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Future productivity and carbon storage limited by terrestrial nutrient availability

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The size of the terrestrial sink remains uncertain. This uncertainty presents a challenge for projecting future climate-carbon cycle feedbacks[1–4]. Terrestrial carbon storage is dependent on the availability of nitrogen for plant growth[5–8], and nitrogen limitation is increasingly included in global models[9–11]. Widespread phosphorus limitation in terrestrial ecosystems[12] may also strongly regulate the global carbon cycle[13–15], but explicit considerations of phosphorus limitation in global models are uncommon[16]. Here we use global state-of-the-art coupled carbon–climate model projections of terrestrial net primary productivity and carbon storage from 1860–2100; estimates of annual new nutrient inputs from deposition, nitrogen fixation, and weathering; and estimates of carbon allocation and stoichiometry to evaluate how simulated CO_2 fertilization effects could be constrained by nutrient availability. We find that the nutrients required for the projected increases in net primary productivity greatly exceed estimated nutrient supply rates, suggesting that projected productivity increases may be unrealistically high. Accounting for nitrogen and nitrogen–phosphorus limitation lowers projected end-of-century estimates of net primary productivity by 19% and 25%, respectively, and turns the land surface into a net source of CO_2 by 2100. We conclude that potential effects of nutrient limitation must be considered in estimates of the terrestrial carbon sink strength through the twenty-first century.

The terrestrial carbon (C) cycle in Earth system models (ESMs) primarily reflects the effects of changing land use, climate and CO_2 on C fluxes driven by net primary productivity (NPP) and heterotrophic respiration, with the balance of these fluxes determining terrestrial C storage. Over the twenty-first century, projected climate warming is expected to increase rates of heterotrophic respiration, yet net ecosystem C storage could increase if, as models also predict, CO_2 fertilization disproportionately stimulates NPP (refs 2,17). The magnitude and duration of terrestrial CO_2 fertilization effects among models remains highly uncertain[3,4], but explicitly considering nitrogen (N) dynamics in ESMs strongly constrains CO_2 fertilization effects[9–11,16]. Yet, only two models in the fifth phase of the Coupled Model Intercomparison Project (CMIP5) archive represent terrestrial C–N biogeochemistry (CESM1-BGC and NorESM1-M). Although phosphorus (P) limitation (or N/P co-limitation) is widespread throughout the terrestrial biosphere[12] and expected to increase in the future[18], the potential effects of P limitation on future climate–C cycle feedbacks are largely unknown[14]. Given these shortcomings, we applied a theoretical framework based on observations of plant C allocation and stoichiometric relationships to diagnose potential biases in climate–C cycle feedbacks simulated by CMIP5 models over the next century.

Increases in NPP and plant biomass require nutrients, mainly N and P, to meet the stoichiometric demands of plant growth[13]. Building on this concept, we explored how the supply of new nutrients could constrain CO_2 fertilization effects from an ensemble of CMIP5 models. We made steady-state assumptions about the models' initial conditions (1860–1869), such that the global supply of N and P could meet plant demand, but that subsequent increases in terrestrial NPP would require exogenous (new) nutrient inputs and/or accelerated mineralization and uptake (recycling) of soil N and P (ref. 13). Here, we focused on the spatial distribution of new nutrient fluxes (for example, N fixation, deposition, and weathering), quantified the potential for these new nutrient

