Reply to comments by reviewers and the editor - bg-2019-118

N_2O *changes from the Last Glacial Maximum to the preindustrial - part II: terrestrial* N_2O *emissions constrain carbon-nitrogen interactions*

We thank the editor and both reviewers for assessing this manuscript and for their time and effort. Please find a revised manuscript, with text changes highlighted and updated figures, at the end of this document. Changes implemented after our reply in the journal's open discussion in response to the comments by the editor are marked in yellow. We hope that the reviewers and the editor find the revised version suitable for publication in Biogeosciences.

The main changes implemented are as follows:

- Reviewer I was concerned that a high value of BNF may invalidate our results. We adjusted the model parameter values, repeated all simulations, and updated figures and text. The simulated global source of reactive N, including BNF, is now in line with empirical estimates and other model results. In spite of this adjustment, our main findings on deglacial change in N_2O emissions remain unchanged.
- The formulation of our working hypotheses apparently lead to misunderstanding. We deleted section 2.3 "Working Hypotheses" and corresponding text in the manuscript. We modified the framing of our results and now discuss uncertainties and different mechanisms to potentially explain the reconstructed N_2O emissions in section 2 and 4, complementing the existing discussion in section 6. We rewrote the abstract and state in the abstract: "The increase [in N_2O emissions] may be explained by an increase in the flux of reactive N entering and leaving ecosystems or by an increase in N_2O yield per unit N converted. ... Our results appear consistent with suggestions of (a) biological controls on ecosystem N acquisition, and (b) flexibility in the coupling of the C and N cycles during periods of rapid environmental change. Alternative mechanisms to explain the reconstructed N2O emissions include changes in N2O yield per N lost through gaseous pathways."
- We restructured and revised the text, in particular parts of the model description in section 3.1, section 5.2 and 6 to avoid redundancy, to adjust to the revised framing of our results and in response of specific review and editor comments.

The original review comments are given below in black, our reply in blue, and quotes from the revised manuscript in gray. Please note that page, line and section numbers refer to the originally submitted manuscript or where indicated in parentheses to the revised manuscript (without track change).

Reply to Reviewer #1

Interactive comment on Biogeosciences Discuss., https://doi.org/10.5194/bg-2019-118, 2019. Received and published: 1 May 2019

This paper takes new ice-core data on nitrous oxide emissions over the deglaciation and compares it to modelled results so as to better understand biological nitrogen fixation (BNF) in the same period. There follows a section on the contribution of different climate drivers on nitrous oxide emissions in separate attribution simulations.

The abstract is rather misleading, focusing on the work of the 'part I' paper which describes the ice-core data, and BNF rather than attribution modelling.

The reconstruction of the marine and terrestrial N_2O emissions is described in part I. Part I also provides a first interpretation of marine emission changes (see page 4 l7 to 9). However, the analysis and interpretation of the reconstructed terrestrial N_2O emission changes is the topic of part II. This is stated in the abstract. The corresponding text is found in sections 4 and 6.1 in the MS. We shorten the text summarizing specific findings of part I on l18 to l24 in abstract. The new text reads: Here we analyse the large increase in terrestrial N_2O emissions over the past 21,000 years as reconstructed from ice-core isotopic data and presented in part I of this study. Remarkably, the increase occurred in two steps, each realized over decades and within maximum two centuries, at the onsets of the major deglacial northern hemisphere warming events. The data suggest a highly dynamic and responsive global N cycle. The increase may be explained by an increase in the flux of reactive N entering and leaving ecosystems or by an increase in N_2O yield per unit N converted.

We modified the last sentence of the introduction (p4, l10) to read: Here in part II we focus on the interpretation of the terrestrial N_2O emission record and discuss terrestrial N_2O emissions and C-N responses in transient deglacial simulations with a dynamical vegetation/terrestrial biogeochemistry model.

However, there are two problems with the main BNF part of this paper: the model's representation of BNF, and the hypotheses posed. These two issues combined make the model runs virtually meaningless and the conclusions baseless.

We understand that the reviewer is concerned about the high value of BNF. We also understand that our formulations of working hypotheses did not help to convey our results as intended. These two issues are now addressed. We present results for modelled BNF (N source) close to the estimate by Cleveland et al., 2013. We revised the presentation of our results and removed section 2.3 "Working hypotheses" and related text from the MS. Nevertheless, some key statements by the reviewer regarding model formulations, model sensitivity, and assumptions are not correct (see below). We address these issues in the discussion below and have revised the text in the MS to clarify these issues.

