

Dear Mr Sato and anonymous referees

we thank very you much for the thoughtful and constructive criticisms which improved the quality of our work. See detailed replies to the specific points in the following. All page and line numbers are referring to the document with tracked changes.

In addition to the changes reported here we improved the language at a few spots (which are not reported here but marked in the document).

Many thanks,
Daniel Goll in behalf of all authors

Interactive comment on “Carbon-nitrogen interactions in idealized simulations with JSBACH (version 3.10)” by Daniel S. Goll et al. Anonymous Referee #1 Received and published: 6 February 2017

The paper of Goll et al. focuses on the carbon-nitrogen interactions in the new version of JSBACH with updated soil organic matter decomposition model and N component. As nutrient limitation plays an important role in land carbon cycles, the work of Goll et al. is very important towards better predicting of future carbon dynamics. The work is novel in making use of nitrogen isotope data to evaluate process based N simulations. The study is generally well conducted and sufficient for recording model behavior, but I have several concerns or questions listed below.

1. To what extent the C-N interactions produced from this paper are reliable?

There is a large uncertainty in N cycle, which makes the C-N interactions difficult to constrain. The N limitation on carbon cycle, or C-N interaction strength, is based on assumptions of CO₂ induced nutrient limitation (CNL) from this paper. The assumption of marginal nitrogen effect on pre-industrial C cycle is debatable.

Reply: The concept of CNL is a carbon centered approach, thereby limiting the applicability of the model. We believe it is an appropriate method to reduce the risk of overestimating the land carbon uptake under increasing CO₂ concentrations by adding an additional constraint with a minimum increase in the model complexity. We added a discussion of the limitation of the CNL approach to the limitation section (see below)

Although the model can be parameterized based on preindustrial conditions (which may have large uncertainties) that have already taking into account of the N effect, it may misrepresent important mechanisms that regulate long term N effects on C. For example, losses of plant uncontrollable nitrogen, such as through fire, erosion, dissolved organic matter, constrains long term N availability and therefore N impacts on C [Thomas et al.,

2015]. Plant uncontrollable nitrogen loss pathways are not represented in the current version of JSBACH.

Reply: The reviewer makes an important point about the importance of uncontrollable losses. We want to stress that JSBACH does account for uncontrollable losses due to leaching, denitrification (see equations 15&16), as well as fire and LULCC. Changing environmental conditions can cause changes in these loss terms. However, due to our concept, these losses do not significantly affect the global terrestrial carbon balance under pre-industrial conditions in JSBACH as the referee correctly states. In this point we agree with the referee.

In this study losses by fire and LULCC are omitted due to the simulation setup (1%CO₂ simulation) as stated on Page 11 Lines 17-22. Erosion losses of soil organic matter have yet to be incorporated into ESM as stated on Page 19 line 10.

Therefore nitrogen limitation cannot be maintained with strong biological controls on N losses and inputs in JSBACH in the long run, but that does not mean there is no N limitation in the long run in a real world. It may capture transient CO₂ responses.

Reply: We agree with the reviewer that the concept of CNL can only be applied to scenarios in which increasing CO₂ is the major agent of change. The model is able to capture positive effects of increasing N availability (N deposition, warming stimulated mineralisation) only if the increase in CO₂ has increased N demand above the background availability in the first place. Positive effects like found in Esser et al (2007) or Warlind et al (2014) can not be captured by the model. However, in general models tend to simulate negative effects of N which outweigh the positive ones in projection for the 21st century.

We revised the manuscript to clarify the mentioned shortcomings of the CNL approach in JSBACH.

We added:

P21L31-P22L6: added "Due to the concept of CO₂-induced nutrient limitation in JSBACH the nitrogen cycle serves primarily as an additional constraint on the carbon uptake. The advantage of the approach is its low complexity and avoidance of assumptions about the initial state of nutrient limitation thereby taking into account (1) the lack of data regarding the nitrogen cycle (Zaehle, 2013) as well as (2) the large uncertainty about the nutrient constraint on plant productivity (Elser et al., 2007, Zaehle, 2013). The shortcomings of this approach are that it limits the applicability of the model to carbon cycle projections for scenarios of increasing atmospheric CO₂ and that it cannot capture any stimulation of the plant productivity due to changes in nitrogen availability itself: In addition to direct increase in nitrogen availability by nitrogen deposition and fertilization, a stimulation of plant productivity can occur due to reduced losses of nitrogen by pathways which are not under control of biota, like fire, leaching, or erosion(Thomas et al., 2015). As a result, the model might underestimate the importance of nitrogen cycling for carbon uptake under elevated CO₂."

As mentioned by the authors, it may misrepresent climate response and potentially the C-N interactions and other aspects that affect C-N interactions. I suggest the authors be cautious about reaching a conclusion about getting the decomposition of soil carbon right first before incorporating C-N interactions as the evaluation should be based on the right representation of C-N interactions and compared to the “true” observation.

Reply: We agree with the referee that this statement cannot be fully backed by the finding of single model, which might not capture the “truth” in particular as it is prone to underestimate the effect of nitrogen on the carbon cycle. We changed the conclusion in abstract to

P1L15-18“These changes are primarily due to the new decomposition model, indicating the importance of soil organic matter decomposition for land carbon feedbacks.”

2. How does reproducing the relative fraction of nitrogen loss pathways affect land carbon?
Or how does C-N models benefit from an accurate representation of the relative N loss pathways?

It seems to me the focus of this paper is on C-N interaction. Does accurate representation of the relative N loss pathway (leaching vs. gaseous) help in correcting C-N interactions? It is possible to have a correct leaching: gaseous loss ratio while have a wrong simulation of leaching loss or gaseous loss. As the ratio can be tuned through parameters, such as the fraction of soil water lost to rivers per day, the fraction of mineral nitrogen in soil solution, and fdenit estimation from ^{15}N relies strongly on climatic conditions, a reasonable representation of the spatial pattern of fdenit does not necessarily mean a good simulation of mineral N and N limitation on biological activities. It makes the ^{15}N based evaluation more valuable if the authors can clarify the merits of such evaluation for the general N cycling and C-N interaction.

Reply: $\delta^{15}\text{N}$ measurements are one of the few sources of spatially extensive data relevant to the N cycle (Houlton et al., 2015). But as the referee states correctly this information does not tell about the total loss rate (or throughput) of N, which is almost impossible to measure (because a large part of the denitrification loss is in the form of N_2). Despite this shortcoming of the data, the good spatial agreement between observed and model loss pathway shows that the model captures the difference in the respective environmental controls on the losses processes. As these losses are not directly under control of vegetation (see point above), it is important to ensure that their sensitivity to climatic changes is realistically implemented in the model (here by substituting space with time). It is not given that ESMs can capture the loss pathways see for example Houghton et al., 2015., in particular not with such high success.

We added to the manuscript a discussion of the benefits and shortcomings of the $\delta^{15}\text{N}$ measurements product, and stress that the fraction of water lost is not tuned but calculated by a soil hydrological scheme:

P12L25: added “ $\delta^{15}\text{N}$ data measurements are one of the few sources of spatially extensive data relevant to the nitrogen cycle, “

P14L30/31: added “However, this comparison does not allow to draw any conclusion about the magnitude of the losses.”

P14L32-P15L2: added: “ The reconstructed f_{denit} from Houlton et al. (2015) maps (Figure (A1&2) presented here are generally similar to those presented by Houlton et al. (2015), with high fractions (ca 80%) in the tropics and mid-latitude deserts, a strong gradient of decreasing fractions with decreasing temperature towards high altitudes and latitudes, and values in the range 0-20% reached in cold, wet climates in the north. For a detailed discussion of differences see SI.”

P10L10-11: added” “ f_{h2o} is computed dynamically accounting for evapotranspiration, precipitation, and changes in the soil water storage using a 5 layer soil hydrological scheme (Hagemann et al. 2014).”

The referee is right that the good agreement between observed and simulated loss pathways does not allow any conclusion about N limitation of vegetation, but we cannot find such a statement in the manuscript. No changes done.

3. Model description is not very clear and is confusing in some parts.

As this paper focus on how N affects land carbon simulation, it is better to let readers know how N limitation regulates photosynthesis (GPP or NPP) and organic matter decomposition which are two key nexus points in C-N interactions. As the model descriptions combine terms from the YASSO model, the old JSBACH model and the updated JSBACH model, it is difficult to follow especially when the structures of these models are not the same. I suggest reworking on model description. More detailed suggestions are available in Minor Points.

Reply: The manuscript reports the changes in the soil part of the nitrogen as the rest is described in detail in Goll et al. (2012) and Parida (2010). We agree that an overview of the C and N cycling and its interactions is beneficial for the reader. We therefore added a scheme (Figure 1) showing the interactions between the N and the C cycle with a comprehensive caption explaining the C-N interactions:

Added P5:

“Figure 1. Schematic representation of carbon (top) and nitrogen (below) cycling in JSBACH. Vegetation is represented by four pools: “active” (leaves and non-lignified tissue) and “wood” (stem and branches), “reserve” (sugar and starches) and “mobile”

(labile nitrogen) (Goll et al., 2012). Dead organic matter is represented by “non-lignified litter”, “lignified litter” (lignified litter and fast-decomposing soil organic matter), and “humus” (slow-decomposing organic matter) (Raddatz et al., 2007). All organic matter pools have fixed C:N ratios, except the pools “reserve”, “labile” and “non-lignified litter”. While the first two pools have no corresponding pool, the C:N ratio of the latter pool varies according the balance between immobilization demand and supply. The carbon in the litter compartment is further refined into the acid-soluble (A), water-soluble (W), ethanol-soluble (E), and non-soluble (N) compounds (Goll et al., 2015) which have no C:N ratio assigned. Soil mineral nitrogen is represented by a single pool (soil mineral pool). The opposing triangle marks carbon fluxes which are downregulated in case the nitrogen demand exceeds the nitrogen supply.”

P3L9-10: added: “ a scheme of the cycling of carbon and nitrogen as well as their interactions are given in Figure 1.

We further included in the appendix the calculation of the nitrogen limitation factor:

P24/25: added:

“The nitrogen limitation factor

The nitrogen limitation factor, f^N_{limit} , is calculated based on a supply and demand approach (Parida 2011, Goll et al., 2012). In a first step, potential carbon fluxes are computed from which the gross mineralisation, immobilization (D_{micr}) and plant uptake of mineral nitrogen (D_{veg}) is diagnosed.

In a second step, all fluxes consuming nitrogen (donor compartment has a higher C:N ratio than the receiving pool as well as plant uptake) are down-regulated in case nitrogen demand cannot be met by the nitrogen supply. Hereby, a common scalar (f^N_{limit}) is used thereby no assumption about the relative competitive strengths of microbial and plant consumption has to be made.

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where the term in square bracket is the maximum rate at which the soil mineral nitrogen pool can supply nitrogen. Note that in the discretized formulation the mineral nitrogen pool can at most be depleted during a single model time step (Δt). We thus set this maximum rate to $\frac{dN_{smin}}{\Delta t}$. “

Please see also the changes done in response to referee #2 points about the model description section.

Minor Points:

1. Is it appropriate to have many citations in abstract?

Reply: we removed all citations from the abstract

2. Page 1, line 10, the reference of Shi et al., 2015 is not relevant. Do you mean Shi Z, Yang Y, Luo Y, Zhou X, Weng E, Finzi A. 2015. Inverse analysis of coupled carbon-nitrogen cycles against multiple datasets at ambient and elevated CO₂. Journal of Plant Ecology, doi:10.1093/jpe/rtv059

Reply: Yes, we meant Shi et al. 2016; we corrected the references at P16L19 and removed the one mentioned here.

3. P4,L5, equation 1, line 9, is there a H component in the matrix equation?

Reply: There is no H component in the matrix equation. We added the equation EQ3 for the dynamics of the Humus pool with its description and corrected the text.

P4L11-12: revised "Matrix C describes the soil carbon pools (A, W, E, N) of the two litter size classes (i) in JSBACH, excluding recalcitrant humic substances (C_H):"

P4L17-P5L1: added: "The dynamics of the humus pool (C_H) are described as:

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where p_H is the relative mass flow parameter and k_H the decomposition rate of the humus pool. "

4. P5, lines 2-3 "lignified litter and fast decomposing organic matter" is confusing as no "fast decomposing organic matter" is mentioned in the carbon part.

Reply: We revised the text to avoid confusions.

P6L11-P7L5: revised/added: "Nitrogen in litter and soil organic matter is separated into three pools, namely slowly-decomposing organic matter C_s , lignified litter and fast decomposing organic matter C_{lw} , as well as non-lignified litter and fast decomposing organic matter C_{la} (Goll et al.,2012). We assigned each of the three nitrogen pools to one or more corresponding YASSO pools (Table~\ref{tab:corr}). A refinement of the representation of nitrogen in decomposing material following strictly the carbon classification is not straightforward as the carbon pools (A,W,E,N) defined by their respective solubility characteristics do not correspond to substance classes with distinguished stoichiometries."

5. P7, equation 10, where is the nitrogen flux from your la class (non-lignified & fast decomposing organic matter)? The third term, the lignified flux is not clear. Why do you have $(r_w - r_{lw}) * F$ for lignified flux while only have $r_{la} * F$ for non-lignified flux in equation 7? The description from Lines 20-21 is not clear. Why do you differentiate N-to-C ratio of lignified litter and biomass?

Reply: We added two sentences to clarify the two mentioned points

Added:

P9L6-11: added: "Due to the lower nitrogen content of litter compared to humus, the decomposition of lignified and non-lignified litter corresponds to a net immobilization of nitrogen, which is part of the D_{micr} . The term $(r_w - r_{lw}) F^{C_{w \rightarrow lw}}$ represents nitrogen leaching from freshly shedded wood given by the decomposition and the stoichiometries assigned to wood (r_w) and lignified litter (r_{lw})."

6. P9, L10, "cchange" to "change "

Reply: typo corrected

7. Section 2.5.2 Nitrogen loss pathway data. I may have missed some part, but the description on how to estimate f_{denitr} is not very clear. You fitted data to equation 19. So in equation 19, what are known and what are need to be estimated? If k is the only factor need to be estimated, what is the purpose to estimate k as equation 20 based on which to estimate f_{denitr} does not need k

reply: In the equation 19, we need to estimate the k **AND** ϵ (gaseous discrimination factor) from soil $\delta^{15}N$ using non-linear least-squares regression method. By re-arranging Eq19 and 20 we can derive f_{denitr} . We revised the text to clarify this.

Changes in the text:

P13L20: revised "*The data were then fitted via epsilon the gaseous discrimination factor and a constant k by non-linear least-squares regression to the relationship*"

P13L26: added: ". Re-arranging Equation 19 and 20 we get $f_{denitr}=(1+k(f(q)/f(T)))-1$ "

See also reply to Referee#2 and revisions on line P12L25-P13L2 which gives additional information regarding the methodology and major differences to approach applied by Houlton et al. (2015).

8. P12, L3-5 No compiled mineral N in Table 5 is available for comparison and indicates simulated mineral nitrogen stock is within the range of estimates. There is no available data in Table 5 to compare denitrification between simulated 1850 vs. observation-based 1850. Comparing between simulated value at 1850 with present is not appropriate as nitrogen cycle is altered strongly by anthropogenic activities since the industrialization.

Reply: we agree with the reviewer about the human impact on the nitrogen cycle. The estimates compiled in Table5 are all estimates we are aware of. We removed the the statement about denitrification and stress that estimates are not available for all variables.

We revised the text:

P14L6-10: revised: "*The model simulates nitrogen stocks and fluxes under pre-industrial conditions well within the wide range of the few available observation based estimates (Table 5). Most of the estimates are for present day conditions and thus are not directly comparable due to the human influence on the nitrogen cycle (Galloway et al., 2013).*"

9. P12,L6, Is nitrogen in Ia (non-lignified litter & fast decomposing organic matter) part of the organic nitrogen stocks? Equation 7 says it is not prescribed based on C:N.

Reply: We added a table with the simulated CN ratios of non-lignified litter & fast decomposing organic matter in comparison with observation to the appendix and state in the main text :

P14L12-13: Added: *“except for non-lignified litter and fast decomposing soil organic matter which shows in general good agreement with observed C:N ratios (see appendix).”*

Added “appendix B” including a Table A1 to appendix :

P26: added: **“Evaluation of dynamically computed C:N ratios**

The only ecosystem compartment in JSBACH which has a flexible stoichiometry is non-lignified litter and fast-decomposing organic matter.

The simulated carbon to nitrogen ratios of this compartment for the six plant functional types in JSBACH are in rather good agreement with observations of foliage litter from the ART-DECO database (Table~\ref{tab:CN}), except for tropical broadleaved deciduous trees and extra-tropical evergreen trees.

Reasons for the overestimation of nitrogen content in litter from extratropical evergreen tree is the global parametrization of leaf stoichiometry applied in JSBACH which does not capture the lower leaf nitrogen concentration in needle-leaved trees compared to broad-leaved trees (Kattge et al., 2011).

The data for tropical species is very scarce and the variability among species is large, which hamper the interpretation of the mismatch between model and observation for the tropical broadleaved deciduous trees.”

10. P13, if climatic forcing is the reason for mismatch, is it feasible to calculate f_{denit} (the isotope approach) based on climatic forcing that drives the JSBACH model simulation instead of CRU CL2.0 and then make comparisons?

Reply: According to the referee’s suggestion, we recalculated f_{denit} map using the climatology from the model in addition to observed climatology. We now use the f_{denit} from simulated climate in the main manuscript and move the map of f_{denit} derived from observed climatology to the appendix. We modified the method section, the discussion section, the conclusion section, and the appendix. We added Figure A1 showing the f_{denit} derived from observed climatology and a comparison of the frequency distributions for the two approaches.

P13L28-P14L3: revised: *“A spatial map of f_{denit} was derived from the empirical relationship between temperature, runoff and f_{denit} using simulated values of $f(q)$ and $f_m(T_m)$ from JSBACH. Thereby, model biases in climate are accounted for in the data derived f_{denit} which allows a straightforward comparison with simulated f_{denit} . In addition, we derived maps of f_{denit} based on monthly grids of observed mean climate from 1961--1990 covering the global land surface at a 10 \unit{minute} spatial resolution (CRU CL2.0) \citep{New2002} which are shown in the appendix.”*

P15L3-P15L18: revised: *“In comparison with the reconstructed fractional gaseous loss from simulated climate (Figure 2a), we find that the model is in good agreement*

(Pearson $R=0.76$, RMSE=0.2, Taylor score=0.83). The model underestimates high values of f_{denit} and overestimate low values (Figure A2). In regions with cold winter temperatures where nitrification losses are small the model overestimates denitrification losses (Figure 2c) These model biases likely derive from the simplistic representation of denitrification as a function of soil moisture and substrate availability, which omits effects of temperature (Butterbach-Bahl et al., 2013). Additionally, other omitted factors like oxygen concentration, soil pH, mineralogy, and transport processes (Butterbach-Bahl et al., 2013) might contribute to the bias.

P23L6-16: revised: “The simulated response of primary productivity to increasing CO₂, simulated litter stoichiometries, as well as the simulated spatial variability in nitrogen loss pathways are in good agreement with observation based estimates. Here we show that a simple representation of mineral nitrogen dynamics can achieve a high agreement with observation in respect to nitrogen loss pathways. Further refinements of denitrification should address the relationship between denitrification and low soil moisture availability and as well as introduce a temperature scaling function.”

P26 added:

“Consistency of nitrogen loss pathways with earlier estimates

The reconstructed f_{denit} map from observed climatology (Figure A1) is generally similar to one presented by Houlton et al. (2015), with high fractions (ca 80%) in the tropics and mid-latitude deserts, a strong gradient of decreasing fractions with decreasing temperature towards high altitudes and latitudes, and values in the range 0-20% reached in cold, wet climates in the north. However, some differences are apparent, most obviously connected with the use of mean annual temperature (MAT) by Houlton et al. (2015) to index microbial activity. MAT becomes extremely low in Eurasia towards the northeast, for example, and accordingly, Houlton et al. (2015) estimates of the denitrification fraction become very low there. Craine et al. (2015) noted that climates with very low MAT (including sites in NE Siberia) showed anomalous values of soil $\delta^{15}\text{N}$, more similar to those of warmer climates. Our approach takes account of this by the use of an index that is much more responsive to the warm summers than to the extreme cold winters found in hypercontinental climates.

When simulated climatology is used to upscale the empirical relationship between temperature, runoff and soil $\delta^{15}\text{N}$, the influence of biases in simulated climatology on f_{denit} become apparent. The overestimation of precipitation and subsequently runoff of about 20% in MPI-ESM (Weedon et al., 2011, Hagemann & Stacke, 2013) leads to a pronounced peak in the histogram of f_{denit} at about 0.1-0.2 (Figure A1), which is mostly in the mid and high latitudes regions in northern hemisphere.”

