

# Flexible foliar stoichiometry reduces the magnitude of the global land carbon sink

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## Key Points (3)

- A flexible, CO<sub>2</sub>-driven parameterization of foliar C:N in the Community Land Model produced a 2-fold reduction in the projected land C sink.
- The flexible foliar C:N parameterization also had large effects on the hydrologic cycle, reducing evapotranspiration and increasing runoff.
- N cycling rates were reduced under the flexible C:N scenario but highlight the need for additional research on modeled plant-soil feedbacks.

## **Abstract**

Increased plant growth under elevated CO<sub>2</sub> slows the pace of climate warming and underlies projections of terrestrial carbon (C) and climate dynamics. However, this important ecosystem service may be diminished by concurrent changes to vegetation carbon to nitrogen (C:N) ratios. Despite clear observational evidence of increasing foliar C:N under elevated CO<sub>2</sub>, our understanding of potential ecological consequences of foliar stoichiometric flexibility is incomplete. Here, we show that incorporating CO<sub>2</sub>-driven foliar stoichiometry into the Community Land Model reduced the projected land C sink two-fold by the end of the century compared to simulations with fixed foliar chemistry. Further, flexible foliar C:N profoundly altered Earth's hydrologic cycle, reducing evapotranspiration and increasing runoff. Belowground N cycling rates were reduced in the flexible scenario, highlighting the urgency of further research examining both the direct and indirect effects of changing foliar stoichiometry on soil N cycling and plant productivity.

## **Plain Language Summary**

As atmospheric carbon dioxide (CO<sub>2</sub>) increases plant growth also increases, which could offset some of the impacts of climate change. However, higher CO<sub>2</sub> dilutes leaf nutrient concentrations, which could ultimately limit plant growth as CO<sub>2</sub> continues to rise. The change in leaf chemistry in response to rising CO<sub>2</sub> is not currently represented in models used to predict future productivity and the land carbon sink. We produced a new representation of leaf chemistry in the Community Land Model to examine potential effects of shifting leaf chemistry on future vegetation growth and global C, nutrient, and hydrologic cycles. We found that our new model simulation reduced the strength of the land C sink 2-fold compared to simulations where foliar

chemistry does not change in response to atmospheric CO<sub>2</sub>. The reduction in plant growth also produced large hydrologic changes, including reduced global evapotranspiration and increased runoff. Nitrogen cycling rates were reduced in the flexible simulation but highlighted a gap in our understanding of aboveground-belowground feedbacks that warrants further research. Thus, the ways we represent foliar chemistry in models are important for understanding the future conditions of the planet and our capacity to respond to climate change.

## **1 Introduction**

Terrestrial ecosystems provide myriad ecosystem services, including a sink for ~30% of historic anthropogenic carbon dioxide (CO<sub>2</sub>) emissions (Friedlingstein et al., 2022; Costanza et al., 1997). Despite the important role of terrestrial ecosystems in reducing the atmospheric CO<sub>2</sub> burden, considerable uncertainty remains about the persistence of this C sink under climate change (Friedlingstein et al., 2022; Arora et al., 2020). Even over the historical record (when observational data are available), land models show significant uncertainty in the magnitude of the terrestrial carbon (C) sink, and especially the role of the CO<sub>2</sub> fertilization effect (O’Sullivan et al., 2022). Therefore, considerable attention has been given to calibrating model parameters that may reduce uncertainty in terrestrial C cycle projections (Dagon et al., 2020; Friend et al., 2007; Smallman et al., 2021). These efforts often reduce the spread in model results, but they also omit other important sources of uncertainty, notably model structural uncertainty related to the representation of some important ecological processes and biotic feedbacks that may regulate the integrated Earth system response to climate change under elevated CO<sub>2</sub>.

Uncertainty surrounding the representation of ecological process in land models originates from both an incomplete understanding of ecological processes and feedbacks themselves, as well as how to mathematically integrate those processes into models (Bonan & Doney, 2018; Bradford et al., 2016; O'Neill & Melnikov, 2008). Both factors contribute to model structural uncertainty that often leads to different outcomes when multiple models attempt to simulate the same phenomena. Large structural uncertainty related to the representation of nitrogen (N) cycling, soil biogeochemistry, and photosynthesis, for example, highlight the importance of considering ecological processes in land models with the goal of more accurately simulating biogeochemical and biophysical dynamics in response to climate change (Bradford et al., 2016; Meyerholt et al., 2020; Wieder et al., 2015). Moreover, integrating new data and insights into global-scale models can reveal outstanding gaps in our mechanistic understanding of Earth systems. Indeed, much of the uncertainty in quantifying Earth's terrestrial C sink originates from model structural uncertainty (Bonan & Doney, 2018), necessitating extensive interdisciplinary research examining ecosystem responses to climate change and increasing CO<sub>2</sub>.

