



Meiyappan, P., Jain, A. K., & House, J. I. (2015). Increased influence of nitrogen limitation on CO₂ emissions from future land use and land use change. *Global Biogeochemical Cycles*, 29(9), 1524-1548.
<https://doi.org/10.1002/2015gb005086>

Peer reviewed version

License (if available):
Unspecified

Link to published version (if available):
[10.1002/2015gb005086](https://doi.org/10.1002/2015gb005086)

[Link to publication record in Explore Bristol Research](#)
PDF-document

An edited version of this paper was published by AGU. Copyright 2015 American Geophysical Union.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/pure/about/ebr-terms>

**Increased influence of nitrogen limitation on CO₂ emissions from future
land use and land-use change**

Running Head: CO₂ emissions from LULUC

Prasanth Meiyappan¹, Atul K. Jain¹, and Joanna I. House²

¹Department of Atmospheric Sciences, University of Illinois, Urbana, IL 61801, USA

²Department of Geography, Cabot Institute, University of Bristol, Bristol, BS8 1SS, UK

Correspondence to: P. Meiyappan (meiyapp2@illinois.edu); A. K. Jain (jain1@illinois.edu)

Keywords: carbon emissions; nitrogen cycle; carbon cycle; CMIP5; uncertainties; IPCC AR5; climate projections.

Type of Paper: Research Article

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/2015GB005086

(Prepared for **Global Biogeochemical Cycles**; Special issue on **Global Land-use Change and Carbon/Climate Dynamics**)

Key points

- **We simulated the effects of nitrogen limitation on future LULUC emissions**
- **LULUC emissions are considerably higher when nitrogen is considered**
- **Nitrogen limitation slows forest recovery and limits CO₂ fertilization effect**

Accepted Article

Abstract

In the latest projections of future greenhouse gas emissions for the Intergovernmental Panel on Climate Change (IPCC), few Earth System Models included the effect of nitrogen limitation, a key process limiting forest regrowth. Few included forest management (wood harvest). We estimate the impacts of nitrogen limitation on the CO₂ emissions from land use and land-use change (LULUC), including wood harvest, for the period 1900-2100. We use a land-surface model that includes a fully coupled carbon and nitrogen cycle, and accounts for forest regrowth processes following agricultural abandonment and wood harvest. Future projections are based on the four Representation Concentration Pathways used in the IPCC Fifth Assessment Report, and we account for uncertainty in future climate for each scenario based on ensembles of climate model outputs. Results show that excluding nitrogen limitation will underestimate global LULUC emissions by 34-52 PgC (20-30%) during the 20th century (range across three different historical LULUC reconstructions) and by 128-187 PgC (90-150%) during the 21st century (range across the four IPCC scenarios). The full range for estimated LULUC emissions during the 21st century including climate model uncertainty is 91 to 227 PgC (with nitrogen limitation included). The underestimation increases with time because: (1) Projected annual wood harvest rates from forests summed over the 21st century are 380-1080% higher compared to those of the 20th century, resulting in more regrowing secondary forests, (2) Nitrogen limitation reduces the CO₂ fertilization effect on net primary production of regrowing secondary forests following wood harvest and agricultural abandonment, and (3) Nitrogen limitation effect is aggravated by the gradual loss of soil nitrogen from LULUC disturbance. Our study implies that: (1) Nitrogen

limitation of CO₂ uptake is substantial and sensitive to nitrogen inputs, (2) If LULUC emissions are larger than previously estimated in studies without nitrogen limitation, then meeting the same climate mitigation target would require an equivalent additional reduction of fossil fuel emissions, (3) The effectiveness of land-based mitigation strategies will critically depend on the interactions between nutrient limitations and secondary forests resulting from LULUC, and (4) It is important for terrestrial biosphere models to consider nitrogen constraint in estimates of the strength of future land carbon uptake.

1. Introduction

The term “land-use change” typically refers to conversion of one land cover type to another, such as clearing forest to grow crops. In contrast, “land use” refers to management without changing the land cover, such as wood harvest and agricultural management (e.g. cropping practices, irrigation). CO₂ emissions from land use and land-use change (LULUC) represents the ‘net effect’ of CO₂ sources (emissions from deforestation, logging and other direct human activities), and CO₂ sinks (as vegetation regrows following land disturbance). LULUC emissions are estimated as 0.9 ± 0.5 PgC/yr ($1 \text{ PgC} = 10^{15} \text{ gC}$) to the atmosphere, for the decade 2004-2013 [Le Quéré et al., 2015]. On a relative scale, LULUC emissions are ~10% of the CO₂ emissions from fossil fuel combustion and cement manufacture (8.9 ± 0.4 PgC/yr), for the same decade [Boden et al., 2013].

To balance the carbon budget, total anthropogenic CO₂ emissions (fossil fuels + LULUC) should equal the sum of CO₂ accumulated in the atmosphere, the oceanic sink, and the remaining

CO₂ exchanged between the atmosphere and terrestrial biosphere. We have a good quantitative understanding and constrained estimates of fossil fuel emissions, atmospheric growth rates, and the oceanic sink. From these better-constrained fluxes, and modeled estimates of LULUC emissions, the remaining terrestrial biosphere flux is inferred as a residual sink of 2.9 ± 0.8 PgC/yr for the decade 2004-2013, thereby offsetting roughly one-quarter of the total anthropogenic carbon emissions [Le Quéré et al., 2015]. The uncertainty in estimating the residual terrestrial sink is mainly attributable to uncertainties in estimating LULUC emissions [Ballantyne et al., 2015; Houghton et al., 2012]. The residual terrestrial sink indicates an increased net carbon accumulation by the terrestrial ecosystems which are sensitive to changing environmental controls (e.g. climate, CO₂ fertilization, nitrogen deposition) [Ballantyne et al., 2015; Ciais et al., 2013; Le Quéré et al., 2015; Schimel et al., 2015; Shevliakova et al., 2013]. Thus, the terrestrial biosphere provides a subsidy to human activities by net absorption of atmospheric CO₂, slowing down the rate of climate change significantly. An understanding of how this subsidy may change in the future, in response to changing environmental controls, is essential to understanding the magnitude of the climate change problem. Constraining the future residual terrestrial sink hinges on our estimates of sources and sinks from LULUC with narrow enough uncertainty bounds. The uncertainties arise not only due to the range of possibilities on how the future world might evolve with respect to LULUC and its environmental controls, but also in our understanding of various processes that affect the LULUC fluxes.

In a recent article, we studied the role of LULUC emissions on the carbon budget for the period 1765-2010. The study used a terrestrial ecosystem component of a land surface model, the

Integrated Science Assessment Model (ISAM) that includes a fully coupled carbon-nitrogen cycle and detailed representation of secondary forest dynamics to account for forest regrowth processes following agricultural abandonment and wood harvest. We showed that failing to account for nitrogen dynamics, a key process limiting forest regrowth, underestimated LULUC emissions by ~70% in the non-tropics, ~10% in the tropics, and ~40% globally during 1990s compared to simulations that included the nitrogen dynamics. The study conveyed two key messages: (1) nitrogen limitation will significantly reduce the effect of carbon sinks on regrowing secondary forests [see Pongratz, 2013], and (2) historically, more secondary forests have resulted from wood harvest than from agricultural abandonment, underscoring the importance of forest management in estimating LULUC emissions (also see Yang et al. [2010]; Ciais et al. [2013]).

The 21st century scenarios based on the Coupled Model Intercomparison Project phase 5 (CMIP5) project a 380-1080% rise in global forest wood harvest rates (area harvested each year summed over the century) compared to those of the 20th century (Table 1), due to rapid increase in demand for bioenergy and wood products [Hurt et al., 2011]. Therefore, the effect of nitrogen limitation on the rates of carbon sink on regrowing secondary forests could be much greater in the future compared to the historical period, having significant implications for the effectiveness of land-based mitigation policies. Accounting for both nitrogen limitation and forest management are beyond the current capabilities of many global climate models involved in CMIP5 [Ciais et al., 2013], thus giving them the tendency to be too optimistic in simulating future carbon sinks [Walker et al., 2015; Wårlind et al., 2014; Wieder et al., 2015a].

Accordingly, the overall aim of this study is to understand how future LULUC emissions are influenced by the interactions among LULUC, nitrogen limitation, and anthropogenic environmental changes (CO₂ fertilization, climate change, and nitrogen deposition that reduce the nitrogen limitation effect). We place specific emphasis on land management. The overall aim can be split into three parts.

First, we study the magnitude of LULUC emissions (with nitrogen limitation effect) attributable to “land use” (management) as compared to “land-use change”, and how the magnitude is influenced by anthropogenic environmental changes. To quantify this effect, first we study the relative contribution of the direct effects of human LULUC activities versus the indirect effects of anthropogenic activity via environmental changes (climate, CO₂, and nitrogen deposition) to total LULUC emissions (see methods; for significance, see Houghton [2013a]). We then breakdown these contributions into its two component activities: “land use” and “land-use change”. The land use activities considered include wood harvested from forests and subsequent regrowth processes. The land-use change activities include clearing of natural ecosystems for expansion of cropland and pastureland and forest regrowth following agricultural abandonment.

Second, we study the impact of nitrogen limitation on the 21st century LULUC fluxes. For this purpose, all LULUC fluxes estimated for the above objective are also simulated without the effect of nitrogen limitation. We quantify the impacts of nitrogen limitation by comparing the LULUC fluxes simulated between with and without nitrogen limitation case. We assess the future impacts of nitrogen limitation on LULUC fluxes relative to that of 20th century.

Third, we carry out a comprehensive assessment of the uncertainties in estimates of future LULUC emissions due to the different mitigation scenarios of the IPCC Fifth Assessment Report [IPCC, 2013], and uncertainties in climate projections underlying each scenario. This is important given that significant uncertainties in simulating future terrestrial carbon fluxes among Earth System Models are attributable to differences in simulated climate [Ciais et al., 2013]. The uncertainties in projected climate (see Fig. S1, S2) reflect uncertainties in emissions scenarios, model initializations, and gaps in process understanding [Knutti and Sedláček, 2012]. Using one terrestrial ecosystem model, but consistently driven by different climate model projections enables us to study how much of total uncertainty in future LULUC emissions are attributable to differences in climate projections alone. Our future climate uncertainty analysis builds on historical uncertainties in quantifying the spatial and temporal patterns of historical LULUC (methods).

2. Materials and methods

We use a data-modeling approach to study the three objectives discussed above. This section briefly describes: the land surface model used to simulate LULUC fluxes, model forcing data, and model simulations performed.

2.1. Model details

We use a terrestrial ecosystem component of a land surface model, Integrated Science Assessment Model (ISAM) to assess the impacts of LULUC on terrestrial carbon fluxes. The terrestrial component of ISAM simulates carbon and nitrogen fluxes between the vegetation and the atmosphere (net land-to-atmosphere flux), above and below ground litter, and soil organic matter at $0.5^{\circ} \times 0.5^{\circ}$ spatial resolution [Jain and Yang, 2005]. ISAM includes detailed representation of nitrogen dynamics [Yang et al., 2009] and secondary forest dynamics [Yang et al., 2010]. The carbon cycle feedbacks modeled includes the influence of: (1) increasing atmospheric [CO_2] on Net Primary Productivity (NPP), (2) temperature and precipitation changes on photosynthesis, autotrophic and heterotrophic respiration, and (3) nitrogen deposition on carbon uptake by plants. The modeled nitrogen cycle accounts for major processes such as denitrification, mineralization, immobilization, nitrification, leaching, symbiotic, and non-symbiotic biological nitrogen fixation. Our water cycle is based on the LINKAGES model [Hanson et al., 2004; Pastor and Post, 1985]. The model operates at two time steps. The vegetation carbon including NPP, litter production, and nitrogen demand by plants are calculated annually. Decomposition of soil and litter, and nitrogen cycle are calculated weekly. The

structure, parameterization, and evaluation of nitrogen cycle in ISAM are detailed in Yang et al. [2009]. Jain et al. [2009] show that the model can simulate the response on historical terrestrial carbon fluxes due to nitrogen limitation, LULUC, and changes in [CO₂], climate change, and nitrogen deposition. ISAM and its extended versions have continually been evaluated and improved using both field observations and model inter-comparison activities [El-Masri et al., 2013; Huntzinger et al., 2012; Ito et al., 2008; Tian et al., 2015; Walker et al., 2014]. Results from ISAM have been a part of the global carbon budget [Le Quéré et al., 2015], and several IPCC Assessment Reports, including the most recent Fifth Assessment Report [Ciais et al., 2013].

Each 0.5°x0.5° lat/lon grid cell in ISAM is occupied by one or more of the 18 land cover types [Yang et al., 2010] that include 5 types of primary forests classified by ecozone, and their corresponding “secondary forests”, 5 types of non-forested vegetation (e.g. grassland, savanna, shrubland), bareland, cropland, and pastureland. The model separately accounts for forest regrowth following agricultural abandonment and wood harvest, here termed as “secondary forest”.

2.2. Net land-to-atmosphere carbon flux calculation in ISAM

Here, we provide an overview of the calculation of the Net Ecosystem Exchange (NEE), the carbon exchanged between the ecosystem and the atmosphere. In the “simulations performed” section, we describe how NEE calculated with different experimental setup is

combined to estimate LULUC fluxes. Our terminology of carbon fluxes follows Chapin et al. [2006].

Following LULUC, the vegetation biomass is released as carbon to the atmosphere as three components in ISAM.

(1) Loss of soil organic carbon due to oxidation of organic matter when native soils are cleared for agriculture. We assume 25% of soil organic carbon stored in the top meter of the soil is lost to the atmosphere upon clearing (E_s), with most loss occurring within the first year of clearing soils. The 25% loss is the average estimate across observational studies [Table 3 of Houghton and Goodale, 2004], and consistent with the assumption of Houghton's bookkeeping model [Houghton, 2010]. We also test the sensitivity of our results to this model parameter.

(2) Part of biomass is shed as litter that enters the soils and decays on-site. As a result of decomposition, there is a heterotrophic respiration (HR) that includes losses by herbivory and the decomposition of organic debris by soil biota.

(3) Part of vegetation biomass enters the wood and fuel product pools and decays at rates dependent on the product pool type following McGuire et al. [2001]. E_p is the emissions from product pools that collectively represents 1 year (agriculture and agriculture products), 10 year (paper and paper products), and 100 year (lumber and long-lived products) product pools. The fraction of vegetation biomass that goes into the three product pools depends on the LULUC activity and region, following Houghton and Hackler [2001]. The three decay pools represent the woody material removed from the site. In reality, the harvest from agriculture and forestry may

be transported to locations far off from the harvested grid cell and allowed to decay. However, due to lack of such global datasets, we assume the product pool decays at the grid cells of origin.

We calculate the NEE carbon flux following LULUC as

$$\text{NEE} = \text{HR} - \text{NPP} + E_p + E_s \quad \text{Eq. (1)}$$

In Eq. (1), positive values for NEE represent flux to the atmosphere. NPP is the carbon accumulated in vegetation (carbon fixed through photosynthesis minus autotrophic respiration). In the case of LULUC, NPP accounts for the carbon accumulated from forest regrowth following agricultural abandonment and wood harvest. The model down regulates NPP depending on the magnitude of simulated nitrogen limitation (nitrogen demand minus supply) (see Yang et al. [2009] for equations). All the right hand side terms of Eq. (1) are influenced by both LULUC, natural (nitrogen limitation) and anthropogenic environmental changes (CO₂ fertilization, climate change, and nitrogen deposition that partly offsets nitrogen limitation effects).

To highlight, NEE following LULUC (Eq. 1) includes three components: emissions following disturbance, legacy fluxes (delayed carbon fluxes from soil and product pool decays), and carbon fluxes induced by anthropogenic environmental changes. Legacy fluxes include both source (decay) and sink terms (regrowth of secondary forests following agricultural abandonment and wood harvest in previous years) and they cause an imbalance between NPP and HR [Pongratz et al., 2014].

2.3. Model forcing data

2.3.1. Overview

The basis of our study is driving data and climate model output from the Coupled Model Intercomparison Project Phase 5 (CMIP5) for future scenarios of land-use change and fossil fuel emissions. The CMIP5 is coordinated by the World Climate Research Programme in support of IPCC Fifth Assessment Report [Taylor et al., 2012]. The IPCC CMIP5 analysis features four Representation Concentration Pathways (RCPs) for the future (>2005 AD) derived from Integrated Assessment Models (IAMs); each describing a possible pathway of future greenhouse gas concentration depending on human behavior including energy use, land use and mitigation policy. No single pathway is more likely than another. The products for each RCP include gridded estimates of LULUC, and atmospheric emissions and concentrations of GHGs for the future that are harmonized to transition smoothly from historical estimates/observations. Coordinated experiments, carried out by more than 20 modeling group from around the world used these data products for conducting a range of climate modeling experiments that included projecting future climate change. The RCPs have been extensively described in literature [Moss et al., 2010; van Vuuren et al., 2011]. We provide a summary of the RCPs with emphasis on its LULUC characteristics in supplementary text S1.

