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Compensatory Effects between CO2, Nitrogen Deposition, and Temperature in Terrestrial Biosphere Models without Nitrogen Compromise Projections of the Future Terrestrial Carbon Sink

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Abstract

The strength of CO2 fertilisation is a major uncertainty across terrestrial biosphere models (TBMs) and is suggested to be overestimated without a representation of nitrogen (N) limitation. Here, we compare TBM projections with and without coupled C and N cycling over alternative future scenarios (the Shared Socioeconomic Pathways) to examine how representing N cycling influences CO2 fertilisation as well as the effects of a comprehensive group of physical and socioeconomic global change drivers. Because elevated N deposition and N mineralisation (driven by elevated temperature) have stimulated terrestrial C sequestration over the historical period, a TBM without N cycling must exaggerate the strength of CO2 fertilisation to compensate for these unrepresented N processes and to reproduce the historical terrestrial C sink. As a result, it cannot reliably project the future terrestrial C sink, overestimating CO2 fertilisation as CO2 increases faster than N deposition and temperature in future scenarios.

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Compensatory Effects between CO_2, Nitrogen Deposition, and Temperature in Terrestrial Biosphere Models without Nitrogen Compromise Projections of the Future Terrestrial Carbon Sink

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Key Points:

- Terrestrial biosphere models without N do not represent N deposition or mineralisation, which have stimulated terrestrial C sequestration
- Exaggerated CO_2 fertilisation compensates for N deposition and mineralisation in order to reproduce the historical terrestrial C sink
- Models cannot reliably project the future terrestrial C sink as CO_2 increases faster than N deposition and temperature in future scenarios

Abstract

The strength of CO_2 fertilisation is a major uncertainty across terrestrial biosphere models (TBMs) and is suggested to be overestimated without a representation of nitrogen (N) limitation. Here, we compare TBM projections with and without coupled C and N cycling over alternative future scenarios (the Shared Socioeconomic Pathways) to examine how representing N cycling influences CO_2 fertilisation as well as the effects of a comprehensive group of physical and socioeconomic global change drivers. Because elevated N deposition and N mineralisation (driven by elevated temperature) have stimulated terrestrial C sequestration over the historical period, a TBM without N cycling must exaggerate the strength of CO_2 fertilisation to compensate for these unrepresented N processes and to reproduce the historical terrestrial C sink. As a result, it cannot reliably project the future terrestrial C sink, overestimating CO_2 fertilisation as CO_2 increases faster than N deposition and temperature in future scenarios.

Plain Language Summary

Climate change models simulate the terrestrial carbon sink (in plant and soil biomass), which takes up a third of anthropogenic CO_2 emissions. However, these models have only recently included representations of nitrogen limitation of plant growth and thus its future influence is unclear. Here we compare a model with and without nitrogen cycling in comprehensive simulations of alternative future scenarios that depend on socioeconomic development over the 21st century. We find that models without nitrogen cycling must exaggerate the influence of elevated atmospheric CO_2 on plant growth to compensate for unrepresented nitrogen cycling processes in order to correctly simulate the historical terrestrial carbon sink. Specifically, these models do not represent how elevated atmospheric nitrogen input (due to intensive agriculture and fossil fuel burning) and how elevated soil nitrogen (due to decomposition driven by rising temperature) have increased plant growth over the historical period. As a result, models without nitrogen cycling cannot reliably project the future terrestrial carbon sink because atmospheric CO_2 increases faster than both atmospheric nitrogen input and temperature. This will lead to an overestimation of the future terrestrial carbon sink with implications for future climate change projections and policy.

1 Introduction

The terrestrial C sink has increased over recent decades driven primarily by CO_2 fertilisation and it currently sequesters approximately 30% of anthropogenic CO_2 emissions (Friedlingstein et al., 2022; Walker et al., 2020). The persistence of the terrestrial C sink over the 21st century is uncertain due to the combined influences of multiple global change drivers – rising CO_2 alongside rising temperature, varying precipitation, and land use change (Huntzinger et al., 2017). In particular, nitrogen (N) is an essential limiting nutrient (Elser et al., 2007a; Fernández-Martínez et al., 2014; LeBauer & Treseder, 2008; Wright et al., 2018) and constrains CO_2 fertilisation (Terrer et al., 2019; S. Wang et al., 2020). However, agricultural activities and fossil fuel use cause elevated N deposition which could alleviate N limitation (O'Sullivan et al., 2019; R. Wang et al., 2017). Elevated temperature drives soil organic matter decomposition which releases plant-available N, i.e., N mineralisation, and this could further alleviate N limitation (Liu et al., 2017). Consequently, the extent to which N limitation will constrain the future terrestrial C sink under this cast of interacting and intensifying global change drivers is unresolved.

