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Influence of dynamic vegetation on carbon-nitrogen cycle feedback in the Community Land Model (CLM4)

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Abstract

Land carbon sensitivity to atmospheric CO₂ concentration (β_L) and climate warming (γ_L) is a crucial part of carbon-climate feedbacks that affect the magnitude of future warming. Although these sensitivities can be estimated by earth system models, their dependence on model representation of land carbon dynamics and the inherent model assumptions has rarely been investigated. Using the widely used Community Land Model version 4 as an example, we examine how β_L and γ_L vary with prescribed versus dynamic vegetation covers. Both sensitivities are found to be larger with dynamic compared to prescribed vegetation on decadal timescale in the late twentieth century, with a more robust difference in γ_L . The latter is a result of dynamic vegetation model deficiencies in representing the competitions between deciduous versus evergreen trees and tree versus grass over the tropics and subtropics. The biased vegetation cover changes the regional characteristics of carbon-nitrogen cycles such that plant productivity responds less strongly to the enhancement of nitrogen mineralization with warming, so more carbon is lost to the atmosphere with rising temperature. The result calls for systematic evaluations of land carbon sensitivities with varying assumptions for land cover representations to help prioritize development effort and constrain uncertainties in carbon-climate feedbacks.

Introduction

Land ecosystems and ocean biogeochemistry play key roles in the carbon cycle that determines the concentration of atmospheric CO₂ ([CO₂]) and consequential changes in surface air temperature (SAT). For example, higher [CO₂] enables plants to achieve better efficiency in carbon uptake, thus providing a negative feedback to the CO₂ emitted to the atmosphere. On the other hand higher SAT can increase plant stress to reduce their productivity and also accelerate litter decomposition, leading to an increase of [CO₂] as a positive feedback to further increase SAT. The so-called carbon cycle feedback is therefore a key property of the climate system related to the magnitude of warming for a given emission of CO₂, and has become quantifiable in global climate

models that include terrestrial and ocean biogeochemical components (commonly referred to as Earth System models, ESMs) (Friedlingstein *et al* 2006, Flato 2011, Taylor *et al* 2012, Shao *et al* 2013). Estimation of the carbon cycle feedback involves calculation of the land carbon sensitivity to [CO₂], denoted as β_L (Pg C ppm⁻¹), and the land carbon sensitivity to temperature, γ_L (Pg C K⁻¹) (e.g. equations (14) and (20) in Gregory *et al* 2009). The former (β_L) represents the terrestrial carbon change per unit change in [CO₂], and the latter (γ_L) represents the terrestrial carbon change per unit change in SAT. Using multiple ESMs, Gregory *et al* (2009) estimated the carbon cycle feedback in a way that was consistent with other climate feedback mechanisms such as clouds, and found that the strength and uncertainty of carbon cycle feedback are comparable to those of other

climate feedbacks. Therefore it is of great importance to identify the magnitude, sources, and pathways of model errors in the simulated carbon cycle feedbacks and ultimately reduce these model errors and the associated uncertainty. Previous studies have identified several factors that influence the carbon cycle feedbacks, which are briefly summarized below.

One of the processes contributing to uncertainty of the carbon cycle feedback is the nitrogen cycle (Arneth *et al* 2010, Zaehle and Dalmonech 2011), which is incorporated in only a small number of ESMs. Thornton *et al* (2009) studied the impact of the coupled carbon-nitrogen biogeochemistry on the land and ocean responses to changing $[\text{CO}_2]$ and climate, noting a reduction of the $[\text{CO}_2]$ fertilization effect due to the nitrogen constraint on plant growth. The nitrogen constraint also has an opposite effect as higher temperature enhances the decomposition of organic matter, hence nitrogen mineralization (NMINN), which increases the nitrogen availability for plants. Other independent studies using global land models or earth system models of intermediate complexity with the nitrogen cycle have also reported similar model responses (Sokolov *et al* 2008, Zaehle *et al* 2010, Piao *et al* 2013).

Another factor that can affect carbon cycle feedback is the change in vegetation cover. The role of anthropogenic land cover change in carbon cycle feedback was studied by Bonan and Levis (2010) (hereafter BL2010). They found recognizable differences in the land carbon sensitivity, particularly γ_L , comparing simulations with and without land use change representations. The effects of land use change on land carbon sensitivities may depend on the carbon-nitrogen interactions, because nitrogen stored in vegetation and/or litter is removed by land-use change activities such as harvesting and burning, which will affect forest regrowth (Gerber *et al* 2010, Jain *et al* 2013). Loss of forest cover also changes the soil moisture and surface energy balance, which influences the soil carbon and nitrogen dynamics (Batlle-Aguilar *et al* 2011). However, at the global scale, BL2010 reported rather small effects of the nitrogen cycle on the simulated carbon loss from land use change.