2.3.2. Atmospheric forcing data

ISAM requires forcing data on climate, atmospheric [CO₂], and nitrogen deposition. Data for atmospheric [CO₂] is as per CMIP5 experiments [Meinshausen et al., 2011] (see Fig. S3 for how the atmospheric [CO₂] varies with time for the RCPs). Gridded estimates of airborne nitrogen deposition are from Lamarque et al. [2011] (see supplementary text S2 and Fig. S4 for

further details). We account for changes in two climate variables: temperature and precipitation. We do not explicitly simulate the effects of radiation on carbon fluxes. Climate data for the historical period is from CRU TS3.21 [Harris et al., 2014]. To account for the climate uncertainties for the RCPs (2006-2100), we use monthly climate projections from a suite of 43 climate models from the CMIP5 multi-model ensemble database (Table S1). All climate data are at $0.5^{\circ} \times 0.5^{\circ}$ lat/lon and interpolated to weekly time steps within the model. Additional details on climate data processing are available in supplementary text S3.

2.3.3. LULUC data

We prescribed LULUC data from the land-use harmonization (LUH) database used for CMIP5 (Hurtt et al. [2011]; <http://luh.umd.edu/>). The data covers the period 1500-2100 annually and at $0.5^{\circ} \times 0.5^{\circ}$ lat/lon resolution. The historical LULUC in the Hurtt data is based on the HYDE 3.1 reconstruction for cropland and pastureland transitions [Klein Goldewijk et al., 2011], and wood harvest from Food and Agriculture Organization (FAO). Specifically, we include three types of wood harvest from LUH database that are provided as fractional area of each grid cell: wood harvest from primary forested land (variable code in LUH: gfsh3), mature secondary forested land (gfsh1), and young secondary forested land (gfsh2). Hurtt et al. [2011] estimated wood harvest area by combining two other estimates: (1) biomass extracted from wood harvest, and (2) model-based estimates of historical above-ground carbon stocks and forest extent.

The future aggregate (for larger world regions) land demands (cropland, pastureland, and wood harvest) in the Hurtt data are based on the four RCPs derived from IAMs. The

“harmonization” in the Hurtt data downscales the aggregate regional land demands to individual grid cells within the region, while simultaneously ensuring that the downscaled maps are spatially consistent with the historical reconstruction.

We use a map of potential natural vegetation and a rule-based approach (Meiyappan and Jain, 2012) to transform the prescribed LULUC information into estimates of annual land cover areas (and underlying land conversions) for each grid cell, consistent with the land cover types of ISAM, similar to the approach taken in other land models [Lawrence et al., 2012; Pitman et al., 2009]. The rules are specific to each LULUC activity, and are broadly consistent with our understanding of historical LULUC dynamics. The rules are generalizations of regional case studies of LULUC drivers, and have been calibrated using remote-sensing observations. Supplementary text S4 gives further details on the LULUC implementation in the model. The LULUC characteristics for the study period (1900-2100), historically and for each future RCP, are shown in Fig. 1 and Table 1, and summarized in the supplementary text S1.

2.4. Simulations Performed

We initialized ISAM with an atmospheric $[\text{CO}_2]$ of 278 ppmv, representative of approximate conditions in the starting year (1765 AD – pre-industrial conditions) of the model simulation, to allow vegetation and soil carbon pools to reach an initial steady state.

The basic approach to calculate LULUC emissions (E_{LULUC} in Eq. 2) is by comparing the NEE (Eq. 1) calculated between two simulations, one with LULUC ($\text{NEE}_{\text{LULUC}}$ in Eq. 3) and the other without LULUC ($\text{NEE}_{\text{noLULUC}}$ in Eq. 4).

$$E_{\text{LULUC}} = \text{NEE}_{\text{LULUC}} - \text{NEE}_{\text{noLULUC}} \quad \text{Eq. (2)}$$

where,

$$\text{NEE}_{\text{LULUC}} = \text{HR}_{\text{LULUC}} - \text{NPP}_{\text{LULUC}} + E_p_{\text{LULUC}} + E_s_{\text{LULUC}} \quad \text{Eq. (3)}$$

$$\text{NEE}_{\text{noLULUC}} = \text{HR}_{\text{noLULUC}} - \text{NPP}_{\text{noLULUC}} \quad \text{Eq. (4)}$$

In Eq. (4), $\text{NEE}_{\text{noLULUC}}$ represents the effects of environmental changes on potential natural vegetation. The E_p and E_s terms do not appear in Eq. (4), because they are zero when there is no LULUC. The LULUC emissions (Eq. 2) are influenced directly by humans through LULUC (Eq. (3); hereafter referred as “direct emissions” from LULUC), and indirectly by human-induced environmental changes on lands undergoing LULUC through Eq. (3, 4) (“indirect emissions” from LULUC). In this paper, the total of direct and indirect emissions is referred to as “total emissions” from LULUC. The definition has been widely adopted for over a decade [McGuire et al., 2001; Pongratz et al., 2014]. All the three emissions (i.e. direct, indirect, and total emissions) are net fluxes and they include both source and sink terms.

We carried out a series of with and without LULUC simulations (Table 2) for the time period 1765-2100. Table 3 summarizes how the results from the simulations listed in Table 2 were combined to estimate Eq. (2) that represents different LULUC flux components, and is further explained in text S5.

In principle, the effects of nitrogen limitation on terrestrial ecosystems are a natural response of the system to human-induced environmental change and hence can be counted as indirect effects of human activity along with climate and $[\text{CO}_2]$ change. However, in our

simulations, we kept nitrogen limitation separate from other environmental effects because our study aims to understand the interactive effects of including nitrogen cycle on LULUC fluxes.

2.4.1. Accounting for uncertainties in future climate projections and LULUC reconstructions:

We carried out the simulations (Table 2) and associated calculations (Table 3) separately for each RCP using corresponding forcing data for LULUC and environmental drivers. Specifically, to account for uncertainties in climate projections within each RCP, we repeated simulations Ref_1, Ref_2, A1, A2, B1 and B2 by varying the climate data listed in Table S1, but keeping the data for other drivers (CO₂, nitrogen deposition, and LULUC) same across the simulations. We carried out simulations C1, C2, D1 and D2 once for each RCP, as they are independent of climate change. The climate-induced uncertainty in simulating total LULUC emissions is purely from indirect effects of human activity on emissions mediated through environmental change, because by design, direct effects of human LULUC activities on emissions are independent of environmental changes. The simulations cover the period 1765-2100, and we present results for 1900-2100.

There are significant uncertainties in quantifying historical LULUC, resulting from differences in inventory datasets [Meiyappan and Jain, 2012] and reconstruction methodologies [Klein Goldewijk and Verburg, 2013]. The HYDE reconstruction for cropland and pastureland used in CMIP5 is just one realization of what could have happened in the past. In an earlier study [Jain et al., 2013] we forced ISAM with three LULUC reconstructions to estimate an array (uncertainty range) of “total LULUC emissions” for the 20th century (including cropland and

pastureland transitions from HYDE, Ramankutty [2012], and FAO [2006]; all using common data for wood harvest based on Hurtt et al. [2011]). Here, we used those estimates for comparison with our future estimates. New to this study is separately calculating direct and indirect LULUC emissions and separating emissions by LULUC activity (i.e. land-use change and wood harvest) for the three historical LULUC reconstructions (from simulations analogous to Table 2 & 3).

3. Results

3.1. Historical simulations: Overview

We first present comparison of two key modeled estimates from our historical simulations with observationally derived global estimates: (1) model simulated above-ground vegetation (tree foliage + woody biomass) carbon in forests vs. FAO-based gridded estimates, and (2) our model simulated NPP vs. NPP modeled from MODIS derived radiation absorption by plants. These comparisons are broadly intended to evaluate how well the historical simulations can reproduce the current conditions. While evaluating the model performance over the historical period is no guarantee of good performance over the 21st century, it does add confidence in the model's suitability for assessing impacts of the interactions between LULUC and environmental change on terrestrial carbon fluxes. While comparison of two model simulated variables is not indicative of overall model performance, the two variables compared here are critical to modeling LULUC emissions. For example, our modeled emissions from wood harvest depend on how well we simulate above-ground vegetation carbon in forests. Similarly, as

our NPP is regulated by modeled nitrogen demand and supply specific to land cover type [Yang et al., 2009], an overall agreement in NPP compared to an independent estimate adds confidence in our modeled nitrogen cycle, and its applicability to scientific questions addressed in this paper. Following this comparison, we present LULUC emission estimates for the 20th century. We highlight model uncertainty in the discussion section.

3.1.1. Model evaluation

Globally, our model simulated above-ground vegetation carbon in forests of 268 PgC (year 2000) compares to 234 PgC estimated from FAO-based gridded statistics [Kindermann et al., 2008; note the study does not provide uncertainty estimates]. A zonal (Fig. 2) and spatial comparison (Fig. S5) indicates that our simulated above-ground carbon in forests is higher in tropics and northern non-tropics, and lower in southern non-tropics. The reasons underlying the systematic latitudinal bias between the two estimates could stem from both data and model sources (e.g. bias from methods used to fill missing country data in FAO and gridding procedure; bias in our model forcing data and errors in model parameter and structure), and includes differences in definition of forest (FAO forest definition of percent cover >10% and height > 5m (Annex 2 of FAO [2005, 2010]) vs. our model definition of percent cover >60% and height >2m based on the IGBP land classification scheme [Loveland and Belward, 1997]).

Next, we compared our model simulated NPP across six land cover types averaged globally over a 5 year period (2001-2005) with that from modeled NPP from MODIS derived radiation absorption by plants [Zhao and Running, 2010; Zhao et al., 2005; Running et al., 2004].

Note that we are comparing two modeled estimates with inherent errors and uncertainties [Cleveland et al., 2015]. Nonetheless, results show that our model simulated NPP across all land cover types fall within the standard deviation range from radiation-based estimates (Fig. 3).

3.1.2. Carbon fluxes from LULUC during the 20th century (with nitrogen limitation effect)

Globally, the total LULUC emissions averaged across the three LULUC reconstructions were 163 PgC (range: 156-174 PgC) cumulated over the 20th century (Table 4) (all numbers discussed include nitrogen limitation effect, unless explicitly noted). The total LULUC emissions are about 58-65% of fossil fuel emissions, and 37-40% of total carbon emissions over the 20th century (266 PgC from fossil fuel combustion and cement production - Boden et al. [2013]). Most of the historical total LULUC emissions were direct emissions (Table 4; Figs. 4a, 5a). The indirect emissions averaged across the three reconstructions were close to zero (-22 to 21 PgC), because of partly offsetting environmental effects. For example, enhanced carbon sinks in regrowing forests under increasing [CO₂], also leads to higher emissions when harvested.

Regionally, the non-tropics accounted for about two-thirds (52-71%) of cumulative 20th century total LULUC emissions (Table 4; Fig. 4). The total LULUC emissions from non-tropics are greater than the tropics mainly because: (1) nitrogen limitation in the non-tropics reduced the carbon uptake rates on regrowing secondary forests (Figs. 4k, 5g; compare with and without nitrogen limitation cases), and (2) historically, two-thirds of global secondary forest area following wood harvest is from the non-tropics (Table 1).

Splitting the total LULUC emissions based on LULUC activity, 60-65% of the total global LULUC emissions are from land-use change, and the rest 35-40% is from wood harvest (55-72 PgC) (Fig. 4a). Breaking down regionally, wood harvest accounted for 11-22% of total LULUC emissions in the tropics (Fig. 4f), and 50-57% in the non-tropics (Fig. 4k).

3.2. Future simulations: Overview

First, using RCP8.5 as example, we describe how the key mechanisms in our model impact nitrogen limitation over time (the mechanisms qualitatively apply to all RCPs). Next, we present the overall effects of these mechanisms on the 21st century LULUC fluxes compared to that of 20th century. For this purpose, we use the mean emissions value of the three LULUC reconstructions for the 20th century. Third, we isolate the effect of nitrogen cycle on LULUC emissions by comparing results between with and without nitrogen cases. Finally, we quantify the uncertainties in LULUC emissions resulting from uncertainty in projections of climate change.

3.2.1. Model response to nitrogen limitation

Nitrogen limitation exists if there is not enough mineral nitrogen available for plant growth and litter decomposition. The difference between nitrogen demand and supply is the magnitude of nitrogen limitation. Results (Fig. 6) show that the total carbon uptake (NPP) by secondary forests increases with time (in both with and without nitrogen cases) due to both CO₂ fertilization effect on regrowing forests, and increase in the area of regrowing forests (following wood harvest and agricultural abandonment). However, the carbon uptake in secondary forests is

significantly lower when nitrogen limitation is included especially in the non-tropics. The tropics have relatively less nitrogen limitation, because warmer and wetter climate enhances nitrogen mineralization in soils. Furthermore, the difference in carbon uptake rates between with and without nitrogen limitation simulations increases over time reflecting the progressively increasing nitrogen limitation effect on CO₂ fertilization (note that the area of secondary forests is the same in both with and without nitrogen simulations). Our modeled response is consistent with ground-based studies that generally indicate that younger regrowing secondary forests require more nitrogen to support new production under increasing [CO₂] [Davidson et al., 2004; Finzi et al., 2006, 2007; Herbert et al., 2003; Hungate et al., 2003; Lebauer and Treseder, 2008; Luo et al., 2004, 2006; Oren et al., 2001; Murty et al., 2002; Reich et al., 2006].

Next, we describe how key nitrogen variables in our model vary with increasing nitrogen limitation. First, biological nitrogen fixation in both primary and secondary forests increases over time, with the increase being greater in secondary forests (Fig. 7a, b). We model nitrogen fixation as a function of evapotranspiration (see discussion section for limitations of this approach). Therefore, tropical forests fix more nitrogen than non-tropical forests in our model, consistent with spatial observations [Cleveland et al., 1999]. Second, increasing nitrogen demands from CO₂ fertilization causes both primary and secondary forests to uptake more nitrogen per unit area with time (Fig. 7e, f), thus reducing ecosystem nitrogen losses (Fig. 6). Third, with increasing nitrogen limitation, the nitrogen-use efficiency (NPP per unit nitrogen uptake; qualitatively similar to Carbon: Nitrogen ratio of vegetation) increases with time, especially in the secondary forests of the nitrogen limited non-tropics (Fig. 6b-h).

Increasing anthropogenic nitrogen deposition (external forcing to our model) provides an additional nitrogen input to terrestrial ecosystems (Fig. 7i). However, its effect on enhancing regrowth sinks (or reducing LULUC emissions) depends on how much of the nitrogen deposition occurs on regrowing forests. There are three major sources of nitrogen losses attributable to LULUC (inferred by comparing “with” and “without” nitrogen limitation simulations). (1) Anaerobic respiration by denitrifying bacteria (soil decomposition) increases with time due to increases in litterfall (leaf litter + dead wood) from LULUC (Fig. 7j). (2) Leaching as soil nitrate dissolves in rainwater and excess water percolates through soil (Fig. 7k). Leaching is higher in the tropics because of more rainfall, and relatively more soil nitrogen compared to the non-tropics. Both denitrification and leaching depends on our simulated soil nitrate content and soil moisture. (3) Removal of nitrogen from soils and vegetation from LULUC disturbance including slash burning and decay from product pools (Fig. 7l) as also documented in earlier studies [Davidson et al., 2007; Herbert et al., 2003; Mathers et al., 2006; Schipper et al., 2007].

In summary, our model simulations suggest that large areas of secondary forests will not respond to CO₂ fertilization as strongly as they would when adequate nitrogen was available to meet the plant demands. In the with-nitrogen cycle simulation, our model responds to increasing nitrogen limitation by increasing nitrogen fixation, reducing nitrogen losses, and increasing nitrogen-use efficiency. LULUC activities result in a gradual loss of nitrogen from the system, thus increasing the nitrogen limitation. In the following section, we explore the overall effects of these mechanisms on the simulated future LULUC emissions.

