

# A model based investigation of the relative importance of CO<sub>2</sub>-fertilization, climate warming, nitrogen deposition and land use change on the global terrestrial carbon uptake in the historical period

N. Devaraju<sup>1,2</sup> · G. Bala<sup>1,2,3</sup> · K. Caldeira<sup>4</sup> · R. Nemani<sup>5</sup>

Received: 26 April 2015 / Accepted: 27 August 2015  
© Springer-Verlag Berlin Heidelberg 2015

**Abstract** In this paper, using the fully coupled NCAR Community Earth System Model (CESM1.0.4), we investigate the relative importance of CO<sub>2</sub>-fertilization, climate warming, anthropogenic nitrogen deposition, and land use and land cover change (LULCC) for terrestrial carbon uptake during the historical period (1850–2005). In our simulations, between the beginning and end of this period, we find an increase in global net primary productivity (NPP) on land of about 4 PgCyr<sup>-1</sup> (8.2 %) with a contribution of 2.3 PgCyr<sup>-1</sup> from CO<sub>2</sub>-fertilization and 2.0 PgCyr<sup>-1</sup> from nitrogen deposition. Climate warming also causes NPP to increase by 0.35 PgCyr<sup>-1</sup> but LULCC causes a decline of 0.7 PgCyr<sup>-1</sup>. These results indicate that the recent increase in vegetation productivity is most likely driven by CO<sub>2</sub> fertilization and nitrogen deposition. Further, we find that this configuration of CESM projects that the global terrestrial ecosystem has been a net source of carbon during 1850–2005 (release of  $45.1 \pm 2.4$  PgC), largely driven by historical LULCC related CO<sub>2</sub> fluxes to the atmosphere. During the recent three decades (early 1970s to early 2000s), however, our model simulations

project that the terrestrial ecosystem acts as a sink, taking up about 10 PgC mainly due to CO<sub>2</sub> fertilization and nitrogen deposition. Our results are in good qualitative agreement with recent studies that indicate an increase in vegetation production and water use efficiency in the satellite era and that the terrestrial ecosystem has been a net sink for carbon in recent decades.

**Keywords** Terrestrial carbon uptake · CO<sub>2</sub> fertilization · Nitrogen deposition · Climate change · Land use land cover change · Net primary productivity

## 1 Introduction

Response of the terrestrial ecosystem to climate change is one of the major uncertainties in projecting the future evolution of the global carbon cycle (Friedlingstein et al. 2014; Ahlstrom et al. 2012; Arora et al. 2013). Though current generation of global land models have improved substantially, they still fail to represent all ecosystem processes adequately. This has led to a large spread in results and hence low confidence on the magnitude of the future changes in land carbon fluxes and stocks (IPCC 2013). The large uncertainty arises because the terrestrial ecosystem is highly heterogeneous and the current observations are inadequate to cover the entire range of diversity found in the global terrestrial ecosystems (Bodman et al. 2013; Norby et al. 2010).

Because of the observational constraints, the role of terrestrial carbon cycle in removing atmospheric CO<sub>2</sub> has been indirectly inferred in recent decades (IPCC 2013). These indirect estimates indicate that land has acted as a carbon sink in recent decades (Le Quéré et al. 2009; Friedlingstein et al. 2010; Zaehle et al. 2011; Pan et al.

---

✉ N. Devaraju  
devarajun@gmail.com

<sup>1</sup> Divecha Centre for Climate Change, Indian Institute of Science, Bangalore 560012, India

<sup>2</sup> Centre for Atmospheric and Oceanic Sciences, Indian Institute of Science, Bangalore 560012, India

<sup>3</sup> Interdisciplinary Centre for Water Research, Indian Institute of Science, Bangalore 560012, India

<sup>4</sup> Department of Global Ecology, Carnegie Institution, 260 Panama Street, Stanford, CA 94305, USA

<sup>5</sup> NASA Ames Research Center, Moffett Field, CA 94035, USA

2011; Bala et al. 2012; Le Quéré et al. 2013; Schimel et al. 2014). Recent satellite observations also suggest that the global vegetation productivity is increasing in recent decades (Anav et al. 2015; Ma et al. 2015; Ichii et al. 2013; Running et al. 2004; Nemani et al. 2003). However, the primary drivers and their contribution for this increase in global vegetation productivity and global land being a sink are not well understood (McGuire et al. 2009; Hayes et al. 2011; Friedlingstein et al. 2014). The likely prominent drivers for terrestrial ecosystem responses are CO<sub>2</sub> fertilization, nitrogen deposition, climate warming and land use and land cover change (LULCC) (Galloway et al. 2004; Canadell et al. 2007; Arneth et al. 2010; Friedlingstein et al. 2010; Houghton et al. 2012; Bala et al. 2012, 2013; Ciais et al. 2013; Devaraju et al. 2015; IPCC 2013).

The atmospheric CO<sub>2</sub> concentration has increased by ~40 % during the historical period (1750–2011; IPCC 2013). A recent study by Schimel et al. (2014) indicates substantial terrestrial carbon uptake in the tropics due to CO<sub>2</sub> fertilization. When combined with extra-tropical fluxes, Schimel et al. find that up to 60 % of the present-day net terrestrial carbon sink is a consequence of increasing atmospheric CO<sub>2</sub> content. This indicates that the increasing CO<sub>2</sub> effect on terrestrial carbon storage is potentially a key negative feedback on future climate change. In most of today's climate models, CO<sub>2</sub> fertilization is one of the largest carbon cycle feedbacks (Schimel et al. 2014; Thornton et al. 2007; Friedlingstein et al. 2006). The CO<sub>2</sub> fertilization effect is difficult to quantify because it operates over large regions and long periods of time and hence is challenging to observe and quantify directly (Schimel et al. 2014). The extent to which CO<sub>2</sub> fertilization is responsible for current and future terrestrial carbon uptake is still not clear and is currently the focus of a large body of active research (IPCC 2013; Zaehle et al. 2010; Krinner et al. 2005).

During the same period (1750–2011) that anthropogenic CO<sub>2</sub> emissions increased by more than tenfold [from about less than 1 Peta gram of carbon per year (PgC yr<sup>-1</sup>) to 10 PgC yr<sup>-1</sup>], the nitrous oxide (N<sub>2</sub>O) emissions have increased six fold (IPCC 2013; Galloway et al. 2004; Jain et al. 2009). Several studies have concluded that terrestrial carbon uptake has increased as a consequence of increased nitrogen deposition from ~10.8 TgNyr<sup>-1</sup> (Tera grams of nitrogen per year) in 1765 to ~60 TgNyr<sup>-1</sup> in the 1990's. Estimates for nitrogen-simulated increase in land carbon uptake range from 0.15–0.35 PgCyr<sup>-1</sup> (10–20 % of terrestrial net uptake; de Vries 2009; de Vries et al. 2008; Zaehle and Dalmonch 2011) to 1.0–2.0 PgCyr<sup>-1</sup> (100 % of terrestrial net uptake; de Vries 2009; de Vries et al. 2008; Holland et al. 1997; Magnani et al. 2007; Zaehle and Dalmonch 2011). However, unlike CO<sub>2</sub> fertilization, there are indications that the sensitivity of terrestrial carbon storage to increased nitrogen deposition is likely to decrease

beyond current nitrogen deposition levels (Reay et al. 2008; Bala et al. 2013).

The global mean surface temperature has increased by 0.8 °C (IPCC 2013) during the historical period (1750–2011). This historical climate warming can alter land carbon fluxes through altered temperatures, shifts in seasonal cycles, changes in precipitation and cloudiness (Bala et al. 2012; Myneni et al. 1997). Terrestrial ecosystems release carbon to the atmosphere through autotrophic (i.e., plant) and heterotrophic (primarily by microbes) respiration which are very sensitive to changes in temperature (Lloyd and Taylor 1994; Boone et al. 1998). These respiratory fluxes are projected to increase in warmer climate and hence cause decline in NPP and Total Ecosystem Carbon (TEC) (Cox et al. 2000; Cramer et al. 2001; Govindasamy et al. 2005; Joos et al. 1991; Lloyd and Taylor 1994; Matthews et al. 2005; Thompson et al. 2004; Zeng et al. 2004).

In addition to the aforementioned three factors, LULCC can also influence the biogeochemical cycles and an ecosystem's level of carbon stocks and carbon fluxes. For instance, when forests are cleared for conversion to agriculture or pasture, a very large proportion of the aboveground biomass may be burned, releasing most of its carbon rapidly into the atmosphere (Boysen et al. 2014; Pongratz et al. 2014; Houghton et al. 2012; Lawrence et al. 2012). According to IPCC (2013), the contribution of LULCC to anthropogenic CO<sub>2</sub> concentration is estimated as  $180 \pm 80$  PgC (33 % of total anthropogenic CO<sub>2</sub> emissions) in the historical period. The LULCC related CO<sub>2</sub> flux during 1980–1989 and 1990–1999 is estimated as  $1.4 \pm 0.8$  and  $1.6 \pm 0.8$  PgCyr<sup>-1</sup>, respectively. For the later decade 2000–2009 the flux has a reduced estimate of  $1.1 \pm 0.8$  PgCyr<sup>-1</sup> and for the most recent decade 2002–2011 the estimate is further reduced to  $0.9 \pm 0.8$  PgCyr<sup>-1</sup>. The reduced LULCC fluxes in the recent decades are likely due to reduction of deforestation and degradation in the tropics and promotion of afforestation/reforestation activities (Houghton et al. 2012; Le Quéré et al. 2014; IPCC 2013). LULCC influences NPP by influencing the amount and type of vegetation that might be present at any particular location. Often, LULCC replaces productive forested ecosystems with less productive grassy ecosystems, resulting in overall reduction in terrestrial carbon stocks.

Based on the above discussion, it is clear that the land biosphere productivity, uptake and release of carbon are governed by several factors such as CO<sub>2</sub>-fertilization, climatic change, nutrient availability, LULCC, fire and regrowth of forests (Ballantyne et al. 2012; Canadell et al. 2007; Friedlingstein et al. 2010; IPCC 2013; Schimel et al. 2014). The possible impacts of primary drivers such as CO<sub>2</sub>-fertilization, nitrogen deposition, climate warming and LULCC on the terrestrial ecosystem have been the subject of various global modelling studies carried out in

recent years (Gerber et al. 2013; Bala et al. 2012, 2013; Lawrence et al. 2012). However the relative contribution of these factors is still uncertain and has not been adequately explored.

Quantification of the individual effect of these factors on global scale is beyond the reach of direct laboratory and field studies and is possible only through a global model—by varying one factor at a time in a series of simulations. Recent work by Bala et al. (2013) uses the offline community land model (CLM4) and investigates the relative contribution of the first three effects. They infer from idealized simulations that terrestrial carbon losses due to warming may have been approximately compensated by effects of increased nitrogen deposition in the industrial era and hence the effect of CO<sub>2</sub>-fertilization is approximately indicative of the current increase in terrestrial carbon stock. However, Bala et al. (2013) does not include LULCC impacts and their inference is based on offline equilibrium simulations. Though offline equilibrium simulations used in that study captures the long term response and hence the long term consequences for the ecosystem, it fails to capture the climate feedbacks and transient historical changes and hence is limited in its usefulness.

Many of the other recent modelling studies (Schimel et al. 2014; Gerber et al. 2013; Bonan and Levis 2010; Jain et al. 2009) on this subject were also offline modelling studies. For example, the models used in a recent land model inter-comparison project TRENDY for investigating the terrestrial ecosystem processes during the historical period are all offline land models (Piao et al. 2013; Schimel et al. 2014; Fisher et al. 2013; Murray-Tortarolo et al. 2013). Thus, these studies do not take into account feedbacks from atmosphere and ocean on the terrestrial ecosystem processes. Further, most of these studies do not also evaluate the influence of nitrogen deposition and LULCC. Though Bala et al. (2012) used a coupled model for investigating the influence of climate warming and CO<sub>2</sub> fertilization, their simulations were equilibrium simulations and they did not study the influence of nitrogen deposition and LULCC. The main focus of the present study is to comprehensively investigate the relative significance of four factors (elevated CO<sub>2</sub> levels, atmospheric nitrogen deposition, climate change and LULCC) during the historical period (1850–2005) using a fully coupled atmosphere–ocean model. Our study is the first to address this question using a coupled model.

Unlike offline models, the coupled models account for feedbacks between the major components of the climate system: atmosphere, land, ocean and ice. They also include the transient effects of climate change. Inclusion of these feedbacks and transient effects in a coupled model frame work leads to high temporal consistency between the atmosphere, ocean and land surface processes (Anav

et al. 2015), and hence improved quantitative carbon flux and stock estimates although biases still exist in the full coupled models which are developed in the recent decades (Anav et al. 2015; Dalmonech et al. 2015; Arora et al. 2013; Brovkin et al. 2013). For instance, Anav et al. (2015) suggest that in coupled models the surface air temperature strongly depends on the surface radiation and thus surface radiation and surface air temperature co-vary in time which in-turn results in covariation for gross primary productivity and hence carbon cycle.

