Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study

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Abstract
Uncertainties in terrestrial carbon (C) cycle projections increase uncertainty of potential climate feedbacks. Efforts to improve model performance often include increased representation of biogeochemical processes, such as coupled carbon–nitrogen (N) cycles. In doing so, models are becoming more complex, generating structural uncertainties in model form that reflect incomplete knowledge of how to represent underlying processes. Here, we explore structural uncertainties associated with biological nitrogen fixation (BNF) and quantify their effects on C cycle projections. We find that alternative plausible structures to represent BNF result in nearly equivalent terrestrial C fluxes and pools through the twentieth century, but the strength of the terrestrial C sink varies by nearly a third (50 Pg C) by the end of the twenty-first century under a business-as-usual climate change scenario representative concentration pathway 8.5. These results indicate that actual uncertainty in future C cycle projections may be larger than previously estimated, and this uncertainty will limit C cycle projections until model structures can be evaluated and refined.

1. Introduction
The global carbon (C) cycle provides a critical set of feedbacks that influences climate change in Earth system model (ESM) simulations of the twenty-first century. However, simulations of the terrestrial C cycle show considerable spread among models, and much of the uncertainty in C cycle feedbacks with climate change arises from terrestrial processes (Friedlingstein et al 2006, Arora et al 2013, Jones et al 2013, Friedlingstein et al 2014). Uncertainty in projections of global surface temperature change arising from C cycle feedbacks compares in magnitude to the uncertainty arising from physical climate processes (Huntingford et al 2009). Moreover, many ESMs poorly simulate key metrics of the present-day terrestrial C cycle such as vegetation and soil C, plant productivity, and C turnover rates, among others (Anav et al 2013, Piao et al 2013, Todd-Brown et al 2013, Carvalhais et al 2014). These uncertainties in the terrestrial C cycle present a critical challenge for the development of the next generation of ESMs, reflecting both an incomplete understanding of the underlying biological and ecological processes themselves, and how to represent them at global scales. Indeed, while the methodology used to derive the C cycle feedback parameters among models varies, and thus results are not directly comparable, the coupled C cycle-climate simulations reported in the IPCC fourth assessment report (Friedlingstein et al 2006, Denman et al 2007) show a similarly broad range in the carbon-concentration feedback and the carbon-climate feedback for land as those reported in the IPCC fifth assessment report (Arora et al 2013, Ciais et al 2013).

Efforts to analyze model uncertainty fall into several broad categories. First, model intercomparisons characterize uncertainty among different models using a multi-model ensemble of simulations, and often compare results with standardized datasets (Anav et al 2013, Todd-Brown et al 2013). A second approach involves perturbing key model parameter values and to show that a wide range of C cycle projections (of equal magnitude to multi-model ensembles) can be obtained from a single model given a plausible range in parameter values (Booth et al 2012, Booth et al 2013, Exbrayat et al 2013, Lambert et al 2013).
Third, data assimilation provides a mathematical framework to constrain a particular model with observations (Smith et al 2013, Hararuk et al 2014). Finally, the mathematical properties of a model in terms of C pools, the partitioning of C input to those pools, and the transfers of C among pools (Xia et al 2013, Luo et al 2014) have been analyzed to assess model uncertainty. While these different approaches yield valuable insight into differences in model states, fluxes and responses to forcings, they often fail to provide insight into the underlying model structures that are collectively responsible for C cycle projections.

Structural uncertainties reflect incomplete knowledge of how to represent processes in models. Structural uncertainty tends to increase with greater model complexity, which often accompanies process-level model development aimed at improving model performance. For example, one key component of ESMs has been the recent inclusion of a terrestrial nitrogen (N) cycle. Terrestrial nutrient availability, specifically nitrogen (N), strongly limits plant productivity and ecosystem C fluxes (Vitousek and Howarth 1991, Hungate et al 2003, Lebauer and Treseder 2008). As such, terrestrial C cycle responses to environmental change, like elevated CO₂ and/or climate change, may be strongly mediated by N availability (Luo et al 2004, Finzi et al 2006, Reich et al 2006a, Norby and Zak 2011), and particularly inputs of new N (Cleveland et al 2013).

Given the importance of nutrient dynamics on global C projections (Hungate et al 2003, Gruber and Galloway 2008, Wang and Houlton 2009, Peñuelas et al 2013, Zaehle et al 2015, Wieder et al 2015a), global land models are increasingly considering coupled C–N biogeochemistry explicitly (Thornton et al 2007, Wang et al 2007, Sokolov et al 2008, Yang et al 2009, Gerber et al 2010, Zaehle et al 2010, Wania et al 2012). Despite the complexities of simulating N biogeochemistry at the global scale, these models consistently demonstrate an attenuation of C-cycle response to environmental change when considering C–N dynamics, relative to C-only simulations. Preliminary efforts to evaluate models that simulate C–N interactions indicate that they partially capture ecosystem responses to elevated CO₂ (Zaehle et al 2014), but also illustrate that representing N inputs, transformations, and losses from terrestrial ecosystems introduces multiple degrees of freedom that increase model uncertainty (Thomas et al 2015). Here, we use one key process in the terrestrial N cycle—N inputs from biological nitrogen fixation (BNF)—to demonstrate the importance of evaluating model structural uncertainty.