3.2.2. Carbon fluxes from LULUC during the 21st century (with nitrogen limitation effect)

Both globally and regionally, the total LULUC emissions estimated across the four RCPs are smaller or comparable to 20th century mean estimates (Table 4). Globally, the direct LULUC emissions due to human activity estimated across the RCPs are a smaller source to the atmosphere by 40-80% compared to 20th century estimates (Table 4; Figs. 4, 5 and S6). In contrast, the indirect LULUC emissions due to human environmental change are a much larger source to the atmosphere for the RCPs (55 to 77 PgC from Table 4) compared to 20th century (-20 to 20 PgC), making the total LULUC emissions much larger than when considering direct emissions alone. In this section, we further explore direct LULUC emissions. Interactions between nitrogen limitation and other environmental factors explain indirect LULUC emissions. We discuss indirect emissions in the next section.

In general, across all the RCPs, the net deforestation rates are significantly lower compared to the 20th century (Table 1; Fig. 1) resulting in smaller direct emissions (Fig. 4). Further, large amount of cropland and pastureland expansion that occurred in the 20th century, are being abandoned in the future (RCP 4.5 and RCP6.0) due to land protection policies (Fig. 1; Table 1). Specifically, forest expansion in RCP4.5 is due to carbon taxation policies that encourage protection of forests (text S1). The higher emissions in the 20th century from land clearing are partly offset in the future under RCP4.5 and RCP6.0 because of carbon accumulation in forests regrowing on abandoned land. This resulted in negative direct emissions from land-use change (sinks) for RCP4.5 globally (Fig. 4c), and for both RCP4.5 and RCP6.0 in the tropics (Fig. 4h, i).

In contrast to land-use change, direct emissions from wood harvest are equal to or larger than the 20th century estimates across all the RCPs (excluding one outlier RCP6.0 elaborated in discussion section), especially in the non-tropics (Fig. 4). This is because the RCPs project a 380-1080% global rise in wood harvest rates compared to 20th century due to rapid increase in demand for bioenergy and wood products (Table 1). The higher wood harvest results in more regrowing forests that become increasingly nitrogen limited due to the mechanisms explained in previous section (excluding [CO₂] down-regulation that is an indirect effect). Thus emissions become much greater compared to slower and smaller sinks in regrowth plus temporary sinks in product pools. As a result, the wood harvest contribution to direct LULUC emissions increase in the future, especially in the already nitrogen limited non-tropics (Table 4; Fig. 4). The higher rates of wood harvest also result in higher direct (and total) LULUC emissions in the non-tropics than in the tropics during the 21st century (Fig. 5; Table 4).

Interestingly, despite large net forest regrowth in the non-tropics under RCP4.5 (Table 1), its direct LULUC emissions (Table 4) are higher than or comparable to RCP2.6 and RCP8.5, both of which show a loss of forest area (Table 1). This is because the direct emissions from wood harvest are higher in RCP4.5 (Fig. 4m) where afforestation provides additional forest biomass to meet the prescribed wood harvest demands.

For both the tropics and non-tropics, the uncertainties in estimating direct emissions for the 20th century based on the three LULUC reconstructions (range from Table 4) is ~50% greater than the scenario-based uncertainty for the 21st century (maximum difference across the four

RCPs from Table 4), indicating that historical LULUC reconstructions are more uncertain regionally than the likely future LULUC outcomes.

3.2.3. Impacts of including nitrogen cycle on LULUC fluxes

All the aforementioned estimates include the effect of nitrogen limitation. To understand the impact of nitrogen cycle, we simulated LULUC fluxes without nitrogen limitation effect i.e. by assuming sufficient nitrogen is available for plant growth and litter decomposition. We quantify the impacts of nitrogen limitation by comparing the LULUC fluxes estimated between with and without nitrogen limitation case.

There are two key results. First, inclusion of nitrogen limitation increases the total LULUC emissions by 128-187 PgC globally for the 21st century, roughly 3-5 times larger compared to the increase for 20th century (Table 4; Fig. 5). This increase is predominantly attributable to two of the component fluxes (Fig. 4): direct emissions from wood harvest in the non-tropics, and indirect emissions from LULUC in both the tropics and non-tropics.

As described before, when we consider nitrogen dynamics, most of the regrowing forests become increasingly nitrogen limited. This restricts the rate of regrowth after harvest resulting in larger total emissions from wood harvest under nitrogen limited conditions, particularly in the non-tropics. When nitrogen dynamics were not considered, direct emissions from wood harvest were smaller, and total LULCC emissions were a sink under two mitigation scenarios (RCP4.5 and RCP6.0; see text S6 for elaboration) globally, and for all scenarios in the non-tropics (Table 4).

Most of the difference in indirect emissions between with and without nitrogen cases can be explained by the interactions between the nitrogen cycle and carbon cycle impacts on areas undergoing land-use change (Fig. 4b-e). Without nitrogen limitation, the higher emissions from deforestation in a CO₂-fertilized world (due to higher carbon stocks) are partly compensated by stronger regrowth sinks (from CO₂-fertilization) on forests regrowing on abandoned land. However, when we include nitrogen limitation, the sinks on forests regrowing on abandoned land are weakened due to CO₂ down-regulation effect, especially in the nitrogen limited non-tropics where the net indirect flux shifts from a sink to a source (Fig. 4l-0). This effect is also reflected in Fig. 5, where the difference in indirect emissions between with and without nitrogen limitation case increases with time for the non-tropics. Under increasing [CO₂], plants need more nitrogen to support production. The insufficient availability of nitrogen limits the CO₂ fertilization effect on plant growth in our model [Fig. 6; also see Norby et al., 2010; Wieder et al., 2015a]. In the tropics, inclusion of nitrogen shifts the indirect flux due to land-use change from a source to a slightly bigger source for RCP2.6, RCP4.5 and RCP6.0 (Fig. 4g-i).

While the above mechanisms apply for land experiencing wood harvest, the indirect wood harvest emissions are small whether nitrogen limitation is considered or not, because weaker sinks from CO₂ fertilization also result in lower emissions in the subsequent harvest cycle (except when wood harvest expands to new areas). This is despite our modeling assumption that wood is preferentially harvested from primary forests or mature secondary forests across most regions (consistent with the assumption made in producing the wood harvest data - Hurtt et al. 2011). In our model, regrowing secondary forests requires roughly 30 (tropics)

to 40 (non-tropics) years to attain 80% maturity, and about 90 (tropics) to 150 (non-tropics) years to attain full maturity (Fig. 8; Text S7). The high wood harvest rates projected for the future (Fig. 1; Table 1) result in harvesting young regrowing secondary forests (as primary or mature secondary forests reduce following LULUC) that have not accumulated sufficient biomass (especially in grid cells with high wood harvest rates; see Fig. S7).

Another key result of our simulations is that the total LULUC emissions from the non-tropics are greater than the tropics for 1900-2100 when nitrogen limitation is considered (Figs. 4, 5, Table 4). In the simulations without nitrogen limitation, the LULUC emissions for the tropics were greater than the non-tropics, after 1940s (Fig. 5). This result is consistent with majority of modeling studies that only include the interactive effects of CO₂ and climate in their calculations of total LULUC emissions [Jain et al., 2013].

It is worth noting that there are other important interactions that determine indirect emissions in our modeled results (Fig. 4). For example, converting forests to agriculture increases indirect emissions in the methodological set up of the model experiments, i.e. comparing a hypothetical no-LULUC case with a representative with-LULUC case. This is because the hypothetical forest that exists in the no-LULCC case has greater sinks from CO₂ fertilization than the sinks in non-forests in the with-LULCC case. This capacity for an additional sink is lost due to deforestation; its magnitude depends on both deforested area and the strength of CO₂ fertilization [Pongratz et al., 2009; Strassman et al., 2008]. Indirect emissions are increasingly affected by climate change in the future, for example, a warmer climate projected for the future (Figs. S1, S2) increases indirect emissions due to enhanced soil decomposition (R_h)

and forest decline in some regions. Concurrently, higher decomposition also releases plant usable mineral nitrogen from soils that enhances carbon uptake in regrowing forests during initial stages [McGuire et al., 2007].

3.2.4. Climate induced uncertainties in simulating carbon fluxes from LULUC (with nitrogen limitation effects)

A key source of uncertainty in projecting future LULUC emissions is that due to the indirect human-induced effects via climate change. Here we evaluate the combined uncertainty from two climate variables: temperature and precipitation.

The range of uncertainties in the 21st century cumulative total LULUC emissions, across all the four RCPs driven by different CMIP5 climate model projections are: 91-227 PgC (globally), 21-96 PgC (tropics), and 51-126 PgC (non-tropics) (Table 5). Globally, for all RCPs the estimated range of total LULUC emissions due to climate uncertainty are roughly 50% of the mean value (Fig. 5, Table 5), and are larger than the scenario-based difference of 54 PgC (estimated from Table 4 as the maximum difference in the mean estimates of total LULUC emissions across the RCPs). In some cases, the climate induced uncertainties in indirect LULUC emissions (Table 5; max-min range) are larger than its mean estimates (Table 4), making even the sign of indirect emissions uncertain (fig. 5h, i). The uncertainty tends to increase with time in the higher emission scenarios (Fig. 5), reflecting the progressively increasing model spread in CMIP5 projected climate [Knutti and Sedláček, 2012]. RCP6.0 has the smallest uncertainty

range across all RCPs, partly because only 24 climate model projections were available for RCP6.0 when we carried out the simulations (Table S1).

Most of the uncertainty results from including wood harvest, because its spatial extent is much larger compared to land-use change (fig. 1; Table 1). The uncertainties in simulated indirect (and total) LULUC emissions are greater over the non-tropics than the tropics (Table 5) mainly because of large uncertainties in projected temperature over the temperate zones of the northern hemisphere (Figs. S1, S2) where most of the non-tropical wood harvest occurs (Fig. 9, S7).

Accepted Article

4. Discussion

4.1. Comparison with previous studies

Previous studies that have examined the future LULUC fluxes using CMIP5 data differ from the LULUC flux estimates presented here on multiple aspects: LULUC activities included (e.g. wood harvest) and their implementation in the model; model processes considered (e.g. nitrogen, secondary forest dynamics); and the type of model itself. A direct one-to-one comparison is confounded by these multiple source of differences. Therefore, our approach is to compile the available estimates and identify the causes of difference from our study.

4.1.1. Wood harvest

Hurtt et al. [2011] provides wood harvest, as biomass extracted from each grid cell. They also provide “wood harvest area” in each grid cell, estimated as the sum of primary, mature secondary, and young secondary forest area required to meet the biomass demand from wood harvest. Therefore, the biomass extracted and the wood harvest area was meant to be consistent with each other. In this study, we implemented “wood harvest area” data in ISAM (section 2.3.3) to calculate biomass extracted (Table 6) and LULUC emissions. The 20th century biomass harvested from forest simulated by the ISAM compares well with Hurtt data, because the available forest area (and average forest biomass per grid area) was adequate to meet the historical demands. However, for all four RCPs, our model estimated forest biomass from wood harvest is much lower compared to Hurtt data, due to two reasons.

First, the forest harvest rates for the RCPs (especially RCP6.0 with highest wood harvest area; Table 1) were higher than the contemporary (circa 2005) forest area (and biomass as evaluated in Fig. 2) in ISAM (Fig. 9). Specifically, RCP 6.0 shows high wood harvest rates for the Himalayas and China (Fig. S7) that seem inconsistent with the contemporary forest area estimated from satellites (Fig. 9; see Fig. S8 for MODIS derived land cover map). Therefore, the modeled forest area could not fully meet the prescribed wood harvest demands. The forest definition in ISAM is consistent with the IGBP land-classification scheme, and its contemporary forest estimates have been calibrated using the most recent version of MODIS land-cover data [Meiyappan and Jain, 2012]. In the year 2005, the MODIS estimated global forest area (~30 million km²) was 25% less than the ~40 million km² estimated by Hurtt et al. [2011].

Second, following wood harvest, regrowing forests require about 90 (non-tropics) to 150 (tropics) years to attain full maturity (fig. 8; text S7). Therefore, lower contemporary forest areas in ISAM compared to Hurtt data implies that we had to use more secondary regrowing forests with lower biomass to meet the future harvest area demands, when enough primary forests or mature secondary forests were not available in the grid cell. Hypothetically, even if our harvest area had equaled Hurtt data, a higher fraction of the total harvested area in our model would be from secondary regrowing forests with lower biomass compared to Hurtt estimates. Most of the discrepancy in forest area stems from the non-tropics (Table 3 of Meiyappan and Jain [2012]), where additionally, the biomass harvested from forests are also higher in Hurtt data than in our model (Table 6).

A part of the discrepancy in forest area between our study and Hurtt et al. is attributable to difference in the definition of forest. Hurtt et al. count savannas as forest (using a different tree density threshold to identify forests), but in ISAM, savannas are classified as herbaceous [Meiyappan and Jain, 2012]. This difference in definition implies that we did not use savannas for wood harvest, and our estimate of deforestation (Table 1 and Fig. 1) does not include savannas converted to cropland and pastureland. Multiple definitions for savannas exist [Scholes and Archer, 1997]. In our model, even counting savannas (as per MODIS-IGBP land cover) within forests will not make much of a difference outside the tropics (Fig. 9). Clearly a lack of consensus on how different land-cover types are defined is a source of uncertainty in LULUC emission estimates.

4.1.2. Historical LULUC emissions

The historical ‘total’ LULUC emissions simulated by ISAM have been compared previously [see Jain et al., 2013; Ciais et al., 2013]. For the historical period, we limit discussion to LULUC fluxes that require elaboration.

The direct LULUC emissions estimated without nitrogen limitation are most comparable to estimates from Houghton’s bookkeeping model [Houghton, 2003, 2008], in terms of definition. Strikingly, our estimated non-tropical emissions for 20th century (63 PgC from Table 4 based on average of three reconstructions) are 57% higher than Houghton’s estimate of 40 PgC (data from Fig. 1b of Richter and Houghton [2011]). Most of the difference is explained by the underlying LULUC datasets. Two of our three LULUC reconstructions (based on Ramankutty

[2012] and HYDE agricultural datasets; see Meiyappan and Jain, 2012] show more net forest loss in the non-tropics compared to the third dataset (based on FRA forest data; FAO [2006]) also used in Houghton's model. Our estimates using FRA data for the non-tropics (41 PgC from Table 4 range) compares with Houghton's bookkeeping estimate.

4.1.3. *Future LULUC emissions*

A comparison of our future LULUC emissions with other published estimates is shown in Table 7. Some climate models participating in CMIP5 did not simulate LULUC emissions for the future, but instead were driven using CO₂ emissions from LULUC estimated by the IAMs which produced the RCPs. These estimates include both wood harvest and land-use change. The definition and methodology of calculating LULUC emissions differed among the IAMs [van Vuuren et al., 2011; Pongratz et al., 2014]. Our total (and direct) LULUC emissions estimated without nitrogen limitation (including wood harvest) are either much smaller emissions or even sinks compared with the IAM estimates. Our total (and direct) LULUC emissions estimated with nitrogen limitation are larger than IAM estimates.

The LUCID-CMIP5 project, using five Earth System Models estimated the range of total LULUC emissions for two RCPs. None of the models account for nitrogen limitation, they vary significantly in their carbon-cycle representations, and only one model (MPI-ESM-LR) included wood harvest. The authors acknowledge that their LULUC emissions from MPI-ESM-LR are overestimated due to high initial carbon stocks. Excluding MPI-ESM-LR, the range is 24-70 PgC (RCP2.6) and 30-67 PgC (RCP8.5). For comparison, our estimated global total LULUC

emissions excluding wood harvest and nitrogen limitation, but including climate uncertainties are (cumulated over the 21st century): 14-43 PgC (RCP2.6) and 5-44 PgC (RCP8.5) (Fig. 4c, e).

Kato et al. [2013] using a terrestrial carbon cycle model, estimated total LULUC emissions for the 21st century. Their estimates do not account for nitrogen limitation, wood harvest, and changes in future climate (static climate corresponding to current conditions are used). Kato et al. estimates are larger compared to our estimates without wood harvest and nitrogen limitation (Table 7).

Using a coupled climate model, Lawrence et al. [2012] reported LULUC emissions from one single with-LULUC simulation, without a reference no-LULUC simulation. Therefore, their LULUC emission estimates include only instantaneous and legacy fluxes from LULUC. Fluxes from regrowth sinks and decomposition of on-site residues are not counted towards LULUC flux [Pongratz et al., 2014]. Their model includes nitrogen cycle, the effect of wood harvested from both forest and non-forest trees, in addition to cropland and pastureland transitions. Their estimates are the larger compared to all published studies and our estimates that include nitrogen limitation and wood harvest across all the scenarios. A large part of their LULUC emissions results from including wood harvest (their Fig. 8a, c).