## 2 Model

The model used for this study is the NCAR (National Centre for Atmospheric Research) Community Earth System Model (CESM1.0.4). An overview of CESM1.0.4 and its performance relative to earlier version CCSM4 is provided in Hurrell et al. (2013). CESM1.0.4 is a coupled climate model consisting of atmosphere, land, ocean and sea-ice components that are linked through a coupler that exchanges state information and fluxes between the components. The atmospheric component of CESM1.0.4 is the Community Atmosphere Model version 5.0 (CAM5.0, Neale et al. 2010). The horizontal spatial resolution of CAM5 used here is 1.9° in latitude and 2.5° in longitude and the time step is 30 min. The number of layer in the vertical is 26. The Parallel Ocean Program version 2 (POP2) is the ocean component in CESM1.0.4 which has a total of 60 levels in the vertical with 10 m vertical resolution in the upper 155 m and coarser resolution in the deep ocean. There is no ocean carbon cycle component in the configuration of CESM1.0.4 adopted for this study.

The CESM1.0.4 sea ice component is the Community Ice Code version 4 and the Community Land Model version 4 (CLM4) is the land model (Lawrence et al. 2011; Oleson et al. 2010). The land component CLM4 succeeds CLM3.5 with revised hydrology and snow models, organic soils, and a 50 m deep soil column (Bonan and Levis 2010). CLM4 also includes carbon–nitrogen biogeochemistry with prognostic carbon and nitrogen in vegetation, litter, and soil organic matter (Randerson et al. 2009; Thornton et al. 2007, 2009). Vegetation is represented by leaf, fine root, respiring and non-respiring stem and coarse root, and storage pools. Leaf area index (LAI) is a prognostic variable in the model and leaf phenology is simulated for evergreen, seasonal deciduous and stress-deciduous plants. The heterotrophic model represents coarse woody debris, three litter pools, and four soil organic matter pools. A prognostic fire model simulates wildfire (Kloster et al. 2010).

In CLM4, nitrogen input into the ecosystem is via biological fixation and nitrogen deposition. Within the ecosystem, nitrogen is released from organic matter (gross

mineralization) in forms that can then be taken up by plants (plant uptake or assimilation) and the remaining is immobilized (immobilization). Nitrogen losses from the ecosystem are through fire loss, denitrification and leaching. The nitrogen deposition data used in CLM4 were generated by the three-dimensional chemistry transport model MOZART-2 (Model for Ozone and Related Tracers, version 2; Horowitz et al. 2003; Lawrence et al. 2012). The model uses transient LULCC annual datasets (includes land cover change along with wood harvest), diagnoses the change in plant functional type (PFT) area and adjusts carbon pools for mass conservation (Bonan and Levis 2010). For example, when PFT area decreases, the loss of carbon is distributed among litter, wood products, and a land cover conversion flux that is released immediately to the atmosphere. A portion of the wood carbon that is transferred to product pools is released to the atmosphere with 10 and 100 year lifespans. Harvesting is similarly implemented except that it does not change PFT composition and instead removes a specified fraction of the vegetation mass. Annual land cover change and harvest area used in this model were derived from the University of New Hampshire version 1 Land-Use History (LUHa.v1) historical dataset based on that of Hurtt et al. (2006).

### 3 Experiments

We perform a set of simulations to investigate the land ecosystem response to increasing atmospheric CO<sub>2</sub> levels, increasing mineral nitrogen deposition, climate warming and LULCC. Our experimental design focuses on assessing the relative importance of each of these factors to the overall land carbon budget and examining the sensitivity of terrestrial carbon pools and fluxes during 1850–2005. The global- and annual-mean atmospheric CO<sub>2</sub> concentrations and mineral nitrogen deposition and also evolution of the areal extent of tree, grass and crop PFTs during 1850–2005 that are used to drive the model are shown in Fig. 1. The model simulated climate warming and cumulative LULCC carbon fluxes for the same period are also shown in Fig. 1. Figure 2 shows the spatial distribution of climate change, nitrogen deposition and cumulative LULCC fluxes during the historical period (1850–2005).

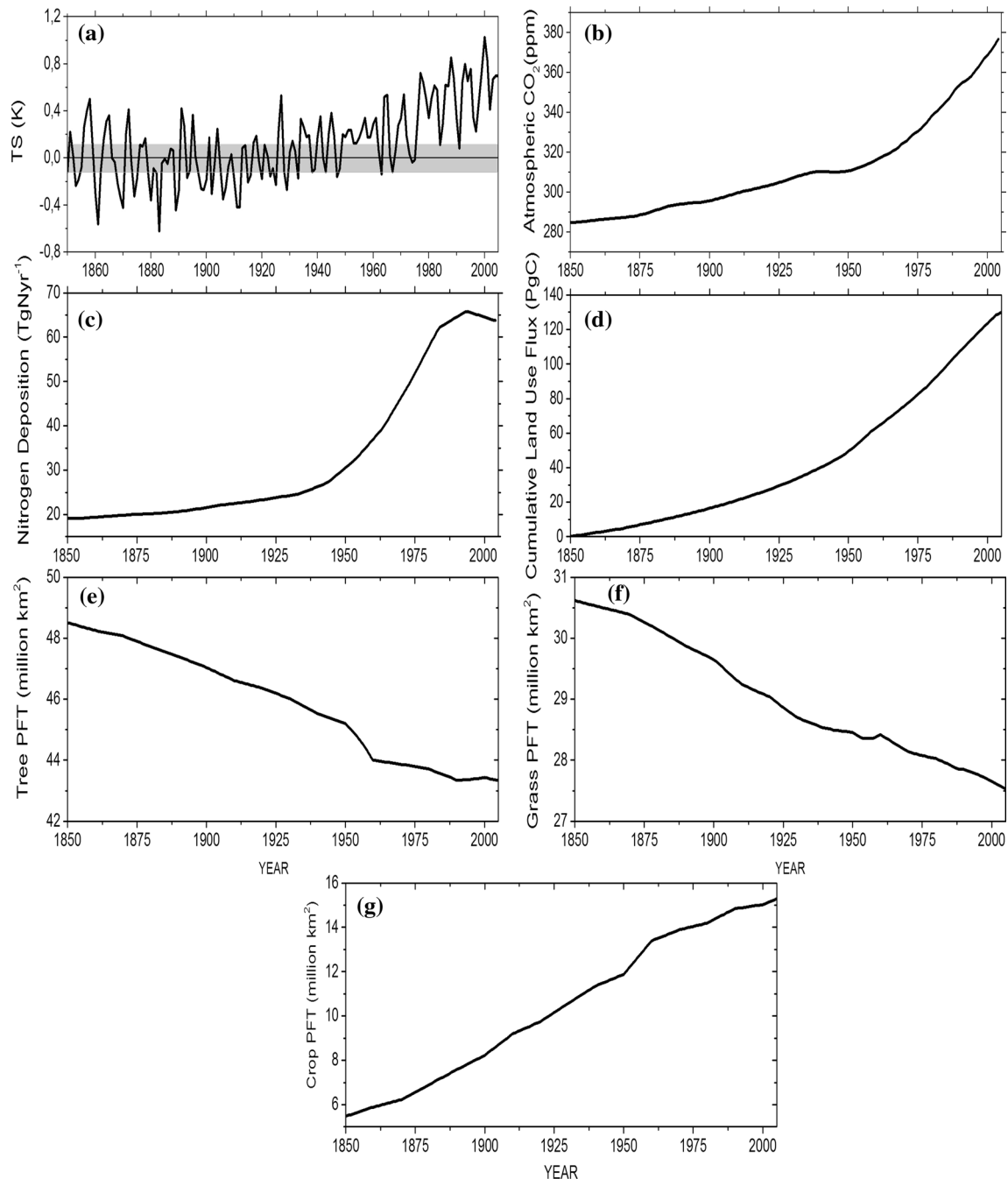
The model was spun up to a steady pre-industrial state at NCAR. The spin up procedure usually reduces the magnitude of the drift in the land surface variables such as vegetation and soil carbon. It involves forcing the model with CO<sub>2</sub> concentration, nitrogen deposition and LULCC data corresponding to the pre-industrial period and allowing it to run for several centuries. In the final spun up state, there is no significant long term trend in land component variables. Using these well spun up conditions from NCAR, we

ran the model for 50 years to verify the steady state conditions. The mean drift during these 50 years of the spin up in global soil carbon and biomass are  $-0.005$  and  $0.031$  PgCyr<sup>-1</sup>, respectively. The drift in global mean surface temperature is only  $-0.0054$  Kyr<sup>-1</sup>. These drifts are small and hence we assume that the model has attained a near-equilibrium state.

Using the initial conditions obtained at the end of our 50 year spin up, we initiated a set of six 156-year experiments for the period 1850–2005 (Table 1). The experiments differ in their treatment of forcing's-atmospheric CO<sub>2</sub> concentration, climate warming, nitrogen deposition and LULCC using either a transient dataset or a fixed pre-industrial distribution. All the experiments use the same transient historical data sets for inputs of aerosols, ozone and incoming solar radiation. Sensitivity to vegetation dynamics has not been incorporated into our century scale simulations since the effect of vegetation changes operates on a time scale of multiple centuries.

Following is a brief description of the six experiments (Table 1).

1. *HISTORICAL* Both CAM5 and CLM4 are forced by transient CO<sub>2</sub> concentrations, nitrogen deposition, non-CO<sub>2</sub> greenhouse gases, ozone, aerosols, solar variability and LULCC for the period 1850–2005.
2. *NO-CO<sub>2</sub>-FERT* same as HISTORICAL except the land model (CLM4) is forced with pre-industrial atmospheric CO<sub>2</sub> concentrations (1850, 284.72 ppm) while the atmosphere model continues to see increasing CO<sub>2</sub> concentrations. Subtraction of the NO-CO<sub>2</sub>-FERT experiment from HISTORICAL would isolate the effect of CO<sub>2</sub>-fertilization (NO-CO<sub>2</sub>-FERT refers to no “CO<sub>2</sub>-fertilization”).
3. *NO-N-CHANGE* same as HISTORICAL except nitrogen deposition is held constant at pre-industrial values (1850, 19.08 TgNyr<sup>-1</sup>). Subtraction of the NO-N-CHANGE experiment from HISTORICAL would isolate the effect of increase in nitrogen deposition (NO-N-CHANGE refers to “no change in nitrogen deposition”).
4. *NO-CO<sub>2</sub>-CHANGE* same as HISTORICAL but CO<sub>2</sub> concentrations in both atmosphere and land models are prescribed at pre-industrial levels. However, the land model still sees increasing nitrogen deposition rates. Subtraction of the NO-CO<sub>2</sub>-CHANGE experiment from NO-CO<sub>2</sub>-FERT would isolate the climate effect of CO<sub>2</sub> on the land biosphere. (NO-CO<sub>2</sub>-CHANGE refers to the fact that CO<sub>2</sub> concentrations are held constant in this simulation). Since the land surface climate could change in an experiment where CO<sub>2</sub> is changed only for radiation model, we do not perform such an experiment for assessing the climate effect.



