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Flexible Foliar Stoichiometry Reduces the Magnitude of the Global Land Carbon Sink

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Key Points:

- A flexible, CO_2-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

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract

Increased plant growth under elevated carbon dioxide (CO_2) 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_2, our understanding of potential ecological consequences of foliar stoichiometric flexibility is incomplete. Here, we illustrate that when we incorporated CO_2-driven increases in foliar stoichiometry into the Community Land Model the projected land C sink decreased two-fold by the end of the century compared to simulations with fixed foliar chemistry. Further, CO_2-driven increases in foliar C:N profoundly altered Earth's hydrologic cycle, reducing evapotranspiration and increasing runoff, and reduced belowground N cycling rates. These findings underscore the urgency of further research to examine 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_2) increases, plants grow more and take up more CO_2, which could slow the pace of climate change. However, higher CO_2 dilutes leaf nutrient concentrations, which could ultimately limit plant growth as CO_2 continues to rise. The change in leaf chemistry in response to rising CO_2 is not well represented in models used to predict future productivity and the land carbon sink. By simulating CO_2-driven changes in leaf chemistry in the Community Land Model, we quantified potential effects of shifting leaf chemistry on future vegetation growth and global C, nutrient, and hydrologic cycles. The 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_2. 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_2) emissions (Costanza et al., 1997; Friedlingstein et al., 2022). Despite the important role of terrestrial ecosystems in reducing the atmospheric CO_2 burden, considerable uncertainty remains about the persistence of this C sink under climate change (Arora et al., 2020; Friedlingstein et al., 2022). 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_2 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_2.

Uncertainty surrounding the representation of ecological processes in land models originates from both an incomplete understanding of ecological processes and feedbacks, 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, Cleveland, Lawrence, & Bonan, 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_2.

Rising atmospheric CO_2 creates multiple ecosystem feedbacks that may interact to regulate long-term CO_2 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_2 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_2 is a well-documented shift in foliar stoichiometry, the ratios of C-to-nutrients in leaf tissues (Gifford et al., 2000; Mason et al., 2022; Myers et al., 2014; Penuelas et al., 2020). Foliar C:N ratios increase under elevated CO_2 in both field and manipulation experiments (Du et al., 2019; Penuelas et al., 2020; C. 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., 2022). Flexible foliar stoichiometry (i.e., ranges of foliar C:N values at which vegetation can still grow) may allow sustained productivity with CO_2 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_2 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_2 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_2, 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_2 (Du et al., 2019; C. Wang et al., 2021). The effects of flexible foliar stoichiometry in response to simulated variations in N deposition and variations in vegetation C for N tradeoffs have been explored in some models (Kou-Giesbrecht et al., 2023; Lawrence et al., 2019; Meyerholt et al., 2020; Meyerholt & Zaehle, 2015; Zhu et al., 2020), but the magnitude of changes to foliar C:N over time in response to rising CO_2 remains poorly evaluated and constrained in models. This leaves a critical gap in our understanding of the ways the land C sink will respond to elevated CO_2.

Here, we conducted a model sensitivity experiment in which we parameterized foliar C:N as a function of atmospheric CO_2 in the Community Land Model, version 5 (CLM5; Lawrence et al., 2019) to reflect empirically observed increases in foliar C:N (C. Wang et al., 2021; Mason et al., 2022; hereafter "flexible C:N"). Although the default parameterization of CLM5 ostensibly represents flexible foliar stoichiometry, we found that foliar C:N ratios simulated in the model were effectively fixed target parameters (hereafter "fixed C:N"). Thus, 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. Our results highlight the potentially critical role of foliar chemistry in driving large-scale ecological responses to elevated CO_2.

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 examined previously published syntheses of Free Air Carbon Enrichment (FACE) studies and other sources available on the

Long Term Ecological Research (LTER) database to estimate the degree of change to foliar C:N under elevated CO_2 (Du et al., 2019; Munger & Wofsy, 2022; Sardans et al., 2012; C. Wang et al., 2021; Welti, 2021; Yang et al., 2011; Yue et al., 2017; Zou et al., 2020). Based on the results of these studies (See Text S1 in Supporting Information S1), we parameterized the change to foliar C:N per ppm atmospheric CO_2 increase:

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

where CN_{now} represents foliar C:N at any given point in the model run. CN_{PFT} is the default parameter foliar C:N value for each plant functional type (PFT) used in CLM5 (Lawrence et al., 2019). CN_{slope} is the slope of the linear relationship between foliar C:N and atmospheric CO_2 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_2 concentration at any given point in time. Finally, CO_{2_base} is a baseline CO_2 concentration when leaf C:N ratios start responding to elevated CO_2; here, we used 310 ppm CO_2, which occurred in year 1936 in our simulations. The global effect of our parameterization on changes in foliar stoichiometry is illustrated in Figure S1 in Supporting Information S1.