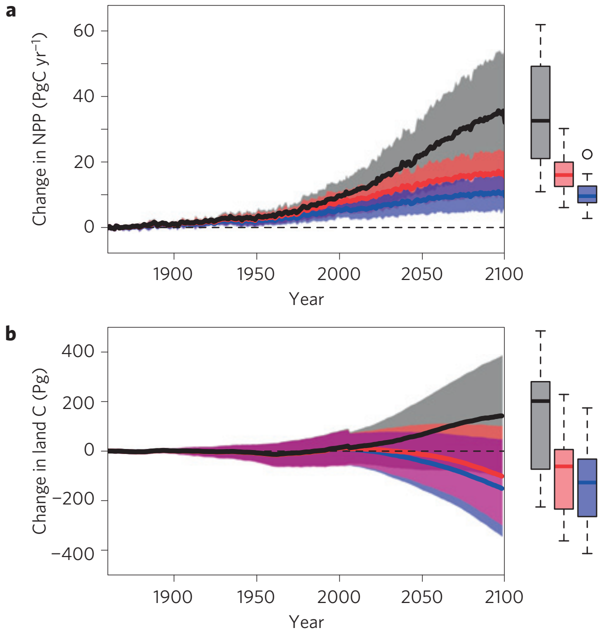

Figure 1 | Change in global NPP and terrestrial C storage from CMIP5 model projections. a,**b**, Difference in global NPP (**a**) and terrestrial C storage (**b**) from initial CMIP5 model values with prescribed CO_2 forcings over the historical period (1860–2004) and RCP 8.5 (2005–2100). Original CMIP5 ensemble mean (±1σ; black), assuming inputs of new N constrain NPP increases (red), and assuming inputs of new N and P constrain NPP increases (blue). Boxplots indicate the median, quartile range, extreme values, and outliers for the end of the twenty-first century (2090–2099).

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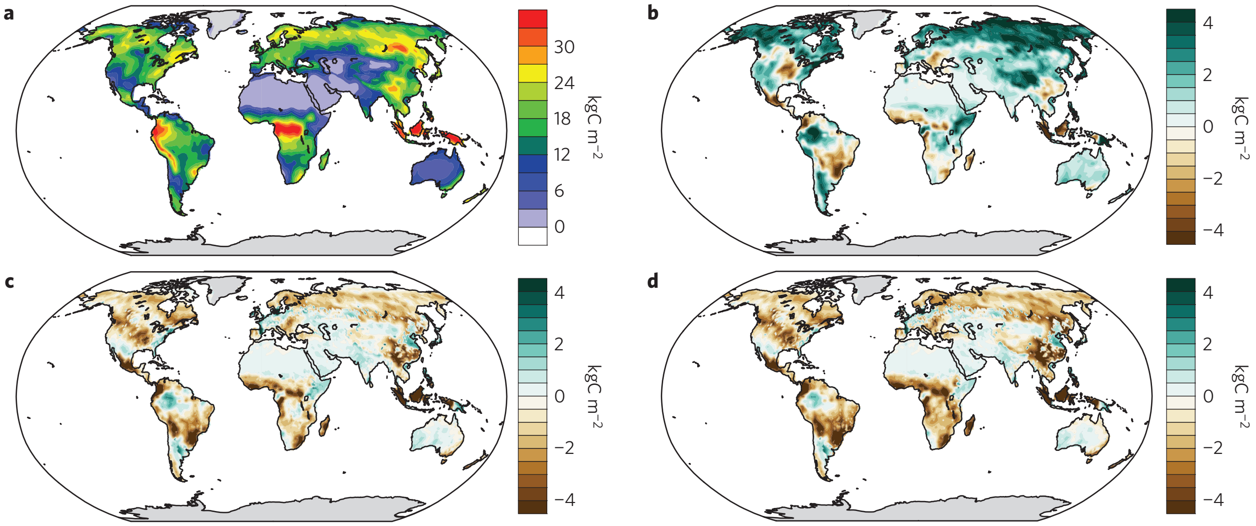

Figure 2 | Multi-model mean terrestrial C storage and changes in C storage with different assumptions about nutrient limitation. a, Mean initial terrestrial C storage for all CMIP5 models (1860–1869). **b**–**d**, Multi-model mean changes in terrestrial C storage at the end of the twenty-first century under RCP 8.5 assuming that increases in NPP are limited by nothing (as in the CMIP5 archive; **b**), new N inputs (**c**), and new N and P (**d**). Individual model results for data summarized are shown in Supplementary Figs 8–10.

Table 1 | Global terrestrial NPP for individual CMIP5 models and the ensemble mean.