Land cover can also be altered via natural vegetation dynamics in response to changing environments. Global-scale models that simulate such natural vegetation dynamics (e.g. establishment, mortality, competition among different vegetation types) are commonly called Dynamic Global Vegetation Models (DGVMs) (Prentice *et al* 2007, Sitch *et al* 2008). The ESMs that participated in Coupled Model Intercomparison Project (CMIP) phase 5 have provided a deeper understanding of the carbon cycle feedback (e.g. Arora *et al* 2013, Friedlingstein *et al* 2014, Wenzel *et al* 2014), with DGVMs included in about half of the ESMs. It is well known that typical DGVMs employ much simplified representations of vegetation dynamics, so their ability

to simulate plant response to changing climate bears a large uncertainty (Fisher *et al* 2010). The influence of nitrogen cycle on simulating vegetation dynamics was also shown to be significant by Gotangco Castillo *et al* (2012), hereafter GC2012, who compared land covers simulated by a DGVM with and without the coupled nitrogen cycle. In their model the nitrogen constraint on plant productivity affects each plant type differently, increasing tree covers and decreasing grass and shrub covers over some regions. Furthermore, previous studies found that other model components, such as soil moisture dynamics, also play significant roles in producing biases in land cover distributions simulated by DGVMs (GC 2012, Shao *et al* 2013). Summarizing those uncertainties associated with DGVMs, Huntingford *et al* (2013) found that the spread among models in projecting the future tropical biomass was broader when different DGVMs were used, compared to the spreads resulting from parameter perturbations or different future climate scenarios.

These previous findings point to the need to quantify how the uncertainty in the land cover distribution in DGVMs alters the land carbon sensitivities, thereby carbon cycle feedback, and to determine the sources of uncertainty. However, such an attempt has rarely been made. This study addresses these issues with a widely used community global land model that incorporates coupled carbon-nitrogen cycles and a DGVM. As more ESMs will include dynamic vegetation and coupled carbon-nitrogen cycle in the near future, our exploration of the linkages between DGVMs and land carbon sensitivities may motivate the need to further improve specific aspects of DGVMs to constrain estimates of land carbon sensitivities by Earth system models.

1. Methods

Models

We used the Community Land Model version 4 (CLM4) (Lawrence *et al* 2011, Oleson *et al* 2010) with coupled carbon-nitrogen biogeochemistry and dynamic vegetation, the same model as also used in BL2010 and GC2012. CLM4 simulates the water and energy cycles across the atmospheric surface layer, vegetation, soil, and bedrock. The terrestrial water-energy cycle requires CLM4 to include photosynthesis that is coupled to transpiration. CLM4 includes a biogeochemistry model that simulates the carbon and nitrogen cycles, CLM4CN (referred to as CN hereafter) (Thornton *et al* 2007), and a DGVM that simulates natural (unmanaged) dynamic vegetation, coupled to the carbon-nitrogen cycle by CN (referred to as CNDV) (GC2012). CN takes the photosynthetic rate simulated by CLM4 and additionally simulates autotrophic and heterotrophic respiration as well as wild fire to close the carbon cycle, keeping track of 20 carbon pools (e.g. leaf, plant litter, soil organic

carbon). CN further couples the carbon and nitrogen cycles that involve 19 different nitrogen pools and fluxes among them. Although plant structures such as height and leaf area are calculated by CN, vegetation cover is prescribed. CN represents anthropogenic land cover change and associated fluxes by using prescribed annual rate of conversions between land-cover categories (e.g. crop, pasture, and natural vegetation). This study (and BL2010) uses the input data developed by Lawrence *et al* (2012) who adapted the standard land use data for CMIP5 (Hurtt *et al* 2011) into the CLM framework.

When the dynamic vegetation module is activated as CNDV, the model predicts large-scale natural vegetation dynamics at the annual time scale (Levis *et al* 2004, Oleson *et al* 2010). The fractional area of each plant functional type (PFT) within a grid cell changes according to the average plant size and population. CNDV records the climate statistics of each grid cell to determine if the climate state is appropriate for the establishment of a new PFT and for the survival of the existing PFTs. The CLM4 framework cannot simultaneously represent anthropogenic alteration and natural vegetation dynamics; therefore CNDV does not include anthropogenic land cover change. The mortality due to fire is the same in CN and CNDV, but mortality due to other causes is different. In CNDV plant mortality varies with annual plant productivity, SAT, and physiological parameters for each PFT, while in CN plant mortality is a constant of 2% carbon loss per year. Except for other minor differences in the tree height calculation and carbon allocation parameters, all biogeophysical and biogeochemical processes are the same between CN and CNDV.

In addition to CN and CNDV, we set up two variations of CNDV (table 1) to attribute the differences in land carbon sensitivities (β_L and γ_L) to the difference in the vegetation biomass and the difference in the land cover characteristics. This assessment is important because the vegetation biomass simulated with CNDV is unreasonably larger than other estimations of contemporary vegetation carbon. In one experiment, CNDV is modified to apply the constant plant mortality of CN as opposed to CNDV's dynamic mortality parameterization, and is referred to as CNDVMO. CNDVMO is motivated by the finding of GC2012 that CNDV's mortality algorithm alone (with little difference in the land cover) can significantly change the characteristics of the mean state from that of CN. The limitation of the mortality parameterizations in CNDV and similar large-scale DGVMs are well recognized, for instance, for the lack of mechanistic representation of local disturbances (e.g. insect attacks) or physiological link between soil hydrology and plant productivity (e.g. hydraulic redistribution) (Galbraith *et al* 2010, Sakaguchi *et al* 2011, Jiang *et al* 2013, Tang *et al* 2015). Improvement of mortality representation is beyond the scope of this study, and here we used the simple change in the

Table 1. Description of the model configurations.

Model configuration	Land cover	Mortality	Atmospheric forcing
CN	Prescribed	Constant (2%)	Renalaysis based (Qian <i>et al</i> 2006)
CNDV	Dynamic	Dynamic	Renalaysis based (Qian <i>et al</i> 2006)
CNDVMO	Dynamic	Constant (2%)	Renalaysis based (Qian <i>et al</i> 2006)
CNDVDF	Dynamic	Dynamic	CCSM4 (Gent <i>et al</i> 2011)

mortality algorithm to explore its possible influence on the feedback parameters.

