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Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model

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Abstract

Recently a considerable amount of effort has been put into quantifying how interactions of the carbon and nitrogen cycle affect future terrestrial carbon sinks. Dynamic vegetation models, representing the nitrogen cycle with varying degree of complexity, have shown diverging constraints of nitrogen dynamics on future carbon sequestration. In this study, we use the dynamic vegetation model LPJ-GUESS to evaluate how population dynamics and resource competition between plant functional types, combined with nitrogen dynamics, have influenced the terrestrial carbon storage in the past and to investigate how terrestrial carbon and nitrogen dynamics might change in the future (1850 to 2100; one exemplary "business-as-usual" climate scenario). Single factor model experiments of CO_2 fertilisation and climate change show generally similar directions of the responses of C–N interactions, compared to the C-only version of the model, as documented in previous studies. Under a RCP 8.5 scenario, nitrogen limitation suppresses potential CO_2 fertilisation, reducing the cumulative net ecosystem carbon uptake between 1850 and 2100 by 61 %, and soil warming-induced increase in nitrogen mineralisation reduces terrestrial carbon loss by 31 %. When environmental changes are considered conjointly, carbon sequestration is limited by nitrogen dynamics until present. However, during the 21st century nitrogen dynamics induce a net increase in carbon sequestration, resulting in an overall larger carbon uptake of 17 % over the full period. This contradicts earlier model results that showed an 8 to 37 % decrease in carbon uptake, questioning the often stated assumption that projections of future terrestrial C dynamics from C-only models are too optimistic.

1 Introduction

The nature of future climate change will depend on anthropogenic emissions of CO_2, and climate and CO_2-mediated feedbacks through carbon (C) cycling in both terrestrial ecosystems and oceans (Friedlingstein et al., 2006; Heimann and Reichstein, 2008;

Sitch et al., 2008; Arneth et al., 2010; Raupach, 2011). Terrestrial ecosystems remove presently about 25 % of the anthropogenic CO_2 fossil-fuel and land-use change emissions (Schulze, 2006; Canadell et al., 2007), but to attribute which mechanisms underlie this uptake, and the key regions where it occurs, is a challenging task. As a conse-
5 quence, projections of how the future C cycle develops in a rapidly changing climate diverge widely (Raupach, 2011; Ahlstrom et al., 2012; Stocker et al., 2013). Considerable attention has focused in recent years on whether and how interactions of the C and nitrogen (N) cycle affect the future terrestrial C sink. Until relatively recently these interactions were not considered in models of the global C cycle, although in many
10 ecosystems N is regarded as a limiting factor, controlling C uptake in present-day environments (Vitousek and Howarth, 1991; Galloway et al., 2008; Arneth et al., 2010). Full-scale ecosystem manipulation studies such as free air CO_2 enrichment (FACE) experiments, that assess ecosystem response to a step-increase in atmospheric [CO_2], have in certain cases seen an initial enhancement in C uptake under elevated [CO_2]
15 declining over time and argued progressive N limitation (Luo et al., 2004) to be abating the initial CO_2 fertilisation (Norby et al., 2010). However, other FACE experiments have shown a sustained enhancement of C uptake in conjunction with CO_2 enrichment (Finzi et al., 2007; McCarthy et al., 2010). Soil warming experiment have shown that an initial decrease in soil C pools due to increase in heterotrophic respiration was al-
20 most offset by an increase in soil N mineralisation, increasing plant C uptake capacity (Melillo et al., 2011). Still, relatively few full-scale multi factorial ecosystem experiments have been conducted to date, and these have been of limited duration, leaving the interaction effects of, and on, future climate change unclear (Beier, 2004; Leuzinger et al., 2011).
25   A few, recent, simulation experiments using dynamic global vegetation models (DGVMs) have begun to investigate the magnitude of C–N interactions on historical and future terrestrial ecosystem C cycling. These studies agree in principle on the main processes, namely that future CO_2 fertilisation of global photosynthesis can be reduced by limitations imposed through N availability, and warmer temperatures can re-

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sult in increased soil N mineralisation, increasing C uptake (Sokolov et al., 2008; Fisher et al., 2010a; Zaehle et al., 2010; Goll et al., 2012). However, the relative magnitude of these competing processes diverges between model studies. If these antagonistic interactions result in a reduction in terrestrial C storage under future climate forcing (Sokolov et al., 2008; Thornton et al., 2009; Arneth et al., 2010; Zaehle et al., 2010) the net feedback effect will be an accelerated warming (Arneth et al., 2010; Arora et al., 2013).

The introduction of N feedbacks will not only alter future land C storage through its effect on CO_2 fertilisation and N mineralisation, but it will also have downstream effects on higher-order ecosystem interactions like population dynamics and competition between plant functional types (PFTs). As a result, shifts in biome distributions may be expected when C–N interactions are taken into account (Smith et al., 2013). In DGVMs, biome patterns and ecosystem composition in terms of presence/absence and relative abundance of different PFTs are determined largely through bioclimatic constraints on the establishment and/or survival of individual PFTs, and through competition between PFTs for resources needed for growth such as light, water and N. Models differ greatly in the level of detail and realism with which the mechanisms underlying competition, their effects on population and community structure, and the resultant feedback to resource uptake, C assimilation and growth are represented (Smith et al., 2001; Wolf et al., 2011). Only a few DGVMs explicitly represent differences in age/size structure among individuals within a PFT and canopy structural variation in time as a result of birth, death and growth of individuals (so called demographics) (Moorcroft et al., 2001; Smith et al., 2001, 2013; Fisher et al., 2010b). It has been suggested that the representation of demographics is a precondition for the accurate representation of the C dynamics and climate feedbacks in forest and savannah ecosystems (Purves and Pacala, 2008; Fisher et al., 2010b; Wolf et al., 2011).