We acknowledge that there is significant uncertainty in some of these parameters. However, the values used provide ranges of foliar stoichiometry that remained within realistic ranges based on the data sets we examined above. Further, prescribing changes in foliar stoichiometry based on CO_2 data alone may not fully capture changes to foliar chemistry in complex ecosystems experiencing multiple disturbances such as N deposition, harvesting, fires, and changes to growing season length. While these ecological changes could be better represented by altering additional model structures alongside our new parameterization, identifying all possible feedbacks that may result from and contribute to increasing foliar C:N and changing additional model structures was beyond the scope of this work.

We implemented Equation 1 into CLM5 and ran the model offline with land only, GSWP3 data atmosphere forcing from 1850 to 2014 following standard protocols (Lawrence et al., 2019; Wieder et al., 2019). We subsequently ran projections from 2015 to 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_2 concentration, nitrogen deposition, and all other forcings followed the Coupled Model Intercomparison Project (CMIP6) protocols as applied in CESM2 and CLM5 simulations (Danabasoglu et al., 2020; Lawrence et al., 2019). 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, Cleveland, Lawrence, & Bonan, 2015).

We compared our newly parameterized flexible C:N simulation to a simulation run under the same conditions but with foliar C:N values set to fixed values specific to each PFT. These values remained constant over the course of the simulation in the fixed C:N scenario, but increased over time in the flexible C:N scenario (Figure S1 in Supporting Information 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_2 driven foliar C:N parameterization.

2.2. Contextualization With CMIP6 and Global Carbon Project 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 data set 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_2 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 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 C:N results presented here, but

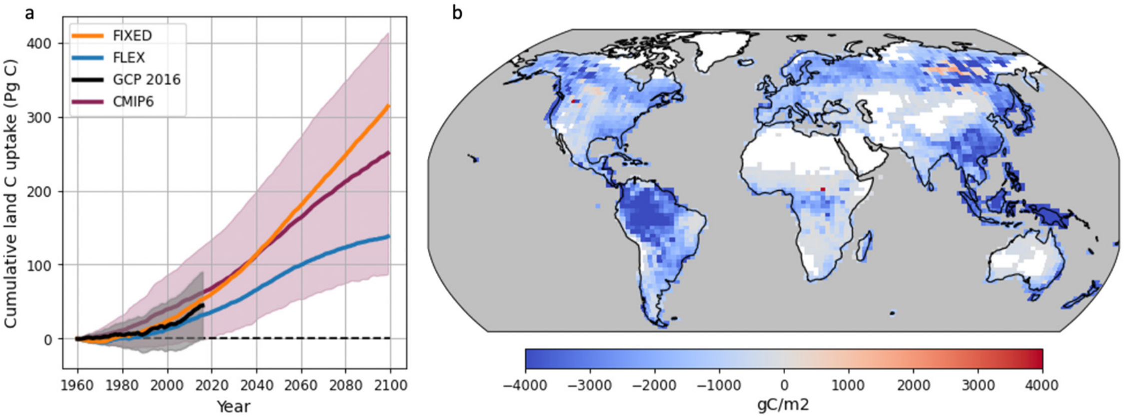

Figure 1. The land C sink is reduced 2-fold in a scenario with flexible foliar C:N (FLEX) compared to a scenario with fixed foliar C:N (FIXED). (a) Cumulative land C uptake from 1960 to 2100 for FIXED and FLEX compared to observation-based estimates of the global land C sink from the Global Carbon Project (GCP, black line, with 95% confidence interval in gray shading) and the average of 11 models from the Coupled Model Intercomparison Project (CMIP6, purple line, with 95% confidence interval in purple 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).