Stocker et al. [2014] using a dynamic global vegetation model reported both total and direct LULUC emissions that include nitrogen cycle, wood harvest, and cropland and pastureland transitions. They accounted for carbon and nitrogen pools between primary and secondary land separately. However, they do not explicitly model secondary forest regrowth dynamics i.e. the process formulations and model parameters are identical between primary and

secondary land. Notably, Stocker et al. used one climate model output (corresponding to model 32 in Table S1) to estimate indirect LULUC emissions (total minus direct emissions) which are smaller compared to our mean estimates (Table 4). However, our multi-model climate sensitivity analysis indicate that the choice of climate data used to force a model can result in substantially different indirect emissions (difference of up to 88PgC globally; Table 5).

Wang et al. [2015] using an Earth System Model reported total LULUC emissions for RCP4.5 and 8.5. In addition to a nitrogen cycle, they also included phosphorous limitation, and wood harvested from both forests and non-forests. Their estimates are lower compared to both our total (and direct) emissions and other studies that include nitrogen limitation and wood harvest.

To summarize, we find that global estimates of LULUC emissions cumulated for 21st century are highly uncertain varying by ~300 PgC (range: -36 to 266 PgC) across published studies (estimates including nitrogen cycle when available). RCP4.5 has the widest range of results varying by ~200 PgC, varying from sink to a source (Table 7). Three studies (ours, Stocker and Wang) that included nitrogen limitation, wood harvest, and regrowth sinks also show widest range of estimates for RCP4.5. There are multiple reasons that could explain these differences, with one possible reason being difference in implementing afforestation data across models [Di Vittorio et al., 2014].

4.2. Model uncertainties

The multi-model comparison presented above characterizes uncertainties across different models. However, an important source of uncertainty is model parameterization i.e. a single model can produce different LULUC emission estimates by varying model parameters within their uncertainty range [Exbrayat et al., 2013]. During model development [e.g. Yang et al., 2009], we have evaluated and calibrated key model parameters based on available observations. However, limited observations also make some of the model parameters highly uncertain. By perturbing two key model parameters as an example, we highlight the impacts of parameter uncertainties on our emission estimates.

First, we test the sensitivity of our assumption that 25% of organic carbon stored in the top meter of the soil is released to the atmosphere when native soils are cleared for cultivation (section 2.2). While numerable meta-analysis [Don et al., 2011; Guo and Gifford, 2002; Murty et al., 2002; Post and Kwon, 2000] broadly report 25-30% loss on an average across all ecosystems, soil types, management practices, and decomposition processes, the variability about the average is large (range: 15-50% from Table 3 of Houghton and Goodale [2004]). We estimated total LULUC emissions (with nitrogen limitation) assuming 22.5% and 32.5% loss roughly corresponding to the 25th and 75th percentile across the observational range. Results show that our global mean estimates (Table 4) could vary by a maximum of -6% (25th %ile) to +18% (75th %ile) across the RCPs (Table S2).

Second, we model biological nitrogen fixation as a function (linear regression) of evapotranspiration, specific to biome type (based on Schimel et al. [1996]). Nitrogen fixation is the largest source of nitrogen input to terrestrial ecosystems; however, its magnitude is also

highly uncertain (overall range of 40-290 TgNyr⁻¹ with estimates being revised downwards; see Cleveland et al. [1999]; Wang and Houlton [2009]; Vitousek et al. [2013]; Sullivan et al. [2014]). By perturbing the regression parameters across all biomes by $\pm 50\%$ (our maximum assumed standard error), the mean estimates for global total LULUC emissions across RCPs (Table 4) vary by -6.4% (+50% perturbation) to +7.3% (-50% perturbation) (Table S3).

The high uncertainty in nitrogen fixation not only reflects limited measurements, but also gaps in mechanistic understanding of nitrogen fixation [Thomas et al., 2015]. Consequently, parameters are just one source of uncertainty in our model. Incomplete understanding on various processes including nitrogen fixation cause structural uncertainties in model. For example, the relationship between nitrogen fixation and evapotranspiration is not from mechanistic understanding, but broadly captures the spatial observation that higher rates of nitrogen fixation are from humid settings with relatively high evapotranspiration [Cleveland et al., 1999]. Further, nitrogen fixation can occur via free-living bacteria or symbiotic relationships [Batterman et al., 2013; Houlton et al., 2008; Vitousek et al., 2013]. Therefore, harvesting of nitrogen-fixing trees may have different consequences for regrowth patterns than evapotranspiration would imply. Nonetheless, most land models to date estimate nitrogen fixation solely as a function of evapotranspiration or NPP [e.g. Hayes et al., 2011; Oleson et al., 2013; Wania et al., 2012; Zaehle and Friend, 2010]; while, both NPP and evapotranspiration based approach have shortcomings, the NPP based approach contradicts empirical knowledge [Wieder et al., 2015b]. Few land models have moved towards a more mechanistic representation of nitrogen fixation that echoes empirical understanding [Gerber et al., 2010; Wang et al., 2010]. Implementing new

approaches in models requires substantial efforts on observational data synthesis to parameterize and evaluate model improvements [Wieder et al., 2015b].

In summary, both parameter and structural uncertainty across all land models including ours extend beyond those discussed above [e.g. Jones et al., 2013; Todd-Brown et al., 2014]. Consequently, these modeling uncertainties impose limits on the accuracy of simulated terrestrial processes.

4.3. *Caveats*

In this study, secondary forests result only from agricultural abandonment and wood harvest. This is because we infer secondary forests from changes in cropland, pastureland and wood harvest areas [Hurtt et al., 2011; Meiyappan and Jain, 2012]. Several countries across the world create more forests through massive reforestation and afforestation efforts that add to the land carbon sink [Fang et al., 2014; FAO, 2010]. We account for carbon sinks from conversion of crops and pastures to secondary forests on lands that were historically forested (reforestation) and non-forested (afforestation). However, we do not account for afforestation on land that is not cropland or pastureland as secondary-to-secondary land conversion information is unavailable [Hurtt et al., 2011]. During 2000-05, Houghton [2013b] estimated that afforestation in the tropics had contributed to ~1% of the region's total gross sinks. Globally, the share might increase in the future, as countries increase their land carbon storage through management practices as modeled in IAM scenarios and even pledged under the United Nations Framework Convention on Climate Change [UNEP, 2013].

This study does not include wood harvested from non-forest tree types and savannas, which Hurtt et al. [2011] count as forest. This is because ISAM classifies these types as herbaceous [Yang et al., 2010]. Herbaceous land-cover types have lesser capacity to store carbon than forests. Our analysis of Hurtt et al. [2011] data indicates that accounting for non-forest wood harvest would have increased our gross carbon source from wood harvest by 10-37% during the 21st century (Table 6). A part of this biomass harvested would be compensated through regrowth sinks thus making a minor difference to our estimated total LULUC emissions.

We infer land-use changes in the model using net changes in cropland and pastureland areas between consecutive years within each grid cell [Hurtt et al., 2011; Meiyappan and Jain, 2012]. This is because existing land use reconstructions (including HYDE used in Hurtt data) draw upon (sub-) national land use statistics at annual time steps that are the net changes. In reality, it is the gross changes (all area gains and losses) that determine the LULUC fluxes. For example, land use statistics collected at administrative level (e.g. state or country level data typically used in historical reconstructions) can indicate zero change in cropland area between two years, but it does not imply that cropland area has remained unchanged in every grid within the administrative region. Similarly, within a grid cell, different sub-grid areas can undergo land cover change (gross changes) in rotation (e.g. crop to forest, forest to grass, and grass to crop), but at the grid cell level the net change in land cover areas could fully or partly cancel out [Fuchs et al., 2014]. However, these sub-grid changes would still affect the carbon fluxes and land carbon storage over time. In such cases, we might be underestimating the total LULUC emissions. Currently, there is no consensus on how a given LULUC data be implemented within

a model [Brovkin et al., 2013; Pitman et al., 2009; Wilkenskield et al., 2014]. Our interpretation of net changes in land-use area within grid cells is consistent with the economic rationale in spatial land-use allocation modules of IAMs that humans tend to lower the cost associated with relocating land areas [Meiyappan et al., 2014; Verburg and Overmars, 2009].

Several other LULUC activities such as shifting cultivation, agricultural management, fire management, land degradation, peatlands, erosion, and woody encroachment have not been included in this study. These factors together could be significant in the global carbon budget, but estimates for some of these factors are highly uncertain even for recent past [Houghton et al., 2012]. From 2000-05, Houghton [2013b] estimated that direct emissions from shifting cultivation (0.082 PgC/yr) accounted for ~7% of total direct emissions in the tropics. Gross sources from shifting cultivation are much larger (~27% of the total gross sources), but regrowth sinks on fallows balances most of the gross sources.

We represent cropland as a ‘generic’ category in our model. Therefore, we do not explicitly simulate the management effects of bioenergy crops/plantations on LULUC emissions. The treatment of bioenergy across the four independent IAM groups that produced the four RCPs is different (test S1). For example, bioenergy is included in wood harvest in RCP8.5, whereas bioenergy is included in cropland in RCP2.6. The ‘land-use change’ effects of implementing bioenergy within croplands (as opposed to its land use/management effects) are however captured by Hurtt et al. [2011] data that drive our land-surface model, and hence by our LULUC emission estimates. For example, Hurtt estimates for RCP2.6 shows the largest increase in cropland area due to bioenergy (Fig. 1), mostly at the expense of forests (table 1).

The study does not account for two key model processes. First is the co-limitation of phosphorus with nitrogen, especially in the moist tropics [Vitousek et al., 2010]. Only recently have models started to include phosphorus dynamics [Goll et al., 2012; Yang et al., 2013; Zhang et al., 2013;], and only Zhang et al. [2013] represent LULUC. Second are the impacts of LULUC on climate realized through biogeophysical pathways [Mahmood et al., 2013]. Brovkin et al. [2013], Kumar et al. [2013], and Lawrence et al. [2012] have examined the biogeophysical impacts of LULUC for the RCPs.

4.4. Summary and implications of results for climate modeling and climate policy

Our analysis offers insight into complex interactions among CO₂ emissions from LULUC, environmental changes, and nitrogen limitation effect on the regrowth sinks. Table 8 summarizes our model estimated uncertainty across different drivers. There are four key conclusions from our modeling study.

First, nitrogen limitation of CO₂ uptake is substantial and sensitive to nitrogen inputs. In our model, excluding nitrogen limitation underestimated global total LULUC emissions by 34-52 PgC (~21-29%) during the 20th century and by 128-187 PgC (90-150%) during the 21st century (Table 8). The difference increases with time because nitrogen limitation will progressively down-regulate the magnitude of CO₂ fertilization effect on regrowing forests, due to decreasing supply of plant-usable mineral nitrogen. Further, regrowing forests become increasingly nitrogen limited due to LULUC-related nitrogen losses from the system. Without large amounts of nitrogen input to the system, the regrowing forests are likely to be nitrogen limited. To meet the

same mitigation target despite larger total LULUC emissions would require an equivalent greater reduction of fossil fuel emissions.

Second, including nitrogen limitation changes the region with the highest total LULUC emissions from the tropics to the non-tropics. The tropics had higher emissions in our simulations without nitrogen limitation, and also earlier studies that considered only the interactive effects of CO₂ and climate. Total LULUC emissions from the non-tropics are greater when the nitrogen cycle is included mainly because the carbon uptake capacity of secondary forests following LULUC is limited by nitrogen deficiency.

Third, historically, the indirect effects of anthropogenic activity through environmental changes in land experiencing LULUC (indirect emissions) are small compared to direct effects of anthropogenic LULUC activity (direct emissions). As a result, including or excluding indirect emissions had a minor influence on the estimated total LULUC emissions historically. In contrast, the indirect LULUC emissions for the 21st century are a much larger source to the atmosphere, in simulations with nitrogen limitation (Table 4). This is because of the gradual weakening of the photosynthetic response to elevated [CO₂] caused by nitrogen limitation.

In this study, we separately accounted for the effects of nitrogen limitation in both direct and indirect LULUC emissions. In principle, the nitrogen limitation effects are also an indirect effect of anthropogenic activity due to environmental change impacts on natural plant processes, hence can be fully counted within indirect emissions (i.e. exclude the effect of nitrogen limitation from direct emissions, and add it to indirect emissions). Following such an accounting procedure will further increase the indirect LULUC emissions for the 21st century (123-162 PgC; calculated

from Table 4 as the difference between total LULUC emissions estimated with nitrogen limitation and direct LULUC emissions estimated without nitrogen limitation), and will dominate over direct emissions (-39–31 PgC; Table 4 without nitrogen limitation case). By either method, our results indicate that treatment of environmental factors can substantially influence the estimated total LULUC emissions for the future (see Houghton [2013a] for an associated discussion).

Fourth, the choice of climate model projection used to force a land model can substantially impact the estimated indirect (and total) LULUC emissions (Table 8). The climate induced uncertainty ranges are larger than the mean estimates of global indirect LULUC emissions cumulated over the 21st century for three RCP scenarios. Further, the indirect LULUC emission estimated for the non-tropics are affected more by climate uncertainties than for the tropics, because larger areas under LULUC (especially wood harvest) in the non-tropics coincide spatially with regions where climate uncertainties are high.

While interpreting our results, the limitations highlighted earlier should be kept in mind. Notably, using one land-surface model is potentially a limiting factor because it does not represent a broad range of model physics response, especially given that there are significant uncertainties in modeling both nitrogen and carbon cycles [Houghton et al., 2012; Friedlingstein and Prentice, 2010], LULUC activities considered [Houghton et al., 2012], and even the method of implementing a given LULUC dataset across biosphere models [Brovkin et al., 2013; Pitman et al., 2009]. Conversely, using a single land-surface model is more appropriate for our analysis because we can consistently isolate the effects on LULUC emissions due to different LULUC

activities, LULUC flux definitions, historical LULUC forcings, and future climate forcings. The above effects cannot be consistently isolated using multi-model comparisons because model-based differences (e.g. different land cover representations) make attribution difficult.

In summary, Hurtt et al. [2011] show that excluding wood harvest alone can underestimate secondary land by 57% on an average for RCPs, and so the associated carbon source. Even if land management is represented, excluding nitrogen limitation will overestimate the carbon sinks on land recovering from LULUC, thereby underestimating total LULUC emissions. It is the total LULUC emissions that the atmosphere sees which can be mitigated by reversing or avoiding any LULUC activity. Notwithstanding the aforementioned caveats, our study implies that the effectiveness of land-based mitigation strategies would critically depend on the interactions between nutrient limitations and secondary forests resulting from LULUC. Therefore, it is important for terrestrial biosphere models to consider nitrogen limitation in estimates of the strength of the future land carbon sink, especially on regrowing forests.

Acknowledgements

Model outputs presented in this study can be obtained from Prasanth Meiyappan (meiyapp2@illinois.edu). We thank Benjamin Houlton and the anonymous reviewers for helpful suggestions. We acknowledge the WCRP's Working Group on Coupled Modelling and the climate modeling groups for producing and making available their model output. The NASA Land Cover and Land Use Change Program (NNX14AD94G), the US National Science Foundation (NSF-AGS-12-43071), and the U.S. Department of Energy (DOE-DE-SC0006706) supported this work. JH was funded by a Leverhulme Early Career Research Fellowship, UK.