11. Figure 2 caption, the tag (a) and (b) should be switched

Reply: corrected

12. P19, 1st paragraph, plant uncontrollable N loss pathways, such as DON and fire losses worth mentioning. You can find the discussion about how plant uncontrollable vs. controllable N losses regulate terrestrial N limitation from the modeling perspective in Thomas et al., [2015]. You can also find an example of a global C-N model with DON loss from Gerber et al., [2010].

Reply: see text revision as a response to the major point of critic #1 (above)

13. P19, 2nd paragraph. I agree BNF is critical in the general terrestrial N cycle simulation, but remains largely unresolved. Gerber et al., [2010] has a more dynamic BNF scheme which takes into N supply, N demand and light availability compared to the NPP or ET approach, but more studies are needed to improve BNF.

Reply: we added references to to more sophisticated BNF models and rephrased the sentence to avoid implying there is no better model around than used in JSBACH:

P22L16-18: revised “BNF models which better resolve the governing mechanisms, for example (Gerber e al., 2010, Fisher et al., 2012), should be incorporated into ESMS to increase the reliability of the simulated pace of changes in BNF (Meyerholt & Zaehle, 2016).

Interactive comment on “Carbon-nitrogen interactions in idealized simulations with JSBACH (version 3.10)” by Daniel S. Goll et al. Anonymous Referee #2 Received and published: 7 March 2017 Review for Groll et al.

This manuscript is a description of global nitrogen cycling and the reporting of standard climate and CO2 feedback parameters from an Earth system model in preparation for CMIP6 simulations. The advancement in modeling is the addition of N cycling to a previously

C only soil decomposition model (YASSO). The unique attribute of the overall modeling framework, with respect to the N cycle, is the assumption that N limitation of plant and microbial activity is not present during the pre-industrial simulation (the CNL assumption). Therefore, the changes in N limitation using the 20 and 21 century simulations are caused by rising atmospheric CO₂ concentrations.

It is difficult to tell whether the disagreement between the N gas loss fraction simulation and estimates is due to differences in the climate driver data or due to the ESM. An offline simulation is needed that uses historical climate driver rather than the coupled model climate drivers to better evaluate the model. Considering the N₁₅-based gas loss fraction is the only spatial evaluation of the model in this manuscript, the simulations used to compare to the observations should allow the most 'clean' comparison possible.

Reply: We agree with the Referee about to need to “clean” the comparison. Unfortunately, it is computational not feasible to repeat the JSBACH simulations, however a clean comparison can also be achieved by recalculating the observed f_{denit} using MPI-ESM climate as Referee #1 suggested. The latter is feasible. In the following we repeat the answer to Referee #1 and the according changes to the manuscript:

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According to the referee's suggestion, we recalculated f_{denit} map using the climatology from the model in addition to observed climatology. We now use the f_{denit} from simulated climate in the main manuscript and move the map of f_{denit} derived from observed climatology to the appendix. We modified the method section, the discussion section, the conclusion section, and the appendix.

P13L7-10: revised: *“A spatial map of f_{denit} was derived from the empirical relationship between temperature, runoff and f_{denit} using simulated values of $f(q)$ and $f_m(T_m)$ from JSBACH. Thereby, model biases in climate are accounted for in the data derived f_{denit} which allows a straightforward comparison with simulated f_{denit} . In addition, we derived maps of f_{denit} based on monthly grids of observed mean climate from 1961--1990 covering the global land surface at a 10 \unit{minute} spatial resolution (CRU CL2.0) \cite{New2002} which are shown in the appendix.”*

P15L3-18: revised: *“In comparison with the reconstructed fractional gaseous loss from simulated climate (Figure 2a), we find that the model is in good agreement (Pearson $R=0.76$, $RMSE=0.2$, Taylor score= 0.83). The model underestimates high values of f_{denit} and overestimate low values Figure A2). In regions with cold winter temperatures where denitrification losses are small the model overestimates denitrification losses Figure 2c) These model biases likely derive from the simplistic representation of denitrification as a function of soil moisture and substrate availability, which omits effects of temperature (Butterbach-Bahl et al., 2013). Additionally, other omitted factors like oxygen concentration, soil pH, mineralogy, and transport processes (Butterbach-Bahl et al., 2013) might contribute to the bias.*

“

P23L6-16: revised: *“The simulated response of primary productivity to increasing CO₂, simulated litter stoichiometries, as well as the simulated spatial variability in nitrogen loss pathways are in good agreement with observation based estimates. Here we show that a simple representation of mineral nitrogen dynamics can achieve a high agreement with observation in respect to nitrogen loss pathways. Further refinements of denitrification should address the relationship between denitrification and low soil moisture availability and as well as introduce a temperature scaling function.”*

P26: added:

“Consistency of nitrogen loss pathways with earlier estimates

The reconstructed f_{denit} map from observed climatology (Figure A1) is generally similar to one presented by Houlton et al. (2015), with high fractions (ca 80%) in the tropics and mid-latitude deserts, a strong gradient of decreasing fractions with decreasing temperature towards high altitudes and latitudes, and values in the range 0-20% reached in cold, wet climates in the north. However, some differences are apparent, most obviously connected with the use of mean annual temperature (MAT) by Houlton et al. (2015) to index microbial activity. MAT becomes extremely low in Eurasia towards the northeast, for example, and accordingly, Houlton et al. (2015) estimates of the denitrification fraction become very low there. Craine et al. (2015) noted that climates with very low MAT (including sites in NE Siberia) showed anomalous values of soil $\delta^{15}\text{N}$, more similar to those of warmer climates. Our approach takes account of this by the use of an index that is much more responsive to the warm summers than to the extreme cold winters found in hypercontinental climates.

When simulated climatology is used to upscale the empirical relationship between temperature, runoff and soil $\delta^{15}\text{N}$, the influence of biases in simulated climatology on f_{denit} become apparent. The overestimation of precipitation and subsequently runoff of about 20% in MPI-ESM (Weedon et al., 2011, Hagemann & Stacke, 2013) leads to a pronounced peak in the histogram of f_{denit} at about 0.1-0.2 (Figure A1), which is mostly in the mid and high latitudes regions in northern hemisphere.”

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Furthermore, more discussion of the uncertainty in the 15N based estimates of N gas loss fraction is needed. How good of a tool is it for evaluating the model?

Reply: We added a discussion about the advantages and shortcomings of using 15N based estimates of N gas loss to the manuscript, as well as discuss the differences to an earlier estimate of Houlton et al. (2015)

P14L24/25: added “, which are one of the few sources of spatially extensive data relevant to the nitrogen cycle, “

P14L30/31 added “However, this comparison does not allow to draw any conclusion about the magnitude of the losses.”

P14L32-P15L2: added: “ The reconstructed f_{denit} from Houlton et al. (2015) maps

(Figure (A1&2) presented here are generally similar to those presented by Houlton et al. (2015), with high fractions (ca 80%) in the tropics and mid-latitude deserts, a strong gradient of decreasing fractions with decreasing temperature towards high altitudes and latitudes, and values in the range 0-20% reached in cold, wet climates in the north. For a detailed discussion of differences see SI.”

More discussion is needed about how the CNL assumption influences the results. It appears that the CNL assumption is achieved by reducing the N limitation during the pre-industrial spin-up but it is unclear how this spin-up process influences the overall predictions.

Reply: We added a discussion of the implications of the CNL approach on the results:

P21L31-P22L7: added “Due to the concept of CO₂-induced nutrient limitation in JSBACH the nitrogen cycle serves primarily as an additional constraint on the carbon uptake. The advantage of the approach is its low complexity and avoidance of assumptions about the initial state of nutrient limitation thereby taking into account (1) the lack of data regarding the nitrogen cycle (Zaehle, 2013) as well as (2) the large uncertainty about the nutrient constraint on plant productivity (Elser et al., 2007, Zaehle, 2013). The shortcomings of this approach are that it limits the applicability of the model to carbon cycle projections for scenarios of increasing atmospheric CO₂ and that it cannot capture any stimulation of the plant productivity due to changes in nitrogen availability itself: In addition to direct increase in nitrogen availability by nitrogen deposition and fertilization, a stimulation of plant productivity can occur due to reduced losses of nitrogen by pathways which are not under control of biota, like fire, leaching, or erosion(Thomas et al., 2015). As a result, the model might underestimate the importance of nitrogen cycling for carbon uptake under elevated CO₂.”

More detailed comments:

Page 1, Line 6: little r is used here but big R is used later on Page 12, Line 19. Which is correct?

Reply: corrected P1L6

Page 1, Line 12: How does CO₂ enhance the turnover of organic nitrogen? This result does not seem to be highlighted explicitly elsewhere. In fact, Page 18, Line 19 states the JSBACH is unable to account for the simulation of organic matter turnover through priming.

Reply: corrected. Turnover is enhanced due to warming not CO₂.

P1L12: revised :*“In line with evidence from elevated carbon dioxide manipulation experiments, pronounced nitrogen scarcity is alleviated by the accumulation of nitrogen due to enhanced nitrogen inputs by biological nitrogen fixation and reduced losses by leaching and volatilization. The stimulation of turnover of organic nitrogen by increasing temperatures further counteracts scarcity.”*

Page 2, Line 12: ‘The exchange of the former. . .’ is awkward to read (did YASSO do the exchanging?).

Reply: corrected. P2L13: change “by the YASSO model” to “with the YASSO model”

Page 2, Line 18: Add an ‘of’ between ‘recycling’ and ‘nitrogen’

Reply: corrected P2L18

Page 2, Line 20: Recommend citing Thomas et al. 2015 (Global Change Biology) here

Reply: reference added P2L20

Page 2, Line 21: The Luo et al 2004 is about progressive nitrogen limitation rather than just nitrogen limitation. I recommend adjusting the language

Reply: added “(progressive)” P2L22

Page 2 Line 23: I recommend adding Zhu and Riley 2015 (Nature Climate Change) to complement the Houlton citation.

Reply: reference added. P2L23

Page 3 Line 12: The manuscript the terms ‘litter size classes’, ‘size classes’, and ‘litter class’) are both used. Please be consistent. (see Page 4 line 17 and Table 1 as examples)

Reply: We revised throughout the text “size class” and “litter size class” to “litter class” and added the following information:

P3L11-15: added /revised: *“The decomposition model (YASSO) is based on a compilation of litter decomposition and soil carbon data and distinguish organic matter fractions according to litter size and solubility (Tuomi et al., 2008,2009, 2011). In JSBACH we use two litter size classes, which correspond to litter from non-lignified and lignified plant material (Goll et al., 2015). Each of the two litter classes is further refined into four solubility classes”*

Page 4, Equation 1. The matrix is missing the humus pool despite being referenced in the prior sentence

Reply: There is no H component in the matrix equation. We added the equation EQ3 for the dynamics of the Humus pool with its description and corrected the text.

P4L11-12: revised *“Matrix $C_{i,j}$ describes the soil carbon pools (A, W, E, N) of the two litter size classes (S_i) in JSBACH, excluding recalcitrant humic substances ($C_{H,S}$):”*

P4L17-P4L20: added: “The dynamics of the humus pool (C_H) are described as:
<<< EQUATION: SEE PDF >>>
where p_H is the relative mass flow parameter and k_H the decomposition rate of the humus pool. “

Table 1. Including the decomposition rates would be useful for understanding how the rate constants compare to other models. Is this a fast turnover model?

Reply: We added mineralisation rates and biomass nitrogen and carbon to Table 5 and discuss the added variables in text.

P14L14-18: added “Mineralisation of organic nitrogen is the major source of nitrogen for vegetation and the simulated flux is less than existing model based estimates for present day ranging between 980--1030 (Smith et al. 2014, Zaehle et al. 2010). In models, nitrogen mineralisation is solely a by-product of decomposition of soil organic carbon and we thus attribute the differences between simulated mineralisation to the use of YASSO decomposition model compared to the use of the CENTRUY decomposition model (Smith et al. 2014, Zaehle et al. 2010) as the soil C:N stoichiometries are comparable among models.“

Section 2.1.1: The exact approach to plant microbe competition needs to be described in this section. Do microbes have first access?

Reply: we revised the methods to add this information:

P6L4-9 revised “In a first step, potential carbon fluxes are computed from which the release, immobilization and plant uptake of mineral nitrogen is diagnosed. In a second step, all fluxes consuming nitrogen (donor compartment has a higher C:N ratio than the receiving pool) are down-regulated in case nitrogen demand cannot be met by the nitrogen supply. Hereby a common scalar (f^N_{limit}) (see appendix) is used thereby no assumption about the relative competitive strengths of microbial and plant consumption has to be made. In case nitrogen demand is met by the supply, the fluxes computed in the first step are taken as actual ones without any modification.”

We further added details on the calculation of the limitation factor to the appendix.

P24/25 added: “**The nitrogen limitation factor**

The nitrogen limitation factor, f^N_{limit} , is calculated based on a supply and demand approach (Parida 2011, Goll et al., 2012). In a first step, potential carbon fluxes are computed from which the gross mineralisation, immobilization (D_{micr}) and plant uptake of mineral nitrogen (D_{veg}) is diagnosed. In a second step, all fluxes consuming nitrogen (donor compartment has a higher C:N ratio than the receiving pool as well as plant uptake) are down-regulated in case nitrogen demand cannot be met by the nitrogen supply. Hereby, a common scalar (f^N_{limit}) is used thereby no assumption about the relative competitive strengths of microbial and plant consumption has to be made.
<<< EQUATION: SEE PDF >>>

where the term in square bracket is the maximum rate at which the soil mineral nitrogen pool can supply nitrogen. Note that in the discretized formulation the mineral nitrogen pool can at most be depleted during a single model time step (Δt). We thus set this maximum rate to $\frac{dN_{smin}}{\Delta t}$. “

Overall, the manuscript needs a better description of the order of operations for the nitrogen cycle.

Reply:, we now explicitly state that losses are prioritized at each timestep. Plant uptake and immobilisation happens simultaneously. See last reply above

Added P10L5: “The losses of nitrogen are given priority over immobilization and plant uptake each time step.”

We added the to the discussion:

P22L23-24: added: “pathways is to a large degree in line with $\delta^{15}\text{N}$ -derived patterns, despite the low performance of another sequential competition model (Houlton et al., 2015; Zhu and Riley, 2015).”

Section 2.1.2. I found the w and g subscript to be confusing. What do the w and g stand for?

Reply: we exchange subscript ‘g’ with ‘a’ for “active” plant tissue. Subscript ‘w’ stands for ‘woody’ plant tissue. We already used the term “active, non-lignified plant tissue” throughout the text. We exchanged the term “lignified plant material” with “lignified (woody) plant material” to make this clear.

Section 2.1.2: It seems that the C:N ratio of non- lignified litter is constant across the globe. Does this mean that the C:N ratio of non-lignified biomass is constant across the globe or is there variable retranslocation? An assumption that the C:N non-lignified litter is constant seems to be ignoring known differences in foliar N across forest types.

Reply: we use globally uniform parametrization of stoichiometry and resorption. The resorption of leaf nitrogen is not that flexible (40-60%) (Sterner & Elser 2005, McGroddy et al. 2004) compared to other nutrients for example leaf phosphorus (McGroddy et al. 2004). Goll et al. (2012) showed that the effect of stoichiometric parametrization on the effect of nutrients on the carbon uptake is rather small in JSBACH. What matters for the effect of nutrients on the carbon uptake is the plasticity in stoichiometry & resorption not the baseline value itself, see for example Meyerholt et al (2015). Plasticity in plant traits is in general omitted in JSBACH.

We added the implications of the omission of plasticity in nitrogen related plant traits to the limitation section:

P21L27: revised “The current understanding of processes governing the terrestrial nitrogen balance is still rather limited \citep{Zaehle2013}, and several processes

which might be of importance, [...], plasticity in stoichiometry and leaf nutrient recycling \citep{Zaehle2014,Meyerholt2015}, [...] are not represented in JSBACH."

Page 9, Line 2: Please expand on what criteria was used to tune the parameter. What does it mean that the 'assumption of regarding the absence of CNL in the pre-industrial state is met'?

Reply: clarified P10L24-25: "so that the assumption regarding the absence of CNL in the pre-industrial state is met which equals to a negligible (<2\%) effect of nitrogen on net primary productivity and carbon stocks"

Section 2.5.2. It should be explicitly stated in this section that the authors reanalyzed existing N15 data. Also, how is the data publically available? Is there a database?

Reply: We added a paragraph to the method section to list the differences in the methods. P12/13

Reply: we explicitly state in the method section that we reanalyzed published data P13L4-7: "*predictors fitted to publicly available data on soil $\delta^{15}\text{N}$ (Patino et al., 2009; Cheng et al., 2009; McCarthy and Pataki, 2010; Fang et al., 2011, 2013; Hilton et al., 2013; Peri et al., 2012; Viani et al., 2011; Sommer et al., 2012; Yi and Yang, 2007).*"

We further make this data available as all other data used in this study as stated in the Data availability section:

"Primary data and scripts used in the analysis and other supplementary information that may be useful in reproducing the author's work are archived by the Max Planck Institute for Meteorology and can be obtained by contacting publications@mpimet.mpg.de."

No changes done.

Overall more description is needed of the dataset that was used. How is the dataset and analysis similar and different from the Houlton 2015 analysis?

Reply: We added to methods detailed information on the differences between the two approaches:

P12L25-P13L2: added " *$\delta^{15}\text{N}$ data measurements are one of the few sources of spatially extensive data relevant to the nitrogen cycle (Houlton et al., 2015) as one can infer information about the nitrogen pathways. Houlton et al. (2015) derived the fraction of nitrogen loss in gaseous form (f_{denit}) based on (Amundson et al., 2003) best-fitting multiple regression equation for soil $\delta^{15}\text{N}$ as a function of mean annual temperature (MAT) and mean annual precipitation (MAP). The data*

set used to generate this equation consisted of 29 samples, and the coefficient of determination was 0.39. Amundson et al. (2003) remarked that ‘pending the availability of more soil $\delta^{15}\text{N}$ analyses, the present Figure ... represents our best estimate of trends ... in global soil $\delta^{15}\text{N}$ values’ (p. 5). We have updated this analysis in three ways: (a) by including a larger number (659) of soil $\delta^{15}\text{N}$ samples; (b) by substituting an annually integrated index of temperature-related microbial activity for MAT, and an index of leaching (derived from runoff) for MAP – i.e. using indices more closely related to the governing processes; and (c) by using non-linear regression to fit a statistical model that is explicitly based on the isotopic mass balance equation of (Houlton & Bai, 2009).”

Page 12, Line 3. The sentence states that the mineral nitrogen stocks were in the wide range of estimates but Table 5 does not provide any global estimates for the Mineral nitrogen pools

Reply: no estimates for mineral N are available. We revised the text P14L6-10: revised: “*The model simulates nitrogen stocks and fluxes under pre-industrial conditions well within the wide range of the few available observation based estimates (Table 5). Most of the estimates are for present day conditions and thus are not directly comparable due to the human influence on the nitrogen cycle (Galloway et al., 2013).*”

Page 12, Line 17. Please provide more information on the consistency between the results used in the manuscript and the Houlton results.

Reply: We added a section to the appendix to discuss the differences in respect of the methodologies:

Added to appendix (Page26): “

Consistency of nitrogen loss pathways with earlier estimates

The reconstructed f_{denit} map (Figure~(\ref{Sfig:15N})) presented here is generally similar to one presented by (Houlton et al., 2015), with high fractions (ca 80%) in the tropics and mid-latitude deserts, a strong gradient of decreasing fractions with decreasing temperature towards high altitudes and latitudes, and values in the range 0-20% reached in cold, wet climates in the north. However, some differences are apparent, most obviously connected with the use of mean annual temperature (MAT) by Houlton et al. (2015) to index microbial activity. MAT becomes extremely low in Eurasia towards the northeast, for example, and accordingly, Houlton et al. (2015) estimates of the denitrification fraction become very low there. Craine et al. (2015) noted that climates with very low MAT (including sites in NE Siberia) showed anomalous values of soil $\delta^{15}\text{N}$, more similar to those of warmer climates. Our approach takes account of this by the use of an index that is much more responsive to the warm summers than to the extreme cold winters found in hypercontinental climates. When simulated climatology is used to upscale the empirical relationship between temperature, runoff and soil $\delta^{15}\text{N}$, the influence of biases in simulated climatology on f_{denit} becomes apparent. The

overestimation of precipitation and subsequently runoff of about 20% in MPI-ESM (Weedon et al., 2011, Hagemann & Stacke, 2013) leads to a pronounced peak in the histogram of f_{denit} at about 0.1-0.2, which is mostly in the mid-and high latitudes regions in northern hemisphere.”

Figure 1. I recommend including a 1:1 plot (simulated vs. reconstructed) as well. It will help the reader understand the bias of the model better.

Reply: We added 1:1 plot to the appendix Fig A2, and added to the discussion:
P15L6-14: added: *“The model underestimates high values of f_{denit} and overestimate low values (Figure A2)”*

Figure 4. I like this figure and find it helpful for visualizing the changes to the N cycle.

