Nitrogen Availability Reduces CMIP5 Projections of Twenty-First-Century Land Carbon Uptake*

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ABSTRACT

Coupled carbon cycle–climate models in the Coupled Model Intercomparison Project, phase 5 (CMIP5), Earth system model ensemble simulate the effects of changes in anthropogenic fossil-fuel emissions and ensuing climatic changes on the global carbon (C) balance but largely ignore the consequences of widespread terrestrial nitrogen (N) limitation. Based on plausible ranges of terrestrial C:N stoichiometry, this study investigates whether the terrestrial C sequestration projections of nine CMIP5 models for four representative concentration pathways (RCPs) are consistent with estimates of N supply from increased biological fixation, atmospheric deposition, and reduced ecosystem N losses. Discrepancies between the timing and places of N demand and supply indicated increases in terrestrial N implicit to the projections of all nine CMIP5 models under all scenarios that are larger than the estimated N supply. Omitting N constraints leads to an overestimation of land C sequestration in these models between the years 1860 and 2100 by between 97 Pg C (69–252 Pg C; RCP 2.6) and 150 Pg C (57–323 Pg C; RCP 8.5), with a large spread across models. The CMIP5 models overestimated the average 2006–2100 fossil-fuel emissions required to keep atmospheric CO₂ levels on the trajectories described in the RCP scenarios by between 0.6 Pg C yr^{−1} (0.4–2.2 Pg C yr^{−1}; RCP 2.6) and 1.2 Pg C yr^{−1} (0.5–3.3 Pg C yr^{−1}; RCP 8.5). If unabated, reduced land C sequestration would enhance CO₂ accumulation in the ocean and atmosphere, increasing atmospheric CO₂ burden by 26 ppm (16–88 ppm; RCP 2.6) to 61 ppm (29–147 ppm; RCP 8.5) by the year 2100.

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1. Introduction

The representative concentration pathways (RCP) describe plausible futures of the anthropogenic radiative forcing, ranging from climate change stabilization at about 2°C (RCP 2.6) to a no climate change mitigation scenario reaching a radiative forcing of 8.5 W m^{−2} (RCP 8.5) by the year 2100 (van Vuuren et al. 2011). Phase 5 of

TABLE 1. CMIP5 Earth system model runs used for these analyses, as described in detail by [Arora et al. 2013](#). C denotes available CMIP5 C cycle model simulations, and CN denotes CMIP5 models that further include an interactive N cycle.

Model name	Modeling center	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
CanESM2	Canadian Centre for Climate Modeling and Analysis	C	C		C
GFDL-ESM2G	National Oceanic and Atmospheric Administration	C		C	C
GFDL-ESM2M			C	C	C
HadGEM2-CC	Met Office Hadley Centre		C		C
HadGEM2-ES		C	C	C	C
IPSL-CM5A-LR	L'Institut Pierre-Simon Laplace	C	C	C	C
IPSL-CM5A-MR		C	C		C
IPSL-CM5B-LR			C		C
MPI-ESM-LR	Max Planck Institute for Meteorology	C	C		C
CESM1(BGC)	National Science Foundation, U.S. Department of Energy, National Center for Atmospheric Research		CN		CN

the Coupled Model Intercomparison Project (CMIP5; [Taylor et al. 2012](#)) has investigated the effects of these scenarios on the climate system using complex Earth system models that include a prognostic global carbon (C) cycle and therefore account for its interactions with the climate system ([Arora et al. 2013](#); [Jones et al. 2013](#)). The global C budgets in these simulations can be used to infer the fossil-fuel emissions trajectories that are compatible with the assumed atmospheric CO₂ burden, thus providing important information on future CO₂ emission targets for climate change mitigation policies ([Friedlingstein et al. 2011](#)).

A potentially important caveat of the CMIP5-based global C projections is that the overwhelming fraction of models in the CMIP5 ensemble do not represent the effects of nitrogen (N) constraints on photosynthesis and organic matter decay ([Table 1](#)). N availability is limited in the natural environment because of the high energy requirement to convert elementary N₂ to biologically available forms and losses of N that escape plant uptake (e.g., denitrification; [Vitousek and Howarth 1991](#); [Houlton et al. 2003](#); [Menge et al. 2008](#)). Free-air CO₂ enrichment (FACE) experiments in temperate, predominantly N-limited forest ecosystems have demonstrated that the capacity of ecosystems to respond to elevated CO₂ levels is strongly affected by the availability of N and the capacity of the vegetation to acquire new sources of N ([Oren et al. 2001](#); [Norby et al. 2010](#); [Zaehle et al. 2014](#)). Conversely, N released from enhanced soil organic matter decomposition because of experimental soil warming in a temperate, predominantly N-limited forest ecosystem has been shown to fertilize plants, leading to above-ground C sequestration at a rate compensating for the warming-related soil carbon loss ([Melillo et al. 2011](#)). Scaling from these experiments to global implications is difficult because of the intricate processes controlling the C–N interaction, as well as

uncertainties in the geographic distribution of N limitation ([Hickler et al. 2008](#); [Zaehle et al. 2014](#)). In particular, the high energy costs of N fixation and its associated decrease from the equator to the poles ([Houlton et al. 2008](#)) causes the constraint of N availability on ecosystem production to increase generally from tropical to boreal environments ([Reich and Oleksyn 2004](#); [McGroddy et al. 2004](#); [Zaehle 2013](#)).

The importance of N dynamics has led to the development of a number of land surface models, suitable for coupling to Earth system models, accounting explicitly for N processes and their effects on the global C cycle [see [Zaehle and Dalmonech \(2011\)](#) for a review]. Future projections from these models ([Sokolov et al. 2008](#); [Thornton et al. 2009](#); [Zaehle et al. 2010](#); [Zhang et al. 2014](#)) have demonstrated that N dynamics attenuate the CO₂ fertilization effect on plant growth and thus the terrestrial C storage in response to increasing atmospheric CO₂. These models have also shown that N dynamics attenuate the terrestrial C loss due to climate warming resulting from increased soil respiration, because the N release associated with higher soil respiration enhances plant growth and increases plant C storage. Taken together, most global C–N models suggest that the net effect of N dynamics results in reduced C accumulation on land between the preindustrial period and the year 2100, which leads to increased estimates for future atmospheric CO₂ and mean annual surface temperatures compared to models that do not represent the N cycle explicitly ([Zaehle and Dalmonech 2011](#)).

Our objective here was to provide spatially and temporally explicit estimates of the N required to sustain the C sequestration projections of the CMIP5 ensemble (herein, the N requirement) and to compare this N requirement to plausible trajectories of terrestrial N availability from increased N inputs (biological fixation and atmospheric deposition) and reduced N losses. Based on

this comparison, we aimed to infer the excess amounts of C sequestration simulated by the CMIP5 models, which are unsupported by N cycle constraints, and to quantify the consequences for the corresponding CMIP5-derived compatible emission pathways. To facilitate comparison to studies on other relevant biogeochemical feedbacks omitted by the current generation of Earth system models (Arneth et al. 2010), we also assessed the effect of ignoring N constraints of the terrestrial C balance on projected atmospheric CO₂ and radiative forcing by tracking the effect of the reduced land C uptake on atmospheric and oceanic C accumulation.

