

Response to reviewer #1

Major concerns:

I appreciate that this is largely a model development and documentation paper, but found some of the discussion surrounding main display items rather hasty and lacking appropriate depth. For example, the spatial patterns of N limitation (Fig. 8) suggest that both tropical and boreal forests are not N limited (indeed, forests globally may have a low sensitivity to N availability)? This is just one example, but on revisions I would encourage the authors to unpack and explore their findings a bit more. Take the opportunity to call out strengths and weaknesses in the current approach and discuss particular model assumptions that are responsible for these features. This doesn't have to be exhaustive, but will help add depth to the results and discussion.

Page 1, Line 6. Significant improvements in crop yields are not apparent in the updated Fig. 10 and SI material uploaded by the authors. Would a plot of global crop yields vs. observations make this point more clearly? If crop model improvements are the big advancement in the current model development, I'd encourage more attention be given to establishing these improvements in the main text. That said, the estimates of N losses (through leaching and N₂O emissions) also have important regional and global consequences and seem to be done well in this version of the model. Should these accomplishments be highlighted in the abstract too?

Answer: The results section has been expanded. We have now structured results into 3 sections: Carbon pools and fluxes, Nitrogen pools and fluxes, Land use and nitrogen dynamics. In particular, Taylor diagrams of regional crop productivities have been added to the manuscript and supplement. They clearly indicate that significant parts of the calibration previously needed are now no longer necessary, as N limitation already reduces simulated crop yields in low-input countries. The strong influence of land use on nitrogen losses is now mentioned in the abstract.

Minor comments

P1, L 8. This suggest the is still scaling occurring in regions with favorable climate and N inputs? Is this true?

Answer: Scaling of yields has still to be done for regions where climate and nitrogen supply are not the main limiting factor, but, e.g. phosphorus, poor pest management or other management aspects not explicitly considered in the model as now mentioned in section 4.4.3.

P1, L 18 Zaehle and co-authors (2015) made similar findings, seems worth citing here? Throughout section 2 is it worth briefly distinguishing the similarities and differences in the approach taken with LPJmL vs. other land models, especially LPJguess (Smith et al 2014) which is referenced throughout?

Answer: In fact, nitrogen dynamics have been incorporated in many other dynamical vegetation models (as described on P1, L22). As LPJ-GUESS, our model considers not only natural vegetation but

also takes into account managed crops. In contrast to LPJ-GUESS nitrogen transformation in soils are simulated in a more sophisticated way in LPJmL5, including immobilization of nitrogen. This is now specified in the introduction and model description.

P4, L 6. It seems odd to introduce table 2 before table 1. Similarly, table 4 is introduced before table 3 (page 7).

Answer: The order of tables has been changed following the suggestions of the referee.

Section 2.2. Is the soil biogeochemistry for this version of the model vertically resolved, as implied with e.g. 7? If so should this be mentioned in section 2: model description?

Answer: Soil processes are vertically resolved in 6 soil layers. A sentence has been added to the model description.

Eq. 13-14, could pft specific root distribution parameters be easily described in the current tables or included elsewhere?

Answer: The parameterization of PFT-specific root distribution is now described in the paper and the corresponding parameters included in Table 2.

P5, L 27. As written this sounds like rates of GPP are reduced by respiration rates? This strikes me as strange. Wouldn't autotrophic respiration be subtracted from GPP to calculate NPP rates (eq. 18). This also isn't clear in Fig 1

Answer: Indeed, for calculating NPP, respiration has to be subtracted from GPP but GPP itself is not directly reduced. This has been clarified in section 2.4. In figure 1, GPP (flux) is not shown, but the process (photosynthesis).

Figure 3: check to see the colors for each arrow are labeled correctly and/or defined. Alternatively, the approach here seems pretty standard, I wonder if the distracting rainbow of flux arrows are really necessary?

Answer: Indeed, the approach is based on standard implementations. We find a colored scheme more helpful than a black-and-white figure but acknowledge that others may have other color preferences. The boxes, however, are now colored in black.

Section 2.6 How are all the competing fates of inorganic N solved (e.g. sequentially, simultaneously, etc)?

Answer: The transformation of nitrogen is calculated in sequential order as now stated in section 2.6.

Section 2.6. Are litter and SOM pools have a fixed C:N ratio or are they flexible (w/in bounds).

Answer: Litter and SOM pools have flexible C:N ratios now explicitly stated in section 2.6.

P 15 L 23 What is a “nodulating leguminous crops pulses”, the phrase seems redundant? Maybe just use “soybeans and pulses”.

Answer: There are non-nodulating legumes (doi:10.14719/pst.2015.2.2.97) as well as non-nodulating soybean varieties (doi:10.1007/978-94-009-4482-4_19) and we wanted to make clear that we're considering these leguminous crops as nodulating varieties with capacities to fix nitrogen.

P17, line 13. What happens to the other 40% of the manure? Is it not really applied, or does it go into SON pools?

Answer: No, the data from Elliott et al. (2015) only provide mineral reactive N forms. In their data set, only the plant available fraction (60% of manure) is specified, the rest is ignored. This is now clarified in the text.

Section 3. What spatial resolution are these simulations? Does each grid cell have a single pft, or is there subgrid variability of vegetation? If there is subgrid PFT variation, do all plants share a soil column, or do they each have individual columns (that is, does manure and fertilizer applied stay on crop only soils, or is it available to plants throughout the grid)?

Answer: Simulations are carried out for a resolution of 0.5 x 0.5°. PFTs can be established concurrently within a cell competing for light, water and nitrogen sharing the same soil resources. This has been explained in more detail in the paper.

Table 4: Although they are described in the main text (section 3) the abbreviations for experiments used in column headings are non-intuitive enough to prevent the information contained in the display item from standing on its own. Consider adding text to the table heading or columns to make these data more understandable.

Answer: The table captions now include an explanation of the different suffixes for the abbreviations of the experiments.

Table 4. I'm surprised global NO₃ pools are an order of magnitude larger than the NH₄ pools. I wonder if there is spatial structure to these patterns (e.g. accumulation of NO₃ in warm or arid regions), or if the patterns are relatively globally distributed. Regardless, it seems surprising given the relatively high mobility and multiple loss pathways of NO₃, compared with NH₄, and suggests that nitrification rates may be too high in the model? Alternatively, decomposition rates may be high, supplying excess inorganic N, or plant NO₃ uptake may be underestimated? This may be worth mentioning in the discussion (section 4.1.1 or 5)?

Answer: This is indeed discussed in section 4.1.1 and we have now expanded this discussion. NH₄ is constantly converted to NO₃ by nitrification, a microbe-mediated process under aerobic conditions, which are often prevailing. NO₃ is lost via leaching or denitrification, again a microbe-mediated process but under anaerobic conditions, which are not dominant conditions in most soils. As a consequence, NO₃ concentrations are typically much higher than NH₄ concentrations, unless N is limiting plant uptake, see e.g. Kabala et al. (2017). Also, NO₃ is accumulated in lower soil layers, despite leaching losses. This phenomenon is reported by Walvoord et al. (2003) and Ascott et al.

(2017) and reproduced by the model. Still, this nitrogen is mostly unavailable to plants, as these have little root access to the lower soil layers at 3m depth. This is now discussed in the paper.

P 18 L 8 Why are agricultural lands (that are presumably being fertilized) becoming increasingly N limited? Is there some metric of N limitation that can illustrate this point more directly, as it's not intuitive from Fig 4a,b. Also, it seems odd to increase carbon use efficiency (NPP:GPP) if the system is becoming more N limited? I see how it occurs in the model, because of higher tissue C:N ration and lower RA costs, but is it ecologically realistic?

Answer: In the simulations, plant growth is enhanced through CO₂ fertilization, whereas fertilizer inputs are static. Also, cropland expansion over the 20th century dominantly expands in areas where fertilizer inputs per hectare are low. As such, the global average fertilizer amount (kg N per hectare) declines. This is now also briefly described in the text (section 4.4.3).

The relationship of RA costs on C:N ratios is well established and was already implemented in the carbon-only model version. There plant organs had a static prescribed C:N ratio that determined respiration costs for maintenance.

Fig 4. How were relative GPP changes calculated, I didn't see this described in the text? Also, consider adding information about line colors to the figure caption, as the legend insets are very small and hard to read.

Answer: Relative changes are calculated by dividing the values by their 1901-1910 average as now stated in the figure caption. The meaning of the different colors in the figures is now explained in the figure caption.

Fig. 4 It looks like the two control models (3.5 and 5) lose vegetation and soil C throughout the 20th century, but GCP data suggests the land surface should be a C sink, at least over then end of the 20th century (e.g., LeQuere et al, 2015). Given increases in plant productivity in Fig 4a,b- this suggests the land use C change flux must be pretty large?

Answer: Yes, see also Table 3 where the NBP (net biome productivity) is listed. For natural vegetation (LPJmL3.5_PNV and LPJmL5_PNV), the terrestrial biosphere is a net carbon sink of about 1.5 and 1.7 PgC/yr, whereas when accounting for current land-use patterns (LPJmL3.5 and LPJmL5), the terrestrial biosphere is a net source.

P 18 L 15. Where is the data showing that N limitation increases by a factor of two? How is N limitation being assessed in this statement?

Answer: In fact, the statement is misleading and has been omitted from the manuscript.

P 18 L 16. What's causing the higher leaching losses with the control model? Does it have to do with vegetation demand for N, rooting profiles of managed vegetation, or other factors?

Answer: The higher leaching under land use is caused by the additional fertilizer input and the irrigation water application under land use, which do not occur in natural vegetation. This is now explained in the text (section 4.3).

Table 4. It's it worth discussing limitations (or uncertainties) of some of the 'observational' estimates presented here

Answer: This discussion is placed in section 4.1.1 and we have extended this now. Certainly, estimates based on only one other model have no value for a model evaluation and only serve as a point of reference.

Fig 6. Agreement on crop C:N ratios doesn't seem that surprising, given the ranges for leaf C:N and allocation that are proscribed in the model (Tables 1,2) . I'm assuming the values for R3 in Table 2 were tuned to provide the spread shown in Fig 6? This is fine, but should be acknowledged. In the text.

Answer: In fact, R3 values were calibrated to the observed values. The approximated relationships between leaf C:N ratios and storage organ C:N ratios based on Bodirsky (2012) lead to consistent but variable C:N ratios in harvested crop organs, as stated in the manuscript.

Fig 7a, it strikes me as odd to have low values (<1) indicative of high leaching losses, especially when points above the 1:1 line show areas of high leaching under present vegetation (fig 7b)

Answer: Values <1 in Fig7a indicate regions where leaching of the potential natural vegetation is less than with land use. This corresponds to points Fig 7b above the 1:1 line. It is not useful to define the ratio the other way round, as leaching under natural vegetation can be very small but very large under land use (irrigation, fertilizer input). We have swapped the x and y axis in Fig7b. Now points are below the 1:1 in panel b for values <1 in panel a. This has been also applied for Fig8.

Fig 9, where do the obs come from- especially for NPP and Veg C. Is each point supposed to represent an individual sites? This are from the same FluxNet sites as in the SI figures? Also, where do the observational error bars come from & how were they calculated? Finally, should correlation coefficients & significance be reported?

Answer: The missing reference to the observational data has been added to the manuscript. The horizontal bars denote the minima and maxima of observed data belonging to the same LPJ grid cell.

Section 4.1.3 Where are the LAI data shown that the addition of N biogeochemistry supposedly fixes? If this is the big advancement with the model presented here should these data also be shown? Is it just the addition of N biogeochemistry that's responsible for the proported improvements, or were other parametric or structural changes made?

Answer: In previous versions without accounting for nitrogen dynamics, the intensity of crop production had been calibrated by scaling the maximum LAI value, the harvest index and the factor for scaling leaf-level photosynthesis to stand level (α_a) of each crop at the national scale as described in Fader et al. (2010). Without this calibration, yield levels are typically overestimated, especially in low-input regions (blue lines in Figures 10, S21-23). Significant parts of this calibration

are now no longer necessary, as N limitation already reduces simulated crop yields in low-input countries. However, the N limitation is not the only mechanism that leads to lower crop yields, so that a further calibration could be performed. However, we did not calibrate yields here to show that N limitation already leads to a better representation of low-input crop production. This is now better discussed in the text (now section 4.4.3).

Fig. 10 A bunch of questions: What are the residuals and how are they calculated? What are units for the y-axis (what is the 'FM')? What are the little numbers in the top of each panel showing? Finally, it looks like global maize production increases over the period shown but the models are all flat. What's driving the increase in yields that the model is apparently missing? Is this true for other major crops?

Answer: FM depicts "fresh matter" (as used for all data reported by the FAOstat) and tFM stands for ton fresh matter and is now explained in the figure caption. The residuals are the detrended observed and simulated values, by subtracting a moving average as described by Müller et al. (2017). The numbers in the panels show the correlation coefficients between the residuals of the FAO-stat data and the residuals of the simulation (dashed lines). This is now also explained in the text. Indeed, simulated crop yields show no trend, as all management assumptions (including fertilizer input) are static, whereas technological advances are driving the observed yield trend. This is now also discussed in the text.

P 26 L 4, What improvements are necessary? What additional complexity may improve things further? What data are critical to getting terrestrial C-N dynamics less wrong? As presented these are kind of empty / throwaway statements. Can the be flushed out with some more detail, both in the main text and in this summary conclusion?

Answer: Thanks for pointing this out. We now discuss further possible improvements in more detail, mainly incorporating aspects that have been implemented in parallel in the carbon-only version (LPJmL4.0, Schaphoff et al. 2017a,b), such as the improved tree phenology, but also more detail in the representation of agricultural management, such as tillage, or fertilizer type and timing.

References in answers:

Ascott, MJ, DC Gooddy, L Wang, ME Stuart, MA Lewis, RS Ward, and AM Binley. 2017, Global patterns of nitrate storage in the vadose zone, *Nat. Commun.*, 8, 1416, doi: 10.1038/s41467-017-01321-w.

Fader, M, S Rost, C Müller, A Bondeau, and D Gerten. 2010, Virtual water content of temperate cereals and maize: Present and potential future patterns, *Journal of Hydrology*, 384, 218-231, doi: 10.1016/j.jhydrol.2009.12.011.

Kabala, C, A Karczewska, B Galka, M Cuske, and J Sowinski. 2017, Seasonal dynamics of nitrate and ammonium ion concentrations in soil solutions collected using MacroRhizon suction cups, *Environ Monit Assess*, 189, 304, doi: 10.1007/s10661-017-6022-3.

Müller, C, J Elliott, J Chryssanthacopoulos, A Arneth, J Balkovic, P Ciais, D Deryng, C Folberth, M Glotter, S Hoek, T Iizumi, RC Izaurralde, C Jones, N Khabarov, P Lawrence, W Liu, S Olin, TAM Pugh, DK Ray, A Reddy, C Rosenzweig, AC Ruane, G Sakurai, E Schmid, R Skalsky, CX Song, X Wang, A de Wit, and H Yang. 2017, Global gridded crop model evaluation: benchmarking, skills, deficiencies and implications, *Geosci. Model Dev.*, 10, 1403-1422, doi: 10.5194/gmd-10-1403-2017.

Schaphoff, S, M Forkel, C Müller, J Knauer, W von Bloh, D Gerten, J Jägermeyr, W Lucht, A Rammig, K Thonicke, and K Waha. 2017, LPJmL4 - a dynamic global vegetation model with managed land: Part II – Model evaluation, *Geosci. Model Dev. Discuss.*, 2017, 1-41, doi: 10.5194/gmd-2017-146.

Schaphoff, S, W von Bloh, A Rammig, K Thonicke, H Biemans, M Forkel, D Gerten, J Heinke, J Jägermeyr, J Knauer, F Langerwisch, W Lucht, C Müller, S Rolinski, and K Waha. 2017, LPJmL4 – a dynamic global vegetation model with managed land: Part I – Model description, *Geosci. Model Dev. Discuss.*, 2017, 1-59, doi: 10.5194/gmd-2017-145.

Walvoord, MA, FM Phillips, DA Stonestrom, RD Evans, PC Hartsough, BD Newman, and RG Striegl. 2003, A Reservoir of Nitrate Beneath Desert Soils, *Science*, 302, 1021.

References: Le Quéré C, et al. (2015) Global Carbon Budget 2015. *Earth System*

Science Data 7: 349-396. DOI:10.5194/essd-7-349-2015

Smith et al. (2014) Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model, *Biogeosciences*, 11, 2027-2054, doi:10.5194/bg-11-2027-2014.

Zaehle, et al. (2015). Nitrogen availability reduces CMIP5 projections of twenty-first century land carbon uptake. *Journal of Climate* 28.6: 2494-2511.

Interactive comment on *Geosci. Model Dev. Discuss.*, <https://doi.org/10.5194/gmd-2017-228>, 2017.

Response to reviewer #2

1. The results part before section 4.1 presents the comparison between outputs from global simulations with various model versions and setups with some interesting findings. However, the section is hard to follow without clear organization of the results, and some interesting findings and important characteristics are presented without proper investigations/explanations. I would suggest authors to make it a sub-section with clearer titles/points indicating the major content of each paragraph. A little deeper investigations or more detailed explanations on the differences between versions/setup would be preferable. In addition, model versions/setup should always be presented along with results (sometimes, it is missing).

Answer: The results section has been restructured and expanded. We have now structured the results into 3 sections: Carbon pools and fluxes, Nitrogen pools and fluxes, Land use and nitrogen dynamics. A new figure plotting Taylor diagrams of regional crop yields have been added to support our findings.

2. Section 4.1.1 and 4.1.2 present the comparison of N and C pools/fluxes at both site-level and globally against literature values. Besides comparing values, some more explanations/discussions in the differences/discrepancies could be helpful for readers to understand the model performance.

Answer: We have expanded the discussion of model results in various aspects e.g. by specifying better the effects of human land use, see also responses to concerns of reviewer #1.

3. The authors present the improvement in simulating crop productivity by model developed in this study very briefly in Section 4.1.3, while it was shown as major results consisting almost half of the Abstract, which might make readers think the evaluation is only done for crop productivity. Even it is the major part of evaluation, I actually did not get the 'improvements' that authors claimed from the text. Though model results and its comparison with data were shown in Fig. 10 and lots of SI Figures, readers can only get little information on the model performance and the improvement due to implementation of N cycle (at least for me). With comparison on many sites, no statistical synthesis of the performance (no numbers), and no further investigations on 'how and why' were shown in the text. It is necessary/critical to show quantitatively how the improvement can be supported by the results. It is not the job of readers to check every figure, compare the lines, and draw the conclusion. In addition, there is no line for LPJmL3.5 in SI Fig. S5-S20, how the 'improvements' can be seen?

Answer: We have now computed the average Willmott coefficients for the NEE and evaporation sites to get a quantitative estimate about the quality of our model. Also, we have extended the discussion on the crop model performance and added an additional figure to the main text and 3 more to the supplementary material. See also answer to the detailed point below.

4. The authors tried to discuss the improvements and limitations of this study in 'Discussion and conclusions' section. But it is lack of clear structure. A synthesis of limitation might be helpful (e.g., listing limitations points by points at first).

Answer: LPJmL5 lifts a major limitation of LPJmL3.5, which is the omission of nitrogen limitations in the simulation of plant growth and biogeochemical cycles. The implementation is based on well-established process descriptions reducing limitations in the form of assumptions to the former version..

Minor comments (there might be some duplicate points as some listed above):

P18L1-3: Need to indicate the results come from which version/setup. The means of red/yellow lines were opposite in the text and the figure.