Accepted Article

References

- Ballantyne, A. P., Andres, R., Houghton, R., Stocker, B. D., Wanninkhof, R., Anderegg, W., Cooper, L. A., DeGrandpre, M., Tans, P. P., Miller, J. B., Alden, C., and White, J. W. C.: Audit of the global carbon budget: estimate errors and their impact on uptake uncertainty, *Biogeosciences*, 12, 2565-2584, 2015.
- Batterman, S. A., Hedin, L. O., Van Breugel, M., Ransijn, J., Craven, D. J., & Hall, J. S. (2013). Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature*, 502(7470), 224-227.
- Boden, T.A., G. Marland, and R.J. Andres. (2013). Global, Regional, and National Fossil-Fuel CO2 Emissions. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A. doi 10.3334/CDIAC/00001_V2013.
- Boysen, L., Brovkin, V., Arora, V. K., Cadule, P., de Noblet-Ducoudré, N., Kato, E., ... & Gayler, V. (2014). Global and regional effects of land-use change on climate in 21st century simulations with interactive carbon cycle. *Earth System Dynamics*, 5, 309-319.
- Brovkin, V., and Coauthors. (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. Climate*, 26, 6859–6881.
- Chapin III, F. S., Woodwell, G. M., Randerson, J. T., Rastetter, E. B., Lovett, G. M., Baldocchi, D. D., ... & Schulze, E. D. (2006). Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, 9(7), 1041-1050.
- Ciais P, Sabine C, Bala G, et al. (2013) Carbon and other biogeochemical cycles. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the International Panel on Climate Change (eds Stocker T, Qin D, Plattner G-K, et al.) Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Cleveland, C. C., Taylor, P., Chadwick, K. D., Dahlin, K., Doughty, C. E., Malhi, Y., ... & Townsend, A. R. (2015). A comparison of plot-based, satellite and Earth system model estimates of tropical forest net primary production. *Global Biogeochemical Cycles*. Doi: 10.1002/2014GB005022.
- Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Howarth, R. W., Hedin, L. O., ... & Wasson, M. F. (1999). Global patterns of terrestrial biological nitrogen (N₂) fixation in natural ecosystems. *Global biogeochemical cycles*, 13(2), 623-645.
- Davidson, E. A., Reis de Carvalho, C. J., Vieira, I. C., Figueiredo, R. D. O., Moutinho, P., Yoko Ishida, F., ... & Tuma Sabá, R. (2004). Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecological Applications*, 14(sp4), 150-163.
- Davidson, E. A., de Carvalho, C. J. R., Figueira, A. M., Ishida, F. Y., Ometto, J. P. H., Nardoto, G. B., ... & Martinelli, L. A. (2007). Recuperation of nitrogen cycling in Amazonian forests following agricultural abandonment. *Nature*, 447(7147), 995-998.
- Di Vittorio, A. V., Chini, L. P., Bond-Lamberty, B., Mao, J., Shi, X., Truesdale, J., ... & Thomson, A. (2014). From land use to land cover: restoring the afforestation signal in a

- coupled integrated assessment–earth system model and the implications for CMIP5 RCP simulations. *Biogeosciences*, 11(22), 6435-6450.
- Don, A., Schumacher, J., & Freibauer, A. (2011). Impact of tropical land-use change on soil organic carbon stocks—a meta-analysis. *Global Change Biology*, 17(4), 1658-1670.
- El-Masri, B., Barman, R., Meiyappan, P., Song, Y., Liang, M., & Jain, A. K. (2013). Carbon dynamics in the Amazonian Basin: Integration of eddy covariance and ecophysiological data with a land surface model. *Agricultural and Forest Meteorology*, 182, 156-167.
- Exbrayat, J. F., Pitman, A. J., Zhang, Q., Abramowitz, G., & Wang, Y. P. (2013). Examining soil carbon uncertainty in a global model: response of microbial decomposition to temperature, moisture and nutrient limitation. *Biogeosciences*, 10(11), 7095-7108.
- Fang, J., Guo, Z., Hu, H., Kato, T., Muraoka, H. and Son, Y. (2014), Forest biomass carbon sinks in East Asia, with special reference to the relative contributions of forest expansion and forest growth. *Global Change Biology*. doi: 10.1111/gcb.12512
- FAO (2006) Global Forest Resources Assessment 2005 . FAO forestry Paper 147, Rome.
- FAO (2010). Global Forest Resources Assessment 2010. FAO forestry Paper 13, Rome.
- Finzi, A. C., Moore, D. J., DeLucia, E. H., Lichter, J., Hofmockel, K. S., Jackson, R. B., ... & Schlesinger, W. H. (2006). Progressive nitrogen limitation of ecosystem processes under elevated CO₂ in a warm-temperate forest. *Ecology*, 87(1), 15-25.
- Finzi, A. C., Norby, R. J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W. E., ... & Ceulemans, R. (2007). Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences*, 104(35), 14014-14019.
- Friedl, M. A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A., & Huang, X. (2010). MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets. *Remote Sensing of Environment*, 114(1), 168-182.
- Friedlingstein, P., & Prentice, I. C. (2010). Carbon–climate feedbacks: a review of model and observation based estimates. *Current Opinion in Environmental Sustainability*, 2(4), 251-257.
- Fuchs, R., Herold, M., Verburg, P., Clevers, J., & Eberle, J. 2014. Gross changes in reconstructions of historic land cover/use for Europe between 1900 and 2010. *Global Change Biology*. doi: 10.1111/gcb.12714.
- Gerber, S., Hedin, L. O., Oppenheimer, M., Pacala, S. W., & Shevliakova, E. (2010). Nitrogen cycling and feedbacks in a global dynamic land model. *Global Biogeochemical Cycles*, 24(1).
- Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., ... & Niinemets, Ü. (2012). Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling. *Biogeosciences*, 9, 3547-3569.
- Guo, L. B., & Gifford, R. M. (2002). Soil carbon stocks and land use change: a meta analysis. *Global change biology*, 8(4), 345-360.

- Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. *International Journal of Climatology*, 34(3), 623-642.
- Hanson, P. J., Amthor, J. S., Wullschlegel, S. D., Wilson, K. B., Grant, R. F., Hartley, A., ... & Cushman, R. M. (2004). Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. *Ecological Monographs*, 74(3), 443-489.
- Hayes, D. J., McGuire, A. D., Kicklighter, D. W., Gurney, K. R., Burnside, T. J., & Melillo, J. M. (2011). Is the northern high-latitude land-based CO₂ sink weakening?. *Global Biogeochemical Cycles*, 25(3).
- Herbert, D. A., Williams, M., & Rastetter, E. B. (2003). A model analysis of N and P limitation on carbon accumulation in Amazonian secondary forest after alternate land-use abandonment. *Biogeochemistry*, 65(1), 121-150.
- Houghton, R. A., & Goodale, C. L. (2004). Effects of Land-Use Change on the Carbon Balance of Terrestrial Ecosystems. *Ecosystems and land use change*, 85-98.
- Houghton, R.A., and J.L. Hackler. (2001). *Carbon Flux to the Atmosphere From Land-use Changes: 1850 to 1990*. NDP-050/R1, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee.
- Houghton RA (2003) Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. *Tellus B*, 55, 378–390.
- Houghton RA (2008) Carbon flux to the atmosphere from land-use changes: 1850-2005. In: *TRENDS: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A.
- Houghton, R. A. (2013a). Keeping management effects separate from environmental effects in terrestrial carbon accounting. *Global change biology*, 19(9), 2609-2612.
- Houghton, R. A. (2013b). The emissions of carbon from deforestation and degradation in the tropics: past trends and future potential. *Carbon Management*, 4(5), 539-546.
- Houghton, R. A., House, J. I., Pongratz, J., Werf, G. R., DeFries, R. S., Hansen, M. C., ... & Ramankutty, nitrogen. (2012). Carbon emissions from land use and land-cover change. *Biogeosciences*, 9(12), 5125-5142.
- Houlton, B. Z., Wang, Y. P., Vitousek, P. M., & Field, C. B. (2008). A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature*, 454(7202), 327-330.
- Hungate, B. A., Dukes, J. S., Shaw, M. R., Luo, Y., & Field, C. B. (2003). Nitrogen and climate change. *Science*, 302(5650), 1512-1513.
- Huntzinger, D. N., Post, W. M., Wei, Y., Michalak, A. M., West, T. O., Jacobson, A. R., ... & Cook, R. (2012). North American Carbon Program (NACP) regional interim synthesis: Terrestrial biospheric model intercomparison. *Ecological Modelling*, 232, 144-157.
- Hurt, G. C., Chini, L. P., Frohling, S., Betts, R. A., Feddema, J., Fischer, G., ... & Wang, Y. P. (2011). Harmonization of land-use scenarios for the period 1500–2100: 600 years of

- global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Climatic Change*, 109(1-2), 117-161.
- IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.
- Ito, A., Penner, J. E., Prather, M. J., De Campos, C. P., Houghton, R. A., Kato, T., ... & Price, D. T. (2008). Can we reconcile differences in estimates of carbon fluxes from land-use change and forestry for the 1990s?. *Atmospheric Chemistry and Physics*, 8(12), 3291-3310.
- Jain AK, Yang X, Kheshgi H, McGuire AD, Post W, Kicklighter D (2009) Nitrogen attenuation of terrestrial carbon cycle response to global environmental factors. *Global Biogeochem.Cycles*, 23, GB4028, doi:10.1029/2009GB003519.
- Jain, A. K., Meiyappan, P., Song, Y. and House, J. I. (2013). CO₂ emissions from land-use change affected more by nitrogen cycle, than by the choice of land-cover data. *Global Change Biology*, 19: 2893–2906.
- Jain, AK, and Yang, X (2005) Modeling the effects of two different land-cover change data sets on the carbon stocks of plants and soils in concert with CO₂ and climate change. *Global Biogeochem.Cycles*, 19(2), 1-20.
- Jones, C., Robertson, E., Arora, V., Friedlingstein, P., Shevliakova, E., Bopp, L., ... & Tjiputra, J. (2013). Twenty-first-century compatible CO₂ emissions and airborne fraction simulated by CMIP5 earth system models under four representative concentration pathways. *Journal of Climate*, 26(13), 4398-4413.
- Kato, E., Kinoshita, T., Ito, A., Kawamiya, M., & Yamagata, Y. (2013). Evaluation of spatially explicit emission scenario of land-use change and biomass burning using a process-based biogeochemical model. *Journal of Land Use Science*, 8(1), 104-122.
- Kindermann, G. E., McCallum, I., Fritz, S., & Obersteiner, M. (2008). A global forest growing stock, biomass and carbon map based on FAO statistics. *Silva Fennica*, 42(3), 387.
- Klein Goldewijk, K., & Verburg, P. H. (2013). Uncertainties in global-scale reconstructions of historical land use: an illustration using the HYDE data set. *Landscape ecology*, 28(5), 861-877.
- Klein Goldewijk, K., Beusen, A., Van Drecht, G., & De Vos, M. (2011). The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, 20(1), 73-86.
- Knutti, R., & Sedláček, J. (2012). Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Climate Change*, 3, 369-373.
- Kumar, S., Dirmeyer, P. A., Merwade, V., DelSole, T., Adams, J. M., & Niyogi, D. (2013). Land use/cover change impacts in CMIP5 climate simulations—a new methodology and 21st century challenges. *Journal of Geophysical Research: Atmospheres*, 118, 6337–6353.

- Lamarque, J. F., Kyle, G. P., Meinshausen, M., Riahi, K., Smith, S. J., van Vuuren, D. P., ... & Vitt, F. (2011). Global and regional evolution of short-lived radiatively-active gases and aerosols in the Representative Concentration Pathways. *Climatic change*, 109(1-2), 191-212.
- Lawrence, P. J., Feddema, J. J., Bonan, G. B., Meehl, G. A., O'Neill, B. C., Oleson, K. W., ... & Thornton, P. E. (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. *Journal of Climate*, 25(9), 3071-3095.
- LeBauer, D. S., & Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89(2), 371-379.
- Le Quéré, C., Moriarty, R., Andrew, R. M., Peters, G. P., Ciais, P., Friedlingstein, P., Jones, S. D., Sitch, S., Tans, P., Arneeth, A., Boden, T. A., Bopp, L., Bozec, Y., Canadell, J. G., Chini, L. P., Chevallier, F., Cosca, C. E., Harris, I., Hoppema, M., Houghton, R. A., House, J. I., Jain, A. K., Johannessen, T., Kato, E., Keeling, R. F., Kitidis, V., Klein Goldewijk, K., Koven, C., Landa, C. S., Landschützer, P., Lenton, A., Lima, I. D., Marland, G., Mathis, J. T., Metzl, N., Nojiri, Y., Olsen, A., Ono, T., Peng, S., Peters, W., Pfeil, B., Poulter, B., Raupach, M. R., Regnier, P., Rödenbeck, C., Saito, S., Salisbury, J. E., Schuster, U., Schwinger, J., Séférian, R., Segsneider, J., Steinhoff, T., Stocker, B. D., Sutton, A. J., Takahashi, T., Tilbrook, B., van der Werf, G. R., Viovy, N., Wang, Y.-P., Wanninkhof, R., Wiltshire, A., and Zeng, N.: Global carbon budget 2014, *Earth Syst. Sci. Data*, 7, 47-85, doi:10.5194/essd-7-47-2015, 2015.
- Loveland, T. R. and Belward, A. S. (1997). The IGBP-DIS Global 1 km Land Cover Data Set, DISCover First Results. *International Journal of Remote Sensing*, v. 18, no. 5, p. 3,289-3,295.
- Luo, Y., Hui, D., & Zhang, D. (2006). Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology*, 87(1), 53-63.
- Luo, Y., Su, B. O., Currie, W. S., Dukes, J. S., Finzi, A., Hartwig, U., ... & Field, C. B. (2004). Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, 54(8), 731-739.
- Mahmood, R., Pielke, R. A., Hubbard, K. G., Niyogi, D., Dirmeyer, P. A., McAlpine, C., ... & Fall, S. (2013). Land cover changes and their biogeophysical effects on climate. *International Journal of Climatology*. doi: 10.1002/joc.3736
- Mathers, N. J., Harms, B., & Dalal, R. C. (2006). Impacts of land-use change on nitrogen status and mineralization in the Mulga Lands of Southern Queensland. *Austral ecology*, 31(6), 708-718.
- McGuire AD, Stitch, S, Clein, JS et al. (2001) Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO₂. climate and land use effects with four process-based ecosystem models, *Global Biogeochemical Cycles*, 15, 183-206.
- McGuire, A. D., Chapin Iii, F. S., Wirth, C., Apps, M., Bhatti, J., Callaghan, T., ... & Vaganov, E. (2007). Responses of high latitude ecosystems to global change: Potential

- consequences for the climate system. In *Terrestrial Ecosystems in a Changing World* (pp. 297-310). Springer Berlin Heidelberg.
- Meinshausen, M., Smith, S. J., Calvin, K., Daniel, J. S., Kainuma, M. L. T., Lamarque, J. F., ... & van Vuuren, D. P. P. (2011). The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change*, 109(1-2), 213-241.
- Meiyappan P and Jain, AK (2012). Three distinct global estimates of historical land-cover change and land-use conversions for over 200 years. *Front. Earth Sci.*, 6(2): 122–139, DOI 10.1007/s11707-012-0314-2.
- Meiyappan, P., Dalton, M., O'Neill, B. C., and Jain, A. K. (2014). Spatial modeling of agricultural land use change at global scale. *Ecological Modelling*. 291: 152-174.
- Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., van Vuuren, D. P., ... & Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, 463(7282), 747-756.
- Murty, D., Kirschbaum, M. U., Mcmurtrie, R. E., & Mcgilvray, H. (2002). Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. *Global Change Biology*, 8(2), 105-123.
- Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., & McMurtrie, R. E. (2010). CO2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences*, 107(45), 19368-19373.
- Oleson, K. W., Lawrence, D. M., Bonan, G. B., Drewniak, B., Huang, M., Koven, C. D., ... & Yang, Z. L. (2013). Technical description of version 4.5 of the Community Land Model (CLM). Ncar Tech. Note NCAR/TN-503+ STR. National Center for Atmospheric Research, Boulder, CO, 422 pp. doi: 10.5065/D6RR1W7M.
- Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., ... & Katul, G. G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. *Nature*, 411(6836), 469-472.
- Pastor, J., & Post, W. M. (1985). *Development of a linked forest productivity-soil process model* (No. ORNL/TM-9519). Oak Ridge National Lab., TN (USA).
- Pitman, A. J., de Noblet-Ducoudré, N., Cruz, F. T., Davin, E. L., Bonan, G. B., Brovkin, V., ... & Voldoire, A. (2009). Uncertainties in climate responses to past land cover change: First results from the LUCID intercomparison study. *Geophysical Research Letters*, 36(14).
- Pongratz, J., Reick, C. H., Raddatz, T., & Claussen, M. (2009). Effects of anthropogenic land cover change on the carbon cycle of the last millennium. *Global Biogeochemical Cycles*, 23(4).
- Pongratz, J. (2013). Climate science: Plant a tree, but tend it well. *Nature*, 498(7452), 47-48.
- Pongratz, J., Reick, C. H., Houghton, R. A., & House, J. I. (2014). Terminology as a key uncertainty in net land use and land cover change carbon flux estimates. *Earth Syst. Dynam.*, 5, 177-195, doi:10.5194/esd-5-177-2014.
- Post, W. M., & Kwon, K. C. (2000). Soil carbon sequestration and land-use change: processes and potential. *Global change biology*, 6(3), 317-327.