Rising atmospheric CO<sub>2</sub> creates multiple ecosystem feedbacks that may interact to regulate long-term CO<sub>2</sub> fertilization effects, but a better understanding of those feedbacks is needed to improve predictions of the terrestrial C sink. Widely reported plant physiological responses to elevated CO<sub>2</sub> include decreases in stomatal conductance, increases in leaf mass per area, and downregulated photosynthesis over time, which are associated with feedbacks on ecosystems and climate (Ellsworth et al., 2004; Kovenock et al., 2021; Medlyn et al., 2015; Sellers et al., 1996; Zarakas et al., 2020). One especially important ecological response to elevated CO<sub>2</sub> is a well-documented shift in foliar stoichiometry, the ratios of C-to-nutrients in leaf tissues (Mason et al.,

2022; Myers et al., 2014; Penuelas et al., 2020). Foliar C:N ratios increase under elevated CO<sub>2</sub> in both field and manipulation experiments (Du et al., 2019; Penuelas et al., 2020; Wang et al., 2021). This direct stoichiometric response is likely due to a combination of processes, including nutrient dilution in leaves with enhanced C uptake, reduced N uptake by vegetation, and reduced soil N availability (Dong et al., 2022; Gojon et al., 2022; Mason et al., 2020). Flexible foliar stoichiometry (i.e. ranges of foliar C:N values at which vegetation can still grow) may allow sustained productivity with CO<sub>2</sub> fertilization even as nutrients become increasingly scarce (Dong et al., 2022; Dynarski et al., 2022; Meyerholt et al., 2020). However, declines in foliar and litter N may directly reduce photosynthetic rates (Ellsworth et al., 2004) as well as produce indirect negative feedbacks on plant production via reduced rates of decomposition and nutrient mineralization that could dampen global terrestrial C storage over time (Liang et al., 2016; Luo et al., 2004). Thus, the relationship between foliar C:N and atmospheric CO<sub>2</sub> concentration may strongly influence the ability of terrestrial ecosystems to act as a global C sink.

While models demonstrate high sensitivity to foliar C:N (Dagon et al., 2020; Fisher et al., 2019), the rate and magnitude of foliar C:N change with increasing CO<sub>2</sub> is unclear. This represents an important source of model structural uncertainty that limits our understanding of terrestrial biogeochemical cycles. While much of this uncertainty reflects a paucity of empirical information about the ways vegetation will respond to elevated CO<sub>2</sub>, it is compounded by the fact that models represent foliar stoichiometry in different ways. For example, many models hold foliar C:N at fixed values that are specific to plant functional types (Goll et al., 2017; Huntingford et al., 2022), despite evidence that foliar C:N changes over time with increasing CO<sub>2</sub> (Du et al., 2019; Wang et al., 2021). Changes in flexible foliar stoichiometry in response to

simulated variations in N deposition and variations in vegetation C for N tradeoffs have been applied in some models (Lawrence et al., 2019; Meyerholt et al., 2020; Meyerholt & Zaehle, 2015; Zhu et al., 2020), but none have parameterized a global scale increase in foliar C:N over time in response to rising CO<sub>2</sub> that reflects observed, directional stoichiometric changes. This leaves a critical gap in our understanding of the ways the land C sink will respond to elevated CO<sub>2</sub>.

Here, we conducted a modeling experiment in which we used empirical data describing changes in foliar C:N under elevated atmospheric CO<sub>2</sub> to parameterize foliar C:N as a function of atmospheric CO<sub>2</sub> in the Community Land Model, version 5 (CLM5; Lawrence et al., 2019). We used this parameterization to explore model sensitivity to fixed versus flexible foliar stoichiometry in response to elevated CO<sub>2</sub>. We ran both flexible and fixed foliar C:N simulations through the year 2100 to quantify the potential effects of changing leaf stoichiometry on global C, N, hydrologic, and energy cycles. Thus, we illuminate the role of foliar chemistry in driving large-scale ecological responses to elevated CO<sub>2</sub>.