Answer: The means of yellow/red lines is now in line with the figure.

Fig. 4: It is necessary to show LPJmL35-PNV too. All lines in the figures of this manuscript should be drawn with thicker lines.

Answer: LPJmL35-PNV has been added to Fig. 4 and line widths have been chosen thicker.

P18L14: It seems not 'quite stable' and not 'slightly increase' in Fig. 5. And how the factor of 2 be derived?

Answer: The terms "quite stable" and "slightly "increase" have been replaced by quantitative numbers. In fact it is unclear how the factor 2 has been derived. The statement has been omitted from the manuscript.

P18L22: Please give model setup.

Answer: The model setup of the experiments is explained in the model setup section on page 16.

P20L9-10:

What ratio? It is not clear. It would be necessary to explain why the ratios above 1 can occur. P21L9-13: I don't understand these 3 sentences. What's the meaning?

Answer: Relative changes are calculated by dividing the values by their 1901-1910 average as now stated in the figure caption. If, e.g. GPP is higher than in the reference period, ratios >1 can occur.

Figure 9: Please indicate the data sources for the observed values.

Answer: A reference to the observed values has been added to the manuscript

P23L5: It is necessary to show in SI figures the LPJmL3.5 output for a real comparison.

Answer: We refer to the supplement of the evaluation paper of LPJmL4, where NEE and evaporation values are shown for all sites. A reference on page 23 has been added. The average of Willmott coefficient is shown for LPJmL4 and LPJmL5 to allow a more quantitative comparison.

P23L9: Please indicate what is 'satisfying', is there any indicators to draw this conclusion?

Answer: We show now a quantitative estimate by using the Willmott coefficient of agreement.

P24L5: Please indicate where the climate conditions are not the only yield limiting factors.

Answer: Crop yields can be limited by climatic conditions or nutrient supply, but also by outbreaks of pests and diseases, unstable social condition and others. We have added pest management as an example to the text.

Sect. 4.1.3:

Please indicate how well the model performance. We can get nothing from the text.

Answer: We have now extended the discussion and included an additional figure on crop performance in the main text and 3 in the supplementary document. As for all other crop models, crop model performance compared to FAO-stat data is very diverse and there is no single metric that would describe it well. The now added Taylor diagram may be the best single indicator that covers a broad range of aspects. The full crop model evaluation with the online tool at <https://mygeohub.org/tools/ggcmevaluation> is included as a zip file in the online material.

Implementing the Nitrogen cycle into the dynamic global vegetation, hydrology and crop growth model LPJmL (version 5)

Werner von Bloh¹, Sibyll Schaphoff¹, Christoph Müller¹, Susanne Rolinski¹, Katharina Waha^{1,2}, and Sönke Zaehle³

¹Potsdam Institute for Climate Impact Research, P.O. Box 60 12 03, 14412 Potsdam, Germany

²CSIRO Agriculture & Food, 306 Carmody Rd, St. Lucia QLD 4067, Australia

³Max Planck Institute for Biogeochemistry, P.O. Box 60 01 64, 07701 Jena, Germany

Correspondence to: Werner von Bloh (bloh@pik-potsdam.de)

Abstract. The well-established dynamical global vegetation, hydrology, and crop growth model LPJmL is extended by a terrestrial nitrogen cycle to account for nutrient limitations. In particular, processes of soil nitrogen dynamics, plant uptake, nitrogen allocation, response of photosynthesis and maintenance respiration to varying nitrogen concentrations in plant organs, and agricultural nitrogen management are included into the model. All new model features are described in full detail and results of a global simulation of the historic past (1901-2009) are presented for evaluation of the model performance. We find that implementation of nitrogen limitation significantly improves the simulation of global patterns of crop productivity. Regional differences in crop productivity, which had to be calibrated via a scaling of the maximum leaf area index can now largely be reproduced by the model, except for regions where fertilizer inputs and climate conditions are not the yield limiting factors. [Furthermore it can be shown that land use has a strong influence on the nitrogen losses increasing leaching by 60%.](#)

1 Introduction

Dynamics of the terrestrial biosphere and the associated terrestrial carbon cycle are of central importance for Earth System science. Climate-carbon cycle feedbacks have become integral parts of Earth System Models (ESMs) for climate change projections. However, the terrestrial carbon cycle dynamic are not only driven by climate and carbon dioxide (CO₂) fertilization (Schimel et al., 2015; Norby et al., 2005), but also by land-use change (Müller et al., 2006, 2016; Arneth et al., 2017; Le Quéré et al., 2016) and vegetation dynamics (Müller et al., 2016, and references therein). Nutrient limitations, especially from nitrogen, are also important constraints on vegetation growth and the terrestrial carbon cycle: Smith et al. (2016) [and Zaehle et al. \(2015\)](#) suggested that Earth System Models contributing to the CMIP5 data archive overestimate the response of net primary productivity to elevated CO₂ because the models largely miss the constraints from nutrient limitation. Also Wieder et al. (2015) find that nitrogen limitation may substantially reduce projected increases in net primary productivity (NPP) under climate change and elevated atmospheric CO₂ concentrations ([CO₂]), possibly even converting the terrestrial biosphere into a net carbon source by the end of the 21st century. Over the last decade, nitrogen limitation has been increasingly accounted for in dynamic global vegetation (DGVM) and ESMs (Thornton et al., 2007; Gerber et al., 2010; Zaehle et al., 2010b; Smith et al., 2014). The Lund Potsdam Jena managed Land (LPJmL) dynamic global vegetation, hydrology and crop growth

model has been widely applied to research questions on the terrestrial carbon cycle, hydrology and agricultural production (Schaphoff et al., 2017b, and references therein) and performed similar to other dynamic vegetation models (Friend et al., 2014; Warszawski et al., 2013; Chang et al., 2017), hydrology models (Schewe et al., 2014) and crop models (Müller et al., 2017). However, LPJmL so far did not explicitly account for nutrient limitations. We here extend the LPJmL model to cover the
5 terrestrial nitrogen cycle, by explicitly adding processes of soil nitrogen dynamics, plant uptake, nitrogen allocation, response of photosynthesis and maintenance respiration to variable nitrogen concentrations in plant organs, and agricultural nitrogen management. Our implementation is based on previous model implementations, but soil processes are e.g. more complex than in Smith et al. (2014) and LPJmL is the only dynamic global vegetation model that explicitly covers natural vegetation, managed crop- and grasslands and the full terrestrial hydrology in one consistent modeling framework (Schaphoff et al., 2017b, a). We
10 describe all new model features in full detail and present results of a global simulation of the historic past (1901-2009) that we use to evaluate model performance.

2 Model description

The Model description focuses on the nitrogen (N) dependent part of the model. A general description of the LPJmL model is supplied by Sitch et al. (2003); Bondeau et al. (2007); Schaphoff et al. (2017b, a). Note that Schaphoff et al. (2017b, a)
15 provide the most comprehensive model description available, which includes a few model features that have been added to the model after the development of the N modules had begun and which are thus not part of the ~~LPJmL-5~~ LPJmL5 version described here. These include several minor amendments of the code as well as the updated grass allocation scheme ~~(?)~~ (Rolinski et al., 2018) and the updated phenology scheme for the natural vegetation (Forkel et al., 2014).

In the ~~predecessor version LPJmL-3.5~~ LPJmL model vegetation is represented by different plant functional types (PFTs)
20 which can establish concurrently within a cell. These established PFTs share the same soil stand and compete for light, water and nitrogen resources, while crop functional types (CFTs) are established exclusively at sowing on their own soil stand.

In the predecessor version LPJmL3.5, all organic matter pools (vegetation, soil) were represented as carbon pools. We now also implemented a corresponding N pool for each of these carbon pools as well as pools for inorganic reactive N forms (NH_4^+ , NO_3^-) in the soil (Fig. 1). ~~In~~ Nitrogen dynamics have been incorporated in other dynamical vegetation models, e.g.,
25 in LPJ-GUESS (Zaehle et al., 2010a). In addition to LPJ-GUESS our model considers not only natural vegetation but also takes into account managed crops. Furthermore nitrogen transformation in soils are simulated in a more sophisticated way incorporating immobilization of nitrogen. In the following sections we describe the implementation of the plants' N demand, uptake, allocation, the effects of N limitation on photosynthesis and maintenance respiration as well as N inputs, transformations and losses in/from soils. All processes are computed at a daily time step, except for fire events (annual) and the allocation
30 of carbon and N in plants, which is computed daily only for crops but annually for natural vegetation and before each harvest event for managed grasslands. Soil processes are vertically resolved in 6 soil layers including one bedrock layer.

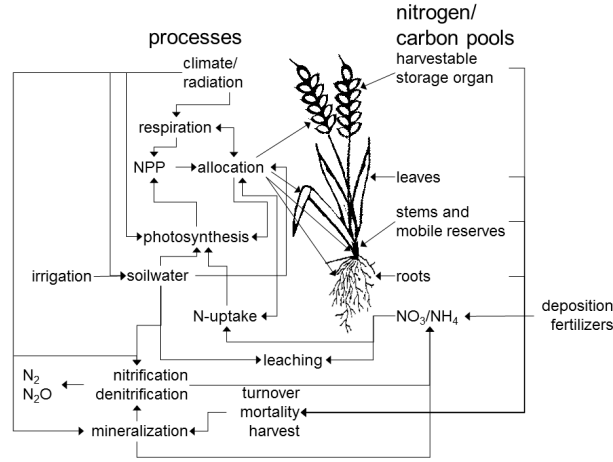


Figure 1. Carbon and nitrogen pools and associated processes for the example of crops.

2.1 Nitrogen demand

Daily photosynthesis and monthly maximum carboxylation capacity (V_{\max}) are computed based on absorbed photosynthetically active radiation (apar) and canopy conductance reflecting the level of water stress (Sitch et al., 2003). This water-stressed carboxylation capacity V_{\max} determines the demand for N of trees, grasses and crops in the leaves. Depending on **plant**
 5 **functional-type (PFT)-specific** requirements for V_{\max} the N demand of leaf, N_{leaf} (gN m^{-2}), is calculated according to Smith et al. (2014) based on Haxeltine and Prentice (1996) as

$$N_{\text{leaf}} = 25 \cdot 0.02314815 / \text{daylength} \cdot V_{\max} \cdot \exp(-0.02 \cdot (T - 25)) \cdot f_{\text{LAI}}(\text{LAI}) + 0.00715 \cdot C_{\text{leaf}} \quad (1)$$

where C_{leaf} is the actual leaf carbon content (gC m^{-2}) and daylength is the duration of daylight (h). The function $f_{\text{LAI}}(\text{LAI})$ is a modifier dependent on current leaf area index (LAI) accounting for a stronger leaf N content decline with canopy depth
 10 compared to incoming sunlight:

$$f_{\text{LAI}}(\text{LAI}) = \begin{cases} \max(0.1, \text{LAI}) & \text{for } \text{LAI} < 1 \\ \exp(0.08 \cdot \min(\text{LAI}, 7)) & \text{otherwise} \end{cases} \quad (2)$$

The pre-factor 0.12 in the exponential term of Smith et al. (2014) has been replaced by 0.08 for two reasons. First, we find that canopy C:N ratios are too low for the original value. Second, the computed values for the average leaf C:N ratio of the canopy should monotonically increase with LAI, whereas they decline again at higher LAI. This unwanted decline is not
 15 completely prevented with our pre-factor of 0.08 but much weaker and occurs only at much higher LAI values than in the original implementation (see SI Fig. S1). We choose a maximum of $\text{LAI} = 7$ and for $\text{LAI} < 1$ a linear decrease to avoid too high respiration rates at low LAI levels, where C:N ratios would become very small otherwise. Daily gross photosynthesis A_{gd}

depends on light-limited photosynthesis rate J_E and Rubisco-limited photosynthesis rate J_C :

$$A_{gd} = \left(J_E + J_C - \sqrt{(J_E + J_C)^2 - 4 \cdot \theta \cdot J_E \cdot J_C} \right) / (2 \cdot \theta) \cdot \text{daylength}, \quad (3)$$

where θ is the shape parameter describing the co-limitation of light and Rubisco activity. The value of θ of ~~LPJmL-3.5~~ [LPJmL3.5](#) has been changed from 0.7 to 0.9 which is in better agreement with Collatz et al. (1990) and results in lower

- 5 Rubisco demand to reach the light-limited photosynthesis rate (see SI Fig. S2). [The factor \$\alpha_a\$ determining the fraction of photosynthetic active radiation \(PAR\) assimilated at ecosystem level relative to leaf level has been changed from 0.5 to 0.6 to counterbalance the reduction GPP due to additional nitrogen limitations.](#)

Because the allocation of carbon and nitrogen for grass and tree PFTs is done on a yearly time interval the actual carbon stored in leaves $C_{\text{leaf},t}$ at time t of the current year is calculated from the carbon stored in leaves at the end of the previous
10 year C_{leaf} :

$$C_{\text{leaf},t} = C_{\text{leaf}} + f_{\text{leaf}} \cdot \sum_{t'=1}^t \text{NPP}_{t'}, \quad (4)$$

where $\sum_{t'} \text{NPP}_{t'}$ is the accumulated biomass increment and f_{leaf} is the fraction of biomass that was allocated to leaves at the end of the previous year. Then the total N demand is determined by the actual (t) carboxylation-based demand for N in leaves $N_{\text{leaf},t}$ (see Eq. (1)), the current N content of the other organs (roots N_{root} and sapwood N_{sapwood} for trees) and the
15 approximated N demand for the newly accumulated NPP (Eq. (5)). For this approximation, we use the allocation shares of the previous year ($f_{\text{root}}, f_{\text{sapwood}}$):

$$N_{\text{demand},t} = N_{\text{leaf},t} + N_{\text{root}} + N_{\text{sapwood}} + \frac{N_{\text{leaf}}}{C_{\text{leaf}}} \cdot (f_{\text{root}}/R_1 + f_{\text{sapwood}}/R_2) \cdot \sum_{t'=1}^t \text{NPP}_{t'}, \quad (5)$$

where R_1, R_2 are the prescribed PFT-specific C:N ratios of roots and sapwood relative to the leaf C:N ratio (Table 1).

- The daily allocation scheme of crops enables the calculation of nitrogen demand by using the carbon compartments itself.
20 Plants maintain a store of labile N, N_{store} (gN m^{-2}), to buffer fluctuations between N demand and supply from the soil mineral N pool (Smith et al., 2014). N demand is therefore increased by a factor of $k_{\text{store}} = 1.15$ for trees and of $k_{\text{store}} = 1.3$ for grass and crops. Thus, the optimum N uptake fulfilling the demand $N_{\text{uptake,opt}}$ can be calculated from the demand increment:

$$N_{\text{uptake,opt}} = (N_{\text{demand},t} - N_{\text{demand},t-1}) \cdot k_{\text{store}} \quad (6)$$

2.2 Nitrogen uptake

- 25 The mechanism for uptake of N (N_{uptake} in $\text{gN m}^{-2} \text{d}^{-1}$) is the same for trees, crops and grasses. Following Smith et al. (2014), plant N_{uptake} is determined by soil mineral N concentrations, fine root mass, soil temperature and porosity, and plant demand for N. This is computed for all soil layers individually and summed up to compute overall N uptake:

$$N_{\text{uptake}} = \sum_{l=1}^{n_{\text{soillayer}}} 2 \cdot N_{\text{up,root}} \cdot f_N(N_{\text{avail},l}) \cdot f_T(T_{\text{soil},l}) \cdot f_{\text{NC}}(\text{NC}_{\text{plant}}) \cdot C_{\text{root}} \cdot \text{rootdist}_l, \quad (7)$$

Table 1. C:N ratios relative to the leaf C:N ratio R_i for the different plant compartments.

Plant	Root R_1	Sapwood R_2	Storage organ R_3	Pool R_4
Tree	1.16	6.9		
Grass	1.16			
Temperate cereals	1.16		0.99	3
Rice	1.16		1.30	3
Maize	1.16		0.83	3
Tropical cereals	1.16		0.79	3
Pulses	1.16		0.45	3
Potatoes	1.16		1.74	3
Sugar beet	1.16		4.46	3
Tropical roots	1.16		3.27	3
Sunflower	1.16		1.04	3
Soybeans	1.16		0.42	3
Groudnut	1.16		0.68	3
Rapeseed	1.16		0.76	3
Sugar cane	1.16		4.57	3

where $N_{\text{up,root}}$ is the maximum N uptake rate per unit fine root mass in each layer, $f_N(N_{\text{avail}})$ parameterizes the dependence on available N, $f_T(T_{\text{soil}})$ parameterizes the temperature dependence, f_{NC} parameterizes the dependence on plant N:C ratio, C_{root} is the carbon stored in the roots, $n_{\text{soillayer}}$ is the number of soil layers ($n_{\text{soillayer}} = 6$) and rootdist_l determines the fraction of roots in each layer. $N_{\text{up,root}}$ is $2.8 \times 10^{-3} \text{ gN gC}^{-1} \text{ d}^{-1}$ for trees and $5.51 \times 10^{-3} \text{ gN gC}^{-1} \text{ d}^{-1}$ for crops and
5 grasses (Smith et al., 2014). The available N is the sum of NO_3^- and NH_4^+ in the soil layer l :

$$N_{\text{avail},l} = \text{NO}_{3,\text{soil},l}^- + \text{NH}_{4,\text{soil},l}^+ \quad (8)$$

The function f_N can be parameterized as a Michaelis-Menten kinetics:

$$f_N(N_{\text{avail},l}) = k_{N,\text{min}} + \frac{N_{\text{avail},l}}{N_{\text{avail},l} + K_{N,\text{min}} \cdot \theta_{\text{max}} \cdot d_{\text{soil},l}}, \quad (9)$$

where $d_{\text{soil},l}$ is the soil column depth (m), θ_{max} is the soil type specific fractional pore space (dimensionless), $K_{N,\text{min}}$ is 1.48
10 gN m^{-3} for woody and 1.19 for grassy PFTs (half saturation concentration of fine root N uptake), and $k_{N,\text{min}}$ (dimensionless) is 0.05, which is the basal rate of N uptake that is not associated with Michaelis-Menten kinetics. The function $f_{\text{NC}}(\text{NC}_{\text{plant}})$ is from Zaehle et al. (2010b):

$$f_{\text{NC}}(\text{NC}_{\text{plant}}) = \frac{\text{NC}_{\text{leaf,high}} - \text{NC}_{\text{plant}}}{\text{NC}_{\text{leaf,high}} - \text{NC}_{\text{leaf,low}}}, \quad (10)$$

where $\text{NC}_{\text{leaf,low}}$ and $\text{NC}_{\text{leaf,high}}$ are the lower and upper limits of N:C ratios and NC_{plant} is the actual plant N:C ratio. The
15 lower and upper limits $\text{NC}_{\text{leaf,low}}$ and $\text{NC}_{\text{leaf,high}}$ are derived from the TRY database (Kattge et al., 2011). Their reciprocal

C:N values for each PFT are shown in Table 2. The actual plant N:C ratio is calculated according to

$$NC_{\text{plant}} = \frac{N_{\text{leaf}} + N_{\text{root}}}{C_{\text{leaf}} + C_{\text{root}}} \quad (11)$$

The temperature function f_T for N uptake is given by Thornley (1991):

$$f_T(T_{\text{soil},l}) = (T_{\text{soil},l} - T_0) \cdot (2 \cdot T_m - T_0 - T_{\text{soil},l}) / (T_r - T_0) / (2 \cdot T_m - T_0 - T_r), \quad (12)$$

- 5 where $T_0 < T_r < 2 \cdot T_m - T_0$. For the chosen $T_m = 15^\circ\text{C}$, $T_r = 15^\circ\text{C}$ and $T_0 = -25^\circ\text{C}$, the maximum of 1 is reached at 15° and the function is positive above -25°C .

