

1           **Flexible foliar stoichiometry reduces the magnitude of the global land carbon sink**

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9           **Key Points (3)**

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

24 **Abstract**

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

37

38 **Plain Language Summary**

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

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

53

## 54 **1 Introduction**

55 Terrestrial ecosystems provide myriad ecosystem services, including a sink for ~30% of historic  
56 anthropogenic carbon dioxide (CO<sub>2</sub>) emissions (Friedlingstein et al., 2022; Costanza et al.,  
57 1997). Despite the important role of terrestrial ecosystems in reducing the atmospheric CO<sub>2</sub>  
58 burden, considerable uncertainty remains about the persistence of this C sink under climate  
59 change (Friedlingstein et al., 2022; Arora et al., 2020). Even over the historical record (when  
60 observational data are available), land models show significant uncertainty in the magnitude of  
61 the terrestrial carbon (C) sink, and especially the role of the CO<sub>2</sub> fertilization effect (O’Sullivan  
62 et al., 2022). Therefore, considerable attention has been given to calibrating model parameters  
63 that may reduce uncertainty in terrestrial C cycle projections (Dagon et al., 2020; Friend et al.,  
64 2007; Smallman et al., 2021). These efforts often reduce the spread in model results, but they  
65 also omit other important sources of uncertainty, notably model structural uncertainty related to  
66 the representation of some important ecological processes and biotic feedbacks that may regulate  
67 the integrated Earth system response to climate change under elevated CO<sub>2</sub>.

68

69 Uncertainty surrounding the representation of ecological process in land models originates from  
70 both an incomplete understanding of ecological processes and feedbacks themselves, as well as  
71 how to mathematically integrate those processes into models (Bonan & Doney, 2018; Bradford  
72 et al., 2016; O'Neill & Melnikov, 2008). Both factors contribute to model structural uncertainty  
73 that often leads to different outcomes when multiple models attempt to simulate the same  
74 phenomena. Large structural uncertainty related to the representation of nitrogen (N) cycling,  
75 soil biogeochemistry, and photosynthesis, for example, highlight the importance of considering  
76 ecological processes in land models with the goal of more accurately simulating biogeochemical  
77 and biophysical dynamics in response to climate change (Bradford et al., 2016; Meyerholt et al.,  
78 2020; Wieder et al., 2015). Moreover, integrating new data and insights into global-scale models  
79 can reveal outstanding gaps in our mechanistic understanding of Earth systems. Indeed, much of  
80 the uncertainty in quantifying Earth's terrestrial C sink originates from model structural  
81 uncertainty (Bonan & Doney, 2018), necessitating extensive interdisciplinary research  
82 examining ecosystem responses to climate change and increasing CO<sub>2</sub>.

83

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

92 2022; Myers et al., 2014; Penuelas et al., 2020). Foliar C:N ratios increase under elevated CO<sub>2</sub> in  
93 both field and manipulation experiments (Du et al., 2019; Penuelas et al., 2020; Wang et al.,  
94 2021). This direct stoichiometric response is likely due to a combination of processes, including  
95 nutrient dilution in leaves with enhanced C uptake, reduced N uptake by vegetation, and reduced  
96 soil N availability (Dong et al., 2022; Gojon et al., 2022; Mason et al., 2020). Flexible foliar  
97 stoichiometry (i.e. ranges of foliar C:N values at which vegetation can still grow) may allow  
98 sustained productivity with CO<sub>2</sub> fertilization even as nutrients become increasingly scarce (Dong  
99 et al., 2022; Dynarski et al., 2022; Meyerholt et al., 2020). However, declines in foliar and litter  
100 N may directly reduce photosynthetic rates (Ellsworth et al., 2004) as well as produce indirect  
101 negative feedbacks on plant production via reduced rates of decomposition and nutrient  
102 mineralization that could dampen global terrestrial C storage over time (Liang et al., 2016; Luo  
103 et al., 2004). Thus, the relationship between foliar C:N and atmospheric CO<sub>2</sub> concentration may  
104 strongly influence the ability of terrestrial ecosystems to act as a global C sink.

