavergne, A., Manzoni, S., Mengoli, G., Morfopoulos, C., Peñuelas, J., Pietsch, S., Rebel, K. T., Ryu, Y., Smith, N. G., Stocker, B. D., and Wright, I. J.: Eco-evolutionary optimality as a means to improve vegetation and land-surface models, *New Phytologist*, <https://doi.org/10.1111/nph.17558>, 2021.

[Reviewer Comment] Besides, since the most important improvement of CEDAR-GPP to other machine learning based GPP products is, they consider the CO₂ in GPP modelling. However, the authors hidden the validation results at tropics, the most important contributor to the global GPP, I highly suspect they have a wrong validation. Therefore, I cannot accept the CEDAR-GPP at the current stage.

Response: We recognize the critical contribution of tropical regions to global ecosystem productivity and would like to provide further clarifications regarding our validation in these regions.

As detailed in Section 3.1.2, Figure 4, and Table S3, we have thoroughly validated monthly, seasonal, interannual, and cross-site GPP variations for tropical sites. Our models show reasonable accuracies in this area aligning with previous studies. However, the validation of GPP long-term trends in tropical areas is constrained by data availability. Across the FLUXNET2015, AmeriFlux OneFlux, and ICOS data that we compiled, only three tropical sites have more than three years of data, and none of them exceed six years (Figure R1 below). Given the strong interannual variabilities, robust detection of long-term trends is not feasible for these sites without longer data records. Figure R1 below shows the GPP time series at these sites from eddy covariance data and our Baseline, CFE-Hybrid, and CFE-ML models (short-term models). Note that none of the sites exhibit statistically significant trends. In the manuscript, we provided validation for individual sites with more than 10 years of data all tropical sites do not meet these criteria (Figure S4, attached below).



Site ID	IGBP	No. of years	Slope			p-value				
			Eddy Covariance	Baseline	CFE-Hybrid	CFE-ML	Eddy Covariance	Baseline	CFE-Hybrid	CFE-ML
AU-DaS	SAV	4	143.77	142.55	145.18	130.34	0.31	0.31	0.31	0.31
AU-How	WSA	6	46.60	9.31	7.81	11.97	0.45	1.00	0.71	1.00
MY-PSO	EBF	5	20.55	-36.66	-21.42	-3.06	0.81	0.46	0.81	1.00

Figure R1. Temporal dynamics of three tropical sites with more than three years of data. (a) Comparison of GPP dynamics from eddy covariance with estimates from Baseline, CFE-Hybrid, and CFE-ML models (short-term models). Eddy covariance GPP is estimated with the night-time partitioning approach. (b) Dynamics of GPP anomalies represented by Z-score. (c) GPP trends estimated by Theil-Sen slopes with p-values from the Mann-Kendall test.