- Ramankutty, N. (2012). Global Cropland and Pasture Data from 1700 - 2007. Available online at (<http://www.geog.mcgill.ca/~nramankutty/Datasets/Datasets.html>) from the LUGE (Land Use and the Global Environment) Laboratory, Department of Geography, McGill University, Montreal, Quebec, Canada. [Accessed on 15 May 2013].
- Ramankutty, N., & Foley, J. A. (1999). Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global biogeochemical cycles*, 13(4), 997-1027.
- Reich, P. B., Hungate, B. A., & Luo, Y. (2006). Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annual Review of Ecology, Evolution, and Systematics*, 611-636.
- Richter, Daniel deB, Jr., & Houghton, R. A. (2011). Gross CO₂ fluxes from land-use change: implications for reducing global emissions and increasing sinks. *Carbon Management*, 2(1), 41-47.
- Running, S. W., Nemani, R. R., Heinsch, F. A., 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, B. B., & Fisher, J. B. (2015). Effect of increasing CO₂ on the terrestrial carbon cycle. *Proceedings of the National Academy of Sciences*, 112(2), 436-441.
- Schimel, D. S., Braswell, B. H., McKeown, R., Ojima, D. S., Parton, W. J., & Pulliam, W. (1996). Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. *Global Biogeochemical Cycles*, 10(4), 677-692.
- Schipper, L. A., Baisden, W. T., Parfitt, R. L., Ross, C., Claydon, J. J., & Arnold, G. (2007). Large losses of soil C and N from soil profiles under pasture in New Zealand during the past 20 years. *Global Change Biology*, 13(6), 1138-1144.
- Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas 1. Annual review of Ecology and Systematics, 28(1), 517-544.
- Shevliakova, E., Stouffer, R. J., Malyshev, S., Krasting, J. P., Hurtt, G. C., & Pacala, S. W. (2013). Historical warming reduced due to enhanced land carbon uptake. *Proceedings of the National Academy of Sciences*, 201314047.
- Stocker, B. D., Feissli, F., Strassmann, K. M., Spahni, R., & Joos, F. (2014). Past and future carbon fluxes from land use change, shifting cultivation and wood harvest. *Tellus B*, 66, 23188.
- Strassmann, K. M., Joos, F., & Fischer, G. (2008). Simulating effects of land use changes on carbon fluxes: past contributions to atmospheric CO₂ increases and future commitments due to losses of terrestrial sink capacity. *Tellus B*, 60(4), 583-603.
- Sullivan, B. W., Smith, W. K., Townsend, A. R., Nasto, M. K., Reed, S. C., Chazdon, R. L., & Cleveland, C. C. (2014). Spatially robust estimates of biological nitrogen (N) fixation imply substantial human alteration of the tropical N cycle. *Proceedings of the National Academy of Sciences*, 111(22), 8101-8106.
- Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, 93(4), 485-498.

- Tian, H., Lu, C., Yang, J., Banger, K., Huntinzger, D. N., Schwalm, C. R., ... & Zeng, N. (2015). Global Patterns and controls of soil organic carbon dynamics as simulated by multiple terrestrial biosphere models: current status and future directions. *Global Biogeochemical Cycles*. doi: 10.1002/2014GB005021
- Thomas, R. Q., Brookshire, E. N., & Gerber, S. (2015). Nitrogen limitation on land: how can it occur in Earth system models?. *Global change biology*, 21(5), 1777-1793.
- Todd-Brown, K. E. O., Randerson, J. T., Hopkins, F., Arora, V., Hajima, T., Jones, C., ... & Allison, S. D. (2014). Changes in soil organic carbon storage predicted by Earth system models during the 21st century. *Biogeosciences*, 11(8), 2341-2356.
- UNEP (2013). The Emissions Gap Report 2013 - A UNEP Synthesis Report, Nairobi, Kenya: UNEP. Available at <http://www.unep.org/emissionsgapreport2013/>
- van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., ... & Rose, S. K. (2011). The representative concentration pathways: an overview. *Climatic Change*, 109(1-2), 5-31.
- Verburg, P. H., & Overmars, K. P. (2009). Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. *Landscape ecology*, 24(9), 1167-1181.
- Vitousek, P. M., Porder, S., Houlton, B. Z., & Chadwick, O. A. (2010). Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, 20(1), 5-15.
- Vitousek, P. M., Menge, D. N., Reed, S. C., & Cleveland, C. C. (2013). Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621), 20130119.
- Walker, A. P., Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Asao, S., Hickler, T., ... & Norby, R. J. (2015). Predicting long-term carbon sequestration in response to CO₂ enrichment: How and why do current ecosystem models differ?. *Global Biogeochemical Cycles*. DOI: 10.1002/2014GB004995.
- Walker, A. P., Hanson, P. J., Jain, A., Lomas, M., Luo, Y., McCarthy, H., ... & Iversen, C. M. (2014). Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO₂ enrichment experiments: model performance at ambient CO₂ concentration.
- Wang, Y. P., Zhang, Q., Pitman, A. J., & Dai, Y. (2015). Nitrogen and phosphorous limitation reduces the effects of land use change on land carbon uptake or emission. *Environmental Research Letters*, 10(1), 014001.
- Wang, Y. P., Law, R. M., & Pak, B. (2010). A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences*, 7(7), 2261-2282.
- Wang, Y. P., & Houlton, B. Z. (2009). Nitrogen constraints on terrestrial carbon uptake: Implications for the global carbon-climate feedback. *Geophysical Research Letters*, 36(24).
- Wania, R., Meissner, K. J., Eby, M., Arora, V. K., Ross, I., & Weaver, A. J. (2012). Carbon-nitrogen feedbacks in the UVic ESCM. *Geoscientific Model Development*, 5(5), 1137-1160.

- Wårilind, D., Smith, B., Hickler, T., & Arneth, A. (2014). Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model. *Biogeosciences*, 11, 6131-6146.
- Wieder, W. R., Cleveland, C. C., Smith, W. K., & Todd-Brown, K. (2015a). Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geoscience*. doi:10.1038/ngeo2413
- Wieder, W. R., Cleveland, C. C., Lawrence, D. M., & Bonan, G. B. (2015b). Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study. *Environmental Research Letters*, 10(4), 044016.
- Wilkenskjeld, S., Kloster, S., Pongratz, J., Raddatz, T., & Reick, C. (2014). Comparing the influence of net and gross anthropogenic land use and land cover changes on the carbon cycle in the MPI-ESM. *Biogeosciences*, 11, 4817-4828.
- Yang X, Richardson TK, and Jain AK (2010) Contributions of secondary forest and nitrogen dynamics to terrestrial carbon uptake *Biogeosciences*, 7, 3041–3050.
- Yang X, Wittig V, Jain A, and Post W (2009) Integration of Nitrogen Dynamics into a Global Terrestrial Ecosystem Model *Global Biogeochem. Cycles*, 23, GB4028, doi:10.1029/2009GB003519.
- Yang, X., Thornton, P. E., Ricciuto, D. M., & Post, W. M. (2013). The role of phosphorus dynamics in tropical forests—a modeling study using CLM-CNP. *Biogeosciences*, 11, 1667-1681.
- Zaehle, S., & Friend, A. D. (2010). Carbon and nitrogen cycle dynamics in the O-CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. *Global Biogeochemical Cycles*, 24(1).
- Zhang, Q., Pitman, A. J., Wang, Y. P., Dai, Y., & Lawrence, P. J. (2013). The impact of nitrogen and phosphorous limitation on the estimated terrestrial carbon balance and warming of land use change over the last 156 yr. *Earth System Dynamics*, 4, 333-345.
- Zhao, M., & Running, S. W. (2010). Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *science*, 329(5994), 940-943.
- Zhao, M., Heinsch, F. A., Nemani, R. R., & Running, S. W. (2005). Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote sensing of Environment*, 95(2), 164-176.

Figure legends

Fig. 1. Annual rates of change in cropland and pastureland, annual wood harvest area from forests and annual net deforestation rates (net forest area loss including afforestation, and forest regrowth following cropland and pastureland abandonment; negative values indicate net forest loss) for 1900-2100. Figure legends are shown in panel (a). All units are in million ha/yr (1 ha = 0.01 km²).

Fig. 2. Zonal breakdown of above-ground carbon in forests (year 2000) based on: (1) our historical model simulations (averaged across estimates obtained using three LULUC datasets; including both primary and secondary forests), and (2) global gridded estimates based on FAO statistics [Kindermann et al., 2008]. Darker grey shades in the background indicate larger forest area fraction along the latitude based on FAO statistics.

Fig. 3. NPP estimated for different land cover types averaged globally over the period 2001-2005. The results are compared between (1) our historical model simulations, and (2) radiation-based modeled estimates of NPP derived from MODIS [Zhao and Running, 2010]. The error bars indicate the standard deviation across the 5-year annual estimates. Our model-based error bars also encompass differences induced by LULUC datasets.

Fig. 4. Break-down of LULUC emission fluxes attributable to land-use change (green bars), and forest wood harvest (brown bars). The fluxes shown are direct, indirect, and total (direct + indirect) emissions. Two sets of estimates are shown, one with and the other without the effect of nitrogen limitation. The first three bars in each panel are estimates that include the effect of nitrogen limitation ('With N lim' - see panel 'a'), and the other three bars are estimates without nitrogen limitation effect ('No N lim'). The historical estimates are averages based on the three LULUC reconstructions. For each RCP, an array of LULUC fluxes were estimated, using outputs from a suite of climate model projections from the CMIP5 multi-model ensemble

database (Table S1). The estimates shown for the RCPs are the mean across the array of estimates. Positive values indicate a land to atmosphere flux. Units are in PgC/century.

Fig. 5. Estimates of direct, indirect and total (direct + indirect) emissions from LULUC averaged over each decade. The dark lines indicate the estimates that include the effect of nitrogen limitation. The grey lines are estimates obtained without nitrogen limitation effect. The historical estimates are averages based on the three LULUC reconstructions. For each RCP, an array of LULUC fluxes were estimated using outputs from a suite of climate model projections from the CMIP5 multi-model ensemble database (Table S1). The lines represent the mean across the array of estimates (for both with and without nitrogen limitation effect). The error bars indicate the uncertainty range in simulated indirect LULUC emissions (for with nitrogen limitation case) that results due to uncertainties in projecting future climate. Uncertainties in simulating indirect LULUC emissions will also introduce uncertainties in estimates of total LULUC emissions. For clarity, uncertainty estimates for total LULUC emissions are not shown, instead provided in Table 5. Units are in PgC/yr. The figure legends are shown in panel (d). See Fig. S6 for figures corresponding to RCP2.6 and RCP6.0.

Fig. 6. Net Primary Productivity (NPP) of secondary forests simulated by ISAM corresponding to RCP8.5. Results are compared between with and without nitrogen limitation case. The historical estimates are based on HYDE LULUC reconstruction. The future estimates shown are mean across the array of estimates obtained by driving ISAM with different climate model projections (for both with and without nitrogen limitation effect).

Fig. 7. Model simulated response to key nitrogen variables illustrated using RCP8.5 simulations (with transient environmental factors) as example. First and second column figures correspond to tropics and the non-tropics respectively, and show the fluxes averaged over primary (unmanaged) and secondary forests (resulting from LULUC). Third column figures show fluxes by region, and includes all land cover types. Panel (a-i, l) is from simulations that include

LULUC effect. Panel (j-k) is obtained by differencing fluxes obtained between “with” and “without” LULUC simulations. (a, b) Biological Nitrogen Fixation which a source of nitrogen to terrestrial ecosystems. (g, h) Nitrogen-Use Efficiency defined as the Net Primary Productivity (NPP; panels c-d) per unit uptake of nitrogen by plants (panels e-f). (i) Anthropogenic nitrogen deposition ($\text{NH}_x + \text{NO}_y$) over land areas (source of nitrogen to both managed and unmanaged land). (j) Denitrification loss attributable to LULUC. (k) Nitrogen leaching loss attributable to LULUC. (k) Nitrogen loss from LULUC disturbance (product pool decays, slash burning and removals).

Fig. 8. Two site-specific simulations (tropical and non-tropical forest site) showing our modeled response to the rate of vegetation carbon accumulation followed wood harvest. The “steady state” indicates the time taken to attain full maturity under ideal conditions (environmental factors unchanged from current site-specific conditions and no LULUC disturbance following wood harvest). An explanation of this figure is provided in text S7.

Fig. 9. Zonal breakdown of prescribed forest harvest area for the four RCPs cumulated over the 21st century (data based on Hurtt et al. [2011]). For comparison, the contemporary (2005 AD) forest areas (and savannas) based on MODIS satellite data [Friedl et al., 2010] are shown. Units are in million km².

Supporting information legends

Text S1. Overview of the RCPs

Text S2. Data for nitrogen deposition

Text S3. Climate forcing data for ISAM

Text S4. Overview of LULUC implementation in ISAM

Text S5. LULUC flux calculations in ISAM

Text S6. Negative direct emissions from wood harvest in without nitrogen limitation case

Text S7. Explanation to Fig. 8

Table S1. List of CMIP5 climate model outputs that were used in this study

Table S2. Sensitivity of total LULUC emissions to assumptions on soil organic carbon loss

Table S3. Sensitivity test of parameter uncertainty in estimating nitrogen fixation

Fig. S1. Future climate projections for the tropical and non-tropical land regions for the RCPs

Fig. S2. Latitudinal breakdown of future temperature projections over the land area for the RCPs

Fig. S3. Global prescribed atmospheric CO₂ concentration for the four RCP storylines

Fig. S4. Global airborne anthropogenic nitrogen deposition rates

Fig. S5. Above-ground vegetation carbon in forests: FAO vs. Model simulations

Fig. S6. Decadal LULUC emissions for RCP2.6 and RCP6.0

Fig. S7. Spatial maps of forest harvest for the RCPs

Fig. S8. The MODIS land cover data for the South and South-East Asia region.

Tables

Table 1. Net change in forest area estimated by the Integrated Science Assessment Model (net forest loss including afforestation, and forest regrowth following cropland and pastureland abandonment; negative values indicate a net loss in forest area) and the annual forest harvested areas summed over a hundred year period (from Hurtt et al. 2011). The historical estimates are averages of the three LULUC reconstructions described in Jain et al. [2013]. The data for the 21st century correspond to the four Representative Concentration Pathways (RCPs). All units in million km²/century.

Region	Net change in forest area					Cumulative wood harvest area from forests [Hurtt et al., 2011]				
	20 th century	21 st century				20 th century	21 st century			
	Historical	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5	Historical	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
Global	-4.6	-2.6	2.3	-0.5	-2.1	16	76	87	188	137
Tropics	-2.2	-1.1	0.9	-0.2	-1.0	6	45	60	98	72

Non-Tropics	-2.4	-1.5	1.4	-0.3	-1.1	10	31	27	90	65
-------------	------	------	-----	------	------	----	----	----	----	----

Accepted Article

Table 2. Design of the simulations. Tick mark (✓) indicates the variable was varied with time. Cross mark (✖) indicates the variable was held static at initial (assumed zero for nitrogen deposition and LULUC) value. Inclusion of nitrogen deposition is irrelevant when nitrogen dynamics is inactive in the model, and is indicated by a hifen (-).

Simulation	CO₂	Climate	Nitrogen Deposition	Land-Use Change	Wood Harvest	Nitrogen Dynamics
Ref_1	✓	✓	✓	✖	✖	Active
A1	✓	✓	✓	✓	✓	Active
B1	✓	✓	✓	✓	✖	Active
C1	✖	✖	✖	✓	✓	Active
D1	✖	✖	✖	✓	✖	Active
Ref_2	✓	✓	-	✖	✖	Inactive
A2	✓	✓	-	✓	✓	Inactive
B2	✓	✓	-	✓	✖	Inactive
C2	✖	✖	-	✓	✓	Inactive
D2	✖	✖	-	✓	✖	Inactive

Table 3. Summary of how the different simulations mentioned in Table 2 were combined to estimate land use and land-use change (LULUC) fluxes with varying environmental factors, LULUC activities, and nitrogen dynamics. Total LULUC emissions are the sum of direct and indirect LULUC emissions. Land-use change is abbreviated as ‘LUC’ and wood harvest as ‘WH’.