Reply: thanks. No changes needed

Page 16, line 32. Please expand on the statement that the overall behavior is in line with mechanisms in Niu et al. 2016. The connection between the model in the manuscript and the conceptual model isn't clear. What does it mean to be 'in line with'?

Reply: we explicitly state what we mean with “overall behaviour”:

P19L30: revised: *“The simulated increase in tightness of the nitrogen cycle as mineral nitrogen stocks deplete is in line with the substrate-based mechanisms “*

Figure 5, Why are the units on Figure 5c (kgC) different from the rest of the units (gC) on the figure?

Reply: We chose to plot kg(C) instead to g(C) in 5c) to avoid small values. No changes done, but if the editor shares the Referee's concern, too, we can change the units.

Page 18, line 12. How does the finding illustrate the need of a multitude of carbon nitrogen models? Please expand on this statement.

Reply: We rephrased the sentence to specify our findings

P20L12-P21L2“*The contrasting findings regarding the effect of nitrogen on the land carbon feedbacks illustrates the need of a multitude of carbon-nitrogen models to draw general conclusions.”*

Page 18, Lines 28: How does elevated CO₂ directly increase respiration? Are you referring the increasing respiration is a requirement to prevent labile C from building up in the plant? Overall, this statement is confusing and needs to be expanded on.

Reply: we rephrased the sentence to clarify

P21L17-19: revised: *“The mechanism by which nitrogen can dampen β_L is via an increasing decoupling of gross primary productivity from biomass accumulation under increasing CO₂ concentration: the incorporation of nitrogen into biomass reduces the mineral nitrogen availability (Luo et al., 2004, Liang et al., 2016) which negatively affects growth (Norby et al., 2010) and increases root respiration (Vicca et al., 2012, McCormack et al., 2015*

Carbon-nitrogen interactions in idealized simulations with JSBACH (version 3.10)

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Abstract. Recent advances in the representation of soil carbon decomposition (Goll et al., 2015) and carbon-nitrogen interactions (Parida, 2011; Goll et al., 2012) implemented previously into separate versions of the land surface scheme JSBACH are here combined in a single version which is set to be used in the upcoming 6th phase of coupled model intercomparison project (CMIP6) (Eyring et al., 2016).

5 Here we demonstrate that the new version of JSBACH is able to reproduce the spatial variability in the reactive nitrogen loss pathways as derived from a compilation of $\delta^{15}\text{N}$ data ($rR=0.63$, $RMSE=0.26$, Taylor score= 0.81). The inclusion of carbon-nitrogen interactions leads to a moderate reduction (-10%) of the carbon-concentration feedback (β_L) and has a negligible effect on the sensitivity of the land carbon cycle to warming (γ_L) compared to the same version of the model without carbon-nitrogen interactions in idealized simulations (1% increase in atmospheric carbon dioxide per yr). In line with evidence from
10 elevated carbon dioxide manipulation experiments (Liang et al., 2016), pronounced nitrogen scarcity is alleviated by (1) the accumulation of nitrogen due to enhanced nitrogen inputs by biological nitrogen fixation and reduced losses by leaching and volatilization as well as the (2) enhanced warming stimulated turnover of organic nitrogen further counteracts scarcity.

The strengths of the land carbon feedbacks of the recent version of JSBACH, with $\beta_L = 0.61 \text{ Pg ppm}^{-1} \text{ Pg ppm}^{-1}$ and $\gamma_L = -27.5 \text{ Pg } ^\circ\text{C}^{-1} \text{ Pg } ^\circ\text{C}^{-1}$, are 34% and 53% less than the averages of CMIP5 models (Arora et al., 2013), although the
15 CMIP5 version of JSBACH simulated β_L and γ_L which are 59% and 42% higher than multi-model average. These changes are primarily due to the new decomposition model, stressing indicating the importance of getting the basics right (here: the decomposition of soil carbon) before increasing the complexity of the model (here: carbon-nitrogen interactions). soil organic matter decomposition for land carbon feedbacks.

1 Introduction

The version of the Max-Planck-Institute Earth System Model (MPI-ESM) used in the 5th phase of the coupled model intercomparison project (CMIP5) experienced pronounced biases in simulated soil carbon (Todd-Brown et al., 2013), soil hydrology (Hagemann and Stacke, 2014), and the lack of carbon-soil nutrient interactions (Zaehle et al., 2014; Wieder et al., 2015), hampering the reliability of the simulated response of land system to increasing carbon dioxide (CO_2), climate and land use and land cover changes. Recent model developments addressed these issues (Goll et al., 2012, 2015; Hagemann and Stacke, 2014) in separate versions of the land surface scheme of the MPI-ESM, JSBACH, but have not been yet combined in a single model version.

The projected carbon balance in JSBACH was substantially affected by recent model developments: The implementation of carbon-, nitrogen- and phosphorus interactions reduced accumulated land carbon uptake by 25% between 1860–2100 under a business as usual scenario (Goll et al., 2012), while the implementation of a new decomposition model (YASSO) reduced the accumulated land carbon uptake by about 60% in the same period (Goll et al., 2015). The exchange of the former CENTURY type soil decomposition model (Parton et al., 1993) ~~by~~ with the YASSO decomposition model (Tuomi et al., 2008, 2009, 2011) improved the present-day state of the carbon cycle compared to observations as well as the response of decomposition to soil warming, and substantially reduced the uncertainties of land use change emissions for a given land use change scenario (Goll et al., 2015). The strong impact on the carbon balance of each of both developments underline the importance of combining them in a single version.

The capacity of land ecosystems to increase their nitrogen storage as well as to enhance recycling of nitrogen in organic matter are major constraints on their ability to increase carbon storage under elevated CO_2 concentrations (Hungate et al., 2003; Liang et al., 2003; Liang et al., 2003; Thomas et al., 2015; Liang et al., 2016). The respective response patterns of nitrogen processes governing the balance and turnover of organic nitrogen are crucial (Niu et al., 2016) to ~~assess the likelihood of the occurrence of~~ asses the likelihood of the occurrence of (progressive) nitrogen limitation (Luo et al., 2004). Recent advances in the interpretation of soil $\delta^{15}\text{N}$ global data sets provide a promising tool (Houlton et al., 2015) (Houlton et al., 2015; Zhu and Riley, 2015) by allowing a more detailed evaluation of the nitrogen loss pathways in land carbon-nitrogen models than previously done (e.g. Parida (2011); Goll et al. (2012)).

Since future scenarios of CO_2 concentrations differ among CMIP phases, an idealized setup of an annual increase in CO_2 concentration by 1% is used to foster the analysis of the carbon cycle feedbacks among models, and to compare emerging properties of different model versions in various CMIPs (Eyring et al., 2016). We adopt this approach taking advantage of existing simulations of climatic changes in this idealized setup of the CMIP5 intercomparison (Arora et al., 2013) to drive the land surface model JSBACH uncoupled from the atmosphere and ocean components of the earth system model.

This article documents the modifications to the soil carbon decomposition (Goll et al., 2015) and nitrogen cycle (Parida, 2011; Goll et al., 2012) submodels and the combination of both developments in a recent version of JSBACH including an advanced soil hydrological scheme (Hagemann and Stacke, 2014), scheduled to be used in CMIP6. We further analyzed the state of the nitrogen cycle ~~and~~ using soil $\delta^{15}\text{N}$ data and quantified the carbon cycle feedbacks to increasing CO_2

concentrations and climate change. The analysis aims at facilitating the interpretation of the models dynamics in the upcoming round of CMIP experiments (Eyring et al., 2016), and allows a straightforward comparison to the result from the previous round of CMIP (Taylor et al., 2012).

2 Methods

5 2.1 Model description

The implementation of the nitrogen cycle and the soil carbon and litter decomposition model YASSO is described in detail in Parida (2011); Goll et al. (2012) and Goll et al. (2015), respectively. In the following, a brief summary of the major concepts is given and afterwards the ~~modification-modifications~~ to the original developments needed to combine them are documented in detail. The notation applied here follows Goll et al. (2012, 2015) and a scheme of the cycling of carbon and nitrogen as well as their interactions are given in Figure 1.

The ~~YASSO-decomposition model~~ decomposition model (YASSO) is based on a compilation of litter decomposition and soil carbon data ~~(Tuomi et al., 2008, 2009, 2011).~~ The model separates decomposing organic matter and distinguish organic matter fractions according to litter size and solubility (Tuomi et al., 2008, 2009, 2011). In JSBACH we use two litter size classes, which correspond to litter from non-lignified and lignified plant material (Goll et al., 2015). Each of the two litter classes is further refined into four solubility classes (acid-soluble (C_A), water-soluble (C_W), ethanol-soluble (C_E), nonsoluble (C_N)) (Eq. 1) ~~and an~~ . One additional pool (C_H) ~~representing-represents~~ humic, slowly-decomposing substances. ~~In JSBACH the organic matter is further separated into two litter size classes, which correspond to lignified (stems and branches) and non-lignified (leaf and fine roots) litter (Goll et al., 2015).~~

The interactions between nitrogen availability and ~~plant productivity as well as decomposition~~ carbon fluxes, namely primary productivity and decomposition, are based on the concept of ~~CO_2~~ CO_2 -induced nutrient limitation (CNL) (Goll et al., 2012). In this framework, we distinguish between CNL and ~~the~~ background nutrient limitation. The latter is assumed to be indirectly considered in the original parametrization of carbon cycle processes as they are based on measurements in present day ecosystems and therefore reflect present day nutrient conditions. CNL is an additional nutrient limitation caused by the increase in atmospheric ~~CO_2~~ CO_2 and is computed dynamically according to nutrient supply and demand. In case microbial and vegetation ~~nitrogen demand cannot be met by the supply, all carbon fluxes of which the donor compartment has a higher C:N ratio than the receiving pool (i. e. the fluxes of carbon from the solubility classes pools to the humus pool) are down-regulated.~~ The concept of CNL allows to introduce carbon-nitrogen interactions to YASSO, as the needed conditions are met, e.g. the parametrization of YASSO indirectly reflects present day nutrient effects on decomposition as it is based on leaf litter experiments.

Following Goll et al. (2012), CNL affects the decomposition of all pools except the slowly-decomposing nutrient-rich pool ~~, which is represented by the "humus" pool in YASSO~~ (Eqs. 2–5). The litter decomposition data on which YASSO is based is not suited to link the fate of nitrogen in litter to the respective solubility pools. Therefore, we assume one single nitrogen pool representing all nitrogen linked to the four carbon solubility pools per litter class (Eq. 7). This can be refined in the future if appropriate data becomes available.

The nitrogen cycling is primarily driven by ~~the nitrogen demand of the carbon cycle by the use of~~ carbon fluxes using constant N-to-C ratios of organic pools (Eqs. 6–7), with the exceptions of the non-lignified litter pool (Eq. 8) (Parida, 2011). Further exceptions are the processes linking the terrestrial carbon cycle with the atmosphere (biological nitrogen fixation and denitrification) and the aquatic systems (leaching) which are computed either as substrate-limited (Eqs. 15–16) or, for the case of biological nitrogen fixation (Eq. 14), as driven by demand due to the ample supply of N_2 in the atmosphere (Parida, 2011). The nitrogen cycle and its interactions with the carbon cycle are not modified. The only exception is that the turnover times of the nitrogen litter and soil organic matter pools are derived from the YASSO decomposition model (Eq. 10) instead of the former decomposition model.

All parameters and variables are given in Table 1&2

10 2.1.1 Nitrogen effect on decomposition

Matrix \mathbf{C} describes the soil carbon pools (~~A, W, E, N, H~~ A, W, E, N) of the two litter ~~size~~ size-classes (i) in JSBACH-~~, excluding~~ recalcitrant humic substances (C_H):

$$\mathbf{C}_i = \begin{pmatrix} C_{A,i} \\ C_{W,i} \\ C_{E,i} \\ C_{N,i} \end{pmatrix} \quad (1)$$

The dynamics of the soil carbon pools are described as

$$15 \quad \frac{d\mathbf{C}_i}{dt} = \mathbf{A}_p \mathbf{k}_i(\mathbf{F}) \mathbf{C}_i + \mathbf{I}_i \quad (2)$$

where \mathbf{A}_p is the mass flow matrix; ~~$\mathbf{k}(\mathbf{F})$~~ $\mathbf{k}_i(\mathbf{F})$ is a diagonal matrix of the decomposition rates $\mathbf{k}_i(\mathbf{F}) = \text{diag}(k_{A,i}, k_{W,i}, k_{E,i}, k_{N,i})(\mathbf{F})$ as a function of climatic conditions (\mathbf{F}); and matrix \mathbf{I}_i is the carbon input of type i to the soil. The dynamics of the humus pool (C_H) are described as

$$\frac{dC_H}{dt} = p_H \sum_{i=1}^N \mathbf{k}_i(\mathbf{F}) \mathbf{C}_i - k_H C_H \quad (3)$$

20 where p_H is the relative mass flow parameter and k_H the decomposition rate of the humus pool. A detail description of decomposition can be found in the supplementary information of Goll et al. (2015), here we only focus on the modification of the original implementation.

The climate dependence of the decomposition rate factor $k_{j,i}$ of the carbon pools was originally implemented by Goll et al. (2015) based on Tuomi et al. (2008) as:

$$25 \quad k_{j,i}(\mathbf{F}) = \alpha_{j,i} \exp(\beta_1 T + \beta_2 T^2) (1 - \exp(\gamma P)), \quad (4)$$

where T is air temperature and P is precipitation, β_1, β_2, γ are parameters, and $\alpha_{j,i}$ are decomposition rates at references conditions ($T = 0$ and $P \rightarrow \infty$) of pool i of litter class j . $\alpha_{j,i}$ is the product of ~~a~~ reference decomposition rate r_j of solubility

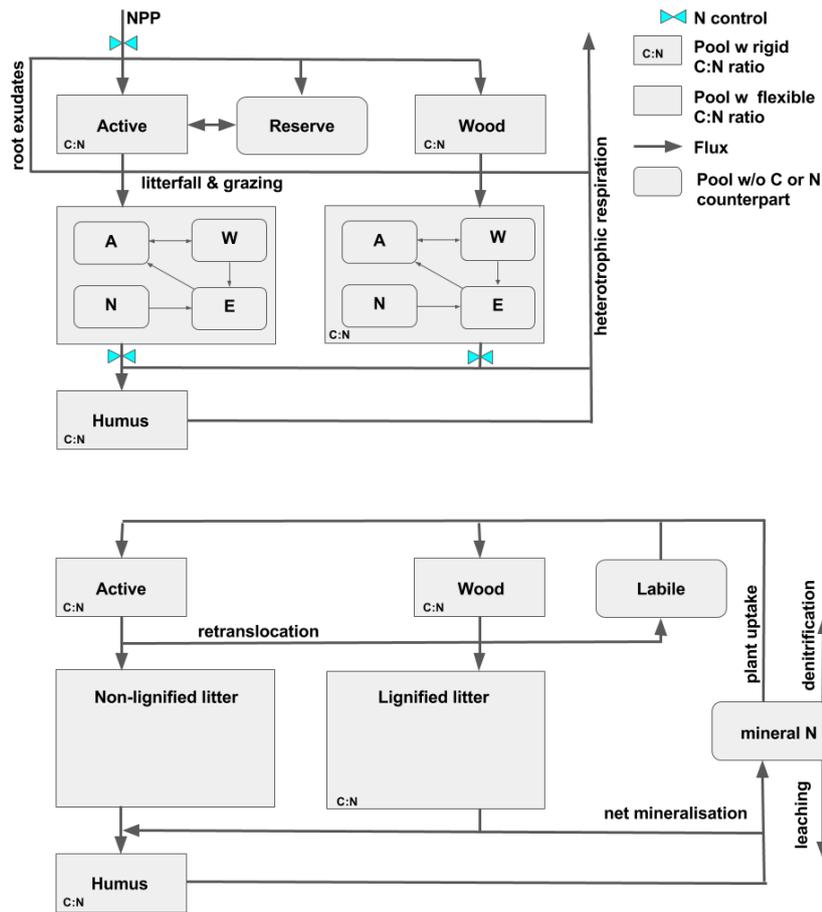


Figure 1. Schematic representation of carbon (top) and nitrogen (below) cycling in JSBACH. Vegetation is represented by four pools: “active” (leaves and non-lignified tissue) and “wood” (stem and branches), “reserve” (sugar and starches) and “mobile” (labile nitrogen) (Goll et al., 2012). Dead organic matter is represented by “non-lignified litter”, “lignified litter” (lignified litter and fast-decomposing soil organic matter), and “humus” (slow-decomposing organic matter) (Raddatz et al., 2007). All organic matter pools have fixed C:N ratios, except the pools “reserve”, “labile” and “non-lignified litter”. While the first two pools have no corresponding pool, the C:N ratio of the latter pool varies according the balance between immobilization demand and supply. The carbon in the litter compartment is further refined into the acid-soluble (A), water-soluble (W), ethanol-soluble (E), and non-soluble (N) compounds (Goll et al., 2015) which have no C:N ratio assigned. Soil mineral nitrogen is represented by a single pool (soil mineral pool). The opposing triangle marks carbon fluxes which are downregulated in case the nitrogen demand exceeds the nitrogen supply.

class j and the litter diameter d_i of litter class i (Tuomi et al., 2011). YASSO uses precipitation instead of the more direct driver of soil moisture due the lack of adequate soil moisture observation to relate the decomposition date the model is based on (Tuomi et al., 2008).

Table 1. Variables of the model.

Variable	Units	Description
P	m day ⁻¹ m day ⁻¹	30 days average of daily precipitation
T	°C °C	30 days average of daily 2m air temperature
$C_{j,i}$	mol(C) m⁻² mol(C) m ⁻²	soil organic carbon of solubility class j and size-litter class i
N_x	mol(N) m⁻² mol(N) m ⁻²	nitrogen in compartment x
\overline{NPP}	mol(C) m⁻² day⁻¹ mol(C) m ⁻² day ⁻¹	annual average of daily net primary productivity
$F_{x>y}^C$	mol(C) m⁻² day⁻¹ mol(C) m ⁻² day ⁻¹	daily flux of carbon from compartment x to compartment y
F_{extr}	mol(C) m⁻² day⁻¹ mol(C) m ⁻² day ⁻¹	daily flux of nitrogen in excrements
F_{extr}	mol(C) m⁻² day⁻¹ mol(C) m ⁻² day ⁻¹	daily flux of nitrogen lost by leaching
BNF	mol(N) m⁻² day⁻¹ mol(N) m ⁻² day ⁻¹	daily nitrogen inputs by biological nitrogen fixation
D_x	mol(N) m⁻² day⁻¹ mol(N) m ⁻² day ⁻¹	nitrogen demand of vegetation ($x = veg$) or immobilization ($x = micr$)
f_{limit}^N	–	nitrogen limitation factor
d_x	day⁻¹ day ⁻¹	decomposition rate of nitrogen in compartment x
$k_{j,i}$	day⁻¹ day ⁻¹	decomposition rate of solubility class j and size-litter class i
k_H	day⁻¹ day ⁻¹	decomposition rate of humus pool
ϵ	day⁻¹ day ⁻¹	consumption rate by herbivores
f_{h2o}	–	daily fraction of soil water lost due to runoff and drainage
α	–	soil moisture stress on biological processes

We introduced a scaling factor, namely the nitrogen limitation factor (f_{limit}^N), to account for the down-regulation of decomposition when nitrogen is in short supply

$$k_{j,i}(\mathbf{F}) = f_{limit}^N \alpha_{j,i} \exp(\beta_1 T + \beta_2 T^2) (1 - \exp(\gamma P)), \quad (5)$$

f_{limit}^N is calculated based on a supply and demand approach (Parida, 2011; Goll et al., 2012). In a first step, potential carbon
5 fluxes are computed from which the ~~release and immobilization~~ gross mineralisation, immobilization and plant uptake of mineral nitrogen is diagnosed. In a second step, all fluxes consuming nitrogen (donor compartment has a higher C:N ratio than the receiving pool as well as plant uptake) are down-regulated in case nitrogen demand cannot be met by the nitrogen supply. Hereby, a common scalar (f_{limit}^N) (see appendix) is used thereby no assumption about the relative competitive strengths of microbial and plant consumption has to be made. In case nitrogen demand is met by the supply, the fluxes computed in the first
10 step are taken as actual ones without any modification.

2.1.2 Dynamics of nitrogen in litter and soil organic matter

~~We substituted the former carbon pools for~~ Nitrogen in litter and soil organic matter is separated into three pools, namely slowly-decomposing organic matter C_s (humus) C_H , lignified litter and fast decomposing organic matter C_{lw} , as well as non-

Table 2. Parameters of the model. (*) $\alpha_{j,i}$ is an array and values can be found in Tuomi et al. (2011).

