

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

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LETTER

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

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William R Wieder¹, Cory C Cleveland², David M Lawrence¹ and Gordon B Bonan¹¹ Climate and Global Dynamics Division, National Center for Atmospheric Research, Boulder, Colorado 80307, USA² Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, Montana 59812, USAE-mail: wwieder@ucar.edu**Keywords:** biological nitrogen fixation, carbon cycle, climate change, community land model, Earth system modeling, structural uncertainty**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).

Table 1. Summary of the global land models that include coupled C–N biogeochemistry, the parameterizations each uses to calculate BNF, and relevant references justifying the chosen parameterization.

Model	BNF approach	N Fixation reference
CLM4cn and CLM4.5bgc (Thornton <i>et al</i> 2007, Oleson <i>et al</i> 2013)	$f(NPP)$	(Cleveland <i>et al</i> 1999)
JSBACH (Parida 2011)	$f(NPP)$	(Cleveland <i>et al</i> 1999)
UVic (Wania <i>et al</i> 2012)	$f(ET)$ (spin-up) $f(NPP)$ (transient)	(Cleveland <i>et al</i> 1999)
Century (Schimel <i>et al</i> 1996)	$f(ET)$	(Cleveland <i>et al</i> 1999)
ISAM (Jain <i>et al</i> 2009, Yang <i>et al</i> 2009)	$f(ET, biome)$	(Schimel <i>et al</i> 1996, Cleveland <i>et al</i> 1999)
OC–N (Zaehle and Friend 2010)	$f(ET)$	(Cleveland <i>et al</i> 1999)
TEM (Hayes <i>et al</i> 2011)	$f(ET)$	(Cleveland <i>et al</i> 1999)
GFDL-LM3V (Gerber <i>et al</i> 2010)	$f(soil\ N, LAI, mortality, disturbance, etc)$	(Rastetter <i>et al</i> 2001)
CASA-CNP (Wang <i>et al</i> 2010)	$f(soil\ N, LAI, P, temperature, etc)$	(Wang <i>et al</i> 2007, Houlton <i>et al</i> 2008)

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

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 (N_2) into a biologically usable form (NH_3) broadly limit rates of BNF (Gutschick 1981). Estimating BNF using relationships between ET and NPP produce similar estimates of pre-industrial BNF inputs, but lead to differing predictions about the response of BNF to changing climate and CO_2 . 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 *et al* 2012). These modifications to CLM4.5bgc improve model agreement 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):

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

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).

$$BNF_{ET} = (0.0102 \times ET + 0.524) / (10 \times 86400 \times 365), \quad (2)$$