In this study, we use LPJ-GUESS to examine the interactions and feedbacks that the combined representation of a dynamic N cycle and forest gap dynamics have on potential natural vegetation (PNV) distribution and C sequestration. To examine this,

a set of simulations have been performed applying a future business-as-usual scenarios in terms of climate change, atmospheric $[CO_2]$, and N deposition. Model runs either include N dynamics (C–N), or have N dynamics turned off (C-only) to analyse and quantify the regional responses of biome structure and C sequestration to future climate change, atmospheric $[CO_2]$, and N deposition scenarios, with and without N dynamics.

2 Methods

Global patterns of natural ecosystem C and N fluxes and pool sizes were simulated with LPJ-GUESS (Smith et al., 2001, 2013) a process-based model of vegetation dynamics and biogeochemistry that incorporates a detailed, individual- and patch-based representation of tree population dynamics and resource competition (Prentice et al., 1993). The competitive strength of a PFT is determined by its bioclimatic limits, phenology, allometry, shade tolerance, specific resource uptake capacity, mortality, and establishment under changing stand structure and environment. For each location, the model simulates a set of replicate patches where PFT age-cohorts compete for light, water and soil available N. A patch represents the area over which one large adult tree would influence its neighbours, a concept commonly used in forest gap models. The patch replicates account for stochastic processes associated with e.g., establishment and mortality. Disturbance is represented by fire (Sitch et al., 2003) and a patch destroying disturbance, representing for example, windstorms and insect-attacks (Smith et al., 2008). A location's ecosystem state and material fluxes are derived as the average over the replicate patches. Plant and soil biogeochemical and biophysical processes are as in Sitch et al. (2003).

The newly implemented C–N interactions in LPJ-GUESS are described in detail in Smith et al. (2013), but will be briefly covered here. The N cycle in LPJ-GUESS simulates dynamically the build-up of a soil mineral N pool through mineralisation of soil organic matter (SOM), atmospheric N deposition and biological N fixation (BNF). BNF

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is estimated annually through an empirical correlation between N fixation and evapo-transpiration (Cleveland et al., 1999). N deposition is an external input from the AC-CMIP global dataset (Lamarque et al., 2010, 2011), providing monthly wet and dry N deposition that varies decadally. In the occurence of a snow lie N deposition is stored

5   in the snow pack and released to the soil mineral N pool in porportion to snow melt. SOM dynamics is modelled by a SOM scheme adopted from the CENTURY model (Parton et al., 1993) with a set of modifications and updates (Comins and McMurtrie, 1993; Kirschbaum and Paul, 2002; Parton et al., 2010). Decomposition of eleven SOM compartments, distinguished with different decay rates and respiration fraction,

10 results in a transfer of C and N between the SOM pools, with associated respiration (CO_2 flux to atmosphere, representing total microbial respiration) and N mineralization or immobilization. The mineral N pool is available for uptake by plants and microbes, or lost from the ecosystem through leaching and a simple representation of trace gas emission (Thomas et al., 2013). The daily plant N demand is driven by optimal leaf N

15 content required for photosynthesis, computed based on the optimisation of carboxylation capacity of Rubisco (Haxeltine and Prentice, 1996a), and leaf N not associated with photosynthesis, connected directly to daily leaf C content. Maximum C content of leaves and roots is determined annually, the daily C content follows the phenological development during the year. The N demand of other compartments of the plant and

20 their N concentrations are proportional in relationship to each other and the optimal leaf N content (Friend et al., 1997; White et al., 2000; Zaehle and Friend, 2010). The daily N uptake capacity, which ideally meets the calculated demand, is directly proportional to plant fine root C mass (Rothstein et al., 2000; Macduff et al., 2002), but with additional constrains imposed by soil mineral N pool, plant N status, and soil tempera-

25 ture (Zaehle and Friend, 2010). If N uptake capacity cannot meet the demand, N from a vegetation storage pool is used. If there still is a shortage, the plant is under N stress and the carboxylation capacity is reduced accordingly, with spill-over effects on leaf and non-green tissue N content. The plant N storage pool is filled during the previous year with retranslocated N from shedding of leaves and fine roots, accompanied by a set

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fraction of total N uptake. If storage capacity is exceeded, less N is retranslocated and the shed leaves and fine roots have a higher N concentration. Such a situation represents a N-rich environment, in which N uptake from the soil mineral N pool is more energy cost efficient for plants compared to retranslocation (Wright and Westoby, 2003; Fisher et al., 2010a). If the daily total N demand/uptake capacity from all PFT cohorts within a single patch cannot be met by the soil mineral N pool, the cohorts have to compete for the resources, where the competitiveness of the cohorts is determined by their fine root C mass and its vertical distribution. N stress consequently also affects the C allocation fraction between shoots and fine roots, making an N stressed cohort allocate more C to its fine roots, compared to shoots, to increase its N uptake capacity and competitiveness compared to other cohorts.

The N cycle in LPJ-GUESS has been extensively evaluated and shown to simulate C and N fluxes observed at a range of field sites (Fleischer et al., 2013; Smith et al., 2013), at FACE experiments simulating future climate change scenarios (De Kauwe et al., 2013), and to agree well with current best-estimates of global C and N pools and fluxes (Smith et al., 2013). Here, we examine the C–N interactions and feedbacks on PNV in a future environment. To do this LPJ-GUESS was forced with output from the MPI-ESM-LR model under the representative concentration pathway (RCP) 8.5 with prescribed atmospheric [CO_2] forcing (Giorgetta et al., 2013). MPI-ESM-LR results were in the middle-range of modelled C sequestration in a recent C-version of LPJ-GUESS in Ahlstrom et al. (2012). CRU TS 3.0 1961–90 climatologies (Mitchell and Jones, 2005) were used to bias correct the climate data, which was interpolated to the CRU grid (0.5° × 0.5° resolution). Historical (Lamarque et al., 2010) and future (Lamarque et al., 2011) RCP 8.5 N deposition forcings are from the CAM model (Gent et al., 2010). Data for the initial 500 yr model spin-up phase was de-trended 1850–1879 climate with a constant 1850 atmospheric [CO_2] and N deposition. After spin-up, historical climate data, atmospheric [CO_2] and N deposition were used, until 2006 when the RCP 8.5 scenario period starts and runs until 2100. The simulations were made with 30 replicate patches to be able to represent the regional vegetation.