Parameter	Value	Units	Description	Source
β_1	0.095	$^{\circ}\text{C}^{-1} \cdot ^{\circ}\text{C}^{-1}$	Temperature dependence of decomposition	Goll et al. (2015)
β_2	-1.4×10^{-3}	$^{\circ}\text{C}^{-2} \cdot ^{\circ}\text{C}^{-2}$	Temperature dependence of decomposition	Goll et al. (2015)
γ_1	-1.21	m^{-1}	Precipitation dependence of decomposition	Goll et al. (2015)
$\alpha_{j,i}$	(*)	$\text{day}^{-1} \cdot \text{day}^{-1}$	decomposition rates at references conditions ($T = 0$ and $P \rightarrow \infty$) of pool i of litter class j	Tuomi et al. (2011)
α_H	4.383×10^{-6}	$\text{day}^{-1} \cdot \text{day}^{-1}$	decomposition rates at references conditions ($T = 0\text{K}$ and $P \rightarrow \infty$) of humus pool	Tuomi et al. (2011)
r_s	10.	$\frac{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}$	N-to-C ratio of slowly decomposing organic matter	Goll et al. (2012)
r_{lw}	330.	$\frac{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}$	N-to-C ratio of lignified litter	Goll et al. (2012)
r_{la}	55.	$\frac{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}$	N-to-C ratio of non-lignified litter	Goll et al. (2012)
r_w	150.	$\frac{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}{\text{mol}(\text{N}) \cdot \text{mol}^{-1}(\text{C})}$	N-to-C ratio of lignified biomass	Goll et al. (2012)
β_3	0.7	–	fraction of nitrogen in excrement in labile form	Parida (2011)
f_{emp}	-3.0×10^{-3}	$\text{day} \cdot \text{g}^{-1}(\text{C}) \cdot \text{day} \cdot \text{g}^{-1}(\text{C})$	NPP dependence of biological nitrogen fixation	Cleveland et al. (2013)
f_{bnf}	0.7	$\frac{\text{g}(\text{N}) \cdot \text{m}^{-2} \cdot \text{day}^{-1}}{\text{g}(\text{N}) \cdot \text{m}^{-2} \cdot \text{day}^{-1}}$	scaling factor of biological nitrogen fixation	this study
f_s	0.1	–	fraction of soil mineral nitrogen in soil solution	this study
k_{denit}	2.0×10^{-3}	–	daily fraction of soil mineral nitrogen lost by denitrification	Parida (2011)
w_C	12.011	$\frac{\text{g}(\text{C}) \cdot \text{mol}^{-1}(\text{C})}{\text{g}(\text{N}) \cdot \text{m}^{-2} \cdot \text{day}^{-1}}$	standard atomic weight of carbon	
w_N	14.007	$\frac{\text{g}(\text{N}) \cdot \text{mol}^{-1}(\text{N})}{\text{g}(\text{N}) \cdot \text{mol}^{-1}(\text{N})}$	standard atomic weight of nitrogen	
t	1	$\text{day} \cdot \text{day}$	time step	

Table 3. The nitrogen pools and the corresponding carbon pools [for humus \(H\) and lignified \(woody\) \(w\) and non-lignified \(active\) \(a\) plant material.](#)

Nitrogen	Carbon
N_s, N_H	C_H
N_{lw}	$C_{A,w} + C_{W,w} + C_{E,w} + C_{N,w}$
N_{la}	$C_{A,g} + C_{W,g} + C_{E,g} + C_{N,g} \cdot C_{A,e} + C_{W,e} + C_{E,e} + C_{N,e}$

lignified litter and fast decomposing organic matter C_{la} ~~with the (Goll et al., 2012). We assigned each of the three nitrogen pools to one or more~~ corresponding YASSO pools (Table 3) ~~to derive the dynamics of the nitrogen pools. A refinement of the representation of nitrogen in decomposing material following strictly the carbon classification is not straightforward as the carbon pools (A, W, E, N) defined by their respective solubility characteristics do not correspond to substance classes with distinguished stoichiometries.~~

In JSBACH, nitrogen in compartments with a fixed N-to-C ratio, namely nitrogen in lignified litter (N_{lw}) as well as nitrogen in slowly decomposing organic matter ($N_s N_H$), are derived from the corresponding YASSO carbon pools ($C_{j,i}$) by:

$$N_H = r_H C_H \quad (6)$$

$$N_{lw} = r_{lw} (C_{A,w} + C_{W,w} + C_{E,w} + C_{N,w}) \quad (7)$$

where $r_s r_H$ is the N-to-C ratio of former slow carbon pool ($C_s C_H$) now applied to the humus pool of YASSO, and r_{lw} of former ~~woody-lignified (woody)~~ litter pool (C_{lw}) now applied to the sum of the solubility class pools for lignified litter of YASSO.

The dynamics of nitrogen in non-lignified litter & fast decomposing organic matter (N_{la}) were not modified from the original nitrogen-enabled version of JSBACH (Parida, 2011) and are given by:

$$15 \quad \frac{dN_{la}}{dt} = r_{la} F_{a>la}^C + (1 - \beta_3) \epsilon N_a - f_{limit}^N d_{la} * N_{la} \quad (8)$$

where the first term describes the nitrogen influx from active, non-lignified plant tissue (N_a), the second term describes the flux of nitrogen from herbivores excrements which is not directly available to biota, and the third term arises from the nitrogen released by biological mineralization of litter and fast-decomposing soil organic matter, ~~where f_{limit}^N is the limitation factor.~~ We assume that active plant material (N_a) is consumed by herbivores at a constant rate (ϵ) and immediately excreted (Parida, 2011). We separate the excrement into labile (β_3) and fast decomposing ($1 - \beta_3$) nitrogen compounds, the latter enters the non-lignified litter pool (N_{la}).

The decomposition rate d_{la} of nitrogen in litter and fast decomposing soil organic matter equals the decomposition rate of the sum of the YASSO carbon pools $C_{A,g} + C_{W,g} + C_{E,g} + C_{N,g}$ ~~$C_{A,a} + C_{W,a} + C_{E,a} + C_{N,a}$~~ and is given by

$$\frac{d(C_{A,a} + C_{W,a} + C_{E,a} + C_{N,a})}{dt} = d_{la} (C_{A,a} + C_{W,a} + C_{E,a} + C_{N,a}) \quad (9)$$

so that d_{la} can be derived from

$$25 \quad d_{la} = \frac{C_{A,a}(t+1) + C_{W,a}(t+1) + C_{E,a}(t+1) + C_{N,a}(t+1)}{C_{A,a}(t) + C_{W,a}(t) + C_{E,a}(t) + C_{N,a}(t)} - 1 \quad (10)$$

As we calculate potential decomposition fluxes in a first step to derive nitrogen demand (see Goll et al. 2012) we know the state of pools for time t and $t + 1$.

The dynamics of the soil mineral nitrogen (N_{smin}) were not modified and are given - as originally formulated by Parida (2011) - by:

$$\frac{dN_{smin}}{dt} = F_{extr} + d_H N_H + (r_w - r_{lw}) F_{w>lw}^C - f_{limit}^N (D_{veg} + D_{micr}) \quad (11)$$

where F_{extr} is the net of fluxes connecting the compartments considered in the model and outside (here: biological dinitrogen (N₂) fixation, leaching, N₂ and nitrous oxide (N₂O) emissions), r_w the N-to-C ratio of lignified plant material, $F_{w>lw}^C$ the litter flux from lignified biomass, D_{micr} and D_{veg} are the nitrogen demands of vegetation and microbes, respectively. Due to the lower nitrogen content of litter compared to humus, the decomposition of lignified and non-lignified litter corresponds to a net immobilization of nitrogen, which is part of the D_{micr} . The term $(r_w - r_{lw}) F_{w>lw}^C$ represents nitrogen leaching from freshly shedded wood given by the decomposition and the stoichiometries assigned to wood (r_w) and lignified litter (r_{lw}).

The decomposition rate of nitrogen in the slow pool (N_s), d_s humus pool (N_H), d_H , equals the decomposition rate of the corresponding YASSO carbon pool C_H , k_H . This rate according to Eq.(4) is given by:

$$k_H(\mathbf{F}) = \alpha_H \exp(\beta_1 T + \beta_2 T^2) (1 - \exp(\gamma P)), \quad (12)$$

Note that there is no nutrient effect on the decomposition of N_s , N_H and k_H is calculated exactly like described in Goll et al. (2015).

For the calculation of the microbial (soil) nutrient demand (D_{micr}) we substituted the pools C_{la} and C_s , C_H with the corresponding YASSO pools in Eq.(15) of Goll et al 2012:

$$D_{micr} = (r_H - \frac{N_{la}}{(C_{A,a} + C_{W,a} + C_{E,a} + C_{N,a})}) F_{la>s}^C + (r_H - r_{lw}) F_{lw>s}^C - \frac{N_{la}}{(C_{A,a} + C_{W,a} + C_{E,a} + C_{N,a})}) F_{la>a}^C - r_{lw} F_{lw>a}^C \quad (13)$$

The fluxes $F_{la>s}^C$ and $F_{lw>s}^C$ are the net fluxes of carbon to the humus from the solubility pools (AWEN) of non-lignified and lignified litter, respectively. $F_{la>a}^C$ and $F_{lw>a}^C$ are the respective sums of respiration fluxes of the AWEN pools.

2.2 The processes governing the terrestrial nitrogen balance in JSBACH

Nitrogen enters terrestrial ecosystems by biological nitrogen fixation (BNF), as well as atmospheric deposition, while nitrogen is lost via leaching, erosion and denitrification.

BNF in global models is commonly represented by an empirical relationship based on a compilation of site measurements (Cleveland et al., 1999). Due to the lack of a process-based alternatives, we use this approach as described in Parida (2011) despite its shortcomings (Thomas et al., 2013; Sullivan et al., 2014; Wieder et al., 2015). In this approach BNF (BNF) is derived from the annual average of daily net primary productivity (\overline{NPP}) using the empirical relationship between BNF and evapotranspiration (Thornton et al., 2007):

$$BNF = (f_{bnf} * (1 - e^{(f_{emp} * w_C \overline{NPP})}) \frac{w_N}{w_C} \quad (14)$$

where $f_{emp} = -0.003 \text{ day}^{-1} \text{ g}^{-1}(\text{C}) - \text{day} \text{ g}^{-1}(\text{C})$ is an empirical relationship from Cleveland et al. (1999), $f_{bnf} = 0.7 \text{ g}(\text{N}) \text{ m}^{-2} \text{ day}^{-1}$ is a calibrated constant to achieve a global sum of BNF of 100 Mt yr^{-1} for a simulated NPP of 65 Gt yr^{-1} based on estimates for present day (Galloway et al., 2013; Ciais et al., 2013), and w_N and w_C the standard atomic weights of nitrogen and carbon, respectively.

- 5 The losses of nitrogen are given priority over immobilization and plant uptake each time step. Following Meixner and Bales (2002); Thornton et al. (2007); Parida (2011), daily losses by leaching are derived from dissolved nitrogen in soil water and the fraction of soil water lost to rivers per day (f_{h2o}) assuming a homogeneous distribution of mineral nitrogen (N_{smin}) in the soil volume :

$$F_{leach} = f_s N_{smin} f_{h2o} \quad (15)$$

- 10 where f_s is the fraction of mineral nitrogen (N_{smin}) in soil solution. f_{h2o} is computed dynamically accounting for evapotranspiration, precipitation, and changes in the soil water storage using a 5 layer soil hydrological scheme (Hagemann and Stacke, 2014)

Following Parida (2011); Goll et al. (2012), daily losses by denitrification are assumed to be at most 0.02% ($k_{denit} = 0.002 \text{ day}^{-1}$) of the soil mineral (N_{smin}):

$$F_{denit} = \alpha k_{denit} N_{smin} \quad (16)$$

- 15 where α is a JSBACH internal indicator of soil moisture stress [0–1] which is dynamically computed from soil moisture and used to scale biological activity (Raddatz et al., 2007).

2.3 Calibration & parametrization of the model

- The parametrization of YASSO (version 3.20) and of the nitrogen cycle in JSBACH was not changed and is described in Goll et al. (2012, 2015). The only exception is the re-calibration of losses of nitrogen by leaching to the new hydrological model in JSBACH (Hagemann and Stacke, 2014). This is achieved, following Goll et al. (2012), by tuning the fraction of mineral nitrogen in soil solution (f_s) so that the assumption regarding the absence of CNL in the pre-industrial state is met which equals to a negligible (<2%) effect of nitrogen on global net primary productivity and carbon storage. We tuned the the fraction of soil mineral nitrogen in soil solution to $f_s = 0.1$, which is lower than in an earlier version (0.2) (Parida, 2011) and in the range of others model (0.02–1.) (Esser et al., 2011; Wang et al., 2010; Warlind et al., 2014). comparable to fractions used in other models (Wang et al., 2010) as well as in observations (Hedin et al., 1995).
- 25

2.4 Simulation setup

- The climatic forcing is derived from MPI-ESM simulations performed for the CMIP5 project (Table 4) (Taylor et al., 2012). We force the land surface model JSBACH with half hourly climatic data simulated by the MPI-ESM instead of running JSBACH coupled with the atmospheric and ocean components of the MPI-ESM. Therefore, our simulations, in contrast to simulations of the MPI-ESM, do not account for the feedback between land and atmosphere with respect to the water and energy cycle. However, the resulting inconsistencies between climate and land surface should not exchange change the results of the present

Table 4. Simulations performed with JSBACH with and without carbon-nitrogen interactions using climatic forcing from MPI-ESM simulations performed for the CMIP5 project (Taylor et al., 2012).

Acronym	C-N interactions	climatic forcing	description
C	without	1pctCO2	1% yr^{-1} increase in CO_2 yr^{-1} increase in CO_2 (to quadrupling)
C_β	without	esmFdbkl	Carbon cycle sees piControl CO_2 - CO_2 concentration, but radiation sees 1% yr^{-1} yr^{-1} rise
C_γ	without	esmFixClim1	Radiation sees piControl CO_2 - CO_2 concentration, but carbon cycle sees 1% yr^{-1} yr^{-1} rise
CN	with	1pctCO2	1% yr^{-1} increase in CO_2 yr^{-1} increase in CO_2 (to quadrupling)
CN_β	with	esmFdbkl	Carbon cycle sees piControl CO_2 - CO_2 concentration, but radiation sees 1% yr^{-1} yr^{-1} rise
CN_γ	with	esmFixClim1	Radiation sees piControl CO_2 - CO_2 concentration, but carbon cycle sees 1% yr^{-1} yr^{-1} rise

study and are anyway partly implicit to the underlying CMIP5 simulations because of the prescribed atmospheric CO_2 - CO_2 levels in case of biogeochemical feedbacks (Taylor et al., 2012). For the sake of simplicity, we will refer to the JSBACH simulations driven by the climate from respective ESM simulations, with the respective label of the ESM simulations.

The climatic forcing is derived from MPI-ESM simulations performed for the CMIP5 project (Table 4) (Taylor et al., 2012).

5

2.4.1 Spinup

The concept of CO_2 - CO_2 induced nutrient limitation (CNL) assumes that nitrogen effects on the carbon cycle are marginal under pre-industrial conditions. Therefore the cycles of carbon and nitrogen can be equilibrated in a two-step procedure in which the carbon cycle is first brought into equilibrium (less than 1% change in global stocks per decade) using the climatic forcing from the pre-industrial control run (Goll et al., 2012). In a second step, we then initialize the nitrogen pools using the prescribed C:N ratios and the equilibrated carbon stocks as well as extremely high mineral nitrogen pools. The model is run again with the climatic forcing from the pre-industrial control run to equilibrate mineral nitrogen dynamics using the same criterion as for the first step. The resulting length of the simulation is 5.5 kyr and 2.6 kyr for step one and step two, respectively. Atmospheric nitrogen depositions are neglected.

15 2.4.2 1% CO_2 - CO_2 increase experiment & climate feedback factors

To analyze the effect of nitrogen limitation on the response of the land carbon cycle to increasing CO_2 - CO_2 concentration and climate change, we perform simulations with JSBACH with and without activated nitrogen cycle (Table 4). The simulations are forced with the climatic conditions from a set of 140 yr - yr long CMIP5 simulations with the MPI-ESM in which atmospheric

CO_2 concentration increases at a rate of $1\% \text{ yr}^{-1}$ from pre-industrial values until concentration quadruples (Arora et al., 2013).

The set of MPI-ESM simulations consist of a simulation where increasing CO_2 affects the climate but not the terrestrial biogeochemistry (radiatively coupled), a second simulation where increasing CO_2 affects the terrestrial biogeochemistry but not the climate (biogeochemically coupled), and a third simulation where increasing CO_2 affects both, climate and biogeochemistry (fully coupled). The biogeochemically-coupled and the radiatively coupled simulations allow us to disentangle the carbon-concentration feedback β_L and carbon-climate feedback γ_L , respectively (Friedlingstein et al., 2006; Arora et al., 2013). β_L is derived from the biogeochemically coupled simulations by dividing the difference in the total land carbon between the first and the last decade by the difference in the atmospheric CO_2 concentration of the same periods. γ_L is derived from the radiatively coupled simulations by dividing the difference in the total land carbon between the first and the last decade by the difference in global land temperature of the same periods. The MPI-ESM simulations do not include the confounding effects of changes in land use, non- CO_2 greenhouse gases, aerosols, etc., and so provide a controlled experiment with which to compare carbon climate interactions in line with the approach by Arora et al. (2013). The model version also does not include dynamic vegetation model and disturbances, such as fire. Natural vegetation cover is prescribed following approach by Pongratz et al. (2008). Cropland and pasture map for 1850 is taken from harmonized landuse dataset by Hurtt et al. (2011).

2.5 Analysis

2.5.1 Pre-industrial state

We average the model data of last three decades of the spinup simulations to derive the pre-industrial state. Differences between model and observation are given by the subtraction of the observation with the simulation. The fraction of denitrification losses to total losses is computed by dividing the annual flux of denitrification by the sum of the annual fluxes of denitrification and leaching. Simulated and observation loss fractions are compared using Pearson correlation coefficients, RMSE, and Taylor scores (Taylor, 2001).

2.5.2 Nitrogen loss pathway data

[δ15N data measurements are one of the few sources of spatially extensive data relevant to the nitrogen cycle \(Houlton et al., 2015\) as one can infer information about the nitrogen pathways. Houlton et al. \(2015\) derived the fraction of nitrogen loss in gaseous form \(\$f_{denit}\$ \) based on Amundson et al. \(2003\) best-fitting multiple regression equation for soil δ15N as a function of mean annual temperature \(MAT\) and mean annual precipitation \(MAP\). The data set used to generate this equation consisted of 29 samples, and the coefficient of determination was 0.39. Amundson et al. \(2003\) remarked that ‘pending the availability of more soil δ15N analyses, the present Figure ... represents our best estimate of trends ... in global soil δ15N values’ \(p. 5\). We have updated this analysis in three ways: \(a\) by including a larger number \(659\) of soil δ15N samples; \(b\) by substituting an annually integrated index of temperature-related microbial activity for MAT, and an index of leaching \(derived from runoff\)](#)

for MAP – i.e. using indices more closely related to the governing processes; and (c) by using non-linear regression to fit a statistical model that is explicitly based on the isotopic mass balance equation of (Houlton and Bai, 2009).

The fraction of N loss in gaseous form (f_{denit}) was estimated using the principle described by e.g. Houlton and Bai (2009); Bai et al. (2012), but using a process-based statistical model for the relationship between soil $\delta^{15}N$ data and environmental predictors fitted to publicly available data on soil $\delta^{15}N$ (Patino et al., 2009; Cheng et al., 2009; McCarthy and Pataki, 2010; Fang et al., 2011, 2013; Hilton et al., 2013; Peri et al., 2012; Viani et al., 2011; Sommer et al., 2012; Yi and Yang, 2007).

It was assumed that soil $\delta^{15}N$ reflects the source (atmospheric) $\delta^{15}N$ modified by isotopic discrimination that occurs during leaching (slight) and gaseous losses (much larger). For simplicity, the source $\delta^{15}N$ was assumed to be zero and discrimination during leaching was neglected. Mean annual runoff (q , in [mm]) was estimated from precipitation and potential evapotranspiration following (Zhang et al., 2004), with $\omega = 3$. Following Xu-Ri et al. (2008) we assumed that leaching losses increase to a maximum dependent on soil water capacity, yielding an annual runoff factor $f(q)$:

$$f(q) = \frac{q}{q + W_{max}} \quad (17)$$

with $W_{max} = 150 \text{ mm}$. Mean monthly soil temperatures (T_m , in K) were estimated for 0.25 m depth following Campbell and Norman. We assigned a generic activation energy of $E_a = 55 \text{ kJ mol}^{-1} K^{-1}$ (Canion et al., 2014) and summed the monthly index values

$$f_m(T_m) = \exp\left(\frac{E_a}{R_{gas}} \left(\frac{1}{T_{ref}} - \frac{1}{T_m}\right)\right) \quad (18)$$

over the 12 months

$$f(T) = \sum_{m=1}^{12} f_m(T_m) \quad (19)$$

yielding the annual soil temperature factor $f(T)$, where $T_{ref} = 293 \text{ K}$.