The root distribution ~~rootdist_l is rootdist_l can be~~ calculated from the proportion of roots from surface to soil depth z , rootdist_z, as in Jackson RB et al. (1996):

$$\text{rootdist}_z = \frac{\int_0^z (\beta_{\text{root}})^{z'} dz'}{\int_0^{z_{\text{bottom}}} (\beta_{\text{root}})^{z'} dz'} = \frac{1 - (\beta_{\text{root}})^z}{1 - (\beta_{\text{root}})^{z_{\text{bottom}}}}, \quad (13)$$

- 10 where β_{root} is a PFT-specific root distribution rootdist_{PFT_l} and the thawing depth parameter (for parameter values see Table 2). rootdist_l is then given by the difference rootdist_{z(l)} – rootdist_{z(l-1)}. If the soil depth of the layer l is greater than the thawing depth then rootdist_l is reduced accordingly. The non-zero rootdist_l are rescaled so that their sum is normalized to one, accounting for the modified root distribution under freezing conditions. Soil NH_4^+ and soil NH_3^- pools are reduced accordingly every simulation day t :

$$15 \quad \text{NO}_{3,\text{soil},l,t+1}^- = \text{NO}_{3,\text{soil},l,t}^- \cdot \left(1 - \text{rootdist}_l \cdot \frac{N_{\text{uptake}}}{\sum_{l=1}^{n_{\text{soil layer}}} N_{\text{avail},l}} \right) \quad (14)$$

$$\text{NH}_{4,\text{soil},l,t+1}^+ = \text{NH}_{4,\text{soil},l,t}^+ \cdot \left(1 - \text{rootdist}_l \cdot \frac{N_{\text{uptake}}}{\sum_{l=1}^{n_{\text{soil layer}}} N_{\text{avail},l}} \right) \quad (15)$$

2.3 Determination of the N limitation scalar

For trees, grass and crops, the N limitation scalar v_{scal} is calculated by ratio of N demand $N_{\text{uptake,opt}}$ and actual N uptake:

$$v_{\text{scal}} = \min(N_{\text{uptake}} / N_{\text{uptake,opt}}, 1) \quad (16)$$

- 20 The scalar v_{scal} is used to account for N limitation in the allocation of N to different plant organs (section 2.5) and is computed as the growing season mean, which is re-initialized to zero every year for natural vegetation and at sowing for crops.

2.4 Net Primary Production under N limitation

To calculate the limitation by N availability, N stress is calculated after determining water stress on photosynthesis. If N demand cannot be fulfilled by N uptake, carboxylation capacity V_{max} has to be reduced. The reduced V_{max} is determined by

- 25 solving Eq. (1) for V_{max} . From this reduced V_{max} , the actual photosynthesis rate can be calculated (Fig. 2). The gross primary production (GPP) derived from the actual photosynthesis rate is reduced by leaf, root and sapwood (for tree PFTs) respiration

Table 2. PFT-specific β_{root} based on Schaphoff et al. (2017b) and minimum and maximum leaf C:N ratios, based on the TRY data base (Kattge et al., 2011) with data from Kurokawa and Nakashizuka (2008); Garnier et al. (2007); Penuelas et al. (2010a); Fyllas et al. (2009); Loveys et al. (2003); Han et al. (2005); Ordonez et al. (2010); Atkin et al. (1999); White et al. (2000); Xu and Baldocchi (2003); Freschet et al. (2010a, b); Laughlin et al. (2010); Niinemets (2001, 1999); Willis et al. (2010); Baker et al. (2009); Patino et al. (2009); Pakeman et al. (2009, 2008); Fortunel et al. (2009); Penuelas et al. (2010b); Cornelissen et al. (1996, 1997, 2004); Qusted et al. (2003); Sardans et al. (2008b, a); Ogaya and Penuelas (2003, 2006, 2007, 2008). The C:N ratios for C3 and C4 grasses and crops are based on White et al. (2000).

Functional type	CN _{leaf,low}	CN _{leaf,high}	Source- β_{root}
Tropical broadleaved evergreen tree	15.6 <u>15.6</u>	46.2 <u>46.2</u>	TRY data 0.962 <u>0.962</u>
Tropical broadleaved raingreen tree	15.4 <u>15.4</u>	34.6 <u>34.6</u>	TRY data 0.961 <u>0.961</u>
Temperate needleleaved evergreen tree	31.8 <u>31.8</u>	63.8 <u>63.8</u>	TRY data 0.976 <u>0.976</u>
Temperate broadleaved evergreen tree	15.6 <u>15.6</u>	46.2 <u>46.2</u>	TRY data 0.964 <u>0.964</u>
Temperate broadleaved summergreen tree	15.4 <u>15.4</u>	34.6 <u>34.6</u>	TRY data 0.966 <u>0.966</u>
Boreal needleleaved evergreen tree	31.8 <u>31.8</u>	63.8 <u>63.8</u>	TRY data 0.943 <u>0.943</u>
Boreal broadleaved summergreen tree	15.4 <u>15.4</u>	34.6 <u>34.6</u>	TRY data 0.943 <u>0.943</u>
Boreal needleleaved summergreen tree	18.4 <u>18.4</u>	36.9 <u>36.9</u>	TRY data 0.943 <u>0.943</u>
C3 perennial grass	10.5 <u>10.5</u>	37.9 <u>37.9</u>	White et al. (2000) 0.972 <u>0.972</u>
C4 perennial grass	17.4 <u>17.4</u>	66.9 <u>66.9</u>	White et al. (2000) 0.943 <u>0.943</u>
Bioenergy tropical tree	15.6 <u>15.6</u>	46.2 <u>46.2</u>	TRY data 0.976 <u>0.976</u>
Bioenergy temperate tree	15.4 <u>15.4</u>	34.6 <u>34.6</u>	TRY data 0.976 <u>0.976</u>
Bioenergy C4 grass	17.4 <u>17.4</u>	66.9 <u>66.9</u>	White et al. (2000) 0.976 <u>0.976</u>
Crops	14.3 <u>14.3</u>	58.8 <u>58.8</u>	White et al. (2000) 0.972 <u>0.972</u>

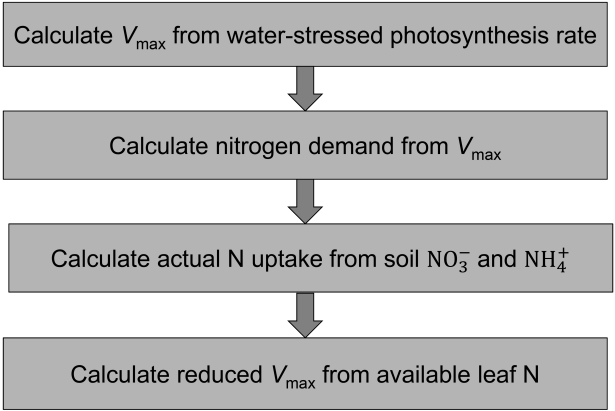


Figure 2. Calculation of N stress of plants.

R_{leaf} , R_{root} , and R_{sapwood} [in order to get the net primary production \(NPP\)](#). Respiration rates of roots and sapwood is assumed to be linearly dependent on the N:C ratio of the corresponding pool, whereas the respiration rate of leaves (R_{leaf}) is a fraction (1.5% for C3 plants, 3.5% for C4 plants) of V_{max} (Sitch et al., 2003):

$$R_{\text{root}} = k_{\text{resp}}(T_{\text{soil}}) \cdot N_{\text{root}} \quad (17)$$

$$5 \quad R_{\text{sapwood}} = k_{\text{resp}}(T_{\text{air}}) \cdot N_{\text{sapwood}}, \quad (18)$$

where $k_{\text{resp}}(T)$ is a temperature dependent respiration rate ($\text{gC gN}^{-1} \text{d}^{-1}$) (as in Sitch et al., 2003). Therefore higher N:C ratios lead to a reduction in net primary production (NPP), which is computed as:

$$\text{NPP} = \text{GPP} - R_{\text{growth}} - R_{\text{leaf}} - R_{\text{root}} - R_{\text{sapwood}}, \quad (19)$$

where R_{growth} is 25% of GPP and R_{sapwood} is zero for all non-woody plants.

10 2.5 Nitrogen allocation and turnover in plants

Carbon allocation to plant compartments follows functional and allometric rules as described by Sitch et al. (2003) and is computed annually for natural vegetation and daily for crops (Bondeau et al., 2007). The allocation rules account for the functional relationships that leaf area needs to be supported by sufficient sapwood (in trees) and fine root biomass. Fine root biomass increases relative to leaf biomass under water stress and also under nitrogen limitation. The allometric rules specify
15 the relationship of stem diameter to plant height and crown diameter (Sitch et al., 2003). Plants require N in varying amounts to satisfy organ-specific C:N ratios. Leaf-N content is determined by the photosynthetic potential and structural requirements and can vary within PFT-specific limits of C:N-ratios. The PFT-specific range of possible C:N-ratios is based on the TRY data base (Kattge et al., 2011, Table 2).

The allocation of N (N_{inc}) to plant compartments follows the allocation rules for carbon and ensures the distribution between
20 the plant compartments as established with the relative ratios given for the C:N ratio of, e.g., roots in comparison to leaves ($\text{CN}_{\text{root}} / \text{CN}_{\text{leaf}}$). These relative ratios for natural vegetation are taken from Friend et al. (1997, Table 4).

For crops the C:N ratios for the storage organ are derived from Bodirsky et al. (2012). For this average crop functional type-specific leaf C:N ratios as simulated by [LPJmL-5](#) [LPJmL5](#) were used to estimate the factors [R₃](#) that relate leaf C:N ratios to storage organ C:N ratios (Table 1). ~~C:N-ratios relative to the leaf C:N-ratio R_i for the different plant compartments. Plant~~
25 ~~Root R_1 Sapwood R_2 Storage organ R_3 Pool R_4 Tree 1.16 6.9 Grass 1.16 Temperate cereals 1.16 0.99 3Rice 1.16 1.30 3Maize 1.16 0.83 3Tropical cereals 1.16 0.79 3Pulses 1.16 0.45 3Potatoes 1.16 1.74 3Sugar beet 1.16 4.46 3Tropical roots 1.16 3.27 3Sunflower 1.16 1.04 3Soybeans 1.16 0.42 3Groundnut 1.16 0.68 3Rapeseed 1.16 0.76 3Sugar cane 1.16 4.57 3~~

The allocation scheme follows the algebraic solution of the following set of equations when there are n plant compartments:

$$\frac{N_1 + a_1 \cdot N_{\text{inc}}}{C_1} = R_1 \cdot \frac{N_2 + a_2 \cdot N_{\text{inc}}}{C_2} \quad (20a)$$

$$\frac{N_1 + a_1 \cdot N_{\text{inc}}}{C_1} = R_2 \cdot \frac{N_3 + a_3 \cdot N_{\text{inc}}}{C_3} \quad (20b)$$

$$\begin{aligned} & \vdots \\ 5 \quad & \frac{N_1 + a_1 \cdot N_{\text{inc}}}{C_1} = R_{n-1} \cdot \frac{N_n + a_n \cdot N_{\text{inc}}}{C_n} \end{aligned} \quad (20c)$$

$$\sum_{i=1}^n a_i = 1 \quad (20d)$$

where C_1, C_2, \dots, C_n , N_1, N_2, \dots, N_n are the C and N pools of plant compartments 1, 2, \dots , n , and R_1, R_2, \dots, R_{n-1} are the relative C:N ratios in comparison to leaves. The system is solved for a_1, a_2, \dots, a_n so that the relative ratios R_1, \dots, R_{n-1} are ensured. Thus, the model has to solve the equation system for $n = 2$ pools for grass, for $n = 3$ pools for trees and for $n = 4$ pools for crops.

If the N:C ratio for a pool is below the PFT-specific minimum N:C ratio allowed then the excess carbon is put into the litter pools. To avoid overly large C fluxes from excess carbon to the litter pools in N-limited environments, we have introduced a sink-limitation for photosynthesis of trees. For this, the excess carbon from the sapwood pool is stored in an additional carbon pool C_{excess} . If this excess pool is filled and if there is a minimum C_{sapwood} pool of at least 1 kg m^{-2} , photosynthesis is downregulated by a scaling factor s in the following year (Eq. (21)). At the end of the year, the newly acquired carbon (NPP) and the C_{excess} are allocated to the plant organs, according to the usual allocation rules. If all carbon can be allocated within allowed compartment-specific C:N ratios, the C_{excess} pool is empty afterwards and photosynthesis no longer downregulated.

$$s = (1 + K_M) \cdot \frac{f}{f + K_M}, f = \min \left(1, \frac{N_{\text{sapwood}}}{C_{\text{sapwood}} + C_{\text{excess}}} \cdot \frac{R_2}{\text{NC}_{\text{leaf,low}}} \right), \quad (21)$$

where $K_M = 0.1$ is the Michaelis constant of the Michaelis-Menten kinetics and R_2 is the relative C:N ratio of sapwood in respect to leaves.

Similar to water stress, we assume that plants allocate more biomass to roots under N limitation. For this, the leaf to root mass ratio lmr_{orm} is modified by the minimum of the N limitation factor v_{scal} and the water limitation factor w_{scal} . Both factors are computed as growing season means with daily updates, i.e. for the entire calendar year for natural vegetation, between harvest events for managed grasslands, and since sowing for crops.

LPJmL employs PFT-specific turnover rates for living leaves and fine roots. At turnover the corresponding amount of carbon is moved into the litter pools, whereas not all of the associated N is disposed but remains in the plant. We assume that grasses and deciduous trees recover $k_{\text{turn}} = 70\%$ of their N upon biomass turnover, whereas evergreen trees only recover $k_{\text{turn}} = 20\%$. At turnover sapwood carbon is transformed into heartwood carbon. Not all nitrogen of the sapwood turnover is going into heartwood, only a fraction $f_{\text{heartwood}} = 0.7$ of nitrogen is transformed.

where

$$R(T_l, M_l) = T_l \cdot (0.04021601 - 5.00505434 \cdot M_l^3 + 4.26937932 \cdot M_l^2 + 0.71890122 \cdot M_l) \quad (23)$$

The mineralization of soil $N_{\text{miner,soil},l}$ in soil layer l is given by

$$N_{\text{miner,soil},l} = F_l^f + F_l^s \quad (24)$$

- 5 Whereas the mineralization fluxes of carbon go completely to the atmosphere as CO_2 , mineralized N goes to the mineral pools, where they are subject to further transformation (Parton et al., 2001).

Decomposition of N in soil organic material (N_{decom}) consists of a mineralization part ($A_f = 0.7$, dimensionless) that forms NH_4^+ (80%) and NO_3^- (20%), and a humification part ($1 - A_f$), in which organic N from the litter pool is transferred to the soil pools. The humification flux is divided into fluxes to slow (s) and fast (f) N soil pools (P); the parameter $F_f = 0.98$

- 10 (dimensionless) specifies the portion that goes to the fast soil pool.

$$P_{l,t+1}^f = P_{l,t}^f + F_f \cdot (1 - A_f) \cdot N_{\text{decom}} \cdot N_{\text{shift},l}^f \quad (25)$$

$$P_{l,t+1}^s = P_{l,t}^s + (1 - F_f) \cdot (1 - A_f) \cdot N_{\text{decom}} \cdot N_{\text{shift},l}^s, \quad (26)$$

where the annual shift rates $N_{\text{shift},l}^{s,f}$ describe the organic matter input from the different PFTs into the respective layer due to cryoturbation and bioturbation (Schaphoff et al., 2013).

- 15 Net mineralized material $N_{\text{miner,litter},l}$ is

$$N_{\text{miner,litter},l} = A_f \cdot N_{\text{decom}} \cdot (F_f \cdot N_{\text{shift},l}^f + (1 - F_f) \cdot N_{\text{shift},l}^s), \quad (27)$$

which adds for N to an intermediate N mineralization pool as well

$$N_{\text{miner},l} = N_{\text{miner,soil},l} + N_{\text{miner,litter},l} \quad (28)$$

A fraction of $K_{\text{nit}} = 0.2$ (dimensionless) of this pool is nitrified directly per day to NO_3^- (see Eq. 2 in Parton et al. (2001)) and

- 20 the fluxes are added to the soil pools of NH_4^+ and NO_3^- (g m^{-2}).

$$\text{NH}_{4,\text{soil},l,t+1}^+ = \text{NH}_{4,\text{soil},l,t}^+ + (1 - K_{\text{nit}}) \cdot N_{\text{miner},l} \quad (29)$$

$$\text{NO}_{3,\text{soil},l,t+1}^- = \text{NO}_{3,\text{soil},l,t}^- + K_{\text{nit}} \cdot N_{\text{miner},l} \quad (30)$$

2.6.2 Nitrogen immobilization

Immobilization, i.e. the transformation of mineral N to organic N in soils, is determined per soil layer directly after soil and

25 litter mineralization, following the CLM approach described by Gerber et al. (2010). If available mineral soil N is constraining immobilization, mineral N is first immobilized into the fast soil pool and then into the slow soil pool. The immobilized N $N_{\text{immo},l}$ is calculated according to

$$N_{\text{immo},l} = F_f \cdot (1 - A_f) \cdot (C_{\text{decom}}/\text{CN}_{\text{soil}} - N_{\text{decom}}) \cdot N_{\text{shift},l}^f \cdot \frac{N_{\text{sum},l}/d_{\text{soil},l}}{k_N + N_{\text{sum},l}/d_{\text{soil},l}}, \quad (31)$$

where CN_{soil} is the desired soil C:N ratio of 15 (dimensionless) for all soil types, $d_{\text{soil},l}$ is the soil depth of layer l in m, $k_N = 5 \times 10^{-3}$ (gN m⁻³) is the half saturation concentration for immobilization in soils (Gerber et al., 2010), and $N_{\text{shift},l}^f$ is the parameter that determines the distribution of the humified organic matter in the topsoil to the different soil layers l (Schaphoff et al., 2013). The available mineral N in the soil layer l ($N_{\text{sum},l}$ in gN m⁻²) is the sum of NH_4^+ and NO_3^- :

$$5 \quad N_{\text{sum},l} = \text{NH}_{4,\text{soil},l}^+ + \text{NO}_{3,\text{soil},l}^- \quad (32)$$

The immobilized N ($N_{\text{immo},l}$) is added to the fast soil N pool of layer l and subtracted from the NH_4^+ and NO_3^- pools:

$$P_{\text{soil},l,t+1}^f = P_{\text{soil},l,t}^f + \min(N_{\text{immo},l}, N_{\text{sum},l}) \quad (33)$$

$$\text{NH}_{4,\text{soil},l,t+1}^+ = \text{NH}_{4,\text{soil},l,t}^+ - \text{NH}_{4,\text{soil},l,t}^+ \cdot \min(N_{\text{immo},l}/N_{\text{sum},l}, 1) \quad (34)$$

$$\text{NO}_{3,\text{soil},l,t+1}^- = \text{NO}_{3,\text{soil},l,t}^- - \text{NO}_{3,\text{soil},l,t}^- \cdot \min(N_{\text{immo},l}/N_{\text{sum},l}, 1) \quad (35)$$

- 10 The immobilization into the slow soil N pool ($P_{\text{soil},l,t+1}^s$) is computed accordingly as in Eq. (31) but with $(1 - F_f)$ instead of F_f .