3 Results

Over the historical time period (1850–2000), total C sequestration in terrestrial ecosystems in the C-only version of LPJ-GUESS exceeded C sequestration in the C–N version by about one third (Table 1 and Fig. 1a). A reduced past-to-present cumulative
[5] C sequestration in C–N versions of terrestrial models seems to emerge as a robust pattern that has also been found in previous studies (Table 1), even though the relative importance of N in LPJ-GUESS is comparatively large compared with other models. The differences imply N-limitation of C cycling over this period, but indirect effects (e.g., initial conditions) vary as the two versions differ in PFT composition and C pool sizes
[10] after the spin-up (Table A2). During the 21st century, warming induces an increase in soil N mineralisation, which in the climate-change only experiment reduces C losses notably, while availability of nitrogen substantially limits photosynthetic C-uptake in the CO_2 only experiment (Fig. 1 and Table A1). Comparable to what is being observed for the historical period, a robust pattern seems to be emerging such that the direction
[15] of individual process-responses to C–N interactions in factorial model experiments is similar (Zaehle et al., 2010). However, when environmental changes are considered conjointly, the net response of the global terrestrial C sink differs between models. In case of LPJ-GUESS, total C accumulated from 1850 to 2100 in the C–N version exceeds the C-only version by 17 %, while previously published model results have
[20] generally found a decline of different magnitude after accounting for C–N interactions (Table 1, Table A1 and Fig. 1a).

The shift to higher C sequestration with N dynamics during the 21st century is mainly due to C–N interactions in the mid-high latitudes (Figs. 1b and 2). Here, the climate-change only experiment induced more soil N available to the plant, reducing the C
[25] losses, whereas the CO_2 only experiments show a reduction in C uptake during CO_2 fertilisation under N limitation. These effects increase with latitude (Fig. 1b), consistent with earlier model studies (Jain et al., 2009; Zaehle et al., 2010). When environmental changes are considered conjointly, the small N limitation during the CO_2 only experi-

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ment in the lower latitudes vanish. In the mid-high latitudes the interaction of soil warming and CO_2 fertilisation results in a higher C sequestration with C–N interactions. For the northernmost latitudes the N limitation persists and the C sequestration in the C–N versions is lower than in the C-only version (Figs. 1b and 2).

Changes in C pools when considering C–N interactions, climate change and changes in atmospheric [CO_2] are not only due to physiological process responses, but also mediated by shifts in vegetation patterns. Figures 3 and 4 summarize modelled large-scale shifts in biome composition (central panels) and highlights changes in more detail for a number of locations indicated by small letters in Fig. 2. These figures show that large-scale biome shifts are influenced by N dynamics mainly in colder regions, e.g. the transition from ecosystems dominated by grass to needleleaf biomes in northern Canada, which is suppressed by N dynamics (Figs. 3 and 4 central panels and location a). For the northernmost latitudes Siberia, N limitation changes both the initial state of biome distribution and C pool sizes, but also the possibility of needle-leafs to outcompete grasses, influencing the C sequestration in long-lived woody tissue (Figs. 3 and 4, central panels and location c). The latitudinal influences are clear in the highlighted changes, were locations in warmer climates experience less influence of N dynamics (Figs. 3 and 4 locations b, e, f, and g), whereas locations in colder climates experience a lower fraction of woody PFT and an inability of newly established PFT to compete for N resource with existing vegetation under N limitation (Figs. 3 and 4 locations a, c, d, and h).

4 Discussion

Even though two versions of the same model are compared here, with respect to their interactions with a changing environment, a direct comparison between the C-only and C–N version of the model is difficult, due to a number of ecosystem-scale feedbacks that are introduced in the C–N version, causing differences in the equilibrium state after the spin-up in the C-pool sizes (Table A2) and the PFT distribution. When comparing

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the different PFT distributions with the Haxeltine and Prentice (1996b) map of PNV, broad agreement of both model versions in geographic locations and ranges of larger biome types appears (Smith et al., 2013). The C–N version shows a better placement of the Northern Hemisphere boreal forest treeline compared to the C-only version of the model, with the exception of eastern Siberia, where the C–N version models a more limited extent of the Siberian Larix belt. The C–N version also improves the southerly extent of the boreal forest in the dry regions of Northern America and Central Asia. For the larger parts the different model versions simulates the PFTs distribution comparable.

Considering the joint impacts of environmental change, the hindcasts simulated with LPJ-GUESS from pre-industrial times up to the end of the 20th century are principally comparable to what has been found in other model studies (Sokolov et al., 2008; Fisher et al., 2010a; Zaehle et al., 2010; Goll et al., 2012), showing a reduction of global C sequestration when N dynamics are considered. Compared to these previous studies, our model simulates the lowest amount of C sequestrated up to present day and the strongest N limitation (Table 1). The influence of N dynamics is most pronounced in the mid- to high-latitude cool climates where they reduce both C sequestration and woody vegetation biomass and, hence, lower the residence time of C. At present, the model does not include organic N uptake which has been found to be a potentially significant source of N for boreal and (sub)arctic vegetation (Näsholm et al., 1998, 2009; Persson et al., 2003; Whiteside et al. 2012). For colder ecosystems, were N availability is limited due to low N mineralisation rates, the ability to represent organic N uptake, conjointly with a better representation of BNF, seems an important step for future development of the model. For low latitude ecosystems, including tropical forests, phosphorus (P) constraints on biogeochemistry may be important to represent (Wang et al., 2010; Peñuelas et al., 2012). Moreover, the representation of SOM decomposition with first order decay kinetics, as it is included in LPJ-GUESS and other global models, has been criticised for being too simplistic (Schimel and Bennett, 2004). This commonly applied approach requires a somewhat artificial division of available N: first,

soil microbes receive N for decomposition (immobilisation), afterwards the remainder is available for plant uptake. In other words, plants have no competitive strength against microbes, resulting in possibly too low N availability for plant growth. A more complex approach, including an active compartment of litter decomposing soil microorganisms that competes with plants for soil mineral N, have been applied on a global scale (Esser et al., 2011) and might be an interesting approach for future development of the model.