## **2 Methods and data**

### *2.1 Development of Community Land Model simulations*

To explore the effects of flexible foliar stoichiometry on modeled C, N, and water cycling, we synthesized data from Free Air Carbon Enrichment (FACE) studies and datasets available on the Long Term Ecological Research database to quantify the degree of change to foliar C:N under elevated CO<sub>2</sub> (See Supporting Information Text S1 and Table S1; Du et al., 2019; Munger & Wofsy, 2022; Sardans et al., 2012; Wang et al., 2021; Welti, 2021; Yang et al., 2011; Yue et al.,

2017; Zou et al., 2020). Our analysis revealed that foliar C:N is ~20% higher under elevated CO<sub>2</sub> treatments compared to ambient CO<sub>2</sub> treatments and that foliar C:N is increasing under elevated CO<sub>2</sub> over time. We used this knowledge to inform a new parameterization of foliar C:N that we implemented into the Community Land Model (CLM, Lawrence et al., 2019). Our new equation represents the change to foliar C:N per ppm atmospheric CO<sub>2</sub> increase:

$$CN_{\text{now}} = CN_{\text{PFT}} + \max(0, CN_{\text{slope}} * \log(CO_{2\_now} / CO_{2\_base})) \quad \text{eqn. 1}$$

where  $CN_{\text{now}}$  represents foliar C:N at any given point in the model run.  $CN_{\text{PFT}}$  is the default parameter foliar C:N values for each plant functional type used in CLM5 (Lawrence et al., 2019).  $CN_{\text{slope}}$  is the slope of the linear relationship between foliar C:N and atmospheric CO<sub>2</sub> concentration, and our simulations used values of 20 and 0 for flexible C:N and fixed C:N simulations, respectively.  $CO_{2\_now}$  represents the atmospheric CO<sub>2</sub> concentration at any given point in time. Finally,  $CO_{2\_base}$  is a baseline CO<sub>2</sub> concentration when leaf C:N ratios start responding to elevated CO<sub>2</sub>; here, we used 310 ppm CO<sub>2</sub>, which occurred in year 1936 in our simulations. The global effect of our parameterization on changes in foliar stoichiometry is illustrated in Supporting Information Fig. S1. We acknowledge that there is significant uncertainty in some of these parameters, but values used here were chosen to provide ranges of foliar stoichiometry in the flexible C:N simulation over the entire 20<sup>th</sup> and 21<sup>st</sup> centuries that remained within realistic ranges based on our data syntheses. Further, prescribing changes in foliar stoichiometry based on empirical data alone may produce ecological changes that could be better represented by altering additional model structures alongside our new parameterization. However, identifying all possible feedbacks that may result from increasing foliar C:N and changing additional model structures was beyond the scope of this work.

We implemented eqn. 1 into CLM5 and ran the model offline with land only, GSWP3 data atmosphere forcing from 1850-2014 following standard protocols (Lawrence et al., 2019; Wieder et al., 2019). We subsequently ran future projections from 2015-2100 by cycling over the GSWP3 input data (2000-2014) and applying a climate change anomaly forcing to atmospheric fields that were derived from the Community Earth System Model 2 (CESM2; Danabasoglu et al., 2020) under the SSP3-7.0 scenario (a business as usual, moderate to high emissions scenario). Land use change, land cover change, atmospheric CO<sub>2</sub> concentration, nitrogen deposition, and all other forcings followed the CMIP6 protocols as applied in CESM2 and CLM5 simulations (Lawrence et al., 2019; Danabasoglu et al., 2020). The use of the anomaly forcing ensures a smooth transition from historical to future climate for land-only simulations and offers a method to isolate potential terrestrial responses to projected climate change (see also Wieder et al., 2015a).

We compared our newly parameterized flexible stoichiometry simulation to a simulation run under the same conditions but with foliar C:N values set to fixed values specific to each plant functional type (PFT). These values remained constant over the course of the simulation in the fixed scenario, but increased over time in the flexible scenario (Supplementary Information Fig. S1). We ran both simulations through the year 2100 to project possible changes to the global C, N and hydrologic cycles in response to the CO<sub>2</sub> driven foliar C:N parameterization.

## *2.2 Contextualization with CMIP6 and GCP data*

To contextualize our findings, we compared CLM simulation results with estimates of the net land C sink from two additional data products. First, we used an observationally derived dataset from the Global Carbon Project (GCP) that spans the years 1960 through 2015 (Le Quéré et al., 2015). More recent iterations of the GCP use land models, including CLM, to estimate the historical terrestrial C sink (Friedlingstein et al., 2022). Data from Le Quéré et al. (2015), however, use a bookkeeping method to estimate land C uptake as the difference between CO<sub>2</sub> emissions estimates and the sum of atmospheric and ocean inventories. Accordingly, the CGP data are intended to provide an observationally based constraint for the magnitude of the historical land C sink and its associated uncertainty that we can compare with our fixed and flexible simulations (as in Lawrence et al. (2019)). Second, we compared our results to an 11-member ensemble of Coupled Model Intercomparison Project (CMIP6) simulations conducted under historical and SSP3-7.0 scenarios that are available on the CMIP6 data portal (<https://esgf-node.llnl.gov/search/cmip6/>). Briefly, monthly grid cell net biome production fluxes were summed to calculate annual fluxes and weighted by model specific grid cell area and land fraction fields and summed to calculate global totals. We acknowledge that our CMIP6 ensemble includes results from CESM2, which includes the fixed stoichiometry results presented here, but from fully coupled simulations. The CMIP6 results provide uncertainty estimates from a multi-model ensemble in anticipated ranges of the potential terrestrial C sink under the SPP3-70 scenario.