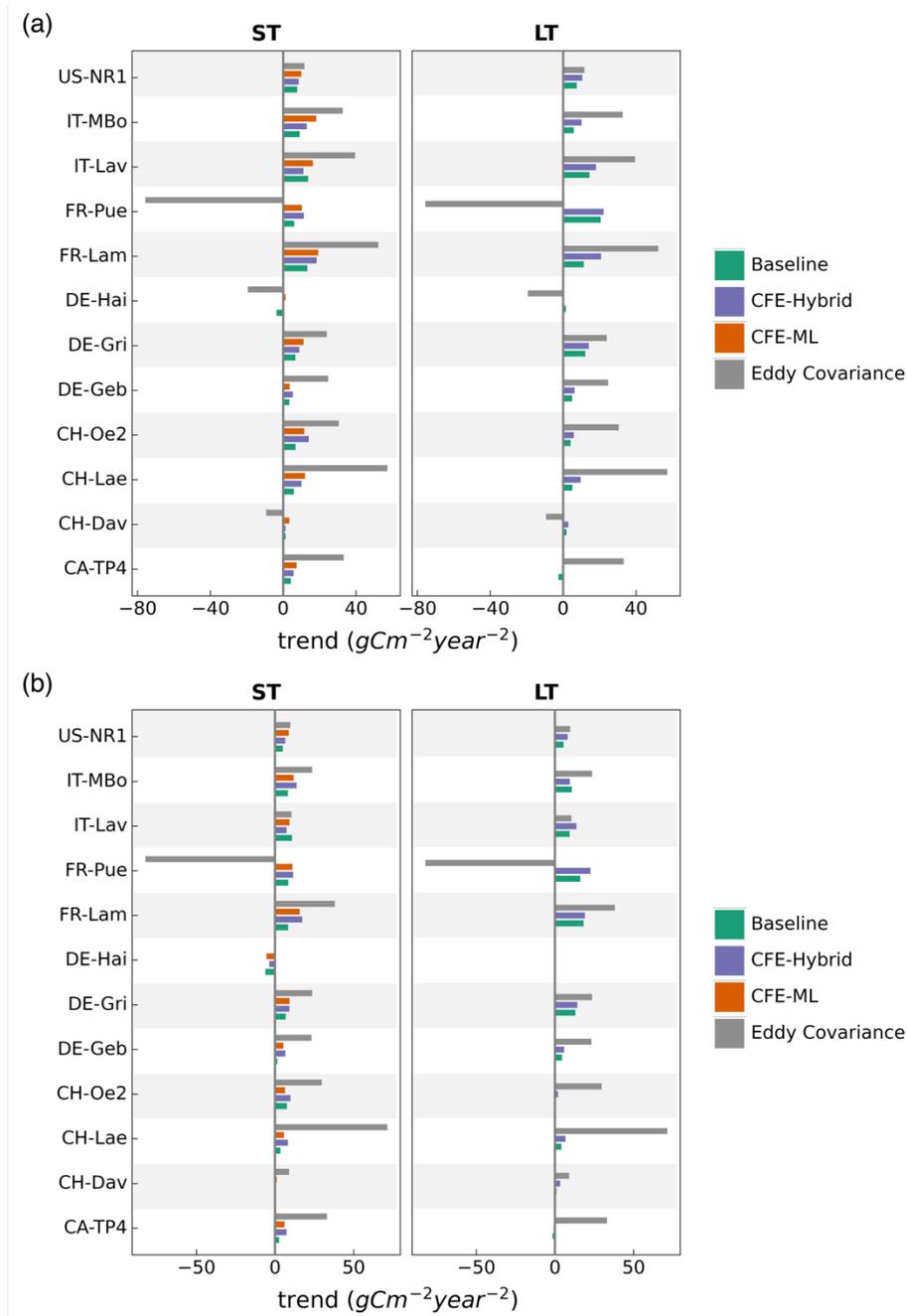


Figure S4. Comparison of observed and predicted GPP trends from (a) NT models and (b) DT models in long-term flux sites. Only sites with at least ten years of data and a significant annual trend (p-value < 0.3) are shown.

To further assess CEDAR-GPP in tropical areas, we compared our estimates of GPP trends to TRENDY-v9 model ensembles. Our CFE models considering direct CO₂ fertilization (CFE-ML and CFE-Hybrid) are much more consistent with TRENDY-v9 than the baseline models and other reference GPP datasets (i.e. FLUXCOM, FLUXSAT, MODIS) (Figure R2, R3). Specifically, both TRENDY-v9 and our CFE models detect a significant increase in tropical GPP which is not captured by the Baseline and other satellite-based datasets (Figure R2, R3). This finding aligns with the relatively stable tropical LAI in the MODIS data, indicating limited indirect CFE (Chen et al., 2019). Furthermore, our CFE models demonstrate the highest consistency with TRENDY in the spatial variations of GPP long-term trends (Figure R4). Notably, among the long-term datasets (Figure R3, R4), CEDAR-GPP is the only product that aligns with TRENDY, while FLUXCOM-ERA5 and rEC-LUE present negative correlations. The consistency of our data-driven approach with purely process-based models in TRENDY demonstrates the robustness and reliability of CEDAR-GPP in representing long-term trends. For presentation clarity and readability, we did not incorporate TRENDY comparisons in this paper.