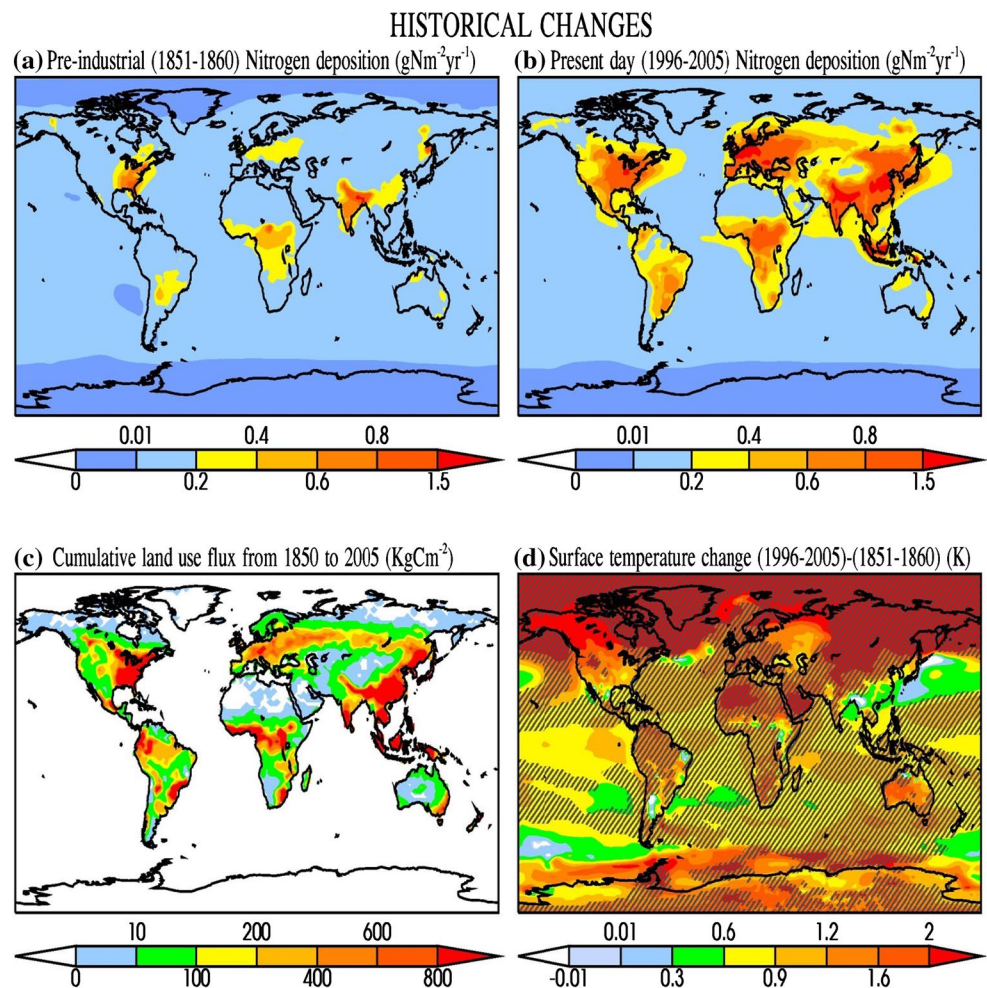
**Fig. 1** The global- and annual- mean **a** surface temperature change, **b** atmospheric CO<sub>2</sub> concentration, **c** nitrogen deposition rate, **d** cumulative land use flux, **e** area covered by tree PFTs, **f** area covered by grass PFTs and **g** area covered by crop PFTs during the historical period (1850–2005). Variables shown in **b**, **c**, and **e–g** are used

as inputs to drive the model and **a**, **d** show changes as simulated by the model. *Shading* in **(a)** represents  $\pm 1$  SDs estimated from the pre-industrial control simulation (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)

5. *NO-LULCC* same as *HISTORICAL* except no change in land cover from pre-industrial level. Wood harvesting is prescribed to be zero. Subtracting this experiment from *HISTORICAL* would isolate the effect of LULCC.
6. *NO-CO<sub>2</sub>-N-LULCC-CHANGE* same as *HISTORICAL* but CO<sub>2</sub> concentration (for both atmosphere and land models), nitrogen deposition and LULCC are fixed at pre-industrial levels. In contrast, ozone, aerosols, and solar fluxes continue to vary. Subtraction of this with *HISTORICAL* would give the combined effect of CO<sub>2</sub>



**Fig. 2** Spatial maps of **a** pre-industrial nitrogen deposition, **b** present-day nitrogen deposition, **c** cumulative land use flux and **d** annual mean surface temperature change during the historical period. Variables shown in **a**, **b** are used as input drivers to the model and **c**, **d** are the changes as simulated by the model. *Hatched areas* in **(d)** are regions where changes are statistically significant at the 95 % confidence level which is achieved when the mean change exceeds two SDs estimated from the last 100 years of the control experiment (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)



**Table 1** Summary of experiments performed in this study

Experiment name	CO <sub>2</sub> forcing to land model	CO <sub>2</sub> forcing to atmosphere model	Nitrogen deposition	LULCC	Other GHGs, ozone, aerosols and solar variability
HISTORICAL	Transient	Transient	Transient	Transient	Transient
NO-CO <sub>2</sub> -FERT	Pre-industrial	Transient	Transient	Transient	Transient
NO-N-CHANGE	Transient	Transient	Pre-industrial	Transient	Transient
NO-CO <sub>2</sub> -CHANGE	Pre-industrial	Pre-industrial	Transient	Transient	Transient
NO-LULCC	Transient	Transient	Transient	Pre-industrial	Transient
NO-CO <sub>2</sub> -N-LULCC-CHANGE	Pre-industrial	Pre-industrial	Pre-industrial	Pre-industrial	Transient

-fertilization, nitrogen deposition, climate warming and LULCC.

In addition to these 6 experiments, we also continued the 50-year spin up by 156 years to produce a pre-industrial control climate. This constant forcing control simulation is used to provide uncertainty estimates in our analysis.

The sixth experiment “NO-CO<sub>2</sub>-N-LULCC-CHANGE” is performed to test if there is any non-linearity when we sum up the four effects. We find that the combined effect (HISTORICAL minus NO-CO<sub>2</sub>-N-LULCC-CHANGE) of CO<sub>2</sub> fertilization, nitrogen deposition, climate warming and LULCC is approximately equal to the sum of four individual effects, indicating near linearity (Table 2).

**Table 2** Global mean changes in key terrestrial ecosystem variables due to CO<sub>2</sub>-fertilization, nitrogen deposition, climate warming, LULCC, the sum of these four effects and combined effect during the

last decade of simulations (1996–2005) relative to the pre-industrial period (1851–1860)

	Control experiment	CO <sub>2</sub> -fertilization	Nitrogen deposition	Climate warming	LULCC	Sum of four effects	Combined effect
NPP (PgCyr <sup>-1</sup> )	45.08 ± 0.57	2.33	2.00	0.35	−0.71	3.97	4.12
HR (PgCyr <sup>-1</sup> )	42.53 ± 0.47	1.53	1.66	0.41	−0.79	2.81	2.50
Total ecosystem carbon (PgC)	1225.48 ± 2.40	55.39	26.11	−15.05	−111.57	−45.12	−50.58
Biomass (PgC)	636.72 ± 2.60	35.99	13.76	−3.36	−108.76	−62.37	−63.05
Soil carbon (PgC)	505.17 ± 0.50	5.77	9.96	−3.13	−1.53	11.07	10.46
LAI	1.89 ± 0.01	0.11	0.09	−0.01	−0.08	0.11	0.14
Canopy transpiration (mmyr <sup>-1</sup> )	295.69 ± 3.3	−6.06	4.87	3.32	1.95	4.08	4.21
Water use efficiency (PgCmm <sup>-1</sup> )	0.22 ± 0.000	0.0154	0.0096	0.0016	−0.0059	0.0207	0.0201

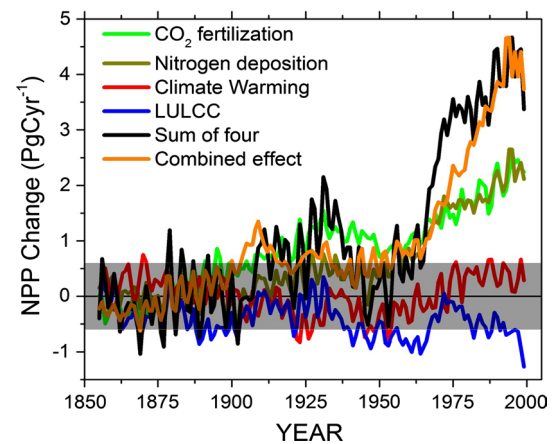
The combined effect is calculated as HISTORICAL minus NO-CO<sub>2</sub>-N-LULCC-CHANGE. The uncertainty is the ±1 SD estimated from the last 100 years of the control experiment (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)

## 4 Results

### 4.1 Trends in net primary productivity

Since NPP reflects the rate of carbon-absorbing capacity of vegetation in a terrestrial ecosystem, studying the response of NPP to the environment, can help us better understand the feedbacks between terrestrial carbon cycle and other components of the climate system. Figure 3 show the time series of change in global NPP during 1850–2005 and Fig. 4 show the spatial pattern of NPP change between 1996 and 2005 and the pre-industrial period (1851–1860) due to each of the four effects, sum of the four effects and the combined effect.

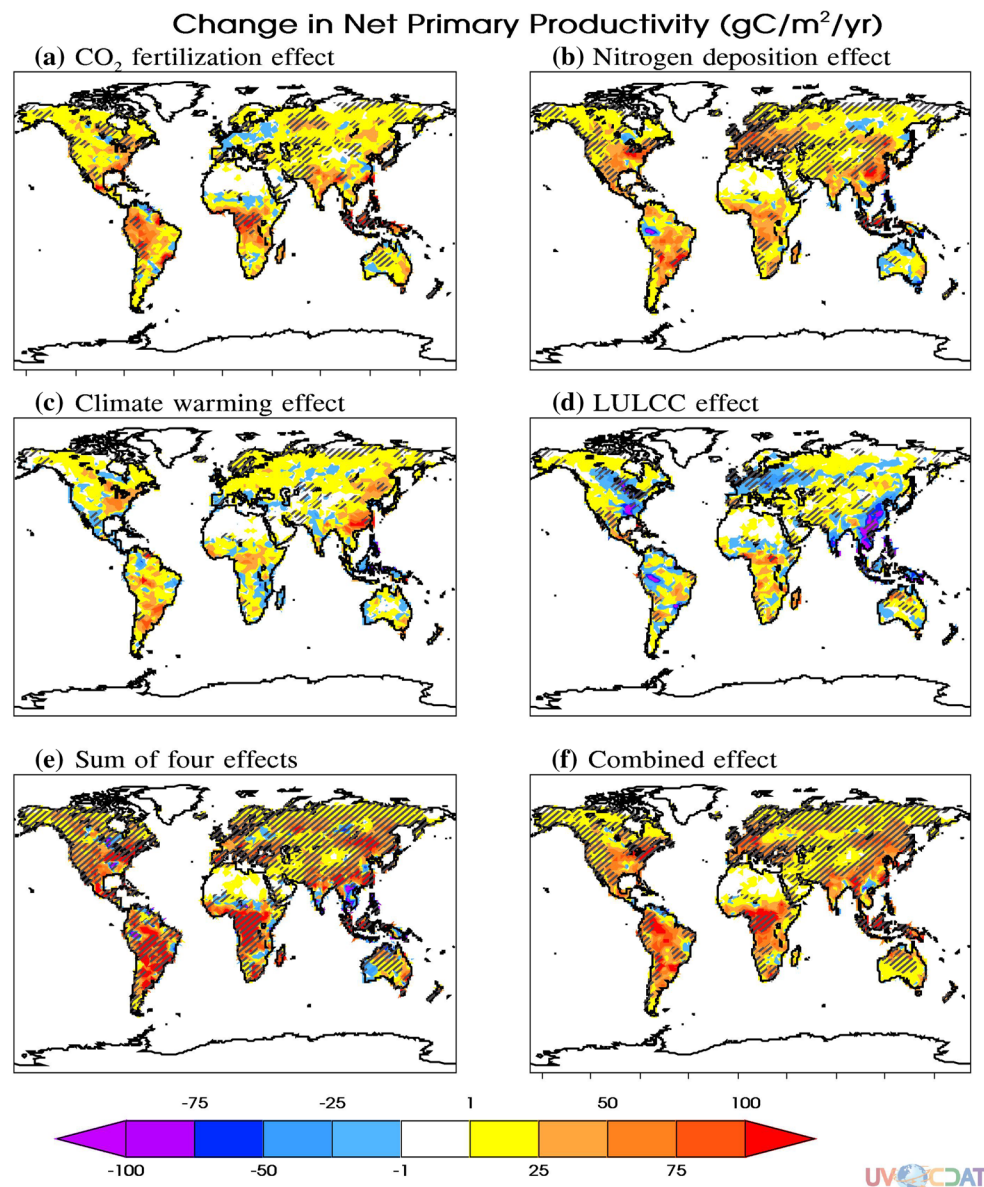
In the model, both CO<sub>2</sub>-fertilization (HISTORICAL minus NO-CO<sub>2</sub>-FERT) and nitrogen deposition (HISTORICAL minus NO-N-CHANGE) cause an increase in the global NPP throughout the historical period and their impact is similar in magnitude as shown by the overlapping time series (Fig. 3). The CO<sub>2</sub>-fertilization effect is dominant in the tropical forests of Amazon, central Africa and South East Asian forests (Fig. 4a) with the contribution on the global scale being around 50 % of the total change in NPP (~2 PgCyr<sup>-1</sup> out of ~4 PgCyr<sup>-1</sup>, Fig. 3). The effect of increased nitrogen deposition is more prominently seen in the highly industrialised regions of Europe and North America due to fossil fuel emissions and also in developing regions such as Southeast Asia where there is large agriculture activity (Fig. 4b). The change in global NPP due to climate warming is small which could be attributed to the decrease in NPP in the tropics (due to climate warming)



**Fig. 3** Simulated global- and annual- mean change in NPP (PgCyr<sup>-1</sup>) due to CO<sub>2</sub> fertilization, nitrogen deposition, climate warming, LULCC, sum of four effects and combined effect during the period 1850–2005. The combined effect is calculated as HISTORICAL simulation results minus the NO-CO<sub>2</sub>-N-LULCC-CHANGE results. A 10 year running average is applied to the original data and hence the first and last 5 years are not shown. Shading represents ±1 SD estimated from the last 100 years of the pre-industrial control simulation (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)

compensated by an increase in NPP in mid and high latitudes (Fig. 4c). In mid- and high-latitudes where the ecosystem is temperature limited, climate warming leads to longer growing season (Bala et al. 2012; Piao et al. 2007; Zhao et al. 2010; Murray-Tortarolo et al. 2013) and hence simulated NPP is increased. The decrease in simulated global NPP throughout the historical period (1850–2005)