Although global increases of N deposition from human activities like fertilizer application and fossil fuel combustion have increased global terrestrial N availability (Townsend et al 1996, Galloway et al 2004), the vast majority of N entering unmanaged ecosystems still comes from BNF (Cleveland et al 1999, Wang et al 2010, Cleveland et al 2013). As such, BNF influences the global C cycle and climate, both now and in the future. Unfortunately, however, estimates of global BNF rates from synthesis and extrapolation are highly uncertain (100–290 Tg N y⁻¹; Cleveland et al 1999), with more recent estimates suggesting that global rates of BNF either fall on the lower end of this range (~125 Tg N y⁻¹; Galloway et al 2004, Wang and Houlton 2009), or are perhaps much lower (40–100 Tg N y⁻¹; Vitousek et al 2013, Sullivan et al 2014). These uncertainties reflect both a paucity of empirical measurements of N fixation, as well as an incomplete understanding of the biophysical controls on BNF across space and through time (Houlton et al 2008, Menge et al 2008, Reed et al 2011). Thus, most C–N models use simple, modified-empirical relationships to generate spatial estimates of BNF based on evapotranspiration (ET) and/or net primary productivity (NPP) (table 1; Cleveland et al 1999). These phenomenological relationships are not derived from mechanistic understanding of BNF, but broadly capture biogeographical observations of higher rates of BNF in humid environments with (seasonally) high

| Model                                    | BNF approach                                      | N Fixation reference                  |
|------------------------------------------|---------------------------------------------------|---------------------------------------|
| CLM4cn and CLM4.5bgc (Thornton et al 2007, Oleson et al 2013) | f(NPP)                                           | (Cleveland et al 1999)                |
| JSBACH (Parida 2011)                     | f(NPP)                                           | (Cleveland et al 1999)                |
| UVic (Wania et al 2012)                  | f(ET) (spin-up) f(NPP) (transient)               | (Cleveland et al 1999)                |
| Century (Schimel et al 1996)             | f(ET)                                            | (Cleveland et al 1999)                |
| ISAM (Jain et al 2009, Yang et al 2009)  | f(ET, biome)                                      | (Schimel et al 1996, Cleveland et al 1999) |
| OC–N (Zaehle and Friend 2010)            | f(ET)                                            | (Cleveland et al 1999)                |
| TEM (Hayes et al 2011)                   | f(ET)                                            | (Cleveland et al 1999)                |
| GFDL-LM3V (Gerber et al 2010)            | f(soil N, LAI, mortality, disturbance, etc)       | (Rastetter et al 2001)                |
| CASA-CNP (Wang et al 2010)               | f(soil N, LAI, P, temperature, etc)                | (Wang et al 2007, Houlton et al 2008) |
solar radiation. Thus, ET and NPP are good bases to derive empirical BNF estimates that are consistent with the view that the energetic costs of ‘fixing’ atmospheric di-nitrogen (N₂) into a biologically usable form (NH₃) broadly limit rates of BNF (Gutschick 1981). Estimating BNF using relationships between ET and NPP produce similar estimates of pre-industrial BNF inputs, but tend to differing predictions about the response of BNF to changing climate and CO₂. Here, we compare the differences in N fixation inputs using these two commonly used approaches, and the associated effects on NPP and the global land C sink using the most recent version of the Community Land Model (CLM4.5bgc).

2. Methods

The CLM4.5bgc (Oleson et al 2013) is a revision to CLM4 (Lawrence et al 2011). Key model improvements pertinent to the C cycle are revisions to the leaf photosynthesis and canopy integration (Bonan et al 2011, Bonan et al 2012), vertically resolved soil C and N biogeochemistry (Koven et al 2013), and permafrost hydrology (Swenson and N biogeochemistry (Koven et al 2013), and key model improvements to CLM4.5bgc that were identical apart from their representation with observed trends in the terrestrial C cycle over previous versions of the model (Koven et al 2013).

We conducted two sets of offline simulations with CLM4.5bgc that were identical apart from their representation of BNF. In the NPP driven case, we use the standard NPP–BNF relationship from Cleveland et al (1999) that is used in CLM (Thornton et al 2007, Oleson et al 2013):

\[
BNF_{NPP} = 1.8 \left(1 - e^{-0.003 \times NPP}\right) / \left(86400 \times 365\right), \tag{1}
\]

where annual NPP fluxes (g C m⁻² y⁻¹) are used to calculate instantaneous BNF rates (g N m⁻² s⁻¹). In the modified case we use the lower bound of ET–BNF relationship reported by Cleveland et al (1999).

\[
BNF_{ET} = (0.0102 \times ET + 0.524) / (10 \times 86400 \times 365), \tag{2}
\]

where instantaneous ET fluxes (converted to an annual rate, mm y⁻¹) are used to calculate instantaneous BNF rates (g N m⁻² s⁻¹). Here, we calculate ET as the sum of canopy evaporation and transpiration fluxes, because preliminary results indicated this would provide initial BNF inputs that were approximately equal to the NPP driven scenario. Specifically, including soil evaporation fluxes in the ET calculation produced a high bias in BNF rates from arid regions, compared to the NPP driven case (W Wieder, unpublished data). For comparison, we also show estimates of BNF simulated by CASA-CNP (Bai and Houlton 2009, Wang and Houlton 2009; see, Cleveland et al 2013). CASA-CNP uses a more process-based approach to estimate global rates of BNF that considers light availability, N and phosphorus (P) supply and demand, as well as putative N fixer abundance (Wang et al 2007, Wang et al 2008, Wang et al 2010).