We have expanded our discussion acknowledging the uncertainties and challenges associated with GPP trend and CO₂ fertilization quantification and validation, highlighting new opportunities provided by current efforts in expanding flux measurements and innovative machine learning approaches.

Revisions:

Line 828 – 839: Lastly, quantifying GPP trends and their causes remain highly uncertain from site to global scales. Trend detection is often complicated by data noises and interannual variabilities, thus requiring long-term records which are limited in certain areas and biomes, such as tropics, polar regions, evergreen broadleaf forests and wetlands (Baldocchi et al., 2018; Zhan et al., 2022). Moreover, isolating the effect of CO₂ is challenging, as it is confounded by other factors, such as forest regrowth, land cover change, and disturbances, which also significantly impacts long-term GPP variations. To this end, continued efforts in expanding ecosystem flux measurements and standardizing data processing are crucial, presenting new opportunities to assess ecosystem productivity responses to changing climate conditions (Delwiche et al., 2024; Pastorello et al., 2020). Future research could also leverage novel machine learning techniques, such as knowledge-guided machine learning (Liu et al., 2024) and hybrid modeling that combines process-based and machine learning approaches (Kraft et al., 2022; Reichstein et al., 2019).

Thank you once again for the time and efforts you dedicated to reviewing our manuscript. We hope that our revisions have sufficiently addressed your comments and concerns and look forward to any further feedback and suggestions you may have.