Terrestrial biosphere models (TBMs) are the principal tool for simulating the terrestrial C sink and they serve as the land components in Earth System Models thereby informing climate change policy (IPCC, 2021). In TBMs, CO_2 fertilisation is suggested to be overestimated without a representation of N limitation: When TBM projections of the future terrestrial C sink under a high atmospheric CO_2 scenario were constrained with observations of N supply and N stoichiometry, terrestrial C sequestration was reduced by 20% (Wieder et al., 2015). However, this study only examined estimated constraints applied post hoc to simulations of TBMs without N cycling rather than including an explicit representation of N cycling in TBMs. More and more TBMs now include a representation of coupled C and N cycling (e.g., in the most recent Global Carbon Project 11 out of 17 TBMs included a representation of N cycling (Friedlingstein et al., 2022)) which allows for intercomparisons between TBMs with and without N cycling. These intercomparisons have found that TBMs with N cycling and TBMs without N cycling perform similarly in reproducing the historical terrestrial C sink (Seiler et al., 2022) but that their responses to different global change drivers acting over the historical period drivers diverge (Huntzinger et al., 2017). In particular, the strength of the CO_2 fertilisation effect over the historical period simulated by TBMs without N cycling was found to be over twice that simulated by TBMs with N cycling, N deposition increased terrestrial C sequestration by approximately 20% over the historical period as simulated by TBMs with N cycling (but was not represented in TBMs without N cycling) (O'Sullivan et al., 2019), and most TBMs with N cycling simulated overall terrestrial C sequestration in response to historical climate variation whereas most TBMs without N cycling simulated overall terrestrial C emissions in response to historical climate variation (Huntzinger et al., 2017). That both TBMs with and without N cycling can reproduce the historical terrestrial C sink despite simulating such divergent responses to individual global change drivers suggests that TBMs are tuned to reproduce the historical terrestrial C sink with unknown consequences for projections of the future terrestrial C sink. However, few studies have examined N cycling in plausible future scenarios that encompass all global change drivers, either examining historical simulations or focusing solely on CO_2 and/or N deposition (Goll et al., 2012; Smith et al., 2014; Sokolov et al., 2008; Thornton et al., 2009; Y. P. Wang et al., 2015; Zaehle et al., 2010).

Here we use the Canadian Land Surface Scheme including Biogeochemical Cycles (CLASSIC), the land component of the Canadian Earth System Model (CanESM5), to examine how representing coupled C and N cycling influences the response of terrestrial C sequestration to global change by comparing simulations of CLASSIC with and without coupled C and N cycling over the 21st century. By examining a single TBM with and without coupled C and N cycling, we can isolate the impact of explicitly representing coupled C and N cycling whereas intercomparisons across TBMs with and without N cycling do not account for other structural and parametric differences between TBMs that may obscure the effects of N cycling. CLASSIC represents both flexible vegetation C:N stoichiometry and the upregulation of symbiotic biological N fixation under N limitation (described and evaluated in Asaadi & Arora (2021) and Kou-Giesbrecht & Arora (2022)) thereby presenting an advanced representation of coupled C and N cycling in a TBM. We evaluate the role of N cycling under individual and combined contributions of a comprehensive group of physical and socioeconomic global change drivers: CO_2, climate, N deposition, and land use change. We simulate the historical period and three alternative future scenarios that are based on the Shared Socioeconomic Pathways (SSP) (Riahi et al., 2017), which are the recent framework adopted by the Intergovernmental Panel on Climate Change (IPCC): SSP126 ("sustainability") has low greenhouse gas emissions, SSP370 ("regional rivalry") has high greenhouse gas emissions, and SSP585 ("fossil-fueled development") has very high greenhouse gas emissions.

2 Materials and Methods

2.1 CLASSIC overview

The Canadian Land Surface Scheme Including Biogeochemical Cycles (CLASSIC) (Melton et al., 2020; Seiler et al., 2021) is the land component in the family of the Canadian Earth System Models (CanESM) (Swart et al., 2019). CLASSIC simulates land-atmosphere fluxes of energy, momentum, water, carbon (C), and nitrogen (N). The physical component of CLASSIC simulates fluxes of energy, momentum, and water (Verseghy, 1991; Verseghy et al., 1993). The biogeochemical component of CLASSIC simulates the land-atmosphere exchange of C via photosynthesis, autotrophic respiration, heterotrophic respiration, land use change, and fire (Arora & Boer, 2005). For biogeochemical processes, vegetation is partitioned into nine plant functional types (PFTs): needleleaf evergreen trees, needleleaf deciduous trees, broadleaf evergreen trees, broadleaf cold deciduous trees, broadleaf drought deciduous trees, C_3 crops, C_4 crops, C_3 grasses, and C_4 grasses. CLASSIC prognostically simulates the amount of C in vegetation, litter, and soil organic matter pools for each PFT and over the bare soil fraction in each grid cell. CLASSIC simulates the land-atmosphere exchange of N via biological N fixation (free-living and symbiotic), specified N deposition and N fertiliser application, nitric oxide (NO) emissions, nitrous oxide (N_2O) emissions, N_2 emissions, ammonia (NH_3) volatilisation, N leaching, and land use change (Asaadi & Arora, 2021; Kou-Giesbrecht & Arora, 2022). CLASSIC prognostically simulates the amount of N in vegetation, litter, soil organic matter, and inorganic soil N (ammonium (NH_4^+) and nitrate (NO_3^-)) pools for each PFT and over the bare soil fraction in each grid cell. See Text S1 for a more detailed description of the physical and biogeochemical components of CLASSIC.