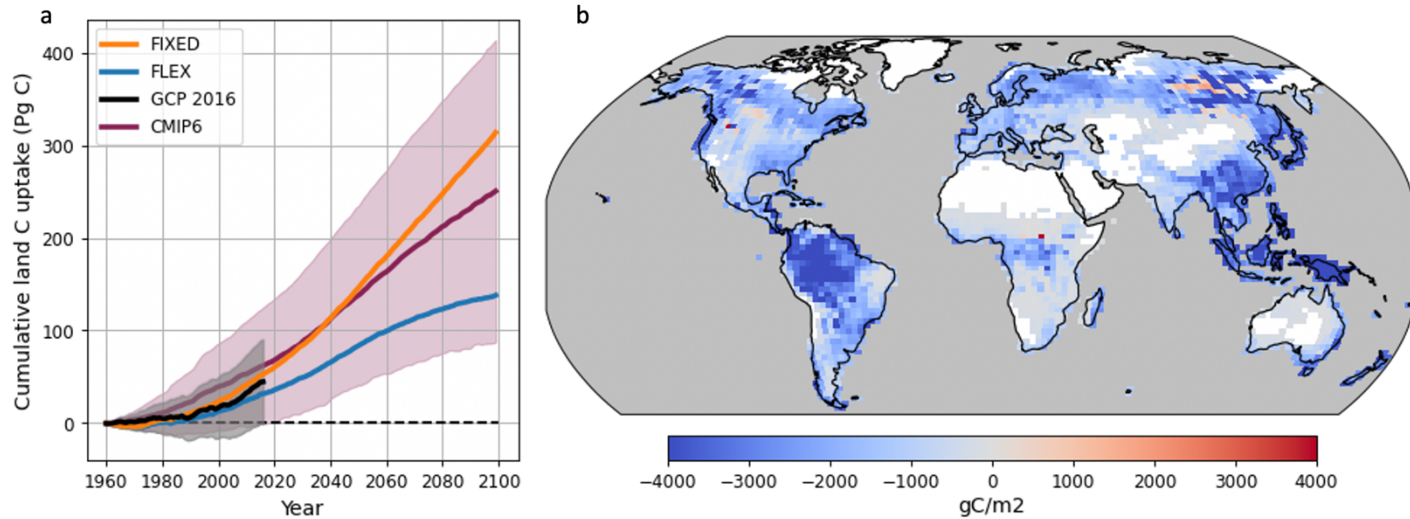
### *2.3 Statistical analyses*

After running the simulations, we analyzed the data using the Xarray (Hoyer & Hamman, 2017) and Matplotlib (Hunter, 2007) packages in Python version 3.9.7 that was run in a Jupyter

notebook. We examined spatial and temporal changes in GPP, NPP, LAI, N mineralization, N fixation, cumulative land C uptake, ecosystem respiration, evapotranspiration, and runoff to quantify biogeochemical and biophysical effects of flexible and fixed foliar stoichiometry on land processes.

### **3 Results and Discussion**

Implementing flexible foliar stoichiometry reduced the global terrestrial C sink more than two-fold (179 Pg C) relative to the fixed scenario by the end of the 21<sup>st</sup> century, from 317 Pg to 138 Pg C (Fig. 1a). For context, by 2100, the difference in the cumulative land C sink between the two scenarios is equivalent to an 84-ppm change in atmospheric CO<sub>2</sub> (Ballantyne et al., 2012), comparable to the increase in atmospheric CO<sub>2</sub> observed over the past 45 years (Keeling et al., 2001). The land C sink is not uniformly distributed across the globe (Supplementary Information Fig. 2Sb), and reductions in the land C sink in the flexible scenario were also unevenly distributed. For example, tropical and boreal forests showed the largest declines in cumulative land C uptake (Fig. 1b). Under the flexible scenario, terrestrial ecosystems remained a net C sink through the end of the century, largely due to consistently high tropical C uptake, although some boreal regions became a C source by 2100 (Supplementary information Fig. 2Sc). On an annual basis, the global rate of land C uptake was reduced by 22.4 Pg C yr<sup>-1</sup> in the flexible scenario, suggesting a weakening of the land C sink when foliar C:N responded to rising CO<sub>2</sub> (Supplementary information Fig. 2Sa). Thus, stoichiometric flexibility in Earth's ecosystems may be a strong determinant of the future strength of the global terrestrial C sink.