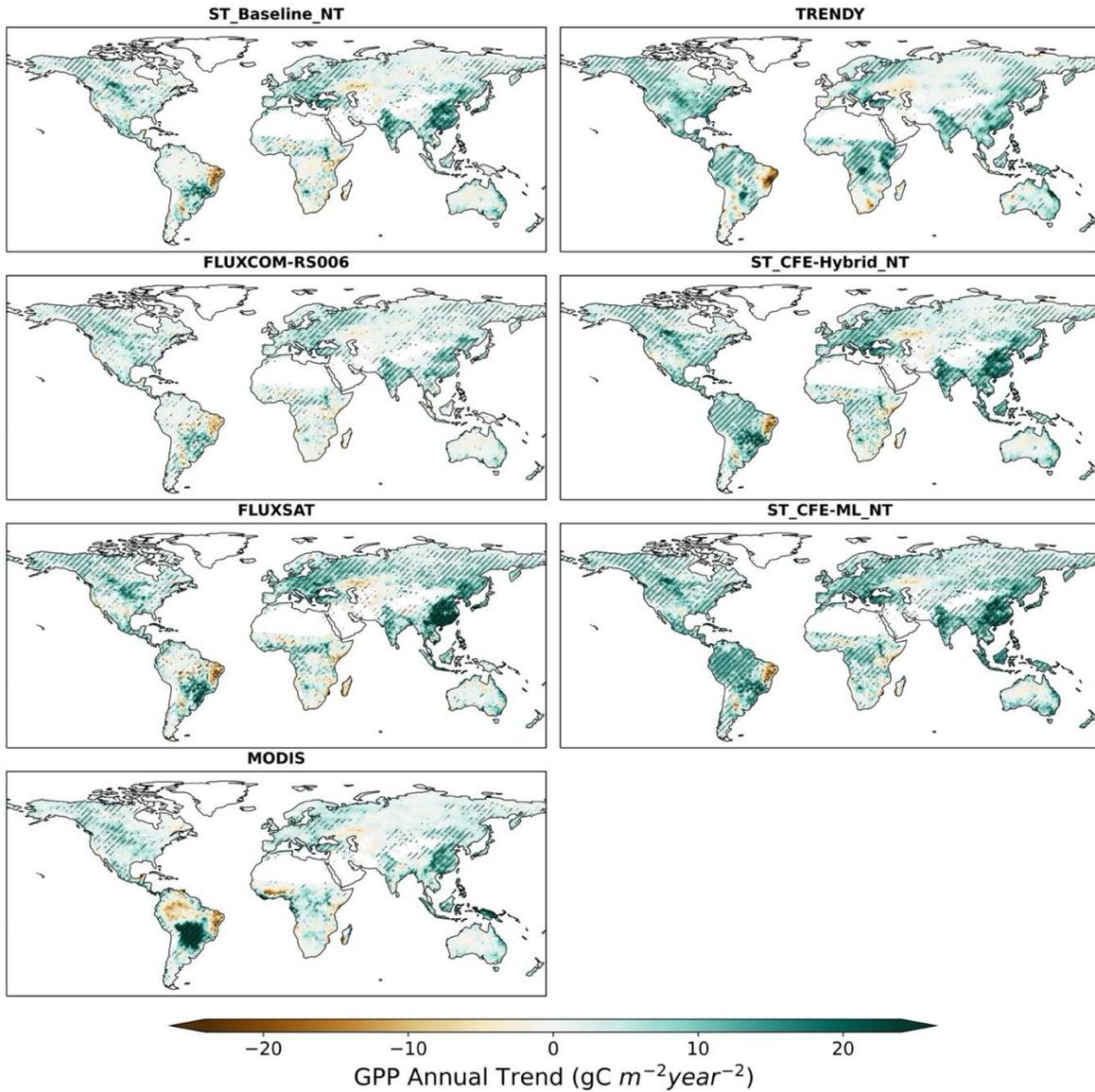


Figure R2. Spatial patterns of GPP trend from 2001 to 2018 estimated by CEDAR models, TRENDY, and reference remote sensing based datasets. Hatch areas indicate a statistically significant trend ($p < 0.05$) from the Mann-Kendall test.