In CLASSIC-CN, photosynthesis is dependent on leaf N such that, when leaf N is low, photosynthesis is downregulated and, when leaf N is high, photosynthesis is upregulated (Asaadi & Arora, 2021; Kou-Giesbrecht & Arora, 2022). Additionally, vegetation exhibits a dynamic response to N limitation of plant growth. First, vegetation upregulates and downregulates symbiotic biological N fixation in response to weak N limitation and strong N limitation respectively (Kou-Giesbrecht & Arora, 2022). Second, vegetation has flexible stoichiometry and thus the vegetation C:N ratio responds to changing N limitation (Asaadi & Arora, 2021). In CLASSIC-C, N cycling is turned off and the downregulation of photosynthesis under increasing CO_2 is controlled by a parameter as explained in Arora et al. (2009). Briefly, this parameter, which ranges between 0 and 0.9, determines the rate of increase of photosynthesis with increasing CO_2. When it is set to 0, photosynthesis does not increase with increasing CO_2. When it is set to 0.9, photosynthesis increases with increasing CO_2 at an unconstrained rate. When it is set to 0.35, CLASSIC-C simulations estimate a global net atmosphere-land CO_2 flux that lies within uncertainty range of estimates from the Global Carbon Project (Friedlingstein et al., 2022).

2.2 Simulations

We use CLASSIC-C and CLASSIC-CN to simulate energy, momentum, water, C, and N fluxes at the global scale over the historical period (1851 – 2014) and over the future period (2015 – 2100) for three Shared Socioeconomic Pathways (SSPs; SSP126, SSP370, and SSP585).

For the historical period, we conducted simulations following the TRENDY protocol (for contributions to the Global Carbon Project (Friedlingstein et al., 2022)). We also conducted historical simulations following the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) protocol (Buchner & Reyer, 2021; Lange & Buchner, 2022) in order to launch future simulations following the ISIMIP protocol. Forcings are described in Table S1. For both the historical period and future period, we conducted simulations with all global change drivers acting concurrently as well as four separate simulation experiments to disentangle the contributions of CO_2, climate, N deposition, and land use change (which includes changes to both crop area and to N fertilisation of crops) to the global net atmosphere-land CO_2 flux. We did not isolate the influence of population density and CH_4 because these forcings regulate fire C emissions and soil CH_4 fluxes respectively, which have minimal influence on the global net atmosphere-land CO_2 flux in comparison to CO_2, climate, land use change, and N deposition. Simulations are described in detail in Text S2 and in Tables S2 and S3.

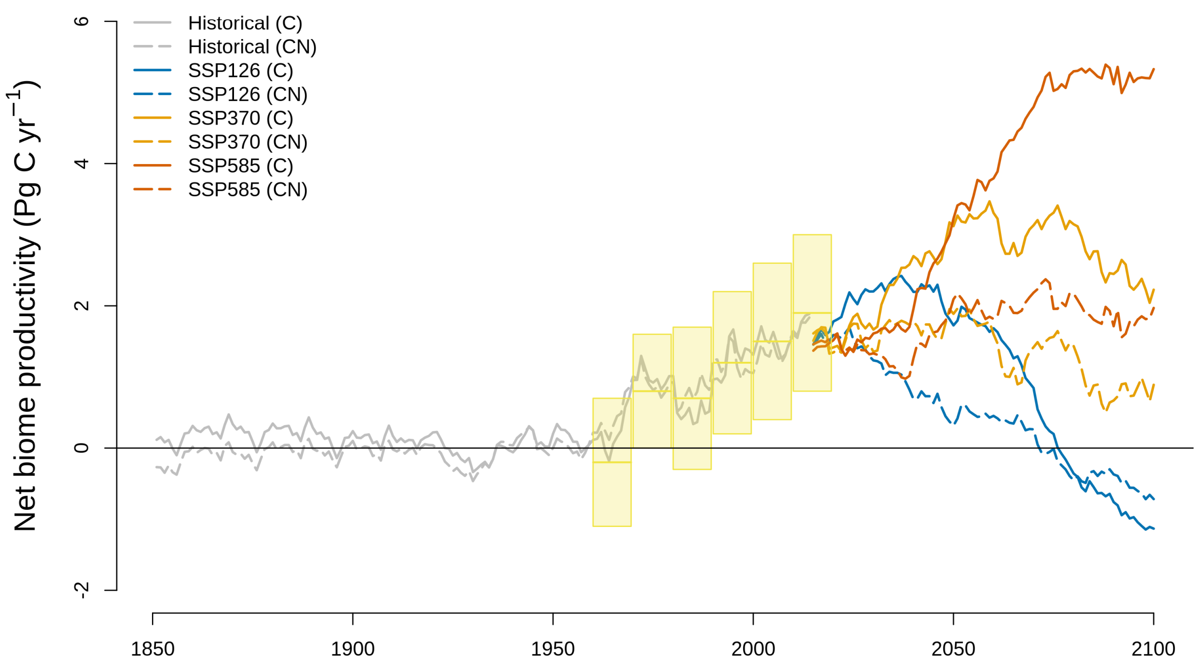
Over the historical period, we compared the global net atmosphere-land CO_2 flux simulated by CLASSIC-C and CLASSIC-CN to estimates from the Global Carbon Project (Friedlingstein et al., 2022). CLASSIC-C and CLASSIC-CN simulations over the historical period have been validated previously in other studies (Asaadi & Arora, 2021; Kou-Giesbrecht & Arora, 2022; Melton et al., 2020; Seiler et al., 2021).