Previous attempts to tackle this question (Hungate et al. 2003; Wang and Houlton 2009) based on earlier model intercomparison studies (Cramer et al. 2001; Friedlingstein et al. 2006) have indicated that models not accounting for N dynamics (herein, C cycle-only models) likely substantially overestimate future terrestrial C sequestration. These studies have assessed the implied N deficit (i.e., the difference between implied N requirement and N supplied) only at the global or hemisphere scales. Furthermore, these studies ignored the trajectories of N requirement relative to N availability. Both simplifications have the potential to bias the assessment of N available to support the projected C sequestration. Thus, in contrast, our analyses are performed at the spatial resolution of the ESMs and on an annual time scale.

2. Methods

a. Framework of the analyses

The N stored in the terrestrial biosphere implied by the CMIP5 simulations can be estimated as

$$N_{\text{tot}} = C_V \frac{N_V}{C_V} + C_L \frac{N_L}{C_L} + C_S \frac{N_S}{C_S} + C_P \frac{N_P}{C_P} \quad [\text{Pg N}], \quad (1)$$

where C_V , C_L , C_S , and C_P are the carbon storage in vegetation (V), litter (L), soil (S), and harvested/stored wood products (P ; including anything from paper to furniture) for each grid cell predicted by the CMIP5 models; and N_i/C_i represents their respective N:C ratios. The N:C ratios are not precisely known, owing to the diversity of chemical compounds that form organic matter. We have assumed wide ranges for the ratios based on (Wang and Houlton 2009): the vegetation C:N ratio ranged between 107 and 278; the soil C:N ratio was 14–16 in tropical and 16–18 temperate and boreal regions, whereas the litter pool was assumed to have a constant value of 120. The product pool was assigned the C:N range of woody biomass (150–400; cf. Wang and Houlton 2009). Lacking a predictive framework of how

the N:C ratios may vary with global change (Zaehle et al. 2014), we have assumed that the N:C ratios for the components (V , L , S , and P) of the terrestrial biosphere are time invariant.

The time-dependent, implied N requirement (fN_{req}) of the terrestrial biosphere can then be calculated as

$$fN_{\text{req}} = \frac{\partial N_{\text{tot}}}{\partial t} = \sum_{i=V,L,S,P} \frac{\partial C_i}{\partial t} \frac{N_i}{C_i} \quad [\text{Pg N yr}^{-1}]. \quad (2)$$

Because of the arrangement of the C:N ratios of the different pools, fN_{req} implicitly accounts for the effects of internal redistribution of N within the terrestrial biosphere. For example, the soil N decline implicit to a reduction of soil C storage can compensate for the implied N requirement of increasing vegetation C storage.

Since the CMIP5 models do not explicitly balance Eq. (1), there was a large interannual variability in the estimate of fN_{req} (Fig. 1b). To avoid this variability causing spurious estimates of the N deficit, we defined, for each ESM and each grid cell, a background N availability term (fN_{nat}) corresponding to twice the detrended, preindustrial (1860–80) standard deviation of fN_{req} , implicitly assuming that there would be sufficient N to support these variations. This assumption is equivalent to the hypothesis that there was no preindustrial N limitation of gross productivity, which is unavoidable in a posteriori analyses. Note that preindustrial rates of N deposition and fixation are implicitly included in the estimate of fN_{nat} . The fN_{nat} term can be interpreted as the upper bound of the annual rate of new organic N resulting from a reduction of ecosystem N losses caused by increased biotic demand for N (Hungate et al. 2003). We derived spatially and temporally explicit datasets of additional terrestrial N from anthropogenic atmospheric N deposition (fN_{dep}) and biological N fixation (fN_{fix}) above their preindustrial rates (section 2c, Fig. 1c) to evaluate whether these N inputs supported the trajectory of the fN_{req} .

We define the implied deficit of N (fN_{def} ; Figs. 1d,e) as

$$fN_{\text{def}} = \max(fN_{\text{req}} - k_d fN_{\text{dep}} - k_b fN_{\text{fix}} - k_n fN_{\text{nat}}, 0) \quad [\text{Pg N yr}^{-1}], \quad (3)$$

where k_n is a scaling constant (range: 0.9–1.1) to assess the sensitivity of fN_{def} to the background availability term, k_d is a scaling coefficient to account for the fraction of N deposition permanently remaining in the terrestrial biosphere (range: 0.1–0.5; Schlesinger 2009), and k_b (range: 0.33–1.0) is a scalar to account for uncertainty in the response of fixation to climate change and CO₂ because of, for example, limitation by micronutrients (Hungate et al. 2004).

FIG. 1. Example of the approach to estimate fC_{exe} and fN_{def} for a grid cell of the HadGEM2-ES RCP 4.5 simulation at 60°N and 95°E. See section 2a for details.

We estimated the associated excess C sequestration in the terrestrial biosphere caused by the N deficit based on the C:N ratios of the C pools increasing in a year and grid cell, in which the N deficit occurs (Figs. 1f,g):

$$fC_{exe} = \left[\frac{\sum_{i=V,L,S,P} \max\left(\frac{\partial C_i}{\partial t}, 0\right)}{\sum_{i=V,L,S,P} \max\left(\frac{\partial N_i}{\partial t}, 0\right)} \right] fN_{def} \quad [Pg \text{ C yr}^{-1}]. \quad (4)$$

Note that Eq. (4) only applies to the fraction of the increase in the projected terrestrial biomass increase that is not supported by available N. Redistribution of N from soil to vegetation is implicitly taken into account in Eq. (2), which decreases the N requirement associated with an increase of, for instance, the vegetation C and N pools in regions where soil C and N decline.

In total, we derived 16 estimates for fN_{def} and the inferred N-induced reduction of terrestrial C sequestration

(fC_{exe}), accounting for the factorial combinations of upper and lower bounds for the values of k_b , k_d , and k_n and the N:C ratios of the pools. Reported values are the globally integrated median and the 90% confidence interval of the distribution, unless stated otherwise. To obtain ensemble results, the results were first aggregated across ensemble members from the same Earth system model family (e.g., GFDL-ESM2, HadGEM2, and IPSL-CM5) and then across different ESMs.

Compatible fossil-fuel emissions (E) were estimated following Jones et al.(2013):

$$E = \frac{dC_A}{dt} + \frac{dC_O}{dt} + \frac{dC_{tot}}{dt} \quad [Pg \text{ C yr}^{-1}], \quad (5)$$

where C_A is the atmospheric CO_2 specified in the RCP scenarios, and C_O is the projected change in ocean C inventory (including sea floor sediments) for each ESM and scenario (section 2b). The expression dC_{tot}/dt is either derived as the time derivative of the CMIP5 projections

of C_V , C_L , C_S , and C_P , which is referred to here as CMIP5, or as the sum of the CMIP5 projections of C_V , C_L , C_S , and C_P reduced by fC_{exce} , which is referred to here as CMIP5-N.