The fourth configuration is called CNDVDF. There is no difference in the model itself between CNDV and CNDVDF; instead, the atmospheric forcing data for CNDVDF is different from that for CNDV (and the other two models), as explained in more detail in the next section. The main purpose of this configuration is again to assess the influence of the overly estimated vegetation biomass by the standard CNDV on the land carbon sensitivities. It will be seen that the vegetation covers in CNDV and CNDVDF are similar while the vegetation biomass is substantially smaller in CNDVDF.

Experiments

All simulations were run on a $0.9^\circ \times 1.25^\circ$ grid with a 30-minute time step. The initial condition for CN was provided with the CLM release, which represents an approximate equilibrium state of the slowest soil carbon and nitrogen pools under the pre-industrial levels of $[\text{CO}_2]$ (284.7 ppm), nitrogen deposition, and aerosol deposition. We used this initial condition for CN's historical simulation starting at 1850. Similar initial conditions for CNDV were not available at the grid resolution we used; therefore CNDV was first spun-up starting from the soil carbon and nitrogen in the CN initial file but with no vegetation cover in all grid points (i.e. bare ground). The same forcing data as the CN spin-up simulation was used, including the atmospheric forcing data by Qian *et al* (2006). During this spin-up, the 25-year atmospheric forcing for the 1948–1972 period, which shows no upward trend in the global mean SAT, was repeatedly cycled. Global net ecosystem exchange reached near-zero values after a few hundred years, implying that the global carbon pools had reached a quasi-equilibrium. As for the PFT distributions, the tropical, temperate, and boreal PFTs reached a quasi-equilibrium state in 200, 500, and 800 years, respectively. Year 1000 from the initial CNDV spin-up was used as the starting point for the subsequent historical simulation of CNDV. The spin-up run for CNDVMO diverged from the CNDV spin-up run at year 800, and continued for 300 years to reach its own quasi-equilibrium state. Similarly, the spin-up run of CNDVDF diverged from the CNDV spin-up at year 800, and continued for 200 years to

reach a quasi-equilibrium state. The CNDVDF spin-up used the same $[\text{CO}_2]$, nitrogen deposition, and aerosol deposition as CNDV, but the meteorological forcing was obtained from a pre-industrial experiment of the Community Climate System Model version 4 (CCSM4) (Gent *et al* 2011).

Following the spin-up simulations, historical simulations were run from 1850 to 2004 during which we applied annually changing $[\text{CO}_2]$, mineral nitrogen and aerosol depositions from Lamarque *et al* (2010). For CN, CNDV, and CNDVMO, the 25-year subset (1948–1972) of the atmospheric forcing data by Qian *et al* (2006) was again cycled during the simulations from 1850 to 1947. From 1948 to 2004, the atmospheric forcing for the corresponding years was used. For CNDVDF, the atmospheric forcing data was replaced with the output from a historical simulation of CCSM4. Since the CCSM4 output was available for the entire period of 1850–2004, the data for the corresponding years were used to force CNDVDF. The other inputs to CNDVDF such as $[\text{CO}_2]$ are the same as the other models. The historical simulations described here are denoted as ‘CONC \times CLIM’ for using both the historical $[\text{CO}_2]$ and atmospheric inputs representing the changing climate.

In addition to ‘CONC \times CLIM’, three simulations were run for each model to estimate β_L and γ_L (table 2). The model inputs, climate forcing, and the simulation period (1973–2004) follow those in BL2010 so that a direct comparison can be made with CN’s land carbon sensitivities obtained in their study. The first sensitivity simulation (‘CTRL’) was driven with a constant $[\text{CO}_2]$ (328.6 ppm, the value for 1973) and the cyclic atmospheric forcing for the 1948–1972 period without a prominent warming trend. In the second simulation (‘CLIM’) we used the constant (328.6 ppm) $[\text{CO}_2]$ level but applied the atmospheric forcing from the 1973–2004 period with the rising SAT, in order to diagnose the model sensitivity to the warming. Variables other than SAT such as precipitation and downward radiative fluxes also change over time, but for simplicity, we refer them together as the warming effect. For the third simulation (‘CONC’) the model was given the historical, increasing $[\text{CO}_2]$, but it received the atmospheric forcing for the 1948–1972 period to assess the model sensitivity to $[\text{CO}_2]$. The same simulation protocols of CTRL, CLIM, and CONC were used for CNDVDF. The only change was to replace the atmospheric forcing data by Qian *et al* (2006) with the outputs from the CCSM4 simulations. Specifically, the CCSM4 output of the 1973–2004 period in its historical experiment was used for CLIM, and a 32-year period was arbitrarily selected from its pre-industrial simulation and applied to CTRL and CONC.

The abbreviations of the experiments follow those in BL2010 and are combined with model names to refer to a specific simulation, such as CN-CLIM or CNDVMO-CTRL. We estimated β_L and γ_L based on how the global land carbon changes over the 1973–2004 period as responding to a single or two

Table 2. Description of the model experiments used to estimate the sensitivity parameters. These four experiments were run for each of the three model configurations.