105

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

115 simulated variations in N deposition and variations in vegetation C for N tradeoffs have been  
116 applied in some models (Lawrence et al., 2019; Meyerholt et al., 2020; Meyerholt & Zaehle,  
117 2015; Zhu et al., 2020), but none have parameterized a global scale increase in foliar C:N over  
118 time in response to rising CO<sub>2</sub> that reflects observed, directional stoichiometric changes. This  
119 leaves a critical gap in our understanding of the ways the land C sink will respond to elevated  
120 CO<sub>2</sub>.

121  
122 Here, we conducted a modeling experiment in which we used empirical data describing changes  
123 in foliar C:N under elevated atmospheric CO<sub>2</sub> to parameterize foliar C:N as a function of  
124 atmospheric CO<sub>2</sub> in the Community Land Model, version 5 (CLM5; Lawrence et al., 2019). We  
125 used this parameterization to explore model sensitivity to fixed versus flexible foliar  
126 stoichiometry in response to elevated CO<sub>2</sub>. We ran both flexible and fixed foliar C:N simulations  
127 through the year 2100 to quantify the potential effects of changing leaf stoichiometry on global  
128 C, N, hydrologic, and energy cycles. Thus, we illuminate the role of foliar chemistry in driving  
129 large-scale ecological responses to elevated CO<sub>2</sub>.

130

## 131 **2 Methods and data**

### 132 *2.1 Development of Community Land Model simulations*

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

138 2017; Zou et al., 2020). Our analysis revealed that foliar C:N is ~20% higher under elevated CO<sub>2</sub>  
139 treatments compared to ambient CO<sub>2</sub> treatments and that foliar C:N is increasing under elevated  
140 CO<sub>2</sub> over time. We used this knowledge to inform a new parameterization of foliar C:N that we  
141 implemented into the Community Land Model (CLM, Lawrence et al., 2019). Our new equation  
142 represents the change to foliar C:N per ppm atmospheric CO<sub>2</sub> increase:

143

$$144 \quad \text{CN}_{\text{now}} = \text{CN}_{\text{PFT}} + \max(0, \text{CN}_{\text{slope}} * \log(\text{CO}_{2\_{\text{now}}} / \text{CO}_{2\_{\text{base}}})) \quad \text{eqn. 1}$$

145

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

162  
163 We implemented eqn. 1 into CLM5 and ran the model offline with land only, GSWP3 data  
164 atmosphere forcing from 1850-2014 following standard protocols (Lawrence et al., 2019; Wieder  
165 et al., 2019). We subsequently ran future projections from 2015-2100 by cycling over the  
166 GSWP3 input data (2000-2014) and applying a climate change anomaly forcing to atmospheric  
167 fields that were derived from the Community Earth System Model 2 (CESM2; Danabasoglu et  
168 al., 2020) under the SSP3-7.0 scenario (a business as usual, moderate to high emissions  
169 scenario). Land use change, land cover change, atmospheric CO<sub>2</sub> concentration, nitrogen  
170 deposition, and all other forcings followed the CMIP6 protocols as applied in CESM2 and  
171 CLM5 simulations (Lawrence et al., 2019; Danabasoglu et al., 2020). The use of the anomaly  
172 forcing ensures a smooth transition from historical to future climate for land-only simulations  
173 and offers a method to isolate potential terrestrial responses to projected climate change (see also  
174 Wieder et al., 2015a).

175  
176 We compared our newly parameterized flexible stoichiometry simulation to a simulation run  
177 under the same conditions but with foliar C:N values set to fixed values specific to each plant  
178 functional type (PFT). These values remained constant over the course of the simulation in the  
179 fixed scenario, but increased over time in the flexible scenario (Supplementary Information Fig.  
180 S1). We ran both simulations through the year 2100 to project possible changes to the global C,  
181 N and hydrologic cycles in response to the CO<sub>2</sub> driven foliar C:N parameterization.