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 SPP3-7.0 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 (Kluyver et al., 2016). We examined spatial and temporal changes in gross primary production (GPP), NPP, leaf area index (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 CO_2-driven flexible foliar stoichiometry reduced the global terrestrial C sink more than two-fold (179 Pg C) relative to the fixed C:N scenario by the end of the 21st century, from 317 Pg to 138 Pg C (Figure 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_2 (Ballantyne et al., 2012), comparable to the increase in atmospheric CO_2 observed over the past 45 years (Keeling et al., 2001). The land C sink is not uniformly distributed across the globe (Figure 2Sb in Supporting Information S1), and reductions in the land C sink in the flexible C:N scenario were also unevenly distributed. For example, tropical and boreal forests showed the largest declines in cumulative land C uptake (Figure 1b). Under the flexible C:N 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 (Figure 2Sc in Supporting Information S1). On an annual basis, the global rate of land C uptake was reduced by 22.4 Pg C yr^{-1} in the flexible scenario, suggesting a weakening of the land C sink when foliar C:N responded to rising CO_2 (Figure 2Sa in Supporting Information S1). Thus, stoichiometric flexibility in Earth's ecosystems may be a strong determinant of the future strength of the global terrestrial C sink.

Results generated in both the fixed and flexible C:N scenarios were within the confidence intervals of observationally derived cumulative land C uptake values generated by the GCP (Figure 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, Figure 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, Cleveland, Smith, & Todd-Brown, 2015). Collectively,

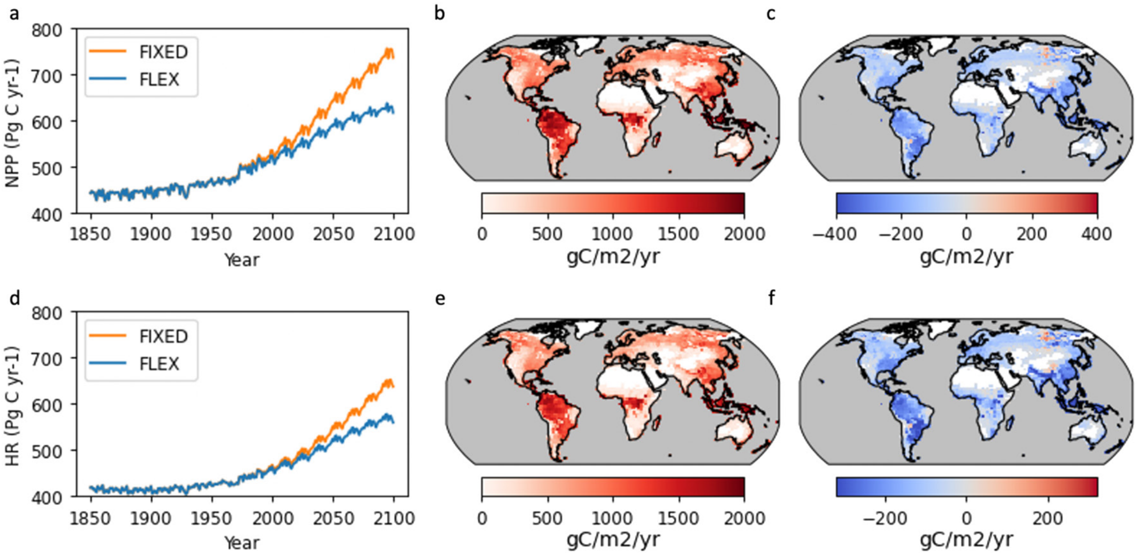

Figure 2. Simulations with flexible foliar C:N (FLEX) produced lower rates of net primary productivity (NPP) and heterotrophic respiration (HR) than scenarios where foliar C:N is held constant (FIXED). (a) NPP over the course of each simulation run. (b) Spatial distribution of NPP averaged over the last 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.