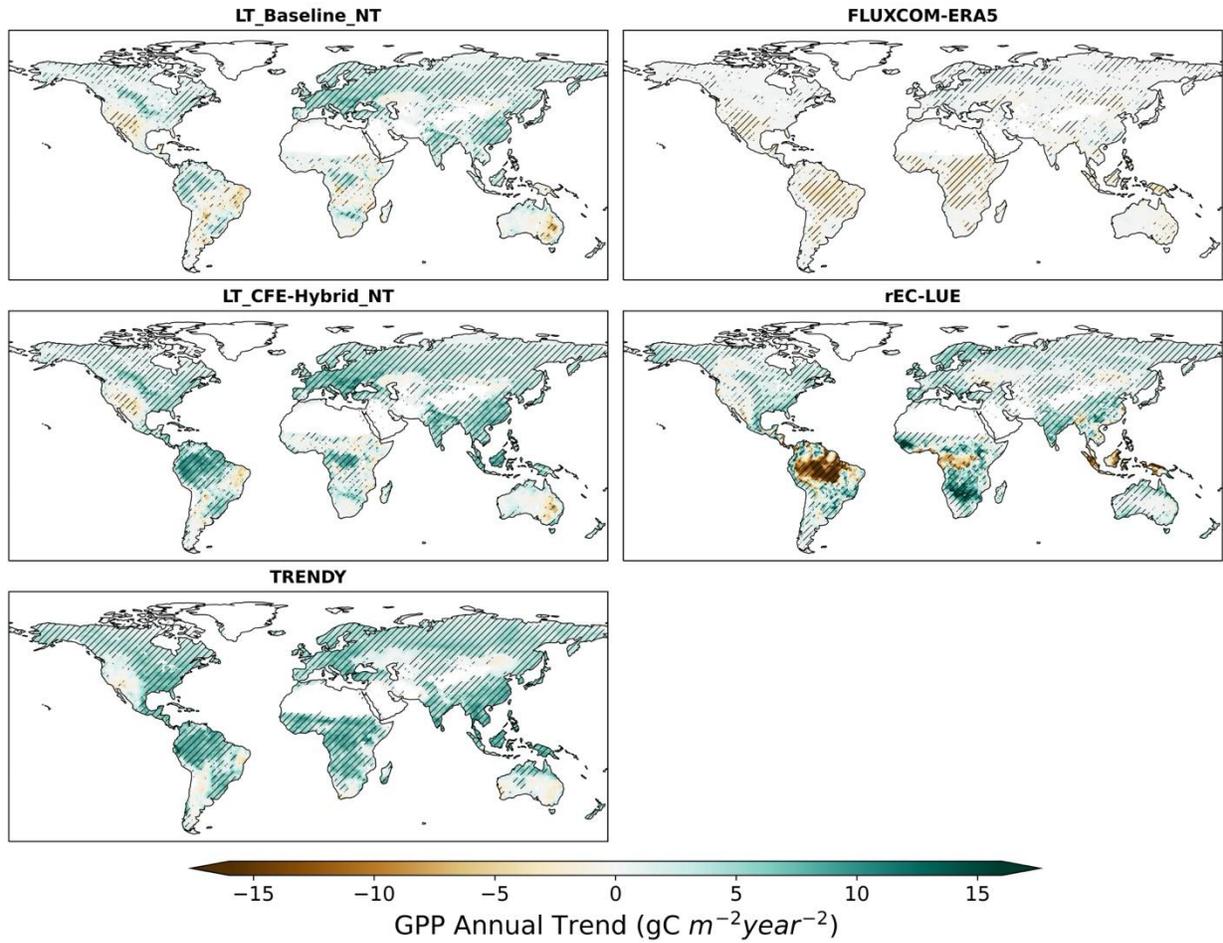


Figure R3. Spatial patterns of GPP trend from 1982 to 2018 estimated by CEDAR models, TRENDY, and reference remote sensing based datasets. Hatch areas indicate a statistically significant trend ($p < 0.05$) from the Mann-Kendall test.

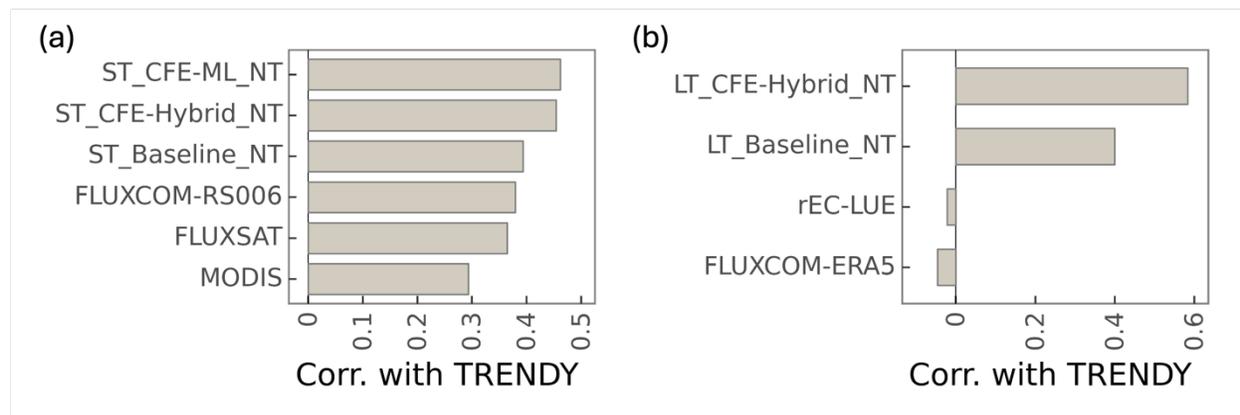


Figure R4. Spatial correlations of long-term GPP trends between TRENDY and remote sensing based estimates for 2001 – 2018 (a) and 1982 – 2018 (b).