Model	Global NPP (PgC yr^{-1})						
	Initial	Historical			Projected		
	CMIP5	CMIP5	N limit	NP limit	CMIP5	N limit	NP limit
BCC-CSM1.1(m)	45.0	54.2	52.5	50.8	80.4	60.2	55.3
BNU-ESM	39.5	48.1	46.1	44.3	72.1	54.3	49.0
CanESM2	48.5	55.6	54.8	53.0	73.8	61.6	56.4
CESM1(BGC)	38.1	42.0	41.9	41.2	51.7	48.8	45.4
GFDL-ESM2G	61.8	74.9	72.7	70.4	114.8	90.9	84.0
HadGEM2-ES	56.9	74.5	69.3	65.1	118.9	79.9	73.3
INM-CM4	55.7	62.9	62.3	60.5	79.1	71.1	65.9
IPSL-CM5A-MR	67.1	81.5	77.6	73.4	112.4	82.7	76.3
MIROC-ESM	56.6	60.0	58.3	57.5	75.2	62.1	59.3
MPI-ESM-MR	73.5	89.2	85.1	80.9	133.4	95.7	88.4
NorESM1-M	41.6	45.6	45.5	44.5	52.5	49.5	46.3
Mean	**53.1**	**62.6**	**60.6**	**58.3**	**87.7**	**68.8**	**63.6**
s.d.	**11.6**	**15.5**	**14.2**	**13.0**	**27.7**	**16.4**	**15.1**

Decadal means were calculated for initial values (1860–1869) and the end of the historical period (1995–2004), and projected under the RCP 8.5 scenario (2090–2099). Data for the historical period and projected under RCP 8.5 are unmodified results from the CMIP5 archive, or assume that new inputs of N or N and P limit increases in terrestrial productivity.

inputs to fuel new plant growth, and explored the implications of nutrient constraints on plant growth and C storage projections. By concentrating on spatially explicit fluxes of C, N and P, this approach most effectively captures the effects of nutrient limitation where and when it occurs—during plant photosynthesis. Moreover, our analysis represents a significant advancement over previous model intercomparisons that have focused on global-to-regional-scale stocks (but not fluxes) of terrestrial C and nutrients[6,7,14].

Most new N inputs enter terrestrial ecosystems through N fixation, with atmospheric N deposition providing regionally important inputs[13]. In contrast, comparatively small inputs of new P come from weathering of parent material and atmospheric deposition, with the largest inputs occurring in arid regions with significant topographic relief and, in many cases, low NPP. We estimate that cumulative new nutrient inputs from 1850–2100 total 51 Pg N and 0.75 Pg P (Supplementary Fig. 1). Assuming that all of these inputs are immediately available to plants and using static, biome-specific estimates of C allocation and stoichiometry[13], we calculated the increases in NPP that could be realized through new nutrient inputs.

The CMIP5 ensemble shows large uncertainty in initial NPP estimates and projected productivity changes (Table 1 and Fig. 1a and Supplementary Figs 2 and 3). Initial NPP estimates vary by a factor of two, averaging 53 ± 12 PgC yr^{-1} (mean $\pm 1\sigma$). By the end of the twenty-first century, models project that NPP will increase $63 \pm 27\%$ under the 'business-as-usual' CO_2 emissions scenario (RCP 8.5). The biological feasibility of these increases remains poorly established, but multiple lines of evidence suggest that they are unrealistically high[6,8,19,20]. If new nutrient inputs constrain projected increases in terrestrial productivity, we find this reduces estimates of mean global NPP in 2100 by $19 \pm 9\%$ and $25 \pm 9\%$ for N and NP simulations respectively, compared with the CMIP5 projections (Table 1 and Supplementary Figs 4 and 5). Projected changes in NPP across biomes generally show a linear relationship with initial NPP estimates and substantial variation among models (Supplementary Fig. 6). Divergent projections in evergreen tropical forests and high-latitude shrublands highlight critical uncertainties about potential NPP changes in these organic C-rich biomes. Simplifying assumptions made in this analysis influence the

Table 2 | Global terrestrial C storage for individual CMIP5 models and the ensemble mean.