2.6.3 Nitrification

- Nitrogen fluxes from nitrification in the soil are modeled modified after Parton et al. (2001) with the schematic representation of a series of pipes for the main flow from NH_4^+ over NO_3^- to N_2 from which N_2O leaks in between. As suggested by Parton et al. (2001, equation 2), nitrification is computed as a fixed fraction of the mineralization flux (see 2.6.1) as well as an explicit transformation flux $F_{\text{NO}_3^-}$ from ammonium to nitrate in gN m⁻² d⁻¹, which is described here.

$$F_{\text{NO}_3^-} = K_{\text{max}} \cdot F_1(T_{\text{soil}}) \cdot F_1(W_{\text{sat}}) \cdot F(\text{pH}) \cdot \text{NH}_{4,\text{soil}}^+ \quad (36)$$

- where $\text{NH}_{4,\text{soil}}^+$ is the model-derived soil ammonium concentration (gN m⁻²), K_{max} is the maximum nitrification rate of NH_4^+ ($K_{\text{max}} = 0.1$ d⁻¹), $F_1(T_{\text{soil}})$ is the limiting function for temperature and $F_1(W_{\text{sat}})$ the corresponding limiting function for water saturation W_{sat} . Parton et al. (2001) show nitrification rates after data of Malhi and McGill (1982) in Table 3 without a formula. Using these data from three different sites in the US, Canada and Australia, we fitted a bell shaped function for the temperature dependence:

$$F_1(T_{\text{soil}}) = \exp(-(T_{\text{soil}} - a)^2 / (2 \cdot b^2)), \quad (37)$$

- where $a = 18.79^\circ\text{C}$ and $b = 5.26$ give the best fit to the data (see SI Fig. S4). The function is applicable also for negative values.

The soil water response function $F_1(W_{\text{sat}})$ is parameterized according to Doran et al. (1988) as described in Parton et al. (1996):

$$F_1(W_{\text{sat}}) = \left(\frac{W_{\text{sat}} - b_{\text{nit}}}{a_{\text{nit}} - b_{\text{nit}}} \right)^{d_{\text{nit}} \cdot (b_{\text{nit}} - a_{\text{nit}}) / (a_{\text{nit}} - c_{\text{nit}})} \cdot \left(\frac{W_{\text{sat}} - c_{\text{nit}}}{a_{\text{nit}} - c_{\text{nit}}} \right)^{d_{\text{nit}}}, \quad (38)$$

where W_{sat} is the water filled pore space of the soil, parameters a_{nit} to d_{nit} are given for sandy and medium soil (SI Table S1).

This soil pH function is based on Parton et al. (1996):

$$F(\text{pH}) = 0.56 + \arctan(\pi \cdot 0.45 \cdot (-5 + \text{pH}))/\pi \quad (39)$$

Soil pH values are taken from the WISE dataset (Batjes, 2000). Part of the N during the nitrification is lost to the atmosphere as nitrous oxide N_2O . Parton et al. (2001) assume that the N_2O flux $F_{\text{N}_2\text{O}}$ (in $\text{gN m}^{-2} \text{d}^{-1}$) is proportional to the nitrification rate with

$$F_{\text{N}_2\text{O}} = K_2 \cdot F_{\text{NO}_3^-}, \quad (40)$$

where K_2 is fraction of nitrified N lost as N_2O flux ($K_2 = 0.02$). Finally, soil NO_3^- and NH_4^+ are updated accordingly:

$$\text{NO}_{3,\text{soil},l,t+1}^- = \text{NO}_{3,\text{soil},l,t}^- + (1 - K_2) \cdot F_{\text{NO}_3^-} \quad (41)$$

$$10 \quad \text{NH}_{4,\text{soil},l,t+1}^+ = \text{NH}_{4,\text{soil},l,t}^+ - F_{\text{NO}_3^-} \quad (42)$$

2.6.4 Denitrification

The reduction of NO_3^- to NO_2 and N_2 is determined for each soil layer using the implementation in SWIM (Krysanova and Wechsung, 2000).

$$D_{\text{NO}_3^-} = F_2(W_{\text{sat}}) \cdot F_2(T_{\text{soil}}, C_{\text{org}}) \cdot \text{NO}_{3,\text{soil}}^- \quad (43)$$

15 where $F_2(W_{\text{sat}})$ is the water response function and $F_2(T, C)$ the soil temperature and carbon reaction function. The water response function depends on the water filled pore space W_{sat} in the following way:

$$F_2(W_{\text{sat}}) = 6.664096 \times 10^{-10} \cdot \exp(21.12912 \cdot W_{\text{sat}}) \quad (44)$$

The water response function shows a qualitatively similar behavior to Eq. 151 from SWIM while ensuring continuity (see SI Fig. S4). Parameters are fitted and adjusted so that for full soil water saturation, the value is not greater than 1. The soil temperature and carbon reaction function is parameterized according to:

$$F_2(T_{\text{soil}}, C_{\text{org}}) = 1 - \exp(-\text{CDN} \cdot F_2(T_{\text{soil}}) \cdot C_{\text{org}}), \quad (45)$$

where $\text{CDN} = 1.4$ is the shape coefficient (Arnold et al., 2012), C_{org} is the sum of the fast and slow C pools and $F_2(T_{\text{soil}})$ is the soil temperature reaction function. $F_2(T_{\text{soil}})$ is replaced by Equation C5 from Smith et al. (2014) which is only valid for positive T_{soil} . The original function from SWAT approaches 1 for high temperatures whereas the function from Smith declines which seems more sensible. Equation C5 of Smith et al. (2014) is taken from Comins and McMurtrie (1993).

$$F_2(T_{\text{soil}}) = \begin{cases} 0.0326 & \text{for } T_{\text{soil}} \leq 0^\circ\text{C} \\ 0.0326 + 0.00351 \cdot T_{\text{soil}}^{1.652} - (T_{\text{soil}}/41.748)^{7.19} & \text{for } 0^\circ\text{C} < T_{\text{soil}} < 45.9^\circ\text{C} \\ 0 & \text{for } T_{\text{soil}} \geq 45.9^\circ\text{C} \end{cases} \quad (46)$$

Bessou et al. (2010) assume that the N_2O flux from NO_3^- , F_{N_2O} (in $gN\ m^{-2}\ d^{-1}$), is proportional to the denitrification rate $D_{NO_3^-}$ with

$$F_{N_2O} = r_{mx} \cdot D_{NO_3^-}, \quad (47)$$

where $r_{mx} = 0.11$ is the fraction of denitrified N lost as N_2O flux. The N_2 flux F_{N_2} is then derived by

$$F_{N_2} = (1 - r_{mx}) \cdot D_{NO_3^-}, \quad (48)$$

The soil NO_3^- pools have to be reduced by the denitrification flux:

$$NO_{3,soil,l,t+1}^- = NO_{3,soil,l,t}^- - D_{NO_3^-} \quad (49)$$

2.6.5 Nitrogen leaching and movement

Nitrate movement with water fluxes is simulated as in SWAT (Neitsch et al., 2002, 2005). Nitrate is assumed to be fully dissolved in water and moves with surface runoff, lateral runoff and percolation water. To compute the amount of nitrate transported with the water from a soil layer, we first calculate the concentration of nitrate in the mobile water. This concentration is then multiplied by the volume of surface runoff, lateral runoff or percolation water between soil layers or into the aquifer, respectively. The amount of nitrate leached depends on the climatic and soil conditions and on the type and intensity of soil management (e.g. plant cover, soil treatment, fertilization).

The concentration of nitrate in the mobile water $conc_{NO_3^-,mobile,l}$ in layer l ($kgN\ m^{-3}$) is:

$$conc_{NO_3^-,mobile,l} = \frac{NO_{3,soil,l}^- \cdot \left(1 - \exp\left(\frac{-w_{mobile,l}}{(1-\theta) \cdot SAT_l}\right)\right)}{w_{mobile,l}}, \quad (50)$$

where $NO_{3,soil,l}^-$ is the content of nitrate in layer l ($gN\ m^{-2}$), w_{mobile} is the amount of mobile water in the layer (mm), $\theta = 0.4$ is the fraction of porosity from which anions are excluded (0.5 in Neitsch et al., 2002), and SAT_l is the saturated water content of the soil layer (mm).

The mobile water $w_{mobile,l}$ in the layer l is the amount of water lost by surface runoff, lateral flow and percolation:

$$w_{mobile,l} = \begin{cases} Q_{surf} + Q_{lat,l=1} + w_{perc,l=1} & \text{for } l = 1 \\ Q_{lat,l} + w_{perc,l} & \text{for } l > 1 \end{cases}, \quad (51)$$

where Q_{surf} is the surface runoff (only in top soil layer, mm), $Q_{lat,l}$ is the water discharged from the layer by lateral flow (mm) and $w_{perc,l}$ is the amount of water percolating to the underlying soil layer on a given day.

Finally, the amount of nitrate that is removed with surface runoff $NO_{3,surf}^-$ and lateral flow $NO_{3,lat,l}^-$ is calculated as:

$$NO_{3,surf}^- = \beta_{NO_3^-} \cdot conc_{NO_3^-,mobile} \cdot Q_{surf} \quad (52)$$

$$NO_{3,lat,l=1}^- = \beta_{NO_3^-} \cdot conc_{NO_3^-,mobile} \cdot Q_{lat,l=1} \quad (53)$$

for the top layer and

$$\text{NO}_3^-_{\text{lat},l} = \text{conc}_{\text{NO}_3^-,\text{mobile},l} \cdot Q_{\text{lat},l} \quad (54)$$

for the lower soil layers, where $\beta_{\text{NO}_3^-}$ is the nitrate percolation coefficient. It controls the amount of NO_3^- removed from the surface layer in runoff relative to the amount removed via percolation (Neitsch et al., 2002). The value for $\beta_{\text{NO}_3^-}$ can range from 0.01 to 1.0. For $\beta_{\text{NO}_3^-} \rightarrow 0$, the concentration of nitrate in the runoff approaches 0. For $\beta_{\text{NO}_3^-} = 1.0$, surface runoff has the same concentration of nitrate as the percolating water. We choose for $\beta_{\text{NO}_3^-}$ a value of 0.4.

Nitrate moved to the lower soil layer with percolation $\text{NO}_3^-_{\text{perc},l}$ is calculated as:

$$\text{NO}_3^-_{\text{perc},l} = \text{conc}_{\text{NO}_3^-,\text{mobile}} \cdot w_{\text{perc},l} \quad (55)$$

$\text{NO}_3^-_{\text{perc},l}$ is subtracted from current NO_3^- in the soil layer and added to the NO_3^- pool of the following soil layer:

$$10 \quad \text{NO}_3^-_{3,\text{soil},l,t+1} = \begin{cases} \text{NO}_3^-_{3,\text{soil},l,t} - \text{NO}_3^-_{\text{perc},l} - \text{NO}_3^-_{\text{surf}} - \text{NO}_3^-_{\text{lat},l} & \text{for } l = 1 \\ \text{NO}_3^-_{3,\text{soil},l,t} + \text{NO}_3^-_{\text{perc},l-1} - \text{NO}_3^-_{\text{perc},l} - \text{NO}_3^-_{\text{lat},l} & \text{for } l > 1 \end{cases} \quad (56)$$

2.6.6 Nitrogen volatilization

Volatilization of NH_4^+ is parameterized according to Montes et al. (2009). A convective mass transfer model is applied where the flux varies with air temperature, air velocity over the surface, and the NH_3 concentration gradient between the ammonium (NH_4^+) in solution and in the air:

$$15 \quad J_{\text{NH}_3} = h_m \cdot ([\text{NH}_3]_{\text{gas}} - [\text{NH}_3]_{\text{air}}), \quad (57)$$

where J_{NH_3} is the NH_3 volatilization flux ($\text{gNH}_3\text{-N m}^{-2} \text{ s}^{-1}$), h_m is the convective mass transfer coefficient (m s^{-1}), $[\text{NH}_3]_{\text{gas}}$ is the concentration of gaseous NH_3 in equilibrium with dissolved NH_3 in solution ($\text{gNH}_3\text{-N m}^{-3} \text{ air}$), and $[\text{NH}_3]_{\text{air}}$ is the concentration of NH_3 in ambient air ($\text{gNH}_3\text{-N m}^{-3} \text{ air}$), which is usually very small and can be neglected. The convective mass transfer coefficient h_m is a function of temperature T (in K), air velocity U (in m s^{-1}) and characteristic length L (in m) of the emitting surface:

$$h_m = 0.000612 \cdot U^{0.8} \cdot T^{0.382} \cdot L^{-0.2} \quad (58)$$

The concentration of gaseous NH_3 in equilibrium with the dissolved NH_3 is determined using Henry's law. The Henry's law K_h constant relates the concentration of dissolved NH_3 in water to an equilibrium concentration of NH_3 in the air:

$$K_h = \frac{[\text{NH}_3]_{\text{gas}}}{[\text{NH}_3]_{\text{solution}}} \quad (59)$$

25 The Henry's law constant K_h can be parameterized as a function of air temperature T_{air} (in K):

$$K_h = K_h(T_{\text{air}}) = (0.2138/T_{\text{air}}) \cdot 10^{6.123-1825/T_{\text{air}}} \quad (60)$$

The fraction of total ammonical N present as NH_3 can be estimated using equilibrium thermodynamic principles:

$$f_{\text{NH}_3} = \frac{[\text{NH}_3]_{\text{solution}}}{[\text{NH}_3]_{\text{solution}} + [\text{NH}_4^+]_{\text{solution}}} \quad (61)$$

$$= \frac{1}{1 + \frac{[\text{H}^+]}{K_a}} = \frac{1}{1 + \frac{10^{-\text{pH}}}{K_a}}, \quad (62)$$

where K_a is the dissociation constant, $[\text{H}^+]$ is the proton concentration in solution, and $\text{pH} = -\log([\text{H}^+])$. The dissociation

constant K_a is parameterized as a function of temperature T (in K):

$$K_a = K_a(T) = 10^{0.05 - 2788/T} \quad (63)$$

Then the volatilization flux F_{vol} (in $\text{gN m}^{-2} \text{d}^{-1}$) is calculated according to

$$F_{\text{vol}} = 86400 \cdot h_m(U, T, L) \cdot K_h(T) \cdot \frac{1}{1 + \frac{10^{-\text{pH}}}{K_a(T)}} \cdot \text{NH}_{4,\text{soil},l=1}^+ / d_{\text{soil},l=1} \quad (64)$$

and soil NH_4^+ is reduced in the top layer $l = 1$ accordingly:

$$\text{NH}_{4,\text{soil},l=1,t+1}^+ = \text{NH}_{4,\text{soil},l=1,t}^+ - F_{\text{vol}} \quad (65)$$

2.7 Nitrogen and fire

Fire creates emissions of N_2O and NO_x and leaves nutrient rich ashes as well as charcoal. Following Gerber et al. (2010), the flux of N due to fire is divided between atmospheric emission and ash introduction to the nitrate pool of the upper soil layer $\text{NO}_{3,\text{soil},l=1}^-$.

$$N_{\text{fire}} = C_{\text{fire}} \cdot N_{\text{pool}} / C_{\text{pool}} \quad (66)$$

$$N_{\text{emission}} = (1 - q_{\text{ash}}) \cdot N_{\text{fire}} \quad (67)$$

$$\text{NO}_{3,\text{soil},l=1,t+1}^- = \text{NO}_{3,\text{soil},l=1,t}^- + q_{\text{ash}} \cdot N_{\text{fire}}, \quad (68)$$

where $q_{\text{ash}} = 0.45$ is the fraction of N going into the top soil layer NO_3^- .

2.8 Biological N-fixation

The biological fixation of N occurs at all stands with an exception for agricultural stands. There, is it applied only for the nodulating leguminous crops pulses and soybean. For these two crops, biological N-fixation (BNF) is simply the difference between N demand and N uptake, basically first using the easily plant-available N from the soils and then fixing extra N at no extra cost. For natural vegetation and grasslands, the function from Cleveland et al. (1999) is applied depending on the 20-year average annual evapotranspiration etp (in mm yr^{-1}). BNF (in $\text{gN m}^{-2} \text{d}^{-1}$) is assumed to only occur if there is a minimum root biomass of 20 gC m^{-2} . All N fixed by BNF is assumed to enter the system as ammonium in the upper soil layer ($l = 1$).

$$\text{BNF} = \begin{cases} \max(0, (0.0234 \cdot \text{etp} - 0.172)/10/365) & \text{if } C_{\text{root}} > 20 \text{ gC m}^{-2} \\ 0 & \text{otherwise} \end{cases} \quad (69)$$

$$\text{NH}_{4,\text{soil},l=1,t+1}^+ = \text{NH}_{4,\text{soil},l=1,t}^+ + \text{BNF} \quad (70)$$

The function gives linearly increasing values which are positive for $\text{etp} > 7.35$ and are set to zero otherwise. Note that in Zaehle et al. (2010a) this function is also cited in the supplementary material but with a positive intercept which is not the original equation from Cleveland et al. (1999).

2.9 Nitrogen fertilization of crops

- 5 Fertilizer is applied at sowing and when the amount of fertilizer is larger than 5 gN m^{-2} , only half of the fertilizer is applied at sowing. The second application occurs when the phenological stage of the crop development fphu exceeds 0.4 to avoid large loss fluxes (leaching, volatilization, nitrification, denitrification) when fertilizing large amounts of N at the beginning of the season.

Nitrogen fertilizer is assumed to be ammonium nitrate (NH_4NO_3), so half of the applied rate is put into the top soil layer nitrate pool ($\text{NO}_{3,\text{soil},l=1}^-$) and the other half into the top soil layer ammonium pool ($\text{NH}_{4,\text{soil},l=1}^+$).

3 Model setup

- For the assessment of model performance, we focus on the historic period 1901-2009. The spatial longitudinal/latitudinal resolution is $0.5^\circ \times 0.5^\circ$. We conduct 6 different sets of simulations, two simulations with the carbon-only predecessor model version ~~LPJmL 3.5~~ LPJmL3.5 and four with the newly implemented nitrogen version ~~LPJmL 5~~ LPJmL5. Both model versions
- 15 are used for a standard historic simulation, with dynamic land-use change, referred to as *LPJmL35* and *LPJmL5* respectively, as well as for a simulation without human land use, where potential natural vegetation (PNV) is simulated on the entire land surface. These runs are referred to as *LPJmL35-PNV* and *LPJmL5-PNV*. For analyzing the current N-limitation, we also conduct a simulation with dynamic land use, but with unlimited N supply (*LPJmL5-nL*) and one with no fertilizer application (*LPJmL5-nF*). Unlimited N supply has been modelled by deposition of $1 \text{ KgN m}^{-2} \text{ d}^{-1}$ on every LPJ cell.

20 3.1 Model input

- Model simulations are driven with observational monthly input data on monthly precipitation from the Global Precipitation Climatology Centre (GPCC Full Data Reanalysis Version 7.0, Becker et al., 2013) and daily mean temperatures from the Climatic Research Unit (CRU TS version 3.23, University of East Anglia Climatic Research Unit; Harris, 2015; Harris et al., 2014). Radiation data, shortwave downward and net downward longwave, are provided by reanalysis data from ERA-Interim
- 25 (Dee et al., 2011). Monthly precipitation is allocated to individual days of the corresponding month by deriving the number of wet days per month synthetically as suggested by New et al. (2000).