Experiment name	Years of atmospheric input data	Atmospheric CO_2 (ppm)
CTRL	1948–1972	328.6
CONC	1948–1972	Historical, 1973–2004
CLIM	1973–2004	328.6
CONC \times CLIM	1973–2004	Historical, 1973–2004

forcings of interests (SAT and $[\text{CO}_2]$) in each simulation. For instance, β_L is obtained by taking the difference between CONC and CTRL in the land carbon changes over the simulation period:

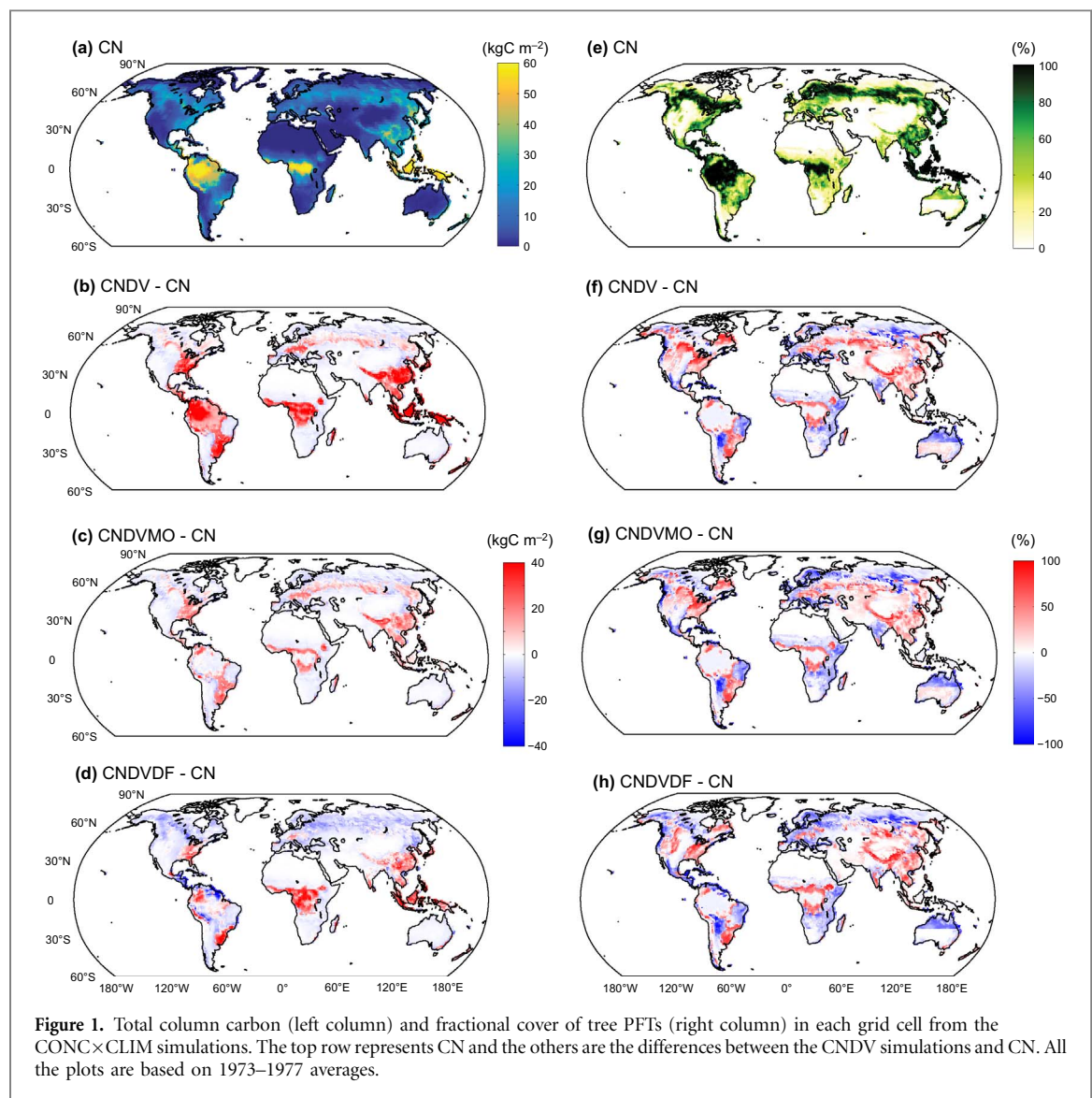
$$\beta_L = \frac{\Delta C_L^{\text{CONC}} - \Delta C_L^{\text{CTRL}}}{\Delta C_A} \quad (1)$$

where ΔC_L (Pg year^{-1}) is the land carbon changes in each simulation (the superscript shows which simulation, CONC or CTRL) and ΔC_A (ppm) is the changes of $[\text{CO}_2]$ imposed on CONC. Note that the signals common to both simulations, such as the background trend in ΔC_L associated with the transient forcing data or (most of) the carbon fluxes associated with the prescribed land cover change in CN, are removed by taking the difference in the numerator. Therefore our experiment extracts only the response of the terrestrial biosphere to the warming and/or $[\text{CO}_2]$ increase. Readers are referred to BL2010 and the supplementary material for more details (stacks.iop.org/ERL/11/124029/mmedia). Note that following BL2010, we also utilized CLM4 as a stand-alone land model, as opposed to being a part of the coupled ESM (e.g. Gent *et al* 2011). Although we cannot consider the feedbacks between the changing land state and the atmosphere or other climate system components, a qualitative agreement was seen in the land carbon sensitivities between the stand-alone (Thornton *et al* 2007) and coupled (Thornton *et al* 2009) simulations using the previous version of CLM.