3 Results

3.1 Historical net biome productivity

The net biome productivity (NBP) is the global net atmosphere-land CO_2 flux and quantifies the terrestrial C sink (or source). NBP ultimately determines changes in atmospheric CO_2 concentration (together with the global net atmosphere-ocean CO_2 flux and fossil fuel CO_2 emissions). Figure 1 shows simulated NBP over the historical period as well as NBP over the 21st century under three SSPs.

Figure 1. Net biome productivity (NBP) over the historical period and for future scenarios simulated by CLASSIC-C (which does not represent N cycling, indicated by solid lines) and CLASSIC-CN (which represents coupled C and N cycling, indicated by dashed lines). Historical simulations follow the TRENDY protocol (1851 – 2014). Future simulations for SSP126 ("sustainability"), SSP370 ("regional rivalry"), and SSP585 ("fossil-fueled development") follow the ISIMIP protocol (2015 – 2100). Yellow boxes indicate the NBP range from other models in the Global Carbon Project.



NBP simulated by CLASSIC-C (which does not represent N cycling) and CLASSIC-CN (which represents coupled C and N cycling) are similar over the historical period (Figure 1). Positive NBP values since the 1960s indicate a terrestrial C sink over the historical period. CLASSIC-C and CLASSIC-CN simulate a NBP of 1.3 Pg C yr^{-1} and 1.2 Pg C yr^{-1} (averaged over 2000 – 2010), respectively. Both these estimates lie within the uncertainty range of NBP estimates from the Global Carbon Project (1.3±0.6 Pg C yr^{-1} from TBMs and 1.0–1.8 Pg C yr^{-1} from atmospheric inversions; averaged over 2000 – 2010).

NBP is driven by contributions from a comprehensive group of physical and socioeconomic global change drivers: CO_2 (Figure 2a), climate (Figure 2b,c), N deposition (Figure 2d), and land use change (which includes changes to both crop area and N fertilisation of crops; Figure 2e,f). Despite both CLASSIC-C and CLASSIC-CN exhibiting a similar NBP when all global change drivers act concurrently that compares well with NBP estimates from the Global Carbon Project (Figure 1), the cumulative NBP contributions over the historical period from each global change driver differ between CLASSIC-C and CLASSIC-CN (Figure 3a). In particular, CLASSIC-C exhibits a significantly stronger NBP increase driven by CO_2 than CLASSIC-CN over the historical period (Figure 3a). Because CLASSIC-C does not represent N cycling, it does not represent the effects of N deposition, N mineralisation, or N fertilisation of crops. In CLASSIC-CN, elevated N deposition relieves N limitation and stimulates NBP over the historical period. In CLASSIC-CN, elevated N mineralisation (which is driven by elevated temperature (Asaadi & Arora, 2021)) also relieves N limitation and stimulates NBP over the historical period. In CLASSIC-C, varying climate over the historical period decreases NBP due to increasing heterotrophic respiration driven by elevated temperature and thus the contribution of climate to cumulative NBP over the historical period is negative. In CLASSIC-CN, this NBP decrease is offset by N mineralisation and the contribution of climate to cumulative NBP over the historical period is positive. Finally, in CLASSIC-CN, elevated N fertilisation of crops also relieves N limitation and stimulates NBP over the historical period. The contribution of land use change to cumulative NBP over the historical period is negative for both CLASSIC-CN and CLASSIC-C due to CO_2 emissions associated with the conversion of natural vegetation to crops but this NBP decrease is weaker for CLASSIC-CN than for CLASSIC-C because it is offset by stimulated NBP due to N fertilisation. In CLASSIC-CN, the contributions of both N deposition and climate (i.e., N mineralisation) to cumulative NBP over the historical period were stronger at higher latitudes, which are often N-limited (Hedin et al., 2009) (Figure S1).