**Fig. 4** Spatial pattern of terrestrial NPP change ( $\text{gCm}^{-2}\text{yr}^{-1}$ ) due to **a**  $\text{CO}_2$  fertilization, **b** nitrogen deposition, **c** climate warming, **d** LULCC, **e** the sum of these four effects, and **f** combined effect during the period 1996–2005 relative to the pre-industrial period (1851–1860). The combined effect is calculated as the difference between the HISTORICAL and NO- $\text{CO}_2$ -N-LULCC-CHANGE simulations. *Hatched areas* are regions where changes are statistically significant at the 95 % confidence level which is achieved when the mean change exceeds two SDs estimated from the last 100 years of the control experiment (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)



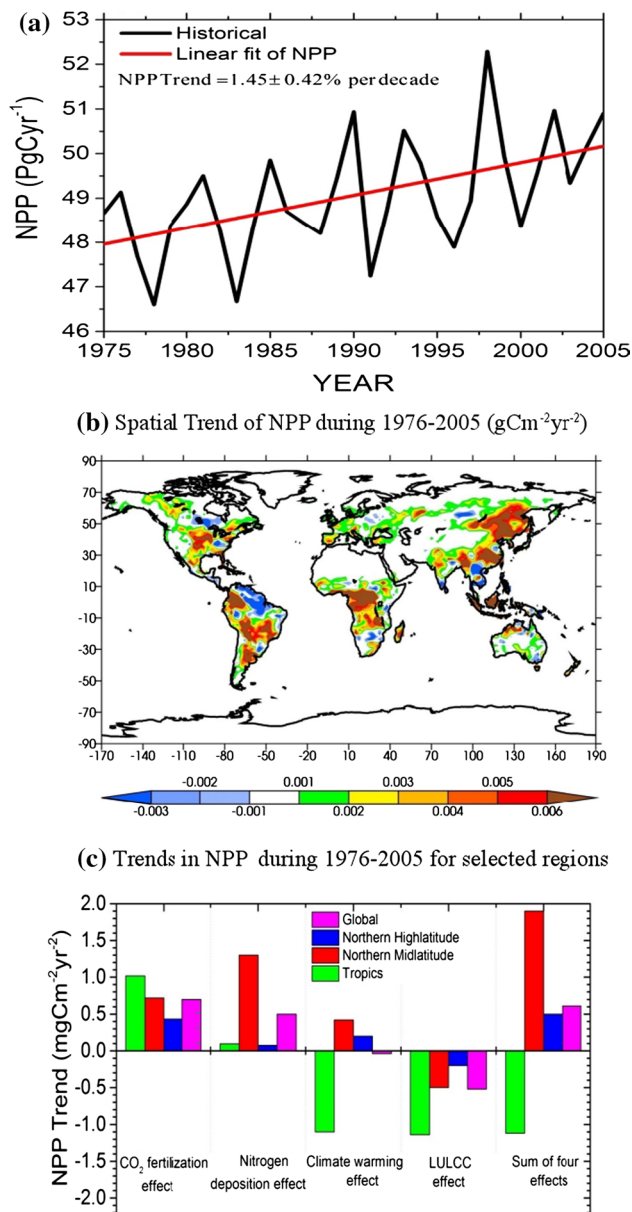
due to LULCC is likely due to historical replacement of forests with less productive plant functional types.

The global NPP increases by  $3.97 \text{ PgCyr}^{-1}$  (8.2 %, sum of the four effects) during 1996–2005 relative to the pre-industrial period (Table 2). While the direct  $\text{CO}_2$ -fertilization causes an average increase of about  $2.33 \text{ PgCyr}^{-1}$  in global NPP anthropogenic nitrogen deposition contributes about  $2.00 \text{ PgCyr}^{-1}$  of additional increase. The contribution of the effects of climate warming and LULCC on the overall NPP change is an increase of  $0.35 \text{ PgCyr}^{-1}$  and a decrease of  $0.71 \text{ PgCyr}^{-1}$ , respectively (Table 2). Thus our simulations suggest that elevated atmospheric  $\text{CO}_2$  and anthropogenic nitrogen deposition are the two major drivers for the increased terrestrial productivity. The impact of LULCC though negative was not large

enough to offset the impact of the first two factors in recent decades.

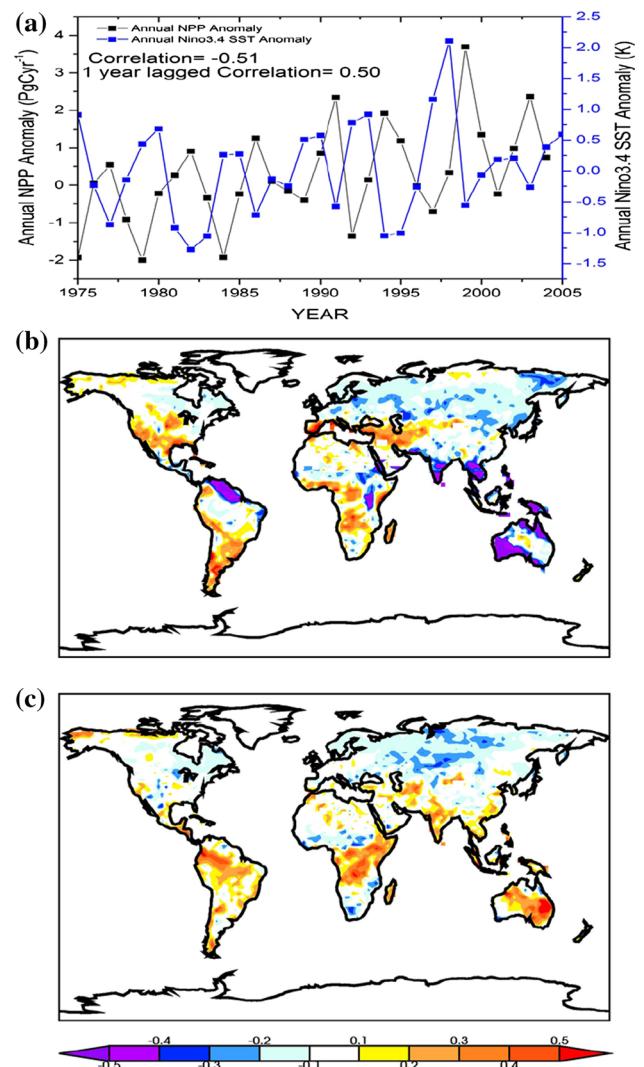
When the NPP changes in the recent decades are analysed, we find that the modelled global NPP increases by  $\sim 5 \%$  ( $2.1 \text{ PgC}$ ) between 1976 and 2005 (Fig. 5a) as simulated by the HISTORICAL simulation. This trend over 30 years is in good qualitative agreement with Nemani et al. (2003) who estimated a 6 % ( $3.4 \text{ PgC}$ ) increase in satellite-derived NPP over an 18 year period (1982–1999). NPP shows positive trends over large areas in the Northern Hemisphere such as North America, Western Europe, India, China, and central Africa but negative trends in the Southern Hemisphere in parts of South America and South Africa (Fig. 5b). These NPP trends have good agreement with Zhao and





**Fig. 5** **a** Time series of the simulated global annual NPP (PgCyr<sup>-1</sup>), **b** the spatial pattern of NPP trend (gCm<sup>-2</sup>yr<sup>-2</sup>), and **c** a comparison of CO<sub>2</sub> fertilization, nitrogen deposition, climate warming and LULCC effects on NPP trends over different regions: Tropics (20°S–20°N), northern mid latitudes (20°N–50°N), northern high latitudes (50°N–90°N) and Global (90°S–90°N). In **(a)** the uncertainty in trends is represented by the SE in the calculation of trends

Running, (2010) who found similar spatial patterns during 2000–2009 in their analysis of satellite-derived NPP. In our coupled model the simulated mean NPP is 48.8 PgCyr<sup>-1</sup> (1976–2005) which is lower than the offline model CLM4 simulated value of 57 PgCyr<sup>-1</sup> (averaged over 1973–2004, Bonan and Levis 2010). This difference is likely due to the missing feedbacks in the offline model (Anav et al. 2015).



**Fig. 6** Simulated anomalies of global NPP (**a** left y-axis), Nino3.4 SST (**a** right y-axis) and their spatial correlation (**b**) and (**c**) during 1976–2005. **b** Correlation between Nino3.4 SST and the NPP during the same year and **c** the correlation in the following year

Figure 5c shows the contribution of different regions to NPP trends during 1976–2005. As simulated in our experiments, CO<sub>2</sub>-fertilization causes positive trends in all the regions: tropics, northern mid- and high latitudes. Nitrogen deposition also causes positive trends in all regions with the mid latitudes showing the largest positive trend due to this effect. In the tropics, CO<sub>2</sub>-fertilization leads to a large positive trend when compared to nitrogen deposition (Fig. 5c). Climate warming causes a large negative trend in the tropics but positive trends in mid- and high-latitudes (Fig. 5c). LULCC leads to negative trends in NPP in all the regions (Fig. 5c). Overall the sum of the four effects is positive in mid- and high latitudes but it is negative for the tropics. The negative trends in the tropics are mainly caused by climate warming and LULCC. The simulated dominant

CO<sub>2</sub>-fertilization effect in the tropics, northern middle and high latitudes is in agreement with a recent study (Schimel et al. 2014): their results show significant tropical uptake and, combining tropical and extra-tropical fluxes, suggest that up to 60 % of the present-day terrestrial sink is caused by increasing atmospheric CO<sub>2</sub>.

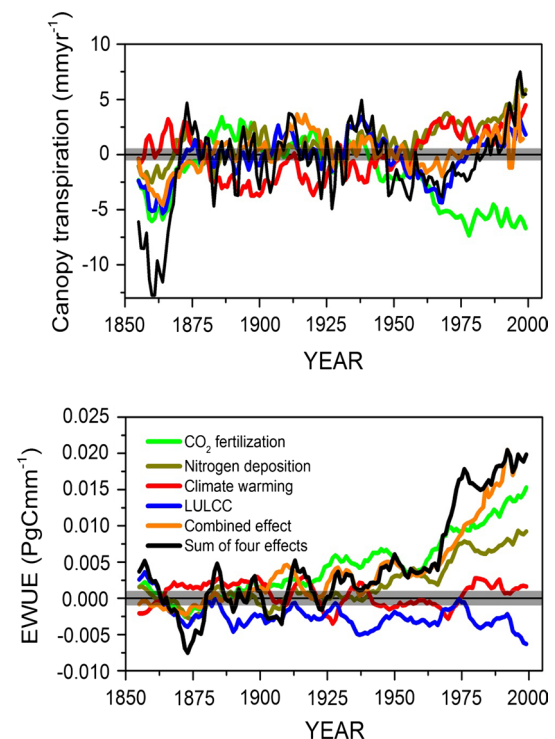
The inter-annual variability in the time series of annual global NPP in Fig. 5a are likely associated with inter-annual climate variability such as El Niño–Southern Oscillation (ENSO) as simulated by the model. We find a correlation of  $-0.52$  between simulated anomalies of annual mean Nino-3.4 sea surface temperature (SST) (as defined by Trenberth 1997) and simulated annual mean NPP (Fig. 6a) indicating declined global vegetation productivity in ENSO years. During the ENSO years, the model simulated NPP declines in Indonesia, India, Australia, East Asia, northern Eurasia and North America and the Amazon (Fig. 6b).

Although the exact link between ENSO and regional NPP has large uncertainty, evidence from atmospheric inversion and ocean models (Le Quéré et al. 2003) indicates that the inter-annual variation of terrestrial ecosystem carbon processes has some correlation with ENSO events. Our simulated result is in agreement with the past studies that have shown negative NPP anomaly during El Niño and positive anomaly during La Niño events (Nemani et al. 2003; Hashimoto et al. 2004; Cao et al. 2002). As shown in Fig. 6a, the correlation becomes positive ( $+0.5$ ) when Nino3.4 SST anomalies are correlated with global NPP of the following year. In the year following ENSO, the tropical vegetation in Indonesia, India, East Asia, Australia, central Africa and the Amazon show increased productivity but northern Eurasia shows continued declines in productivity (Fig. 6c).