For the 21st century, the single-factor responses simulated by LPJ-GUESS are similar to what has been found earlier using other DGVMs (Sokolov et al., 2008; Fisher et al., 2010a; Zaehle et al., 2010; Goll et al., 2012). The model simulates lower C sequestration under a single-factor CO_2 fertilisation scenario when N dynamics are enabled, which is consistent with ecological understanding (Vitousek and Howarth, 1991; Luo et al., 2004) and results from FACE experiments (Norby et al., 2010). The 61 % reduction in C sequestration by the end of the 21st century in the C–N simulation with our model, compared to the C-only version, is in agreement with a previous study using the O-CN DGVMs (Zaehle et al., 2010), where an increased influence of N dynamics on C balance at higher latitudes, reducing the CO_2 fertilisation effect, was likewise observed (Jain et al., 2009; Zaehle et al., 2010).

A warming-induced increase in soil N mineralisation under climate change (Figs. A2 and A3) counteracts the relatively lower C uptake in mid-high latitudes found in the CO_2 experiment. Similar to the historical simulations, accounting for N dynamics does not greatly influence future vegetation, litter and soil C dynamics in the lower latitudes; a similar decline under climate change occurred in both the C-only and C–N simulations. Globally, enhanced N mineralisation under warmer temperatures reduces cumulative C loss by c. 30 % compared to the C-only version, which may be compared to a 16 % loss reported by Zaehle et al. (2010). By contrast to effects of enhanced $[CO_2]$ and globally warmer temperatures, effects of changing N deposition on C sequestration are negligible in LPJ-GUESS, partly because, during the 21st century, most areas that experience N-limitation under present-day climate will see rather small changes in N deposition fluxes according to the projections adopted for our study (Fig. A4). A limited

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effect of changing N deposition on global C sequestration has also been observed in other studies (Esser et al., 2011).

A striking finding of our study is the presence of highly non-linear, synergistic, N-mediated effects of multiple forcing factors on future global C balance. Whereas climate and [CO_2], applied independently, cause a decline in ecosystem C balance during the 21st century, when these forcing factors are considered conjointly, the impacts on C balance are not only reduced but actually reversed, more C being sequestrated by the global biosphere when N cycle dynamics are included. This result stands in contrast to findings with a range of other DGVMs in which increasing N limitations, particularly at mid-high latitudes, lead to a decline in biospheric C storage globally in a business-as-usual 21st century climate, [CO_2] and N-deposition projection (Sokolov et al., 2008; Fisher et al., 2010a; Zaehle et al., 2010; Goll et al., 2012; see Table 1).

Shifting from strong N limitation of C-uptake in the 20th century to high C sequestration during the 21st century might seem puzzling from a mass balance perspective, but Smith et al. (2013) showed that the model response is within stoichiometric limits of how much N is needed to sustain C uptake (Hungate et al., 2003). This is also confirmed by the finding that the terrestrial ecosystem shifts from being a net N sink in the end of the 20th century to a net source by the end of the 21st century (Table A3), implying that many regions are becoming N saturated. Regionally, differences in C balance response between the C-only and C–N simulations are mainly apparent in mid-high latitudes, where the C–N version simulates a stronger increase in vegetation biomass, which is accompanied by an increase in litter C, augmenting soil C pools (Table A1). These shifts for the C–N version can also be seen in the increase of global C : N ratio of both vegetation and soils (Table A3). Simulated shifts in vegetation structure and PFT composition are fundamental to these adjustments in C and N balance.

In the C–N simulation, woody vegetation abundance is initially lower, and the increase in litter pool sizes with N dynamics is due to the slightly larger increase of woody vegetation C over the 21st century and lower initial litter pool sizes compared to the C-only version. Increased litter input more than compensates for warming-induced res-

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piratory C loss through decomposition (Fig. A1). In lower latitudes, N dynamics do not significantly limit CO_2 fertilization because of faster soil N mineralisation in a warmer climate (Fig. A5). As a result, C sequestration rates remain similar in the C–N simulations compared to the C-only version for these areas. It should be borne in mind that, while low-latitude ecosystems may not be sensitive to N dynamics, P availability may impose limitations on C storage (Vitousek and Howarth, 1991; Vitousek et al., 2010; Wang et al., 2010). P limitations are not considered by our model.

N dynamics affect future vegetation composition most strongly in northern high latitudes in our simulations. Severe N limitation associated with low N mineralisation rates constrains the possibility for woody vegetation to compete for light and space with grasses (which may also be taken to represent other herbaceous vegetation and dwarf shrubs of tundra vegetation in these areas). As a result, poleward shifts in the taiga-tundra boundary, simulated in the C-only simulation, were not replicated in the C–N simulation. This reduces the C sequestration in the stems of growing trees and results in smaller C sinks at high northern latitudes in the C–N simulation compared to the C-only simulation (Figs. 3 and 4). This is most evident when comparing the future changes for highlights a and d in Figs. 3 and 4. The bioclimatic limits enabling establishment of trees are reached simultaneously in both simulations, but due to continuing low soil temperatures, N mineralisation remains insufficient to sustain the establishment of new vegetation. In addition, the resident "tundra" (C_3 grass) vegetation has a competitive advantage with respect to the uptake of N, further suppressing the establishment of trees. For highlights c and h (Figs. 3 and 4), N limitation has historically suppressed woody vegetation, whereas in the future the limitation is removed. The level of suppression of trees under the present climate is too large for highlight c and might be explained by the failure to account for uptake of organic N by plants, which is believed to provide an important source of N in high latitude ecosystems such as boreal forest (Näsholm et al., 1998, 2009; Persson et al., 2003; Whiteside et al., 2012). The explicit representation of competition among PFTs and its effects on vegetation structure and composition, mediated by population demographics, acts to retard the