182

183 *2.2 Contextualization with CMIP6 and GCP data*

184 To contextualize our findings, we compared CLM simulation results with estimates of the net  
185 land C sink from two additional data products. First, we used an observationally derived dataset  
186 from the Global Carbon Project (GCP) that spans the years 1960 through 2015 (Le Quéré et al.,  
187 2015). More recent iterations of the GCP use land models, including CLM, to estimate the  
188 historical terrestrial C sink (Friedlingstein et al., 2022). Data from Le Quéré et al. (2015),  
189 however, use a bookkeeping method to estimate land C uptake as the difference between CO<sub>2</sub>  
190 emissions estimates and the sum of atmospheric and ocean inventories. Accordingly, the CGP  
191 data are intended to provide an observationally based constraint for the magnitude of the  
192 historical land C sink and its associated uncertainty that we can compare with our fixed and  
193 flexible simulations (as in Lawrence et al. (2019)). Second, we compared our results to an 11-  
194 member ensemble of Coupled Model Intercomparison Project (CMIP6) simulations conducted  
195 under historical and SSP3-7.0 scenarios that are available on the CMIP6 data portal ([https://esgf-  
197 node.llnl.gov/search/cmip6/](https://esgf-<br/>196 node.llnl.gov/search/cmip6/)). Briefly, monthly grid cell net biome production fluxes were  
198 summed to calculate annual fluxes and weighted by model specific grid cell area and land  
199 fraction fields and summed to calculate global totals. We acknowledge that our CMIP6 ensemble  
200 includes results from CESM2, which includes the fixed stoichiometry results presented here, but  
201 from fully coupled simulations. The CMIP6 results provide uncertainty estimates from a multi-  
202 model ensemble in anticipated ranges of the potential terrestrial C sink under the SPP3-70  
203 scenario.

203

### 204 *2.3 Statistical analyses*

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

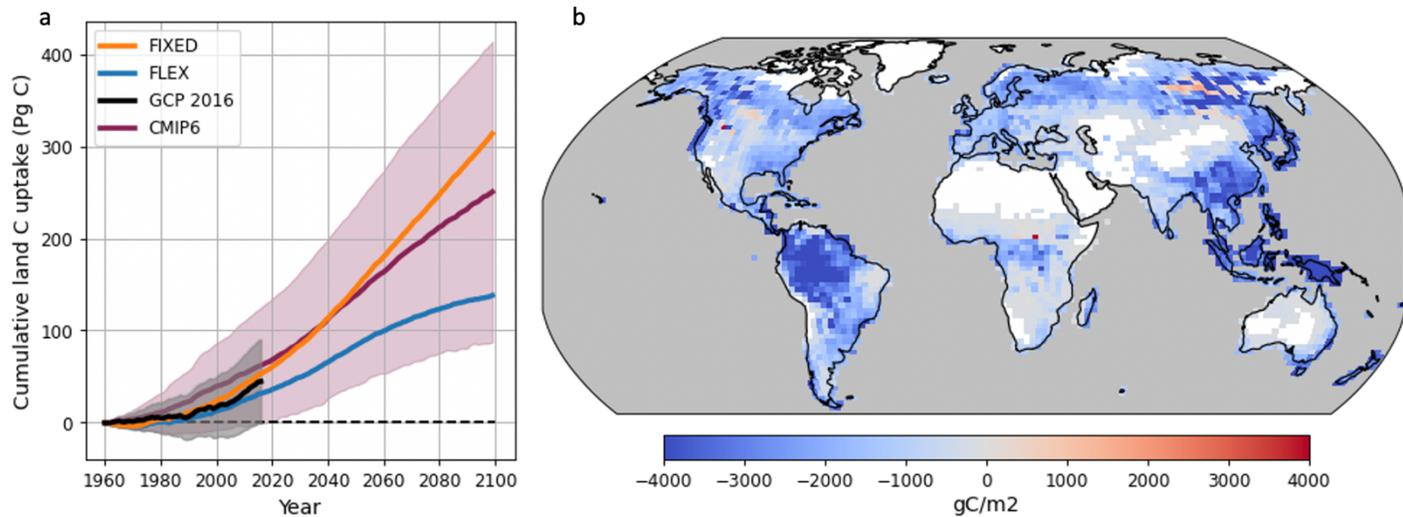
207 notebook. We examined spatial and temporal changes in GPP, NPP, LAI, N mineralization, N  
208 fixation, cumulative land C uptake, ecosystem respiration, evapotranspiration, and runoff to  
209 quantify biogeochemical and biophysical effects of flexible and fixed foliar stoichiometry on  
210 land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