We also estimated the additional atmospheric CO_2 burden and radiative forcing resulting from fC_{exce} assuming unchanged CMIP5-based fossil-fuel emissions. Consistent estimates of the net air–ocean C flux and atmospheric CO_2 burden were obtained by driving a pulse-response ocean C cycle model (3D model; Joos et al. 1996) with the RCP-compatible fossil-fuel emissions derived from integrated assessment models (van Vuuren et al. 2011), the estimated net land C fluxes, and the ESMs' sea surface temperature (SST) projections. The 3D ocean model's parameter for the ocean's mixed layer depth h was calibrated such that, given the 1860–2005 observed atmospheric CO_2 and SST trends, the simulated net ocean uptake corresponded to observation-based estimates for the period 1960–99 (1.7 Pg C yr^{-1} ; Le Quéré et al. 2013). The radiative effect of simulated atmospheric CO_2 abundance was then estimated following the IPCC TAR (Ramaswamy et al. 2001).

b. CMIP5 C storage and surface temperature data

The simulations used for this study were the historical (1860–2005) and future (2006–2100) RCP simulations (CMIP5 experiment numbers 4.1–4.4; Taylor et al. 2012) obtained from the standard CMIP5 output from the Program for Climate Model Diagnosis and Intercomparison (<http://cmip-pcmdi.llnl.gov/cmip5/>). The ESMs were run using specified abundances of atmospheric CO_2 and greenhouse gases, emissions of aerosols, and natural forcings such as solar and volcanic aerosol emissions. Scenarios of land-use change were also available and used by the models, but their implementation differs considerably between models (Brovkin et al. 2013). The year 1860 was chosen as a starting date for the analyses, because not all simulations were available from 1850.

Data from nine ESMs (CanESM2, GFDL-ESM2G, GFDL-ESM2M, HadGEM2-CC, HadGEM2-ES, IPSL-CM5A-LR, IPSL-CM5A-MR, IPSL-CM5B, and MPI-ESM-LR) and four RCP scenarios (RCP 2.6, 4.5, 6.0, and 8.5) were used for this study; but not all models ran all scenarios (Table 1). None of these models include C–N interactions. In addition, we analyzed the results of the Community Earth System Model, version 1–Biogeochemistry [CESM1(BGC)], which included the Community Land Model, version 4 (CLM4; Thornton et al. 2009), and thus accounted for C–N cycle interactions explicitly. Of the available output, we used annual means of living above- and below-ground biomass (cVeg), undecomposed dead plant material (cLitter), and soil organic matter (cSoil), as well as carbon stored in wood products (cProduct). The HadGEM2

and GFDL-ESM2 models did not report litter carbon. For these models, the fraction of reported soil carbon that was litter was assumed to vary between 30% and 40%, which is approximately the global average estimate based on the other CMIP5 simulations (Wang and Houlton 2009). For the derivation of the compatible emissions [Eq. (5)] we also used the annual, globally integrated change in the ocean C inventory from the CMIP5 simulation. We used the simulated annual mean surface temperature (TAS) for the calculation of biological N fixation (section 2c). TAS was also used to simulate the ocean net C flux, given specified land C uptake and fossil emissions, in order to diagnose atmospheric CO_2 abundance in emissions-driven runs (section 2a). All results were conservatively interpolated to a common $1^\circ \times 1^\circ$ grid, with the land fraction of each grid cell determined from the $0.5^\circ \times 0.5^\circ$ GTOPO30 dataset (<https://lta.cr.usgs.gov/GTOPO30>).

c. N fixation and atmospheric N deposition

Spatially explicit changes in annual biological N_2 fixation from preindustrial conditions were estimated based on the results of a process-based ecological model of biological N fixation (Houlton et al. 2008; Wang and Houlton 2009), for which spatially explicit sensitivities to changes in surface temperature and atmospheric CO_2 have been derived. This reduced-form model was driven with the ESMs' gridded annual mean surface temperature (section 2b) and the RCP-specific annual atmospheric CO_2 burden projections (Taylor et al. 2012). Based on this model, global N fixation increases by up to 85 Tg N yr^{-1} relative to a preindustrial baseline of about 120 Tg N yr^{-1} (see Fig. S1 in Wang and Houlton 2009). Cumulated over time, this leads to 2.9–8.8 Pg N (RCP 2.6) to 3.3–10.1 Pg N (RCP 8.5) of additional N input (fN_{fix}) over the period 1860–2100, with much higher inputs in tropical versus temperate and boreal ecosystems (Fig. S1).

Spatially explicit changes in anthropogenic N inputs between 1860 and 2100 were taken from simulations with the chemistry–climate Community Atmosphere Model (CAM-chem), driven with reactive N emission inventories according to the RCP scenarios, including emissions from biomass burning and soils (Lamarque et al. 2012, 2011). However, no climate or N cycle-related feedbacks from burning or soil emissions on N deposition were included. Not all of this deposited N is sequestered in the biosphere (section 2a). Between 1860 and 2100, 0.6–3.0 Pg N (RCP 4.5) to 0.7–3.7 Pg N (RCP 8.5) are estimated to become biologically available, with a clear regional pattern with highest rates in areas with high population and industry density (Fig. S1).

FIG. 2. CMIP5 projections of (a) cumulative C sequestration and (b) the implied cumulative N sequestration required to support the cumulative C sequestration between 1860 and 2100 for the four representative concentration pathways (RCP 2.6, 4.5, 6.0, and 8.5), as well as (c) the relationship between cumulated C sequestration and N requirements for the year 2100. The black points in (a) and (b) denote the 2005 values; colored points indicate the 2100 values; error bars indicate the range due to uncertainty in the pool's C:N ratios (section 2a). In (a) and (b), only the results from the CanESM2, GFDL-ESM2G, HadGEM2-ES, IPSL-CM5A-LR, MPI-ESM-LR, and CESM1(BGC) models are plotted for clarity. Corresponding simulations of the other ESMs (GFDL-ESM2M, HadGEM2-CC, IPSL-CM5A-MR, and IPSL-CM5B-LR) were quantitatively similar.

3. Results

a. Projections of C sequestration and implied N requirements

Cumulative terrestrial C losses and gains nearly balanced out during the historical period for most models in the CMIP5 ensemble (Fig. 2a), with an implied cumulative N requirement of 1.2 Pg N (-0.6 – 6.3 Pg N; Fig. 2b). Exceptions were the GFDL-ESM2 models, which simulated a strong decline in terrestrial C and associated net N loss, and the MPI-ESM-LR, which showed a small net C uptake of 15 Pg C, with soil C gains compensating for vegetation C losses, associated with an increase in the implied terrestrial N stock of 7.5 Pg N, mostly in soils. The C sequestration and implied N requirements were larger for the scenario period for most models and scenarios, with—for each model—the RCP 2.6 showing generally the lowest and the RCP 4.5 generally the largest C sequestration (Figs. 2a,b). Cumulated between 1860 and 2100, the CMIP5 ensemble projected a change in global land C storage between -26 and 488 Pg C, with a larger spread between models than between scenarios (Fig. 2a).