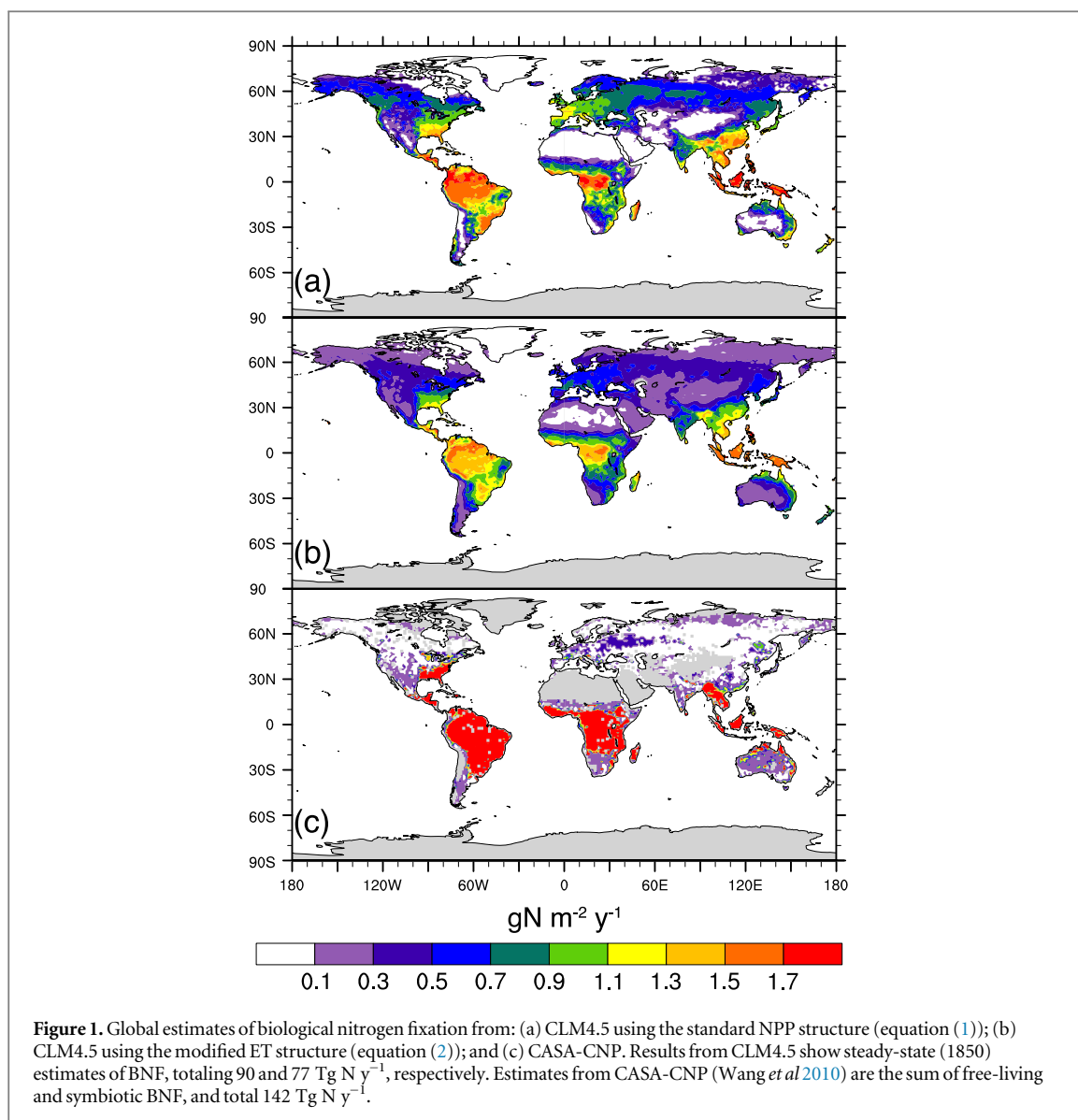
where instantaneous ET fluxes (converted to an annual rate, $mm y^{-1}$) are used to calculate instantaneous BNF rates ($g N m^{-2} s^{-1}$). Here, we calculate ET as the sum of canopy evaporation and transpiration fluxes, because preliminary results indicated this would provide initial BNF inputs that 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, Houlton *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 [CO_2], 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