rate of vegetation response to changing environmental forcing, compared to models in which spatial changes in vegetation are strongly driven by bioclimatic thresholds for the presence or absence of PFTs (Pavlick et al., 2012). As future climate change is, under most emission scenarios, projected to occur at a higher pace than any historical cli-
5 mate change, shifts in the bioclimatic envelopes within which different vegetation types occur under present climate conditions may be expected to occur faster than observed before. However, studies of past climate change episodes generally point to considerable lags in migration rates of major vegetation types, due to dispersal, colonisation and demographic process that hinder and slow the establishment of new species on
10 sites rendered climatically favourable by climate change (Malcolm et al., 2002; Gonzalez et al., 2010; Meier et al., 2012; Iverson and McKenzie, 2013). In our simulations, adjustments in C sequestration in the future projection are strongly tied to transient sinks of carbon in the stems of growing trees. The vegetation-mediated lags inter alia in the vicinity of the taiga-tundra boundary play a key role in such dynamics.

15 Would not similar, vegetation-dynamics mediated responses to N cycle dynamics, be expected in conventional DGVMs, lacking individual- and patch-based representations of vegetation structure and dynamics? In a comparison of LPJ-GUESS and the LPJ model, the latter incorporating identical representations of plant physiological and ecosystem biogeochemical processes, but a generalised, area-based representation of
20 vegetation dynamics, Smith et al. (2001) showed that the explicit separation of individual and population growth in LPJ-GUESS resulted in different, and apparently more accurate, temporal evolution (succession) and equilibrium PFT composition of vegetation across the climate zones of Europe. Shortcomings in the performance of conventional DGVMs with respect to reproducing *structural* features of vegetation have been high-
25 lighted in recent work. For example, Wolf et al. (2011) showed that models employing "big wood" schemes that combine environmental and structural dependencies of individual and population growth into a single, common parametisation generally fail to reproduce allometric scaling relationships revealed by forest inventory data. Similarly, some conventional DGVMs fail to account for the influence of disturbance on ecosys-

tem structure at the landscape scale (Haverd et al., 2013). The explicit, individual- and patch-based representation of vegetation structural dynamics of our model may largely explain the contrasting predictions of C–N dynamics under climate warming and CO_2 enrichment, compared with previous findings based on other models.

5 Concluding remarks

The results shown in this study add a new perspective to the previous inconclusive evidence on how strongly – and in what direction – terrestrial N cycle dynamics will affect future C sequestration by the terrestrial biosphere. Results from our individual-based DGVM exhibit slightly *increased* C sequestration under a business-as-usual future climate scenario when N cycle dynamics are accounted for, contrasting with results previously reported from other models, which universally point to a decline in ecosystem C stocks under climate projections for the coming century (Sokolov et al., 2008; Fisher et al., 2010a; Zaehle et al., 2010; Goll et al., 2012). Transient sinks for C in the stems of trees colonising new areas, or undergoing demographic adjustment within existing forest stands, account for such dynamics in our model, and likely explain why the results deviate from other studies with models lacking explicit representation of population dynamics, neighbourhood-level resource competition, and associated lags in the response of vegetation structure and distribution to climate change.

LPJ-GUESS, like most current DGVMs, lacks a dynamic representation of organic N uptake, and it is possible that N limitations, and the subsequent release from limitation through climate warming, in mid-high latitudes might therefore be overestimated.

Our contrasting – but plausible – results of future C–N coupling add to the still considerable uncertainty as to the likely fate of present-day biospheric carbon sinks, and the influence of C–N interactions on these, in a future high-CO_2 world. As ecosystem and Earth system models are developed to account for N cycle dynamics there is still a need for carefully designed empirical studies of N cycle impacts on C biogeochem-

istry in a range of ecosystem types and in response to multiple environmental forcing factors, emulating global change, to adequately constrain the models.

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Table 1. Modelled C sequestration [Pg C] for periods 1850 to 2000 and 1850 to 2100 with LPJ-GUESS and four additional C–N models with % difference between C-only and C–N versions.

Model[*]	1850 to 2000			1850 to 2100		
	C-only	C–N	% diff	C-only	C–N	% diff
LPJ-GUESS	76	45	−41	317	372	17
TEM	90	80	−11	332	242	−27
ORCHIDEE	108	83	−23	388	244	−37
FUN	85	78	−8	288	264	−8
JSBACH	158	150	−5	550	479	−13

[*] LPJ-GUESS – this paper; TEM – Sokolov et al. (2008); ORCHIDEE – Zaehle et al. (2010); FUN – Fisher et al. (2010a); JSBACH – Goll et al. (2012).

Table A1. Modelled C sequestration between 1850 to 2100 [Pg C] for climate change (CLIM), atmospheric [CO_2] (CO_2), N deposition (NDEP) alone, and all together (ALL).

		Veg C	Litter C	Soil C	Total	% diff
ALL	C-only	373	−23	−33	317	
	C–N	372	28	−28	372	17
CLIM	C-only	−200	−164	−101	−465	
	C–N	−120	−108	−92	−320	−31
CO_2	C-only	633	193	97	924	
	C–N	239	65	57	361	−61
NDEP	C-only	–	–	–	–	
	C–N	58	−6	3	55	

Table A2. Initial conditions for the C-only and C–N model versions, after spin-up.