- Land-use input is derived from MIRCA2000 (Portmann et al., 2010) using the maximum monthly growing areas per crop and grid cell combined with the extent of areas equipped for irrigation (Siebert et al., 2015). HYDE3 (Klein Goldewijk and van Drecht, 2006) gives the relative changes of cropland and pasture extent backward to 1700. Further information are given
- 30 by Fader et al. (2010).

The global dataset "Simulated Topological Network" (STN-30) drainage direction map (Vorosmarty and Fekete, 2011) gives transport directions of the river routing scheme. We use the GRanD database (Lehner et al., 2011), which provides detailed information on water reservoirs that includes information on storage capacity, total area and main purpose. Furthermore, information on natural lakes are obtained from Lehner and Döll (2004).

- 5 Nitrogen deposition is based on the ACCMIP database (Lamarque et al., 2013) for NO_3^- and NH_4^+ separately, which is applied daily to the corresponding mineral N pools of the top soil layer. Dry and wet deposition is not distinguished. Soil pH data are taken from the WISE dataset (Batjes, 2000). Fertilizer data is crop-specific, but static in time. We use the data supplied by the Global Gridded Crop Model Intercomparison (GGCMI phase 1 Elliott et al., 2015), which is based on gridded mineral fertilizer data (Mueller et al., 2012) and manure data (Potter et al., 2010) from which 60% is assumed to be plant
10 available (~~Elliott et al., 2015~~) and thus included in the data, whereas the remainder is ignored and not included in the data of Elliott et al. (2015).

3.2 Model initialization, spin up and equilibration of soil

- All carbon and water pools are initialized to zero except soil water, soil carbon and soil temperatures, which are computed from a 30 yr averaged climate. Then a spin-up simulation of 5000 years is performed to bring permafrost extent, vegetation patterns
15 and carbon stocks into dynamic equilibriums. The long spin-up time is necessary for reaching these equilibrium states in the permafrost regions (Schaphoff et al., 2013).

- Soil N pools (organic and mineral) are initialized with assumptions to allow for initial vegetation growth. Organic N pools (slow, fast) as well as mineral N pools (NO_3^- and NH_4^+) are set to 10^4 gN m^{-2} . After 1320 simulation years, vegetation composition is assumed to have reached an equilibrium (Schaphoff et al., 2013) and litterfall is tracked for another 3680 years
20 to allow for estimating soil carbon and soil N stocks. Based on these estimates for carbon and N fluxes under equilibrium conditions, nitrogen and carbon pools are re-initialized following Sitch et al. (2003). Hence, all N from the initialization is removed that is not supporting plant growth because of other constraints such as water shortage (e.g. in deserts).

- A second spin up phase of 390 yrs is conducted for all versions, including land-use change (except in the PNV runs *LPJmL35-PNV* and *LPJmL5-PNV*) by using land-use input of Fader et al. (2010) to capture the influence of historic land-
25 use change on the carbon and nitrogen pools in soil and vegetation.

4 Results

~~Simulations with LPJmL5~~

4.1 Carbon pools and fluxes

- Simulations with LPJmL5 result in carbon pools and net biome productivity (NBP), NPP and GPP fluxes comparable to the
30 carbon-only ~~LPJmL3.5~~ LPJmL3.5 version (Table 3) and show a similar temporal dynamic (Fig. 4). The actual vegetation carbon pool is strongly limited by current N levels and increases substantially across all ecosystems, when N limitations are

Table 3. Global carbon pools (soil and vegetation carbon) and fluxes (net biome productivity NBP, net primary productivity NPP, and gross primary productivity GPP) for the 6 different experiments (averages over the period 2000 to 2009). The suffix *-PNV* denotes experiments with potential natural vegetation, *-nL* with unlimited N supply, and *-nF* without fertilizer input.

C pools/fluxes	<i>LPJmL35</i>	<i>LPJmL35-PNV</i>	<i>LPJmL5</i>	<i>LPJmL5-nL</i>	<i>LPJmL5-nF</i>	<i>LPJmL5-PNV</i>
NBP (PgC yr ⁻¹)	0.269	-1.561	0.297	0.329	0.277	-1.744
NPP (PgC yr ⁻¹)	57.12	58.90	58.85	67.71	58.24	67.74
GPP (PgC yr ⁻¹)	129.9	143.0	134.6	153.7	133.6	168.5
Soil C (PgC)	2034	2156	2394	2461	2389	2578
Vegetation C (PgC)	450.7	627.4	466.3	611.5	465.9	659.8

lifted (*LPJmL5-nL*). Under actual N limitations and static current fertilizer levels (Elliott et al., 2015), global GPP is relatively stable throughout the simulation period (1901-2009, ~~yellow-red~~ line in Fig. 4a) as the expansion of cropland into increasingly low-input areas compensates the increase in GPP in the natural vegetation (~~red-orange~~ line in Fig. 4a). NPP increases in the standard simulation with dynamic land use (*LPJmL5*), but not as strongly as for natural vegetation (compare red and ~~yellow~~ ~~orange~~ lines in Fig. 4b). ~~, indicating that the agricultural land is increasingly limited, so that C:N-ratio dependent maintenance respiration declines and NPP increases whereas GPP does not.~~ The difference in global annual NPP between simulations with natural vegetation only and dynamic land use increases significantly from 3% (*LPJmL35-PNV-LPJmL3.5*) to 16% (*LPJmL5-PNV-LPJmL5*). This indicates that the agricultural land is increasingly N limited, so that C:N-ratio dependent maintenance respiration declines and NPP increases whereas GPP does not. This is in part because simulations are conducted with static fertilizer inputs and because land-use change predominantly causes cropland expansion in countries with low fertilizer use, so that the global average fertilizer use declines, causing higher N limitation on agricultural land. Land-use driven declines in vegetation carbon over the 20th century are similar between the carbon-only *LPJmL35* and the simulation with nitrogen *LPJmL5* (Fig. 4c), but soil carbon stocks decline with nitrogen, whereas increases in the natural vegetation balance the land-use change induced losses in the carbon-only version (Fig. 4d).

~~The role of human land-use for the limitation of plant growth by nitrogen availability is apparent when comparing simulations with land use (When N limitations are lifted through unlimited N supply (*LPJmL5*, red lines in Fig. 6) and natural vegetation only (*LPJmL-PNV*, orange lines in *LPJmL5-nL*), GPP is mostly increased, except in very dry environments. The scatter plot (Fig. 6). The nitrogen pool in the natural vegetation remains quite stable (Fig. 6a) and 5b) shows that the GPP increase mainly occurs in low to moderately productive areas. Decreases in GPP under unlimited N supply are possible where other factors are strongly limiting (e.g. water) and the higher N supply leads to higher maintenance respiration under lower tissue C:N ratios only slightly increase (Fig. 6b) whereas vegetation nitrogen with the inclusion of the historical land use declines and limitation increases by a factor of 2. The predominant difference between both simulations is the 60% increase in losses of by leaching under land use (Fig. 6e)., so that less biomass is available for leaves and thus less light can be intercepted.~~

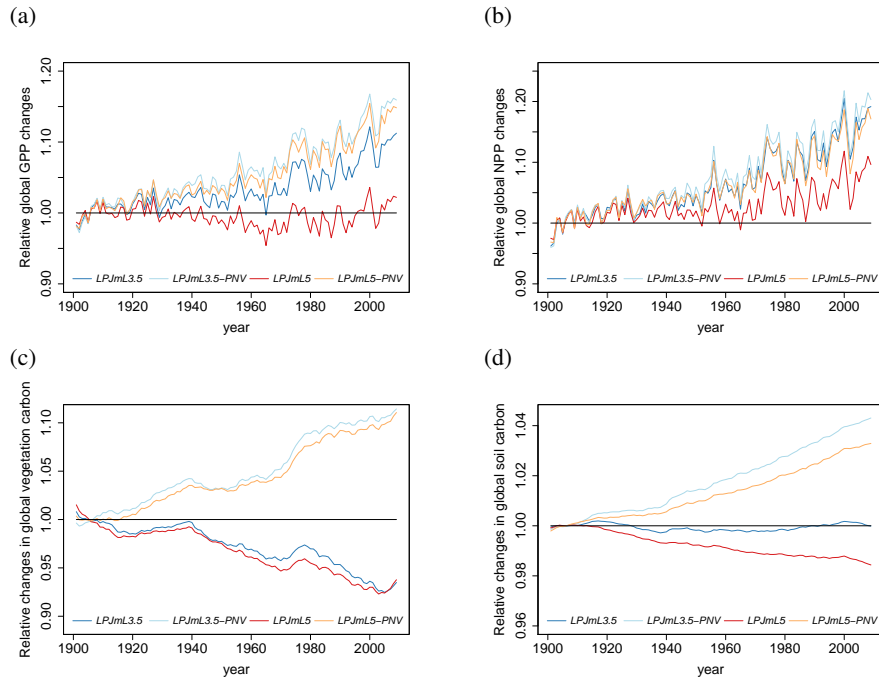


Figure 4. Relative global changes of GPP (a), NPP (b), vegetation carbon (c) and soil carbon (d). Values-Relative changes are normalized to calculated by dividing the values by their 1901-1910 average to make the different model versions and settings comparable. The blue lines denote values for LPJmL3.5 with land use (LPJmL3.5), the light blue lines for LPJmL3.5 with natural vegetation only (LPJmL3.5-PNV), the red lines for LPJmL5 with land use (LPJmL5) and the orange lines for LPJmL5 with natural vegetation only (LPJmL5-PNV).

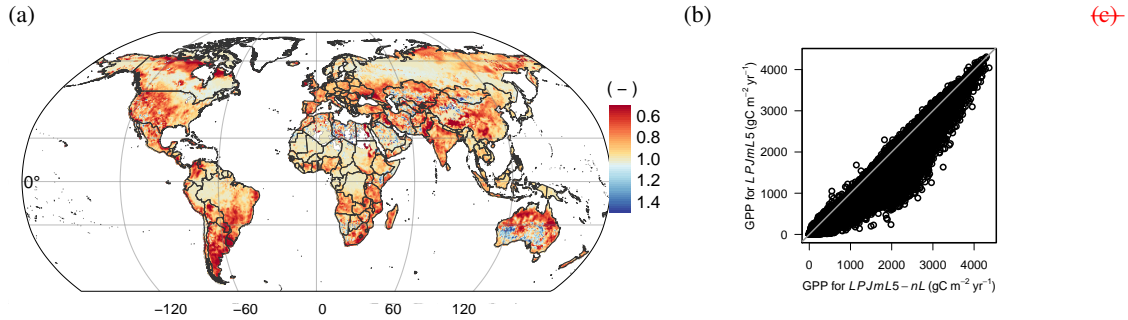


Figure 5. Simulated global time-series Ratio of vegetation nitrogen-GPP under actual N limitations (aLPJmL5) ,vegetation C:N-ratios to unlimited N supply (bLPJmL5-nL) and-leaching (ea) with land-use; values less than 1 indicate higher GPP under unlimited N supply. The scatter plot (LPJmL5b) and-potential natural vegetation (LPJmL5-PNV)shows that GPP is increased through additional N supply mostly in low to moderately productive regions.

4.2 Nitrogen pools and fluxes

The comparison of global N values to literature estimates is divided between values including natural vegetation only and those considering land-use dynamics (Table 4). Whereas several estimates exist for global N pools and fluxes under natural vegetation, those including land-use dynamics are rather rare and given mostly for emissions from the soil (e.g. denitrification or N₂O). Lifting N limitation (*LPJmL5-nL*) results in similar responses for all global nitrogen pools (Table 4). Vegetation N and plant uptake increase substantially by ≈ 75 and $\approx 100\%$ respectively, whereas soil N pools only increase slightly by 6%. The omission of N fertilizers has little effects on N pools, which are dominated by the natural ecosystems, but strongly affect nitrogen losses, especially leaching and volatilization fluxes (Table 4). A comparison to literature estimates are discussed further in section 4.4.1.

4.3 Land use and nitrogen dynamics

The role of human land use for the limitation of plant growth by nitrogen availability is apparent when comparing simulations with land use (*LPJmL5*, red lines in Fig. 6) and natural vegetation only (*LPJmL-PNV*, orange lines in Fig. 6). The nitrogen pool in the natural vegetation slightly increases by 3% (Fig. 6a) and C:N ratios increase by 5.5% (Fig. 6b) whereas vegetation nitrogen with the inclusion of the historical land use declines. The predominant difference between both simulations is the 60% increase in losses of N by leaching under land use (Fig. 6c), which is caused by the additional fertilizer and irrigation water inputs under land use.

The approximated relationships between leaf C:N ratios and storage organ C:N ratios based on Boudirsky et al. (2012) lead to consistent but variable C:N ratios in harvested crop organs, reflecting differences between crop types (Fig. 7). The leguminous crops (soybean, pulses) are not limited by N, as they can acquire the necessary N via biological N fixation. For these, C:N ratios of harvested organs are typically underestimated. Under unlimited N supply, C:N ratios are typically reduced (Fig. 7b).

We find that agricultural land use and associated fertilizer application greatly increases nitrogen pollution. Leaching (+60%) and ammonia volatilization (+25%) increase strongly, which is almost entirely driven by fertilizer inputs, not by land-use change (compare *LPJmL5* with *LPJmL5-PNV* and *LPJmL5-nF* in Table 4). On the contrary, N₂O emissions only change slightly, when agricultural land use is accounted for as increases in denitrification are partially compensated by decreases in nitrification under reduced net mineralization (mineralization minus immobilization flux) of soil organic matter (Table 4). The effect of agricultural land use and fertilizer application is also clearly detectable in the spatial patterns of leaching. The ratio of *LPJmL5-PNV* to *LPJmL5* (Fig. 8a) is mostly below 1 indicating higher leaching in agricultural areas. In natural vegetation under dry conditions also ratios above 1 can occur (Fig. 8b).

~~When limitations are lifted through unlimited supply (*LPJmL5-nL*), GPP is mostly increased, except in very dry environments. The scatter plot (Fig. 5b) shows that the GPP increase mainly occurs in low to moderately productive areas. Decreases in GPP under unlimited supply are possible where other factors are strongly limiting (e.g. water) and the higher supply leads to higher maintenance respiration under lower tissue C:N ratios, so that less biomass is available for leaves and thus less light can be intercepted.~~

Table 4. Global nitrogen pools and fluxes for the 4 different experiments with **LPJmL5-LPJmL5** and literature estimates (averages over the period 2000 to 2009). The suffix *-PNV* denotes experiments with potential natural vegetation, *-nL* with unlimited N supply, and *-nF* without fertilizer input.

N pools/fluxes	<i>LPJmL5</i>	Literature estimates LU	<i>LPJmL5-PNV</i>	Literature estimates PNV	<i>LPJmL5-nL</i>	<i>LPJmL5-nF</i>
Vegetation (PgN)	2.29	-	3.21	3.6 ¹ , 3.8 ² , 5.3 ³ , 16 ⁴	4.00	2.28
Soil organic matter (PgN)	130.9	-	138.9	120 ¹ , 101 ² , 61.4 ³ , 280 ⁴ , 95 ⁵	138.8	130.6
Soil NH ₄ ⁺ (TgN)	640.7	-	650.7	361 ³	-	637.7
Soil NO ₃ ⁻ (TgN)	5873	-	6282	580 ³	-	5636
Plant uptake (TgN yr ⁻¹)	751	-	836	970 ¹ , 1130 ² , 1080 ³ , 620 ⁴	1526	718
Mineralization (TgN yr ⁻¹)	1422	-	1715	980 ¹ , 1030 ² , 6300 ⁴	1766	1404
Immobilization (TgN yr ⁻¹)	781.6	-	937.3	-	774.7	778.2
Leaching (TgN yr ⁻¹)	72.63	93 ⁶ , 95 ⁷	45.39	13 ¹ , 87 ² , 5 ⁴	-	46.17
Volatilization (TgN yr ⁻¹)	19.11	-	15.27	-	-	14.03
Denitrification N ₂ O emissions (TgN yr ⁻¹)	6.43	-	5.89	-	-	5.67
Denitrification N ₂ emissions (TgN yr ⁻¹)	52.05	68 ⁶	47.63	-	-	45.88
Denitrification total (TgN yr ⁻¹)	58.48	72-85 ⁶ , 25 ⁷ , 67 ⁹	53.52	-	-	51.55
Nitrification N ₂ O (TgN yr ⁻¹)	7.37	-	8.33	-	-	6.74
total N ₂ O emissions (TgN yr ⁻¹)	13.80	11 ⁸ , 15 ⁹	12.63	-	-	12.41
Biological N fixation (TgN yr ⁻¹)	134.4	92 ⁶ , 118 ⁷ , 104-108 ⁸ , 107 ⁹	102.9	34 ¹ , 108 ² , 211 ⁴ , 58 ¹⁰	136.3	134.3

¹ Smith et al. (2014), ² Zaehle et al. (2010a), ³ Xu-Ri and Prentice (2008), ⁴ Lin et al. (2000), ⁵ Post et al. (1985), ⁶ Bouwman et al. (2013), ⁷ Sutton et al. (2013), ⁸ Galloway et al. (2013), ⁹ Galloway et al. (2004), ¹⁰ Vitousek et al. (2013)

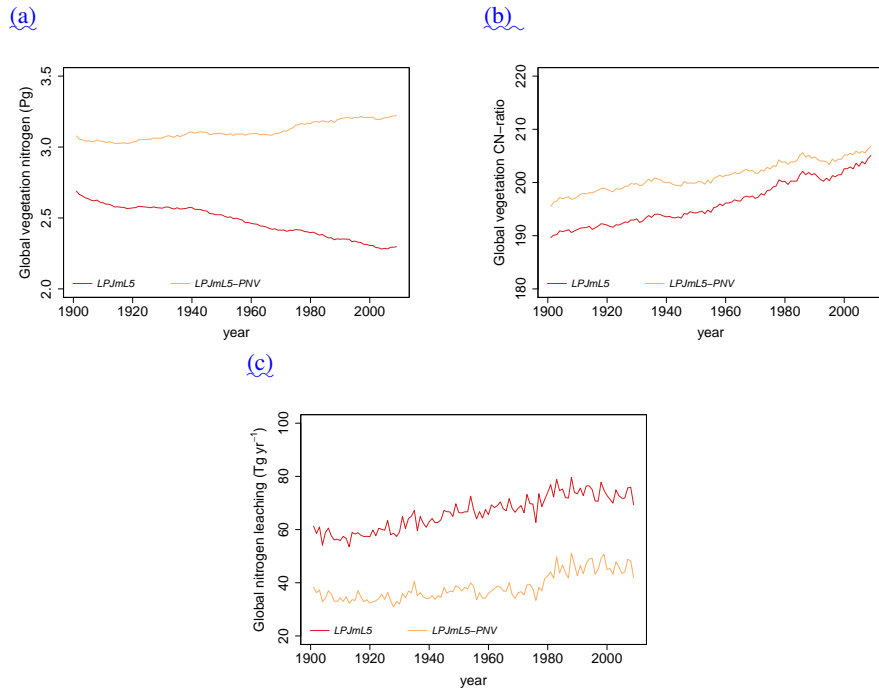


Figure 6. Simulated global time series of vegetation nitrogen (a), vegetation C:N ratios (b) and leaching (c) with land use (*LPJmL5*, red line) and potential natural vegetation (*LPJmL5-PNV*, orange line).

(a) (b) Ratio of GPP under actual limitations (*LPJmL5*) to unlimited supply (*LPJmL5-nL*) (a); values less than 1 indicate higher GPP under unlimited supply. The scatter plot (b) shows that GPP is increased through additional supply mostly in low to moderately productive regions.