LULUC flux estimated	Effects Included			Calculation Method
	LULUC activities	Changing environmental factors	Nitrogen Dynamics	
Total emissions with nitrogen limitation	LUC+WH	CO ₂ + nitrogen deposition + climate	Active	A1 – Ref1
	LUC			B1 – Ref1
	WH			(A1 – B1)
Total emissions without nitrogen limitation	LUC+WH	CO ₂ + climate	Inactive ^a	A2 – Ref2
	LUC			B2 – Ref2
	WH			(A2 – B2)
Direct emissions with nitrogen limitation	LUC+WH	None	Active	C1
	LUC			D1
	WH			(C1 – D1)
Direct emissions without nitrogen limitation	LUC+WH	None	Inactive ^a	C2
	LUC			D2
	WH			(C2 – D2)
Indirect emissions with nitrogen limitation	LUC+WH	CO ₂ + nitrogen deposition + climate	Active	(A1 – Ref1) – C1
	LUC			(B1 – Ref1) – D1
	WH			(A1 – B1) – (C1 – D1)
Indirect emissions without nitrogen	LUC+WH	CO ₂ + climate	Inactive ^a	(A2 – Ref2) – C2
	LUC			(B2 – Ref2) – D2

limitation	WH			$(A2 - B2) - (C2 - D2)$
------------	----	--	--	-------------------------

^a Inclusion of nitrogen deposition is irrelevant for “without” nitrogen limitation case.

Table 4. Direct, indirect, and total emissions from land use and land-use change (LULUC). The estimates for the 20th century are based on the three LULUC reconstructions. The estimates for the 21st century are based on the four Representative Concentration Pathways (RCPs). Two sets of estimates are shown, one with and the other without the effect of nitrogen limitation. For each RCP, an array of LULUC fluxes were estimated, using outputs from a suite of climate model projections from the CMIP5 multi-model ensemble database (Table S1). The estimates shown for the RCPs are the mean across the array of estimates. Positive values indicate a land to atmosphere flux. Units are in PgC/century.

Land-use affected ecosystem exchange	With Nitrogen Limitation Effect					Without Nitrogen Limitation Effect				
	20 th century	21 st century				20 th century	21 st century			
	Mean (& range)	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5	Mean (& range)	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
Global										
Direct LULUC emissions	+167 (135 to 186)	+81	+68	+35	+96	+123 (93 to 142)	+14	-39	-31	+31
Indirect LULUC emissions	-4 (-22 to 21)	+56	+55	+77	+71	0 (-18 to 29)	-5	-25	+6	-13
Total LULUC emissions	+163 (156 to 174)	+137	+123	+112	+167	+123 (122 to 124)	+9	-64	-25	+18
Tropics										
Direct LULUC emissions	+61 (43 to 85)	+22	-2	+5	+25	+60 (43 to 84)	+15	-17	-3	+33
Indirect LULUC emissions	-1 (-9 to 8)	+29	+31	+37	+40	0 (-8 to 18)	+8	0	+8	+11
Total LULUC emissions	+60 (51 to 76)	+51	+29	+42	+65	+60 (35 to 76)	+23	-17	+5	+44
Non-Tropics										
Direct LULUC emissions	+106 (80 to 143)	+59	+70	+30	+71	+63 (41 to 89)	-1	-22	-28	-2
Indirect LULUC emissions	-3 (-20 to 25)	+27	+24	+40	+31	0 (-10 to 11)	-13	-25	-2	-24
Total LULUC emissions	+103 (82 to 123)	+86	+94	+70	+102	+63 (48 to 87)	-14	-47	-30	-26

Table 5. Climate projections induced uncertainties in simulating total (direct + indirect) LULUC emissions for the 21st century. The numbers shown for total LULUC emissions are the maximum range of estimates obtained by forcing the Integrated Science Assessment Model (ISAM) with multiple climate model outputs (Table S1). The “(Max – Min) value” is calculated as the difference between the maximum and minimum value range. The mean values for land to estimates the effect of nitrogen limitation. Units are in PgC/century.

Region	Range of cumulative total LULUC emissions				(Max – Min) value			
	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
Global	116–180	107–165	91–150	139–227	64	60	59	88
Tropics	33–72	21–50	32–59	48–96	39	29	27	48
Non-Tropics	67–119	74–126	51–99	77–146	52	52	48	69

maximum and from the estimated estimates are Table 4. Positive emissions indicate a atmosphere flux. The provided here include

	Hurtt et al. [2011]	This study
--	---------------------	------------

Table 6. Comparison of biomass harvested from forests between Hurtt et al. [2011] and this study. The numbers provided within brackets are estimates of biomass harvested from non-forested tree types which we do not account for. The range of estimates provided for the historical period (corresponding to this study) is obtained using the three different LULUC reconstructions. The range of estimates provided for the RCPs, are based on estimates with and without the effects of nitrogen limitation. Lower end values are generally the estimates that include the effect of nitrogen limitation. Both the estimates with and without the effect of nitrogen limitation for the RCPs are mean estimates obtained by driving the Integrated Science Assessment Model (ISAM) using multiple climate model projections (Table S1). Units are in PgC/century.

Region	20 th century	21 st century				20 th century	21 st century			
	Historical	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5	Historical	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
Global	70 (3)	144 (22)	165 (17)	150 (35)	182 (68)	69–76	88–93	113–116	69–77	143–146
Tropics	18 (2)	38 (18)	54 (14)	53 (22)	61 (30)	11–13	28–33	33–37	37–41	57–62
Non-Tropics	52 (1)	106 (4)	111 (3)	97 (13)	121 (38)	56–65	56–65	77–83	29–41	82–90

Table 7: Global comparison of our model estimated cumulative (2001-2100) LULUC fluxes for the four RCPs with previous studies. Units are in PgC/century.

Reference	RCP2.6	RCP4.5	RCP6.0	RCP8.5	Notes	Nitrogen cycle	Wood harvest
-----------	--------	--------	--------	--------	-------	----------------	--------------

<i>This study</i>							
Data from Table 4	14 9	-39 -64	-31 -25	31 18	Direct emissions Total emissions	x	✓
Data from Fig. 4	25	-46	4	31	Total emissions	x	x
Data from Table 4	81 137	68 123	35 112	96 167	Direct emissions Total emissions	✓	✓
<i>Other studies</i>							
IAMs that produced the RCPs	68	30	6	60	Data from http://cmip-pcmdi.llnl.gov/cmip5/forcing.html	x	✓
Brovkin et al. [2013]: LUCID-CMIP5	24 to 180	-	-	30 to 210	Range from five Earth System Models (one model included wood harvest)	x	See notes
	24 to 70	-	-	30 to 67	Range excluding MPI-ESM-LR	x	x
Boysen et al. [2014]: LUCID-CMIP5 (extension to Brovkin et al.)	-	-	-	34 to 218	Range from four Earth System Models (one model included wood harvest)	x	See notes
	-	-	-	34 to 57	Range excluding MPI-ESM-LR	x	x
Kato et al. [2013]	118	-36	16	82	Data from their Fig. 7	x	x
Lawrence et al. [2012]	185	158	191	266	Data from their Fig. 8a	✓	✓
Stocker et al. [2014]	91	30	91	127	Direct emissions	✓	✓
	111	33	103	157	Total emissions	✓	✓
Wang et al. [2015]	-	-16	-	61	They provide estimates for 2006-2100 to which we added estimates for 2001- 2005 based on the same model provided in Zhang et al. (2013).	✓	✓
Range	24 to 185	-36 to 158	6 to 191	30 to 266	Range across "Other studies"	-	-

Table 8: Summary of relative uncertainties in estimated ‘total LULUC emissions’ due to: (1) uncertainty in climate projections underlying future scenarios (‘Climate’), (2) including nitrogen cycle (‘Nitrogen cycle’), and (3) including wood harvest (‘LULUC activities’) under both with and without nitrogen limitation cases (‘N lim’ and ‘No N lim’ respectively). The ranges shown are minimum and maximum values of uncertainty estimated across the three historical reconstructions (for the 20th century), and across the four RCP scenarios (for the 21st century). We estimate the uncertainty for each LULUC history and RCP as follows. For ‘Climate’, the uncertainty values correspond to ‘(Max-Min) value’ column in Table 5. For ‘Nitrogen cycle’, we calculated the difference in LULUC emission estimates between with and without nitrogen limitation case (from Table 4). For ‘LULUC activities’, we extracted the values corresponding to ‘wood harvest’ from figure 4 (brown bars). Units are in PgC/century.

Region	Climate	Nitrogen cycle	LULUC activities (N lim)	LULUC activities (No N lim)
20th century				
Global	-	34 to 52	55 to 64	-20 to 40
Tropics	-	0 to 16	8 to 11	8 to 10
Non-Tropics	-	34 to 53	47 to 56	-28 to 30
21st century				
Global	59 to 88	128 to 187	38 to 125	-29 to 11
Tropics	27 to 48	21 to 46	13 to 41	-8 to 11
Non-Tropics	48 to 69	100 to 141	17 to 84	-28 to 0

Accepted Article

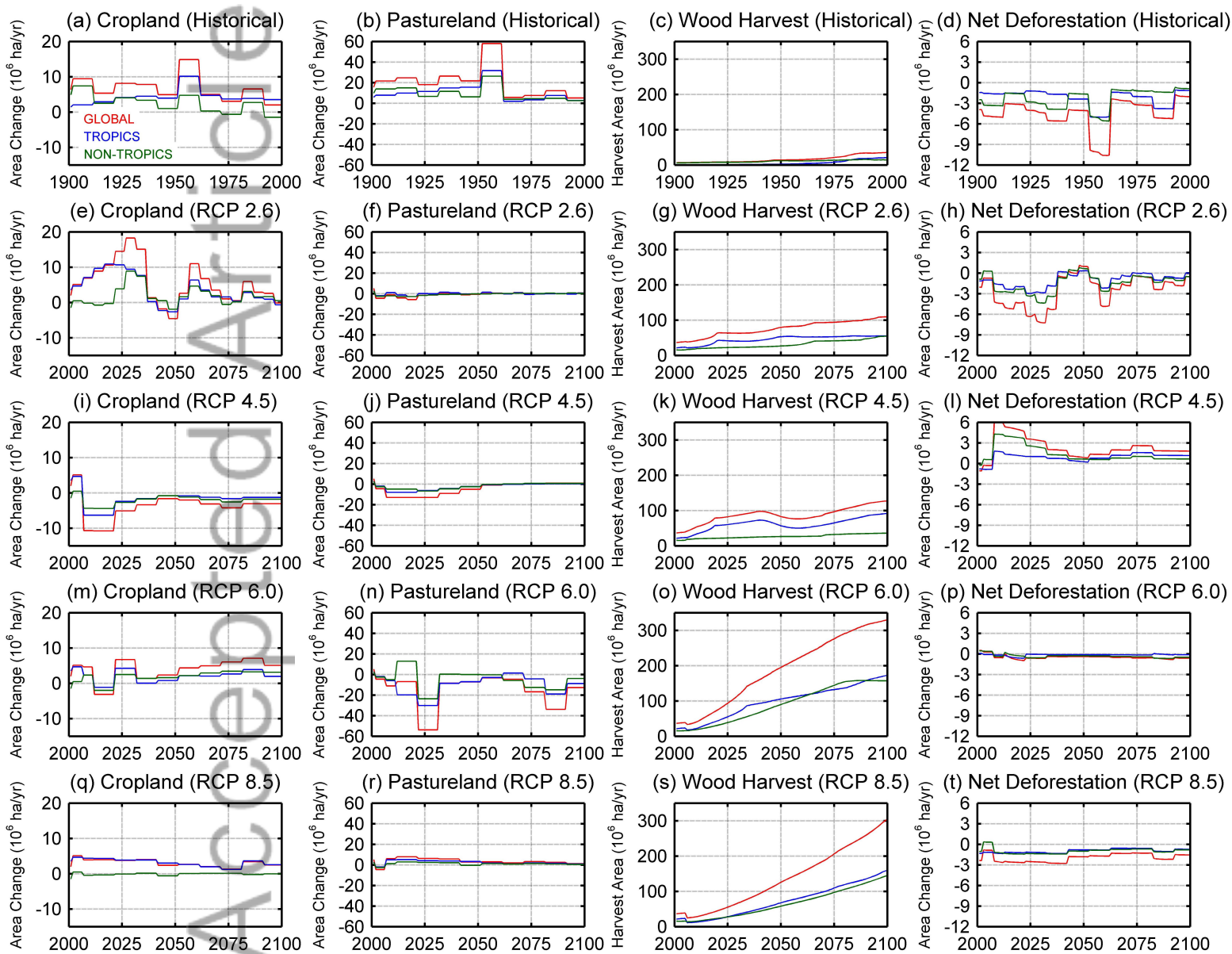


fig1.jpg

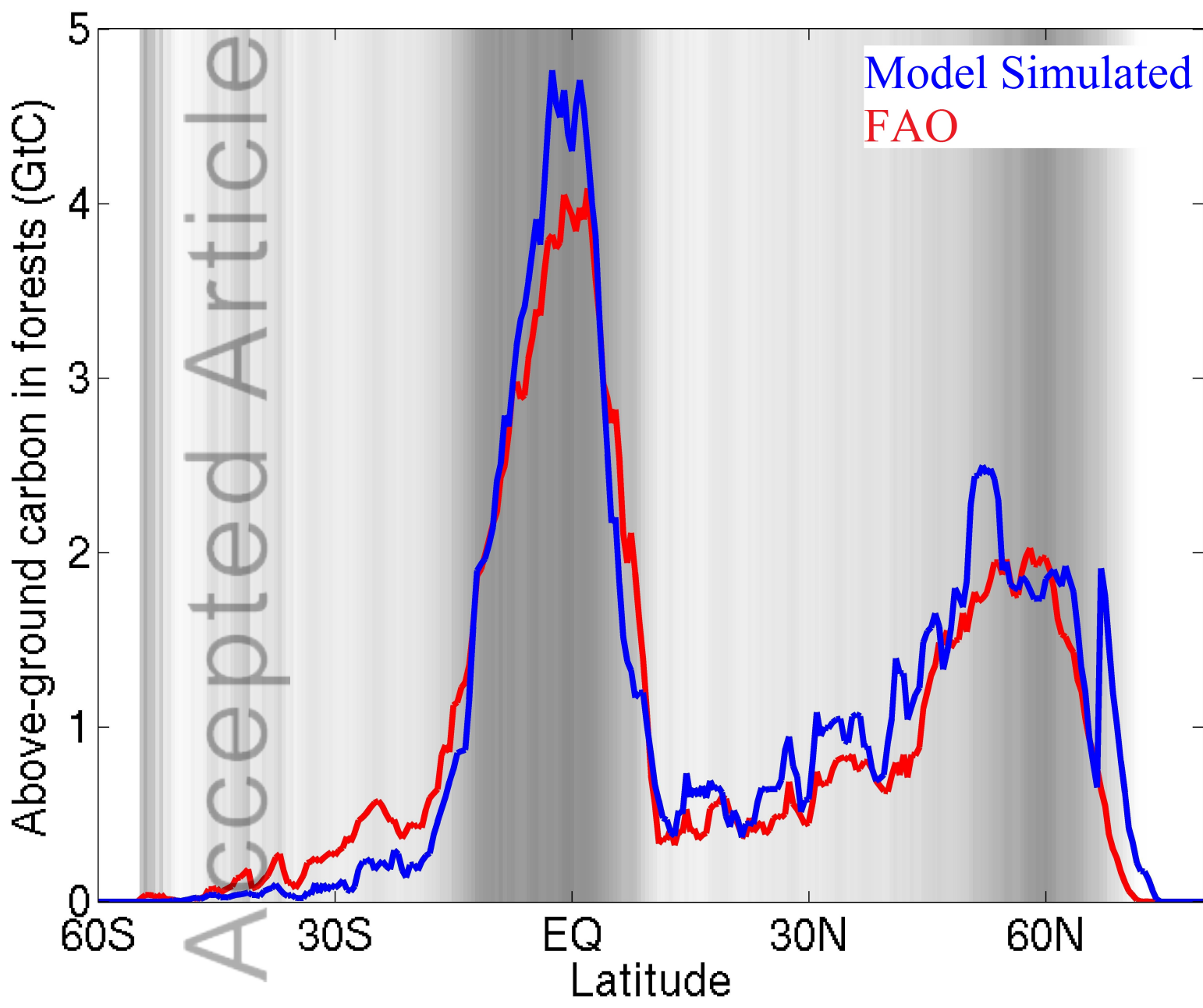
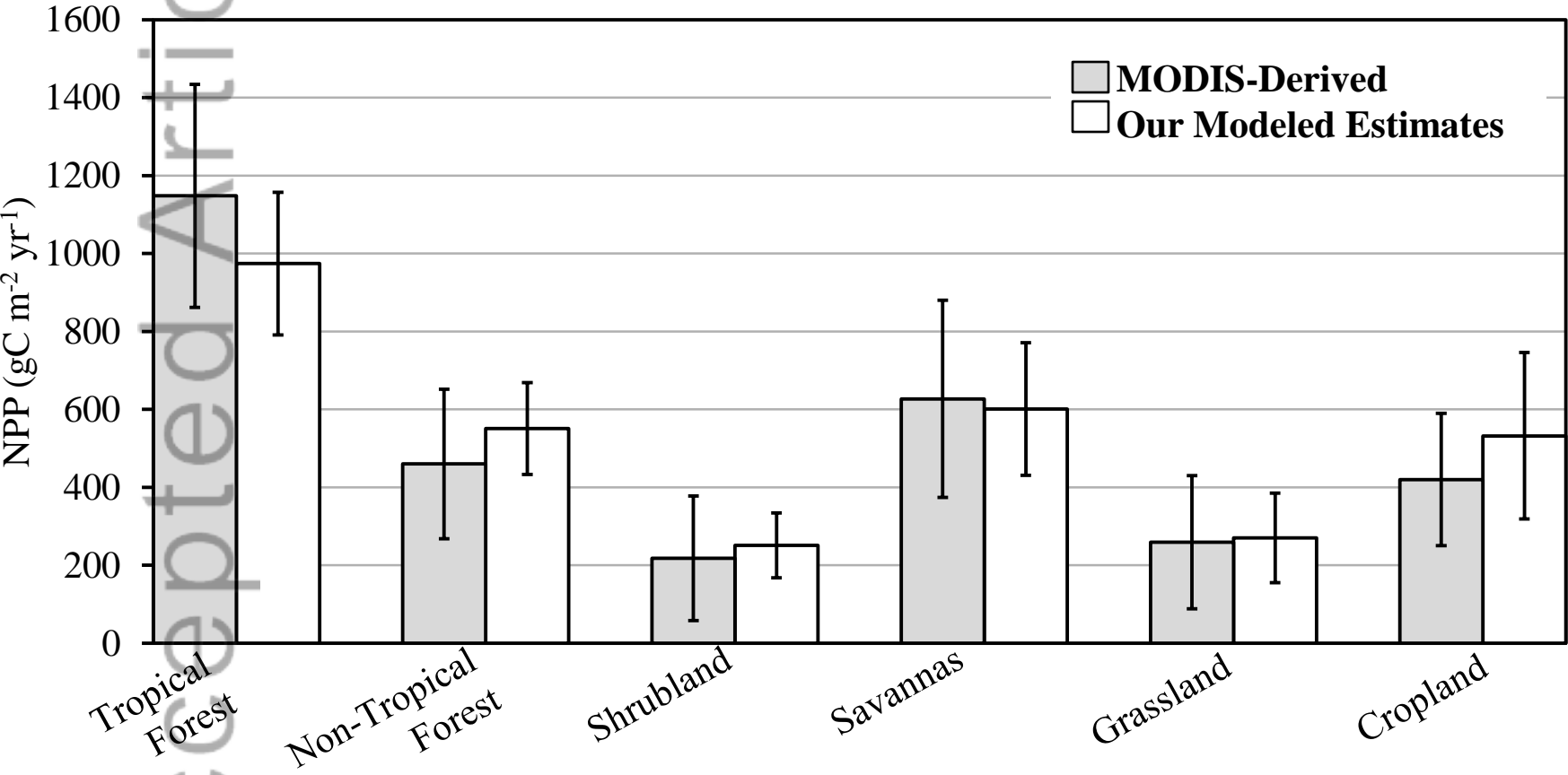