Variable[*]	NPP	R_h	BB	NCB	Veg C	Litter C	Soil C	Total C
Unit	$PgC\,yr^{-1}$	$PgC\,yr^{-1}$	$PgC\,yr^{-1}$	$PgC\,yr^{-1}$	Pg C	Pg C	Pg C	Pg C
C-only	56.0	49.4	6.4	−0.2	697	435	1245	2377
C–N	53.1	48.5	4.5	−0.1	519	297	1197	2014

[*] NPP = net primary production; R_h = heterotrophic respiration; BB = biomass burning by wildfires; NCB = net ecosystem C balance = R_h + BB − NPP; Veg C = vegetation C.

Table A3. Changes in N stocks and fluxes for the C–N version of the model under all scenarios.

Variable	Units	1961 to 1990	2071 to 2100	Units	1976 to 2086
Vegetation C : N	kg C (kg N)$^{-1}$	142.9	159.9	%[a]	11.9
Soil + litter C : N	kg C (kg N)$^{-1}$	12.6	12.8	%[a]	1.0
Vegetation N	Pg N	3.9	5.3	Pg N[b]	1.4
Soil + litter N	Pg N	117.0	116.8	Pg N[b]	−0.1
N storage change				Pg N[b]	1.3
N deposition	Tg N yr^{-1}	−52.1	−78.2	Pg N[c]	−7.7
N fixation	Tg N yr^{-1}	−28.6	−26.6	Pg N[c]	−3.0
N leaching	Tg N yr^{-1}	17.8	26.5	Pg N[c]	6.9
N emission	Tg N yr^{-1}	47.4	79.2	Pg N[c]	2.5
Net flux	Tg N yr^{-1}	−15.4	0.8	Pg N[c]	−1.3

[a] Percentage change in C : N ratios between periods 1961 to 1990 and 2071 to 2100.
[b] Change in N storage between periods 1961 to 1990 and 2071 to 2100.
[c] Cumulative N fluxes between periods 1961 to 1990 and 2071 to 2100.
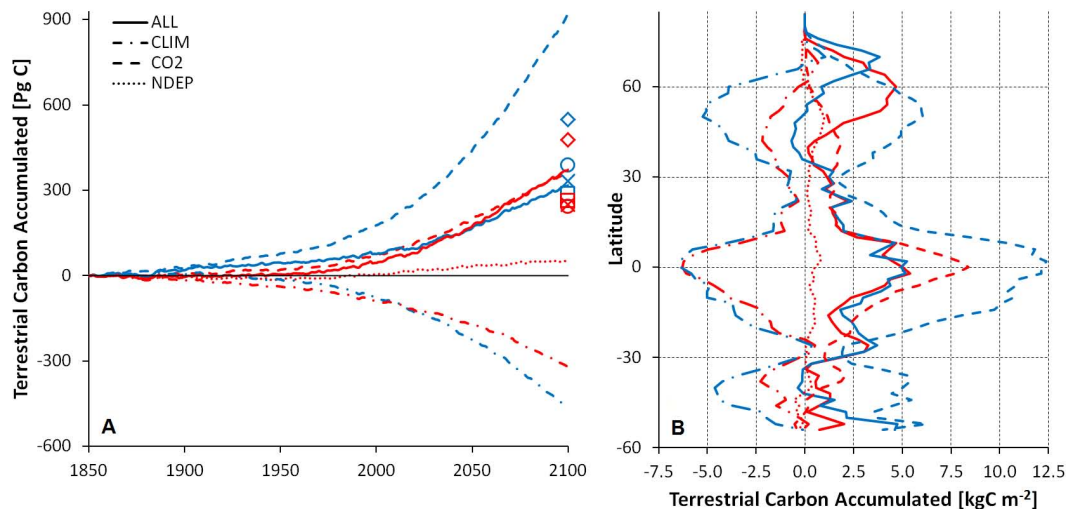
Fig. 1. Accumulative terrestrial C sequestrated between 1850 and 2100 **(A)** simulated with historical and future change in climate (CLIM), atmospheric [CO_2] (CO2), N deposition (NDEP) alone, and all together (ALL). Other model results are for TEM (X), ORCHIDEE (O), FUN (□), and JSBACH (◇). Latitudinal accumulated terrestrial C sequestration between 2000 and 2100 **(B)**. Blue lines are C-only version and red lines are C–N version.