2. Results

Sensitivity of β_L and γ_L to the use of CN versus CNDV

We first compare the CN and CNDV simulations and discuss results from the two other sets (CNDVMO and CNDVDF) in the next section. Figure 1b shows that the total column carbon in CNDV is substantially higher than that in CN, particularly over the tropical and subtropical forests. The difference is partly explained by CNDV’s higher tree cover (figure 1(f)), but a more important contribution comes from the lower mortality rate for plants in CNDV compared to CN as discussed in the next section. At the global scale, the terrestrial



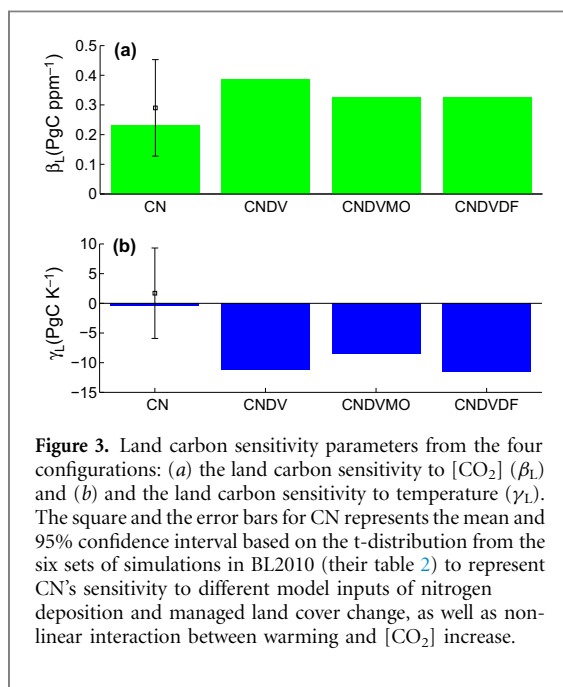
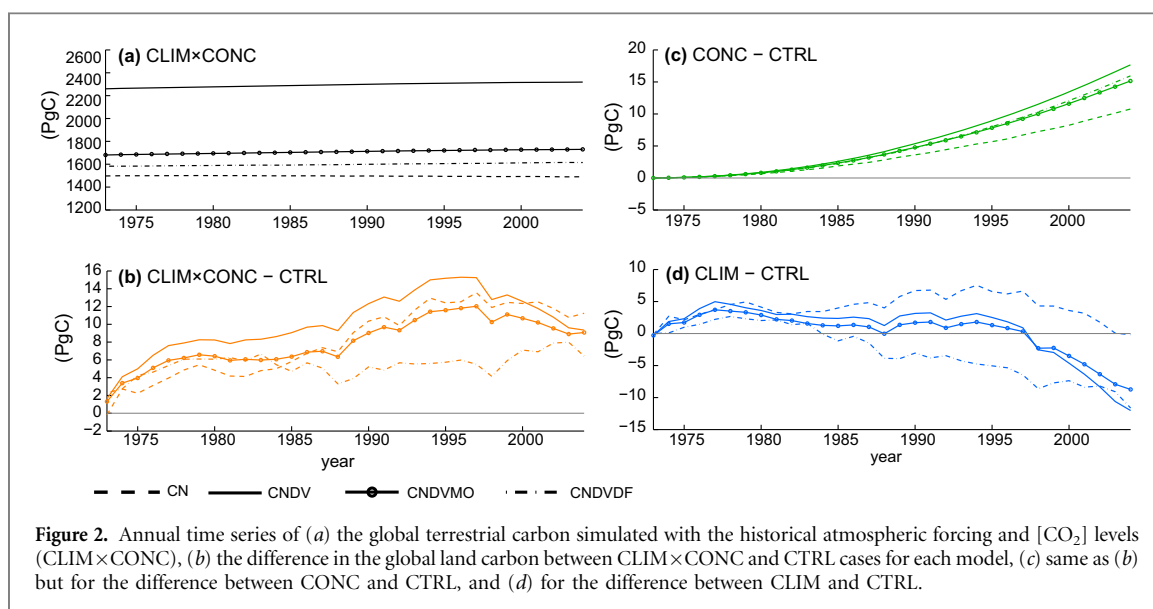
ecosystem stores ~ 800 PgC more carbon in CNDV than in CN (figure 2(a), solid and dashed lines, respectively).

Despite the differences in the vegetation cover and terrestrial carbon stocks, the response to the rising SAT and $[\text{CO}_2]$ together is fairly similar between the two configurations, shown as the difference between CONC×CLIM and CTRL in each model (figure 2(b)). However, the model responses to *each* of the two forcings are more distinct. The differences between CONC and CTRL depict a smaller gain of terrestrial carbon with higher $[\text{CO}_2]$ in CN than in CNDV (figure 2(c)). Comparing CLIM and CTRL for the effect of warming climate, the land carbon in CNDV-CLIM starts to fall below the levels of CNDV-CTRL from around 1998, the year with a strong warming (figure 2(d)). The land carbon remains higher in CN-CLIM than in CN-CTRL throughout the analysis period.

The difference between the terrestrial carbon storage averaged over the last (2000–2004) and first (1973–1977) five years is used to calculate β_L and γ_L (BL2010, Supplementary Material). Calculations using linear trends instead of the difference support the same

conclusion. We use the 95% confidence interval of β_L and γ_L obtained from the six CN experiments in BL2010 to determine if the difference between CN and CNDV is statistically significant; BL2010 provided multiple values of β_L and γ_L by sampling the influence of anthropogenic land cover change, nitrogen deposition, and non-linear interaction between warming and $[\text{CO}_2]$ increase (Supplementary Material). Based on this criterion, CNDV's β_L does not appear to differ substantially from those of CN (figure 3(a)). On the other hand, γ_L shows a distinct difference between CNDV and CN (figure 3(b)).