Figure 2. Global change drivers over the historical period (1851 – 2014) and for future scenarios (2015 – 2100) for SSP126 ("sustainability"), SSP370 ("regional rivalry"), and SSP585 ("fossil-fueled development"). a. CO_2. b. Temperature (globally averaged over land excluding Greenland and Antarctica). c. N deposition. d. Land cover. e. N fertilisation of crops. f. Ratio of CO_2 to N deposition. g. Ratio of CO_2 to temperature. Historical forcings are from the TRENDY protocol. Future forcings for SSP126 ("sustainability"), SSP370 ("regional rivalry"), and SSP585 ("fossil-fueled development") are from the ISIMIP protocol. In f, decreasing CO_2 : N deposition ratio over the historical period indicates that N deposition is increasing faster than CO_2, whereas increasing CO_2 : N deposition ratio in the future scenarios indicates that CO_2 is increasing faster than N deposition. In g, increasing CO_2 : temperature ratio is due to the logarithmic relationship between temperature and CO_2 (Shine et al., 1990).

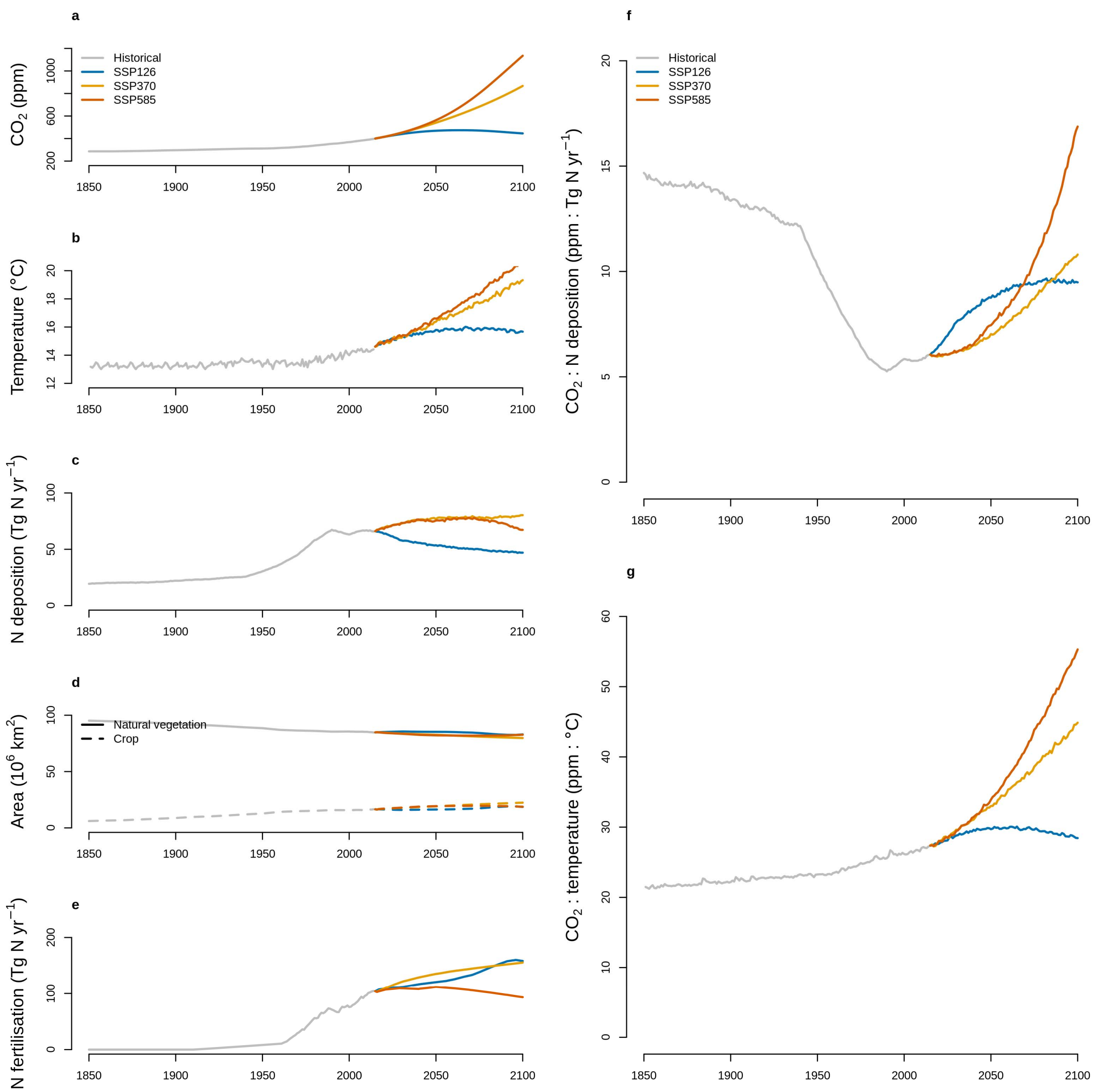
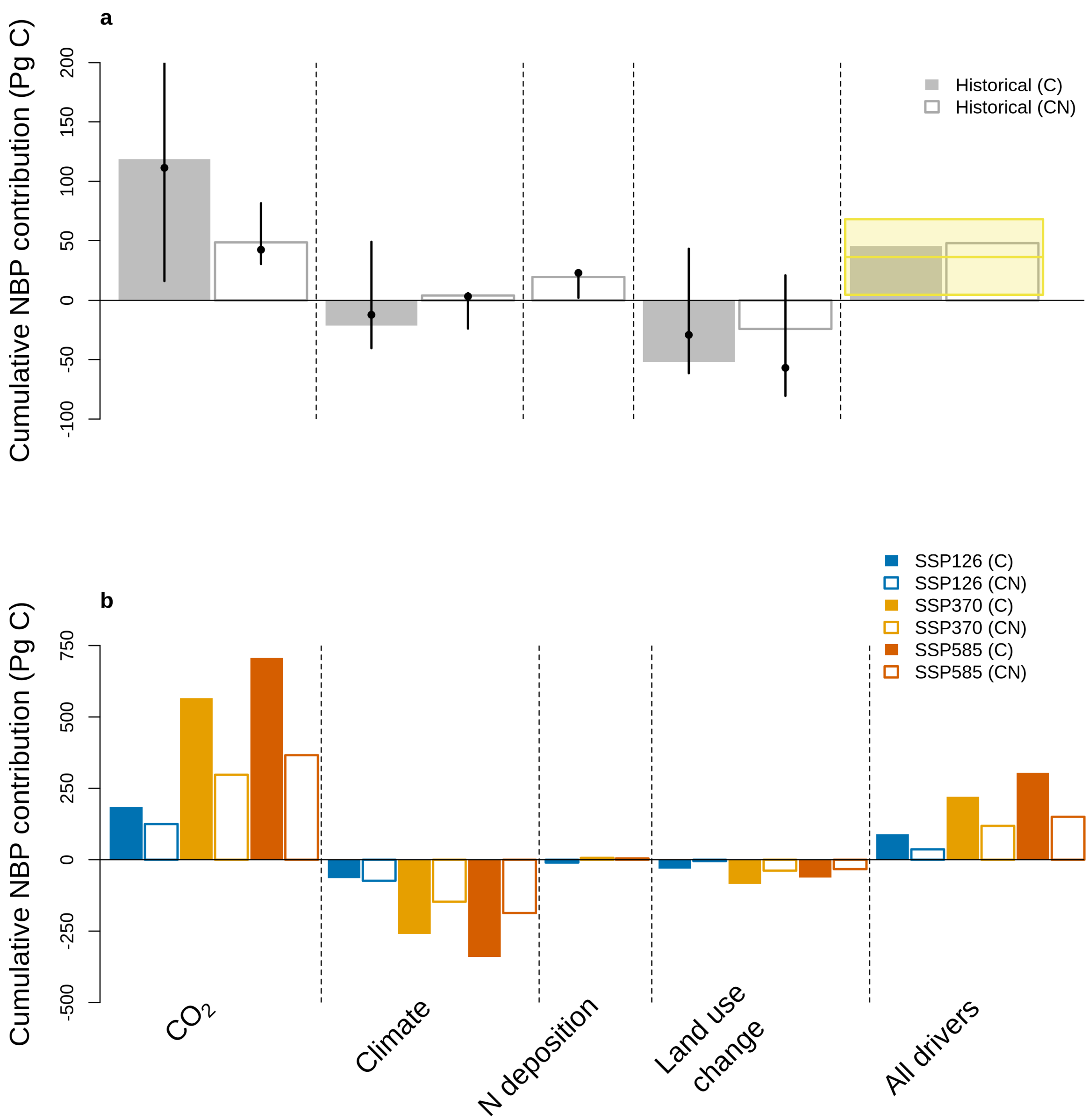


Figure 3. Contributions of CO_2, climate, N deposition, and land use change (includes both changes to both crop area and to N fertilisation of crops) to cumulative net biome productivity (NBP) over the historical period (1851 – 2014; a) and for future scenarios (2015 – 2100; b) simulated by CLASSIC-C (which does not represent N cycling) and CLASSIC-CN (which represents coupled C and N cycling). Historical simulations follow the TRENDY protocol. Future simulations for SSP126 (“sustainability”), SSP370 (“regional rivalry”), and SSP585 (“fossil-fueled development”) follow the ISIMIP protocol. The yellow box indicates the range from other models in the Global Carbon Project. Black dots and lines indicate the median and 95% confidence interval of other models with coupled C and N cycling from Huntzinger et al. (2017). Figure S2 shows the time series of the contribution of each global change driver to cumulative NBP.