Subsequently we ran parallel CLM4.5bgc simulations that only differed in their BNF assumptions (equations (1) and (2)). We used 1900–1919 meteorology, 1850 [CO₂], N deposition, and land cover (see, Koven et al 2015) and an accelerated spin-up procedure (Koven et al 2013) to approximate steady-state pools and fluxes using the NPP driven configuration, which was followed by another 500-year standard spin-up phase for both NPP and ET driven cases. The initialized simulations were forced with CRU-NCEP re-analysis data over this historical period (1850–2005), transient land cover change (Lawrence et al 2012, Oleson et al 2013), and an anomaly forcing protocol to replicate a single CCSM4 projection (Gent et al 2011, Meehl et al 2012) of climate change under the ‘business-as-usual’ representative concentration pathway 8.5 (RCP8.5) (Moss et al 2010). Although we apply transient land cover scenarios with active timber harvest and agricultural management that extract C from the system, they do not represent the complex interactions among disturbance, the site micro-environment (e.g., increased light), and C–N biogeochemistry and are the focus of ongoing model developments (Levis et al 2012, Thomas and Williams 2014, Thomas et al 2015). The anomaly forcing provides a smooth transition between the observed historical period and the projected RCP8.5 CCSM4 projection. We quantified global differences in mean steady-state (1850–1859) C and N pools and fluxes between these two cases. We examined changes in projected C and N pools and fluxes through the historical period and RCP8.5.

3. Results

Initial estimates of global BNF were approximately 15% higher when simulated as a function of NPP than when simulated as a function of ET, totaling 90 and 77 Tg N y⁻¹, respectively (figures 1(a) and (b)). Both of these values are lower than the BNF estimates of Cleveland et al (1999), and at the upper end of the uncertainty estimates in Vitousek et al (2013). In the ET driven case, rates of BNF across much of the northern hemisphere were 25–35% lower than in the NPP driven case. By contrast, rates of BNF were higher in many arid ecosystems and savannas using the ET parameterization, and generally similar across tropical forests. By comparison, estimates of BNF simulated by CASA-CNP show much higher N inputs in the tropics and lower rates of BNF in extra-tropical regions compared to either ET or NPP parameterizations (figure 1(c)), resulting in larger total rates of BNF (142 Tg N y⁻¹) (Wang et al 2010; see, Cleveland et al 2013). Few observational data points and high uncertainty (Cleveland et al 1999) preclude robust
corroboration of these estimates, although we argue they all represent plausible approximations of pre-industrial BNF rates.

Despite the differences in BNF using the two alternative parameterizations (figures 1(a) and (b)), we found negligible differences in steady-state C fluxes and pools between cases. Global estimates of plant productivity from NPP- and ET-driven cases totaled 46.1 and 44.8 Pg C y$^{-1}$, respectively. Nitrogen limitation in CLM occurs through the instantaneous downregulation of photosynthesis based on the availability and demand for N (Thornton et al 2007). Modifications to the leaf photosynthesis and canopy integration (Bonan et al 2011, 2012) and soil N biogeochemistry (Koven et al 2013) have made the model less sensitive to N inputs, as extant soil N pools can largely meet plant demand (figure 2); although, specific aspects of the representation of N biogeochemistry in CLM warrant more focused attention (Thomas et al 2013a, 2013b, 2015). In our ET-driven case, estimates of NPP were <10% lower at high latitudes than in the NPP-driven case, but elsewhere they were very similar (figures 2(a) and (b)). Differences between initial total ecosystem C (the sum of all vegetation, litter, and soil C pools) from NPP and ET cases were more subtle, totaling 4500 and 4460 Pg C (0–3 m depth), respectively (2610 and 2570 Pg C (0–1 m depth)), and representing N fixation using the different approaches generated few obvious spatial differences in C pools (figures 2(c) and (d)). Given the steady-state similarities, we focus on the evolution of terrestrial C and N dynamics in transient simulations with changing climate and [CO$_2$] through 2100.