fig2.jpg



ACCEPTED MANUSCRIPT

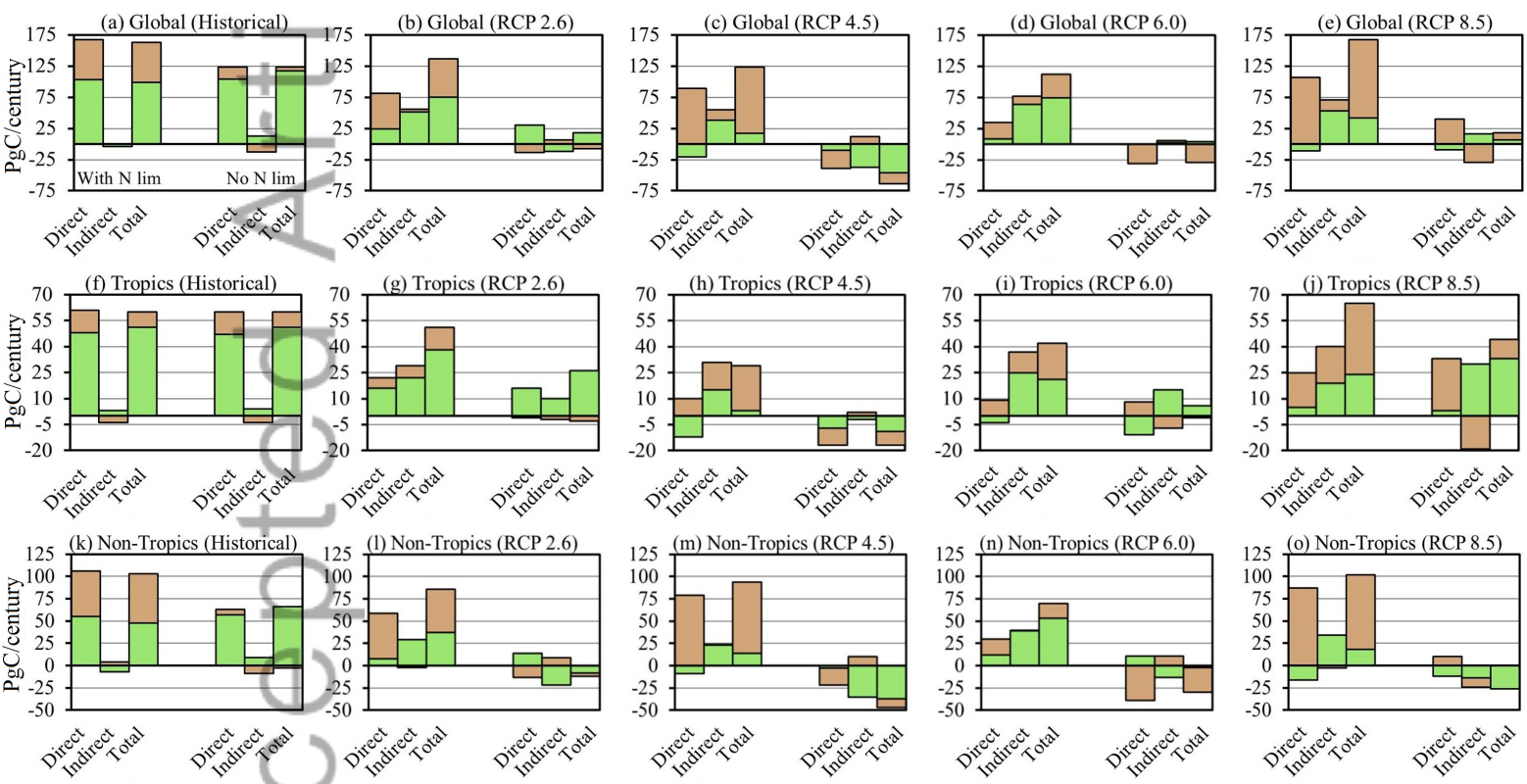
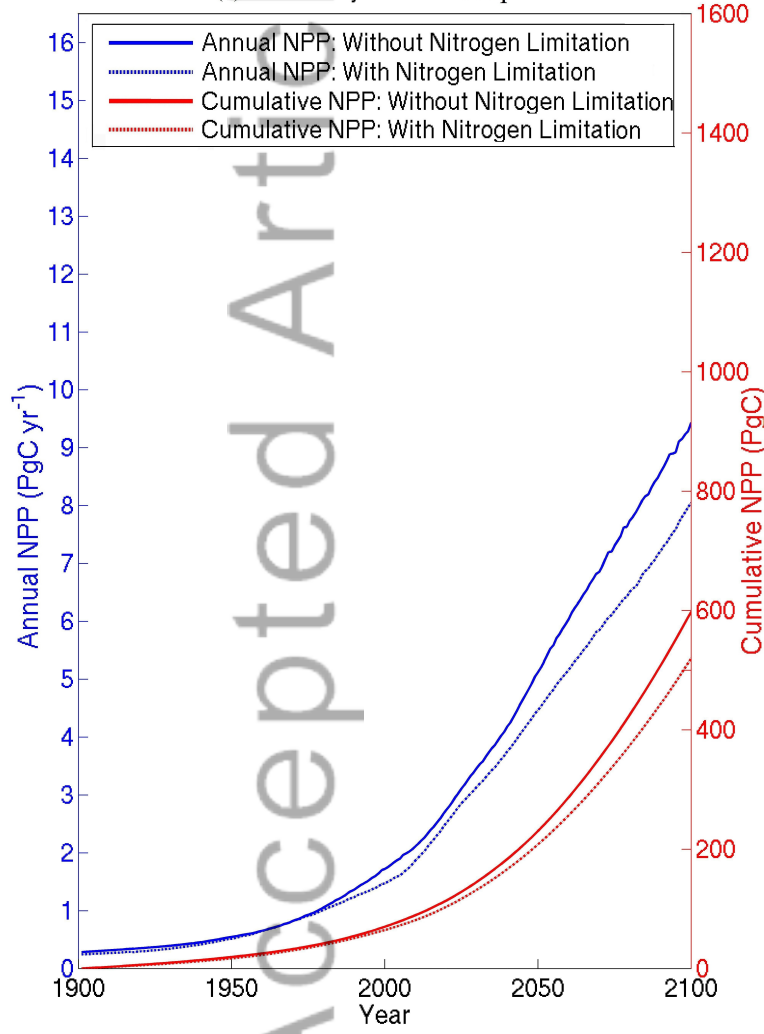


fig4.jpg

(a) Secondary Forests: Tropics



(b) Secondary Forests: Non-Tropics

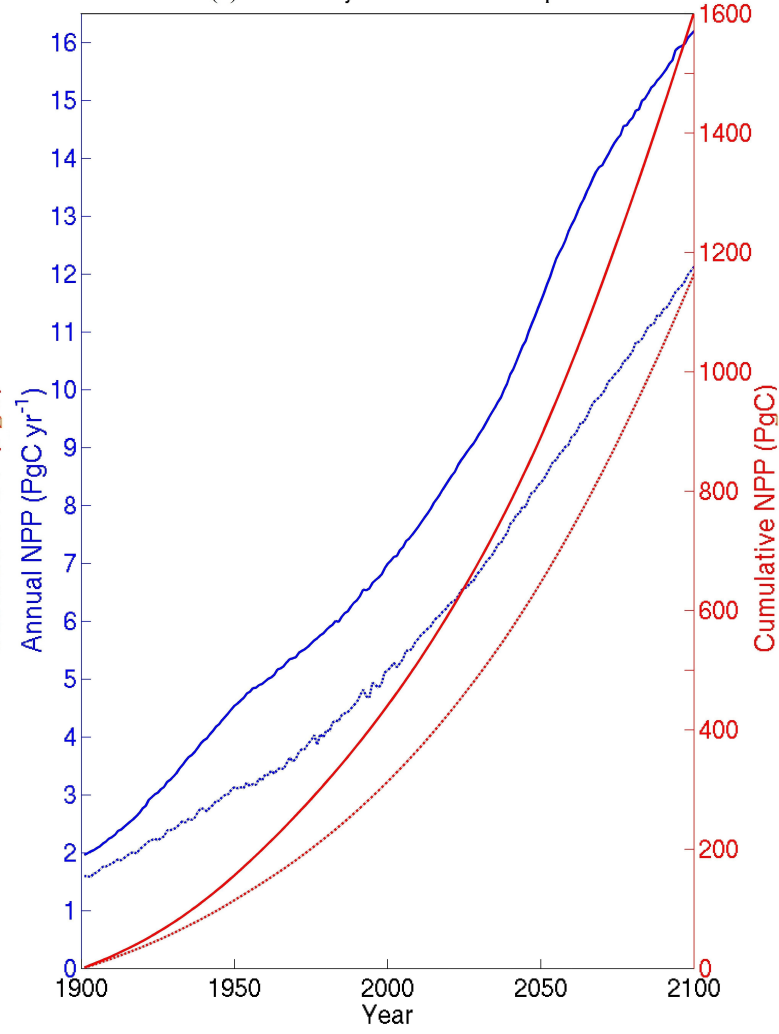


fig6.jpg

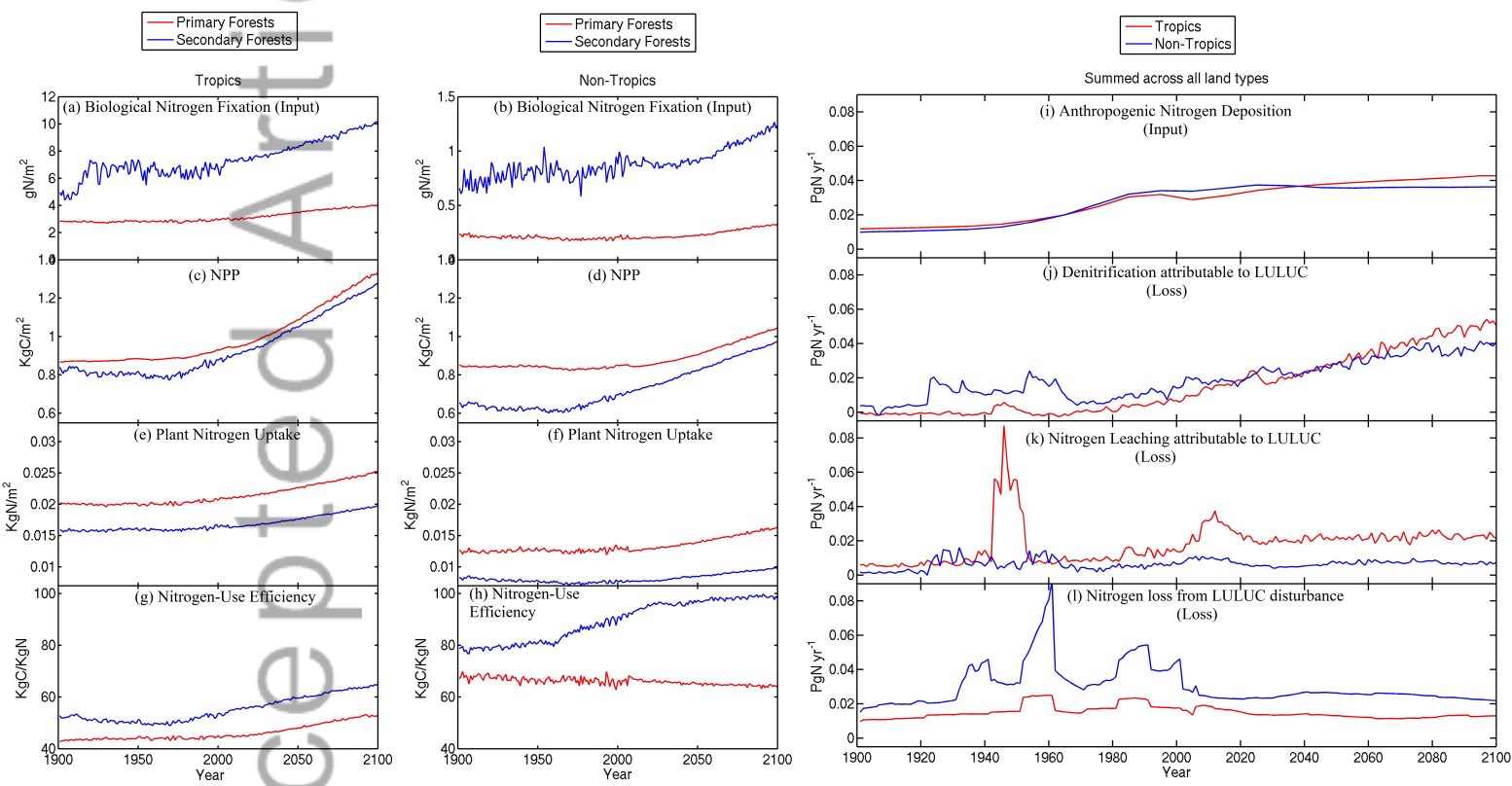


fig7.jpg

Vegetation Carbon →