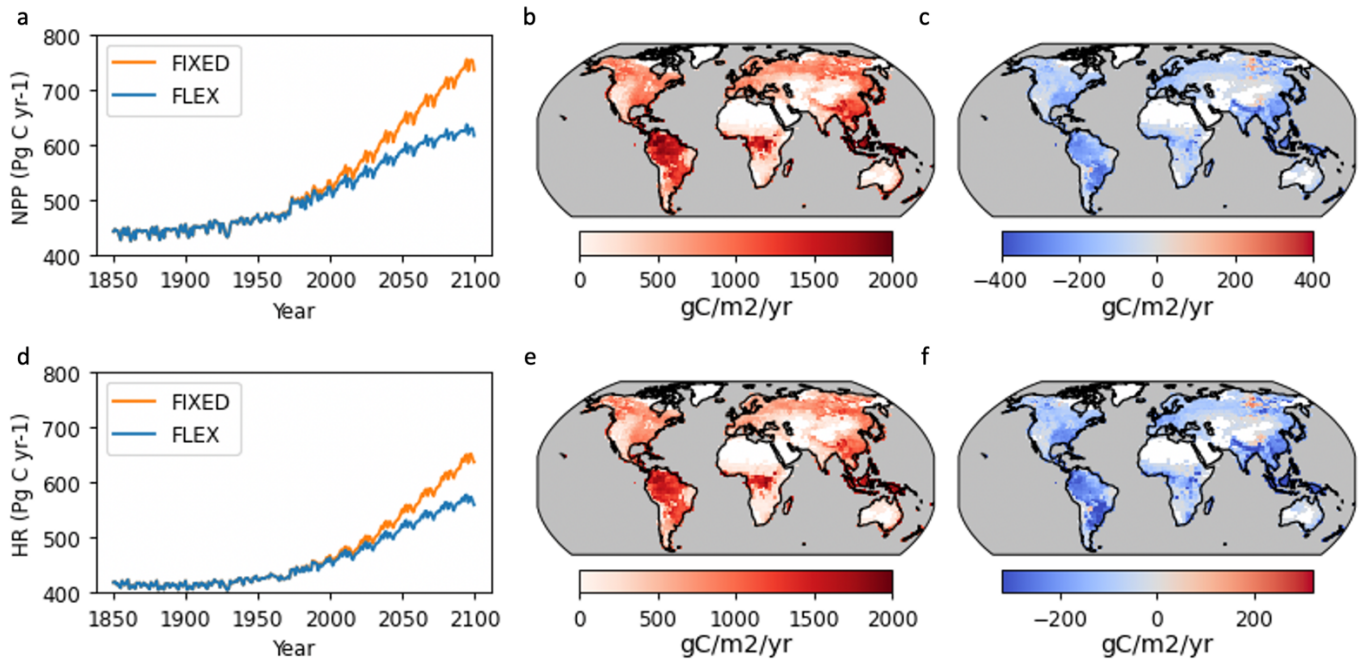


**Figure 1.** The land C sink is reduced 2-fold in a scenario with flexible foliar C:N (FLEX) compared to a scenario with fixed foliar C:N (FIXED). (a) Cumulative land C uptake from 1960 to 2100 for FIXED and FLEX compared to observation-based estimates of the global land C sink from the Global Carbon Project (GCP, black with grey shading) and the average of 11 models from the Coupled Model Intercomparison Project (CMIP6, purple line and shading) (b) Spatial difference in land C uptake generated by the FIXED and FLEX scenarios averaged over the last 10 years of the simulation (2091-2100, calculated as FLEX – FIXED).

Results generated in both the fixed and flexible scenarios were within the confidence intervals of observationally derived cumulative land C uptake values generated by the Global Carbon Project (GCP; Fig 1a, black line, Le Quéré et al., 2015), as well as results generated by 11 models from the sixth phase of the Coupled Model Intercomparison Project (CMIP6, Fig. 1a, purple line). Similarities between the models and GCP observations suggest that both fixed and flexible CLM5 simulations represent plausible land C sinks over the historical record. However, the future trajectory will depend on ecological processes that remain poorly understood and have not been fully incorporated into models. Nevertheless, our findings are comparable to other

simulated reductions in land C uptake due to future N and P constraints (240 Pg C; Wieder et al., 2015b). Collectively, these findings suggest that the future global C sink will likely be smaller than current model projections, but accurately characterizing the extent of future land C uptake requires a more complete understanding of ecological responses to rising CO<sub>2</sub> and improved model structures that represent those processes.