#### 4.2 Ecosystem water use efficiency (EWUE)

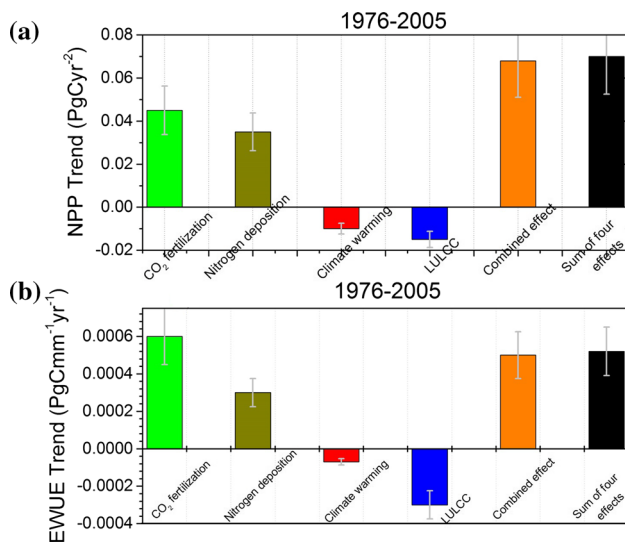
The global ecosystem annual mean water use efficiency is an indicator of adjustment of vegetation productivity to plant transpiration. EWUE is defined as the ratio of annual gross primary productivity to the annual evapotranspiration and it is widely used in many previous studies (Huang et al. 2015; Zhu et al. 2011; Beer et al. 2009; Hu et al. 2008; Ponton et al. 2006). Similar to NPP discussed above, CO<sub>2</sub>-fertilization is the major driver for the increase in EWUE followed by nitrogen deposition and climate warming during the historical period (Fig. 7) which is in agreement with a recent modelling study (Huang et al. 2015). However, LULCC leads to a decrease in EWUE throughout the historical period in our simulations.

During the recent three decades (1976–2005), our simulation show that CO<sub>2</sub>-fertilization and nitrogen deposition contribute significantly to positive trends in NPP and EWUE but climate change has very little effect (Fig. 8).



**Fig. 7** Time series of changes in global- and annual-mean Canopy transpiration ( $\text{mm yr}^{-1}$ ) and EWUE ( $\text{PgCmm}^{-1}$ ) due to CO<sub>2</sub>-fertilization, nitrogen deposition, climate warming, LULCC, sum of these four effects, and combined effect during the historical period 1850–2005. The combined effect is calculated as the difference between the HISTORICAL and NO-CO<sub>2</sub>-N-LULCC-CHANGE simulations. Shading represents  $\pm 1$  SD estimated from the last 100 years of the pre-industrial control simulation (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)

The LULCC contributes significantly to negative trends in NPP and EWUE (Fig. 8). Overall the sum of the four effects in our simulations is a positive NPP trend of  $0.07 \text{ PgCyr}^{-2}$  and EWUE trend of  $0.0005 \text{ PgCmm}^{-1}\text{yr}^{-1}$  in the recent three decades (Fig. 8). In the last decade (1996–2005) relative to the pre-industrial period, except LULCC all the other three factors contribute to increased NPP and water use efficiency (Table 2). Under CO<sub>2</sub> fertilization we simulate a decrease in canopy transpiration (Fig. 7; Table 2) which is mainly due to CO<sub>2</sub> physiological effect (less widely opened plant stomata under elevated CO<sub>2</sub> concentration, Collatz et al. 1992; Bala et al. 2012). The increase in LAI is likely to partly offset this decrease. Under climate change the evaporative demand increases because of warmer temperatures. The increase in LAI is likely to result in increased transpiration in the nitrogen deposition case. For LULCC, we simulate an increase in canopy transpiration during the last decade (Fig. 7; Table 2), though forest cover has decreased in recent decades (Fig. 1e). It is likely that the altered climate due to LULCC results in larger mean evaporative demand. The increase in canopy



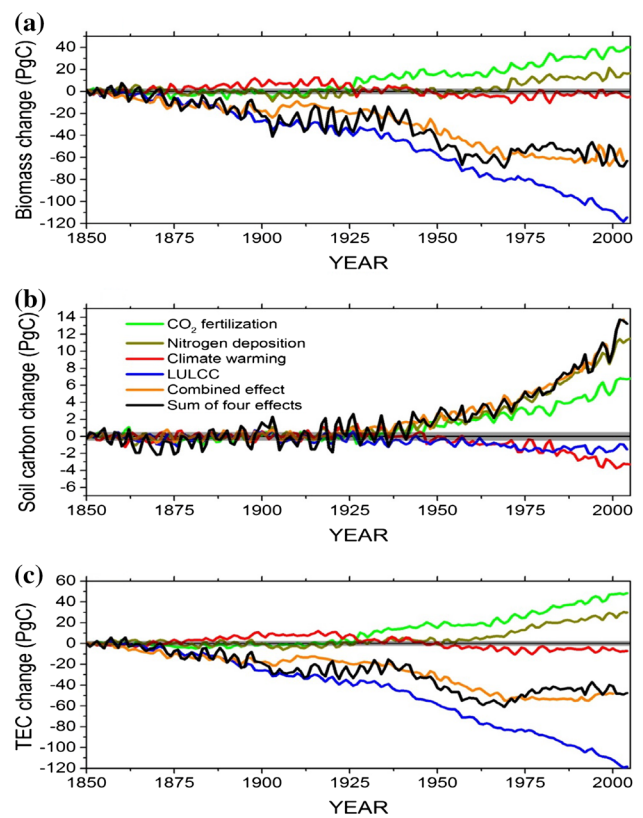
**Fig. 8** Trends in global and annual **a** NPP (PgCyr<sup>-2</sup>) and **b** EWUE (PgCmm<sup>-1</sup>yr<sup>-1</sup>) due to CO<sub>2</sub> fertilization (HISTORICAL minus NO-CO<sub>2</sub>-FERT), nitrogen deposition (HISTORICAL minus NO-N-CHANGE), climate warming (NO-CO<sub>2</sub>-FERT minus NO-CO<sub>2</sub>-CHANGE), LULCC effects (HISTORICAL minus NO-LULCC), sum of these four, and combined effects (HISTORICAL minus NO-CO<sub>2</sub>-N-LULCC-CHANGE) during the last three decades (1976–2005). The trends are calculated using linear regression. Uncertainty is represented by the SE in the calculations of trends

transpiration under LULCC needs further investigations and we intend to study this issue in a future work.

### 4.3 Changes in land carbon stocks

Figure 9 shows the simulated response of the global terrestrial carbon pools (soil carbon, total biomass and TEC) resulting from changes in CO<sub>2</sub> concentration, nitrogen deposition, climate warming and LULCC during the period 1850–2005. Both CO<sub>2</sub>-fertilization and nitrogen deposition increase the size of land carbon pools, with the effect of increased atmospheric CO<sub>2</sub> being more pronounced than the effect of nitrogen deposition in the case of total biomass carbon and TEC (Fig. 9). The relative importance of these two factors is opposite in case of soil carbon in our simulations i.e., the nitrogen deposition effect is larger in increasing the soil carbon stock than the CO<sub>2</sub>-fertilization effect. This is because additional nitrogen deposition impedes organic matter decomposition, reduces soil respiration and thus enhanced soil carbon stock, especially in temperate forest soils where nitrogen is not limiting microbial growth (Janssens et al. 2010).

The overall effect of climate warming during the 20<sup>th</sup> century reduces the land carbon sink. This is largely due to increased respiratory fluxes (autotrophic and heterotrophic) in warmer climates (Cox et al. 2000; Cramer et al. 2001; Lloyd and Taylor 1994; Govindasamy et al. 2005). Our



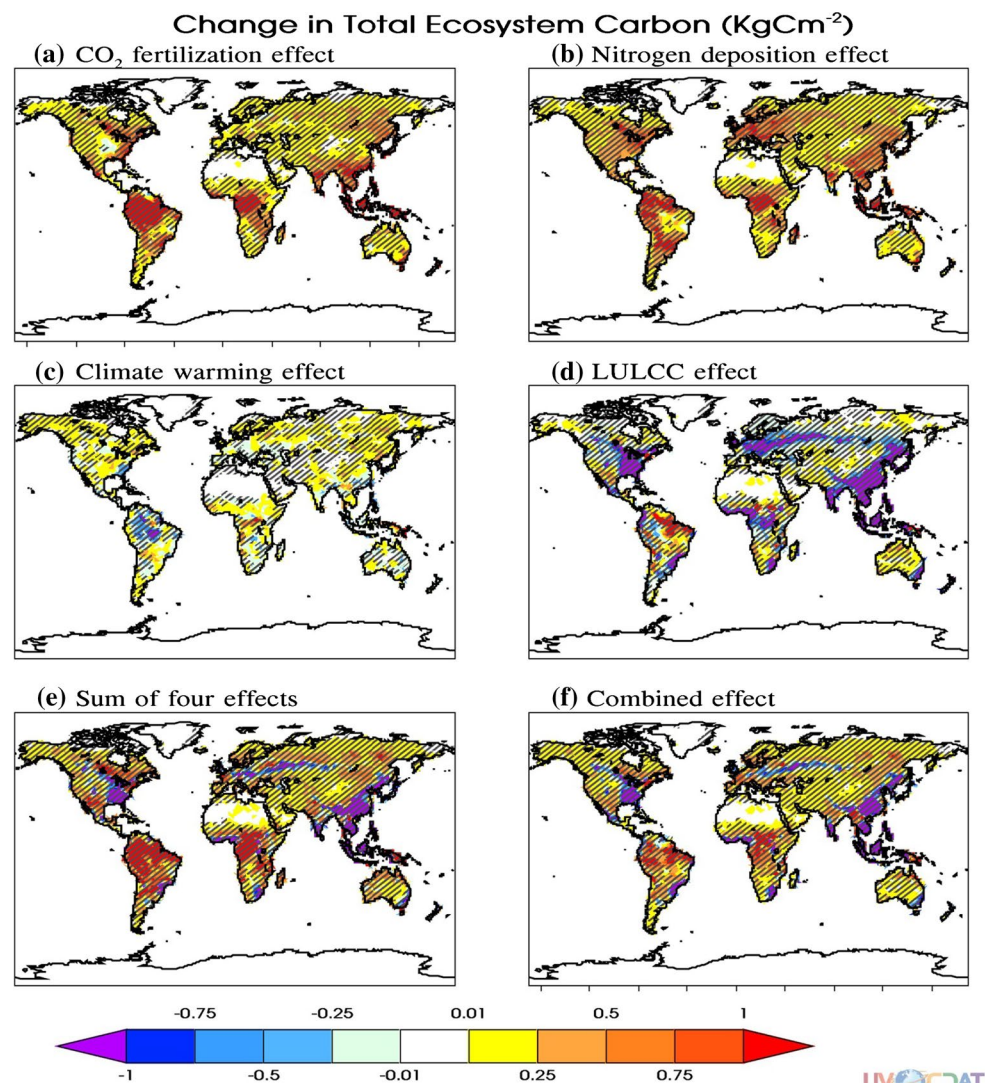
**Fig. 9** Time series of changes in global- and annual-mean **a** biomass, **b** soil carbon, **c** total ecosystem carbon (TEC) due to CO<sub>2</sub>-fertilization, nitrogen deposition, climate warming, LULCC, sum of these four effects, and combined effect (PgC) during the period 1850–2005 as simulated by the model. The combined effect is calculated as the difference between the HISTORICAL and NO-CO<sub>2</sub>-N-LULCC-CHANGE simulations. Shading represents  $\pm 1$  SD estimated from the last 100 years of the pre-industrial control simulation (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)

simulations show that LULCC causes a considerable loss of TEC with biomass decline being the largest contributor. Soils carbon accounts for a very small portion of this TEC decrease. The net effect of the four factors on soils is a gain of about 11.1 PgC by 1996–2005 relative to the pre-industrial period (Table 2). During the same period, the biomass and total ecosystem loose carbon by 62.37 and 45.12 PgC respectively. As for the individual contributions of the four factors, LULCC and climate warming cause declines of 111.57 and 15.05 PgC in TEC while CO<sub>2</sub>-fertilization and nitrogen deposition cause gains of 55.39 and 26.11 PgC, respectively. The increase in heterotrophic respiration is larger than the increase in global NPP for climate warming (Table 2) which explains the loss in TEC due to climate warming during the historical period. The net loss due to the sum of these four effects is 45.12 PgC (Table 2).

Changes in TEC in the last 10 years of simulations (1996–2005) relative to the pre-industrial period



**Fig. 10** Spatial pattern of total ecosystem carbon change ( $\text{KgCm}^{-2}$ ) due to **a**  $\text{CO}_2$  fertilization, **b** nitrogen deposition, **c** climate warming, **d** LULCC, **e** the sum of these four effects, and **f** combined effect during the period 1996–2005 relative to the pre-industrial period (1851–1860). The combined effect is calculated as the difference between the HISTORICAL and NO- $\text{CO}_2$ -N-LULCC-CHANGE simulations. *Hatched areas* are regions where changes are statistically significant at the 95 % confidence level which is achieved when the mean change exceeds two SDs estimated from the last 100 years of the control experiment (changes are statistically assessed relative to the variability in the unforced pre-industrial climate state)



(1851–1860) show distinct regional patterns (Fig. 10). These patterns resemble the respective spatial pattern of changes in NPP (Fig. 4). In response to  $\text{CO}_2$ -fertilization effect, Amazon and central African forests gain TEC larger than  $1 \text{ KgCm}^{-2}$  and gains of up to  $0.6 \text{ KgCm}^{-2}$  in Southeast Asia and temperate forests of Eurasia and North America (Fig. 10a) are simulated. The forest regions in the tropics and more industrialized regions North America and Europe show increases in TEC for nitrogen deposition (Fig. 10b). Climate warming has little effect on TEC in most regions except in some parts of Amazon where there is a decline of about  $0.9 \text{ KgCm}^{-2}$  (Fig. 10c). The effect of historical LULCC is a large decline in TEC in present-day cropland areas in India, Southeast Asia, Europe and North America (Fig. 10d).