Reviewer #2

The authors have well respond to most of my concerns and suggestions. I only have one minor suggestions here. As presented by the authors, they did not use the observations from flux sites before 2001 as the inputs, and used a constant χ value for the generation of long-term GPP datasets. Please noted that both these factors will affect the long-term trend of GPP. For example, as the CO₂ increases, the stomatal conductance will likely to be reduced, and the χ value also will be changed. So the variation of χ value is also a part of the CO₂ fertilization effect on GPP, but this dataset did not comprehensively consider this. I understand the difficulty, that the authors can hardly accurately modelling the variation in χ value, especially in global scale. But as this GPP dataset certainly will be widely used after published, a detailed and comprehensively discussion of these caveats may be better, to avoid the wrong use by non-specialist in this area. Overall, my humble suggestion is that the authors could add a point-to-point discussion of the limitations that affect the accuracy of this GPP dataset, and better to present some attentions that which situation this product is not fit for. Other parts of this manuscript is very good and clear now. Songhan.

Responses:

Dear Dr. Wang,

Thank you very much for your thorough review of our manuscript! We are pleased that our revisions have sufficiently addressed most of your comments. We also appreciate your insightful feedback regarding the uncertainty associated with modeling χ , i.e. the ratio of leaf internal and atmospheric CO₂ concentration. We evaluated an alternative model where χ is dynamically quantified based on air temperature and VPD following eco-optimality theory, which provided highly consistent results with the fixed χ approach. We note that the results confirm the robustness of our original conclusions, in part because although c_i certainly increases with CO₂, the ratio of c_i to c_a , χ , is relatively constant (as observed in experimental and manipulation studies).

We found that the estimated direct CO₂ effects and GPP trends are consistent between the dynamical and fixed χ approaches (Figure S11, included below). At monthly intervals across 233 flux sites, the simulated c_i/c_a ratios center closely around a mean and median value of 0.70, with a standard deviation of only 0.04 (Figure S11a). This mean value is consistent with the global average value used in the fixed model. Moreover, the direct CO₂ effects, quantified by the ratio of actual light use efficiency (LUE) under ambient CO₂ effects to the reference LUE at a fixed CO₂ level of year 2001, show remarkable consistency between the two approaches. The linear regression line between the two approaches has a slope of 0.99 and r^2 of 0.99 across global sites (Figure S11b). Finally, the aggregated GPP trend across global sites from the fixed and dynamic approaches also show minimum differences (dynamic χ : 4.15, fixed χ : 4.25 g C m⁻² year⁻²) (Figure S11c).

These results suggest that sensitivity of χ to environmental variations may not significantly affect the direct CO₂ effect or the GPP long-term trend. However, modeling χ responses to varied environmental factors remains challenging. Further research is needed to evaluate different representations of χ and LUE sensitivity to CO₂ to gain a deeper understanding of how these factors affect the quantification of GPP and its variation. In the revised manuscript, we discussed these results and implications and presented the relevant figure.

We also greatly appreciate your concerns about excluding flux tower data before 2001 and would like to provide further clarifications. Our short-term predictions are based on MODIS data, which is only available after 2000. Thus, earlier flux measurements could not be incorporated into our training sample. For long-term predictions, omitting these earlier data should not pose significant extrapolation issues in the Baseline and CFE-Hybrid model. This is because long-term climatic and environmental changes (excluding CO₂) before and after 2001 are considerably smaller than the seasonal, interannual, and spatial variations of the factors, which are sufficiently represented by data from 2001 to 2020. Additionally, only four of the over 230 sites have data before 1996 representing a very small fraction of the dataset. As such, the inclusion or exclusion of data before 2001 likely have a minimal effect on the GPP predictions by the Baseline and CFE-Hybrid models. Excluding these data also ensures the consistency in training samples used for the long-term and short-term predictions. Note that, given the continuous increase of CO₂ over the years, we chose not to produce long-term predictions from the CFE-ML model due to concerns about the potential for biased extrapolation of the CO₂ effect, given the limited data available before 2001. We have incorporated these considerations in our revised manuscript.