The model BNF

The model BNF (page 9, 13 and Fig.1) is 523 TgN/yr globally in the pre-industrial simulation. The authors acknowledge this is "higher than the published range" but are selective about what range they are referring to and what the implication of this is. Their BNF is an order of magnitude more than low budget-based estimates (Vitousek et al., 2013) (44/58 TgN/yr) and almost 200TgN/yr larger than the upper model estimate (Xu-Ri and Prentice, 2017) (340 TgN/yr) they reference. The authors cite Cleveland et al., (1999) (195 TgN/yr), but interestingly fail to cite the more recent paper by the same author, revising the estimate down to 127.5 TgN/yr (Cleveland et al., 2013). The authors' reference to Lenhart et al., (2015) (page 9, line 16) as part of the "published range" of global BNF estimates is baffling, as the paper discusses nitrous oxide and methane emissions, not BNF. Moreover, the authors fail to mention that of all estimates of BNF in the last half century, only one (Xu-Ri and Prentice, 2017) is over 300 TgN/yr and most are around 100 – 150 TgN/yr.

We added the following text on line p9, l10 (revised MS: p8, l21) Estimates of the global BNF for non-agricultural ecosystems are uncertain. They range from 40 to 470 TgN yr^{-1}, with most published estimates around 100 to 150 TgN yr^{-1}. Cleveland et al. (1999) used 100 plot-scale estimates of BNF to estimate global BNF on natural ecosystems to 195 TgN yr^{-1} (range: 100 to 290 Tg N yr^{-1}). Vitousek et al. (2013) suggest a plausible range for preindustrial BNF of 40 to 100 TgN yr^{-1} by computing BNF as the difference from all other global sources and sink fluxes of N. Cleveland et al. (2013) estimate symbiotic BNF to 105 TgN yr^{-1}, based on cost-benefit modelling for N fixation. The same authors estimate asymbiotic N fixation to 22 TgN yr^{-1} by upscaling measurements reported in Cleveland et al. (1999). In contrast, Elbert et al. (2012) estimate asymbiotic N fixation by cryptogamic covers alone to 49 TgN yr^{-1} (27-99 TgN yr^{-1}) by integrating experimental data from 200 studies. In addition, rock weathering is estimated to add 10 to 20 TgN yr^{-1} to land ecosystems (Houlton et al, 2018). Xu-Ri and Prentice, (2017) estimated global N sources to 340 (230–470) TgN yr-1 for the parameter settings they adopted within the LPJ-DyN model; this estimate includes contributions from rock weathering and other inputs that are not explicitly prescribed or simulated by LPJ-DyN. Meyerholt et al. (2016) implemented six different BNF formulations in their model and predict modern BNF ranging from 108 to 148 TgN yr^{-1}.

Lenhart et al. 2015 discuss N_2O emissions from cryptogamic cover and summarize the results for N fixation by cryptogamic covers from Elbert et al., 2012. We deleted the reference to Lenhart et al., 2015 and added the reference to Cleveland et al., 2013 on p9, l16. We now explicitly cite the results of Elbert et al., 2012 on p9, l10 (see above).

These global BNF estimates of around 100 TgN/yr are because field experiments show that nitrogen fixation is relatively unusual in the terrestrial biosphere. Whilst individual nitrogen fixing plants or organisms have the potential to fix large amounts of nitrogen, they are best suited to 'pioneer' environments with low soil nitrogen, are usually found at very low densities in mature ecosystems, and may be facultative (rather than obligate) fixers. Taking one example, tropical forest is generally thought to be the highest BNF region due to its high NPP and low nitrogen limitation. Recent work by Sullivan et al., (2014) found that tropical forest in Costa Rica has BNF of 0.5 gN/m2/yr. From the map of pre-industrial BNF in LPJ-Bern (Figure 5 A) it seems BNF in Costa Rica is modelled at 10 gN/m2/yr. i.e. the model overestimates BNF in the tropics by a factor of 20. Though no present day BNF value is given in the paper, from the information available the present-day modelled value for Costa Rica is likely higher. Even compared to the upper bound for tropical forest of 6 gN/m2/yr from the meta-analysis done by Cleveland et al., (1999), the values in LPJ-Bern are high. Cleveland et al., (1999) said their upper limit was "extremely unlikely" and the global BNF from those upper values was 290 TgN/yr (compared to LPJ-Bern's 523 TgN/yr).

The parameters accounting for N immobilization were inadvertently set to low values by Lienert and Joos (2018). This in turn leads to a high N source in the model. We decided to use this published version for the originally submitted MS, complemented by the results from sensitivity simulations with a higher N flux representing immobilization and lower BNF. This approach was selected for reasons of traceability and transparency. We re-ran all simulations with an updated parameter set to yield a global preindustrial and modern N source of 128 and 140 TgN yr^{-1}, respectively. This flux of reactive N to ecosystems implicitly includes contributions from symbiotic and asymbiotic N fixation, rock weathering, and possibly other, yet to be discovered, pathways. In view of this, we adjusted the text and now refer to 'ecosystem N inputs' or 'N source' in general rather than BNF.