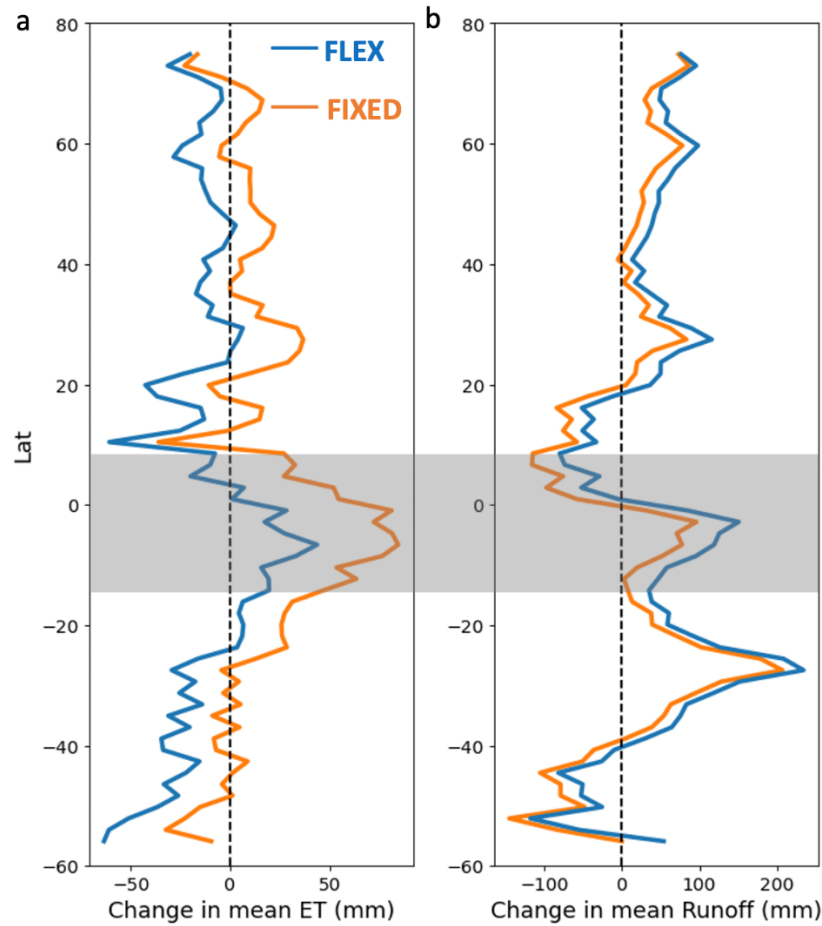
The reduced strength of the terrestrial C sink in the flexible scenario was a direct result of reduced plant photosynthetic capacity with increasing foliar C:N. Gross primary production (GPP), net primary production (NPP), leaf area index (LAI), and heterotrophic respiration all declined in the flexible scenario relative to the fixed scenario (Fig. 2, Supplementary Information Figs. S3 & S4). These findings are consistent with previous results showing a dampening of CO<sub>2</sub> fertilization effects on photosynthesis over time (Wang et al., 2020). In our study, reductions in NPP occurred globally but were strongest in tropical and boreal forest regions. The decline in NPP stemmed directly from the fact that foliar N concentrations determine leaf-level photosynthetic rates, as seen in observations (Reich et al., 1997) and as implemented in CLM (Lawrence et al., 2019; Ali et al., 2016). In the flexible scenario, reductions in leaf-level photosynthesis rates were compounded by canopy-scale feedbacks from concurrent reductions in LAI. Thus, our simulations revealed that foliar chemistry strongly influenced leaf- and canopy-level photosynthetic activity, which directly governs the magnitude of the terrestrial C sink and the uncertainty surrounding it.



**Figure 2.** Simulations with flexible foliar C:N (FLEX) produced lower rates of net primary productivity (NPP) and heterotrophic respiration (HR) than scenarios where foliar C:N is held constant (FIXED). (a) NPP over the course of each simulation run. (b) Spatial distribution of NPP averaged over the last 10 years of the FIXED control scenario (2091 – 2100). (c) Spatial distribution of the differences between the FIXED and FLEX scenario over the last 10 years of the simulation. (d) Change in HR in the two scenarios over time. (e) HR in the control (FIXED) scenario in the last 10 years of the simulation. (f) Map of spatial differences in HR between the FIXED and FLEX scenario over the last 10 years of the simulation. C and F are calculated as FLEX - FIXED. Both HR and NPP are reduced in the flexible C:N scenario.