Model	Global Terrestrial C Storage (PgC)						
	Initial	Historical			Projected		
	CMIP5	CMIP5	N limit	NP limit	CMIP5	N limit	NP limit
BCC-CSM1.1(m)	1,139	1,245	1,244	1,243	1,666	1,375	1,326
BNU-ESM	1,497	1,599	1,583	1,582	1,716	1,503	1,466
CanESM2	1,775	1,800	1,800	1,799	1,872	1,694	1,637
CESM1(BGC)	999	957	956	956	884	855	828
GFDL-ESM2G	2,160	2,059	2,048	2,048	2,116	1,910	1,879
HadGEM2-ES	1,569	1,581	1,578	1,578	1,899	1,498	1,469
INM-CM4	2,023	2,135	2,135	2,134	2,291	2,190	2,128
IPSL-CM5A-MR	1,957	1,983	1,981	1,981	2,277	1,942	1,910
MIROC-ESM	2,900	2,840	2,833	2,833	2,784	2,492	2,447
MPI-ESM-MR	3,327	3,347	3,334	3,334	3,614	3,035	2,985
NorESM1-M	1,106	1,061	1,061	1,060	862	832	810
Mean	**1,859**	**1,873**	**1,868**	**1,868**	**1,998**	**1,757**	**1,717**
s.d.	**736**	**727**	**724**	**724**	**784**	**661**	**653**

Decadal means were calculated for initial values (1860–1869) and the end of the historical period (1995–2004), and projected under the RCP 8.5 scenario (2090–2099). Data for this historical period and projected under RCP 8.5 include unmodified results from the CMIP5 archive, or assume that new inputs of N or N and P limit increases in terrestrial productivity.

magnitude of projected NPP changes, and have a greater influence on N-limited scenarios (±3.0% values reported in Table 1) than NP-limited scenarios (±0.7%, see Methods). We suspect that these low-uncertainty estimates are driven by low nutrient input rates, especially P, and conclude that—irrespective of assumptions—new nutrient inputs cannot meet projected increases in NPP from the CMIP5 archive. Thus, nutrient demand would have to be met by accelerated recycling of endogenous sources, processes that are largely omitted in our analysis, but are discussed below.

In the absence of sufficient new nutrient inputs, could accelerated recycling of extant soil nutrient pools account for the predicted CMIP5 increases in NPP? It seems plausible that modest NPP increases over the historical period could have been met through accelerated mineralization of soil N pools from warming[21] or greater below-ground C allocation in response to elevated $[CO_2]$ (ref. 5). We calculated potential increases in N availability that could be realized from accelerated soil organic matter decomposition. Although this analysis includes several assumptions (see Methods), including the magnitude of sustained soil N mineralization through time given constant soil C/N ratios, they are consistent with estimates typically made in ESMs that represent coupled C–N biogeochemistry[9]. Warming-induced increases in N availability could, in theory, provide enough N to meet projected increases in terrestrial NPP across the CMIP5 models (Supplementary Fig. 7). However, increases in NPP fuelled by indefinite increases in N mineralization rates are unlikely over the long term as soil organic matter pools become rapidly depleted[19].

Whereas new inputs and accelerated mineralization could be sufficient to meet the N demands, similar outcomes seem unlikely for P. Low soil P availability could potentially be overcome through physical, chemical or biological mechanisms that reduce P constraints under elevated $[CO_2]$ (ref. 22), but these mechanisms remain poorly understood and quantified[14,23]. In particular, diffusion of phosphate ions from adsorbed and occluded P pools to plant-available P pools probably takes place over decades to centuries, and is unlikely to keep pace with the rapid increases in P demand[23]. Plant investment of C resources to root exudates, mycorrhizal associations and phosphatase enzymes could increase rates of P mineralization and acquisition, yet evidence for shifting strategies of plant C allocation in response to increasing nutrient demand are also poorly documented across biomes and soil types[24–26]. We stress that direct observations of temperature and elevated CO_2 effects on P mineralization rates and changes in below-ground C allocation are sparse, especially in tropical forests and savannahs where P probably limits productivity[13,27]. Uncertainties in the availability and dynamics of soil P across the land surface present significant challenges in projecting potential changes in plant P acquisition in global change scenarios, as P availability could substantially limit future productivity over much of the terrestrial land surface[13–15,18] (Fig. 1a). The importance of filling these knowledge gaps is reinforced by our findings that the CMIP5 ensemble generated unrealistically high estimates of future terrestrial productivity by failing to account for potential biogeochemical constraints.