The TEC change for the historical period can be calculated by integrating Net Ecosystem Exchange (NEE) from 1850 to 2005 in the “HISTORICAL” simulation. NEE is the net carbon exchange between the ecosystem and the

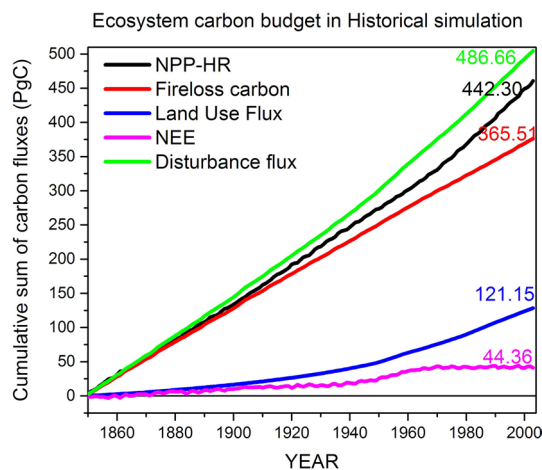
atmosphere, which comprises of mainly two terms as given below in Eq. (1):

$$\text{NEE} = \text{disturbance flux} - \text{NEP}, \quad (1)$$

where disturbance flux is land use flux (includes wood harvest carbon loss) plus fire loss carbon and NEP represents net ecosystem productivity (NPP-HR). HR is the heterotrophic respiration by the ecosystem. Here a positive value of NEE indicates a source of carbon to atmosphere from the land biosphere.

Figure 11 shows the cumulative NEE, disturbance flux and NEP during the historical period (1850–2005). We find that the cumulative NEE ( $44.36 \text{ PgC}$ ) is nearly equal to the difference between cumulative disturbance flux (fire loss carbon of  $365.51 \text{ PgC}$  plus LULCC flux of  $121.15 \text{ PgC}$ ) and cumulative NEP ( $442.30 \text{ PgC}$ ). The positive value of NEE ( $\sim 44.36 \text{ PgC}$ ) indicates that the ecosystem acts as a source of carbon to the atmosphere during the entire period (1850–2005). This cumulative NEE ( $44.36 \text{ PgC}$ ) is about





**Fig. 11** Time series of the budget for the cumulative net ecosystem exchange (NEE) ( $\text{PgCyr}^{-1}$ ) during the period 1850–2005 as simulated by the model in the HISTORICAL experiment. A positive value indicates a flux of carbon from land to the atmosphere. For instance, the land has been a source of carbon to the atmosphere (cumulative NEE is positive) during the historical period. The numbers at the right of each line refers to the corresponding cumulative flux in year 2005. The cumulative NEE in 2005 is positive (land is a source of CO<sub>2</sub> to the atmosphere) because the cumulative disturbance flux is larger than the cumulative net ecosystem productivity

the same as TEC loss (45.12 PgC) due to sum of four factors discussed above for the historical period. The cumulative NEE in 2005 is positive (land is a source of CO<sub>2</sub> to the atmosphere) because the cumulative disturbance flux is larger than the cumulative net ecosystem productivity (Fig. 11). This result for our HISTORICAL simulation is in agreement with multi-model mean ensemble of CMIP5 (Friedlingstein et al. 2014) and also consistent with another study that used an earlier version of the same model (CCSM4, Lawrence et al. 2012). But the magnitude of our simulated value (44.36 PgC) is larger than the value estimated in CMIP5 ( $26 \pm 36$  PgC, Friedlingstein et al. 2014) and smaller than Lawrence et al. (2012) which simulate a cumulative NEE flux of about 64.5 PgC.

The global carbon budget studies (Pan et al. 2011; Le Quéré et al. 2014; Ballantyne et al. 2012; Canadell et al. 2007; Beck and Goetz 2011) indicate that the terrestrial biosphere is a sink for carbon in the recent decades. We estimate the changes in TEC between the early 1970s and early 2000s in our simulations. For this recent 3 decades, we calculate a 24 PgC increase due to CO<sub>2</sub>-fertilization, 17.5 PgC due to nitrogen deposition and 0.16 PgC due to climate warming. LULCC causes a decline of about 31 PgC and the net TEC increase is about 10 PgC. Thus our simulations of changes in TEC for the recent decades are *qualitatively* in agreement with recent global carbon budget estimates and further they suggest that the CO<sub>2</sub>-fertilization and nitrogen deposition are the main drivers for land being a sink for carbon in the recent decades.

#### 4.4 Carbon storage sensitivity

The carbon storage sensitivity is an important parameter for quantifying the feedbacks between the terrestrial biosphere and changes in global environmental factors. In the past, 3 such parameters have been defined (Bala et al. 2013) describing the sensitivity of the total ecosystem carbon stock to changes in CO<sub>2</sub>, climate warming and nitrogen deposition. The carbon storage sensitivity over land to CO<sub>2</sub>,  $\beta$  (Bala et al. 2012; Friedlingstein et al. 2006) is defined as the change in TEC associated with a unit change in atmospheric CO<sub>2</sub>. The carbon storage sensitivity over land to climate warming ( $\gamma$ ) is defined as the change in TEC associated with a unit change in surface temperature and carbon storage sensitivity over land to nitrogen deposition ( $\delta$ ) as the change in TEC associated with unit change in atmospheric nitrogen deposition rate:

$$\beta = \Delta \text{TEC} / \Delta C_a$$

$$\gamma = \Delta \text{TEC} / \Delta T$$

$$\delta = \Delta \text{TEC} / \Delta N$$

where  $C_a$ ,  $T$  and  $N$  here refer to atmospheric CO<sub>2</sub> concentrations, global-mean surface temperature and atmospheric nitrogen deposition rate.

The values of these three parameters are estimated as the change in TEC between the last decade (1996–2005) and the pre-industrial period. The values of  $\beta$  and  $\gamma$  are found to be 0.50 PgC per ppm and  $-20.33$  PgC per K, respectively. A positive value of  $\beta$  for the global domain suggests that each unit increase in the atmospheric CO<sub>2</sub> concentration leads to an increases in TEC in the absence of climate warming, nitrogen deposition and LULCC effects. In contrast,  $\gamma$  being negative is indicative of the reduction in TEC solely due to an increase in temperature. Also, a positive  $\beta$  suggests a negative “carbon-concentration” feedback which acts to remove CO<sub>2</sub> from the atmosphere via enhanced uptake of CO<sub>2</sub> while a negative  $\gamma$  indicates a positive “carbon-temperature” feedback which acts to increase CO<sub>2</sub> flux to the atmosphere as temperatures warms (Boer and Arora 2009).

The value of  $\delta$  is calculated as the ratio of TEC changes in the last 10 years (1996–2005) relative to the pre-industrial period and the change in mean nitrogen deposition rate between the two periods. We estimate a  $\delta$  of 0.59 PgC per  $\text{TgNyr}^{-1}$  in our simulations. The value of  $\delta$  has been estimated in the past by Bala et al. (2013) which estimates a range of  $\delta$  values from a set of equilibrium simulations ( $2.47$ – $3.41$  PgC per  $\text{TgNyr}^{-1}$ ) and these values are larger than our present value. The large difference in  $\delta$  values estimated in this study and between Bala et al. (2013) is likely due to nature of the scenarios in the two studies—the

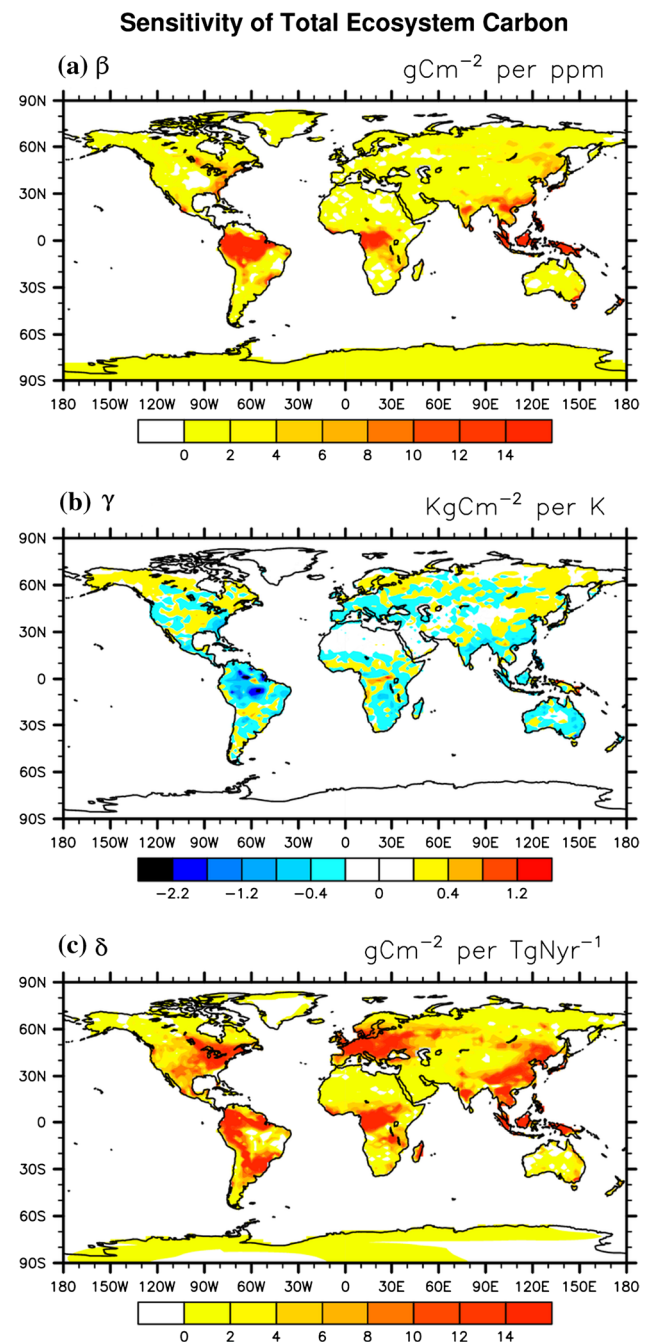
present estimate relates to a transient scenario and Bala et al. (2013) considered equilibrium simulations. This is corroborated by the fact that the values of  $\beta$  and  $\gamma$  estimated in this present study are in close agreement with many previous transient simulations (Thornton et al. 2009; Bonan and Levis 2010; Zaehle et al. 2010) but not in agreement with the equilibrium values ( $\beta = 2.2\text{--}2.7$  PgC per ppm and  $\gamma = -152$  to  $-182$  PgC per K) of Bala et al. (2013). The values of sensitivity parameters  $\beta$ ,  $\gamma$  and  $\delta$  in the transient scenario are smaller than *equilibrium* simulations because of lags in terrestrial ecosystem response (Jones et al. 2009, 2010; Bala et al. 2012, 2013).

Figure 12 shows the spatial patterns of  $\beta$ ,  $\gamma$  and  $\delta$  during 1996–2005 relative to pre-industrial period. The sensitivity of TEC is larger in the thickly vegetated regions: Amazon, central Africa, India, North eastern North America and Southeast Asia.  $\beta$  and  $\delta$  are positive over all regions due to  $\text{CO}_2$  fertilization and nitrogen deposition (Fig. 12a, c), but  $\gamma$  is negative in most of the vegetated regions of the tropics and is positive in high-latitudes and some parts of tropics (Fig. 12b). The negative value of  $\gamma$  is associated with a decrease in NPP (Fig. 4c) and the consequent decline in vegetation and soil carbon. The positive value of  $\gamma$  in high-latitudes forests is mainly due to longer growing season as discussed in Sect. 4.1. Though  $\gamma$  is negative in Amazon ( $\sim -2$   $\text{KgCm}^{-2}$  per K), the positive value in the southeastern region adjacent to Amazon is likely because of increased rainfall under climate warming. This is consistent with Bala et al. (2012), where they find increased rainfall in that region under climate warming and hence increased NPP (Fig. 4c). We also simulate positive values of  $\gamma$  ( $\sim 0.4$   $\text{KgCm}^{-2}$  per K) in central Africa and East Asia (Fig. 12b).

## 5 Discussion and conclusions

We have investigated the impact of four important factors ( $\text{CO}_2$ -fertilization, climate warming, nitrogen deposition and LULCC) in driving the global terrestrial carbon cycle during the historical period using transient simulations from a fully coupled climate model. Our simulations suggest that the global NPP increase during the historical period can be largely attributed to  $\text{CO}_2$ -fertilization effect with anthropogenic nitrogen deposition making equally important contribution. Further, our model simulations also indicate that the positive trends in satellite-derived NPP (Nemani et al. 2003; Running et al. 2004; Donohue et al. 2013) in recent decades is likely driven by  $\text{CO}_2$ -fertilization and nitrogen deposition.