Between 1860 and 2100, the CanESM2 simulated to a globally integrated negative N requirement (-2.8 to -1.3 Pg N) despite a globally integrated positive C sequestration under most scenarios (-19 – 93 Pg C). This resulted from a combination of concurrent regional C and N losses south of 20° N and increases in terrestrial C

north of 40° N (Fig. 3), which were not associated with increases in terrestrial N as a result of N redistribution from soils to vegetation. The projected change in land C in the GFDL-ESM2 models implied only little change in the global terrestrial N pool (0.7 – 2.2 Pg N) and showed no distinct latitudinal pattern. Larger N requirements with average increases of 3 – 8 Pg N associated with larger terrestrial C sequestration occurred for the HadGEM2 and IPSL-CM5 models. These N requirements were still much lower than the 18 – 24 Pg N implied by the MPI-ESM-LR simulations, although the global C sequestration estimates between the HadGEM2, IPSL-CM5, and MPI-ESM-LR models were broadly comparable.

The primary reason for this large model difference was the fate of the sequestered C. The fraction of C stored in high C:N vegetation versus low C:N soils was different between the models, with a large vegetation share in the IPSL-CM5 models, a fairly equal share in the HadGEM2 models, and a low share in the MPI-ESM. The regional distribution of C sequestration and associated N requirements were also strikingly different between these models (Fig. 3): the HadGEM2 models showed large C sequestration north of 50° N, mostly in former sparsely forested tundra, while the MPI-ESM simulated the largest C sequestration in dry land soils at most latitudinal bands. The IPSL-CM5 models suggested the largest C sequestration in tropical forests, with a secondary peak around 60° N. The different distribution of additional C storage between vegetation

FIG. 3. Latitudinal distribution of (a) the projected CMIP5 terrestrial C storage and (b) implied N sequestration between 1860 and 2100 under the RCP8.5 scenario, as simulated by the CanESM2, GFDL-ESM2G, HadGEM2-ES, IPSL-CM5A-LR, MPI-ESM-LR, and CESM1 (BGC) models. The red lines, labelled CMIP5, represent the CMIP5 simulations; blue lines, labelled CMIP5-N, represent the estimates compatible with the N budget estimate, as described in sections 3b and 3c. The blue shaded area represents the uncertainty range of the implied N sequestration estimate; the yellow shaded area represents the diagnosed fC_{exe} and fN_{def} , respectively.

and soils is also the cause for the differences in the latitudinal patterns of N requirements and C sequestration between the HadGEM2 and IPSL-CM5 models north of 50°N (Fig. 3), with HadGEM2 requiring roughly 4 times the amount of N for about the same level of C sequestration, owing to the larger share of soil C sequestration.

b. Calculation of the nitrogen deficit 1860–2100

We next evaluated whether reducing N losses or increasing terrestrial N inputs could support these implied N requirements. Taking the HadGEM2-ES RCP 8.5 simulation as an example (Fig. 4; see Fig. S2 for the other models), the spatially and temporally explicit overlay of the estimates for N requirement with N input from fixation and deposition resulted in a small increase in new terrestrial N from fixation and deposition during the

twentieth century but notable increases during the twenty-first century (Fig. 4b). The by-far largest source of additional terrestrial N during 1860 to 2100 was an increase in the terrestrial N pool derived from background N availability (Fig. 4c), which can be interpreted as increases in ecosystem N pools because of reduced terrestrial N losses (see section 2a). Note that Fig. 4c displays the global effective net flux from the assumed time-invariant background N availability minus N losses from regions with a permanently negative N balance. The primary reason for the comparatively small contribution of fixation and deposition to the new terrestrial N storage was that most of the N requirement occurred in boreal regions with low projected increases in fixation and deposition; conversely, most of the projected increase in N fixation and deposition occurred in regions

FIG. 4. Estimates of the cumulative N fluxes between 1860 and 2100 for the HadGEM2-ES RCP 8.5 simulation: (a) CMIP5 implied fN_{req} and the plausible range of N sequestration derived in section 3b ($fN_{\text{req}} - fN_{\text{def}}$); (b) N supply that supports fN_{req} from fN_{fix} and fN_{dep} ; (c) global net N supply from fN_{nat} (note that this estimate accounts for N losses in some and N gains in other regions), as well as the diagnosed fN_{def} remaining after accounting for these N sources. Shaded areas represent the 90% confidence interval. See Fig. S3 for CanESM2, GFDL-ESM2G, IPSL-CM5A-LR, MPI-ESM-LR, and CESM1(BGC).

that did not show large increases in N storage. Based on these fluxes, we diagnosed an implied, cumulative N deficit for the year 2100 of 3.4 Pg N (2.6–4.5 Pg N; Fig. 4c). Accounting for this N deficit, the cumulative N requirement for the HadGEM2-ES simulation would be reduced to 0.9 Pg N (0.7–1.1 Pg N) until 2005 and to 3.8 Pg N (3.1–4.5 Pg N) in 2100 (Fig. 4a).

Across models, the new terrestrial N derived from fN_{nat} ranged between an additional 3.1 Pg N (0.8–14.0 Pg N) in

RCP 2.6 and 3.4 Pg N (0.7–12.7 Pg N) in RCP 8.5, with a larger spread across models than scenarios (Fig. 5a). These model differences were associated with differences in preindustrial N stocks, from which fN_{nat} was derived. Another important factor was that in some models (most importantly the MPI-ESM), terrestrial N increased gradually in time, thus allowing for a nearly continuous supply of N from fN_{nat} . This was not the case for the other models, which showed the large interannual variability in the terrestrial N requirement. The additional terrestrial N storage due to fixation was only 0.3 Pg N (0.1–1.0 Pg N; RCP 2.6) to 0.4 Pg N (0.1–1.4 Pg N; RCP 8.5; Fig. 5a). The difference between the cumulative increase in potential N fixation and N-fixation-based N was caused by large potential N fixation increases in the tropics, where not much N was required in most CMIP5 models (Figs. 3 and S1). Our analysis further suggested that additional input from N deposition supplied 0.2 Pg N (0.1–1.0; RCP 2.6) to 0.3 Pg N (0.1 to 1.2 Pg N; RCP 8.5; Fig. 5a). The main reason for the large difference between the additional N stored in the terrestrial biosphere based on N deposition and the larger input from N deposition are low N requirements in areas of high N deposition.