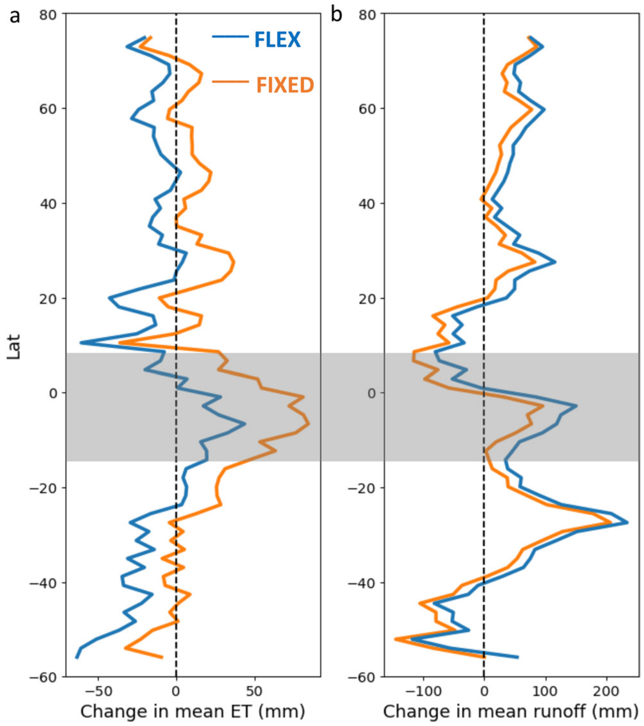

Figure 3. In a model scenario with flexible foliar C:N (FLEX), global evapotranspiration (ET) decreased and global runoff increased compared to a scenario with fixed foliar C:N (FIXED). (a) Change in ET between present day and the year 2100 in the FLEX and FIXED scenarios averaged across latitudes. (b)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

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_2 and improved model structures that represent those processes.

The reduced strength of the terrestrial C sink in the flexible C:N scenario was a direct result of reduced plant photosynthetic capacity with increasing foliar C:N. GPP, NPP, LAI, and heterotrophic respiration all declined in the flexible scenario relative to the fixed scenario (Figure 2, Figures S3 and S4 in Supporting Information S1). These findings are consistent with previous results showing a dampening of CO_2 fertilization effects on photosynthesis over time (S. 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 (Ali et al., 2016; Lawrence et al., 2019). 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.

In addition to changes in C cycling, we observed strong effects of flexible stoichiometry on hydrologic cycling. In the flexible C:N simulation, global runoff increased by 38 mm yr^{-1} by the end of the century, while global evapotranspiration (ET) declined by the same amount relative to the fixed C:N simulation (Figure 3, Figure S5 in Supporting Information S1). 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 Figures S3–S5 in Supporting

Information S1). 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.

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 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 C:N 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_2 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 (Figures S1d–S1f in Supporting Information S1) are also known to reduce decomposition and N mineralization rates, which could further suppress plant production indirectly via enhanced N limitation (Figure S6 in Supporting Information S1; 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 by 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_2. Given theoretical expectations that changes in plant stoichiometry should elicit strong indirect effects on ecosystem responses to elevated CO_2 (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_2 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 (Figure 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_2 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 $CO_{2.}$

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_2 and foliar stoichiometry could greatly reduce the strength of the global terrestrial C sink. If so, more rapid increases in atmospheric CO_2 could accelerate the pace of climate change, exacerbate climate hazards, food and water security risks, and 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 are 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 atmospheric CO_2 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_2 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; G. Wang & Feng, 2012). Our study presents a model sensitivity experiment that represents an important first step toward understanding possible global ecosystem responses to CO_2-driven changes to foliar stoichiometry. However, additional empirical and experimental 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 new empirical and modeling efforts will increase our confidence in the validity of those predictions.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Data from Community Land Model simulations are found in Wieder (2023). CMIP6 data are available through the Earth System Grid Federation system (ESGF; https://esgf-node.llnl.gov/search/cmip6/). The models and ensemble members used can be found in Table S1 in Supporting Information S1. Global Carbon Project data used for this analysis are included in the Zenodo repository for this manuscript (Hauser, 2023), along with code used to download data, run analyses, produce graphics and process CMIP6 data. Data from Harvard Forest are available in Munger & Wofsy, 2022 and data from Konza Prairie LTER are available in Welti (2021). Data from SPRUCE are available in Phillips et al. (2021). FACE data are available from Du et al. (2019), Sardans et al. (2012), C. Wang et al. (2021), Yang et al. (2011), Yue et al. (2017), and Zou et al. (2020).

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References

Ali, A. A., Xu, C., Rogers, A., Fisher, R. A., Wullschleger, S. D., Massoud, E. C., et al. (2016). A global scale mechanistic model of photosynthetic capacity (LUNA V1. 0). *Geoscientific Model Development*, *9*(2), 587–606. https://doi.org/10.5194/gmd-9-587-2016

Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein, P., et al. (2020). Carbon–concentration and carbon–climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences*, *17*(16), 4173–4222. https://doi.org/10.5194/bg-17-4173-2020

Ballantyne, A. Á., Alden, C. Á., Miller, J. Á., Tans, P. Á., & White, J. W. C. (2012). Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature*, *488*(7409), 70–72. https://doi.org/10.1038/nature11299

Bonan, G. B., & Doney, S. C. (2018). Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models. *Science*, *359*(6375), eaam8328. https://doi.org/10.1126/science.aam8328