How might nutrient constraints on future NPP modify the strength of the terrestrial C sink? Estimates of initial terrestrial C storage vary threefold across CMIP5 models (Table 2 and Supplementary Fig. 8). Under RCP 8.5, increases in NPP outpace increases in heterotrophic respiration, resulting in terrestrial C uptake of 140 ± 240 PgC (Figs 1b and 2), although four of the models analysed show net C release to the atmosphere. Notably, many models project significant terrestrial C storage at high latitudes (Supplementary Fig. 9), which is inconsistent with observations[28] and models[29] that show climate-driven soil C losses (from heterotrophic respiration) outpace C accumulation (from NPP) in these ecosystems. Nonetheless, warming-induced increases in soil N mineralization—combined with small but chronic new N inputs—could be sufficient to overcome potential N constraints on NPP. Thus, we see negligible changes from CMIP5 projections in terrestrial C storage through 2100 (Supplementary Fig. 7). Long-term global increases in NPP, however, will be more likely realized with new N inputs from N fixation and deposition[13]. If so, the terrestrial biosphere becomes a net C source, losing 100 ± 200 PgC to the atmosphere by 2100, with eight models showing net terrestrial C release to the atmosphere. These findings are consistent with theoretical results suggesting that N limitation could reduce terrestrial C storage by 16 to 149 PgC by 2050 (ref. 7), and models that show reductions in the strength of the land C sink with N limitation—although these simulations maintained a terrestrial C sink over the twenty-first century[9,11].

Our analysis indicates that the effects of both N and P limitation on NPP could result in net terrestrial C losses to the atmosphere of 140 ± 190 PgC (Fig. 2d and Supplementary Fig. 10); a total roughly equivalent to 14 years of current anthropogenic CO_2 emissions that would increase the atmospheric CO_2 burden by 66 ppm. These findings reflect the ability of terrestrial N supply to conceivably keep pace with plant N demands, whereas P inputs and mineralization rates are low and expected to broadly limit NPP in the future[13,18]. The extent to which soil P availability will actually limit CO_2 fertilization effects and the future strength of the terrestrial C sink remains unknown[14,22,23], but our findings are generally consistent with other models[15]. Our results demonstrate that considering nutrient limitation reduces both the magnitude and variability in NPP changes, but expose strong temperature sensitivities among the CMIP5 models[30] that drive terrestrial C losses in nutrient-limited scenarios (Fig. 1). Although accelerated recycling of extant nutrient pools may meet increased plant N and P demand, it will probably result from modifications of plant nutrient acquisition strategies or patterns of C and nutrient allocation[5,19,24–26]—with uncertain effects on global C and nutrient cycles. Thus, future work should focus on improving the theory, observations and models of ecosystem C–nutrient biogeochemistry.

Collectively, these results indicate that:C cycle projections from CMIP5 models probably overestimate the ability of the land surface to absorb atmospheric CO_2; and nutrient limitation is critical for projecting climate–C feedbacks. Our analysis demonstrates that new inputs of N and P are probably insufficient to meet the nutrient demand generated from projected productivity increases, and highlights the potential for P limitation to ultimately constraint NPP, especially in tropical ecosystems[13,14,18]. These findings raise important questions about the feasibility of projected terrestrial uptake of anthropogenic CO_2 emissions, and emphasize the need to better quantify and represent shifting patterns of plant C allocation in the face of nutrient limitation across biomes and soil fertility gradients. Thus far, terrestrial C uptake has curtailed accumulation of CO_2 in the atmosphere. If nutrients limit the terrestrial biosphere's capacity to continue providing this critical ecosystem service, allowable emissions from human activities will have to be further curtailed to meet stable $[CO_2]$ targets and avoid warming beyond RCP 8.5 projections[15]. Resolving these questions has profound policy and social implications as we consider climate change adaptation and mitigation strategies.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