Representing BNF using the ET relationship (equation (2); green lines, figure 3) produces equivalent estimates of BNF, NPP, and total ecosystem C storage through the historical period (1850–2005). By contrast, in the NPP driven case (equation (1)), rates of BNF accelerated because of increases in NPP from CO$_2$ fertilization under the RCP8.5 scenario (black lines, figure 3), creating a positive feedback between BNF and NPP that resulted in sustained increases in

Figure 1. Global estimates of biological nitrogen fixation from: (a) CLM4.5 using the standard NPP structure (equation (1)); (b) CLM4.5 using the modified ET structure (equation (2)); and (c) CASA-CNP. Results from CLM4.5 show steady-state (1850) estimates of BNF, totaling 90 and 77 Tg N y$^{-1}$, respectively. Estimates from CASA-CNP (Wang et al 2010) are the sum of free-living and symbiotic BNF, and total 142 Tg N y$^{-1}$.
NPP and large increases in terrestrial C storage through the 21st century. Notably, the trajectories of terrestrial C storage are virtually identical for both cases through the historical period, with initial terrestrial C losses driven by land use and land cover that recover by the end of the 20th century, with slight (<2 Pg C) difference in terrestrial C accumulated by 2005. We cannot find empirical support from elevated [CO2] experiments for the sustained increases in BNF suggested by the current, NPP-based, configuration of CLM4.5 (Hungate et al. 2004, van Groenigen et al. 2006, Reich et al. 2006b, Hungate et al. 2013). Moreover, disturbance currently has no effect on BNF in CLM4.5, which is inconsistent with empirical work showing the highest rates of N fixation immediately following disturbance (Batterman et al. 2013, Sullivan et al. 2014). By contrast, in the ET driven case N demand outpaces BNF, which increasingly attenuates CO2 fertilization effects in the modified case. Thus, reducing terrestrial C accumulation by nearly 50 Pg C (~40%) by 2100, which would increase the atmospheric [CO2] burden by approximately 25 ppm.

4. Discussion

Representing N fixation as a function of either NPP or ET produces comparable initial land C stocks and fluxes in CLM4.5bgc (figures 1 and 2), but generate significant differences in trends of BNF that have large effects on the global C cycle in transient simulations (figure 3). These results illustrate one key model uncertainty that more broadly reflects the status of the theoretical understanding and numerical implementation of terrestrial C–N biogeochemistry in ESMs (Thomas et al. 2015). Uncertainty in the representation of BNF is important, but structural uncertainties in the representation of C and N cycles extend far beyond representations of BNF, and include processes like plant N uptake (Thomas et al. 2013a, Brzostek et al. 2014) and soil microbial dynamics (Wieder et al. 2013, 2015b), among others. These uncertainties broadly limit the ability to accurately simulate changes in the terrestrial C cycle, and by extension to project future climate. We contend that evaluating these structural uncertainties in ESMs can simultaneously improve the theoretical understanding of biogeochemical processes, inform prognostic climate models, and highlight critical observational needs in the most uncertain aspects of the C–N system. This argues for replacing the empirical approaches (such as those for BNF described here), with more a mechanistic representation of biogeochemical processes. Several approaches for BNF already exist (Gerber et al. 2010, Wang et al. 2010, Brzostek et al. 2014; discussed below), however additional efforts are needed to evaluate how any of these approaches may improve confidence in future model projections.

Poor understanding and representation of the factors that regulate rates of biogeochemical processes significantly impede the ability to improve C-nutrient dynamics in ESMs. Specifically, we lack both a detailed theoretical understanding and sufficient empirical data to validate models and inform likely responses of BNF to elevated [CO2] and climate change across biomes. Current approaches that represent BNF rates as a function of NPP are contradictory (equation (1); table 1), especially when the purpose of C–N models is to explore how terrestrial nutrient limitation may mediate C cycle response. Moreover, data from field
manipulation experiments do not support the persistent increases in BNF rates that are projected by the NPP driven case (Hungate et al. 2004, van Groenigen et al. 2006, Reich et al. 2006b, Hungate et al. 2013). Yet, this approach is currently applied in several land models, including CLM (table 1), but should likely be revised.

We recommend alternative model structures be considered to describe rates of BNF—the largest source of N inputs to terrestrial ecosystems. In the short-term, revisions to BNF parameterizations could include empirical relationships with ET and/or assignment of biome-level rates (Cleveland et al. 1999). Both approaches still have shortcomings, but they would still represent an improvement over model structures that directly contradict empirical results. Longer-term efforts should focus on exploring large-scale and mechanistic drivers of BNF and potential C–N interactions in response to environmental change. Alternative structures that represent competing hypotheses about the relative importance of different factors effecting BNF rates are already available (table 1, figure 1). For example, the structure of the GFDL-LMV3 model suggests disturbance history controls BNF rates (Gerber et al. 2010), whereas phosphorus (P) availability is more important in CASA-CNP (Wang et al. 2007, Wang et al. 2010, figure 1(c)), and N availability and plant N demand is critical in the fixation and uptake of nitrogen model (FUN; Fisher et al. 2010, Brzostek et al. 2014). These more mechanistic approaches are consistent with recent empirical work showing that disturbance history (Battarman et al. 2013, Sullivan et al. 2014) and soil P dynamics (Houlton et al. 2008, Reed et al. 2011, Nasto et al. 2014) influence BNF. Given the complexity of representing the global N cycle in ESMs, new efforts to mechanistically simulate BNF will require a significant investment in model development and the simultaneous collection of appropriate observational datasets to parameterize and evaluate different model structures and assumptions. Such developments may introduce many more degrees of freedom and uncertainty to land models, but will simultaneously present opportunities to address more scientifically and societally relevant questions about coupled biogeochemical cycles.