Bradford, M. A., Wieder, W. R., Bonan, G. B., Fierer, N., Raymond, P. A., & Crowther, T. W. (2016). Managing uncertainty in soil carbon feedbacks to climate change. *Nature Climate Change*, *6*(8), 751–758. https://doi.org/10.1038/nclimate3071

Caretta, A. M. M. A., Arfanuzzaman, R. B. M., Morgan, S. M. R., & Kumar, M. (2022). Water. In *Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., et al. (1997). The value of the world's ecosystem services and natural capital. *Nature*, *387*(6630), 253–260. https://doi.org/10.1038/387253a0

Craine, J. M., Elmore, A. J., Wang, L., Aranibar, J., Bauters, M., Boeckx, P., et al. (2018). Isotopic evidence for oligotrophication of terrestrial ecosystems. *Nature Ecology & Evolution*, *2*(11), 1735–1744. https://doi.org/10.1038/s41559-018-0694-0

Cui, J., Lian, X., Huntingford, C., Gimeno, L., Wang, T., Ding, J., et al. (2022). Global water availability boosted by vegetation-driven changes in atmospheric moisture transport. *Nature Geoscience*, *15*(12), 982–988. https://doi.org/10.1038/s41561-022-01061-7

Dagon, K., Sanderson, B. M., Fisher, R. A., & Lawrence, D. M. (2020). A machine learning approach to emulation and biophysical parameter estimation with the Community Land Model, version 5. *Advances in Statistical Climatology, Meteorology and Oceanography*, *6*(2), 223–244. https://doi.org/10.5194/ascmo-6-223-2020

Danabasoglu, G., Lamarque, J. F., Bacmeister, J., Bailey, D. A., DuVivier, A. K., Edwards, J., et al. (2020). The community Earth system model version 2 (CESM2. *Journal of Advances in Modeling Earth Systems*, *12*(2), e2019MS001916. https://doi.org/10.1029/2019ms001916

Dietze, M. C., Fox, A., Beck-Johnson, L. M., Betancourt, J. L., Hooten, M. B., Jarnevich, C. S., et al. (2018). Iterative near-term ecological forecasting: Needs, opportunities, and challenges. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(7), 1424–1432. https://doi.org/10.1073/pnas.1710231115

Dong, N., Wright, I. J., Chen, J. M., Luo, X., Wang, H., Keenan, T. F., et al. (2022). Rising CO_2 and warming reduce global canopy demand for nitrogen. *New Phytologist*, *235*(5), 1692–1700. https://doi.org/10.1111/nph.18076

Du, C., Wang, X., Zhang, M., Jing, J., & Gao, Y. (2019). Effects of elevated CO_2 on plant C-N-P stoichiometry in terrestrial ecosystems: A meta-analysis. *Science of the Total Environment*, *650*, 697–708. https://doi.org/10.1016/j.scitotenv.2018.09.051

Dynarski, K. A., Soper, F. M., Reed, S. C., Wieder, W. R., & Cleveland, C. C. (2022). Patterns and controls of foliar nutrient stoichiometry and flexibility across United States forests. *Ecology*, *104*(2), e3909. https://doi.org/10.1002/ecy.3909

Ellsworth, D. S., Reich, P. B., Naumburg, E. S., Koch, G. W., Kubiske, M. E., & Smith, S. D. (2004). Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland and desert. *Global Change Biology*, *10*(12), 2121–2138. https://doi.org/10.1111/j.1365-2486.2004.00867.x

Fisher, R. A., Wieder, W. R., Sanderson, B. M., Koven, C. D., Oleson, K. W., Xu, C., et al. (2019). Parametric controls on vegetation responses to biogeochemical forcing in the CLM5. *Journal of Advances in Modeling Earth Systems*, *11*(9), 2879–2895. https://doi.org/10.1029/2019ms001609

Friedlingstein, P., Jones, M. W., O'Sullivan, M., Andrew, R. M., Bakker, D. C. E., Hauck, J., et al. (2022). Global carbon budget 2021. *Earth System Science Data*, *14*(4), 1917–2005. https://doi.org/10.5194/essd-14-1917-2022

Friend, A. D., Arneth, A., Kiang, N. Y., Lomas, M., Ogee, J., Rödenbeck, C., et al. (2007). FLUXNET and modelling the global carbon cycle. *Global Change Biology*, *13*(3), 610–633. https://doi.org/10.1111/j.1365-2486.2006.01223.x

Gifford, R. M., Barrett, D. J., & Lutze, J. L. (2000). The effects of elevated [CO_2] on the C: Nand C:P mass ratios of plant tissues. *Plant and Soil*, *224*, 1–14. https://doi.org/10.1023/a:1004790612630