Despite these increases in terrestrial N inputs, N deficit—that is, a larger implied N requirement than N supply [Eq. (3)]—occurred for all models and scenarios (Fig. 5a). For each model, the implied N deficit showed a scenario dependence, with a comparatively low N deficit of 1.4 Pg N (1.0–8.8 Pg N) in the low- CO_2 scenario RCP 2.6 and a larger N deficit [2.0 Pg N (1.4–12.0 Pg N)] in the high- CO_2 scenario RCP 8.5. Taking the RCP 8.5 scenario as an example, the N deficit was fairly similar between the GFDL-ESM2 [1.6 Pg N (0.8–2.7 Pg N)], CanESM2 [1.7 Pg N (1.3–2.2 Pg N)], and IPSL-CM5 models [2.0 Pg N (1.3–3.0 Pg N)], significantly larger for the HadGEM2 models [3.7 (2.6–5.1) Pg N], and largest in the MPI-ESM-LR [12.0 Pg N (10.0–14.1 Pg N)].

Differences in the spatial pattern of N requirement due to diverging geographical distributions of projected C sequestration and its partitioning between high C:N vegetation and low C:N soil organic matter were the main reason for the large intermodel difference in the implied N deficit. The HadGEM2 models showed the largest rate of N accumulation in the boreal/tundra zone and, to a lesser extent, in putatively N-limited temperate forests, leading to a large implied N deficit (Fig. 3b). Despite similar C sequestration in this region, as projected by the IPSL-CM5 models, the lower N requirement due to a larger share of vegetation C storage (and its higher C:N ratio) resulted in a smaller implied N deficit. The large increase in tropical vegetation biomass in the IPSL-CM5 simulations (Fig. 3b) caused N requirement in excess of the N available from increased N fixation, partly because of limits of tropical N

FIG. 5. (a) Cumulative N budget and (b) cumulative C budget of the CMIP5 simulations, split into N (or C) derived from fN_{nat} , fN_{dep} , and fN_{fix} , as well as the diagnosed fN_{def} or fC_{exe} , respectively, not supported by any source of N. In (a), points denote the implied CMIP5 N requirements; in (b), they denote the CMIP5 C sequestration estimate. Negative values can occur when cumulative N or C losses in some regions are not compensated for by N or C gains in other regions.

fixation induced by climate warming. The MPI-ESM projected substantial rates of C sequestration in the soils of semiarid ecosystems, resulting in a very high implied N deficit between 20° and 70°N and south of 20°S (Fig. 3b).

c. Implied excess C sequestration

Corresponding to the results in section 3b, natural N availability was responsible for most of the plausible C sequestration in the CMIP5 simulations (Fig. 5b). Across all models, fN_{nat} accounted for 133 Pg C (48–214 Pg C; RCP 2.6) to 238 Pg C (104–339 Pg C; RCP 4.5) stored in the biosphere between 1860 and 2100. This estimated C implicitly accounts for the C sequestration effect of redistributing N from low C:N soils to high C:N vegetation to the extent where soil C losses occurred simultaneous to vegetation C increases. Across models, the effects of N redistribution from soils to vegetation (i.e., the fertilization effect from enhanced soil C losses) was an increase of vegetation C by 7.2 Pg C (1.6–30.8 Pg C) in the RCP 2.6 to 10.2 Pg C (1.7–44.5 Pg C) in the RCP 8.5 scenario, with a large spread across models: 2.4 Pg C (1.0–4.9 Pg C) in the HadGEM2 models up to 29.5 Pg C (12.6–61.1 Pg C) in the CanESM2 model.

We estimated that, across models, anthropogenic N deposition contributed to terrestrial C storage on the

order of 13.0 Pg C (9.6–17.0 Pg C; RCP 2.6) and 21.2 Pg C (15.8–24.7 Pg C; RCP 8.5; Fig. 5b; see also Fig. S3). Again, there were consistent differences between the models: lowest for CanESM2 [11.0 Pg C (4.0–27.4 Pg C)] and highest for MPI-ESM-LR [17.5 Pg C (5.7–36.5 Pg C)]. Biological N fixation contributed to additional C sequestration between 12.0 Pg C (7.2–18.0 Pg C; RCP 2.6) and 23.4 Pg C (13.2–34.4 Pg C; RCP 8.5; Fig. 5b; see also Fig. S3). Some models, in particular the IPSL-CM5 models, for which N supply from tropical N fixation was important, showed that the fixation effect was lower in the RCP 8.5 scenario than in the RCP 4.5 scenario because of reduction in tropical N fixation as temperatures increased above the optimal temperature threshold (Houlton et al. 2008). Again, there were large differences across models, with CanESM2 showing the lowest effect of changed biological N fixation [10.4 Pg C (4.5–17.2 Pg C)] and MPI-ESM-LR showing the largest effect [22.2 Pg C (11.9–44.2 Pg C)].

Taking the RCP 8.5 scenario as an example, the globally integrated excess C across models between 1860 and 2100 ranged from 97 Pg C (78–121 Pg C) for the CanESM2 to 112 Pg C (77–162 Pg C) for the IPSL-CM5 models. The GFDL-ESM2 models with an equally moderate N deficit suggested a slightly larger excess C

FIG. 6. Cumulative C sequestration from the CMIP5 models (as in Fig. 1a) and plausible range of C sequestration considering N constraints (CMIP5-N) for the CanESM2, GFDL-ESM2G, HadGEM2-ES, IPSL-CM5A-LR, MPI-ESM-LR, and CESM1(BGC) models.

[165 Pg C (119–274 Pg C)]. For the HadGEM2 models, the N deficit resulted in a global C excess sequestration of 218 Pg C (172–274 Pg C). This C excess estimate is still substantially smaller than that of MPI-ESM [383 Pg C (339–429 Pg C)]. Excess C occurred mainly in the boreal zone for the CanESM2 and HadGEM2 models, whereas it was more equally distributed for the GFDL and IPSL-CM5 models (Fig. 3a). The large projected increases in dry land soil C across most latitudinal bounds in the MPI-ESM were found to be largely unsupported by potential sources of N, according to our study (Fig. 3a).

The temporal explicit nature of our analysis allows us to diagnose the temporal development of excess C

sequestration and estimate a corrected time series of the C sequestration estimates by models participating in CMIP5, which is commensurate with our estimates of the terrestrial N balance (Fig. 6). Some of the excess C sequestration occurred during the twentieth century as the result of increasing C sequestration due to CO₂ fertilization (Fig. S4). The development of the excess C accelerated after the year 2000, when C sequestration in the original simulations started to rapidly increase. Taken together, during the scenario period, N limitation reduced the projected CMIP5 net land C uptake by 37% (median for RCP 2.6) and 58% (median for RCP 8.5), with a larger difference between models than across scenarios (Fig. 7).