4.4 Model evaluation

- 5 To evaluate model performance, we here focus on carbon and nitrogen pools and fluxes at global and specific sites. Many estimates are also model-based, so that these cannot be used for model evaluation but only for putting our simulation results into context.

4.4.1 N pools and fluxes

- Typically, simulated N pools and fluxes are within literature estimates (Table 4), although literature estimates are often broad, reflecting substantial uncertainty in these values. [Values from other model simulations are generally not suitable for an evaluation of model results as they may be wrong \(Kelley et al., 2013\), and we only include them here for pools and fluxes where no independent data is available. These model-based reference points include the vegetation N pool, soil mineral N pools, plant uptake rates, mineralization rates, and most global values assessed for potential natural vegetation \(PNV\). Vegetation N of the potential natural vegetation simulation, *LPJmL5-PNV*, is slightly below the other model-based estimates \(Table](#)

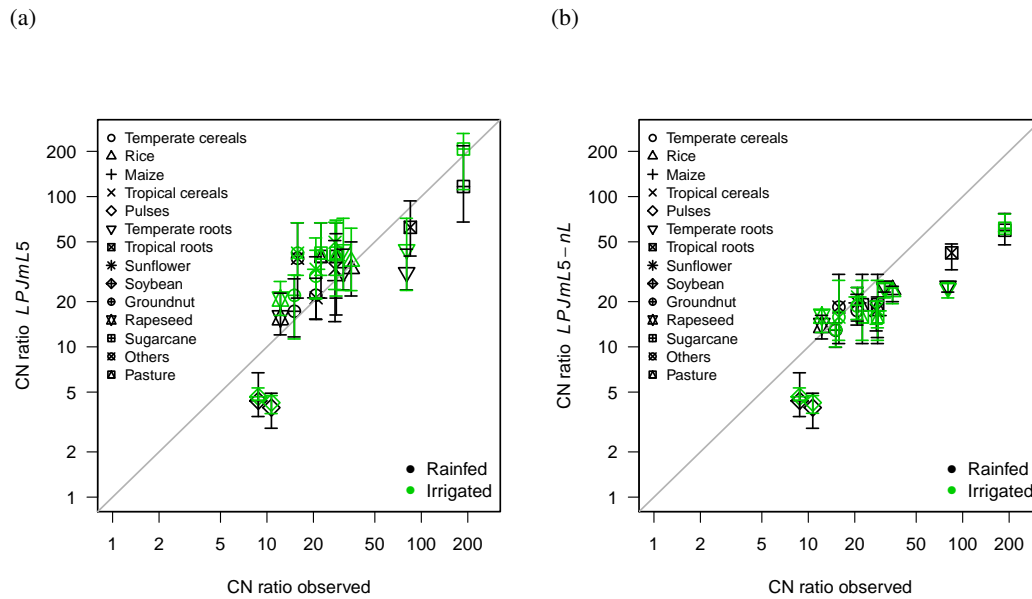


Figure 7. Observed C:N ratios of harvested crops versus simulated mean ratios for the crop PFTs (a) with N limitation ($LPJmL5$) and (b) without N limitation ($LPJmL5-nL$). The vertical error bars denote the 95% percentile.

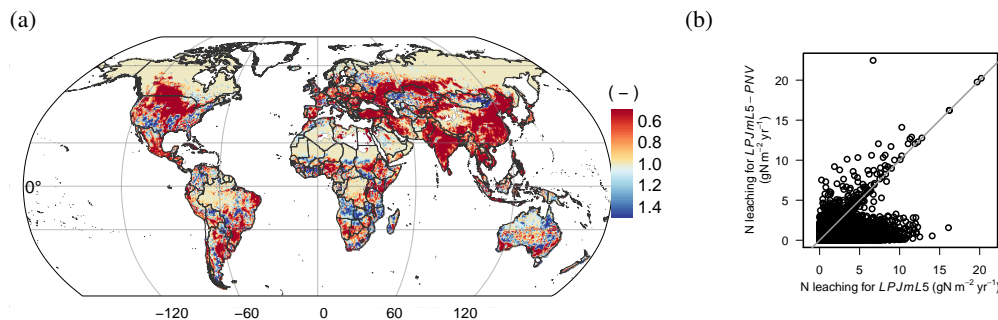


Figure 8. Ratio of leaching flux under potential natural vegetation ($LPJmL5-PNV$) to the leaching flux under actual land-use patterns ($LPJmL5$) (a); values less than 1 indicate higher leaching under actual land-use patterns. The scatter plot (b) shows that leaching is increased strongly mostly in regions where leaching is low under potential natural vegetation.

4), whereas other fluxes (e.g. plant uptake of N or mineralization) and pools (soil organic N) are within the range of reported values. For simulations with land use history, $LPJmL5$ ~~comparison~~ a comparison with independent data is possible for most of the emissions from the soil. There our values for leaching and N_2 emissions are slightly below other estimates. For the complimentary flux, N_2O emissions from denitrification, there is no other estimate, but total N_2O emissions from denitrifi-

5 cation and nitrification are within the range of other estimates again (Table 4). Xu-Ri and Prentice (2008) are the only study reporting global soil pools of mineral N forms, but for potential natural vegetation only and for the upper 1.5 m soil layer and this estimate is based on their model application, not on independent data. Our values, which are the inventory of 3 m soil, are

much higher than the estimates of Xu-Ri and Prentice (2008) by a factor of 2 and 10, respectively, for soil NH_4^+ and NO_3^- . Accounting for the content of the first 1.5 m, soil NO_3^- amounts to 847 TgN and soil NH_4^+ to 228 TgN. Therefore, in comparison to Xu-Ri and Prentice (2008) we overestimate NO_3^- values and underestimate NH_4^+ values in the soil but are in the same order of magnitude. The accumulation of NO_3^- in lower soil layers is a phenomenon also reported by Walvoord et al. (2003) and Ascott et al. (2017), although they report lower values than we find. In any case, this nitrogen pool is largely inaccessible to plants, as they have very little root access to these layers in our model. Also, higher NO_3^- than NH_4^+ concentrations are common in soils, as, e.g. reported by Kabala et al. (2017).

4.4.2 Carbon cycle dynamics

Carbon dynamics are mostly unchanged to the predecessor version ~~LPJmL-3.5~~ LPJmL3.5 (Table 3 and Fig. 4). In comparison to measured site-level GPP, NPP and vegetation carbon, ~~LPJmL-5~~ LPJmL5 (Luyssaert et al., 2007), LPJmL5 performs well, especially for GPP and NPP, but with a tendency to underestimate vegetation carbon (Fig. 9). The correlation of observed and simulated GPP and NPP values is statistically significant, the values of vegetation carbon are less correlated owing to the often broad spread of observations within one grid cell (error bars) and general difficulties to exactly reproduce disturbances, mortality, and age class distributions (Schaphoff et al., 2017a). Still the comparison shows that simulated values are in the right order of magnitude and are also often within the range of observations (error bar crosses 1:1 line in Fig. 9). Best correlation with observational data can be found for GPP. We also provide comparisons to eddy flux tower measurements (ORNL DAAC, 2011) in the supplement. SI Figs. S5-S11 show modelled versus observed net ecosystem exchange (NEE) rate defined as

$$\text{NEE} = \text{NPP} - \text{R}_{\text{h}}, \quad (71)$$

where R_h is the heterotrophic respiration. For some sites a time lag (e.g. site Renon/Ritten) between modelled and observed is visible. Because ~~LPJmL-5~~ LPJmL5 uses the phenology scheme of ~~LPJmL-3.5~~ LPJmL3.5 incorporating the new phenology of ~~LPJmL-4~~ LPJmL4 might reduce these deviations (for a comparison, see supplement of Schaphoff et al., 2017a). The overall agreement between modelled and observed NEE is satisfying. While LPJmL4 has an averaged Willmott coefficient of agreement (Willmott, 1982) of $\overline{W} = 0.63$, LPJmL5 results in $\overline{W} = 0.51$. Also the simulated evapotranspiration fluxes shown in SI Figs. S12-S20 agree very well with the observations ($\overline{W} = 0.79$).

4.4.3 Crop yields

The implementation of nitrogen limitation also greatly helps to improve the simulation of global patterns of crop productivity. Regional differences in crop productivity, ~~which~~ had to be calibrated via a scaling of the maximum leaf area index (LAI_{max}), the harvest index and the factor for scaling leaf-level photosynthesis to stand level (α_a), as described in Fader et al. (2010), because the LPJmL3.5 version could only distinguish irrigated from rainfed production but not other inputs such as fertilizers. The difference in crop productivity between low- and high-input regions can now largely be reproduced by the model, except for (compare yellow asterisk for uncalibrated with blue asterisk for calibrated LPJmL3.5 simulations with red circle and cross for LPJmL5 in Fig. 10 and SI Figs. S21–S23), which are based on the evaluation procedure as described by Müller et al. (2017).

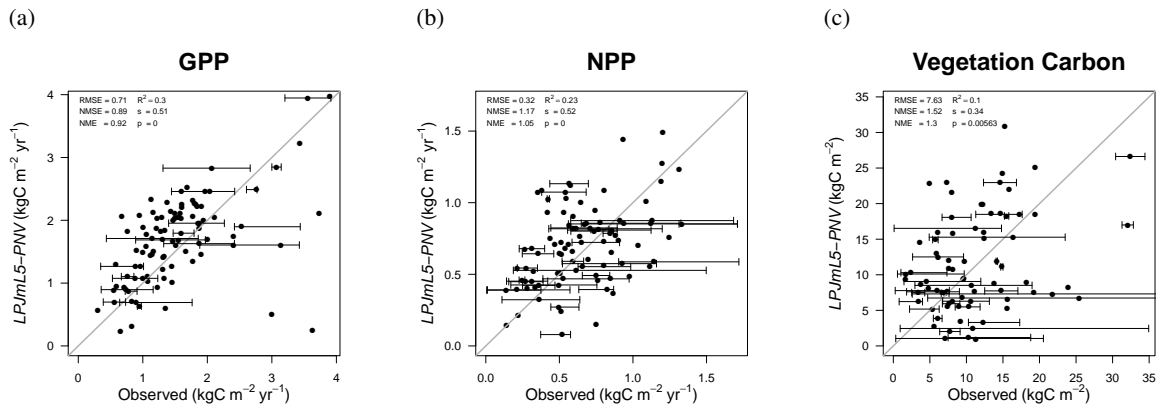


Figure 9. Observed ~~versus simulated~~-GPP (a), NPP (b) and vegetation carbon (c) data (Luyssaert et al., 2007) versus simulated data for natural vegetation (LPJmL5-PNV). The horizontal error bars denote the minima and maxima of observed site data belonging to the same LPJmL grid cell and the open dot is the mean. The thin black line denotes the 1:1 line. RMSE: root-mean-square error, NMSE: normalized mean square error, NME: normalized mean error, s: slope, p: significance.

In regions where fertilizer inputs and climate conditions are not the only yield limiting factors, e.g. in regions with poor pest management, an additional calibration of yield levels could be performed as described by Fader et al. (2010), but is not performed here. The temporal variance of simulated crop yields is often not affected much by accounting for N limitation and sometimes improves or worsens the time series correlation with FAO yield statistics (FAOSTAT), (Fig. 11 and SI Figs. S24–S26

5 in the supplementary material).

We also use the online tool as supplied by Müller et al. (2017) for comparing the crop yield simulations against the Global Gridded Crop Model Intercomparison (GGCMI) model ensemble. Also here, results show that ~~LPJmL-5~~ LPJmL5 improves with respect to reproducing absolute yield levels across different countries, but ~~that~~ there is little effect on the simulated inter-annual variability of crop yields. As with the calibrated ~~LPJmL-3.5~~ LPJmL3.5 version (Fader et al., 2010), the uncalibrated

10 ~~LPJmL-5~~ LPJmL5 simulations perform well in comparison to the other GGCMI models. We supply the output of that online model evaluation tool as supplementary material.

5 Discussion and conclusions

The current implementation of nitrogen dynamics into ~~LPJmL-3.5~~ forming LPJmL-5 ~~LPJmL3.5~~ forming LPJmL5 introduces a missing feature into a unique modeling framework of the terrestrial biosphere. ~~LPJmL-5~~ LPJmL5 combines natural vegetation

15 dynamics, the full terrestrial hydrology and managed grass- and croplands in one consistent framework with the associated carbon, water, and now also nitrogen pools and fluxes. Owing to parallel model development efforts, ~~LPJmL-5~~ LPJmL5 does not yet include all model features of the first open source version of LPJmL, ~~LPJmL-4~~ LPJmL4 (Schaphoff et al., 2017b, a),

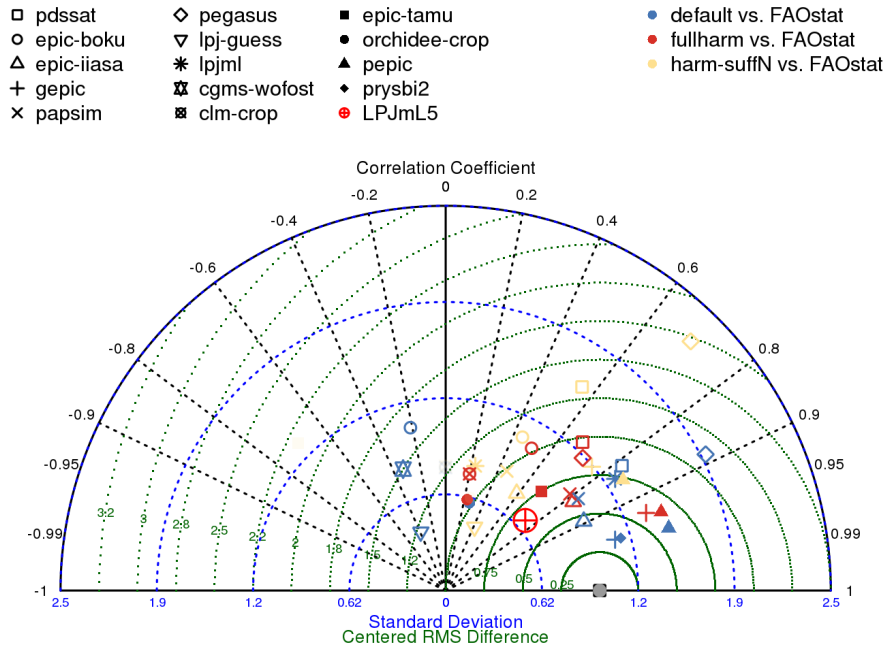


Figure 10. ~~Maize yield simulations~~ Taylor diagram of the spatial patterns (in $tFM ha^{-1}$ national mean yields) ~~for~~ of maize productivity. The performance of *LPJmL5* is depicted as the ~~10 top-producing countries for~~ red circlecross (\oplus) and should be compared to the ~~carbon-only~~ *LPJmL3.5* version *LPJmL3.5* simulations, the version with limitation depicted as stars (*) in yellow (uncalibrated) and with unlimited supply blue (calibrated). This figure was produced by the online crop model evaluation tool of Müller et al. (2017).

such as the updated allocation scheme for managed grasslands (?) (Rolinski et al., 2018) and the updated phenology scheme for natural vegetation (Forkel et al., 2014).

With the implementation of the nitrogen dynamics, the model simulations require new inputs, especially on atmospheric deposition, but also on fertilizer applications, where we currently use a static crop- and irrigation-specific data set, developed for the harmonization of crop models in the Agricultural Model Intercomparison and Improvement Project (AgMIP) (Elliott et al., 2015). This static fertilizer set also affects the simulation of historic carbon cycle dynamics, as high-input regions, such as large parts of Europe or northern America receive current high N inputs also in the early 20th century, whereas historic land expansion mostly moves into regions with currently lower input systems. As a consequence, land-use change leads to increasing nitrogen limitation and increasing C:N ratios, which may be an artifact from the static fertilizer input data set used.

As the historic land-use development and fertilizer application are important for simulated current biogeochemical cycles, historic time series of crop-specific fertilizer application would be desirable. Also, global data sets on crop rotations (Kollas et al., 2015), timing of field operations (Hutchings et al., 2012) or crop residue management, as well as livestock management

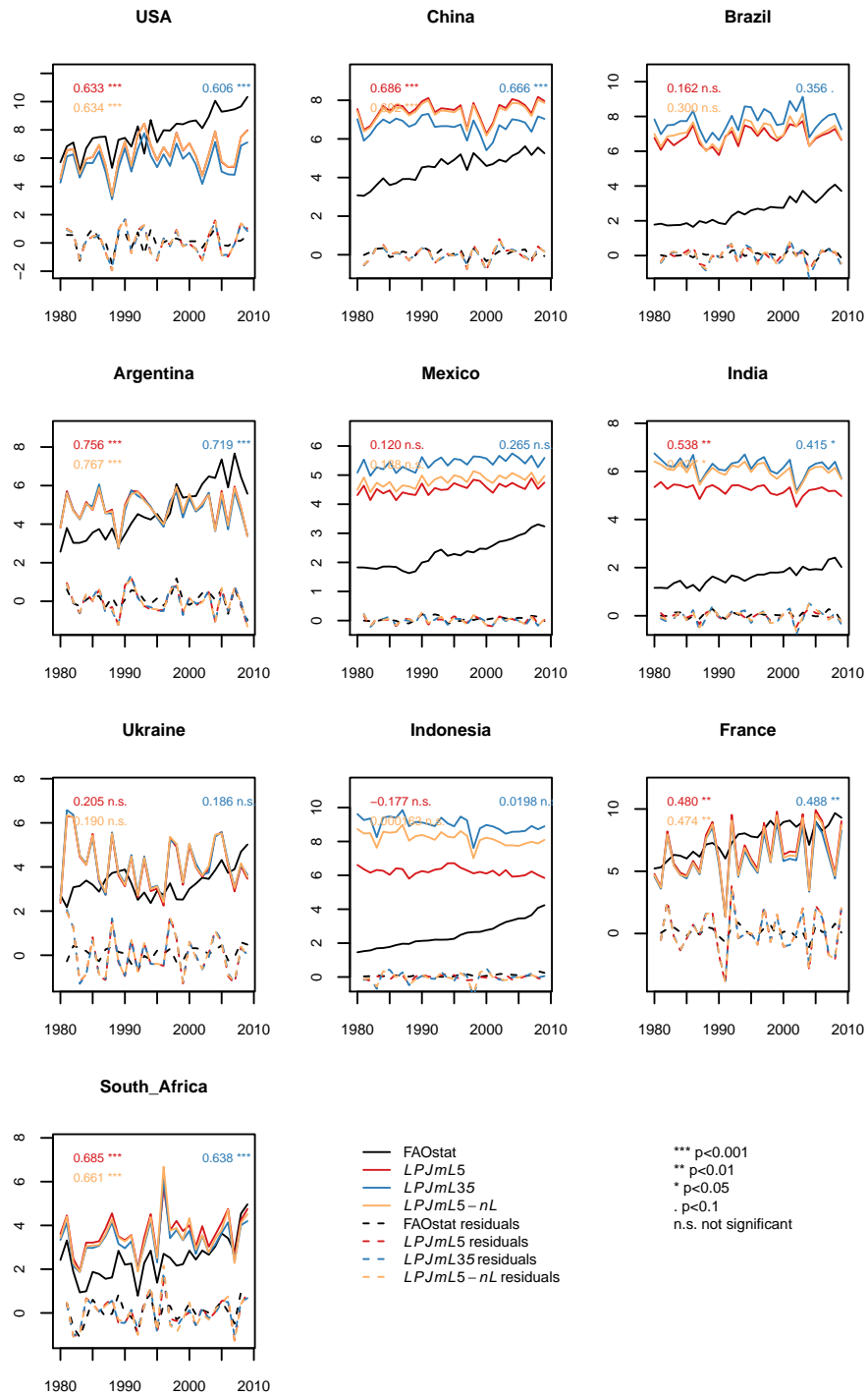


Figure 11. Maize yield simulations (in t fresh matter (FM) ha⁻¹) for the 10 top-producing countries for the carbon-only LPJmL3.5 version (LPJmL35), the version with N limitation (LPJmL5) and with unlimited N supply (LPJmL5-nL). The residuals plotted are the detrended observed and simulated yields.

systems ~~(?)~~ (Rolinski et al., 2018) would be an asset, as the interaction of different cropping systems and natural vegetation is now further increased via the nitrogen cycle.