Given the larger disparity in γ_L , we focus on the CLIM and CTRL experiments with CN and CNDV. In the CLIM simulations, terrestrial carbon declines due to increased wild fires, heterotrophic respiration (HR), and also due to the reduction in plant uptake of carbon (i.e. NPP). After integrating the global carbon loss by wild fires and HR over time (1973–2004) and subtracting the same quantities from the respective CTRL runs, both are found to be larger in CNDV than in CN by about 0.2 PgC and 0.9 PgC, respectively. The dominant contribution to the difference between CNDV and CN comes from the NPP. The accumulated



NPP is smaller in CNDV-CLIM than CN-CLIM by 4.1 PgC.

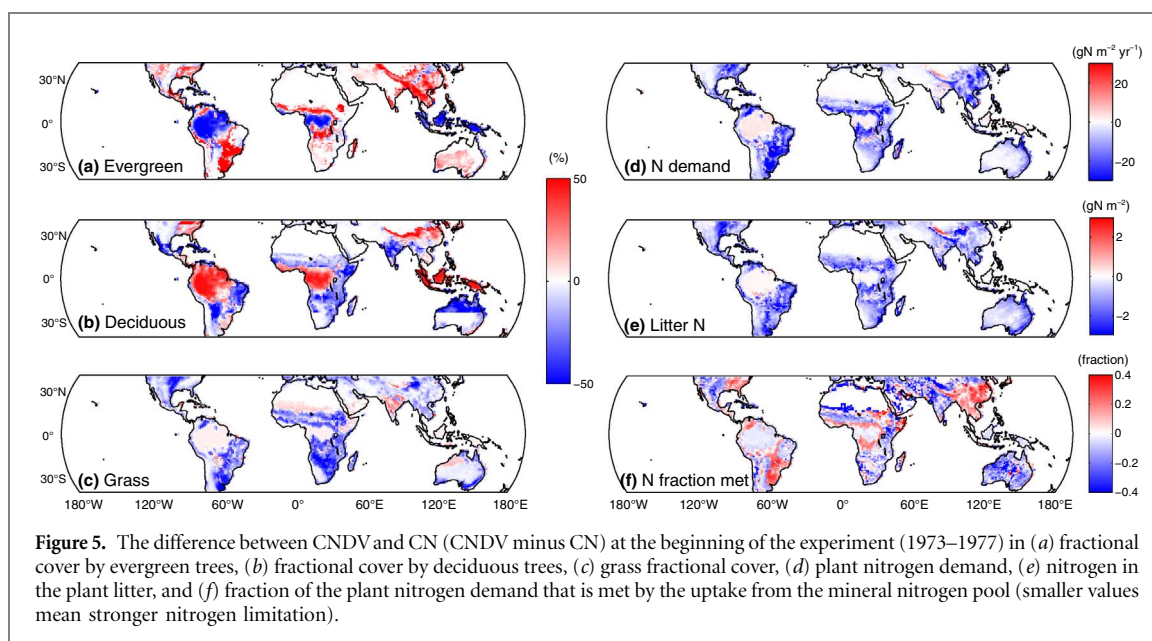
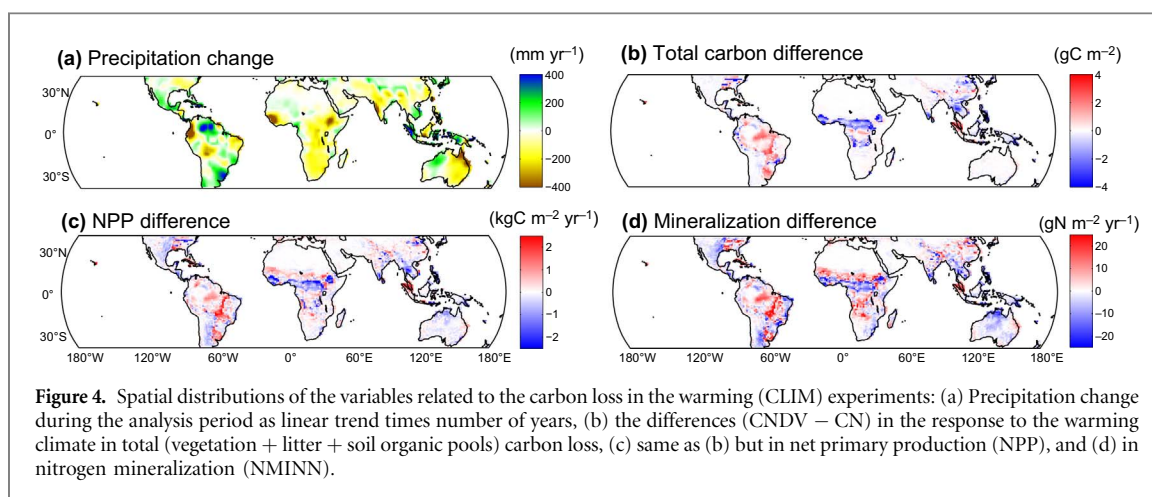
Geographically, most substantial carbon loss in the CLIM experiments takes place in the tropics and subtropics (figure S1), particularly in Africa where precipitation decreases during the analysis period (figure 4(a)). These regions are also where we see the greatest disparity between CNDV and CN in the terrestrial carbon (figure 4(b)). The NPP difference (figure 4(c)) shows almost identical spatial patterns as the carbon loss difference.