Sincerely,

Yanghui Kang
On behalf of all co-authors

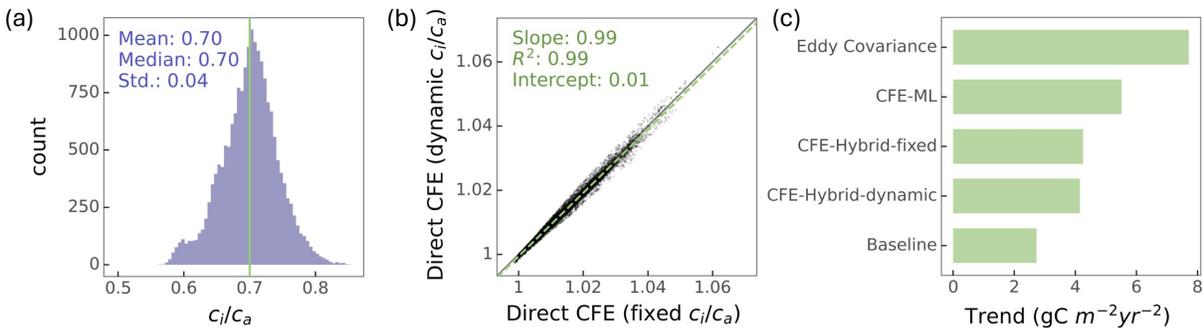


Figure S11. Comparison of CO₂ sensitivity of LUE with dynamic vs. fixed values of χ , i.e. the leaf internal to atmospheric CO₂ concentration ratio (c_i/c_a). The dynamic model simulates χ as a function of air temperature and VPD, whereas the other approach has a fixed χ at the global long-term average ($\chi=0.7$). (a) Statistical distribution of c_i/c_a (monthly values) across global eddy covariance tower. (b) Comparison of the direct CO₂ fertilization effect (CFE) between the two models. The direct CFE is quantified as the ratio between LUE under ambient CO₂ levels and LUE at a reference CO₂ level (the value of year 2001). This corresponds to the $(\phi_{CO_2}^t/\phi_{CO_2}^{t_0})$ term in eq. A8. (c) Aggregated GPP trends across global flux towers over 2002 to 2019 from eddy covariance data and model estimates. The CFE-Hybrid-fixed model assumes a constant c_i/c_a and the CFE-Hybrid-dynamic model computes c_i/c_a as a function of air temperature and VPD based on an eco-evolutionary optimality theory.

Revisions:

Line 137 – 140: Note that we did not include eddy covariance data before 2001, since it was limited to only a few sites with only four sites containing data before 1996. This scarcity might introduce biases in the machine learning models, particularly in the relationship between GPP

and CO₂, leading to unreliable extrapolations across space and time in the long-term predictions.

Line 777 – 790: CEDAR's CFE-Hybrid setup offered a conservative estimation of the direct CO₂ effects by simulating the CO₂ sensitivity of light-limited LUE for C3 plants (Walker et al., 2021). However, the model did not account for the impacts of nutrient availability, which could potentially constrain CO₂ fertilization (Reich et al., 2014; Peñuelas et al., 2017; Terrer et al., 2019). Robust modeling of LUE responses to rising CO₂ under various environmental conditions remains challenging (Wang et al., 2017). Future work is needed to better understand how these factors affect the quantification of GPP and its long-term temporal variations.

Line 943 – 951: We further tested a dynamic model that quantified χ as a function of air temperature and vapor pressure deficit following an eco-evolutionary theory across global flux sites (Keenan et al., 2023). The estimated χ had a mean and median of 0.7 and a standard deviation of 0.04 (Figure S11a). Differences in the direct CO₂ effect between the dynamic and fixed χ approaches were minimal, with an R² of 0.99 and a slope of 0.99 from a least squares linear regression line (Figure S11b). GPP trends across flux towers were also highly consistent between the two approaches (Figure S11b, c). Since these results indicated that χ is relatively stable, we used the fixed χ approach to produce the CEDAR-GPP dataset.