211

### 212 **3 Results and Discussion**

213 Implementing flexible foliar stoichiometry reduced the global terrestrial C sink more than two-  
214 fold (179 Pg C) relative to the fixed scenario by the end of the 21<sup>st</sup> century, from 317 Pg to 138  
215 Pg C (Fig. 1a). For context, by 2100, the difference in the cumulative land C sink between the  
216 two scenarios is equivalent to an 84-ppm change in atmospheric CO<sub>2</sub> (Ballantyne et al., 2012),  
217 comparable to the increase in atmospheric CO<sub>2</sub> observed over the past 45 years (Keeling et al.,  
218 2001). The land C sink is not uniformly distributed across the globe (Supplementary Information  
219 Fig. 2Sb), and reductions in the land C sink in the flexible scenario were also unevenly  
220 distributed. For example, tropical and boreal forests showed the largest declines in cumulative  
221 land C uptake (Fig. 1b). Under the flexible scenario, terrestrial ecosystems remained a net C sink  
222 through the end of the century, largely due to consistently high tropical C uptake, although some  
223 boreal regions became a C source by 2100 (Supplementary information Fig. 2Sc). On an annual  
224 basis, the global rate of land C uptake was reduced by 22.4 Pg C yr<sup>-1</sup> in the flexible scenario,  
225 suggesting a weakening of the land C sink when foliar C:N responded to rising CO<sub>2</sub>  
226 (Supplementary information Fig. 2Sa). Thus, stoichiometric flexibility in Earth's ecosystems  
227 may be a strong determinant of the future strength of the global terrestrial C sink.

228



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230

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

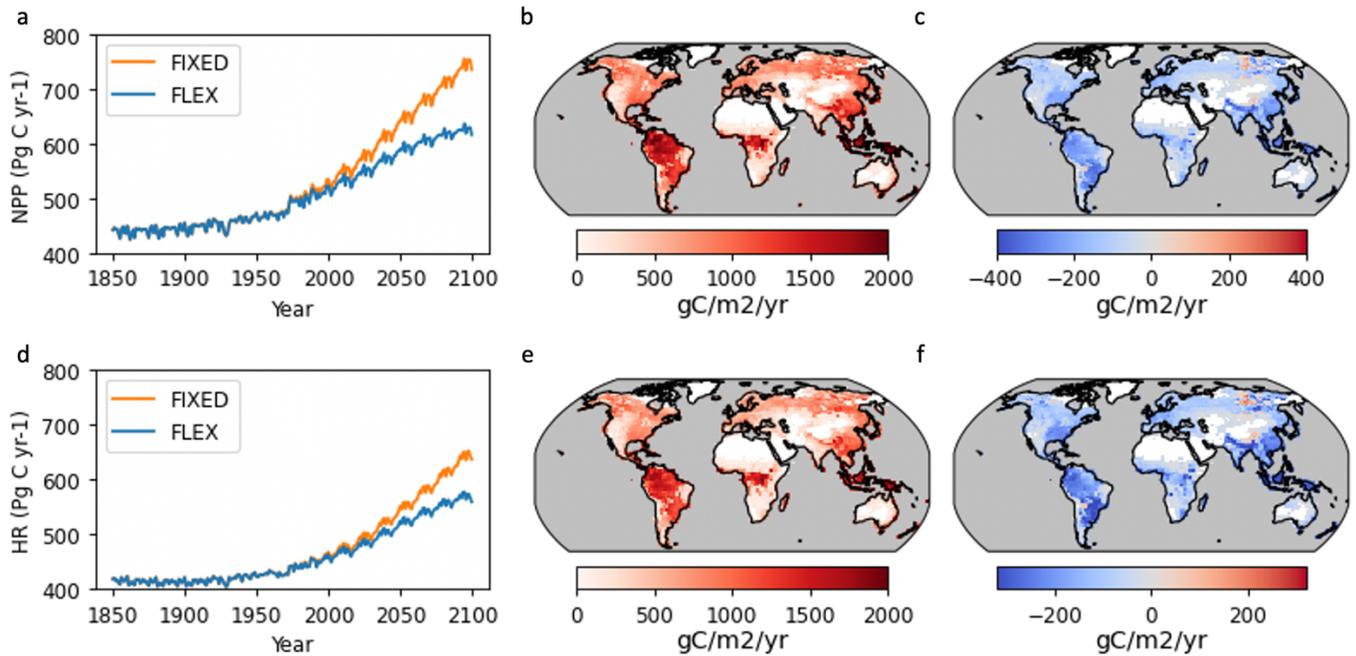
238

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

247 simulated reductions in land C uptake due to future N and P constraints (240 Pg C; Wieder et al.,  
248 2015b). Collectively, these findings suggest that the future global C sink will likely be smaller  
249 than current model projections, but accurately characterizing the extent of future land C uptake  
250 requires a more complete understanding of ecological responses to rising CO<sub>2</sub> and improved  
251 model structures that represent those processes.