Gojon, A., Cassan, O., Bach, L., Lejay, L., & Martin, A. (2022). The decline of plant mineral nutrition under rising CO_2: Physiological and molecular aspects of a bad deal. *Trends in Plant Science*, *28*(2), 185–198. https://doi.org/10.1016/j.tplants.2022.09.002

Goll, D. S., Winkler, A. J., Raddatz, T., Dong, N., Prentice, I. C., Ciais, P., & Brovkin, V. (2017). Carbon–nitrogen interactions in idealized simulations with JSBACH (version 3.10). *Geoscientific Model Development*, *10*(5), 2009–2030. https://doi.org/10.5194/gmd-10-2009-2017

Hauser, E. (2023). Emhauser/FlexibleFoliarCN: Flexible foliar stoichiometry reduces the Magnitude of the global land carbon sink [Software]. Zenodo. https://doi.org/10.5281/zenodo.7814787

Hoyer, S., & Hamman, J. (2017). xarray: ND labeled arrays and datasets in Python. *Journal of Open Research Software*, *5*(1), 10. https://doi.org/10.5334/jors.148

Hunter, J. D. (2007). Matplotlib: A 2D graphics environment. *Computing in Science & Engineering*, *9*(03), 90–95. https://doi.org/10.1109/mcse.2007.55

Huntingford, C., Burke, E. J., Jones, C. D., Jeffers, E. S., & Wiltshire, A. J. (2022). Nitrogen cycle impacts on CO_2 fertilisation and climate forcing of land carbon stores. *Environmental Research Letters*, *17*(4), 044072. https://doi.org/10.1088/1748-9326/ac6148

Keeling, C. D., Piper, S. C., Bacastow, R. B., Wahlen, M., Whorf, T. P., Heimann, M., & Meijer, H. A. (2001). *Exchanges of atmospheric CO_2 and $13CO_2$ with the terrestrial biosphere and oceans from 1978 to 2000. I. Global aspects*. UC San Diego: Scripps Institution of Oceanography.

Kluyver, T., Ragan-Kelley, B., Pérez, F., Granger, B., Bussonnier, M., Frederic, J., et al. (2016). Jupyter Notebooks - a publishing format for reproducible computational workflows. In F. Loizides & B. Schmidt (Eds.), *Positioning and power in academic publishing: Players, agents and agendas* (pp. 87–90).

Kou-Giesbrecht, S., Arora, V., Seiler, C., Arneth, A., Falk, S., Jain, A., et al. (2023). Evaluating nitrogen cycling in terrestrial biosphere models: Implications for the future terrestrial carbon sink. https://doi.org/10.5194/egusphere-2023-167

Kovenock, M., Koven, C. D., Knox, R. G., Fisher, R. A., & Swann, A. L. S. (2021). Leaf trait plasticity alters competitive ability and functioning of simulated tropical trees in response to elevated carbon dioxide. *Global Biogeochemical Cycles*, *35*(2), e2020GB006807. https://doi.org/10.1029/2020gb006807

Kyker-Snowman, E., Lombardozzi, D. L., Bonan, G. B., Cheng, S. J., Dukes, J. S., Frey, S. D., et al. (2022). Increasing the spatial and temporal impact of ecological research: A roadmap for integrating a novel terrestrial process into an Earth system model. *Global Change Biology*, *28*(2), 665–684. https://doi.org/10.1111/gcb.15894

Langenbrunner, B., Pritchard, M. S., Kooperman, G. J., & Randerson, J. T. (2019). Why does Amazon precipitation decrease when tropical forests respond to increasing CO_2? *Earth's Future*, *7*, 450–468.

Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., et al. (2019). The community land model version 5: Description of new features, benchmarking, and impact of forcing uncertainty. *Journal of Advances in Modeling Earth Systems*, *11*(12), 4245–4287. https://doi.org/10.1029/2018ms001583

Lemordant, L., Gentine, P., Swann, A. S., Cook, B. I., & Scheff, J. (2018). Critical impact of vegetation physiology on the continental hydrologic cycle in response to increasing CO_2. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16), 4093–4098. https://doi.org/10.1073/pnas.1720712115

Le Quéré, C., Moriarty, R., Andrew, R. M., Canadell, J. G., Sitch, S., Korsbakken, J. I., et al. (2015). Global carbon budget 2014. *Earth System Science Data*, *7*(1), 47–85. https://doi.org/10.5194/essd-7-47-2015