The lack of real progress in representing N fixation in models is not surprising—reflecting the fact that actual rates of BNF in most terrestrial ecosystems are poorly understood or measured, and in some cases, completely unknown. Thus, lack of data availability will significantly hinder the evaluation of model developments advocated here. The empirical relationships that inform the BNF parameterizations used in the majority of land models were formed based on extremely limited data (Cleveland et al. 1999, table 1), and subsequent progress to generate new estimates has been slow (Cleveland et al. 2010, Reed et al. 2011). The lack of a robust method for generating point measurements of symbiotic BNF remains a key limitation to generating ecosystem level estimates, although some promising new field sampling approaches may help overcome this issue (Sullivan et al. 2014). Observations of free-living BNF rates are even more rare than data

Figure 3. Changes in global (a) N fixation rates, (b) terrestrial NPP, and (c) terrestrial C storage from fully transient run from 1850–2100 under RCP8.5 using different structures to simulate rates of BNF. First, BNF rates were estimated as a function of NPP, as currently applied in CLM4.5 (black lines; Thornton et al. 2007). Thus, as plant productivity increases in response to elevated CO2 and climate change, BNF also increases. By contrast, when BNF was estimated from ET (green line, Cleveland et al. 1999), terrestrial N inputs do not keep pace with N demand from elevated CO2. This attenuates the rate of NPP increase and reduces the size of the terrestrial C sink nearly 50 Pg by the end of this century.
on symbiotic nitrogen fixation rates, and completely absent from some ecosystems (Reed et al 2011). Nitrogen inputs from symbiotic and free-living pathways likely vary over space and through time (Batterman et al 2013), and may be subject to different environmental controls. Collectively, these observations provide a strong theoretical justification for considering symbiotic and free-living BNF separately in land models (Wang et al 2010, Hayes et al 2011, Thomas et al 2013a). For example, in the terrestrial ecosystem model (TEM), Hayes et al (2011) add N from symbiotic BNF to vegetation N pools, while free-living inputs contributing to soil N pools. Similar approaches may be feasible in the near-term with CLM; although we stress that more attention needs to focus on evaluating the C-cycle implications of such structural changes in models.

Model response uncertainties extend beyond representations of N fixation and generate wide variation in C cycle projections both among and within models (Jones et al 2013). For example, multi-model analyses illustrate six-fold variation in steady-state soil C pools among models represented in the CMIP5 archive, and highly uncertain soil C responses through the 21st century (Todd-Brown et al 2013, Exbrayat et al 2014, Todd-Brown et al 2014). Uncertainty within the parameter space of a single land model can generate uncertainty estimates similar to multi-model ensembles (Exbrayat et al 2013). Finally, alternative model structures generate plausible steady-state soil C estimates, but simulate very different predictions about the fate of soil C in a changing world (Wieder et al 2013, Sulman et al 2014, Wieder et al 2015b). Existing mathematical techniques, generally known as model-data fusion, can help improve model predictions and reduce model response uncertainty by: (1) estimating model parameters that best fit observations, and quantifying their associated uncertainty; (2) improving the model state through data assimilation; and (3) identifying key data deficiencies and model development needs (Wang et al 2009, Williams et al 2009, Dietze et al 2014, Hararuk et al 2014, Luo et al 2014). Although these techniques provide robust ways to constrain model parameters for interpolation, they may not provide reliable insight into how biologically driven processes may respond to environmental change as they overlook the theoretical underpinnings and structural assumptions responsible for process-level representation in particular models. Structural errors can more formally be identified—but not necessarily attributed—with recursive prediction error algorithms (Lin and Beck 2007), although to our knowledge similar approaches have not been applied to ESMs. Our results indicate that considerations of alternative model structures are critical to improving both the theoretical understanding of important biogeochemical processes (like BNF) and the accuracy of C cycle projections. As an increasing number of models represent C–N biogeochemistry, structural uncertainties associated with the representation of N inputs, transformations, uptake, and losses need to be evaluated.