W.R.W. and C.C.C. designed the study. W.R.W. coordinated the experiments and wrote the manuscript. W.K.S. provided nutrient input estimations. K.T-B. modified the CMIP5 simulation results to reflect the nutrient limitations. All authors contributed significantly to the final analysis and revisions of the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to W.R.W.

Competing financial interests

The authors declare no competing financial interests.

Methods

Annual inputs of new N and P were estimated from previously published results for the experimental period (1850–2100). We applied a constant land cover map derived from the MODIS land cover data sets. Cumulative nutrient input data and the dominant MODIS land cover were regridded to a 1° grid (Supplementary Fig. 1). Raw data from the CMIP5 archive can be found on the Earth System Grid Federation repository (https://www.earthsystemgrid.org). From these initial NPP estimates, we applied static, biome-specific estimates of plant C allocation and stoichiometry (from ref. 13) to calculate the maximum amount of new NPP that could be met with new inputs of N and P to each grid cell. We assumed that in any given year, 100% of new nutrient inputs were plant available and that new nutrient inputs were additive over the course of the simulation; new nutrients are added to the cumulative bio-available nutrient pool that plants may draw on to support new NPP. In all simulations we assume fixed plant allocation of NPP to roots, stems and leaves[13]. We evaluated the sensitivity of our findings to these simplifying assumptions by propagating a 20% uncertainty in nutrient inputs and stoichiometric demands (both individually and combined) and quantified the ensuing effects on changes in NPP projections (see Supplementary Methods). Further, we assume that soil mineralization liberates C and N in a specific ratio, and N mineralization can support NPP. Thus, new nutrients that can support new NPP accumulate in and are immediately recycled by terrestrial ecosystems. This approach differs from previous studies that assumed only a fraction of soil nutrient pools and new inputs were plant available[6,7,14]. Thus, our approach probably underestimates the effects of nutrient limitation on NPP in response to CO_2 fertilization. Finally, we assumed no nutrient limitation of NPP in agricultural lands in our analysis, and that increases in NPP in these ecosystems would simply reflect unconstrained CO_2 fertilization effects.

Terrestrial NPP and total C pools were downloaded from the CMIP5 archive over the experimental period and regridded to a 1° grid. We defined annual N-limited (or NP-limited) increases in NPP as the minimum of individual model NPP and the NPP that could be supported by new N inputs (or N and P inputs; Table 1 and Fig. 1). Separately, we calculated potential increases in N mineralization rates assuming constant, biome-specific soil C/N ratios[16] and calculated the additional N that would be mineralized from projected warming through 2100 and repeated our N- and NP-limited analyses (Supplementary Fig. 7).

To estimate how changes in NPP may affect terrestrial C storage we adjusted annual C inputs to vegetation and soil C pools for each CMIP5 model from our time series of modified NPP estimates (Fig. 1a). Vegetation carbon was recalculated at each time step; specifically, vegetation input and outputs were adjusted proportionally to the nutrient limitation applied to NPP. Soil carbon stocks were rescaled to be proportional to the change in nutrient-limited NPP and decomposition rates were adjusted to maintain terrestrial C storage estimates (the sum of all vegetation C and soil C pools; Figs 1b and 2) simulated from each model over the historical period. These modifications maintained individual model projections of terrestrial C pools through the historical period, and preserved the trajectory of terrestrial C response to climate change.

Code availability. Code used for analyses and figures have been archived in a GitHub repository (https://github.com/ktoddbrown/CMIP5_NP_Limitation/releases/tag/v1.0.0).