In addition to changes in C cycling, we observed strong effects of flexible stoichiometry on hydrologic cycling. In the flexible simulation, global runoff increased by 38 mm yr<sup>-1</sup> by the end of the century, while global evapotranspiration (ET) declined by the same amount relative to the fixed stoichiometry simulation (Fig. 3, Supplemental Information Fig. S5). The hydrologic

perturbations were especially strong in tropical regions and mirrored declines in GPP, LAI, and plant water use efficiency in the flexible scenario compared to the fixed scenario (compare Supplemental Information Figs. S3-S5). Thus, beyond the biogeochemical changes stemming from reduced photosynthetic capacity with flexible stoichiometry, the observed plant physiological responses also catalyzed ecohydrological changes that would modify terrestrial climate feedbacks in coupled simulations with an interactive model atmosphere (Langenbrunner et al., 2019; Zarakas et al., 2020). For example, lower rates of evapotranspiration would likely reduce surface humidity and evaporative cooling, thereby warming local temperatures, reducing cloud cover, altering boundary-layer dynamics, and changing regional precipitation (Cui et al., 2022; Lemordant et al., 2018). Future work should consider the potential magnitude of these biophysical effects in fully coupled simulations. However, our findings highlight how nutrient feedbacks can moderate both C and water cycles in terrestrial ecosystems and underscore the importance of considering integrated Earth system responses to improve our ability to predict future biogeochemical and climate dynamics.



**Figure 3.** In a model scenario with flexible foliar C:N (FLEX), global evapotranspiration (ET) decreased and global runoff increased compared to a scenario with fixed foliar C:N (FIXED). (a) Change in ET between present day and the year 2100 in the FLEX and fixed foliar C:N (FIXED) scenarios averaged across latitudes. (b) Changes in runoff between present day and the year 2100 in the FLEX and FIXED scenarios averaged across latitudes. Grey shading highlights that the largest changes to ET and runoff are in the tropics.

More accurately predicting the effects of changing ecosystem stoichiometry on C and hydrologic cycles will require at least two important advances: First, a more complete understanding

surrounding of the ecological drivers and effects of stoichiometric flexibility; and second, improved model structures that accurately represent those ecological processes. Our empirical understanding of the consequences of stoichiometric flexibility is still poor, but our results provide compelling evidence of its importance. Moreover, the large declines in C storage we observed in the flexible scenario most strongly reflect the direct effects of declining plant productivity as foliar C:N ratios increase. This is consistent with the downregulation of photosynthesis under elevated CO<sub>2</sub> commonly observed in longer-term studies (Ellsworth et al, 2004) as vegetation optimizes photosynthetic processes to cope with reduced plant N. However, concurrent declines in litter quality (Supplemental Information Fig. S1d-f) are also known to reduce decomposition and N mineralization rates, which could further suppress plant production indirectly via enhanced N limitation (Supplemental information Fig. S6; Craine et al., 2018; Luo et al., 2004; Mason et al., 2022).

Our experimental design did not allow for direct quantification of indirect biogeochemical effects because soil organic matter stocks in CLM – which also have fixed stoichiometry – are much larger than litter pools and provide the bulk of mineral N required plant growth in the model. Future empirical work should evaluate this assumption by quantifying indirect effects of plant-soil feedbacks on ecosystem responses to elevated CO<sub>2</sub>. Given theoretical expectations that changes in plant stoichiometry should elicit strong indirect effects on ecosystem responses to elevated CO<sub>2</sub> (Liang et al., 2016; Mason et al., 2022), the overall declines in C and water cycling we observed under the flexible foliar C:N scenario may be conservative. Therefore, future studies exploring the indirect effects of shifting foliar C:N and potential feedbacks on plant

productivity are critical for more accurately predicting the land C sink as atmospheric CO<sub>2</sub> concentrations continue to rise.

As our understanding of the effects of stoichiometric flexibility improves, model structures will need to be modified. No model includes all possible ecological processes and feedbacks, creating opportunities for additional structural improvement. Such advances would reduce model structural uncertainty, a key step toward improving our ability to realistically predict the ways ecosystems will function in the future. Structural uncertainty analyses reveal areas where models may be able to predict historic patterns, but in ways that are not necessarily consistent with underlying ecological processes (i.e. we might be getting the right answer but for the wrong reason; Bonan & Doney 2018; Dietze et al., 2018; Medlyn et al., 2015). As an example, both of our simulations capture the magnitude of the historic land C sink but show large divergence in their future projections (Fig 1a). Further, another recent study implementing three different model structures to represent vegetation stoichiometry produced a larger land C sink with flexible plant tissue C:N relative to control scenarios with fixed C:N values, the opposite of our observed trends (Zhu et al., 2020). Together, these findings highlight that model structures that recreate observed patterns without fully representing underlying ecological processes limit the predictive capacity of models to accurately simulate appropriate ecosystem responses to global change (Dietze et al., 2018; Medlyn et al., 2015). The link between pattern and process can be strengthened by integrating modeling and empirical disciplines because model fidelity to ecological processes hinges on our ability to translate ecological knowledge into mathematical equations (Bonan & Doney 2018; Bradford et al., 2016; Kyker-Snowman et al., 2022). Integrating results from manipulative experiments, especially long-term elevated CO<sub>2</sub> studies,

with model future scenarios examining the indirect effects of foliar and litter stoichiometry (Kyker-Snowman et al., 2022; Wieder et al., 2019) will help reduce model structural uncertainty that underlies the numerous and divergent predictions of the terrestrial C sink. While there are other model structural changes that likely need to follow from our change to foliar C:N, we present this parameterization of foliar chemistry as a first step toward addressing our growing understanding of the ways ecosystems are changing under elevated CO<sub>2</sub>.