The data were then fitted via ϵ the gaseous discrimination factor and a constant k by non-linear least-squares regression to the relationship

$$\delta = \delta_0 + \epsilon \left(1 + k \left(\frac{f(q)}{f(T)}\right)\right)^{-1} \quad (20)$$

where δ is soil $\delta^{15}N$, δ_0 is the $\delta^{15}N$ of the N inputs, ϵ is the gaseous discrimination factor and k is a constant to be estimated.

Assuming the leaching discrimination factor is 0, f_{denit} can be expressed as

$$f_{denit} = \frac{\delta - \delta_0}{\epsilon} \quad (21)$$

from the first principle (Houlton and Bai, 2009). Re-arranging Equation 20 and 21 we get

$$f_{denit} = \left(1 + k \left(\frac{f(q)}{f(T)}\right)\right)^{-1} \quad (22)$$

A spatial map of f_{denit} were derived from the calculated empirical relationship between temperature, runoff and f_{denit} using simulated values of $f(q)$ and $f_m(T_m)$ across each grid cell from JSBACH. Thereby, model biases in climate are

accounted for in the data derived f_{denit} which allows a straightforward comparison with simulated f_{denit} . In addition, we derived maps of f_{denit} based on monthly grids of observed mean climate from 1961–1990 covering the global land surface at a 10 minute-minute spatial resolution (CRU CL2.0) (New et al., 2002) -which are shown in the appendix.

3 Results & discussion

5 3.1 Model evaluation: pre-industrial state

The model simulates mineral-nitrogen stocks and fluxes under pre-industrial conditions well within the wide range of the few available observation based estimates (Table 5). The simulated losses by leaching and denitrification are rather at the lower end of estimates, while the calibrated inputs by biological nitrogen fixation are at the higher end of estimates. Most of the estimates are for present day conditions and thus are not directly comparable due to the human influence on the nitrogen cycle (Galloway et al., 2013).

The organic nitrogen stocks and fluxes are given by the prescribed C:N stoichiometry and the state variables of the carbon cycle and thus are not affected by the changes we introduced here. Thus, we, except for non-lignified litter and fast decomposing soil organic matter which shows in general good agreement with observed C:N ratios for most biomes (see appendix). Mineralisation of organic nitrogen is the major source of nitrogen for vegetation and the simulated flux is less than existing model based estimates for present day ranging between 980–1030 (Smith et al., 2014; Zaehle et al., 2010). In models, nitrogen mineralisation is solely a by-product of decomposition of soil organic carbon and we thus attribute the differences between simulated mineralisation to the use of YASSO decomposition model compared to the use of the CENTRUY decomposition model (Smith et al., 2014; Zaehle et al., 2010) as the soil C:N stoichiometries are comparable among models. We refer to the evaluation of the carbon cycle in JSBACH elsewhere (Anav et al., 2013; Goll et al., 2015) (Anav et al., 2013; Goll et al., 2015), as the concept of CO_2 - CO_2 induced nutrient limitation prevents an effect of nitrogen on the carbon cycle under pre-industrial CO_2 - CO_2 concentrations.

The large uncertainty in estimates of global fluxes and stocks of nitrogen hampers are often lacking or associated with large uncertainties, thus a detailed analysis of the simulated nitrogen cycle is hampered (Zaehle, 2013). However, recent advances in the use of $\delta^{15}\text{N}$ data (Houlton et al., 2015), which are one of the few sources of spatially extensive data relevant to the nitrogen cycle, allow the evaluation of the respective importance of nitrogen loss pathways in space. Due to the different environmental controls of the loss pathways, which are on first order represented in the model, we can test the models underlying assumptions by comparing the simulated fraction of denitrification losses to total nitrogen losses (f_{denit}) to f_{denit} reconstructed from $\delta^{15}\text{N}$ data. We estimate from collected $\delta^{15}\text{N}$ data the highest values of fractional gaseous loss in arid regions, where leaching losses are minimal in these regions. Gaseous N loss is also predicted to be the dominant pathway over much of the tropics, with lower values towards high latitudes. However, this comparison does not allow to draw any conclusion about the magnitude of total losses. The pattern is generally consistent with earlier estimates of

The reconstructed f_{denit} from Houlton et al. (2015) maps (Figure (A1&2) presented here are generally similar to those presented by Houlton et al. (2015), with high fractions (ca 80%) in the tropics and mid-latitude deserts, a strong gradient of

Table 5. Comparison of simulated net primary productivity and biomass carbon as well ~~all-mineral~~-nitrogen stocks and fluxes for pre-industrial conditions with observation based estimates for 1850 and present day.

	simulated		observation-based	
	1850	1850	present day	reference
NPP (Gt yr^{-1})	65.1	–	50–56	Ito (2011)
leaching (Mt yr^{-1}) <u>biomass carbon (Gt)</u>	<u>514.7</u>	<u>–</u>	<u>470–650</u>	<u>Saugier and Roy (2001); Ciais et al. (2013)</u>
<u>biomass nitrogen (Gt)</u>	<u>4.6</u>	<u>–</u>	<u>3.5</u>	<u>Schlesinger (1997)</u>
<u>mineral nitrogen (Gt)</u>	<u>1.3</u>	<u>–</u>	<u>–</u>	
<u>total nitrogen (Gt)</u>	<u>63.6</u>	<u>–</u>	<u>60–75</u>	<u>Galloway et al. (2013)</u>
<u>leaching (Mtyr^{-1})</u>	50.0	70	13–180	Galloway et al. (2004, 2013)
denitrification (Mt yr^{-1})	49.2	–	43–290	Galloway et al. (2013)
BNF (Mt yr^{-1})	98.3	40–120	100–139	Galloway et al. (2004); Vitousek et al. (2013)
Mineral nitrogen (Gt) <u>mineralisation (Mtyr^{-1})</u>	<u>1.3–717.3</u>	–	Total nitrogen (Gt) 63.6–	60–75 Galloway et al. (2013)

decreasing fractions with decreasing temperature towards high altitudes and latitudes, and values in the range 0-20% reached in cold, wet climates in the north. For a detailed discussion of differences see SI.

In comparison with the reconstructed fractional gaseous loss from simulated climate (Figure 2a), we find that the model is in ~~rather~~ good agreement (Pearson $R=0.63$ 0.76, RMSE=0.260.2, Taylor score=0.81). ~~However, some regions substantially~~
5 ~~differ between model and observation~~ 0.83). ~~The model underestimates high values of f_{denit} and overestimate low values~~
(Figure 2) ~~which can be attributed to the use of the MPI-ESM climate which in some regions deviates significantly from the~~
~~observed climate: The biases in denitrification losses resemble biases in surface temperature and precipitation in the climatic~~
~~forcing from MPI-ESM (Hagemann et al., 2013). The strong underestimation of denitrification losses at the West coast of~~
10 ~~North and South America, Central Asia, and the Southwest coast of Africa can be attributed to the strong overestimation of~~
~~precipitation in the climatic forcing compared to observations (Weedon et al., 2011; Hagemann et al., 2013). The pronounced~~
~~positive bias in boreal winter temperatures of 0.5–5.5 K between 40–80°N in Eurasia as well as East part of North America~~
~~resembles regions with a strong overestimation of denitrification losses. The frequency distribution of simulated and observed~~
 ~~f_{denit} indicates that the occurrence of regions of where denitrification dominates are underestimated while regions where~~
~~leaching dominates are overestimated in the model.~~ A2). In regions with cold winter temperatures where denitrification losses
15 are small the model overestimates denitrification losses (Figure 2c) These model biases likely derive from the simplistic
representation of denitrification as a function of soil moisture and substrate availability, which omits effects of temperature
(Butterbach-Bahl et al., 2013). Additionally, other omitted factors like oxygen concentration, soil pH, mineralogy, and transport
processes (Butterbach-Bahl et al., 2013) might contribute to the bias.

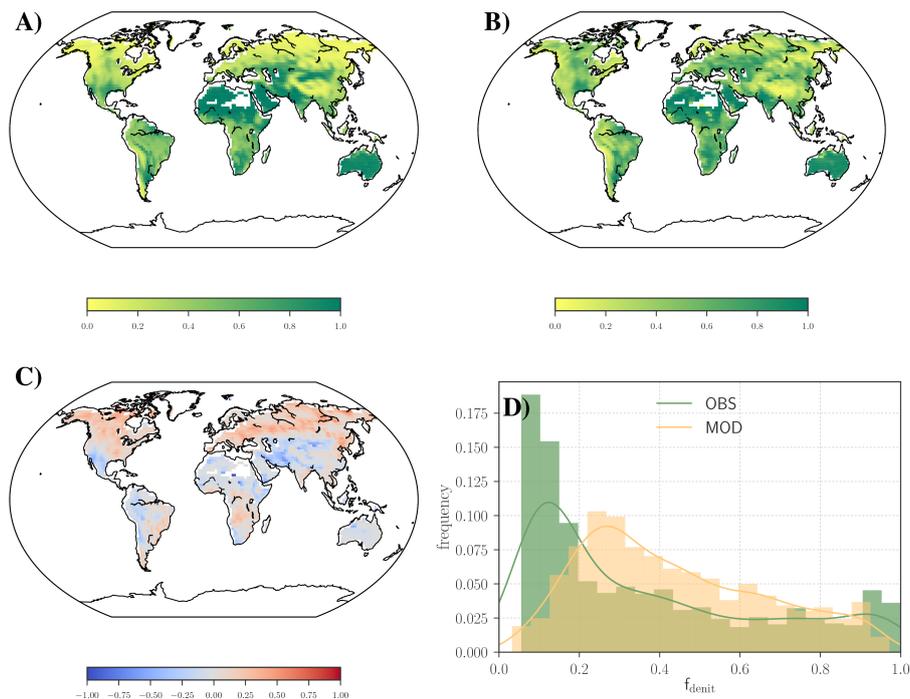


Figure 2. Comparison of simulated and reconstructed fractions of nitrogen lost by denitrification relative to as a fraction of total nitrogen losses (f_{denit}). Shown are loss fractions f_{denit} reconstructed from observational data on $\delta^{15}N$ measurements and simulated climate (aA), f_{denit} as simulated (bB), the difference between simulated and reconstructed f_{denit} (cC), as well as the frequency distribution of simulated (yellow) and reconstructed (green) f_{denit} (dD).

Table 6. Simulated response ratios of gross and net primary productivity to elevated $\text{CO}_2\text{-CO}_2$ in comparison with observation based estimates.

Response ratio	simulated	observed	reference
$\text{GPP}_{396}/\text{GPP}_{295}$	1.23 ± 0.03	1.25	Ehlers et al. (2015)
$\text{NPP}_{550}/\text{NPP}_{370}$	1.16 ± 0.03	1.23 ± 0.02	Norby et al. (2005)

3.2 Changes in the land carbon cycle in the 1% $\text{CO}_2\text{-CO}_2$ increase simulations

JSBACH simulates a strong increase in net plant productivity (NPP) due to increasing $\text{CO}_2\text{-CO}_2$ from pre-industrial level to $4 \times$ pre-industrial level (Figure 3). The simulated increase in NPP of 16.0% for a rise in atmospheric $\text{CO}_2\text{-CO}_2$ from 370 ppm-ppm to 550 ppm-ppm is somewhat lower than the estimated increase of 25% from 4 free air carbon dioxide enrichment (FACE) experiments (Norby et al., 2005) (Table 6). A lower increase than in the FACE experiment can be expected as the long-term effect of elevated $\text{CO}_2\text{-CO}_2$ is likely to be less than the one derived from short duration FACE experiments (Norby

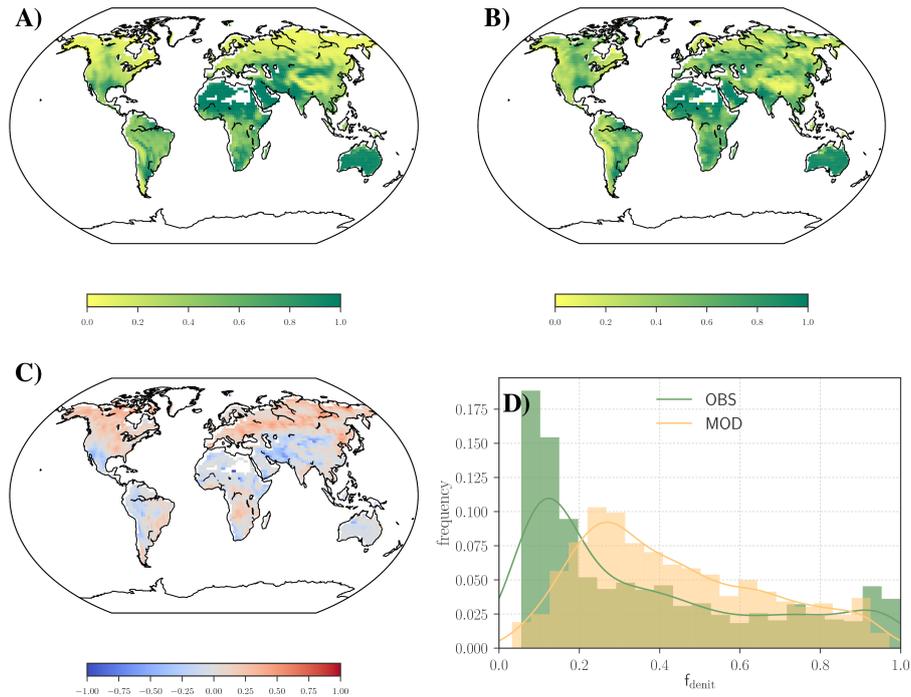


Figure 3. Changes in ~~global net primary productivity~~ total land carbon (a) and ~~total land carbon~~ global net primary productivity (b) and in the set of 1% CO_2 - CO_2 increase simulations with (solid line) and without (dashed line) carbon-nitrogen interactions.

et al., 2010) on early successional forests (Norby et al., 2015). The simulated increase in GPP of 23.1% for an increase in atmospheric CO_2 - CO_2 concentration from the level of the year 1900 to 2013 is close to the 25% increase for the same increase in CO_2 - CO_2 estimated from intramolecular isotope distributions (isotopomers), a methodology for detecting shifts in plant carbon metabolism over long times (Ehlers et al., 2015).

- 5 The increase in NPP translates to an increase in carbon storage of approximately 600 Gt-Gt by end of the biogeochemically-coupled simulation (Figure 3). Climate change, in particular increasing temperature, overall has a slightly negative effect on global NPP: the carbon losses by autotrophic respiration in low latitudes outweigh the increases in NPP in temperature limited ecosystems. Globally, warming stimulates the decomposition of soil organic matter (not shown) which leads to a smaller increase in carbon storage in the fully-coupled simulation compared to the biogeochemically-coupled simulation, and even a
- 10 reduction in carbon storage in the radiatively-coupled simulations. The effect of CO_2 - CO_2 and climate change on land carbon storage is much less pronounced in the recent version of JSBACH than in the CMIP5 version and the responses of the new version lie well within the range of CMIP5 models (Arora et al., 2013). The more moderate response can mainly be attributed to the recent improvement in respect to the carbon cycle and are discussed in detail later.

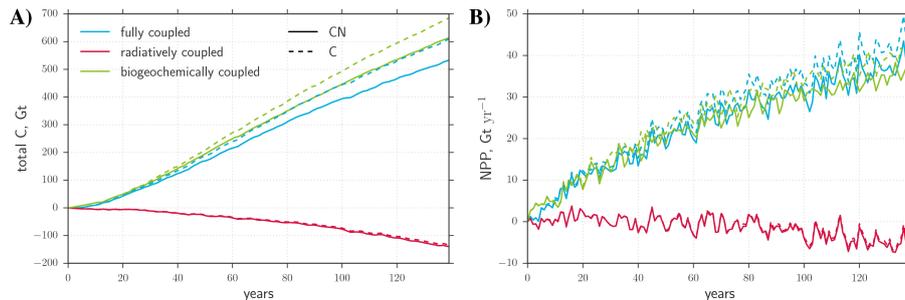


Figure 4. Changes in the nitrogen cycling in the set of 1% CO_2 - CO_2 increase simulations with carbon-nitrogen interactions: (a) total nitrogen, (b) mineral N, (c) biological nitrogen fixation, (d) net mineralisation, (e) leaching, and (f) denitrification.

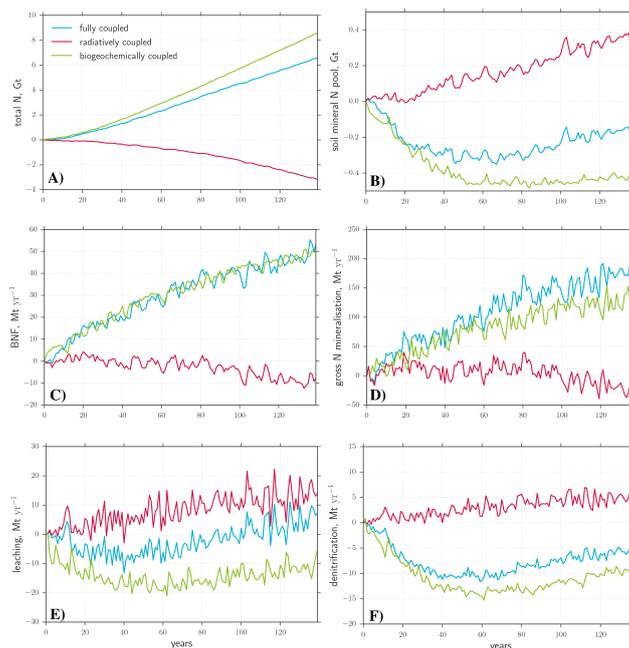


Figure 5. The terrestrial nitrogen balance during the fully “coupled” simulation. Shown are the average fluxes and stocks for 10 yr time period for initial conditions (year=0; 284 ppm), fourth decade (year=35; 400 ppm) and the last decade (year=135; 4 × 284 ppm).

3.3 Changes in the land nitrogen cycle in the 1% CO_2 - CO_2 increase simulations

Increasing atmospheric CO_2 - CO_2 concentration leads to the accumulation of nitrogen in the terrestrial system (Figure 4a), due to elevated inputs by biological nitrogen fixation (BNF) (Figure 4c) in combination with reduced losses by leaching and denitrification (Figure 4d). The increasing primary productivity and the subsequent incorporation of soil mineral nitrogen are the main drivers behind the accumulation. Increasing NPP (Figure 3) directly stimulates the demand-driven process of BNF

and therefore BNF rates increase nearly as strong as NPP (50% compared to 59% by end of the simulations). The decline in soil mineral nitrogen (Figure 4b) due to the incorporation of nitrogen in accumulating biomass leads to reduced losses by leaching and denitrification.

An increase in the nitrogen stock by 8.5% was found in a ~~15-yr ecosystem scale CO₂ enrichment experiment (?)~~ ecosystem scale CO₂ enrichment experiment (Shi et al., 2016), which is more pronounced than the simulated increase in the nitrogen stock of 3.2% for a comparable increase in ~~CO₂-CO₂~~ (year 29–69; 369–551ppm). A strong stimulation of BNF by 44%, with a strong decline in leaching by 42% and no significant changes in denitrification, mineralisation and soil organic nitrogen were found in a compilation of ~~CO₂-CO₂~~ CO₂ enrichment experiments (Liang et al., 2016). However the representativeness of these findings was questioned recently (Rütting, 2016). In addition to that, ~~CO₂-CO₂~~ was increased abruptly in ~~CO₂~~ CO₂ enrichment experiments while it increased gradually in our simulations. As the different nitrogen processes have different response patterns, ~~they t hey~~ are likely to react differently to an abrupt than to a gradual increase in ~~CO₂~~ CO₂. Although the relative contributions of reduced losses and increased inputs to an accumulation remain somewhat elusive due to methodological biases (Rütting, 2016) and limited data, an accumulation of nitrogen under elevated ~~CO₂~~ CO₂ is a plausible scenario.

We find that the processes governing the nitrogen balance operate on different time scales (Figure 5). The mineral nitrogen stocks decline from 1.33 ~~Gt-Gt~~ to 1.06 ~~Gt-Gt~~ during the first 35 ~~yr~~ and thereby reduce the substrate driven nitrogen losses (Figure 5) from 98 ~~Mt-yr⁻¹~~ to 83 ~~Mt-yr⁻¹~~. However, losses by leaching start to increase afterwards and are higher by the end of the simulation than at the start. While the reduction in losses and gains in inputs contribute to equally parts to the accumulation in the first decades of the simulation, the stimulated BNF dominates the accumulation in later (Figure 5). This highlights the importance of long term manipulation experiments for improving our understanding about the long term effects of increasing ~~CO₂~~ CO₂ on the terrestrial biosphere.