Liang, J., Qi, X., Souza, L., & Luo, Y. (2016). Processes regulating progressive nitrogen limitation under elevated carbon dioxide: A meta-analysis. *Biogeosciences*, *13*(9), 2689–2699. https://doi.org/10.5194/bg-13-2689-2016

Lincoln, D. E., Fajer, E. D., & Johnson, R. H. (1993). Plant-insect herbivore interactions in elevated CO_2 environments. *Trends in Ecology and Evolution*, *8*(2), 64–68. https://doi.org/10.1016/0169-5347(93)90161-h

Luo, Y., Su, B. O., Currie, W. S., Dukes, J. S., Finzi, A., Hartwig, U., et al. (2004). Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, *54*(8), 731–739. https://doi.org/10.1641/0006-3568(2004)054[0731:pnloer]2.0.co;2

Mason, R. E., Craine, J. M., Lany, N. K., Jonard, M., Ollinger, S. V., Groffman, P. M., et al. (2022). Evidence, causes, and consequences of declining nitrogen availability in terrestrial ecosystems. *Science*, *376*(6590), eabh3767. https://doi.org/10.1126/science.abh3767

Medlyn, B. E., Zaehle, S., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hanson, P. J., et al. (2015). Using ecosystem experiments to improve vegetation models. *Nature Climate Change*, *5*(6), 528–534. https://doi.org/10.1038/nclimate2621

Meyerholt, J., Sickel, K., & Zaehle, S. (2020). Ensemble projections elucidate effects of uncertainty in terrestrial nitrogen limitation on future carbon uptake. *Global Change Biology*, *26*(7), 3978–3996. https://doi.org/10.1111/gcb.15114

Meyerholt, J., & Zaehle, S. (2015). The role of stoichiometric flexibility in modelling forest ecosystem responses to nitrogen fertilization. *New Phytologist*, *208*(4), 1042–1055. https://doi.org/10.1111/nph.13547

Munger, W., & Wofsy, S. (2022). Biomass inventories at Harvard forest EMS tower since 1993. Harvard forest data archive: HF069 (v.37) [Dataset]. Environmental Data Initiative. https://doi.org/10.6073/pasta/cd913a57d7f138b832b7f90b53ae21be

Myers, S. S., Zanobetti, A., Kloog, I., Huybers, P., Leakey, A. D., Bloom, A. J., et al. (2014). Increasing CO_2 threatens human nutrition. *Nature*, *510*(7503), 139–142. https://doi.org/10.1038/nature13179

O'Neill, B. C., & Melnikov, N. B. (2008). Learning about parameter and structural uncertainty in carbon cycle models. *Climatic Change*, *89*(1–2), 23–44. https://doi.org/10.1007/s10584-008-9404-2

O'sullivan, M., Friedlingstein, P., Sitch, S., Anthoni, P., Arneth, A., Arora, V. K., et al. (2022). Process-oriented analysis of dominant sources of uncertainty in the land carbon sink. *Nature Communications*, *13*, 1–10. https://doi.org/10.1038/s41467-022-32416-8

Penuelas, J., Fernández-Martínez, M., Vallicrosa, H., Maspons, J., Zuccarini, P., Carnicer, J., et al. (2020). Increasing atmospheric CO_2 concentrations correlate with declining nutritional status of European forests. *Communications Biology*, *3*(1), 125. https://doi.org/10.1038/s42003-020-0839-y

Phillips, J. R., Hanson, P. J., & Warren, J. M. (2021). SPRUCE Plant tissue analyses from experimental plots beginning 2017. Oak Ridge National Laboratory, TES SFA, U.S. [Dataset]. Department of Energy. https://doi.org/10.25581/spruce.090/1780604

Pörtner, H. O., Roberts, D. C., Adams, H., Adler, C., Aldunce, P., Ali, E., et al. (2022). *Climate change 2022: Impacts, adaptation and vulnerability* (p. 3056). IPCC.

Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(25), 13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Sardans, J., Rivas-Ubach, A., & Peñuelas, J. (2012). The C:N:P stoichiometry of organisms and ecosystems in a changing world: A review and perspectives. *Perspectives in Plant Ecology, Evolution and Systematics*, *14*(1), 33–47. https://doi.org/10.1016/j.ppees.2011.08.002

Sellers, P. J., Bounoua, L., Collatz, G. J., Randall, D. A., Dazlich, D. A., Los, S. O., et al. (1996). Comparison of radiative and physiological effects of doubled atmospheric CO_2 on climate. *Science*, *271*(5254), 1402–1406. https://doi.org/10.1126/science.271.5254.1402

Smallman, T. L., Milodowski, D. T., Neto, E. S., Koren, G., Ometto, J., & Williams, M. (2021). Parameter uncertainty dominates C-cycle forecast errors over most of Brazil for the 21st century. *Earth System Dynamics*, *12*(4), 1191–1237. https://doi.org/10.5194/esd-12-1191-2021

Wang, C., Sun, Y., Chen, H. Y. H., & Ruan, H. (2021). Effects of elevated CO_2 on the C:N stoichiometry of plants, soils, and microorganisms in terrestrial ecosystems. *Catena*, *201*, 105219. https://doi.org/10.1016/j.catena.2021.105219

Wang, G., & Feng, X. (2012). Response of plants' water use efficiency to increasing atmospheric CO_2 concentration. *Environmental Science & Technology*, *46*(16), 8610–8620. https://doi.org/10.1021/es301323m

Wang, S., Zhang, Y., Ju, W., Chen, J. M., Ciais, P., Cescatti, A., et al. (2020). Recent global decline of CO_2 fertilization effects on vegetation photosynthesis. *Science*, *370*(6522), 1295–1300. https://doi.org/10.1126/science.abb7772

Welti, E. (2021). PEC01 Elemental chemistry of plant tissue collected for the Konza LTER aboveground plant biomass on Konza Prairie core watersheds [Dataset]. Environmental Data Initiative. https://doi.org/10.6073/pasta/ea69ebede543bed70ecd316a5a0a104f

Wieder, W. R. (2023). Flexible foliar stoichiometry with CTSM5.1 (Version 1.0) [Dataset]. GDEX. https://doi.org/10.5065/8spx-e662

Wieder, W. R., Cleveland, C. C., Lawrence, D. M., & Bonan, G. B. (2015). Effects of model structural uncertainty on carbon cycle projections: Biological nitrogen fixation as a case study. *Environmental Research Letters*, *10*(4), 044016. https://doi.org/10.1088/1748-9326/10/4/044016

Wieder, W. R., Cleveland, C. C., Smith, W. K., & Todd-Brown, K. (2015). Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geoscience*, *8*(6), 441–444. https://doi.org/10.1038/ngeo2413

Wieder, W. R., Lawrence, D. M., Fisher, R. A., Bonan, G. B., Cheng, S. J., Goodale, C. L., et al. (2019). Beyond static benchmarking: Using experimental manipulations to evaluate land model assumptions. *Global Biogeochemical Cycles*, *33*(10), 1289–1309. https://doi.org/10.1029/2018GB006141

Yang, Y., Luo, Y., Lu, M., Schädel, C., & Han, W. (2011). Terrestrial C:N stoichiometry in response to elevated CO_2 and N addition: A synthesis of two meta-analyses. *Plant and Soil*, *343*(1–2), 393–400. https://doi.org/10.1007/s11104-011-0736-8

Yue, K., Fornara, D. A., Yang, W., Peng, Y., Li, Z., Wu, F., & Peng, C. (2017). Effects of three global change drivers on terrestrial C: N: P stoichiometry: A global synthesis. *Global Change Biology*, *23*(6), 2450–2463. https://doi.org/10.1111/gcb.13569

Zarakas, C. M., Swann, A. L. S., Laguë, M. M., Armour, K. C., & Randerson, J. T. (2020). Plant physiology increases the magnitude and spread of the transient climate response to CO_2 in CMIP6 Earth system models. *Journal of Climate*, *33*(19), 8561–8578. https://doi.org/10.1175/jcli-d-20-0078.1

Zhu, Q., Riley, W. J., Iversen, C. M., & Kattge, J. (2020). Assessing impacts of plant stoichiometric traits on terrestrial ecosystem carbon accumulation using the E3SM land model. *Journal of Advances in Modeling Earth Systems*, *12*(4), e2019MS001841. https://doi.org/10.1029/2019ms001841

Zou, J., Li, Q., Osborne, B., & Luo, Y. (2020). Dominant role of nitrogen stoichiometric flexibility in ecosystem carbon storage under elevated CO_2. *Science of the Total Environment*, *747*, 141308. https://doi.org/10.1016/j.scitotenv.2020.141308

References From the Supporting Information

Jubb, I., Canadell, P., & Dix, M. (2013). *Representative concentration pathways (RCPs)*. Australian Government, Department of the Environment.