This is also relevant for comparing this flux with empirical estimates. Accounting for the N weathering flux of around 15 TgN yr^{-1} (Houlton et al. 2018), the simulated flux of reactive N inputs presented here implies a modern BNF close to the reviewers preferred value of 127.5 TgN yr^{-1}. As noted already in the original MS (p9, l20-23), relative changes in modelled N source and N_2O emissions and related model-based conclusions are not sensitive to the exact parameter values. In addition, the yield factor for nitrification is assumed to vary with temperature in the same way as the yield for denitrification in this revised setup. This has a modest impact on modelled N_2O as only 10 % of the simulated N_2O flux stems from nitrification.

All figures in the manuscript were updated with results for this new parameter setting and included in the draft provided at the end of this document. Specifically, Fig, 5A displays the N source (BNF plus weathering and potential other abiotic sources) simulated by LPX-Bern. Typical values in Central America are around 1 gN m^{-2} yr^{-1} for the new setup, and comparable to field measurements (Sullivan et al., 2014; Wurzburg and Hedin, 2016). For example, Wurzburg and Hedin, 2016, report BNF of N fixers

from 0 (for about half of the trees) to up to 12 gN m^{-2} yr^{-1} in their supplementary material. New text is added in section 5.2 (revised MS: p14, l31) to describe results displayed in Figure 5:
The N source (Fig. 5A) is typically smaller than 0.5 gN m^{-2} yr^{-1} in northern mid and high latitude and around 1 gN m^{-2} yr^{-1} in tropical rainforest and in Central America, comparable to observational estimates (Sullivan et al., 2014;Wurzburger and Hedin, 2016a, b). An N source of 2 to 6 gN m^{-2} yr^{-1} is simulated in many semi-arid regions, including southern Africa, the sub-Sahara region, India, northern Australia, and in the southern parts of North America. Soil mineral N is typically below 0.5 TgN m^{-2} in the tropics ....

The BNF in LPJ-Bern is entirely disjointed from reality. This puts significant doubt on the ability of this model to produce meaningful results about or based on BNF. The authors infer on page 9 that the high BNF is irrelevant to their results. They describe two sensitivity experiments with lower global BNF and the nitrous oxide emissions are broadly similar. However, the two sensitivity experiment global BNF values (310 and 188 TgN/yr) are still unrealistically high. Therefore, these sensitivity experiments reveal that the problem with BNF in the model may not be a parameter based issue but could be something more fundamental.

As outlined above, the assumption by the reviewer regarding the sensitivity of the model to the absolute value of the N source and BNF is not correct. The text starting on p9, l11 (revised MS: p9, l26) is modified to read: The two-step calibration described above resulted in yield factors that are higher than the range of published estimates. The global mean yield for denitrification, expressed as N_2O per N_2 produced, is 5.6 % and thus higher than the range of estimates (0.2–4.7 %) summarized by Xu-Ri and Prentice (2008). Similarly, the global yield for nitrification (0.26 %) is higher than observation-based estimates (0.01-0.2 %). The mismatches in these estimates for yield may suggest that current best estimates for the N source, N_2O yield, and preindustrial N_2O emissions are not fully consistent. We carried out a sensitivity simulation to explore uncertainties: the immobilization fraction is set to 0 % for litter and to 26.39 % for soil mineralization, leading to a preindustrial N source of 523 TgN yr^{-1}. This is about a factor of four higher than in the standard setup. Correspondingly, yield factors are about a factor four lower in this sensitivity run than in the standard simulation.

The sensitivity of simulated N2O emission changes over the deglacial period to these parameter choices is relatively small, while the absolute magnitude of the N source has some implications for N stress and thus NPP. The increase in NPP over the deglaciation is larger in simulations with a high compared to a low N source (10.1 versus 5.9 GtC yr^{-1} in the standard). Importantly, the difference in relative changes in modelled global N source is small (16 % versus 10 % in the standard) and the deglacial increase in N_2O emissions is only 0.2 TgN yr^{-1} higher in the sensitivity than in the standard run (see Sect. 3.2 and 5), despite the large difference in the implied N source. Thus, related model-based conclusions for N_2O emissions are not sensitive to the parameter settings for the yield and the flux representing immobilization.