Our results indicate that increases in foliar C:N could have important and far-reaching effects on biogeochemical cycles, ecosystems, and climate, and could therefore have profound implications for human societies. We show that feedbacks between CO<sub>2</sub> and foliar stoichiometry could greatly reduce the strength of the global terrestrial C sink. If so, more rapid increases in atmospheric CO<sub>2</sub> could accelerate the pace of climate change, exacerbate climate hazards, food and water security risks, biodiversity loss, among other adverse consequences (Pörtner et al., 2022). Further, water security is central to climate change adaptation and mitigation (Caretta et al., 2022). Our results suggest strong perturbations to the global hydrologic cycle due to changes to foliar stoichiometry, which is likely to alter global water distributions and the ability of communities to adapt to change.

#### **4 Conclusion**

The actual response of Earth's terrestrial ecosystems to ongoing increases in atmosphere CO<sub>2</sub> concentrations will be complex, as indicated by the numerous model structures and conflicting results presented by our study and others (Friedlingstein et al. 2022; Kovenock et al., 2021; Zhu et al., 2020). Rising CO<sub>2</sub> has already created a cascade of feedbacks in Earth's terrestrial

ecosystems, including enhanced plant production, reduced N availability, changes in plant water use efficiency, declines in food quality, and altered trophic interactions (Friedlingstein et al., 2022, Lincoln et al., 1993, Mason et al., 2022; Myers et al., 2014; Wang & Feng, 2012). Our study introduces a new, CO<sub>2</sub> driven parameterization of foliar chemistry into CLM to attempt to explore global ecosystem responses to observed stoichiometric patterns. However, parallel empirical and experimental efforts – including modified model structures informed from those efforts – are critically needed to predict the effects of changing stoichiometry more accurately. Estimating the future of Earth’s terrestrial C sink will undoubtedly include some uncertainty but integrating new empirical and modeling and efforts will increase our confidence in the validity of those predictions.

## **Acknowledgements**

This research was supported by a National Science Foundation Research Coordination Grant (INCyTE; DEB-1754126) to CCC and WRW to investigate nutrient cycling in terrestrial ecosystems. We would also like to thank S. Levis at the National Center for Atmospheric Research (NCAR) for assistance with the model simulations. This material is based upon work supported by NCAR, which is a major facility sponsored by the National Science Foundation (NSF) under Cooperative Agreement No. 1852977. WRW was supported in part by NSF award numbers 1926413, 2031238, and 2224439.

## **Open Research Statement**

Data from Community Land Model simulations can be found at the following link:  
<https://doi.org/10.5065/8spx-e662>. Data from CMIP6 can be retrieved from <https://esgf->

node.llnl.gov/search/cmip6/. Global Carbon Project dataset used for this analysis is included in the repository for this manuscript, <https://doi.org/10.5281/zenodo.7814787>.

Code used to download data, run analyses, produce graphics and process CMIP6 data can be found on Zenodo at <https://doi.org/10.5281/zenodo.7814787>. Data from the Harvard Forest and Konza Prairie LTERs detailed in the Supplementary Information can be found at the following links respectively:

<https://harvardforest1.fas.harvard.edu/sites/harvardforest.fas.harvard.edu/files/data/p06/hf069/hf069-04-canopy-chem.csv> (Munger et al., 2022).

<http://dx.doi.org/10.6073/pasta/6cff694ce8fecb3e589e415b762b091e> (Welti et al., 2021).

Data from SPRUCE can be downloaded from: <https://doi.org/10.25581/spruce.090/1780604>.

FACE data summarized for these analyses are available from Du et al. (2019), Sardans et al. (2012), Wang et al. (2021), Yang et al. (2011), Yue et al. (2017), Zou et al. (2020).

#### **Author Contributions**

CC, EH, and WW conceived of the original idea. WW ran the model simulations and processed the CMIP6 results. EH analyzed the data and wrote the first draft of the manuscript. EH, CC, GB and WW all contributed to revisions and production of the final version of the manuscript.

#### **Declaration of Competing Interest**

The authors declare that they have no competing interests.

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