We find that the effect of increasing ~~CO₂~~ CO₂ and climate change on the nitrogen balance differ. Elevated ~~CO₂~~ CO₂ alone leads to a shift from inorganic nitrogen to organic nitrogen (Figure 4a&b), whereas climate change is dampening this shift as warming stimulates the decomposition of organic nitrogen (Figure 4d) and thereby slow down the progressive immobilization of mineral nitrogen into biomass and soil organic matter. Climate change alone leads to a loss of nitrogen from the system (Figure 4a): The enhanced net mineralisation of organic nitrogen due to warming leads to increased losses of nitrogen via leaching and denitrification. We further found that changes in the water cycle due to climate change are increasing losses by leaching, while denitrification follows primarily the changes in substrate availability despite the influence of soil moisture in Eq. 16 (Figure 5). Overall, we find that total nitrogen losses are intensified relative to the substrate availability at the end compared to the start of the simulations (Figure 5).

The ~~overall behavior simulated increase in tightness~~ of the nitrogen ~~cycle cycle as mineral nitrogen stocks deplete~~ is in line with the substrate-based mechanisms proposed based on recent compilation of ecosystem nitrogen addition experiments (Niu et al., 2016), in which the mineral nitrogen exerts a major control on the mineral nitrogen consuming processes. However, the respective observed response patterns of ecosystem nitrogen processes remain to a large degree unknown and are represented in a strongly simplified way in JSBACH. In general, we find that the effect of nitrogen availability on carbon storage is rather moderate in all simulation (Figure 3) due to the adjustments of the nitrogen balance to changes in the carbon cycle (Figure 5).

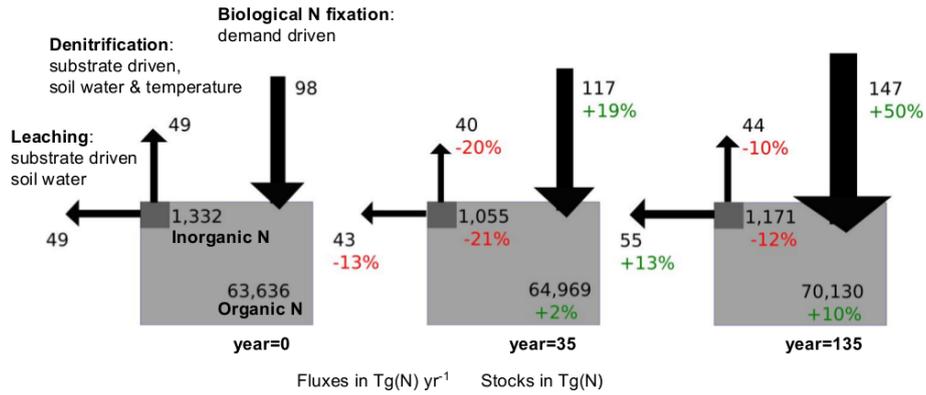


Figure 6. Spatial map of the carbon concentration feedback β_L (a) and the carbon climate feedback γ_L (eb) (of the simulations with carbon-nitrogen interactions) as well as the effect of the nitrogen cycling on the respective feedbacks (bc,d)(as the difference in the feedback strengths between simulations with and without carbon-nitrogen interactions).

Table 7. Carbon cycle feedbacks in simulations with JSBACH compared to results from CMIP5.

	Land carbon-concentration feedback [Pg ppm ⁻¹]	Land carbon-climate feedback [Pg °C ⁻¹]	reference
CMIP5 MPI-ESM-LR	1.46	-83.2	Arora et al. (2013)
CMIP5 multi model mean	0.92±0.44	-58.5±28.5	Arora et al. (2013)
JSBACH C	0.74	-26.2	this study
JSBACH CN	0.61	-27.5	this study

3.4 The effect of nitrogen on the carbon feedbacks

We quantify the strengths of the climate carbon-feedback (γ_L) and the carbon-concentration feedback (β_L) from the radiatively “coupled” and biogeochemically “coupled” simulations, respectively (Figure 6a,c). Both land feedbacks, with a global β_L of 0.61 Pg ppm⁻¹ Pg(C) ppm⁻¹ and a global γ_L of -27.5 Pg °C⁻¹ Pg(C) °C⁻¹, are 34% and 53% smaller than the multi-model averages of the CMIP5 models, despite that the CMIP5 version of JSBACH simulated global β_L and γ_L which are 59% and 42% times larger than the average of CMIP5 models (Table 7).

In CMIP5 the two ESMs with nitrogen limitation (which shared the same terrestrial biosphere component) had feedback strengths 70–75% lower than averaged across models (Arora et al., 2013), suggesting a prominent role of nitrogen in dampening both carbon cycle feedbacks. Here, we find that the dampened response is primarily related to the modifications of the soil and litter carbon decomposition module, rather than to the inclusion of the nitrogen cycle. The global β_L in the simulation without nitrogen cycle is only 10% larger than in the simulation with nitrogen, while there is hardly any difference in global γ_L between simulation, as the small positive and negative differences cancel out (Figure 6). [This finding](#) [The contrasting findings regarding](#)

[the effect of nitrogen on the land carbon feedbacks](#) illustrates the need of a multitude of carbon-nitrogen models to draw [conclusions regarding the effect of nitrogen on the land carbon feedbacks](#) [general conclusions](#).

The large difference between the CMIP5 version of JSBACH and the recent version described here can primarily be attributed to the new decomposition model. The drastically reduced γ_L is primarily caused by the smaller initial soil carbon stock, as well as by the long-term acclimation of decomposition to warming due to substrate depletion in YASSO (Goll et al., 2015). The importance of the initial soil carbon stock for the carbon losses due to warming was illustrated by Todd-Brown et al. (2014). The lower β_L can be attributed to a much lower fraction of biomass which is converted into stable soil organic matter. Therefore, the increasing productivity translates to a much smaller increase in carbon storage. JSBACH does not account for the stimulation of decomposition of recalcitrant carbon under elevated CO_2 due to increases in labile organic matter (from of priming effect) observed in lab incubation experiments (Kuzyakov et al., 2000), which could potentially alter the response of soil carbon to increasing CO_2 , but for which there is no evidence of its relevance on multi-decadal time scales (Cardinael et al., 2015).

A dampening effect of the nitrogen cycle on the response of the terrestrial carbon cycle to climate change and increasing CO_2 is in line with the majority of carbon-nitrogen model studies (Ciais et al., 2013; Zaehle, 2013), but not all (Esser et al., 2011; Warlind et al., 2014). The mechanism by which nitrogen can dampen β_L is via an increasing decoupling of gross primary productivity from biomass accumulation under increasing ~~CO_2 concentration as mineral nitrogen availability decreases.~~ [In this case, the lack of nitrogen reduces the accumulation of carbon in vegetation biomass and respiration losses increase.](#) CO_2 [concentration: the incorporation of nitrogen into biomass reduces the mineral nitrogen availability \(Luo et al., 2004; Liang et al., 2016\) which negatively affects growth \(Norby et al., 2010\) and increases root respiration \(Vicca et al., 2012; McCormack et al., 2015\).](#) The dampening of γ_L is mainly via an enhanced nitrogen mineralisation in cold regions due to warming (Zaehle, 2013; Warlind et al., 2014; Koven et al., 2015), which cannot be fully captured by JSBACH due to assumption of CO_2 -induced nutrient limitation, and therefore the model is prone to underestimate the effect of nitrogen on γ_L .

3.5 Model limitations and future development directions

The current understanding of processes governing the terrestrial nitrogen balance is still rather limited (Zaehle, 2013), and several processes which might be of importance, in particular stand dynamics (Warlind et al., 2014) which can potentially alter biomass turnover (Brienen et al., 2015), interactions between plants and microbes which can stimulate nitrogen scarcity by non-altruistic symbioses (Franklin et al., 2014), [plasticity in stoichiometry and leaf nutrient recycling \(Zaehle et al., 2014; Meyerholt and Zaehle](#) and the availability of other nutrients (Goll et al., 2012) are not represented in JSBACH. In addition, the loss of organic matter in general due to erosion, although potentially of importance (?), is not yet represented in global land surface models, but development are underway (Naipal et al., 2015, 2016).

[Due to the concept of \$\text{CO}_2\$ -induced nutrient limitation in JSBACH the nitrogen cycle serves primarily as an additional constraint on the carbon uptake. The advantage of the approach is its low complexity and avoidance of assumptions about the initial state of nutrient limitation thereby taking into account \(1\) the lack of data regarding the nitrogen cycle \(Zaehle, 2013\) as well as \(2\) the large uncertainty about the nutrient constraint on plant productivity \(Letters et al., 2007; Zaehle, 2013\). The](#)

shortcomings of this approach are that it limits the applicability of the model to carbon cycle projections for scenarios of increasing atmospheric CO₂ and that it cannot capture any stimulation of the plant productivity due to changes in nitrogen availability itself: In addition to direct increase in nitrogen availability by nitrogen deposition and fertilization, a stimulation of plant productivity can occur due to reduced losses of nitrogen by pathways which are not under control of biota, like fire, leaching, or erosion (Thomas et al., 2015). As a result, the model might underestimate the importance of nitrogen cycling for carbon uptake under elevated CO₂.

Regarding the processes resolved in JSBACH, the extent of BNF increase has to be regarded as highly uncertain, despite its agreement with short-term experiments (Liang et al., 2016): the formulation of BNF used here is based on an empirical correlation between evapotranspiration and BNF and therefore the rate at which BNF rates increase strictly follows the increase in productivity whereas in reality the different processes leading to changes in BNF on ecosystem scales operate on a different time scale: The control of plants on their symbiotic partners via glucose export, and in case of nodules via oxygen regulation, result in changes in BNF from hours to months. On longer time scales, the composition of the ecosystem, namely the fraction of BNF associated species, affects nitrogen inputs to the system. While for tropical ecosystems there is evidence that any governing mechanism(s) ought to operate at a synoptic scale (Hedin et al., 2009), higher latitude system might experience longer lag times. Additionally, other nutrients, like phosphorus or molybdenum, might slow down or reduce the potential of BNF to increase (Vitousek et al., 2013). ~~Next-generation BNF models, need to~~ BNF models which better resolve the governing mechanisms, for example (Gerber et al., 2010; Fisher et al., 2012), should be incorporated into ESMs to increase the reliability of the simulated pace of changes in BNF (Meyerholt et al., 2016).

Models which simulate simultaneous competition for soil nitrogen substrates by multiple processes match the observed patterns of nitrogen losses better than models like JSBACH which are based on sequential competition (Niu et al., 2016). Here we find that despite the sequential competition, the simulated behavior is in general agreement with the dynamics of substrate-based mechanisms derived from manipulation experiments (Niu et al., 2016) and the spatial variability in the respective loss pathways is to a large degree in line with $\delta^{15}\text{N}$ -derived patterns, ~~despite the low performance of another sequential competition model (Houlton et al., 2015; Zhu and Riley, 2015)~~

The high-latitude permafrost processes are not represented here but were shown to be of importance for the effect on warming on carbon and nitrogen losses. Permafrost regions store about 1,000 Gt C within the upper few meters of soil (Hugelius et al., 2014). The thawing of permafrost and deepening of the active layer in response to global warming can potentially lead to a much stronger climate carbon feedback (Schneider Von Deimling et al., 2012; Schuur et al., 2015). The recent study of Koven et al. (2015) with the CLM model showed these carbon losses in high latitudes can be partly offset by increased nitrogen mineralisation, and in turn productivity and input to the soils.

Finally, as advocated by for example in Prentice et al. (2014); Medlyn et al. (2015), the stringent use of observational data set to evaluate the present day state of ecosystems as well as their response to manipulations must drive and guide new model developments whenever possible. With respect to JSBACH and other land surface models, the use of observation-derived climatology instead of the ESM climate as well as the use of site-specific simulations to allow a straightforward comparison to manipulation experiments is a research priority to increase the model reliability (Luo et al., 2012). In this study, the use of the

ESM climatology is justified by a focus on the feedback analysis in the framework of idealized simulations as suggested in the climate-carbon cycle model intercomparison project C4MIP (Anav et al., 2013; Jones et al., 2016). For further evaluation of the nitrogen limitation, however the preferable setup includes site-level simulations driven by observation-derived climatology (Zaehle et al., 2014).

5 4 Conclusions

The simulated response of primary productivity ~~and the simulated to increasing~~ CO₂, simulated litter stoichiometries, as well as the simulated spatial variability in nitrogen loss pathways are in ~~rather~~ good agreement with observation based estimates ~~despite the use of the simulated climate from an earth system model which in some regions deviates significantly from the observed climate (Hagemann et al., 2013). Regions with substantial bias in nitrogen loss pathways resemble regions with strong biases in either precipitation or surface temperature (Hagemann et al., 2013). The use of simulated climatology hampers a more detailed analysis of the~~. Here we show that a simple representation of mineral nitrogen dynamics can achieve a high agreement with observation in respect to nitrogen loss pathways ~~and limits hampers the ability to evaluate land processes using observational based constraint. A more stringent use of observed climatology in the calibration of JSBACH is recommended due to increasingly more common application of JSBACH outside the earth system model. Further refinements of denitrification should address the relationship between denitrification and low soil moisture availability and as well as the increasing availability of observational constraints. introduce a temperature scaling function.~~

The effect of nitrogen cycling on the land carbon uptake in idealized simulations with JSBACH is globally minor, but not negligible. In particular, the carbon-concentration feedback is affected by mineral nitrogen availability, but the extent is moderate compared to earlier studies (Arora et al., 2013; Zaehle, 2013). During the first decades of the simulations, nitrogen limitation is circumvented by a strong initial decline in loss terms in combination with increases in biological nitrogen fixation. Afterwards progressive increases in biological nitrogen fixation drive the accumulation of nitrogen in ecosystems. On top of that, warming enhances mineralisation and counteracts the immobilization of nitrogen in biomass. Our study is in line with the majority of carbon dioxide enrichment studies (Liang et al., 2016), showing that progressive nitrogen limitation under elevated carbon dioxide concentrations is less likely to occur than originally suggested (Luo et al., 2004).

The timescale and the extent to which the nitrogen cycle adjusts to increasing carbon dioxide and changing climate depend on the response of the input and loss processes of nitrogen as well as turnover of organic nitrogen. Here, we illustrate that the processes counteracting nitrogen scarcity operate on different time scales and have different trajectories due to differences in the respective environmental drivers, which indicates a picture more complicated than drawn from environmental response functions (Niu et al., 2016; Liang et al., 2016). It is difficult to assess to what extent the timescales in our experiments are realistic, as timescale on which these processes operate is well beyond the typical duration of manipulation experiments.

Our results suggest that nitrogen limitation of land carbon uptake of natural ecosystems could be temporally restricted, being the result of the inertia of the balancing processes (Altabet et al., 1995; Hedin et al., 2009). Ultimately, other nutrients like phosphorus which sources are depleted over time, are likely to dominate the long-term capacity of carbon storage.

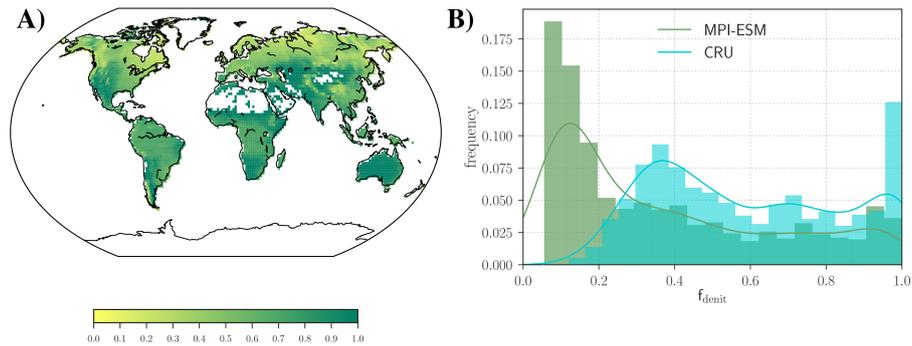


Figure A1. Reconstructed fractions of nitrogen lost by denitrification relative to total losses (f_{denit}). Shown are loss fractions reconstructed from observational data on $\delta^{15}N$ and observed climatology (A) and the frequency distribution of reconstructed f_{denit} from observed (turquoise) and simulated (green) climatology, respectively (D).

5 Code availability

The JSBACH model version 3.10 used here includes the soil module YASSO and nitrogen components. The model version corresponds to the revision 8691 from the 19th July 2016 in the Apache version control system (SVN) of the Max Planck Institute for Meteorology (<https://svn.zmaw.de/svn/cosmos/branches/mpiesm-landveg>). This version will be used in the CMIP6 simulations, where other components (landuse, dynamic vegetation, fire) will be included as well. The source code of the CMIP6 version of JSBACH as a part of MPI-ESM will be available in 2017 under the MPI-M Software License Agreement obtained at <http://www.mpimet.mpg.de/en/science/models/license/>. In meantime, please contact Thomas Raddatz (thomas.raddatz@mpimet.mpg.de) for the code of the JSBACH if you plan an application of the model and envisage longer-term scientific collaboration.

10 6 Data availability

Primary data and scripts used in the analysis and other supplementary information that may be useful in reproducing the author's work are archived by the Max Planck Institute for Meteorology and can be obtained by contacting publications@mpimet.mpg.de.

Appendix A: The nitrogen limitation factor

The nitrogen limitation factor, f_{limit}^N , is calculated based on a supply and demand approach (Parida, 2011; Goll et al., 2012). In a first step, potential carbon fluxes are computed from which the gross mineralisation, immobilization (D_{micr}) and plant uptake of mineral nitrogen (D_{veg}) is diagnosed. In a second step, all fluxes consuming nitrogen (donor compartment has a higher C:N ratio than the receiving pool as well as plant uptake) are down-regulated in case nitrogen demand cannot be met by the nitrogen supply. Hereby, a common scalar (f_{limit}^N) is used thereby no assumption about the relative competitive strengths

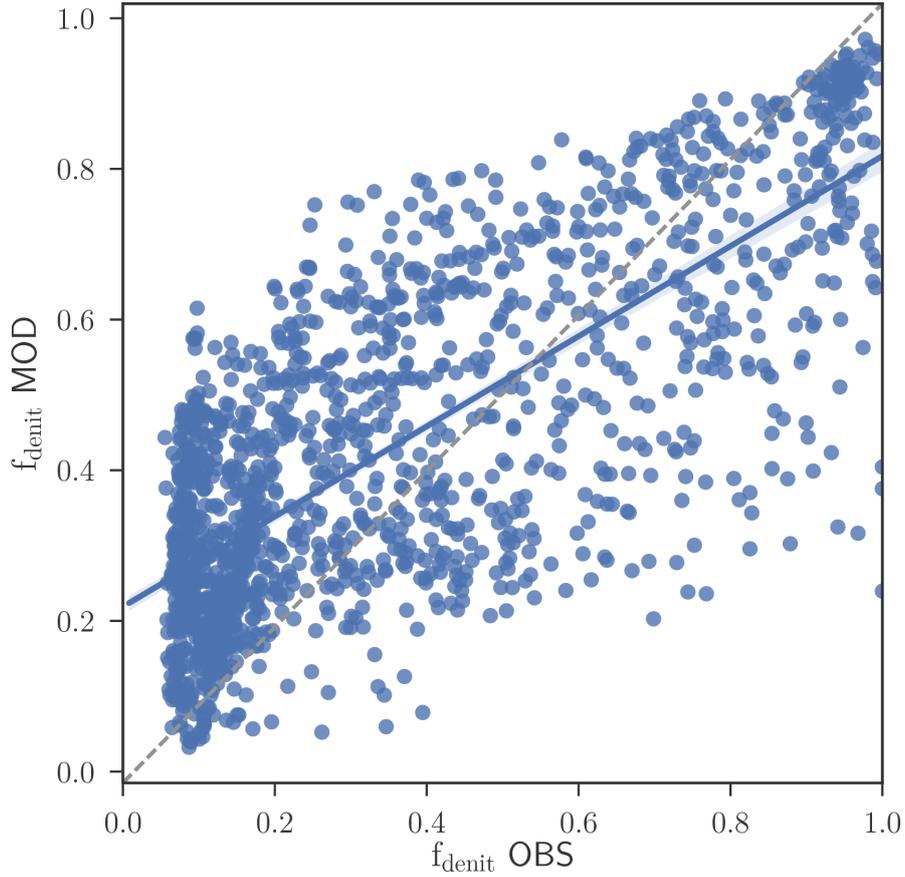


Figure A2. Scatter plot of simulated and reconstructed denitrification fractions (f_{denit}) derived from simulated climatology.

Table A1. Carbon to nitrogen mass ratio [g(C)g⁻¹(N)] of non-lignified litter compared to observations of foliage litter from Cornwell et al. (2008); Brovkin et al. (2012)

<u>PFT</u>	<u>simulated</u>	<u>observed</u>
<u>tropical broadleaved evergreen trees</u>	<u>53.5</u>	<u>55.9</u>
<u>tropical broadleaved deciduous trees</u>	<u>55.1</u>	<u>29.4</u>
<u>extra-tropical evergreen trees</u>	<u>50.4</u>	<u>68.3</u>
<u>extra-tropical deciduous trees</u>	<u>54.4</u>	<u>55.9</u>
<u>C3 perennial grass</u>	<u>54.5</u>	<u>47.6</u>
<u>C4 perennial grass</u>	<u>53.4</u>	<u>54.1</u>

of microbial and plant consumption has to be made.

$$f_{limit}^N = \begin{cases} \frac{[\frac{dN_{smin}}{dt}]^{max}}{D_{micr} + D_{veg}} & \text{for } (D_{micr} + D_{veg}) > [\frac{dN_{smin}}{dt}]^{max} \\ 1 & \text{otherwise} \end{cases} \quad (\text{A1})$$

where the term in square bracket is the maximum rate at which the soil mineral nitrogen pool can supply nitrogen. Note that in the discretized formulation the mineral nitrogen pool can at most be depleted during a single model time step (Δt). We thus set this maximum rate to $\frac{dN_{smin}}{\Delta t}$.