This first implementation of nitrogen dynamics into LPJmL constitutes an operational modeling framework with many detailed processes resolved explicitly. Specific processes are currently implemented in a simplified manner, even though more
5 detailed approaches are available, as, e.g., for biological N fixation (Fisher et al., 2010). As such, some process may have to be revised upon further testing against new reference data. Additional reference data would greatly help to evaluate model performance, which currently is largely constrained to comparisons against other modeling results.

~~LPJmL-5~~ LPJmL5 constitutes a unique modeling framework that can now simulate global terrestrial carbon, water and nitrogen dynamics, consistently accounting for natural vegetation dynamics, agricultural crop- and grassland management and
10 water management.

Code and data availability. The source code is available upon request from the main author for the review process and for selected collaborative projects. We are in the process of setting up a publicly accessible open-source model code repository where the code as described here will be released. The source code will be generally available after final publication of this paper and a DOI for access will be provided. Data from the simulations conducted here is available upon request from the main author.

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

Acknowledgements. This study was supported by the German Federal Ministry of Education and Research's (BMBF's) "PalMod 2.3 Methankreislauf, Teilprojekt 2 Modellierung der Methanemissionen von Feucht- und Permafrostgebieten mit Hilfe von LPJmL", (FKZ 01LP1507C). C.M. and S.R. acknowledge financial support from the MACMIT project (01LN1317A) funded through the German Federal Ministry of Education and Research (BMBF). S.Z. was supported by the European Research Council (ERC) under the European Union's Horizon 2020
20 research and innovation programme (QUINCY; grant no. 647204).

References

- Arneth, A., Sitch, S., Pongratz, J., Stocker, B. D., Ciais, P., Poulter, B., Bayer, A. D., Bondeau, A., Calle, L., Chini, L. P., Gasser, T., Fader, M., Friedlingstein, P., Kato, E., Li, W., Lindeskog, M., Nabel, J. E. M. S., Pugh, T. A. M., Robertson, E., Viovy, N., Yue, C., and Zaehle, S.: Historical carbon dioxide emissions caused by land-use changes are possibly larger than assumed, *Nature Geosci*, 10, 79–84, doi:10.1038/ngeo2882, 2017.
- Arnold, J. G., Kiniry, J. R., Williams, J. R., Haney, E. B., and Neitsch, S. L.: Soil and water assessment tool input/output documentation version 2012, Texas Water Resources Institute, College Station, Texas, 2012.
- Ascott, M. J., Gooddy, D. C., Wang, L., Stuart, M. E., Lewis, M. A., Ward, R. S., and Binley, A. M.: Global patterns of nitrate storage in the vadose zone, *Nature Communications*, 8, 1416, doi:10.1038/s41467-017-01321-w, <https://doi.org/10.1038/s41467-017-01321-w>, 2017.
- Atkin, O., Schortemeyer, M., McFarlane, N., and Evans, J.: The response of fast- and slow-growing *Acacia* species to elevated atmospheric CO₂: an analysis of the underlying components of relative growth rate, *Oecologica*, 120, 544–554, doi:10.1007/s004420050889, 1999.
- Baker, T. R., Phillips, O. L., Laurance, W. F., Pitman, N. C. A., Almeida, S., Arroyo, L., DiFiore, A., Erwin, T., Higuchi, N., Killeen, T. J., Laurance, S. G., Nascimento, H., Monteagudo, A., Neill, D. A., Silva, J. N. M., Malhi, Y., Gonzalez, G. L., Peacock, J., Quesada, C. A., Lewis, S. L., and Lloyd, J.: Do species traits determine patterns of wood production in Amazonian forests?, *Biogeosciences*, 6, 297–307, 2009.
- Batjes, N. H., ed.: Global Data Set of Derived Soil Properties, 0.5-Degree Grid (ISRIC-WISE), Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A., doi:10.3334/ORNLDAAAC/546., 2000.
- Becker, A., Finger, P., Meyer-Christoffer, A., Rudolf, B., Schamm, K., Schneider, U., and Ziese, M.: A description of the global land-surface precipitation data products of the Global Precipitation Climatology Centre with sample applications including centennial (trend) analysis from 1901–present, *Earth System Science Data*, 5, 71–99, doi:10.5194/essd-5-71-2013, 2013.
- Bessou, C., Mary, B., Léonard, J., Roussel, M., Gréhan, E., and Gabrielle, B.: Modelling soil compaction impacts on nitrous oxide emissions in arable fields, *European Journal of Soil Science*, 61, 348–363, doi:10.1111/j.1365-2389.2010.01243.x, 2010.
- Bodirsky, B. L., Popp, A., Weindl, I., Dietrich, J. P., Rolinski, S., Scheffele, L., Schmitz, C., and Lotze-Campen, H.: N₂O emissions from the global agricultural nitrogen cycle – current state and future scenarios, *Biogeosciences*, 9, 4169–4197, doi:10.5194/bg-9-4169-2012, 2012.
- Bondeau, A., Smith, P. C., Zaehle, S., Schaphoff, S., Lucht, W., Cramer, W., and Gerten, D.: Modelling the role of agriculture for the 20th century global terrestrial carbon balance, *Global Change Biology*, 13, 679–706, 2007.
- Bouwman, A. F., Beusen, A. H. W., Griffioen, J., Van Groenigen, J. W., Hefting, M. M., Oenema, O., Van Puijenbroek, P. J. T. M., Seitzinger, S., Slomp, C. P., and Stehfest, E.: Global trends and uncertainties in terrestrial denitrification and N₂O emissions, *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 368, doi:10.1098/rstb.2013.0112, 2013.
- Chang, J., Ciais, P., Wang, X., Piao, S., Asrar, G., Betts, R., Chevallier, F., Dury, M., François, L., Frieler, K., Ros, A. G. C., Henrot, A.-J., Hickler, T., Ito, A., Morfopoulos, C., Munhoven, G., Nishina, K., Ostberg, S., Pan, S., Peng, S., Rafique, R., Rey, C., Rödenbeck, C., Schaphoff, S., Steinkamp, J., Tian, H., Viovy, N., Yang, J., Zeng, N., and Zhao, F.: Benchmarking carbon fluxes of the ISIMIP2a biome models, *Environmental Research Letters*, 12, 045 002, 2017.
- Cleveland, C. C., Townsend, A. R., Schimel, D. S., Fisher, H., Howarth, R. W., Hedin, L. O., Perakis, S. S., Latty, E. F., Von Fischer, J. C., 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, 1999.

- Collatz, G. J., Berry, J. A., Farquhar, G. D., and Pierce, J.: The relationship between the Rubisco reaction mechanism and models of photosynthesis, *Plant, Cell and Environment*, 13, 219–225, 1990.
- Comins, H. N. and McMurtrie, R. E.: Long-Term Response of Nutrient-Limited Forests to CO₂ Enrichment; Equilibrium Behavior of Plant-Soil Models, *Ecological Applications*, 3, 666–681, doi:10.2307/1942099, 1993.
- 5 Cornelissen, J., Diez, P., and Hunt, R.: Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types, *Journal of Ecology*, 84, 755–765, doi:10.2307/2261337, 1996.
- Cornelissen, J., Werger, M., CastroDiez, P., vanRheenen, J., and Rowland, A.: Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types, *Oecologia*, 111, 460–469, doi:10.1007/s004420050259, 1997.
- Cornelissen, J., Qusteded, H., Gwynn-Jones, D., Van Logtestijn, R., De Beus, M., Kondratchuk, A., Callaghan, T., and Aerts, R.: Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types, *Functional Ecology*, 18, 779–786, doi:10.1111/j.0269-8463.2004.00900.x, 2004.
- 10 Dee, D. P., Uppala, S. M., Simmons, A. J., Berrisford, P., Poli, P., Kobayashi, S., Andrae, U., Balmaseda, M. A., Balsamo, G., Bauer, P., Bechtold, P., Beljaars, A. C. M., van de Berg, L., Bidlot, J., Bormann, N., Delsol, C., Dragani, R., Fuentes, M., Geer, A. J., Haimberger, L., Healy, S. B., Hersbach, H., Hólm, E. V., Isaksen, I., Kållberg, P., Köhler, M., Matricardi, M., McNally, A. P., Monge-Sanz, B. M., Morcrette, J.-J., Park, B.-K., Peubey, C., de Rosnay, P., Tavolato, C., Thépaut, J.-N., and Vitart, F.: The ERA-Interim reanalysis: configuration and performance of the data assimilation system, *Quarterly Journal of the Royal Meteorological Society*, 137, 553–597, doi:10.1002/qj.828, 2011.
- 15 Doran, J. W., Mielke, L. N., and Stamatiadis, S.: Microbial activity and N cycling as regulated by soil water-filled pore space, in: 11th International Conference, Int. Soil Tillage Res. Orgo (ISTRO), Edinburgh, Scotland, 1988.
- 20 Elliott, J., Müller, C., Deryng, D., Chrysanthacopoulos, J., Boote, K. J., Büchner, M., Foster, I., Glotter, M., Heinke, J., Iizumi, T., Izaurralde, R. C., Mueller, N. D., Ray, D. K., Rosenzweig, C., Ruane, A. C., and Sheffield, J.: The Global Gridded Crop Model Intercomparison: data and modeling protocols for Phase 1 (v1.0), *Geosci. Model Dev.*, 8, 261–277, doi:10.5194/gmd-8-261-2015, 2015.
- Fader, M., Rost, S., Müller, C., Bondeau, A., and Gerten, D.: Virtual water content of temperate cereals and maize: Present and potential future patterns, *Journal of Hydrology*, 384, 218–231, doi:10.1016/j.jhydrol.2009.12.011, 2010.
- 25 FAOSTAT: FAOSTAT, <http://www.fao.org/faostat/en/#data/QC>.
- Fisher, J. B., Sitch, S., Malhi, Y., Fisher, R. A., Huntingford, C., and Tan, S.-Y.: Carbon cost of plant nitrogen acquisition: A mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and fixation, *Global Biogeochemical Cycles*, 24, GB1014, doi:10.1029/2009GB003621, 2010.
- Forkel, M., Carvalhais, N., Schaphoff, S., von Bloh, W., Migliavacca, M., Thurner, M., and Thonicke, K.: Identifying environmental controls on vegetation greenness phenology through model–data integration, *Biogeosciences*, 11, 7025–7050, doi:10.5194/bg-11-7025-2014, 2014.
- 30 Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Qusteded, H., Grigulis, K., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Freitas, H., Golodets, C., Jouany, C., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V. P., Quetier, F., Robson, M., Sternberg, M., Theau, J.-P., Thebault, A., and Zarovali, M.: Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe, *Ecology*, 90, 598–611, doi:10.1890/08-0418.1, 2009.
- 35 Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P., and Aerts, R.: Evidence of the ‘plant economics spectrum’ in a subarctic flora, *Journal of Ecology*, 98, 362–373, doi:10.1111/j.1365-2745.2009.01615.x, 2010a.

- Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P., and Aerts, R.: Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits?, *New Phytologist*, 186, 879–889, doi:10.1111/j.1469-8137.2010.03228.x, 2010b.
- Friend, A. D., Stevens, A. K., Knox, R. G., and Cannell, M. G. R.: A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0), *Ecological Modelling*, 95, 249–287, doi:10.1016/S0304-3800(96)00034-8, 1997.
- Friend, A. D., Lucht, W., Rademacher, T. T., Kerbin, R., Betts, R., Cadule, P., Ciais, P., Clark, D. B., Dankers, R., Falloon, P. D., Ito, A., Kahana, R., Kleidon, A., Lomas, M. R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A., and Woodward, F. I.: Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO₂, *Proceedings of the National Academy of Sciences*, 111, 3280–3285, doi:10.1073/pnas.1222477110, 2014.
- 10 Fyllas, N. M., Patino, S., Baker, T. R., Nardoto, G. B., Martinelli, L. A., Quesada, C. A., Paiva, R., Schwarz, M., Horna, V., Mercado, L. M., Santos, A., Arroyo, L., Jimenez, E. M., Luizao, F. J., Neill, D. A., Silva, N., Prieto, A., Rudas, A., Silviera, M., Vieira, I. C. G., Lopez-Gonzalez, G., Malhi, Y., Phillips, O. L., and Lloyd, J.: Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate, *Biogeosciences*, 6, 2677–2708, doi:10.5194/bg-6-2677-2009, 2009.
- 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., 15 Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, A. R., and Vöosmarty, C. J.: Nitrogen Cycles: Past, Present, and Future, *Biogeochemistry*, 70, 153–226, doi:10.1007/s10533-004-0370-0, 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 B: Biological Sciences*, 368, doi:10.1098/rstb.2013.0120, 2013.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., 20 Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V. P., Quested, H., Quetier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.-P., Thebault, A., Vile, D., and Zarovali, M. P.: Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites, *Annals of Botany*, 99, 967–985, doi:10.1093/aob/mcm215, 90th Annual Meeting of the Ecological-Society-of-America/9th International Congress of Ecology, Montreal, Canada, Aug. 2005, 2007.
- 25 Gerber, S., Hedin, L. O., Oppenheimer, M., Pacala, S. W., and Shevliakova, E.: Nitrogen cycling and feedbacks in a global dynamic land model, *Global Biogeochemical Cycles*, 24, doi:10.1029/2008GB003336, 2010.
- Han, W., Fang, J., Guo, D., and Zhang, Y.: Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China, *New Phytologist*, 168, 377–385, doi:10.1111/j.1469-8137.2005.01530.x, 2005.
- Harris, I., Jones, P., Osborn, T., and Lister, D.: Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset, 30 *International Journal of Climatology*, 34, 623–642, doi:10.1002/joc.3711, 2014.
- Haxeltine, A. and Prentice, I. C.: A General Model for the Light-Use Efficiency of Primary Production, *Functional Ecology*, 10, 551–561, doi:10.2307/2390165, 1996.
- Hutchings, N. J., Reinds, G. J., Leip, A., Wattenbach, M., Bienkowski, J. F., Dalgaard, T., Dragosits, U., Drouet, J. L., Durand, P., Maury, O., and de Vries, W.: A model for simulating the timelines of field operations at a European scale for use in complex dynamic models, 35 *Biogeosciences*, 9, 4487–4496, doi:10.5194/bg-9-4487-2012, 2012.
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, and Schulze ED: A global analysis of root distributions for terrestrial biomes, *Oecologia*, 108, 389–411, doi:10.1007/BF00333714, 1996.

- Kabala, C., Karczewska, A., Gałka, B., Cuske, M., and Sowiński, J.: Seasonal dynamics of nitrate and ammonium ion concentrations in soil solutions collected using MacroRhizon suction cups, *Environmental Monitoring and Assessment*, 189, 304, doi:10.1007/s10661-017-6022-3, <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC5487726/>, 2017.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. 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., Chambers, J. Q., Chapin Iii, 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. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A., Kerkhoff, A. J., Kirkup, D., 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., Llusià, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., Müller, S. C., Nadrowski, K., Naeem, S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W. 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., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E., and Wirth, C.: TRY – a global database of plant traits, *Global Change Biology*, 17, 2905–2935, doi:10.1111/j.1365-2486.2011.02451.x, 2011.
- Kelley, D. I., Prentice, I. C., Harrison, S. P., Wang, H., Simard, M., Fisher, J. B., and Willis, K. O.: A comprehensive benchmarking system for evaluating global vegetation models, *Biogeosciences*, pp. 3313–3340, doi:10.5194/bg-10-3313-2013, 2013.
- Klein Goldewijk, K. and van Drecht, G.: HYDE 3: Current and historical population and land cover, in: *Integrated modelling of global environmental change. An overview of IMAGE 2.4.*, edited by Bouwman, A., T. K., and Klein Goldewijk, K., pp. 93–111, Netherlands Environmental Assessment Agency (MNP), Bilthoven, The Netherlands, 2006.
- Kollas, C., Kersebaum, K. C., Nendel, C., Manevski, K., Müller, C., Palosuo, T., Armas-Herrera, C. M., Beaudoin, N., Bindi, M., Charfeddine, M., Conradt, T., Constantin, J., Eitzinger, J., Ewert, F., Ferrise, R., Gaiser, T., Cortazar-Atauri, I. G. d., Giglio, L., Hlavinka, P., Hoffmann, H., Hoffmann, M. P., Launay, M., Manderscheid, R., Mary, B., Mirschel, W., Moriondo, M., Olesen, J. E., Öztürk, I., Pacholski, A., Ripoche-Wachter, D., Roggero, P. P., Roncossek, S., Rötter, R. P., Ruget, F., Sharif, B., Trnka, M., Ventrella, D., Waha, K., Wegehenkel, M., Weigel, H.-J., and Wu, L.: Crop rotation modelling—A European model intercomparison, *European Journal of Agronomy*, 70, 98–111, doi:10.1016/j.eja.2015.06.007, 2015.
- Krysanova, V. and Wechsung, F.: SWIM (Soil and Water Integrated Model) User Manual, <https://www.pik-potsdam.de/members/valen/swim>, 2000.
- Kurokawa, H. and Nakashizuka, T.: Leaf herbivory and decomposability in a Malaysian tropical rain forest, *Ecology*, 89, 2645–2656, doi:10.1890/07-1352.1, 2008.
- Lamarque, J.-F., Dentener, F., McConnell, J., Ro, C.-U., Shaw, M., Vet, R., Bergmann, D., Cameron-Smith, P., Dalsoren, S., Doherty, R., Faluvegi, G., Ghan, S. J., Josse, B., Lee, Y. H., MacKenzie, I. A., Plummer, D., Shindell, D. T., Skeie, R. B., Stevenson, D. S., Strode, S., Zeng, G., Curran, M., Dahl-Jensen, D., Das, S., Fritzsche, D., and Nolan, M.: Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): evaluation of historical and projected future changes, *Atmospheric Chemistry and Physics*, 13, 7997–8018, doi:10.5194/acp-13-7997-2013, 2013.