252

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



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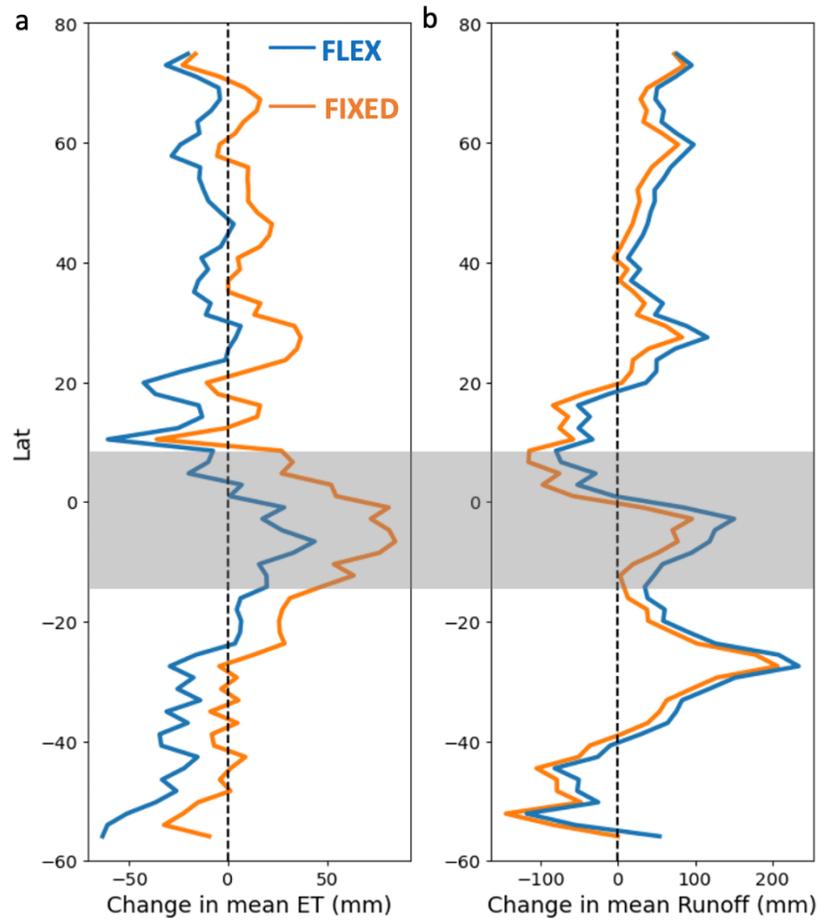
269 **Figure 2.** Simulations with flexible foliar C:N (FLEX) produced lower rates of net primary productivity  
 270 (NPP) and heterotrophic respiration (HR) than scenarios where foliar C:N is held constant (FIXED). (a)  
 271 NPP over the course of each simulation run. (b) Spatial distribution of NPP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

278

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

283 perturbations were especially strong in tropical regions and mirrored declines in GPP, LAI, and  
284 plant water use efficiency in the flexible scenario compared to the fixed scenario (compare  
285 Supplemental Information Figs. S3-S5). Thus, beyond the biogeochemical changes stemming  
286 from reduced photosynthetic capacity with flexible stoichiometry, the observed plant  
287 physiological responses also catalyzed ecohydrological changes that would modify terrestrial  
288 climate feedbacks in coupled simulations with an interactive model atmosphere (Langenbrunner  
289 et al., 2019; Zarakas et al., 2020). For example, lower rates of evapotranspiration would likely  
290 reduce surface humidity and evaporative cooling, thereby warming local temperatures, reducing  
291 cloud cover, altering boundary-layer dynamics, and changing regional precipitation (Cui et al.,  
292 2022; Lemordant et al., 2018). Future work should consider the potential magnitude of these  
293 biophysical effects in fully coupled simulations. However, our findings highlight how nutrient  
294 feedbacks can moderate both C and water cycles in terrestrial ecosystems and underscore the  
295 importance of considering integrated Earth system responses to improve our ability to predict  
296 future biogeochemical and climate dynamics.