Fig. 2. Simulated terrestrial C sequestration differences between the C-only and C–N version for the 21st century (calculated as C–N total pool change for 1990–2000 to 2090–2100 subtracted by C-only total pool change for 1990–2000 to 2090–2100). Negative values indicating a larger cumulative uptake for the C-only version than for the C–N version. Letters a–h indicates regions detailed in Figs. 3 and 4.
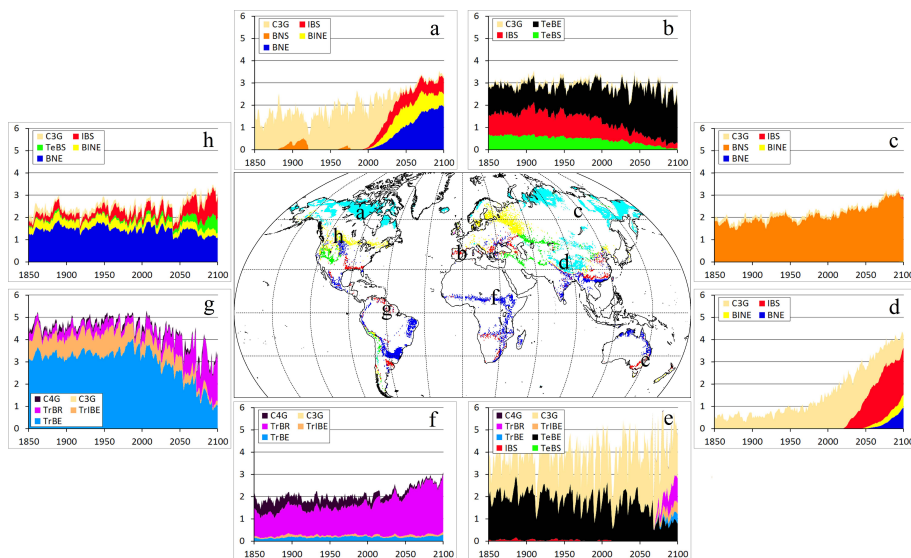
Fig. 3. Major biome shift for the C-only version from year 2000 to 2100 using three broad biome classifications; grass (G), broadleaf (B), and needleleaf (N) dominated. Shifts denoted as biome to biome, e.g. shift from grass to broadleaf dominated is denoted as "GtoB". "No" is implying no major shift of biome over the period. Eight hotspots from Fig. 2 are inserted with accumulated LAI [$m^2\,m^{-2}$] for all present PFTs over the simulated period.
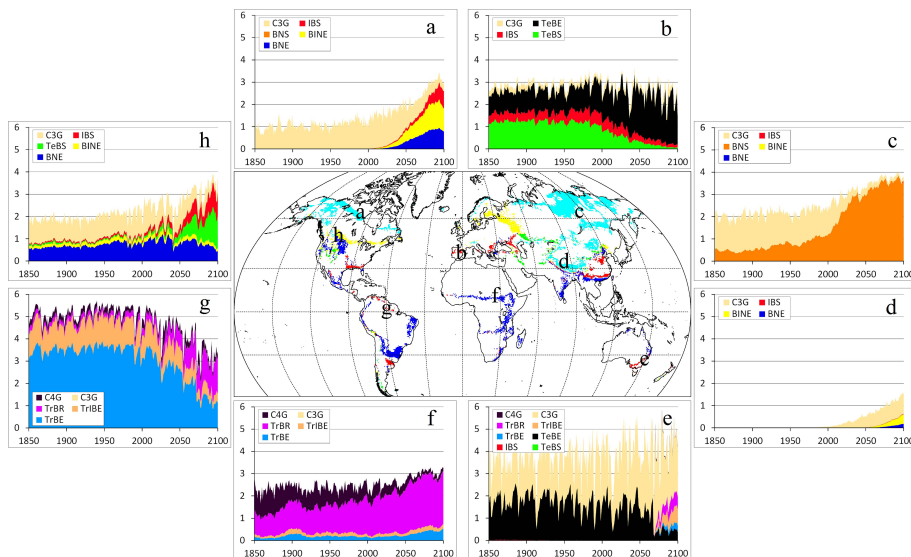
Fig. 4. Major biome shift for the C–N version from year 2000 to 2100 with same classification as in Fig. 3. Eight hotspots from Fig. 2 are inserted with accumulated LAI [$m^2\,m^{-2}$] for all present PFTs over the simulated period.
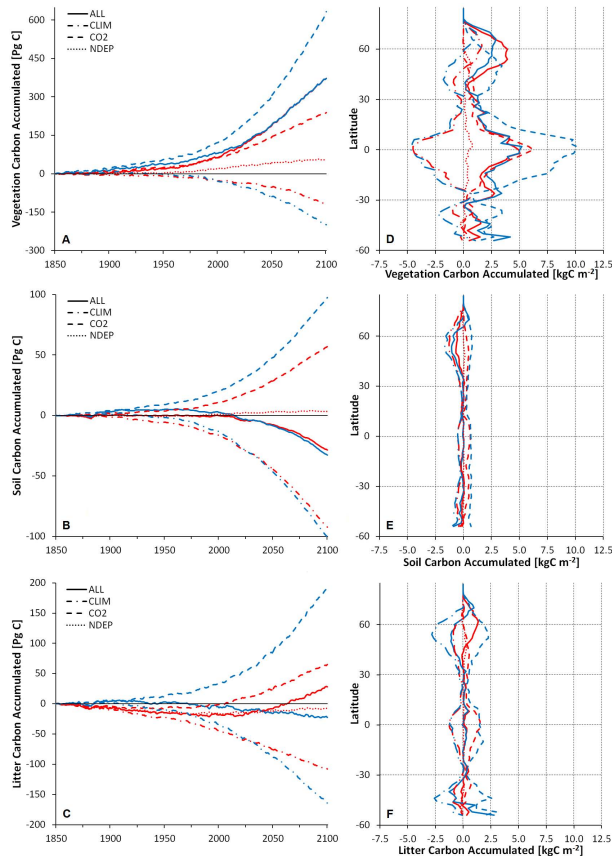
Fig. A1. Accumulative vegetation **(A)**, soil **(B)**, and litter **(C)** C sequestrated between 1850 and 2100 simulated with historical and future change in climate (CLIM), atmospheric [CO_2] (CO2), N deposition (NDEP) alone, and all together (ALL). **(D–F)** show accumulated C by latitude over the period 2000–2100. Blue lines C-only version and red lines are C–N version.