FIG. 7. Ensemble median of (a) terrestrial N sequestration and (b) terrestrial C sequestration for the historical (1860–2005) and scenario (2006–2100) period with (CMIP5-N) and without (CMIP5) taking N constraints into account. Points mark the median result for each model and scenario.

d. Effect of the CMIP5 excess C sequestration on estimates of the RCP-compatible emissions

Using the revised terrestrial C sequestration estimates, we estimated revised trajectories of the RCP-compatible emissions, given the RCP atmospheric CO_2 abundance and the CMIP5 models' net ocean C fluxes (Fig. 8). The compatible emissions for the scenario period (2006–2100) would have had to be reduced by 62 Pg C (40–194 Pg C) in the low- CO_2 scenario RCP2.6 to 126 Pg C (61–290 Pg C) in the high-emission scenario RCP 8.5 (Fig. 8b). Relative to the estimate based on the original nine CMIP5 models, this reduction corresponds to 19%, 14%, 8%, and 7% of the compatible emissions for RCP 2.6, 4.5, 6.0, and 8.5, respectively, with only modest shifts in the timing of the compatible peak emissions (Fig. 8c). In the RCP 2.6 scenario, the average 2076–2100 compatible emissions [$0.39 \text{ Pg C yr}^{-1}$ (-1.01 – $1.15 \text{ Pg C yr}^{-1}$) in the CMIP5 simulations] needed to be reduced to $-0.50 \text{ Pg C yr}^{-1}$ (-1.63 – $0.07 \text{ Pg C yr}^{-1}$), thus increasing the percentage of simulations requiring net C capture by the end of the twenty-first century to meet the atmospheric CO_2 trajectory from 40% ($n = 5$) in the CMIP5 ensemble to 80% ($n = 80$), considering N constraints in our study.

e. Effect of the CMIP5 excess C sequestration on estimates of atmospheric CO_2 and radiative forcing

To facilitate comparison to studies on other relevant biogeochemical feedbacks omitted by CMIP5, we further estimated the effect of not considering the N-induced constraints on terrestrial C sequestration in calculating emission targets on the levels of atmospheric

CO_2 and its radiative forcing. Using a temperature-sensitive pulse-response ocean C cycle model to estimate the fate of the excess C in ocean and atmosphere (section 2b), we found that the lower cumulative land C uptake caused the cumulative ocean C uptake to increase by 24 Pg C (16–121 Pg C) to 36 Pg C (20–90 Pg C) for the RCP 2.6 and 8.5 scenarios, respectively (Fig. 9a). The remaining excess C accumulated in the atmosphere, causing an extra burden of 26 ppm (16–88 ppm) to 61 ppm (29–147 ppm) by the year 2100 for the RCP 2.6 and 8.5 scenarios, respectively (Fig. 9b). Because of the non-linearity of radiative forcing with atmospheric CO_2 , the additional median radiative forcing in the year 2100 was similar for the RCP 2.6 and 8.5 scenarios at 0.34 W m^{-2} and highest in the RCP 4.5 at 0.46 W m^{-2} (Fig. 9c), thus increasing the expected climate change for a given scenario of anthropogenic fossil-fuel emissions.

4. Discussion

The analyses presented above are based on a range of simplifying assumptions, which can only be resolved properly within dynamic ecosystem models accounting for all relevant C–N interactions. In the following, we discuss the implications of these assumptions.

a. Methodological limitations

Lacking a framework to account for potential changes in tissue C:N ratios, we did not include such effects. Foliar C:N ratios have been reported to increase with elevated CO_2 (Ainsworth and Long 2005), while they decrease with N additions (Hyvönen et al. 2007). However, the C:N of the entire vegetation were

FIG. 8. (a) N-induced reduction of annual RCP-compatible emissions under the four RCP scenarios; (b) cumulative N-induced reduction of RCP-compatible emissions; (c) the annual RCP-compatible emissions derived from the CMIP5 ensemble excluding (dashed) and including (solid) nitrogen constraints; and (d) the cumulative RCP-compatible emissions derived from the integrated assessment models (IAM; [van Vuuren et al. 2011](#)), the CMIP5 ensemble ([Jones et al. 2013](#)), and CMIP5-N. The middle bars denote the ensemble median, the boxes denote the 25%, and 75% quantile, and the bars denote the 90% confidence interval. Points mark individual models. The scenarios RCP 2.6, 4.5, 6.0, and 8.5 refer to the period 2006–2100. The value n indicates the number of ESMs upon which these plots are made (see also [Table 1](#)).

largely unaffected in free-air CO₂ enrichment experiments ([Finzi et al. 2007](#)), and it is not clear that gradual changes in atmospheric CO₂ or N inputs, as they occur in the RCP scenarios, would lead to a similar magnitude of changes in foliar chemistry to that observed in these manipulation experiments ([Zaehle et al. 2014](#)). The potential maximal effect of changing stoichiometry of new biomass can be estimated from the difference in excess C for the upper and lower bounds of C:N ratios [RCP 2.6: 7 Pg C (1.1–14.4 Pg C); RCP 8.5: 18.4 Pg C (3.9–26.0 Pg C)], which was less than 10% of the excess C for most models. The exception was the IPSL-CM5 models (difference < 20%), which had a large share of vegetation C sequestration with the largest plausible range of C:N values.

The key source of N to support the implied N requirement was the assumed background N availability (fN_{nat}), which is unknown from observations. We defined this term as twice the standard deviation of the interannual variations of the 1860–80 N budget, implicitly assuming that there would be sufficient N to support

these variations. In other words, we assumed that there would be no preindustrial N limitation anywhere in the world. This assumption is inevitable in the a posteriori approach taken here, but it introduces a tendency for the method to underestimate the N limitation of future C sequestration, because the assumption that there would be no preindustrial N limitation is too strong within all reasonable understanding of the N cycle ([Menge et al. 2012](#); [Vitousek and Howarth 1991](#)). In consequence, we tend to overestimate fN_{nat} over large parts of the world.

The average N derived from fN_{nat} was about 50 Tg N yr⁻¹ for the MPI-ESM-LR, which corresponds to a third of the preindustrial N losses from the terrestrial biosphere ([Zaehle 2013](#)). This high estimate was associated with high preindustrial soil C (and, with them, soil N) stocks, which contributed to a large fN_{nat} , and fairly continuous soil C (and thus soil N) accrual throughout the simulation across large areas. For the other models, as a result of lower estimates of fN_{nat} and a temporally more variable N requirement, the N derived from fN_{nat} was much lower and corresponded to reduced N losses of

FIG. 9. (a) Additional net ocean C uptake, (c) atmospheric CO_2 burden, and (e) additional radiative forcing in the year 2100 due to terrestrial N limitation, obtained by comparing the (b) year 2100 net ocean uptake, (d) atmospheric CO_2 burden, and (f) radiative forcing simulated with (CMIP5-N) and without (CMIP5) N constraints. These values were obtained with a simple ocean–atmosphere C cycle model (see section 2a). Points mark individual model projections and are displaced slightly on the x axis for clearer visibility. The boxes denote the 25% and 75% quantile, the bars denote the ensemble range, and the middle bars denote the ensemble median.

$4\text{--}17\text{ Tg N yr}^{-1}$. This latter estimate is broadly compatible with the up to 20% decrease in N losses under elevated CO_2 hypothesized by [Hungate et al. \(2003\)](#).