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References

Anav A, Friedlingstein P, Kidston M, Bopp L, Ciais P, Cox P, Jones C, Jung M, Myneni R and Zhu Z 2013 Evaluating the land and ocean components of the global carbon cycle in the CMIP5 Earth system models J. Clim. 26 6801–43

Arora V K et al 2013 Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth system models J. Clim. 26 5289–314

Bai E and Houlton B Z 2009 Coupled isotopic and process-based modeling of gaseous nitrogen losses from tropical rain forests Glob. Biogeoch. Cycles 23 GB2011

Batterman S A, Hedin L O, van Breugel M, Ransijn J, Craven D J and Hall J S 2013 Key role of symbiotic dinitrogen fixation in tropical forest secondary succession Nature 502 224–7

Bonan G B, Lawrence P J, Oleson K W, Levis S, Jung M, Reichstein M, Lawrence D M and Swenson S C 2011 Improving canopy processes in the community land model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data J. Geophys. Res. 116 G02041

Bonan G B, Oleson K W, Fisher R A, Laslop G and Reichstein M 2012 Reconciling leaf physiological traits and canopy flux data: use of the TRY and FLUXNET databases in the community land model version 4 (J. Geophys. Res.: Biogeoosci. 117 G03026

Booth B B B, Bernie D, McNeall D, Hawkins E, Caesar J, Boulton C, Friedlingstein P and Sexton D M H 2013 Scenario and modelling uncertainty in global mean temperature change derived from emission-driven global climate models Earth Syst. Dyn. 4 95–108

Booth B B B, Jones C D, Collins M, Totterdell I J, Cox P M, Sitch S, Huntingford C, Betts R A, Harris G R and Lloyd J 2012 High sensitivity of future global warming to land carbon cycle processes Environ. Res. Lett. 7 024002

Brzostek E R, Fisher J B and Phillips R P 2014 Modeling the carbon cost of plant nitrogen acquisition: mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation J. Geophys. Res.: Biogeoosci. 119 1684–97

Carvalhais N et al 2014 Global covariation of carbon turnover times with climate in terrestrial ecosystems Nature 514 213–7

Ciais P et al 2013 Carbon and other biogeochemical cycles Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change ed T F Stocker et al (Cambridge: Cambridge University Press)

Cleveland C C, Houlton B Z, Smith W K, Marklein A R, Reed S C, Parton W, Del Grosso S J and Running S W 2013 Patterns of new versus recycled primary production in the terrestrial biosphere Proc. Natl Acad. Sci. USA 110 12753–7

Cleveland C C, et al 1999 Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems Glob. Biogeoch. Cycles 13 623–45

Cleveland C C, Houlton B Z,Neill C, Reed S C, Townsend A R and Wang Y P 2010 Using indirect methods to constrain symbiotic nitrogen fixation rates: a case study from an Amazonian rain forest Biogeochocmistry 99 1–13
Denman K L et al 2007 Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge: Cambridge University Press) pp 499–587

Dietze M C et al 2014 A quantitative assessment of a terrestrial biosphere model’s data needs across North American biomes J. Geophys. Res.: Biogeosci. 119 2013JG002392

Exbrayat J F, Pitman A J and Abramowitz G 2014 Response of microbial decomposition to spin-up explains CMIP5 soil carbon range until 2100 Geosci. Model Dev. 7 2683–92

Exbrayat J F, Pitman A J, Zhang Q, Abramowitz G and Wang Y P 2013 Examining soil carbon uncertainty in a global model: response of microbial decomposition to temperature, moisture and nutrient limitation Biogeosciences 10 7095–108

Finzi A C et al 2016 Progressive nitrogen limitation of ecosystem processes under elevated CO2 in a warm–temperate forest Ecology 87 15–25

Fisher J B, Sitch S, Malhi Y, Fisher R A, Huntingford C and Tan S Y 2013 Examining soil carbon uncertainty in a global model: mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and fixation Glob. Biogeochem. Cycles 24 GB1014

Friedlingstein P et al 2006 Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison J. Clim. 19 3337–53

Friedlingstein P, Meinshausen M, Arora V K, Jones C D, Anav A, Liddicoat S K and Knutti R 2014 Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks J. Clim. 27 511–26

Galloway J N et al 2004 Nitrogen cycles: past, present, and future Biogeochemistry 70 153–226

Gen R P, Danabasoglu G, Donner L J, Holland M M, Hunke E C, Jayne S R, Lawrence D M, Neale R B, Rasch P J and Vertenstein M 2011 The community climate system model version 4 J. Clim. 24 4973–91

Gerber S, Hedin L O, Oppenheimer M, Pacala S W and Shevlakova E 2010 Nitrogen cycling and feedbacks in a global dynamic land model Glob. Biogeochem. Cycles 24 GB1001

van Groenigen K J, Xu J, Huntingford C, A de Graaff M A, van Breemen N and van Kessel C 2006 Element interactions limit soil carbon storage Proc. Natl Acad. Sci. USA 103 6571–4

Gruber N and Galloway J N 2008 An Earth–system perspective of the global nitrogen cycle Nature 451 293–6

Gutschick V P 1981 Evolved strategies of nitrogen fixation in plants Am. Naturalist 118 607–37

Hararuk O, Xia J and Luo Y 2014 Evaluation and improvement of a terrestrial biosphere model’s data needs across North American biomes J. Geophys. Res.: Biogeosci. 119 2013JG002392

Hayes D J, McGuire A D, Kicklighter D W, Gurney K R, Burnside T J and Meillo J M 2011 Is the northern high-latitude land-based CO2 sink weakening? Glob. Biogeochem. Cycles 25 GB3018

Houghton B Z, Wang Y P, Vitousek P M and Field C B 2008 A unifying framework for dinitrogen fixation in the terrestrial biosphere Nature 454 327–34