Vegetation cover changes differently in CNDV-CLIM and CNDV-CTRL over the analysis period, but their magnitudes are rather minor in the above regions (on average, less than 5% of the grid area, figure S2). Different land cover evolution would play a more important role in coupled simulations through

changes in the surface energy and water fluxes at the surface, such as amplifying warming and heat stress (Jiang *et al* 2013). However, Rauscher *et al* (2015) showed that such feedbacks were not significant in the coupled CNDV simulation in the historical period (1970–1999). Note that there is no difference in the PFT fractional cover between CN-CLIM and CN-CTRL because these two simulations use the same prescribed land cover data.

A close inspection revealed that the spatial pattern in the difference between CNDV and CN in the NPP response to the warming (figure 4(c)) is very similar to that in nitrogen mineralization (figure 4(d)), indicating that it is the favourable effect of warming on vegetation growth, through enhanced mineralization, that causes CN and CNDV to have distinct γ_L . Furthermore, the regions with greater decline in CNDV of carbon, NPP, and mineralization coincide with the areas where CNDV overestimates the fractional cover of evergreen trees and underestimates the fractional covers of deciduous tree and grass PFTs, particularly the dry forest north of the equatorial rainforest in Africa (figure 5(a)–(c)).

The evergreen trees are parameterized with slightly lower nitrogen:carbon stoichiometry ratio than the deciduous trees and require less nitrogen for a unit carbon allocation (Chapter 13 in Oleson *et al* 2013, figure S3). Grass, without woody stems, has even higher nitrogen:carbon ratio than these trees, so removing grass also reduces nitrogen requirement for a given growth. These physiological traits and CNDV's land cover result in a less-active nitrogen cycle, characterized by smaller nitrogen demands from the vegetation (figure 5(d), figure S4a), less nitrogen in plant litter (figure 5(e)), and overall weaker nitrogen constraint on plant growth (figure 5(f)), compared to those in CN. The greater nitrogen demand in CN, thereby stronger nitrogen constraint on plant growth, also explains why CN's response to the increasing $[\text{CO}_2]$ levels is somewhat smaller than that of CNDV



(figures 2(c) and 3(a)). The drying trend of precipitation likely has a negative effect on the heterotrophic decomposition, but the enhancement of NMINN with warming still takes place and it helps counter the moisture stress on plants in CN. With the smaller nitrogen constraint associated with CNDV's vegetation cover, such mediation of moisture stress is likely weaker and contributes to the greater decline of NPP and the land carbon with warming.

Robustness of the results and related discussion

The diagnoses in the previous section illustrate the link between the change in γ_L from CN to CNDV and the model bias in vegetation distribution, by way of the coupled carbon-nitrogen cycle. Yet, the gross overestimation of the terrestrial carbon pool by CNDV deserves a check to determine if the large disparity in the carbon storage may play a role in changing γ_L . We addressed this question using two additional sets of CNDV simulations (section 2): one switching the plant mortality representation to that of CN (CNDVMO), and the other forced by atmospheric data from a historical simulation of the fully coupled

CCSM4 (CNDVDF) instead of observationally-constrained reanalysis-based data by Qian *et al* (2006).

The PFT distribution in CNDVMO is quite similar to that in the standard CNDV (figure 1(f) and (g)), indicating little sensitivity of CNDV biogeography to the plant mortality difference. On the other hand, figures 1(c) and 2(a) show that the land carbon storage is substantially reduced with CN's constant mortality. The major contributor to this reduction is the tropical region (figure 1(b) and (c)). In the CNDVDF simulation using the CCSM4 forcing, tree cover over the mid-latitudes shrinks to some extent, but overall its forest cover is quite similar to that of CNDV (figure 1(f) and (h)). Terrestrial carbon pool becomes much smaller compared to CNDV (figures 1(d) and (2a)). The atmospheric forcing from CCSM4 shows sizable difference in SAT, precipitation, and surface shortwave radiation compared to Qian *et al* (2006) as shown in figure S5 and noted by Gent *et al* (2011) and D. Lawrence *et al* (2012). In particular, the smaller biomass of the Amazon forest in CNDVDF is likely the result of the underestimation of precipitation by CCSM4 over the same region (figure S5b).

However in figure 3, both of these two CNDV simulation sets exhibit γ_L quite similar to that of the standard CNDV. Indeed both sets of simulations are found to be very similar to the standard CNDV in terms of the tropical and sub-tropical biogeography as well as the carbon-nitrogen cycle coupling (figure S6). The result of CNDVMO strongly suggests that the difference we see in γ_L between CNDV and CN is not a simple translation of the difference in the terrestrial carbon storage, but is rooted in CNDV's biogeography and its coupling to the carbon-nitrogen cycle. The same conclusion is also supported by CNDVDF from which surprisingly persistent characteristics of CNDV's vegetation cover and associated carbon-nitrogen cycle coupling are found. Although the result of CNDVDF can be used to refute the hypothesis that the difference in the size of the terrestrial carbon pool is the main reason for the difference in γ_L , we note that not all aspects of the interactions between vegetation and carbon-nitrogen biogeochemistry are the same between CNDV and CNDVDF. Indeed some caution in interpreting the result of CNDVDF is warranted. This is because unlike CN vs. CNDV, we do not directly compare CNDVDF to the CN simulations with the CCSM4 forcing. It is also possible that the result of CNDVDF depends on ensemble members from which the forcing data was created, and on the period of the pre-industrial forcing data selected for the CTRL and CONC simulations. Detailed investigations on CNDVDF with additional simulations are beyond the scope of this work.