Using our definition of preindustrial N availability, rather than the total 1860–80 range, avoided small-scale, but large, single-year perturbations inflating the estimate of background availability. However, statistically, this approach created a 2.3% chance to detect N limitation, even if there was no change in the implied terrestrial N budget (i.e., continued preindustrial variability), which would have been unrelated to the trends between 1860 and 2100 that we meant to detect. We estimated this “spurious” excess C sequestration as lower than 20 Pg C based on extrapolating the excess C inferred for the period 1860–80 until the year 2100. We believe that this error is defensible, because the spurious excess C is small compared to the excess C estimates we obtained and because the CMIP5 simulations were not assuming unchanged conditions between 1860 and 1880, in particular with respect to land use; thus, not all of this excess C was indeed spurious.

Observation-based studies of the N retained from atmospheric N deposition, which are limited to time scales of decades at most, have suggested that, in strongly N-limited systems, up to 75% of the deposition had been retained ([Schlesinger 2009](#)). This estimate is consistent with simulations from a process-based N cycle model in highly N-limited ecosystems ([Zaehle 2013](#)). Increasing the range of N available for C storage from the 50% assumed here to 75% would have led to a decrease in the upper-range estimate of excess C by 13.7 Pg C in the most extreme case (for the HadGEM2 models, estimated from extrapolating the results of the factorial analysis), with lesser effect on the median estimates. However, as the time scale of our analyses is two-and-a-half centuries and, thus, longer than these multiannual studies, we deliberately limited the range of N deposition retention to values below 50%, because sustained N deposition gradually reduces N retention ([Aber et al. 1998](#)), which cannot be represented by the simple nature of this a posteriori analysis.

Biological N fixation may increase in response to enhanced plant N demand under elevated CO_2 ([Houlton](#)

et al. 2008) if other limitations, such as from micronutrient availability, do not suppress the increase (Hungate et al. 2004). A decade of FACE experiments did not result in any significant increases of biological fixation in temperate, N-limited forest ecosystems and did not have any strong effect on the C cycle response to elevated CO₂ (Hofmockel and Schlesinger 2007; Hofmockel et al. 2011). Because we could not estimate N fixation based on the net primary production (NPP) simulated by the CMIP5 models directly but used the temperature and CO₂ sensitivities of an independent model to simulate potential N fixation changes, there might be spatial offsets between the potential N fixation increase dataset and the N demands simulated by the CMIP5 models. However, it is unlikely that these differences will strongly affect our conclusions, as most of the projected N deficit occurred either in dry land ecosystems or in boreal and tundra ecosystems with low NPPs and therefore also low potential changes in N fixation.

Warmer soil temperatures under climate change will spur soil organic matter decomposition. The ensuing release of N is expected to fertilize plants in N-limited ecosystems and increase above-ground C storage (Melillo et al. 2011). Our estimate of fN_{req} implicitly included redistribution of N from soils to vegetation if a warmer climate reduced soil C storage. However, the resulting estimate of additional C storage is likely an underestimate, because the a posteriori analysis cannot account for the effect of increased N availability on plant production and, thus, additional C uptake not accounted for in the CMIP5 simulations. We can derive an upper bound of the potential C sequestration rate (not accounting for constraints on C accumulation other than N limitation) based on the implied net N loss from soils in the CMIP5 simulations to estimate the potential additional C storage in vegetation. Assuming that 5% and 20% of the N released were recovered in plants (Melillo et al. 2002), N redistribution from soils to plants could have caused additional vegetation C increases between 15.7 Pg C (13.7–45.8 Pg C) for the RCP 2.6 and 22.7 Pg C (15.2–66.7 Pg C) under the RCP 8.5 scenario, about double the estimate included in fC_{exce} .

The a posteriori approach can also not account for the so-called priming effect, whereby increased C exudation of N deficient plants increase soil organic matter decomposition to increase the plant N uptake (Phillips et al. 2011; Drake et al. 2011; Hungate et al. 2013). While this process contributed strongly to C storage in some FACE experiments, it has not in others (Iversen 2010; Iversen et al. 2011). It is unclear whether transient increases of atmospheric CO₂ would have the same effects as those of step increases of atmospheric CO₂ by around 200 ppm (Luo and Reynolds 1999), and given the ambiguous evidence, the omission of this process is justified.

b. Comparison to other studies

The inferred 1860–2005 cumulative change in terrestrial N from the CMIP5 simulations was 1.2 Pg N (−0.6–6.3 Pg N; Fig. 1). Our revised net N budget estimate compatible with potential N sources amounted to 0.5 Pg N (−1.1–4.0 Pg N). Few alternative, comprehensive terrestrial N budget estimates exists, because most coupled C–N models only report their C budgets. One such terrestrial model estimated an increase in terrestrial N between 1860 and 2010 of 0.6 Pg N (Zaehle 2013) as a result of the historical changes in atmospheric CO₂, climate, N deposition, and land use. This suggests that the implied net N budgets of the original CanESM2, the HadGEM2 models, and the MPI-ESM-LR were substantially larger than plausible. The revised range of N accrual in the biosphere is plausible for all but the MPI-ESM simulation, which remains higher than plausible.

A method to evaluate the possibility that the framework applied here erroneously detects N limitation where it does not exist is to apply the framework also to the CMIP5 projections of CESM1(BGC), which explicitly accounted for terrestrial N availability due to the prognostic C–N cycle of CLM4 (Thornton et al. 2009). Spatial differences in the assumed background N availability and uncertainty primarily in background N availability and C:N stoichiometry results in an average “erroneous” implied N deficit of 0.7 Pg N (0.4–1.1 Pg N) accumulated over the period 1860–2100, giving rise to an excess C estimate of 24 Pg C (12–41 Pg C). This is considerably lower than the lowest implied N deficit estimated for the C cycle-only CMIP5 ensemble [2.0 Pg N (1.4–12.0 Pg N)].

The estimate of the ensemble N effect on year 2100 cumulative reduction in land C uptake and on atmospheric CO₂ for the RCP 8.5 scenario is broadly comparable to results from one particular coupled C–N cycle model forced with the comparable SRES A2 scenario (150 Pg C and 48 ppm, respectively; Zaehle et al. 2010). Using a model that considered N and phosphorus limitation but no land-use changes, Zhang et al. (2014) estimated that N limitation reduced historical (1860–2005) terrestrial C sequestration by 90 Pg C, compared to our estimate of about 35 Pg C. Scenario projections with this model showed reduced land C storage because of N limitation of 73 Pg C (RCP 2.6) to 150 Pg C (RCP 8.5), which compares to 62 Pg C (40–194 Pg C) and 126 Pg C (61–290 Pg C) for RCPs 2.6 and 8.5 from our study.

The results of our analyses are broadly compatible with previous a posteriori analyses of C cycle model projections (Hungate et al. 2003; Wang and Houlton 2009) in that they suggest that ecosystem models not explicitly accounting for N dynamics tend to overestimate C sequestration. Our

spatially explicit approach allowed us to separate regions with diverging C cycle trends (and thus diverging N requirements) within the same latitudinal band, compared to the globally integrated study of [Hungate et al. \(2003\)](#) and the study by [Wang and Houlton \(2009\)](#), which differentiated tropical and extratropical latitudes. In consequence, while both studies would have identified the large N requirement of the MPI-ESM-LR as implausible, they would have underestimated the excess C estimate by about 100 Pg C for the MPI-ESM-LR RCP 8.5 scenario (Table S1). For the other models, for which our analyses consistently indicated excess C sequestration because of the spatial and temporal structure of the simulated C sequestration, both previous studies would have included the case of no N limitation of terrestrial C sequestration, as well as consistently lower median estimates of N limitation for each model (Table S1). This underestimation results from integrating over regions with N gains and losses, implying a lateral, but mechanistically unexplained, N transfer between grid cells.