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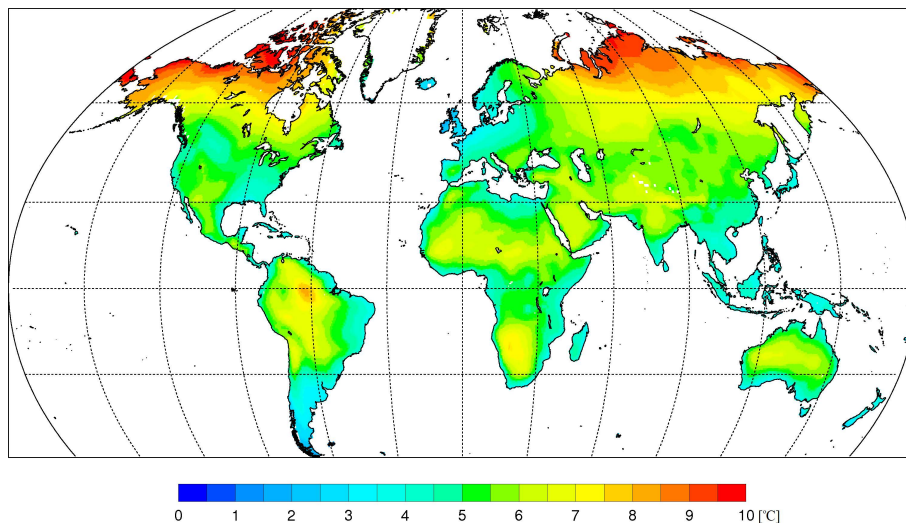
Fig. A2. Change in temperature change during the 21st century simulated with MPI-ESM-LR under RCP 8.5. Shown is the difference between average values computed for 1990–2000 and 2090–2100. Data were bias-corrected following Ahlström et al. (2013).
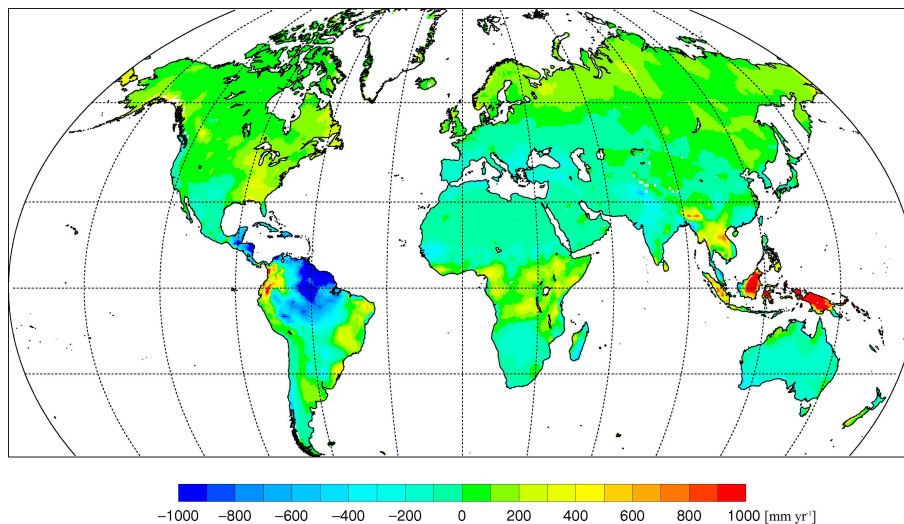
Fig. A3. Changes in precipitation change during the 21st century simulated with MPI-ESM-LR under RCP 8.5. Shown is the difference between average values computed for 1990–2000 and 2090–2100. Data were bias-corrected following Ahlström et al. (2013).
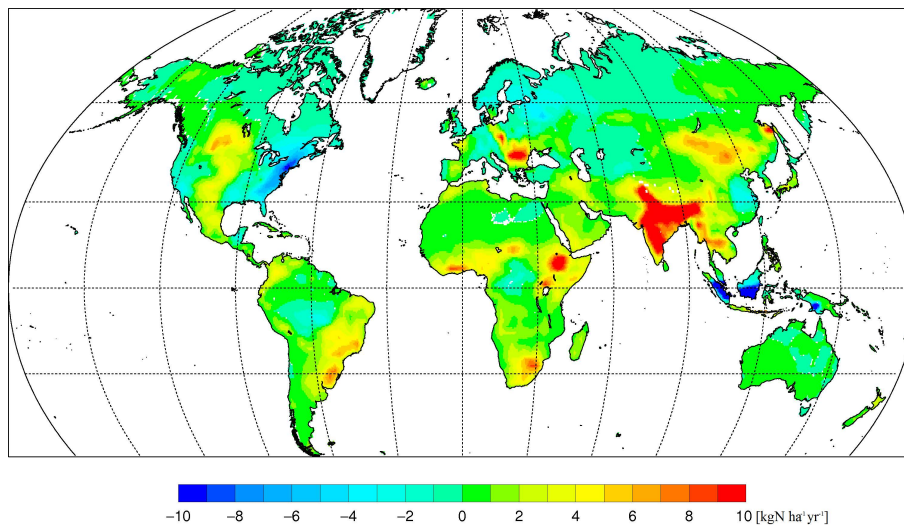
Fig. A4. Change in anthropogenic N-deposition during the 21st century, simulated with the CAM model (Gent et al., 2010) under RCP 8.5. Shown is the difference between average values computed for 1990–2000 and 2090–2100.
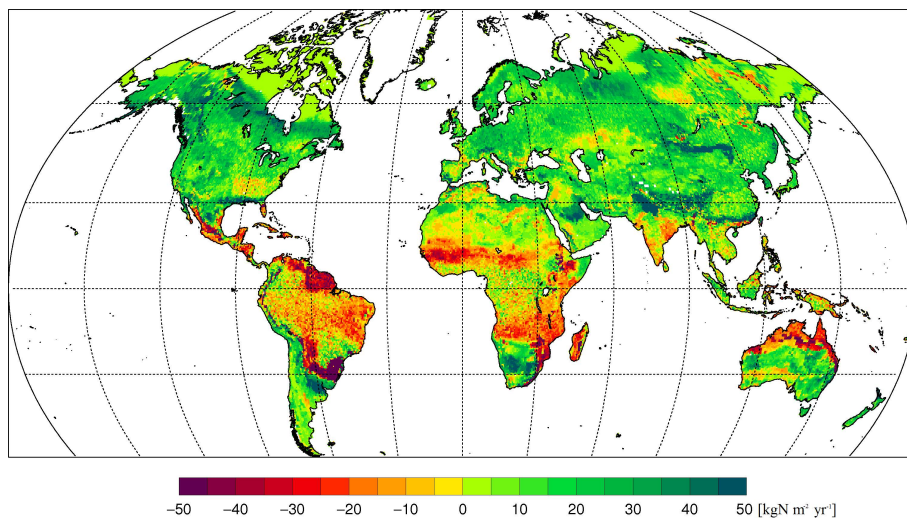
Fig. A5. Change in net N-mineralisation during the 21st century, under the ALL scenario. Shown is the difference between average values computed for 1990–2000 and 2090–2100.