Though vegetation productivity has increased in the recent decades, we find the global land has overall lost carbon during the historical period. This is because the



**Fig. 12** Spatial pattern of total ecosystem carbon sensitivity to **a**  $\text{CO}_2$  fertilization ( $\beta$ ,  $\text{gCm}^{-2}$  per ppm), **b** climate warming ( $\gamma$ ,  $\text{KgCm}^{-2}$  per K) and **c** nitrogen deposition ( $\delta$ ,  $\text{gCm}^{-2}$  per  $\text{TgNyr}^{-1}$ ) during the period 1996–2005 relative to pre-industrial state

cumulative disturbance fluxes (fire plus LULCC fluxes) are larger than the cumulative NEP during this period. Our results are qualitatively in agreement with a recent model inter-comparison project study (Friedlingstein et al. 2014) and also with another study that used an earlier version of CESM (Lawrence et al. 2012). In our simulations, the individual contributions to the change in total ecosystem

carbon (TEC) by CO<sub>2</sub>-fertilization, nitrogen deposition, climate warming and LULCC are 55.51 PgC, 25.9 PgC, −15.05 PgC and −111.57 PgC, respectively, during the same period (1850–2005). Thus the reduction in land carbon stocks due to the sum of the four effects is around 45.12 PgC and LULCC dynamics is the major driver for this source of carbon from land to the atmosphere during the historical period.

However, during the recent three decades (between the early 1970s and early 2000s), simulated TEC increases by about 10 PgC (land is a sink) which is *qualitatively* in agreement with recent global carbon budget estimates (Baltantyne et al. 2012; Canadell et al. 2007; Beck and Goetz 2011; Fensholt et al. 2012) which infer indirectly that land is net sink for carbon in recent decades. In our simulations, this 10 PgC increase is the result of a 24 PgC increase due to CO<sub>2</sub>-fertilization, a 17.5 PgC increase due to nitrogen deposition and a 0.16 PgC increase due to climate warming. LULCC causes a decrease of about 31 PgC. Thus our simulations suggest that the CO<sub>2</sub>-fertilization and nitrogen deposition are the main drivers for land being a sink for carbon in the recent decades.

There are many unaccounted effects associated nitrogen deposition on land in our modelling study. Nitrogen, though being an essential element for plant growth, can lead to reduced plant productivity if present in excess. Often areas of high nitrous oxide emissions also have high ozone concentration which is likely to suppress growth of plants (Chameides et al. 1994). Such effects associated with high nitrogen loads would dampen the positive effect of increased nitrogen availability on plant productivity. These effects are not included in the model. This model also lacks the representation for other essential elements like phosphorus.

The soil carbon which is a major reservoir of terrestrial carbon is underestimated in our simulations. The conventionally accepted value of the soil carbon pool size is around 1500 PgC (Bonan and Levis 2010) while it is only 505 PgC in our control simulation (Table 2). However, since we have focussed only on changes and differences in carbon stocks with respect to the pre-industrial period, this limitation is likely to have only small influence on our results. However, biases of this huge magnitude are not desirable and future model improvements should address this bias.

CLM4 (like many other global land models) does not have representation of high latitude permafrost carbon reservoir which contains large quantity of organic carbon matter because of low temperatures in the high latitudes. As global temperature increases due to climate change, the thawing of permafrost could result in microbial decomposition of frozen organic carbon and eventually this region could become a large source of CO<sub>2</sub> (Schuur et al. 2008,

2009). This positive feedback of soil carbon respiration to global warming scenario is not simulated by CLM4. However this effect will not affect our HISTORICAL simulation results because permafrost feedback operates on century to millennial timescales (Schuur et al. 2015). Another limitation of this study is that it does not include the ocean carbon cycle, which is a very important part of global carbon cycle. The changes in ocean carbon cycle and the consequent changes in atmospheric CO<sub>2</sub> can potentially change the quantitative results of this work but unlikely to change the key conclusions.

This study has investigated only the four dominant drivers of the terrestrial carbon cycle and it does not account for the contributions made by other factors like non-CO<sub>2</sub> gases, ozone, aerosols and solar variability. The effect of these factors on land carbon uptake is likely to be small because as discussed in Sect. 4 the changes in terrestrial carbon stock in our “HISTORICAL” simulations are nearly accounted for by the sum of four effects investigated in this study.

Our present study and its findings assume significance due to the fact that we have used a full coupled model to study the transient response of the land carbon cycle for the historical period while most of the previous studies (Bala et al. 2013; Bonan and Levis 2010; Thornton et al. 2007) have used offline models which may have missed important feedbacks and transient effects. The use of a coupled model is likely to result in better quantitative estimates. The missing feedbacks and transient effects in offline models could cause overestimation of the carbon fluxes of terrestrial ecosystem (Anav et al. 2015). For instance, the magnitude of the sensitivity parameters,  $\beta$ ,  $\gamma$  and  $\delta$  are overestimated in a recent offline modelling study that used the same land model (Bala et al. 2013). A detailed investigation of the possible causes for the terrestrial carbon uptake due to temporal consistency in coupled models is beyond the scope of this paper and will be the subject of future paper.

The full coupled model results obtained in this study are from single model. Though our results are qualitatively consistent with many previous studies, the magnitude of ecosystem carbon fluxes and stocks may differ from model to model. Therefore, a multi-model analysis will be required to better quantify the ecosystem carbon stocks and fluxes and to provide uncertainty estimates.

The sensitivity parameters  $\beta$  and  $\gamma$  estimated in our simulations and in previous modelling studies span a wide range of values (Bala et al. 2012: Table 2) which suggests large uncertainties in model-based estimates of the climate- and concentration-carbon cycle feedbacks. Our understanding of nutrient limitations on carbon cycle is limited and models, for example, lack of carbon-phosphorous interactions (Dolman et al. 2010; Reay et al. 2008; Zaehle and Dalmonech 2011). The uncertainties in terrestrial carbon



cycle can be reduced through expanded network of observations and by representing the processes that are missing in current generation of land models. Hence, more observational and multi-model inter-comparisons will be required to provide more confidence in our understanding of the terrestrial carbon dynamics.

In summary, the main message from this modelling study is that increased atmospheric CO<sub>2</sub> and anthropogenic nitrogen deposition are the two most important factors that are responsible for the enhanced terrestrial vegetation productivity in recent years. These two factors are also likely driving the terrestrial carbon sink in the recent decades. However, when the entire duration of the historical period (1850–2005) is considered, there has been a cumulative loss of carbon from land which has been driven primarily by LULCC.

**Acknowledgments** We thank the funding from Department of Science and Technology under the Grant DST0948. Dr. Devaraju is supported by the Divecha Center for Climate Change. Computations were carried out at CAOS HPC facility funded by FIST, Department of Science and Technology and Divecha Center for Climate Change.

## References

- Ahlstrom A, Schurgers G, Arneth A, Smith B (2012) Robustness and uncertainty in terrestrial ecosystem carbon response to CMIP5 climate change projections. *Environ Res Lett* 7(044008):1–9
- Anav A, Friedlingstein P, Beer C, Ciais P, Harper A, Jones C, Murray-Tortarolo G, Papale D, Parazoo NC, Peylin P et al (2015) Spatio-temporal patterns of terrestrial gross primary production: a review. *Rev Geophys*. doi:[10.1002/2015RG000483](https://doi.org/10.1002/2015RG000483)
- Arneth et al (2010) Terrestrial biogeochemical feedbacks in the climate system. *Nat Geosci* 3:525–532. doi:[10.1038/ngeo905](https://doi.org/10.1038/ngeo905)
- Arora VK et al (2013) Carbon-concentration and carbon-climate feedbacks in CMIP5 earth system models. *J Clim* 26:5289–5314
- Bala G, Krishna S, Devaraju N, Cao L, Caldeira K, Nemani R (2012) An estimate of equilibrium sensitivity of global terrestrial carbon cycle using NCAR CCSM4. *Clim Dyn*. doi:[10.1007/s00382-012-1495-9](https://doi.org/10.1007/s00382-012-1495-9)
- Bala G, Devaraju N, Chaturvedi RK, Caldeira K, Nemani R (2013) Nitrogen deposition: how important is it for global terrestrial carbon uptake? *Biogeosciences* 10:7147–7160
- Ballantyne AP, Alden CB, Miller JB, Tans PP, White JWC (2012) Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature* 488(7409):70–72. doi:[10.1038/nature11299](https://doi.org/10.1038/nature11299)
- Beck PS, Goetz SJ (2011) Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. *Environ Res Lett* 6(4):045501
- Beer C, Reichstein M et al (2009) Temporal and among-site variability of inherent water use efficiency at the ecosystem level. *Global Biogeochem Cycles* 23:GB2018. doi:[10.1029/2008GB003233](https://doi.org/10.1029/2008GB003233)
- Bodman RW et al (2013) Uncertainty in temperature projections reduced using carbon cycle and climate observations. *Nat Clim Change* 3:725–729
- Boer GJ, Arora V (2009) Temperature and concentration feedbacks in the carbon cycle. *Geophys Res Lett* 36:L02704. doi:[10.1029/L036220](https://doi.org/10.1029/L036220)
- Bonan GB, Levis S (2010) Quantifying carbon–nitrogen feedbacks in the Community Land Model (CLM4). *Geophys Res Lett* 37:L0740. doi:[10.1029/2010GL042430](https://doi.org/10.1029/2010GL042430)
- Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP (1998) Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature* 396(6711):570–572
- Boysen LR, Brovkin V, Arora VK, Cadule P, de Noblet-Ducoudré N, Kato E, Pongratz J, Gayler V (2014) Global and regional effects of land-use change on climate in 21st century simulations with interactive carbon cycle. *Earth Syst Dyn* 5:309–319. doi:[10.5194/esd-5-309-2014](https://doi.org/10.5194/esd-5-309-2014)
- Brovkin V, Boysen L, Arora VK, Boisier JP, Cadule P, Chini L, Weiss M et al (2013) Effect of anthropogenic land-use and land-cover changes on climate and land carbon storage in CMIP5 projections for the twenty-first century. *J Clim* 26(18):6859–6881
- Canadell JG, Le Quéré C, Raupach MR, Field CB, Buitenhuis ET, Ciais P, Conway TJ, Gillett NP, Houghton RA, Marland G (2007) Contributions to accelerating atmospheric CO<sub>2</sub> growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc Natl Acad Sci USA* 104(47):18866–18870
- Cao M, Prince SD, Shugart HH (2002) Increasing terrestrial carbon uptake from the 1980s to the 1990s with changes in climate and atmospheric CO<sub>2</sub>. *Glob Biogeochem Cycles* 16(4):1069. doi:[10.1029/2001GB001553](https://doi.org/10.1029/2001GB001553)
- Chameides WL, Kasibhatla PS, Yienger JJ, Levy H II, Moxim WJ (1994) The growth of continental-scale metro-agro-plexes, regional ozone pollution, and world food production. *Science* 264:74–78
- Ciais P et al (2013) Carbon and other biogeochemical cycles. Climate change 2013: the physical science basis. In: Stocker TF et al (eds) Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge Univ Press, Cambridge, pp 465–570
- Collatz GJ, Ribas-Carbo M, Berry JA (1992) Coupled photosynthesis-stomatal conductance model for leaves of C4 plants. *Aust J Plant Physiol* 19(5):519–538
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408(6809):184–187
- Cramer W et al (2001) Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Glob Change Biol* 7(4):357–373
- Dalmonech D, Zaehle S, Schürmann GJ, Brovkin V, Reick C, Schnur R (2015) Separation of the effects of land and climate model errors on simulated contemporary land carbon cycle trends in the MPI earth system model version 1. *J Clim* 28:272–291
- de Vries W (2009) Assessment of the relative importance of nitrogen deposition and climate change on the sequestration of carbon by forests in Europe: an overview. *Introd For Ecol Manag* 258:1–302
- de Vries W, Solberg S, Dobbervin M, Sterba H, Laubhahn D, Reinds GJ, Nabuurs GJ, Gundersen P, Sutton MA (2008) Ecologically implausible carbon response? *Nature* 451:E1–E3
- Devaraju N, Bala G, Nemani R (2015) Modelling the influence of land-use changes on biophysical and biochemical interactions at regional and global scales. *Plant Cell Environ* 38:1931–1946. doi:[10.1111/pce.12488](https://doi.org/10.1111/pce.12488)
- Dolman AJ, van der Werf GR, van der Molen MK, Ganssen G, Erisman JW, Strengers B (2010) A Carbon cycle science update since IPCC AR-4. *Ambio* 39:402–412
- Donohue RJ, Roderick ML, McVicar TR, Farquhar GD (2013) CO<sub>2</sub> fertilisation has increased maximum foliage cover across the globe's warm, arid environments. *Geophys Res Lett*. doi:[10.1002/grl.50563](https://doi.org/10.1002/grl.50563)
- Fensholt R, Langanke T, Rasmussen R, Reenberg A, Prince SD, Tucker CJ, Scholes RJ, Bao Le Q, Bondeau A, Eastman R,