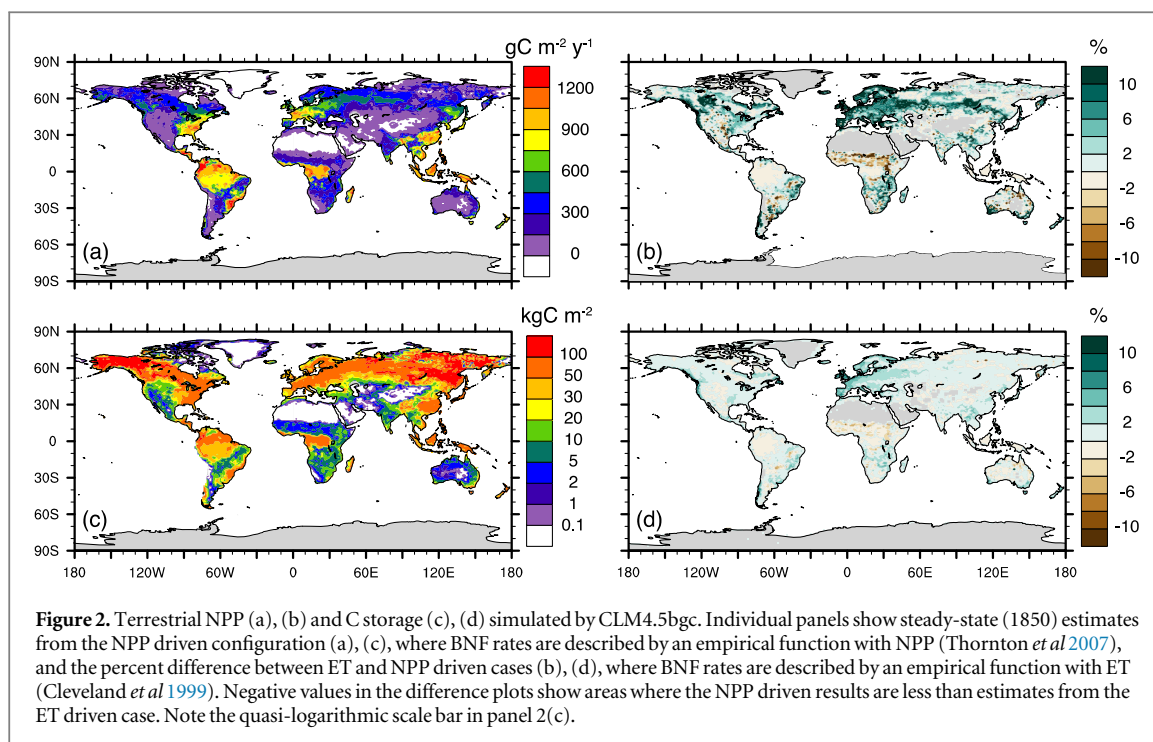


corroboration of these estimates, although we argue they all represent plausible approximations of pre-industrial BNF rates.

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 down-regulation 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 [CO₂] 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 CO₂ fertilization under the RCP8.5 scenario (black lines, figure 3), creating a positive feedback between BNF and NPP that resulted in sustained increases in



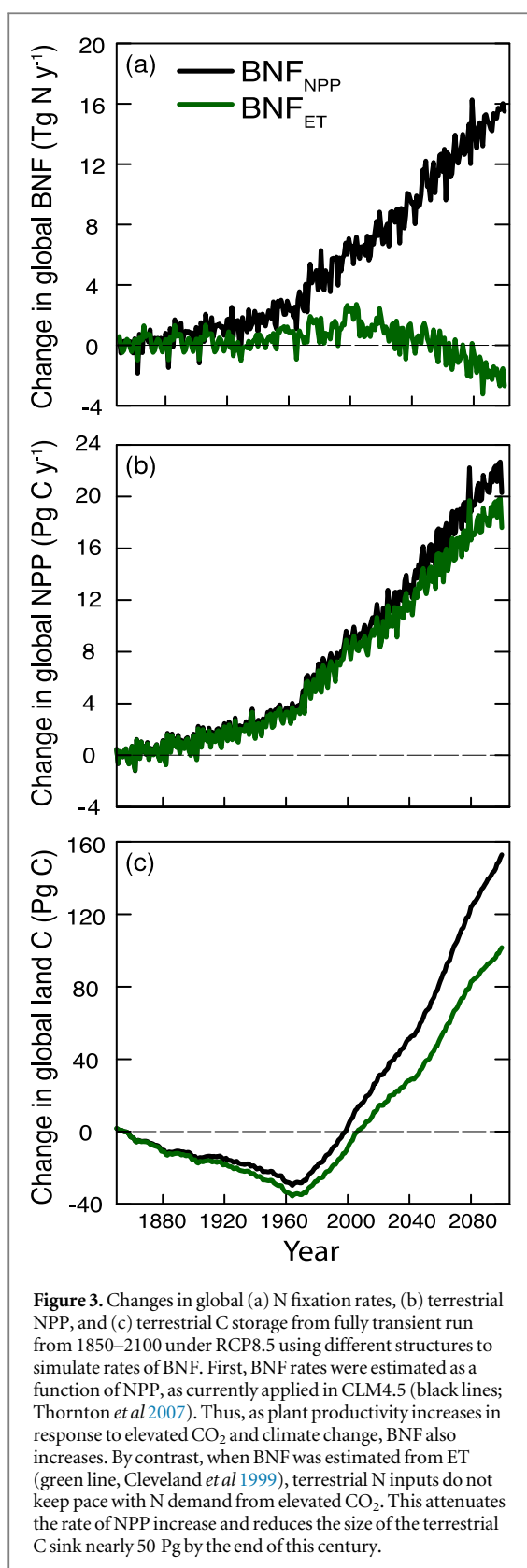
NPP and large increases in terrestrial C storage through the 21st century. Notably, the trajectories of terrestrial C storage are virtually identical for both cases through the historical period, with initial terrestrial C losses driven by land use and land cover that recover by the end of the 20th century, 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 (Batterman *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 socially 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

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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