Huntingford C, Lowe J A, Booth B B, Jones C D, Harrison G R, Hymus G J, Hinkle C R and Drake B G 2004 CO2 enrichment and biogeochemical feedbacks in lowland tropical rain forests Ecol. Lett. 7 1282–9

Jones C D et al 2013 Twenty-first-century compatible CO2 emissions and airborne fraction simulated by CMIP5 Earth system models under four representative concentration pathways J. Clim. 26 4398–413

Koven C D, Lawrence D M and Riley W J 2015 Permafrost carbon-climate feedback is sensitive to deep soil decomposability but not deep soil nitrogen dynamics Proc. Natl Acad. Sci. USA 112 3752–72

Koven C D, Riley W J, Subin Z M, Tang Y J, Torn M S, Collins W D, Bonan G B, Lawrence D M and Swenson S C 2013 The effect of vertically-resolved soil biogeochemistry and alternate soil C and N models on C dynamics of CLM4 Biogeosciences 10 7109–31

Lambert F H, Harriss R, Collins M, Murphy J, Sexton D H and Booth B B 2013 Interactions between perturbations to different Earth system components simulated by a fully-coupled climate model Clim. Dyn. 41 3055–72

Lawrence D M et al 2011 Parameterization improvements and functional and structural advances in version 4 of the community land model J. Adv. Model. Earth Syst. 3 M03001

Lawrence P J et al 2012 Simulating the biogeochemical and biophysical impacts of transient land cover change and wood harvest in the Community Climate System Model (CCSM4) from 1850 to 2100 J. Climate 25 3071–95

Lebauer D S and Treseder K K 2008 Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed Ecology 89 371–9

Levis S, Bonan G B, Kluzek E, Thornton P E, Jones C D, Sacks W J and Kucharik C J 2012 Interactive crop management in the community Earth system model (CESM1): seasonal influences on land–atmosphere fluxes J. Clim. 25 4839–59

Lin Z and Beck M B 2007 On the identification of model structure in hydrological and environmental systems Water Resour. Res. 43 W02402

Luo Y, Keenan T F and Smith M 2014 Predictability of the terrestrial carbon cycle Glob. Change Biol. at press

Luo Y et al 2004 Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide Biogeochemistry 54 731–9

Mehl G A et al 2012 Climate system response to external forcings and climate change projections in CCSM4 J. Clim. 25 3661–83

Meng X et al 2010 The next generation of scenarios for climate change research and assessment Nature 463 747–56

Nasto M K, Levin S A and Hedin L O 2004 Nitrogen fixation in plants Systematics and Evolutionary Biology (Berlin: Springer) pp 221–41

Norby R J and Ziska L H 2011 Ecological consequences of free-air CO2 enrichment (FACE) experiments Annu. Rev. Ecol., Evol. Systematics 42 181–203

Oleson K et al 2013 Technical description of version 4.5 of the Community Land Model (CLM) NCAR Technical Note NCAR/TN-503+STR p 420

Patadia B 2011 The Influence of Plant Nitrogen Availability on the Global Carbon Cycle and N2O Emissions (Hamburg: University of Hamburg)

Peñuelas J et al 2013 Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe Nat. Commun. 4 2934

Piao S et al 2013 Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO2 trends Glob. Change Biol. 19 2117–32

Rastetter E, Vitousek P, Field C, Shaver G and Herbert D 2001 Resource optimization and symbiotic nitrogen fixation Ecosystems 4 369–88
Thornton P E, Lamarque J F, Rosenbloom N A and Mahowald N M 2011 Functional ecology of free-living nitrogen fixation: a contemporary perspective Annu. Rev. Ecol., Evol. Systematics 42 489–512

Reich P B, Hobbs S E, Lee T, Ellsworth D S, West J B, Tilman D, Knops J M H, Naeem S and Trost J 2006a Nitrogen limitation constrains sustainability of ecosystem response to CO2 Nature 440 922–5

Reich P B, Hungate B A and Luo Y Q 2006b Carbon–nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide Annu. Rev. Ecol., Evol. Systematics 37 611–36

Schimel D S, Brasswell B H, McKeon R, Ojima D S, Parton W J and Puliaim W 1996 Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling Glob. Biogeochem. Cycles 10 677–92

Smith M J, Parvez D, Vanderwel M, Lyutsarev V and Emmott S 2013a The climate dependence of the terrestrial carbon cycle, including parameter and structural uncertainties Biogeosciences 10 583–606

Sokolov A P, Kicklighter D W, Melillo J M, Felzer B S, Schlosser CA and Cronin TW 2008 Consequences of considering carbon–nitrogen interactions on the feedbacks between climate and the terrestrial carbon cycle J. Clim. 21 3776–96

Sullivan B W, Smith W K, Townsend A R, Nasto M K, Reed S C, Chadzon R L and Cleveland C C 2014 Spatially robust estimates of biological nitrogen (N) fixation imply substantial human alteration of the tropical N cycle Proc. Natl Acad. Sci. USA 111 8101–6