Overall, because CLASSIC-C and other similar TBMs that do not represent N cycling (Huntzinger et al., 2017) are unable to represent the stimulation of terrestrial C sequestration by N deposition, N mineralisation, or N fertilisation of crops over the historical period. Therefore, the stimulation of terrestrial C sequestration by elevated CO_2 over the historical period must be exaggerated to compensate for these unrepresented N processes in order to reproduce the historical terrestrial C sink. Essentially, in TBMs that do not represent N cycling, the sensitivity of terrestrial photosynthesis to CO_2 is calibrated to reproduce the terrestrial C sink over the historical period (Arora et al., 2009; Delire et al., 2020; Krinner et al., 2005). This introduces these compensatory effects and overestimates the CO_2 effect by design. We now explore the consequences of these compensatory effects in projections of the future terrestrial C sink.

2.2 Future net biome productivity

Despite the agreement between NBP simulated by CLASSIC-C and CLASSIC-CN over the historical period and their agreement with NBP estimates from the Global Carbon Project, there are major differences between NBP projected by CLASSIC-C and CLASSIC-CN over the 21st century, especially in future scenarios characterised by high atmospheric CO_2. At the end of the 21st century, projections of NBP by CLASSIC-C and CLASSIC-CN differ by 0.5 Pg C yr^{-1} for SSP126, by 1.4 Pg C yr^{-1} for SSP370, and by 3.3 Pg C yr^{-1} for SSP585 (averaged over 2090 – 2100; Figure 1).

In SSP126 ("sustainability"), CO_2 and temperature stabilise then decrease after 2050 while N deposition decreases (Figure 2). Thus, CLASSIC-C and CLASSIC-CN project decreasing NBP over the 21st century due to the contributions of climate and land use change (Figures 1 and 3b). Note that, in SSP126, the terrestrial C sink transitions to a terrestrial C source because photosynthesis decreases due to decreasing CO_2 while heterotrophic respiration persists given its longer timescale. In both SSP370 ("regional rivalry") and SSP585 ("fossil-fueled development"), CO_2, temperature, and N deposition increase (Figure 2). CLASSIC-C and CLASSIC-CN project increasing NBP for SSP370 over the 21st century primarily due to increasing CO_2 (Figures 1 and 3b).

Under SSP370 ("regional rivalry"), although CO_2, temperature, and N deposition increase simultaneously as in the historical period, CO_2 increases at a faster rate than N deposition (Figure 2f) and temperature (Figure 2g). Under SSP585 ("fossil-fueled development"), CO_2 and temperature increase whereas N deposition peaks then decreases as opposed to the historical period over which CO_2, temperature, and N deposition all increase simultaneously (Figure 2fg). Similar to SSP370, CO_2 increases at a faster rate than temperature in SSP585 (Figure 2g). Over the historical period, the contribution of N deposition to cumulative NBP was 19.6 Pg C (20% of 96.5 Pg C) whereas the contribution of CO_2 to cumulative NBP was 48.5 Pg C (51% of 96.5 Pg C) for CLASSIC-CN and 118.6 Pg C (62% of 191.8 Pg C) for CLASSIC-C (Figure 3b and Table S4). The contribution of N deposition relative to that of CO_2 to cumulative NBP is much weaker in future scenarios than over the historical period. For SSP370 and SSP585, the contributions of N deposition to cumulative NBP were only 6.6 Pg C (1% of 489.6 Pg C) and 4.4 Pg C (1% of 590.2 Pg C), respectively. In comparison, the contributions of CO_2 to cumulative NBP were 297.5 Pg C (60% of 489.6 Pg C) in SSP370 and 365.9 Pg C (61% of 590.2 Pg C) in SSP585 for CLASSIC-CN and were 565.2 Pg C (62% of 910.6 Pg C) in SSP370 and 707.1 Pg C (63% of 1109.8 Pg C) in SSP585 for CLASSIC-C (Figure 3b and Table S4).

Therefore, for SSP370, CLASSIC-CN projects a terrestrial C sink that is 1.4 Pg C yr^{-1} lower (58% lower) than that projected by CLASSIC-C at the end of the 21st century (Figure 1). For SSP585, the discrepancy between CLASSIC-C and CLASSIC-CN is substantial: CLASSIC-CN projects a terrestrial C sink that is 3.3 Pg C yr^{-1} lower (64% lower) than that projected by CLASSIC-C at the end of the 21st century (Figure 1).