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300

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

307

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

310 surrounding of the ecological drivers and effects of stoichiometric flexibility; and second,  
311 improved model structures that accurately represent those ecological processes. Our empirical  
312 understanding of the consequences of stoichiometric flexibility is still poor, but our results  
313 provide compelling evidence of its importance. Moreover, the large declines in C storage we  
314 observed in the flexible scenario most strongly reflect the direct effects of declining plant  
315 productivity as foliar C:N ratios increase. This is consistent with the downregulation of  
316 photosynthesis under elevated CO<sub>2</sub> commonly observed in longer-term studies (Ellsworth et al,  
317 2004) as vegetation optimizes photosynthetic processes to cope with reduced plant N. However,  
318 concurrent declines in litter quality (Supplemental Information Fig. S1d-f) are also known to  
319 reduce decomposition and N mineralization rates, which could further suppress plant production  
320 indirectly via enhanced N limitation (Supplemental information Fig. S6; Craine et al., 2018; Luo  
321 et al., 2004; Mason et al., 2022).

322

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

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

334

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

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

361

362 Our results indicate that increases in foliar C:N could have important and far-reaching effects on  
363 biogeochemical cycles, ecosystems, and climate, and could therefore have profound implications  
364 for human societies. We show that feedbacks between CO<sub>2</sub> and foliar stoichiometry could greatly  
365 reduce the strength of the global terrestrial C sink. If so, more rapid increases in atmospheric  
366 CO<sub>2</sub> could accelerate the pace of climate change, exacerbate climate hazards, food and water  
367 security risks, biodiversity loss, among other adverse consequences (Pörtner et al., 2022).  
368 Further, water security is central to climate change adaptation and mitigation (Caretta et al.,  
369 2022). Our results suggest strong perturbations to the global hydrologic cycle due to changes to  
370 foliar stoichiometry, which is likely to alter global water distributions and the ability of  
371 communities to adapt to change.

372

#### 373 **4 Conclusion**

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

378 ecosystems, including enhanced plant production, reduced N availability, changes in plant water  
379 use efficiency, declines in food quality, and altered trophic interactions (Friedlingstein et al.,  
380 2022, Lincoln et al., 1993, Mason et al., 2022; Myers et al., 2014; Wang & Feng, 2012). Our  
381 study introduces a new, CO<sub>2</sub> driven parameterization of foliar chemistry into CLM to attempt to  
382 explore global ecosystem responses to observed stoichiometric patterns. However, parallel  
383 empirical and experimental efforts – including modified model structures informed from those  
384 efforts – are critically needed to predict the effects of changing stoichiometry more accurately.  
385 Estimating the future of Earth’s terrestrial C sink will undoubtedly include some uncertainty but  
386 integrating new empirical and modeling and efforts will increase our confidence in the validity of  
387 those predictions.

388

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397

### 398 **Open Research Statement**

399 Data from Community Land Model simulations can be found at the following link:

400 <https://doi.org/10.5065/8spx-e662>. Data from CMIP6 can be retrieved from <https://esgf->

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

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

407 [https://harvardforest1.fas.harvard.edu/sites/harvardforest.fas.harvard.edu/files/data/p06/hf069/hf](https://harvardforest1.fas.harvard.edu/sites/harvardforest.fas.harvard.edu/files/data/p06/hf069/hf069-04-canopy-chem.csv)  
408 [069-04-canopy-chem.csv](https://harvardforest1.fas.harvard.edu/sites/harvardforest.fas.harvard.edu/files/data/p06/hf069/hf069-04-canopy-chem.csv) (Munger et al., 2022).

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

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

411 FACE data summarized for these analyses are available from Du et al. (2019), Sardans et al.  
412 (2012), Wang et al. (2021), Yang et al. (2011), Yue et al. (2017), Zou et al. (2020).

413

#### 414 **Author Contributions**

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

418

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

420 The authors declare that they have no competing interests.

421

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423

424 **References**

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