Sulman B N, Phillips R P, Oishi A C, Shevliakova E and Pacala S W 2014 Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO2 Nat. Clim. Change 4 1099–102

Swenson S C, Lawrence D M and Lee H 2012 Improved simulation of the terrestrial hydrological cycle in permafrost regions by the Community Land Model J. Adv. Model. Earth Syst. 4 M08002

Thomas R Q, Bonan G B and Goodale C L 2013a Insights into mechanisms governing forest carbon response to nitrogen deposition: a model-data comparison using observed responses to nitrogen addition Biogeosciences 10 3869–87

Thomas R Q, Brookshire E N J and Gerber S 2015 Nitrogen limitation on land: how can it occur in Earth system models? Glob. Change Biol. doi:10.1111/gcb.12813

Thomas R Q and Williams M 2014 A model using marginal efficiency of investment to analyze carbon and nitrogen interactions in terrestrial ecosystems (ACONITE version 1) Geosci. Model Dev. 7 2015–37

Thomas R Q, Zaehle S, Templer P H and Goodale C L 2013b Global patterns of nitrogen limitation: confronting two global biogeochemical models with observations Glob. Change Biol. 19 2986–98

Thornton P E, Lamarque J F, Rosenbloom N A and Mahowald N M 2007 Influence of carbon–nitrogen cycle coupling on land model response to CO2 fertilization and climate variability Glob. Biogeochem. Cycles 21 GB0108

Todd-Brown K E O et al 2014 Changes in soil organic carbon storage predicted by Earth system models during the 21st century Biogeosciences 11 2341–56

Todd-Brown K E O, Randerson J T, Post W M, Hoffman F M, Tarnocai C, Schuur E A G and Allison S D 2013 Causes of variation in soil carbon predictions from CMIP5 Earth system models and comparison with observations Biogeosciences 10 1717–36

Townsend A R, Brasswell B H, Holland E A and Penner J E 1996 Spatial and temporal patterns in terrestrial carbon storage due to deposition of anthropogenic nitrogen Ecol. Appl. 6 806–14

Vitousek P M and Howarth R W 1991 Nitrogen limitation on land and sea: how can it occur Biochemistry 13 87–115

Vitousek P M, Menge D N L, Reed S C and Cleveland C C 2013 Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems Phil. Trans. R. Soc. B 368

Wang Y P and Houlton B Z 2009 Nitrogen constraints on terrestrial carbon uptake: implications for the global carbon–climate feedback Geophys. Res. Lett. 36 L24403

Wang Y P, Houlton B Z and Field C B 2007 A model of biogeochemical cycles of carbon, nitrogen, and phosphorus including symbiotic nitrogen fixation and phosphaite production Glob. Biogeochem. Cycles 21 GB1018

Wang Y P, Law R M and Pak B 2010 A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere Biogeosciences 7 2261–82

Wang Y-P, Trudinger C M and Enting I G 2009 A review of applications of model–data fusion to studies of terrestrial carbon fluxes at different scales Agric. Forest Meteorol. 149 1829–42

Wania R, Meissner K J, Eby M, Arora V K, Ross I and Weaver A J 2012 Carbon–nitrogen feedbacks in the UVic ESM Geosci. Model Dev. 5 1137–60

Wieder W R, Bonan G B and Allison S D 2013 Global soil carbon projections are improved by modelling microbial processes Wieder W R, Cleveland C C, Smith W K and Todd–Brown K E O 2015a Future productivity and carbon storage limited by terrestrial nutrient availability Nat. Geosci. at press

Wieder W R, Grandy A S, Kallenbach C M, Taylor P G and Bonan G B 2015b Representing life in the Earth system with soil microbial functional traits in the MIMICS model Geosci. Model Dev. 8 2011–92

Williams M et al 2009 Improving land surface models with FLUXNET data Biogeosciences 6 1341–59

Xia J, Luo Y, Wang Y P and Hararak D 2013 Traceable components of terrestrial carbon storage capacity in biogeochemical models Glob. Change Biol. 19 19204–16

Yang X, Wittig V, Jain A K and Post W 2009 Integration of nitrogen cycle dynamics into the Integrated Science Assessment Model for the study of terrestrial ecosystem responses to global change Geosci. Model Dev. 24 GB4029

Zaehle S, Friedlingstein P and Friend A D 2010 Terrestrial nitrogen feedbacks may accelerate future climate change Geophys. Res. Lett. 37 101401

Zaehle S and Friend A D 2010 Carbon and nitrogen cycle dynamics in the O–CN land surface model: L Model description, site-scale evaluation, and sensitivity to parameter estimates Glob. Biogeochem. Cycles 24 GB1005

Zaehle S, Jones C D, Houlton B, Lamarque J F and Robertson E 2015 Nitrogen availability reduces CMIP5 projections of twenty-first-century land carbon uptake J. Clim. 28 2494–513

Zaehle S et al 2014 Evaluation of I1 terrestrial carbon–nitrogen cycle models against observations from two temperate free-air CO2 enrichment studies New Phytol. 202 803–22