- Epstein HE, Gaughan AE, Hellden U, Mbow C, Olsson L, Paruelo J, Schweitzer C, Seaquist J, Wessels K (2012) Greenness in semi-arid areas across the globe 1981–2007— an earth observing satellite based analysis of trends and drivers. *Remote Sens Environ* 121:144–158
- Fisher JB et al (2013) African tropical rainforest net carbon dioxide fluxes in the twentieth century. *Philos Trans R Soc B Biol Sci* 368(1625):20120376
- Friedlingstein P et al (2006) Climate-carbon cycle feedback analysis: results from the (CMIP)-M-4 model intercomparison. *J Clim* 19(14):3337–3353
- Friedlingstein P, Houghton RA, Marland G, Hackler J, Boden TA, Conway TJ, Canadell JG, Raupach MR, Ciais P, Le Quéré C (2010) Update on CO<sub>2</sub> emissions. *Nat Geosci* 3(12):811–812. doi:10.1038/ngeo1022
- Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, Liddicoat SK, Knutti R (2014) Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *J Clim* 27:511–526
- Galloway JN et al (2004) nitrogen cycles: past, present, and future. *Biogeochemistry* 70(2):153–226
- Gerber S, Hedin LO, Keel SG, Pacala SW, Shevliakova E (2013) Land use change and nitrogen feedbacks constrain the trajectory of the land carbon sink. *Geophys Res Lett* 40:5218–5222. doi:10.1002/grl.50957
- Govindasamy B, Thompson S, Mirin A, Wickett M, Caldeira K, Delire C (2005) Increase of carbon cycle feedback with climate sensitivity: results from a coupled climate and carbon cycle model. *Tellus B* 57(2):153–163
- Hashimoto H, Nemani RR, White MA, Jolly WM, Piper SC, Keeling CD, Myneni RB, Running SW (2004) El Niño – Southern Oscillation – induced variability in terrestrial carbon cycling. *J Geophys Res* 109:D23110. doi:10.1029/2004JD004959
- Hayes DJ, McGuire AD, Kicklighter DW, Gurney KR, Burnside TJ, Melillo JM (2011) Is the northern high latitude land-based CO<sub>2</sub> sink weakening? *Global Biogeochem Cycles* 25:GB3018. doi:10.1029/2010GB003813
- Holland EA, Braswell BH, Lamarque J-F, Townsend A, Sulzman J, Müller J-F, Dentener F, Brasseur G, Levy H II, Penner JE, Roelofs GJ (1997) Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *J Geophys Res Atmos* 102:15849–15866
- Horowitz LW, Walters S, Mauzerall DL, Emmons LK, Rasch PJ, Granier C, Tie X, Lamarque J-F, Schultz MG, Tyndall GS, Orlando JJ, Brasseur GP (2003) A global simulation of tropospheric ozone and related tracers: description and evaluation of MOZART, version 2. *J Geophys Res-Atmos* 108:4784. doi:10.1029/2002JD002853
- Houghton RA, House JI, Pongratz J, van der Werf GR, DeFries RS, Hansen MC, Le Quéré C, Ramankutty N (2012) Carbon emissions from land use and land-cover change. *Biogeosciences* 9:5125–5142. doi:10.5194/bg-9-5125-2012
- Hu Z, Yu G, Fu Y et al (2008) Effects of vegetation control on ecosystem water use efficiency within and among four grassland ecosystems in China. *Glob Change Biol* 14:1609–1619
- Huang M, Piao S, Sun Y, Ciais P, Cheng L, Mao J, Poulter B, Shi X, Zeng Z, Wang Y (2015) Change in terrestrial ecosystem water-use efficiency over the last three decades. *Glob Change Biol*. doi:10.1111/gcb.12873
- Hurrell JW et al (2013) The community earth system model: a framework for collaborative research. *Bull Am Meteorol Soc* 94:1339–1360
- Hurt GC, Frolking S, Fearon MG, Moore B, Shevliakova E, Malyshev S, Pacala SW, Houghton RA (2006) The under pinnings of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. *Glob Change Biol* 12:1208–1229. doi:10.1111/j.1365-2486.2006.01150.x
- Ichii K, Kondo M, Okabe Y, Ueyama M, Kobayashi H, Lee S-J, Saigusa N, Zhu Z, Myneni RB (2013) Recent changes in terrestrial gross primary productivity in Asia from 1982 to 2011. *Remote Sens* 5(11):6043–6062
- IPCC (2013) Climate change 2013: the physical science basis. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, p 1535. doi:10.1017/CBO9781107415324
- Jain A, Yang XJ, Khesghi H, McGuire AD, Post W, Kicklighter D (2009) Nitrogen attenuation of terrestrial carbon cycle response to global environmental factors. *Glob Biogeochem Cycles* 23(GB4028):1–13
- Janssens IA et al (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nat Geosci* 3:315–322
- Jones C, Jason L, Spencer L, Betts R (2009) Committed terrestrial ecosystem changes due to climate change. *Nat Geosci* 2:484–487
- Jones C, Jason L, Spencer L, Betts R (2010) Role of terrestrial ecosystems in determining CO<sub>2</sub> stabilization and recovery behaviour. *Tellus Ser B Chem Phys Meteorol* 62(5):682–699
- Joos F, Sarmiento JL, Siegenthaler U (1991) Estimates of the effect of Southern-Ocean iron fertilization on atmospheric CO<sub>2</sub> concentrations. *Nature* 349(6312):772–775
- Kloster S et al (2010) Fire dynamics during the 20th century simulated by the Community Land Model. *Biogeosciences* 7(6):1877–1902
- Krinner G et al (2005) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob Biogeochem Cycles* 19:1–33
- Lawrence DM 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. doi:10.1029/2011ms000045
- Lawrence PJ et al (2012) Simulating the biogeochemical and biogeophysical impacts of transient land cover change and wood harvest in the Community Climate System Model (CCSM4) from 1850 to 2100. *J Clim* 25:3071–3095
- Le Quéré C et al (2003) Two decades of ocean CO<sub>2</sub> sink and variability. *Tellus Ser B* 55:649–656
- Le Quéré C et al (2009) Trends in the sources and sinks of carbon dioxide. *Nat Geosci* 2(12):831–883
- Le Quéré C et al (2013) The global carbon budget 1959–2011. *Earth Syst Sci Data* 5:165–185. doi:10.5194/essd-5-165-2013
- Le Quéré C et al (2014) Global carbon budget 2013. *Earth Syst Sci Data* 6:235–263. doi:10.5194/essd-6-235-2014
- Lloyd J, Taylor JA (1994) On the temperature-dependence of soil respiration. *Funct Ecol* 8(3):315–323
- Ma J, Yan X, Dong W, Chou J (2015) Gross primary production of global forest ecosystems has been overestimated. *Nat Sci Rep* 5:10820. doi:10.1038/srep10820
- Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P, Jarvis PG, Kolari P, Kowalski AS, Lankreijer H, Law BE, Lindroth A, Loustau D, Manca G, Moncrieff JB, Rayment M, Tedeschi V, Valentini R, Grace J (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447:848–850
- Matthews HD, Weaver AJ, Meissner KJ (2005) Terrestrial carbon cycle dynamics under recent and future climate change. *J Clim* 18:1609–1628
- McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo L, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW, Roulet N (2009) Sensitivity of the carbon cycle in the Arctic to climate change. *Ecol Monogr* 79:523–555

- Murray-Tortarolo G et al (2013) Evaluation of land surface models in reproducing satellite-derived LAI over the high-latitude Northern Hemisphere part I: uncoupled DGVMs. *Remote Sens* 5(10):4819–4838
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702
- Neale RB, Chen CC, Gettelman A, Lauritzen PH, Park S, Williamson DL, Conley AJ, Garcia R, Kinnison D, Lamarque JF, Marsh D, Mills M, Smith AK, Tilmes S, Vitt F, Morrison H, Cameron-Smith P, Collins WD, Iacono MJ, Easter RC, Ghan SJ, Liu XH, Rasch PJ, Taylor MA (2010) Description of the NCAR Community Atmosphere Model (CAM5.0). Tech. Rep. NCAR/TN-486-STR, NCAR. <http://www.cesm.ucar.edu/models/cesm1.0/cam/>. Last Access 8 Jan 2013
- Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running SW (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300(5625):1560–1563
- Norby RJ, Warrena JM, Iversena CM, Medlynb BE, McMurtriec RE (2010) CO<sub>2</sub> enhancement of forest productivity constrained by limited nitrogen availability. *Proc Natl Acad Sci* 107(45):19368–19373
- Oleson KW, Lawrence DM, Bonan GB, Flanner MG, Kluzek E, Lawrence PJ, Levis S, Swenson SC, Thornton P et al (2010) Technical description of version 4.0 of the Community Land Model (CLM) Rep. National Center for Atmospheric Research, Boulder, p 266
- Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D (2011) A large and persistent carbon sink in the world's forests. *Science* 333:988–993
- Piao S, Friedlingstein P, Ciais P, Viovy N, Demarty J (2007) Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Glob Biogeochem Cycles* 21:GB3018. doi:10.1029/2006GB002888
- Piao S et al (2013) Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO<sub>2</sub> trends. *Glob Change Biol* 19(7):2117–2132
- Pongratz J, Reick CH, Houghton RA, House JI (2014) Terminology as a key uncertainty in net land use and land cover change carbon flux estimates. *Earth Syst Dyn* 5:177–195. doi:10.5194/esd-5-177-2014
- Ponton S, Flanagan LB, Alstad KP et al (2006) Comparison of ecosystem water-use efficiency among Douglas-fir forest, aspen forest and grassland using eddy covariance and carbon isotope techniques. *Glob Change Biol* 12:294–310
- Randerson JT et al (2009) Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. *Glob Change Biol* 15(10):2462–2484
- Reay DS, Dentener F, Smith P, Grace J, Feely RA (2008) Global nitrogen deposition and carbon sinks. *Nat Geosci* 1:430–437
- Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H (2004) A continuous satellite-derived measure of global terrestrial primary production. *Bioscience* 54(6):547–560
- Schimel D, Stephens BB, Fisher JB (2014) Effect of increasing CO<sub>2</sub> on the terrestrial carbon cycle. *Proc Natl Acad Sci* 112(2):436–441
- Schuur EAG et al (2008) Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. *Bioscience* 58(8):701–714
- Schuur EAG et al (2009) The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* 459(7246):556–559
- Schuur EAG et al (2015) Climate change and the permafrost carbon feedback. *Nature* 520:171–179
- Thompson SL et al (2004) Quantifying the effects of CO<sub>2</sub>-fertilized vegetation on future global climate and carbon dynamics. *Geophys Res Lett* 31(23):L23211. doi:10.1029/2004GL021239
- Thornton PE et al (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needle leaf forests. *Agric For Meteorol* 113(1–4):185–222
- Thornton PE, Lamarque JF, Rosenbloom NA, Mahowald NM (2007) Influence of carbon–nitrogen cycle coupling on land model response to CO<sub>2</sub> fertilization and climate variability. *Glob Biogeochem Cycles* 21:GB4018. doi:10.1029/2006GB002868
- Thornton PE, Doney SC, Lindsay K, Moore JK, Mahowald N, Randerson JT, Fung I, Lamarque JF, Feddes JJ, Lee YH (2009) Carbon–nitrogen interactions regulate climate-carbon cycle feedbacks: results from an atmosphere–ocean general circulation model. *Biogeosciences* 6(10):2099–2120
- Trenberth KE (1997) The definition of El Niño. *Bull Am Meteorol Soc* 78(12):2771–2777
- Zaehle S, Dalmonech D (2011) Carbon–nitrogen interactions on land at global scales: current understanding in modelling climate biosphere feedbacks. *Curr Opin Environ Sustain* 3:311–320
- Zaehle S et al (2010) Carbon and nitrogen cycle dynamics in the O-CN land surface model, II: the role of the nitrogen cycle in the historical terrestrial C balance. *Glob Biogeochem Cycles* 24:1–14
- Zaehle S, Ciais P, Friend AD, Prieur V (2011) Carbon benefits of anthropogenic reactive nitrogen offset by nitrous oxide emissions. *Nat Geosci* 4:601–605
- Zeng N, Qian HF, Munoz E, Iacono R (2004) How strong is carbon cycle-climate feedback under global warming? *Geophys Res Lett* 31:L20203. doi:10.1029/2004GL020904
- Zhao M, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329:940–943
- Zhu Q, Jiang H, Peng C, Liu J, Wei X, Fang X, Liu S, Zhou G, Yu S (2011) Evaluating the effects of future climate change and elevated CO<sub>2</sub> on the water use efficiency in terrestrial ecosystems of China. *Ecol Model* 222(14):2414–2429