Appendix B: Evaluation of dynamically computed C:N ratios

5 The only ecosystem compartment in JSBACH which has a flexible stoichiometry is non-lignified litter and fast-decomposing organic matter. The simulated carbon to nitrogen ratios of this compartment for the six plant functional types in JSBACH are in rather good agreement with observations of foliage litter from the ART-DECO database (Table A1), except for tropical broadleaved deciduous trees and extra-tropical evergreen trees. The reason for the overestimation of nitrogen content in litter from extratropical evergreen trees is the global parametrization of leaf stoichiometry applied in JSBACH which does not
10 capture the lower leaf nitrogen concentration in needle-leaved trees compared to broad-leaved trees (KATTGE et al., 2011). The data for tropical species is very scarce and the variability among species is large, which hamper the interpretation of the mismatch between model and observation for the tropical broadleaved deciduous trees.

Appendix C: Consistency of nitrogen loss pathways with earlier estimates

The reconstructed f_{denit} map from observed climatology (Figure (A1) is generally similar to one presented by Houlton et al. (2015),
15 with high fractions (ca 80%) in the tropics and mid-latitude deserts, a strong gradient of decreasing fractions with decreasing temperature towards high altitudes and latitudes, and values in the range 0-20% reached in cold, wet climates in the north. However, some differences are apparent, most obviously connected with the use of mean annual temperature (MAT) by Houlton et al. (2015) to index microbial activity. MAT becomes extremely low in Eurasia towards the northeast, for example, and accordingly, Houlton et al. (2015) estimates of the denitrification fraction become very low there. Craine et al. (2015) noted
20 that climates with very low MAT (including sites in NE Siberia) showed anomalous values of soil $\delta^{15}\text{N}$, more similar to those of warmer climates. Our approach takes account of this by the use of an index that is much more responsive to the warm summers than to the extreme cold winters found in hypercontinental climates.

When simulated climatology is used to upscale the empirical relationship between temperature, runoff and soil $\delta^{15}\text{N}$, the influence of biases in simulated climatology on f_{denit} become apparent. The overestimation of precipitation and subsequently
25 runoff of about 20% in MPI-ESM (Weedon et al., 2011; Hagemann et al., 2013) leads to a pronounced peak in the histogram of f_{denit} at about 0.1-0.2 (Figure A1), which is mostly in the mid and high latitudes regions in northern hemisphere.

Author contributions. The study was led by Daniel S. Goll who developed the model concept and implemented it into JSBACH. Victor Brovkin, Alexander J. Winkler and Thomas Raddatz designed and performed the model experiment. Alexander J. Winkler analysed and visualized the data. Ning Dong and Colin Prentice performed the estimation of the nitrogen loss pathways. Philippe Ciais contributed to the
30 analysis and evaluation of the model. The draft of the manuscript was written by Daniel S. Goll with all authors contributing to its final form.

Competing interests. The authors declare that they have no conflict of interest.

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References

- Altabet, M. a., Francois, R., Murray, D. W., and Prell, W. L.: Climate-related variations in denitrification in the Arabian Sea from sediment 15N/14N ratios, *Nature*, 373, 506–509, doi:10.1038/373506a0, 1995.
- 5 [Amundson, R., Austin, A., Schuur, E., Yoo, K., Matzek, V., Kendall, C., Uebersax, A., Brenner, D., and Baisden W.T.: Global patterns of the isotopic composition of soil and plant nitrogen, *Global Biogeochem. Cycles*, 17, 31/1–31/10, doi:10.1029/2002GB001903, http://www.agu.org/journals/gb/gb0301/2002GB001903/2002GB001903.pdf, 2003.](#)
- Anav, A., Friedlingstein, P., Kidston, M., Bopp, L., Ciais, P., Cox, P., Jones, C., Jung, M., Myneni, R., and Zhu, Z.: Evaluating the Land and Ocean Components of the Global Carbon Cycle in the Cmp5 Earth System Models, *J. Clim.*, p. 130401082723008, doi:10.1175/JCLI-D-12-00417.1, http://journals.ametsoc.org/doi/abs/10.1175/JCLI-D-12-00417.1, 2013.
- 10 Arora, V. K., Boer, G. J., Friedlingstein, P., Eby, M., Jones, C. D., Christian, J. R., Bonan, G., Bopp, L., Brovkin, V., Cadule, P., Hajima, T., Ilyina, T., Lindsay, K., Tjiputra, J. F., and Wu, T.: Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth system models, *Journal of Climate*, p. 130208091306008, doi:10.1175/JCLI-D-12-00494.1, http://journals.ametsoc.org/doi/abs/10.1175/JCLI-D-12-00494.1, 2013.
- Bai, E., Houlton, B. Z., and Wang, Y. P.: Isotopic identification of nitrogen hotspots across natural terrestrial ecosystems, *Biogeosciences*, 9, 3287–3304, doi:10.5194/bg-9-3287-2012, 2012.
- 15 Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., and Et Al.: Long-term decline of the Amazon carbon sink, *Nature*, 519, 344–348, doi:10.1038/nature14283, http://dx.doi.org/10.1038/nature14283, 2015.
- [Brovkin, V., Van Bodegom, P. M., Kleinen, T., Wirth, C., Cornwell, W. K., Cornelissen, J. H. C., and Kattge, J.: Plant-driven variation in decomposition rates improves projections of global litter stock distribution, *Biogeosciences*, 9, 565–576, doi:10.5194/bg-9-565-2012, 2012.](#)
- 20 [Butterbach-Bahl, K., Baggs, E. M., Dannenmann, M., Kiese, R., and Zechmeister-Boltenstern, S.: Nitrous oxide emissions from soils: how well do we understand the processes and their controls?, *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 368, 20130122, doi:10.1098/rstb.2013.0122, http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3682742{&}tool=pmcentrez{&}rendertype=abstract, 2013.](#)
- 25 Campbell, G. S. and Norman, J. M.: *An Introduction to Environmental Biophysics*, Springer-Verlag New York, 2 edn., doi:10.1007/978-1-4612-1626-1.
- Canion, A., Kostka, J. E., Gihring, T. M., Huettel, M., Van Beusekom, J. E. E., Gao, H., Lavik, G., and Kuypers, M. M. M.: Temperature response of denitrification and anammox reveals the adaptation of microbial communities to in situ temperatures in permeable marine sediments that span 50 in latitude, *Biogeosciences*, 11, 309–320, doi:10.5194/bg-11-309-2014, 2014.
- 30 Cardinael, R., Eglin, T., Guenet, B., Neill, C., Houot, S., and Chenu, C.: Is priming effect a significant process for long-term SOC dynamics? Analysis of a 52-years old experiment, *Biogeochemistry*, 123, 203–219, doi:10.1007/s10533-014-0063-2, http://dx.doi.org/10.1007/s10533-014-0063-2, 2015.
- Cheng, W., Chen, Q., Xu, Y., Han, X., and Li, L.: Climate and ecosystem¹⁵N natural abundance along a transect of Inner Mongolian grasslands: Contrasting regional patterns and global patterns, *Global Biogeochemical Cycles*, 23, 1–11, doi:10.1029/2008GB003315, 35 2009.
- Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, a., DeFries, R., Galloway, J., Heimann, M., Jones, C., Quéré, C. L., Myneni, R., Piao, S., Thornton, P., France, P. C., Willem, J., Friedlingstein, P., and Munhoven, G.: 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 Intergovernmental Panel on Climate Change.*, edited by Stocker, T., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Y., X., Bex, V., and Midgley, P. M., chap. Carbon and, pp. 465–570, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, doi:10.1017/CBO9781107415324.015, 2013.
- 5 Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Hedin, L. O., Perakis, S., Latty, E. F., Fischer, C. V., Elseroad, A., and Wasson, M. F.: Global patterns of terrestrial biological nitrogen (N₂) fixation in natural ecosystems, *Global Biogeochemical Cycles*, 13, 623–645, doi:10.1029/1999GB900014, <http://onlinelibrary.wiley.com/doi/10.1029/1999GB900014/pdf>, 1999.
- [Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Díaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V., and Westoby, M.: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide, *Ecol. Lett.*, 11, 1065–1071, doi:10.1111/j.1461-0248.2008.01219.x, 2008.](#)
- 10 [Craine, J. M., Elmore, A. J., Wang, L., Augusto, L., Baisden, W. T., Brookshire, E. N. J., Cramer, M. D., Hasselquist, N. J., Hobbie, E. A., Kahmen, A., Koba, K., Kranabetter, J. M., Mack, M. C., Marin-Spiotta, E., Mayor, J. R., McLauchlan, K. K., Michelsen, A., Nardoto, G. B., Oliveira, R. S., Perakis, S. S., Peri, P. L., Quesada, C. A., Richter, A., Schipper, L. A., Stevenson, B. A., Turner, B. L., Viani, R. A. G., Wanek, W., and Zeller, B.: Convergence of soil nitrogen isotopes across global climate gradients., *Sci. Rep.*, 5, 8280, doi:10.1038/srep08280, <http://www.nature.com/srep/2015/150206/srep08280/full/srep08280.html>, 2015.](#)
- 15 Ehlers, I., Augusti, A., Betson, T. R., Nilsson, M. B., Marshall, J. D., and Schleucher, J.: Detecting long-term metabolic shifts using isotopomers : CO₂ -driven suppression of photorespiration in C₃ plants over the 20th century, *Proceedings of the National Academy of Sciences*, pp. 1–6, doi:10.1073/pnas.1504493112, 2015.
- 20 Esser, G., Kattge, J., Sakalli, A., and Use, L.: Feedback of carbon and nitrogen cycles enhances carbon sequestration in the terrestrial biosphere, *GLOBAL CHANGE BIOLOGY*, 17, 819–842, doi:10.1111/j.1365-2486.2010.02261.x, 2011.
- Eyring, V., Bony, S., Meehl, J., Senior, C., Stouffer, R., Taylor, K., and Panel, C.: Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) Experimental Design and Organization Coupled Model Intercomparison Project (CMIP), 6, doi:10.5194/gmd-9-1937-2016, 2016.
- 25 Fang, Y., Yoh, M., Koba, K., Zhu, W., Takebayashi, Y., Xiao, Y., Lei, C., Mo, J., Zhang, W., and Lu, X.: Nitrogen deposition and forest nitrogen cycling along an urban-rural transect in southern China, *Global Change Biology*, 17, 872–885, doi:10.1111/j.1365-2486.2010.02283.x, 2011.
- Fang, Y., Koba, K., Yoh, M., Makabe, A., and Liu, X.: Patterns of foliar 15N and their control in Eastern Asian forests, *Ecological Research*, 30, 735–748, doi:10.1007/s11284-012-0934-8, <http://dx.doi.org/10.1007/s11284-012-0934-8>, 2013.
- [Fisher, J. B., Badgley, G., and Blyth, E.: Global nutrient limitation in terrestrial vegetation, *Global Biogeochem. Cycles*, 26, GB3007, <http://www.agu.org/pubs/crossref/2012/2011GB004252.shtml><http://www.agu.org/pubs/crossref/pip/2011GB004252.shtml>, 2012.](#)
- Franklin, O., Näsholm, T., Höglberg, P., and Höglberg, M. N.: Forests trapped in nitrogen limitation - an ecological market perspective on ectomycorrhizal symbiosis, *New Phytologist*, 203, 657–666, doi:10.1111/nph.12840, <http://www.ncbi.nlm.nih.gov/pubmed/24824576>, 35 2014.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler,

- K. G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N.: Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison, *JOURNAL OF CLIMATE*, 19, 3337–3353, 2006.
- Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., Asner, G. P., Cleveland, C. C., Green, P. a., Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, a. R., and Vo, C. J.: Nitrogen cycles : past, present , and future, *BIOGEOCHEMISTRY*, 70, 153–226, 2004.
- Galloway, J. N., Leach, A. M., Bleeker, A., and Erisman, J. W.: A chronology of human understanding of the nitrogen cycle., *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368, 20130 120, doi:10.1098/rstb.2013.0120, <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3682740>{& }tool=pmcentrez{& }rendertype=abstract, 2013.
- [Gerber, S., Hedin, L. O., Oppenheimer, M., Pacala, S. W., and Shevliakova, E.: Nitrogen cycling and feedbacks in a global dynamic land model, *Global Biogeochem. Cycles*, 24, 1–15, doi:10.1029/2008GB003336, 2010.](#)
- Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., Van Bodegom, P. M., and Niinemets, Ü.: Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon, nitrogen and phosphorus cycling, *Biogeosciences*, 9, 3547–3569, doi:10.5194/bg-9-3547-2012, <http://www.biogeosciences-discuss.net/9/3173/2012/http://www.biogeosciences.net/9/3547/2012/>, 2012.
- Goll, D. S., Brovkin, V., Liski, J., Raddatz, T., Thum, T., and Todd-Brown, K. E. O.: Strong dependence of CO₂ emissions from anthropogenic land cover change on soil carbon parametrization and initial land cover, *Global Biogeochemical Cycles*, 29, 1–58, doi:10.1002/2014GB004988.Abstract, 2015.
- Hagemann, S. and Stacke, T.: Impact of the soil hydrology scheme on simulated soil moisture memory, *Climate Dynamics*, pp. 1731–1750, doi:10.1007/s00382-014-2221-6, 2014.
- Hagemann, S., Loew, A., and Andersson, A.: Combined evaluation of MPI-ESM land surface water and energy fluxes, *J. Adv. Model. Earth Syst.*, 5, n/a–n/a, doi:10.1029/2012MS000173, <http://doi.wiley.com/10.1029/2012MS000173>, 2013.
- Hedin, L. O., Armesto, J. J., and Johnson, R. A. H.: Patterns of Nutrient Loss from Unpolluted, Old-Growth Temperate Forests: Evaluation of Biogeochemical Theory, *ECOLOGY*, 76, 493–509, doi:10.2307/1941208, 1995.
- Hedin, L. O., Brookshire, E. J., Menge, D. N., and Barron, A. R.: The Nitrogen Paradox in Tropical Forest Ecosystems, *Annual Review of Ecology, Evolution, and Systematics*, 40, 613–635, doi:10.1146/annurev.ecolsys.37.091305.110246, <http://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.37.091305.110246>, 2009.
- Hilton, R. G., Galy, A., West, A. J., Hovius, N., and Roberts, G. G.: Geomorphic control on the ¹⁵N of mountain forests, *Biogeosciences*, 10, 1693–1705, doi:10.5194/bg-10-1693-2013, 2013.
- Houlton, B. Z. and Bai, E.: Imprint of denitrifying bacteria on the global terrestrial biosphere, *Proc. Natl. Acad. Sci. USA*, 106, 21 713–21 716, doi:10.1073/pnas.0912111106, 2009.
- Houlton, B. Z., Marklein, A. R., and Bai, E.: Representation of nitrogen in climate change forecasts, *Nature Climate Change*, 5, 398–401, doi:10.1038/nclimate2538, <http://www.nature.com/doi/10.1038/nclimate2538>, 2015.
- Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C. L., Schirmermeister, L., Grosse, G., Michaelson, G. J., Koven, C. D., O'Donnell, J. A., Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J., and Kuhry, P.: Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps, *Biogeosciences*, 11, 6573–6593, doi:10.5194/bg-11-6573-2014, 2014.
- Hungate, B. a., Dukes, J. S., Shaw, M. R., Luo, Y., and Field, C. B.: Nitrogen and Climate Change, *Science*, 302, 1512–1513, doi:10.1126/science.1091390, <http://www.sciencemag.org/content/302/5650/1512.short>, 2003.

- Hurt, G. C., Chini, L. P., Frohling, S., Betts, R. a., Feddema, J., Fischer, G., Fisk, J. P., Hibbard, K., Houghton, R. a., Janetos, A., Jones, C. D., Kindermann, G., Kinoshita, T., Klein Goldewijk, Kees, Riahi, K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Thornton, P., Vuuren, D. P., and Wang, Y. P.: 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, *Clim. Change*, 109, 117–161, doi:10.1007/s10584-011-0153-2, 2011.
- 5 Ito, A.: A historical meta-analysis of global terrestrial net primary productivity: are estimates converging?, *Global Change Biology*, 17, 3161–3175, doi:10.1111/j.1365-2486.2011.02450.x, <http://doi.wiley.com/10.1111/j.1365-2486.2011.02450.x>, 2011.
- Jones, C. D., Arora, V., Friedlingstein, P., Bopp, L., Brovkin, V., Dunne, J., Graven, H., Hoffman, F., Ilyina, T., John, J. G., Jung, M., Kawamiya, M., Koven, C., Pongratz, J., Raddatz, T., Randerson, J., and Zaehle, S.: The C4MIP experimental protocol for CMIP6, *Geoscientific Model Development Discussions*, pp. 1–52, doi:10.5194/gmd-2016-36, <http://www.geosci-model-dev-discuss.net/gmd-2016-36/>,
10 2016.
- [KATTGE, J., DÍAZ, S., LAVOREL, S., PRENTICE, I. C., LEADLEY, P., BÖNISCH, G., GARNIER, E., WESTOBY, M., REICH, P. B., WRIGHT, I. A. N. J., CORNELISSEN, J. H. C., VIOLLE, C., HARRISON, S. P., van BODEGOM, P. M., REICHSTEIN, M., ENQUIST, B. J., SOUDZILOVSKAIA, N. A., ACKERLY, D. D., ANAND, M., ATKIN, O., BAHN, M., BAKER, T. R., BALDOCCHI, D., BEKKER, R., BLANCO, C. C., BLONDER, B., BOND, W. J., BRADSTOCK, R., BUNKER, D. E., CASANOVES, F., CAVENDER-BARES, J.,
15 CHAMBERS, J. Q., CHAPIN, F. S., CHAVE, J., COOMES, D., CORNWELL, W. K., CRAINE, J. M., DOBRIN, B. H., DUARTE, L., DURKA, W., ELSER, J., ESSER, G., ESTIARTE, M., FAGAN, W. F., FANG, J., FERNÁNDEZ-MÉNDEZ, F., FIDELIS, A., FINEGAN, B., FLORES, O., FORD, H., FRANK, D., FRESCHET, G. T., FYLLAS, N. M., GALLAGHER, R. V., GREEN, W. A., GUTIERREZ, A. G., HICKLER, T., HIGGINS, S., HODGSON, J. G., JALILI, A., JANSEN, S., JOLY, C., KERKHOFF, A. J., KIRKUP, D. O. N., KITAJIMA, K., KLEYER, M., KLOTZ, S., KNOPS, J. M. H., KRAMER, K., KÜHN, I., KUROKAWA, H., LAUGHLIN, D., LEE, T. D., LEISHMAN, M., LENS, F., LENZ, T., LEWIS, S. L., LLOYD, J. O. N., LLUSIÀ, J., LOUAULT, F., MA, S., MAHECHA, M. D., MANNING, P., MASSAD, T., MEDLYN, B., MESSIER, J., MOLES, A. T., MÜLLER, S. C., NADROWSKI, K., NAEEM, S., NIINEMETS, Ü. L. O., NÖLLERT, S., NÜSKE, A., OGAYA, R., OLEKSYN, J., ONIPCHENKO, V. G., ONODA, Y., ORDOÑEZ, J., OVERBECK, G., OZINGA, W. I. M. A., PATIÑO, S., PAULA, S., PAUSAS, J. G., PEÑUELAS, J., PHILLIPS, O. L., PILLAR, V., POORTER, H., POORTER, L., POSCHLOD, P., PRINZING, A., PROULX, R., RAMMIG, A., REINSCH, S., REU, B., SACK, L.,
20 SALGADO-NEGRET, B., SARDANS, J., SHIODERA, S., SHIPLEY, B., SIEFERT, A., SOSINSKI, E., SOUSSANA, J.-F., SWAINE, E., SWENSON, N., THOMPSON, K. E. N., THORNTON, P., WALDRAM, M., WEIHER, E., WHITE, M., WHITE, S., WRIGHT, S. J., YGUEL, B., ZAEHLE, S., ZANNE, A. M. Y. E., and WIRTH, C.: TRY – a global database of plant traits. *Glob. Chang. Biol.*, pp. no—no, doi:10.1111/j.1365-2486.2011.02451.x, <http://dx.doi.org/10.1111/j.1365-2486.2011.02451.x>, 2011.](#)
- Koven, C. D., Lawrence, D. M., and Riley, W. J.: Permafrost carbon-climate feedback is sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics., *Proceedings of the National Academy of Sciences of the United States of America*, 112, 3752–7, doi:10.1073/pnas.1415123112, <http://www.pnas.org/content/112/12/3752.full>, 2015.
- Kuzyakov, Y., Friedel, J. K., and Stahr, K.: Review of mechanisms and quantification of priming effects, *Soil Biology and Biochemistry*, 32, 1485–1498, doi:10.1016/S0038-0717(00)00084-5, 2000.
- Lal2002 Lal, R.: Soil erosion and the global carbon budget, *Environment International*, 29, 437–450, doi:10.1016/S0160-4120(02)00192-7,
35 2002.
- [Letters, E., Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., and Smith, J. E.: Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.*, 10, 1135–1142, doi:10.1111/j.1461-0248.2007.01113.x, <http://www.ncbi.nlm.nih.gov/pubmed/17922835>, 2007.](#)