The enhanced spatial detail employed here allowed the identification of key factors that caused divergent N limitation estimates between the models. These were mostly related to differing assumptions about (i) the regional distribution of C accumulation, which—next to the climate sensitivity of photosynthesis and respiration—was likely related to the representation of land-use changes and vegetation dynamics (i.e., the extent of woody biomass increase in tundra regions or the extent of drought-related forest cover loss in tropical rain forest); (ii) the turnover times of vegetation carbon, and therefore the fraction of new C remaining in comparatively low N biomass over the simulation period; and (iii) the regional distribution of soil C turnover times, which made dry land soil C sequestration of the MPI-ESM-LR stand out from the rest of the ensemble. We also note that the ESM with the lowest estimate of excess C sequestration (CanESM2) implicitly accounted for the N-related down regulation of the CO₂ response of photosynthesis and, thus, had the lowest C cycle response to elevated CO₂ in the ensemble considered here ([Arora et al. 2013](#)).

c. Outlook

The principle purpose of this paper was to estimate whether the CMIP5 ensemble projections are commensurate with the current understanding of the terrestrial N cycle and, in particular, potential increases in N availability with time. Our analyses revealed that, regionally, the projections exceeded plausible ranges of N availability to an extent that, integrated globally, significantly different trajectories of global land C storage were to be expected if N limitation had been explicitly taken into account ([Fig. 6](#)). While there are

important caveats in an a posteriori analysis, as discussed above, we quantified the associated errors and found that they are not negligible but small compared to the N limitation effect on C storage. Despite these uncertainties, the results clearly suggest that the RCP-compatible emissions as reported in [Jones et al. \(2013\)](#) may be too optimistic. Because the effect is large enough to provide a feedback to the climate system, and because of the limitations of the a posteriori approach, it is important that the next generation of coupled carbon cycle–climate models include N cycle interactions with the terrestrial C cycle explicitly.

Developments along these lines are on the way ([Gerber et al. 2010](#); [Wania et al. 2012](#); [Zhang et al. 2014](#); [Goll et al. 2012](#)) such that there is now a suite of models available to address global carbon–nitrogen cycle feedbacks interactively ([Zaehle and Dalmonech 2011](#)). The grand challenge will be to suitably constrain these models to give reliable projections despite the increased complexity and degrees of freedom of the enhanced modeling systems. Conventional benchmarking systems ([Piao et al. 2013](#); [Anav et al. 2013](#)) will fail to deliver this constraint, because the N cycle constraint will be most important with respect to its effect on the response of the terrestrial C to changed environmental conditions. Despite the large body of ecological research on nitrogen–carbon coupling ([Hyvönen et al. 2007](#)), which helps us to understand ecological processes and judge the adequacy of model formulations to represent these processes ([Zaehle et al. 2014](#)), currently these data offer only little constraint on the quantitative estimates of land C storage projected by global models because of the complexity of the interactions and confounding biological trends.

Along with N, other nutrients, such as phosphorus (P), also affect plant productivity ([Elser et al. 2007](#)) and thereby potentially also the capacity of the biosphere to sequester additional C. The biogeochemistry of P is fundamentally different from that of N in that inorganic soil process (weathering, leaching, and occlusion) have a strong control on the amount of plant available P [[Vitousek et al. \(2010\)](#); but see [Morford et al. \(2011\)](#) for the role of N weathering]; also, the physiological effects of P deficiency differ from those of N deficiency ([Kornfeld et al. 2013](#)). Increases in plant productivity in the terrestrial biosphere may be substantially limited by P ([Cleveland et al. 2013](#)), largely reflecting its closed cycling and slow turnover relative to N. Terrestrial C:P ratios are not as tightly constrained as C:N ratios ([Kattge et al. 2011](#)), and there is little quantitative, observational evidence to estimate the potential implications of P limitation on projections of global C storage. While it is therefore not possible to estimate a clear C:P stoichiometric constraint of C sequestration in CMIP5, plant

production limitation by P availability is thought to be stronger than the effect of N availability on very old soils (Vitousek et al. 2010), such as occur in the Amazon basin or Australia. The analysis presented here, which quantified the N-based stoichiometric limits to C sequestration projections in CMIP5, might thus be overestimating the C sequestration capacity and underestimating the buildup of excess C in these regions.

5. Conclusions

Taking the uncertainties in the understanding of the limits to terrestrial N availability into account, the analysis provided here suggests that constrained terrestrial N availability will significantly reduce C sequestration projections from all C-only models within the CMIP5 model ensemble over the entire range of RCP scenarios despite the assumed high-end increases in biological N fixation and scenarios of anthropogenic N deposition. While the two latter factors contributed to enhanced C storage in the terrestrial biosphere, the preindustrial natural N availability was the strongest factor affecting the strength of N limitation within any model, illustrating the importance of the initial state of the N cycle in determining future N limitation. Across models, next to spatial offsets between increases in N availability and implied N requirements, a substantial factor affecting the extent of N limitation was how much of the additionally assimilated C became stored in soil organic matter within the timeframe of the simulation. These findings are in general agreement with results of ecosystem manipulation studies and the projection of coupled C–N models that N availability strongly affects CO₂ fertilization.

Our results show that CMIP5 simulations from 1860 to 2100 require 1.4 Pg N (1.05–7.1 Pg N; RCP 2.6) to 1.9 Pg N (1.1–8.3 Pg N; RCP 8.5) more N than can be plausibly provided given a wide range of estimates of future N availability. As a result, the CMIP5 models likely overestimate land carbon sequestration by between 37% (median for RCP 2.6) and 58% (median for RCP 8.5), with a large spread across models. This reduction necessitates a decrease of the 2006–2100 fossil-fuel emissions by 56 Pg C (40–165 Pg C; RCP 2.6) to 104 Pg C (36–246 Pg C; RCP 8.5) to keep atmospheric CO₂ levels on the trajectories described in the RCP scenarios, relative to the projections of the CMIP5 models (Jones et al. 2013)). If these N-induced emission reductions were not implemented, an additional atmospheric CO₂ burden of 26 ppm (17–88 ppm; RCP 2.6) to 61 ppm (29–147 ppm; RCP 8.5) is likely to occur by the year 2100, increasing the expected climate change for a given scenario of anthropogenic fossil-fuel emissions.

Caution is therefore warranted when interpreting the CMIP5 model projections in terms of their implications for either the diagnosis of RCP-compatible CO₂ emissions or the net climate effect of anthropogenic fossil-fuel CO₂ emissions.

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