The PFT distributions in our CNDV simulations are consistent with GC2012, who found that the drought-deciduous phenology adapted from CN into CNDV is responsible for the biased competition between tropical evergreen and deciduous trees. Improving this particular leaf phenology in CLM4 is quite challenging as noted by Dahlin *et al* (2015), mainly because of the tight coupling between plant productivity and soil hydrology, an issue recognized for other ecosystem models as well (Christoffersen *et al* 2014). Tang *et al* (2015) also faced a difficulty in their attempt to improve the soil-plant linkage in the CLM framework by incorporating root hydraulic redistribution, thus noting the necessity of a significant change in the model structure. Underestimated grass cover has been recognized in CNDV and its base model LPJ (Bonan *et al* 2003, Sitch *et al* 2003), which would require substantial changes in model representation of forest structure and plant trait trade-offs (e.g. Baudena *et al* 2015, Fisher *et al* 2015). Previous studies also found that several aspects of the carbon-nitrogen biogeochemistry of CN require improvements (e.g. Thomas *et al* 2013). In particular, the strong model response to nitrogen in tropical areas is not completely consistent with the general understanding (BL2010, Wang *et al* 2010), which is another model uncertainty important to our result.

Given these limitations, the two main processes considered in this study, the nitrogen cycle and dynamic vegetation, appear to increase the uncertainty of the model's feedback parameters. However, the lack of nutrient limitation can lead to unrealistic terrestrial carbon sink for future climate projections (Wang and Houlton 2009, Wieder *et al* 2015), and there is no guarantee that a prescribed land cover such as produced by Integrated Assessment Models (Moss *et al* 2010, van Vuuren *et al* 2011) will be consistent with the climate simulated by a coupled climate model. In this respect, a DGVM will be more consistent and has been shown to be important for regional climate projections (e.g. Strengers *et al* 2010).

Lastly, the magnitudes of γ_L explored in our analysis period are rather small and only about 20% of β_L if we scale them in the same units as $\text{W m}^{-2} \text{K}^{-1}$ following Gregory *et al* (2009) (using the ensemble mean values of the related quantities in their table 3 for their equation 20); with this scaling γ_L is about -0.07 while β_L is about 0.36 for CNDV, making the impact on γ_L appears not as important. Nevertheless, it is important to note that in most of the ESM projections, β_L tends to asymptote at certain values or decrease after the middle of the 21st century while γ_L keeps decreasing (strengthening in the negative direction) under increasing $[\text{CO}_2]$ (Arora *et al* 2013, also seen in our unpublished future simulations extended from CNDVDF). Therefore the difference in γ_L may not be significant in the near-term climate change, but it may have more serious implications for the long-term projections.

3. Conclusion

The land carbon sensitivities to $[\text{CO}_2]$ (β_L) and warming (γ_L) are essential parts of the carbon cycle feedbacks, which in turn play a key role in determining the magnitude of warming for a given emission of CO_2 . Therefore the land carbon sensitivities represented in earth system models should be critically assessed and continuously improved for reliable projections of the future climate. The main questions of this study are how β_L and γ_L are affected by the natural vegetation dynamics simulated by a global land model with coupled carbon-nitrogen cycle, and how relevant model errors propagate to the land carbon sensitivities. These questions are addressed by comparing the present-day (1973–2004) simulations of a global carbon-nitrogen biogeochemistry model (CLM4) with prescribed vegetation cover (CN) and with dynamic global vegetation model (CNDV). It is found that β_L is not significantly different between the two treatments of vegetation cover but γ_L is distinct and more negative in CNDV compared to CN. The latter result arises not from the differences in the concurrent vegetation dynamics induced by the

warming during the study period, but from the difference in the characteristics of the coupled carbon-nitrogen cycle that developed differently in the prescribed (CN) and dynamically evolved (CNDV) vegetation distributions during the long simulations of the pre- and post-industrial periods. Specifically, CNDV's quasi-equilibrium vegetation distribution includes biases in the distribution of tropical evergreen trees, deciduous trees, and grass, so the tropical dry forests demand less nitrogen for a given amount of plant growth in CNDV than in CN with prescribed vegetation. The weaker dependence of plant productivity on available nitrogen reduces the positive effect of warming on the carbon uptake through enhanced nitrogen mineralization, which results in smaller land carbon sink in CNDV with warming climate. Such a pathway for a dynamic global vegetation model to influence the carbon cycle feedback is rather indirect and has not been widely recognized, presumably because this pathway is only possible for models that incorporate both dynamic vegetation and coupled carbon-nitrogen cycle (or other nutrient limitations). The above result is reproduced by additional sets of CNDV simulations using either the constant plant mortality of CN (instead of CNDV's variable mortality) or different atmospheric forcing data derived from a historical simulation of the fully coupled CCSM4, demonstrating the persistence of the aforementioned bias of CNDV biogeography and associated characteristics of the plant-carbon-nitrogen relationship.

Although the result here is based on a single land model, the relevant model processes—phenology parameterizations and closely related soil hydrology-plant interactions, poorly represented competition between tree and grass PFTs, and the strength of nitrogen constraint on plant growth—are known to be difficult for other models as well (Christoffersen *et al* 2014, Fu *et al* 2014, Baudena *et al* 2015). Hence we believe that the outcome of this study is useful for other modelling groups and encourage more systematic evaluations of land carbon sensitivities in ESMs with varying assumptions in their land cover representations. Given the large magnitude and uncertainty in the current estimates for carbon-climate feedbacks, such efforts will be necessary to more effectively direct resources in model development and rapidly constrain the new estimates for carbon-climate feedbacks, for instance by the new generation of ESMs participating in the upcoming CMIP6.

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