- Liang, J., Qi, X., Souza, L., and Luo, Y.: Processes regulating progressive nitrogen limitation under elevated carbon dioxide: A meta-analysis, *Biogeosciences*, 13, 2689–2699, doi:10.5194/bg-13-2689-2016, 2016.
- Luo, Y., Su, B., Currie, W. S., Dukes, J. S., Finzi, A. C., Hartwig, U., Hungate, B., McMurtrie, R. E., Oren, R., Parton, W. J., Pataki, D. E., Shaw, M. R., Zak, D. R., and Field, C. B.: Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide, *BIOSCIENCE*, 54, 731–739, doi:10.1641/0006-3568(2004)054[0731:PNLOER]2.0.CO;2, 2004.
- McCarthy, H. R. and Pataki, D. E.: Drivers of variability in water use of native and non-native urban trees in the greater Los Angeles area, *Urban Ecosystems*, 13, 393–414, doi:10.1007/s11252-010-0127-6, 2010.
- [McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., Erik, A., Iversen, C. M., Jackson, R. B., Leppalammi-Kujansuu, J., Norby, R. J., Phillips, R. P., Pregitzer, K. S., Pritchard, S., Rewald, B., and Zadworny, M.: Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes, *New Phytol.*, doi:doi: 10.1111/nph.13363 Key, 2015.](#)
- Medlyn, B. E., Kauwe, M. G. D., Walker, A. P., Dietze, C., Hanson, P., Hickler, T., Jain, A., Luo, Y., Parton, W., Colin, I., Wang, S., Wang, Y.-p., Weng, E., Iversen, C. M., Mccarthy, H., Warren, J., Oren, R., Norby, R., Division, E. S., Ridge, O., Goethe, G., and Collins, F.: Using Ecosystem Experiments to Improve Vegetation Models : Lessons Learnt from the Free-Air CO₂ Enrichment Model-Data Synthesis, *Nature Climate Change*, 5, 528–534, doi:10.1038/nclimate2621, 2015.
- Meixner, T. and Bales, R. C.: Hydrochemical modeling of coupled C and N cycling in high-elevation catchments: importance of snow cover, *Biogeochemistry*, 62, 289–308, doi:10.1023/A:1021118922787, 2002.
- [Meyerholt, J. and Zaehle, S.: The role of stoichiometric flexibility in modelling forest ecosystem responses to nitrogen fertilization, *New Phytol.*, 208, 1042–1055, doi:10.1111/nph.13547, 2015.](#)
- [Meyerholt, J., Zaehle, S., and Smith, M. J.: Variability of projected terrestrial biosphere responses to elevated levels of atmospheric CO₂ due to uncertainty in biological nitrogen fixation, *Biogeosciences*, 13, 1491–1518, doi:10.5194/bg-13-1491-2016, 2016.](#)
- Naipal, V., Reick, C., Pongratz, J., and Oost, K. V.: Improving the global applicability of the RUSLE model – adjustment of the topographical and rainfall erosivity factors, *Geosci. Model Dev.*, 8, 2893–2913, doi:10.5194/gmd-8-2893-2015, 2015.
- Naipal, V., Reick, C., Van Oost, K., Hoffmann, T., and Pongratz, J.: Modeling long-term, large-scale sediment storage using a simple sediment budget approach, *Earth Surface Dynamics*, 4, 407–423, doi:10.5194/esurf-4-407-2016, 2016.
- New, M., Lister, D., Hulme, M., and Makin, I.: A high-resolution data set of surface climate over global land areas, *Climate Research*, 21, 1–25, doi:10.3354/cr021001, 2002.
- Niu, S., Classen, A. T., Dukes, J. S., Kardol, P., Liu, L., Luo, Y., Rustad, L., Sun, J., Tang, J., Templer, P. H., Thomas, R. Q., Tian, D., Vicca, S., Wang, Y. P., Xia, J., and Zaehle, S.: Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle, *Ecology Letters*, 19, 697–709, doi:10.1111/ele.12591, 2016.
- Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., Ledford, J., McCarthy, H. R., Moore, D. J. P., Ceulemans, R., De Angelis, P., Finzi, A. C., Karnosky, D. F., Kubiske, M. E., Lukac, M., Pregitzer, K. S., Scarascia-Mugnozza, G. E., Schlesinger, W. H., and Oren, R.: Forest response to elevated CO₂ is conserved across a broad range of productivity, *Proceedings of the National Academy of Sciences*, 102, 18 052–18 056, doi:10.1073/pnas.0509478102, <http://www.pnas.org/cgi/doi/10.1073/pnas.0509478102>{%}5Cn<http://www.pnas.org/content/102/50/18052.full>{%}5Cn<http://www.pnas.org/cgi/doi/10.1073/pnas.0509478102>, 2005.

- Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., and McMurtrie, R. E.: CO₂ enhancement of forest productivity constrained by limited nitrogen availability., *Proceedings of the National Academy of Sciences of the United States of America*, 107, 19368–19373, doi:10.1073/pnas.1006463107, 2010.
- Norby, R. J., De Kauwe, M. G., Domingues, T. F., Duursma, R. A., Ellsworth, D. S., Goll, D. S., Lapola, D. M., Luus, K. A., MacKenzie, A. R., Medlyn, B. E., Pavlick, R., Rammig, A., Smith, B., Thomas, R., Thonicke, K., Walker, A. P., Yang, X., and Zaehle, S.: Model-data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments., *The New phytologist*, doi:10.1111/nph.13593, <http://www.ncbi.nlm.nih.gov/pubmed/26249015>, 2015.
- Parida, B. R.: The influence of plant nitrogen availability on the global carbon cycle and N₂O emissions, in: *Berichte zur Erdsystemforschung*, 2011.
- 10 Parton, W. J., Scurlock, J. M. O., Ojima, D. S., Gilmanov, T. G., Scholes, R. J., Schimel, D. S., Kirchner, T., Menaut, J.-C., Seastedt, T. R., Garcia Moya, E., Kamnalrut, A., and Kinyamario, J. I.: Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide, *Global Biogeochemical Cycles*, 7, 785–809, doi:10.1029/93GB02042, 1993.
- Patino, S., Lloyd, J., Paiva, R., Baker, T. R., Quesada, C. A., Mercado, L. M., Schmerler, J., Schwarz, M., Santos, A. J. B., Aguilar, A., Czimeczik, C. I., Gallo, J., Horna, V., Hoyos, E. J., Jimenez, E. M., Palomino, W., Peacock, J., Pena-Cruz, A., Sarmiento, C., Sota, A., 15 Turriago, J. D., Villanueva, B., Vitzthum, P., Alvarez, E., Arroyo, L., Baraloto, C., Bonal, D., Chave, J., Costa, A. C. L., Herrera, R., Higuchi, N., Killeen, T., Leal, E., Luizao, F., Meir, P., Monteagudo, A., Neil, D., Nunez-Vargas, P., Penuela, M. C., Pitman, N., Priante Filho, N., Prieto, A., Panfil, S. N., Rudas, A., Salomao, R., Silva, N., Silveira, M., DeAlmeida, S. S., Torres-Lezama, A., Vasquez-Martinez, R., Vieira, I., Malhi, Y., and Phillips, O. L.: Branch xylem density variations across the Amazon Basin, *BIOGEOSCIENCES*, 6, 545–568, 2009.
- 20 Peri, P. L., Ladd, B., Pepper, D. A., Bonser, S. P., Laffan, S. W., and Amelung, W.: Carbon (?? ¹³C) and nitrogen (?? ¹⁵N) stable isotope composition in plant and soil in Southern Patagonia’s native forests, *Global Change Biology*, 18, 311–321, doi:10.1111/j.1365-2486.2011.02494.x, 2012.
- Prentice, I. C., Liang, X., Medlyn, B. E., and Wang, Y.-P.: Reliable, robust and realistic: the three R’s of next-generation land surface modelling, *Atmospheric Chemistry and Physics Discussions*, 14, 24811–24861, doi:10.5194/acpd-14-24811-2014, <http://www.atmos-chem-phys-discuss.net/14/24811/2014/>, 2014.
- 25 , Pongratz, J., C. Reick, T. Raddatz, and M. Claussen: A reconstruction of global agricultural areas and land cover for the last millennium, *Global Biogeochem. Cycles*, 22, doi:10.1029/2007GB003153, 2008.
- Raddatz, T. J., Reick, C. H., Knorr, W., Kattge, J., Roeckner, E., Schnur, R., Schnitzler, K.-G. G., Wetzels, P., and Jungclaus, J.: Will the tropical land biosphere dominate the climate-carbon cycle feedback during the twenty-first century?, *CLIMATE DYNAMICS*, 29, 565– 30 574, doi:10.1007/s00382-007-0247-8, 2007.
- Rütting, T.: Nitrogen mineralization, not N₂<sub>2</sub><sub>2</sub> fixation alleviates progressive nitrogen limitation – Comment on “Processes regulating progressive nitrogen limitation under elevated carbon dioxide: a meta-analysis” b, *Biogeosciences Discussions*, pp. 1–8, doi:10.5194/bg-2016-456, <http://www.biogeosciences-discuss.net/bg-2016-456/>, 2016.
- [Saugier, B. and Roy, J.: Estimations of global terrestrial productivity: Converging towards a single number?. *Global Terrestrial Productivity: Past, Present and Future*, p. 573, Academic, San Diego, 2001.](#)
- 35 [Schlesinger, W. H.: *Biogeochemistry: An Analysis of Global Change*, ACADEMIC PRESS, San Diego, 2nd editio edn., 1997.](#)
- Schneider Von Deimling, T., Meinshausen, M., Levermann, A., Huber, V., Frieler, K., Lawrence, D. M., and Brovkin, V.: Estimating the near-surface permafrost-carbon feedback on global warming, *Biogeosciences*, 9, 649–665, doi:10.5194/bg-9-649-2012, 2012.

- Schuur, E. a. G., McGuire, a. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., Hugelius, G., Koven, C. D., Kuhry, P., Lawrence, D. M., Natali, S. M., Olefeldt, D., Romanovsky, V. E., Schaefer, K., Turetsky, M. R., Treat, C. C., and Vonk, J. E.: Climate change and the permafrost carbon feedback, *Nature*, 520, 171–179, doi:10.1038/nature14338, <http://www.nature.com/doi/10.1038/nature14338>, 2015.
- 5 Shi, Z., ~~Sherry, R., Xu Yang, Y., Zhou, X., Hararuk, O., Souza, L., Jiang, L., Xia Weng, E., Finzi, A. C., and Luo, Y.:~~ [Inverse analysis of coupled carbon-nitrogen cycles against multiple datasets at ambient and elevated CO₂](#), *J. Plant Ecol.*, 9, ~~Liang~~285–295, doi:10.1093/jpe/rtv059, 2016.
- ~~Smith, B., Wärlind, D., Arneith, A., Hickler, T., Leadley, P., Siltberg, J., and Luo, Y.~~ [Zaehle, S.: Evidence for long-term shift in plant community composition under decadal experimental warming](#) [Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model](#), *Journal of Ecology*, 103, 1131–1140, 2015. *Biogeosciences*, 11, 2027–2054, doi:10.5194/bg-11-2027-2014, <http://www.biogeosciences.net/11/2027/2014/>, 2014.
- 10 Sommer, J., Pausch, J., Brundrett, M. C., Dixon, K. W., Bidartondo, M. I., and Gebauer, G.: Limited carbon and mineral nutrient gain from mycorrhizal fungi by adult Australian Orchids, *American Journal of Botany*, 99, 1133–1145, doi:10.3732/ajb.1100575, 2012.
- Sullivan, B. W., Smith, W. K., Townsend, A. R., Nasto, M. K., Reed, S. C., Chazdon, R. L., and Cleveland, C. C.: Spatially robust estimates of biological nitrogen (N) fixation imply substantial human alteration of the tropical N cycle., *Proceedings of the National Academy of Sciences of the United States of America*, 111, 8101–6, doi:10.1073/pnas.1320646111, <http://www.ncbi.nlm.nih.gov/pubmed/24843146>, 2014.
- Taylor, K. E.: Summarizing multiple aspects of model performance in a single diagram, *Journal of Geophysical Research*, 106, 7183–7192, 2001.
- 20 Taylor, K. E., Stouffer, R. J., and Meehl, G. a.: An Overview of CMIP5 and the Experiment Design, *Bull. Am. Meteorol. Soc.*, 93, 485–498, doi:10.1175/BAMS-D-11-00094.1, <http://journals.ametsoc.org/doi/abs/10.1175/BAMS-D-11-00094.1>, 2012.
- Thomas, R. Q., Zaehle, S., Templer, P. H., and Goodale, C. L.: Global patterns of nitrogen limitation: Confronting two global biogeochemical models with observations, *Global Change Biology*, 19, 2986–2998, doi:10.1111/gcb.12281, 2013.
- ~~Thomas, R. Q., Brookshire, E. J., and Gerber, S.:~~ [Nitrogen limitation on land : How can it occur in Earth System Models ?](#), *Glob. Chang. Biol.*, doi:10.1111/gcb.12813, 2015.
- 25 Thornton, P. E., Rosenbloom, N. a., Mahowald, N. M., Lamarque, J. F. J.-F., Rosenbloom, N. a., and Mahowald, N. M.: Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability, *GLOBAL BIOGEOCHEMICAL CYCLES*, 21, 1–15, doi:10.1029/2006GB002868, 2007.
- Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E. a. G., and Allison, S. D.: Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations, *Biogeosciences*, 10, 1717–1736, doi:10.5194/bg-10-1717-2013, <http://www.biogeosciences.net/10/1717/2013/>, 2013.
- 30 Todd-Brown, K. E. O., Randerson, J. T., Hopkins, F., Arora, V., Hajima, T., Jones, C., Shevliakova, E., Tjiputra, J., Volodin, E., Wu, T., Zhang, Q., and Allison, S. D.: Changes in soil organic carbon storage predicted by Earth system models during the 21st century, *Biogeosciences*, 11, 2341–2356, doi:10.5194/bg-11-2341-2014, <http://www.biogeosciences.net/11/2341/2014/>, 2014.
- 35 Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., and Liski, J.: Heterotrophic soil respiration—Comparison of different models describing its temperature dependence, *Ecological Modelling*, 211, 182–190, doi:10.1016/j.ecolmodel.2007.09.003, <http://linkinghub.elsevier.com/retrieve/pii/S030438000700453X>, 2008.

- Tuomi, M., Thum, T., Järvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofymow, J., Sevanto, S., and Liski, J.: Leaf litter decomposition—Estimates of global variability based on Yasso07 model, *Ecological Modelling*, 220, 3362–3371, doi:10.1016/j.ecolmodel.2009.05.016, <http://linkinghub.elsevier.com/retrieve/pii/S030438000900386X>, 2009.
- Tuomi, M., Laiho, R., Repo, A., and Liski, J.: Wood decomposition model for boreal forests, *Ecological Modelling*, 222, 709–718, doi:10.1016/j.ecolmodel.2010.10.025, <http://linkinghub.elsevier.com/retrieve/pii/S0304380010005855>, 2011.
- Viani, R. A. G., Rodrigues, R. R., Dawson, T. E., and Oliveira, R. S.: Functional differences between woodland savannas and seasonally dry forests from south-eastern Brazil: Evidence from 15N natural abundance studies, *Austral Ecology*, 36, 974–982, doi:10.1111/j.1442-9993.2010.02233.x, 2011.
- [Vicca, S., Luyssaert, S., Peñuelas, J., Campioli, M., Chapin, F. S., Ciais, P., Heinemeyer, A., Högberg, P., Kutsch, W. L., Law, B. E., Malhi, Y., Papale, D., Piao, S. L., Reichstein, M., Schulze, E. D., and Janssens, I. A.: Fertile forests produce biomass more efficiently, *Ecol. Lett.*, 15, 520–526, doi:10.1111/j.1461-0248.2012.01775.x, 2012.](#)
- Vitousek, P. M., Menge, D. N. L., Reed, S. C., and Cleveland, C. C.: Biological nitrogen fixation: rates, patterns and ecological controls in terrestrial ecosystems., *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368, 20130 119, doi:10.1098/rstb.2013.0119, <http://www.ncbi.nlm.nih.gov/pubmed/23713117>, 2013.
- Wang, Y.-P. P., Law, R. M., and Pak, B.: A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere, *Biogeosciences*, 7, 2261–2282, doi:10.5194/bg-7-2261-2010, 2010.
- Warland, D., Smith, B., Hickler, T., and Arneth, A.: Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model, *Biogeosciences*, 11, 6131–6146, doi:10.5194/bg-11-6131-2014, 2014.
- Weedon, G. P., Gomes, S., Viterbo, P., Shuttleworth, W. J., Blyth, E., Österle, H., Adam, J. C., Bellouin, N., Boucher, O., and Best, M.: Creation of the WATCH Forcing Data and Its Use to Assess Global and Regional Reference Crop Evaporation over Land during the Twentieth Century, *Journal of Hydrometeorology*, 12, 823–848, doi:10.1175/2011JHM1369.1, <http://journals.ametsoc.org/doi/abs/10.1175/2011JHM1369.1>, 2011.
- Wieder, W. R., Cleveland, C. C., Smith, W. K., and Todd-Brown, K.: Future productivity and carbon storage limited by terrestrial nutrient availability, *Nature Geoscience*, 8, 1–15, doi:10.1038/ngeo2413, <http://www.nature.com/doi/abs/10.1038/ngeo2413>, 2015.
- Xu-Ri, Prentice, I. C., and Academy, C.: Terrestrial nitrogen cycle simulation with a dynamic global vegetation model, *Global Change Biol.*, 14, 1745–1764, doi:10.1111/j.1365-2486.2008.01625.x, <http://dx.doi.org/10.1111/j.1365-2486.2008.01625.x>, 2008.
- Yi, X. and Yang, Y.: Independence of alpine meadow plants from soil organic matter for nitrogen supply: evidence from stable nitrogen isotopes, *Isotopes in environmental and health studies*, 43, 51–56, 2007.
- [Zaehle, S., Friend, A. D., Friedlingstein, P., Dentener, F., Peylin, P., Schulz, M., and Cleve, V.: Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance, *Global Biogeochem. Cycles*, 24, 1–14, doi:10.1029/2009GB003522, 2010.](#)
- Zaehle, S.: Terrestrial nitrogen - carbon cycle interactions at the global scale, *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368, doi:<http://dx.doi.org/10.1098/rstb.2013.0125>, 2013.
- Zaehle, S., Jones, C. D., Houlton, B., Lamarque, J.-F., and Robertson, E.: Nitrogen availability reduces CMIP5 projections of 21st century land carbon uptake, *Journal of Climate*, doi:10.1175/JCLI-D-13-00776.1, <http://journals.ametsoc.org/doi/abs/10.1175/JCLI-D-13-00776.1>, 2014.
- Zaehle, Sönke, Medlyn, Belinda E, De Kauwe, Martin G, Walker, Anthony P, Dietze, Michael C, Hickler, Thomas, Luo, Yiqi, Wang, Ying-Ping, El-masri, Bassil, Thornton, Peter, Jain, Atul, Wang, Shusen, Warland, David, Weng, Ensheng, Parton, William, Iversen, Colleen

M, Gallet-budynek, Anne, Mccarthy, Heather, Finzi, Adrien C., Hanson, Paul J., Prentice, Iain Colin, Oren, Ram, and Norby, Richard J.: Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO₂ Enrichment studies, *New Phytologist*, doi:10.1111/nph.12697, 2014.

5 Zhang, L., Hickel, K., Dawes, W. R., Chiew, F. H. S., Western, A. W., and Briggs, P. R.: A rational function approach for estimating mean annual evapotranspiration, *Water Resources Research*, 40, 1–14, doi:10.1029/2003WR002710, 2004.

[Zhu, Q. and Riley, W. J.: Improved modelling of soil nitrogen losses, *Nat. Clim. Chang.*, 5, 705–706, doi:10.1038/nclimate2696, http://www.nature.com/nclimate/journal/v5/n8/full/nclimate2696.html, 2015.](https://doi.org/10.1038/nclimate2696)