- Laughlin, D. C., Leppert, J. J., Moore, M. M., and Sieg, C. H.: A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora, *Functional Ecology*, 24, 493–501, doi:10.1111/j.1365-2435.2009.01672.x, 2010.
- Le Quéré, C., Andrew, R. M., Canadell, J. G., Sitch, S., Korsbakken, J. I., Peters, G. P., Manning, A. C., Boden, T. A., Tans, P. P., Houghton, R. A., Keeling, R. F., Alin, S., Andrews, O. D., Anthoni, P., Barbero, L., Bopp, L., Chevallier, F., Chini, L. P., Ciais, P., Currie, K., Delire, C., Doney, S. C., Friedlingstein, P., Gkritzalis, T., Harris, I., Hauck, J., Haverd, V., Hoppema, M., Klein Goldewijk, K., Jain, A. K., Kato, E., Körtzinger, A., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Lombardozzi, D., Melton, J. R., Metzl, N., Millero, F., Monteiro, P. M. S., Munro, D. R., Nabel, J. E. M. S., Nakaoka, S.-I., O'Brien, K., Olsen, A., Omar, A. M., Ono, T., Pierrot, D., Poulter, B., Rödenbeck, C., Salisbury, J., Schuster, U., Schwinger, J., Séférian, R., Skjelvan, I., Stocker, B. D., Sutton, A. J., Takahashi, T., Tian, H., Tilbrook, B., van der Laan-Luijkx, I. T., van der Werf, G. R., Viovy, N., Walker, A. P., Wiltshire, A. J., and Zaehle, S.: Global Carbon Budget 2016, *Earth System Science Data*, 8, 605–649, doi:10.5194/essd-8-605-2016, 2016.
- Lehner, B. and Döll, P.: Development and validation of a global database of lakes, reservoirs and wetlands, *Journal of Hydrology*, 296, 1–22, doi:10.1016/j.jhydrol.2004.03.028, 2004.
- Lehner, B., Liermann, C. R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., and Magome, J.: High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management, *Frontiers in Ecology and the Environment*, 9, 494–502, doi:10.1890/100125, 2011.
- Lin, B.-L., Sakoda, A., Shibasaki, R., Goto, N., and Suzuki, M.: Modelling a global biogeochemical nitrogen cycle in terrestrial ecosystems, *Ecological Modelling*, 135, 89–110, doi:10.1016/S0304-3800(00)00372-0, 2000.
- Loveys, B., Atkinson, L., Sherlock, D., Roberts, R., Fitter, A., and Atkin, O.: Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast- and slow-growing plant species, *Global Change Biology*, 9, 895–910, doi:10.1046/j.1365-2486.2003.00611.x, 2003.
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J. M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, A. J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutya, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J. W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Rouspard, O., Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C., Smith, M. L., Tang, J., Valentini, R., Vesala, T., and Janssens, I. A.: CO₂ balance of boreal, temperate, and tropical forests derived from a global database, *Global Change Biology*, 13, 2509–2537, doi:10.1111/j.1365-2486.2007.01439.x, 2007.
- Malhi, S. S. and McGill, W. B.: Nitrification in three Alberta soils: Effect of temperature, moisture and substrate concentration, *Soil Biology and Biochemistry*, 14, 393–399, doi:10.1016/0038-0717(82)90011-6, 1982.
- Montes, F., Rotz, C. A., and Chaoui, H.: Process Modeling of Ammonia Volatilization from Ammonium Solution and Manure Surfaces: A Review with Recommended Models, *Transactions of the ASABE*, 52, 1707–1720, doi:10.13031/2013.29133, 2009.
- Mueller, N. D., Gerber, J. S., Johnston, M., Ray, D. K., Ramankutty, N., and Foley, J. A.: Closing yield gaps through nutrient and water management, *Nature*, 490, 254–257, doi:10.1038/nature11420, 2012.
- Müller, C., Bondeau, A., Lotze-Campen, H., Cramer, W., and Lucht, W.: Comparative impact of climatic and nonclimatic factors on global terrestrial carbon and water cycles, *Global Biogeochemical Cycles*, 20, GB4015, doi:10.1029/2006GB002742, 2006.

- Müller, C., Stehfest, E., van Minnen, J. G., Strengers, B., von Bloh, W., Beusen, A. H., Schaphoff, S., Kram, T., and Lucht, W.: Drivers and patterns of land biosphere carbon balance reversal, *Environmental Research Letters*, 11, 044 002, doi:10.1088/1748-9326/11/4/044002, 2016.
- Müller, C., Elliott, J., Chrysanthacopoulos, J., Arneth, A., Balkovic, J., Ciais, P., Deryng, D., Folberth, C., Glotter, M., Hoek, S., Iizumi, T., Izaurrealde, R. C., Jones, C., Khabarov, N., Lawrence, P., Liu, W., Olin, S., Pugh, T. A. M., Ray, D. K., Reddy, A., Rosenzweig, C., Ruane, A. C., Sakurai, G., Schmid, E., Skalsky, R., Song, C. X., Wang, X., de Wit, A., and Yang, H.: Global gridded crop model evaluation: benchmarking, skills, deficiencies and implications, *Geoscientific Model Development*, 10, 1403–1422, doi:10.5194/gmd-10-1403-2017, 2017.
- Neitsch, S. L., Arnold, J. G., Kiniry, J. R., Srinivasan, R., and Williams, J. R.: Soil and water assessment tool user’s manual version 2000, GSWRL report, 202, 2002.
- Neitsch, S. L., Arnold, J. G., Kiniry, J. R., and Williams, J. R.: Soil and water assessment tool theoretical documentation, Texas Water Resources Institute, College Station, Texas, 2005.
- New, M., Hulme, M., and Jones, P.: Representing Twentieth-Century Space–Time Climate Variability. Part II: Development of 1901–96 Monthly Grids of Terrestrial Surface Climate, *Journal of Climate*, 13, 2217–2238, doi:10.1175/1520-0442(2000)013<2217:RTCSTC>2.0.CO;2, 2000.
- Niinemets, U.: Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants, *New Phytologist*, 144, 35–47, doi:10.1046/j.1469-8137.1999.00466.x, 4th New Phytologist Symposium, Montpellier, France, Oct 05-06, 1998, 1999.
- Niinemets, U.: Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs, *Ecology*, 82, 453–469, doi:10.1890/0012-9658(2001)082[0453:GSCCOL]2.0.CO;2, 2001.
- 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 of the United States of America*, 102, 18 052–18 056, doi:10.1073/pnas.0509478102, 2005.
- Ogaya, R. and Penuelas, J.: Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: photosynthetic response to experimental drought conditions, *Environmental and Experimental Botany*, 50, 137–148, doi:10.1016/S0098-8472(03)00019-4, 2003.
- Ogaya, R. and Penuelas, J.: Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*, *Biologia Plantarum*, 50, 373–382, doi:10.1007/s10535-006-0052-y, 2006.
- Ogaya, R. and Penuelas, J.: Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought, *Plant Ecology*, 189, 291–299, doi:10.1007/s11258-006-9184-6, 2007.
- Ogaya, R. and Penuelas, J.: Changes in leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for three Mediterranean tree species in relation to soil water availability, *Acta Oecologica-International Journal of Ecology*, 34, 331–338, doi:10.1016/j.actao.2008.06.005, 2008.
- Ordóñez, J. C., van Bodegom, P. M., Witte, J.-P. M., Bartholomeus, R. P., van Hal, J. R., and Aerts, R.: Plant Strategies in Relation to Resource Supply in Mesic to Wet Environments: Does Theory Mirror Nature?, *American Naturalist*, 175, 225–239, doi:10.1086/649582, 2010.
- ORNL DAAC, Oak Ridge, T. U.: Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC), <http://fluxnet.ornl.gov/>, 2011.

- Pakeman, R. J., Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Freitas, H., Golodets, C., Kigel, J., Kleyer, M., Leps, J., Meier, T., Papadimitriou, M., Papanastasis, V. P., Qusteded, H., Quetier, F., Rusch, G., Sternberg, M., Theau, J.-P., Thebault, A., and Vile, D.: Impact of abundance weighting on the response of seed traits to climate and land use, *Journal of Ecology*, 96, 355–366, doi:10.1111/j.1365-2745.2007.01336.x, 2008.
- 5 Pakeman, R. J., Leps, J., Kleyer, M., Lavorel, S., Garnier, E., and Consortium, V.: Relative climatic, edaphic and management controls of plant functional trait signatures, *Journal of Vegetation Science*, 20, 148–159, doi:10.1111/j.1654-1103.2009.05548.x, 2009.
- Parton, W. J., Mosier, A. R., Ojima, D. S., Valentine, D. W., Schimel, D. S., Weier, K., and Kulmala, A. E.: Generalized model for N₂ and N₂O production from nitrification and denitrification, *Global Biogeochemical Cycles*, 10, 401–412, doi:10.1029/96GB01455, 1996.
- Parton, W. J., Holland, E. A., Del Grosso, S. J., Hartman, M. D., Martin, R. E., Mosier, A. R., Ojima, D. S., and Schimel, D. S.:
10 Generalized model for NO₂ and N₂O emissions from soils, *Journal of Geophysical Research: Atmospheres*, 106, 17 403–17 419, doi:10.1029/2001JD900101, 2001.
- 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., Czimczik, C. I., Gallo, J., Horna, V., Hoyos, E. J., Jimenez, E. M., Palomino, W., Peacock, J., Pena-Cruz, A., Sarmiento, C., Sota, A., Turriago, J. D., Villanueva, B., Vitzthum, P., Alvarez, E., Arroyo, L., Baraloto, C., Bonal, D., Chave, J., Costa, A. C. L., Herrera,
15 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, doi:10.5194/bg-6-545-2009, 2009.
- Penuelas, J., Sardans, J., Llusia, J., Owen, S. M., Carnicer, J., Giambelluca, T. W., Rezende, E. L., Waite, M., and Niinemets, U.: Faster
20 returns on ‘leaf economics’ and different biogeochemical niche in invasive compared with native plant species, *Global Change Biology*, 16, 2171–2185, doi:10.1111/j.1365-2486.2009.02054.x, 2010a.
- Penuelas, J., Sardans, J., Llusia, J., Owen, S. M., Silva, J., and Niinemets, U.: Higher Allocation to Low Cost Chemical Defenses in Invasive Species of Hawaii, *Journal of Chemical Ecology*, 36, 1255–1270, doi:10.1007/s10886-010-9862-7, 2010b.
- Portmann, F. T., Siebert, S., and Döll, P.: MIRCA2000 - Global monthly irrigated and rainfed crop areas around the year 2000: A new high-
25 resolution data set for agricultural and hydrological modeling, *Global Biogeochemical Cycles*, 24, 1–24, doi:10.1029/2008GB003435, 2010.
- Post, W. M., Pastor, J., Zinke, P. J., and Stangenberger, A. G.: Global patterns of soil nitrogen storage, *Nature*, 317, 613–616, doi:10.1038/317613a0, 1985.
- Potter, P., Ramankutty, N., Bennett, E. M., and Donner, S. D.: Characterizing the Spatial Patterns of Global Fertilizer Application and Manure
30 Production, *Earth Interactions*, 14, 1–22, doi:10.1175/2009EI288.1, 2010.
- Qusteded, H., Cornelissen, J., Press, M., Callaghan, T., Aerts, R., Trosien, F., Riemann, P., Gwynn-Jones, D., Kondratchuk, A., and Jonasson, S.: Decomposition of sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites, *Ecology*, 84, 3209–3221, doi:10.1890/02-0426, 2003.
- Rolinski, S., Müller, C., Heinke, J., Weindl, I., Biewald, A., Boudirsky, B. L., Bondeau, A., Boons-Prins, E. R., Bouwman, A. F., Leffelaar,
35 P. A., te Roller, J. A., Schaphoff, S., and Thonicke, K.: Modeling vegetation and carbon dynamics of managed grasslands at the global scale with LPJmL 3.6, *Geoscientific Model Development*, 11, 429–451, doi:10.5194/gmd-11-429-2018, 2018.
- Sardans, J., Penuelas, J., and Ogaya, R.: Drought-induced changes in C and N stoichiometry in a *Quercus ilex* Mediterranean forest, *Forest Science*, 54, 513–522, 2008a.

- Sardans, J., Penuelas, J., Prieto, P., and Estiarte, M.: Changes in Ca, Fe, Mg, Mo, Na, and S content in a Mediterranean shrubland under warming and drought, *Journal of Geophysical Research-Biogeosciences*, 113, doi:10.1029/2008JG000795, 2008b.
- Schaphoff, S., Heyder, U., Ostberg, S., Gerten, D., Heinke, J., and Lucht, W.: Contribution of permafrost soils to the global carbon budget, *Environmental Research Letters*, 8, 014 026, 2013.
- 5 Schaphoff, S., Forkel, M., Müller, C., Knauer, J., von Bloh, W., Biemans, H., Gerten, D., Heinke, J., Jägermeyr, J., Lucht, W., Rammig, A., Thonicke, K., and Waha, K.: LPJmL4 – a dynamic global vegetation model with managed land: Part II – Model evaluation, *Geoscientific Model Development Discussions*, 2017, 1–41, doi:10.5194/gmd-2017-146, 2017a.
- Schaphoff, S., von Bloh, W., Rammig, A., Thonicke, K., Forkel, M., Biemans, H., Gerten, D., Heinke, J., Jägermeyr, J., Knauer, J., Lucht, W., Müller, C., Rolinski, S., and Waha, K.: LPJmL4 – a dynamic global vegetation model with managed land: Part I – Model description, *Geoscientific Model Development Discussions*, 2017, 1–59, doi:10.5194/gmd-2017-145, 2017b.
- 10 Schewe, J., Heinke, J., Gerten, D., Haddeland, I., Arnell, N. W., Clark, D. B., Dankers, R., Eisner, S., Fekete, B. M., Colón-González, F. J., Gosling, S. N., Kim, H., Liu, X., Masaki, Y., Portmann, F. T., Satoh, Y., Stacke, T., Tang, Q., Wada, Y., Wisser, D., Albrecht, T., Frieler, K., Piontek, F., Warszawski, L., and Kabat, P.: Multimodel assessment of water scarcity under climate change, *Proceedings of the National Academy of Sciences*, 111, 3245–3250, doi:10.1073/pnas.1222460110, 2014.
- 15 Schimel, D., Stephens, B. B., and Fisher, J. B.: Effect of increasing CO₂ on the terrestrial carbon cycle, *Proceedings of the National Academy of Sciences*, 112, 436–441, doi:10.1073/pnas.1407302112, 2015.
- Siebert, S., Kumm, M., Porkka, M., Döll, P., Ramankutty, N., and Scanlon, B. R.: A global data set of the extent of irrigated land from 1900 to 2005, *Hydrology and Earth System Sciences*, 19, 1521–1545, doi:10.13019/M20599, 2015.
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Global Change Biology*, 9, 161–185, doi:10.1046/j.1365-2486.2003.00569.x, 2003.
- 20 Smith, B., Warlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., and Zaehle, S.: Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model, *Biogeosciences*, 11, 2027–2054, doi:10.5194/bg-11-2027-2014, 2014.
- 25 Smith, W., Reed, S., Cleveland, C., Ballantyne, A., Anderegg, W., Wieder, W., Liu, Y., and Running, S.: Large divergence of satellite and Earth system model estimates of global terrestrial CO₂ fertilization, *Nature Climate Change*, 6, 306–310, doi:10.1038/nclimate2879, cited By 25, 2016.
- Sutton, M., Bleeker, A., Howard, C., Bekunda, M., Grizzetti, B., de Vries, W., van Grinsven, H., Abrol, Y., Adhya, T., Billen, G., Davidson, E., Datta, A., Diaz, R., Erisman, J., Liu, X., Oenema, O., Palm, C., Raghuram, N., Reis, S., Scholz, R., Sims, T., Westhoek, H., and Zhang, F.: Our nutrient world: the challenge to produce more food and energy with less pollution, NERC/Centre for Ecology & Hydrology, Edinburgh, <http://nora.nerc.ac.uk/500700/>, prepared by the Global Partnership on Nutrient Management (GPNM) in collaboration with the International Nitrogen Initiative (INI). Freely available online - see Official URL link., 2013.
- 30 Thornley, J. H. M.: A Transport-resistance Model of Forest Growth and Partitioning, *Annals of Botany*, 68, 211–216, 1991.
- Thornton, P. E., Lamarque, 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, GB4018, doi:10.1029/2006GB002868, 2007.
- University of East Anglia Climatic Research Unit; Harris, I.C.; Jones, P. : CRU TS3.23: Climatic Research Unit (CRU) Time-Series (TS) Version 3.23 of High Resolution Gridded Data of Month-by-month Variation in Climate (Jan. 1901- Dec. 2014)., Centre for Environmental Data Analysis, 2015.

- 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 B: Biological Sciences*, 368, doi:10.1098/rstb.2013.0119, 2013.
- Vorosmarty, C. and Fekete, B.: ISLSCP II River Routing Data (STN-30p), in: ISLSCP Initiative II Collection. Data set., edited by Hall, F. G.,
5 Collatz, G., Meeson, B., Los, S., Brown de Colstoun, E., and Landis, D., ORNL Distributed Active Archive Center, <https://doi.org/10.3334/ORNLDAAAC/1005>, 2011.
- Walvoord, M. A., Phillips, F. M., Stonestrom, D. A., Evans, R. D., Hartsough, P. C., Newman, B. D., and Striegl, R. G.: A Reservoir of Nitrate Beneath Desert Soils, *Science*, 302, 1021–1024, doi:10.1126/science.1086435, <http://science.sciencemag.org/content/302/5647/1021>, 2003.
- 10 Warszawski, L., Friend, A., Ostberg, S., Frieler, K., Lucht, W., Schaphoff, S., Beerling, D., Cadule, P., Ciais, P., Clark, D. B., Kahana, R., Ito, A., Keribin, R., Kleidon, A., Lomas, M., Nishina, K., Pavlick, R., Rademacher, T. T., Buechner, M., Piontek, F., Schewe, J., Serdeczny, O., and Schellnhuber, H. J.: A multi-model analysis of risk of ecosystem shifts under climate change, *Environmental Research Letters*, 8, 044 018, 2013.
- White, M. A., Thornton, P. E., Running, S. W., and Nemani, R. R.: Parameterization and Sensitivity Analysis of the
15 BIOME–BGC Terrestrial Ecosystem Model: Net Primary Production Controls, *Earth Interactions*, 4, 1–85, doi:10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2, 2000.
- 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, 441–444, doi:10.1038/ngeo2413, 2015.
- Willis, C. G., Halina, M., Lehman, C., Reich, P. B., Keen, A., McCarthy, S., and Cavender-Bares, J.: Phylogenetic community structure
20 in Minnesota oak savanna is influenced by spatial extent and environmental variation, *Ecography*, 33, 565–577, doi:10.1111/j.1600-0587.2009.05975.x, 2010.
- Willmott, C. J.: Some comments on the evaluation of model performance, *Bulletin American Meteorological Society*, pp. 1309–1313, doi:10.1175/1520-0477(1982)063<1309:SCOTEO>2.0.CO;2, 1982.
- Xu, L. and Baldocchi, D.: Seasonal trends in photosynthetic parameters and stomatal conductance of blue oak (*Quercus douglasii*) under
25 prolonged summer drought and high temperature, *Tree Physiology*, 23, 865–877, 2003.
- Xu-Ri and Prentice, I. C.: Terrestrial nitrogen cycle simulation with a dynamic global vegetation model, *Global Change Biology*, 14, 1745–1764, doi:10.1111/j.1365-2486.2008.01625.x, 2008.
- Zaehle, S. Jones, C. D., Houlton, B., Lamarque, J.-F., and Robertson, E.: Nitrogen availability reduces CMIP5 projections of twenty-first-century land carbon uptake, *Journal of Climate*, 28, 2494–2511, doi:10.1175/JCLI-D-13-00776.1, 2015.
- 30 Zaehle, S., Friend, A. D., Friedlingstein, P., Dentener, F., Peylin, P., and Schulz, M.: 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 Biogeochemical Cycles*, 24, GB1006, doi:10.1029/2009GB003522, 2010a.
- Zaehle, S., Sitch, S., Prentice, I. C., Liski, J., Cramer, W., Erhard, M., Hickler, T., and Smith, B.: The importance of age-related decline in forest NPP for modeling regional carbon balances, *Ecological Applications*, 16, 1555–1574, doi:10.1890/1051-
35 0761(2006)016[1555:TIOADI]2.0.CO;2, 2010b.