4 Discussion

Of critical importance, as we show here, is that while a TBM that does not represent coupled C and N cycling can reproduce the historical terrestrial C sink, it cannot reliably project the future terrestrial C sink. This is because, in a TBM that does not represent coupled C and N cycling, calibrating the sensitivity of terrestrial photosynthesis to CO_2 to reproduce the historical terrestrial C sink in the absence of N cycling introduces compensatory effects: the stimulation of terrestrial C sequestration by elevated CO_2 over the historical period (i.e., the CO_2 fertilisation effect) must be exaggerated to compensate for the absence of N cycling, i.e., the stimulation of terrestrial C sequestration by elevated N deposition and elevated N mineralisation (driven by elevated temperature) over the historical period. The result of these compensatory effects is that a TBM that does not represent coupled C and N cycling but reproduces the historical terrestrial C sink correctly cannot reliably project the future terrestrial C sink as global change drivers follow divergent trajectories and occur in unprecedented combinations. Specifically, it will overestimate the CO_2 fertilisation effect as CO_2 increases faster than N deposition (which also decreases in some future scenarios) and temperature. This is supported by our simulations of the terrestrial C sink in future scenarios characterised by high atmospheric CO_2: the TBM used here with coupled C and N cycling projects a global net atmosphere-land CO_2 flux that is between 1.4 and 3.3 Pg C yr^{-1} lower (58% to 64% lower) than that projected by the TBM used here without coupled C and N cycling at the end of the 21st century.

Numerous lines of evidence have suggested the importance of N limitation in constraining CO_2 fertilisation, including meta-analyses of elevated CO_2 experiments (Terrer et al., 2019) and temporal analyses of satellite-based estimates of terrestrial photosynthesis paired with foliar N observations (S. Wang et al., 2020). Consistent with these studies, we show that explicitly representing N limitation in a TBM reduces the CO_2 fertilisation effect. Additionally, it has been proposed that the dynamic response of vegetation to N limitation, whereby vegetation invests C in N uptake strategies (such as symbiotic biological N fixation (Vitousek et al., 2013), mycorrhizae (Phillips et al., 2013), rhizosphere priming (Cheng et al., 2014; Finzi et al., 2015), and increasing root:shoot ratio (Poorter et al., 2012; Z. Wang & Wang, 2021)) and/or N retention strategies (such as increasing N resorption (Reed et al., 2012; Z. Wang & Wang, 2021) and increasing C:N ratios (Elser et al., 2010; Sistla & Schimel, 2012; Z. Wang & Wang, 2021)) could allow vegetation to overcome N limitation. The TBM used here includes an advanced representation of symbiotic biological N fixation (Kou-Giesbrecht & Arora, 2022) as well as a representation of flexible C:N stoichiometry (Asaadi & Arora, 2021), suggesting that the dynamic response of vegetation to N limitation (via these two strategies) is insufficient to relieve N limitation of CO_2 fertilisation. Finally, phosphorus (P) could also be imperative in constraining CO_2 fertilisation, especially in tropical regions (Elser et al., 2007b). Additional compensatory effects could exist in TBMs to compensate for the absence of P cycling and require further analysis.

The overestimation of the CO_2 fertilisation effect by TBMs without coupled C and N cycling extends to climate change projections by Earth System Models. CLASSIC serves as the land component of the Canadian Earth System Model (CanESM5) (Swart et al., 2019), which contributed to the sixth phase of the Coupled Model Intercomparison Project (CMIP6) (Eyring et al., 2016). In CanESM5, which includes the older version of CLASSIC that does not represent coupled C and N cycling, the projected global net atmosphere-land CO_2 flux reaches a staggering 12.0 Pg C yr^{-1} at the end of the 21st century for the future scenario with the highest CO_2 (SSP585). This estimate was the highest among participating Earth System Models in CMIP6, despite CanESM5's ability to reproduce several aspects of the historical global C budget (Arora & Scinocca, 2016), and was closely followed by estimates from two other Earth System Models without a representation of coupled terrestrial C and N cycling (Arora et al., 2020; Koven et al., 2022).

5 Conclusions

Our analyses show that reproduction of the historical terrestrial C sink, which is achieved successfully by most TBMs (Friedlingstein et al., 2022), cannot be considered an indicator for the reliability of their projections of the future terrestrial C sink. Our findings show that a TBM that does not represent coupled C and N cycling cannot represent the combined influences of multiple global change drivers, overestimating CO_2 fertilisation as CO_2 increases faster than N deposition and temperature over the 21st century. Scaling fundamental ecological understanding of C and N interactions to the global scale through the explicit representation of physical and biological processes rather than calibration to reproduce the historical terrestrial C sink is key for reliably projecting the future terrestrial C sink under global change with TBMs and ultimately climate change with Earth System Models.

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Open Research

The source code for CLASSIC is available on the CLASSIC community Zenodo page (https://zenodo.org/record/6499554#.YmrLy-3MKUl).

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