The hypotheses

The hypotheses set out on page 7 present a false dilemma. They are based on the premise that the nitrous oxide emissions are attributable to a nitrogen system that is either ‘open’ or ‘closed’. The idea of either an open or closed system stems from the assumption that the nitrogen cycle is in equilibrium during the deglaciation (stated by the authors on page 6, line 5). However, there’s no evidence either way on this question. Even if the assumption of equilibrium is accepted, an open system is not the only mechanism of increasing nitrous oxide emissions, thus the hypotheses are a false dilemma. The changes in nitrous oxide could also be caused by changes to the internal dynamics of the system (e.g. soil nitrogen turnover, or flexible C:N ratios, or the authors’ assumption of homogeneous nitrous oxide yield fractions over space and time (page 8, line 26)).

We do not assume equilibrium over the deglaciation – neither when discussing the ice core record, nor the model results. The model applied here accounts for the transient dynamics of all C and N pools and fluxes and the main underlying principle is mass conservation. The highly transient nature of the ice core N_2O emission record and of the N cycle in LPX-Bern is evident in Figs. 3, 4, 6, 7, 8, 10, and 11. To avoid the misunderstanding by the reviewer, we modified the sentence on p6, l5 (revised MS p6, l21) to read: Following mass balance, losses of reactive N from ecosystems and changes in ecosystem and abiotic N stocks have to be compensated by N inputs, mainly by BNF. In addition, we modified the last sentence of the introduction (p4, l10) to point the reader early on to the transient nature of our simulations. .. and discuss terrestrial N_2O emissions and C-N responses in transient deglacial simulations with a dynamical vegetation/terrestrial biogeochemistry model.

Furthermore, we do not assume a constant N_2O yield factor in space and time as asserted by the reviewer. The yield factor for denitrification, responsible for more than 85 % of the N_2O flux in our model, is significantly varying in space and time as described on p8 l20 to l23 in the original MS.

It was not our intention to present a dilemma, but rather to guide the reader and place our analysis in the wider scientific context, connecting to fundamental question about ecosystem functioning and the nature of N limitation. We deleted section 2.3 and all text related to working hypotheses to avoid potential misinterpretations. Alternative explanations for the deglacial N_2O increase are discussed in the original MS, e.g. related to abiotic N source (p6, l23), related to pre-existing stocks of reactive N on p18 l14 to 26), and related to changes in the yield factor per unit N converted on p19, l1 to 25. However, these additional explanations may be viewed as coming too late in the MS. We therefore adjusted the abstract as described in the second bullet at the beginning of this reply and added text in section 2 and 4. We added the following text at the end of section

2.1 on production mechanisms: The amount of N_2O produced per unit of N converted varies with environmental conditions and production pathway. For nitrification and denitrification this yield (or emission) factor depends on substrate availability linked to soil organic matter decomposition and C:N stoichiometry, on oxygen level influenced by soil moisture status, on acidity and temperature (Diem et al., 2017;Davidson et al., 2000;Firestone and Davidson, 1989;Smith, 1997;Phillips et al., 2015;Saggar et al., 2013). In addition, different N_2O production pathways and N loss processes and their relative importance may evolve through time and influence the N_2O yield on local to global scales.

We added the following text at the end of section 2.2 on C-N-N_2O coupling: In summary of section 2.1 and 2.2, changes in terrestrial N_2O emissions may be linked (i) to changes in the magnitude of reactive N entering and leaving ecosystems, and (ii) to changes in the N_2O yield per unit reactive N converted in land ecosystems. We added the following text towards the end of section 4 on reconstructed N_2O emission: The rapid increase in terrestrial N_2O emissions at the onset of the B/A and at the end of the YD and the overall increase in emissions over the past 21,000 years either point (i) to an increase in N_2O yield per unit N converted for emissions to the atmosphere, averaged globally and across all N_2O production pathways, or/and (ii) to an increase in the global flux of converted N.

The answer to the false dilemma presented is pre-decided by the definitions the authors give on page 6. Under the false dilemma, an ‘open’ (high-input-high-output) system is presented as the only mechanism that can produce high terrestrial nitrous oxide emissions. We know we have increasing (nitrous oxide) output, so under the assumption of either ‘open’ (high-input-high-output) or ‘closed’ (low-input-low-output), there is only one possible answer. This pre-determined result is exacerbated by the model. The high BNF in the model means the N cycle in the model must be ‘leaky’ and ‘open’ otherwise there would be no N limitation at all (contrary to the evidence, see LeBauer and Treseder, (2008)). Some models take a more ‘closed’ approach (often resulting in low BNF). But it stands to reason that closing the input of N in a model reliant on high N input will cause the model to produce results inconsistent with reality. These simulations might inform somewhat about the model but can’t say anything about real world BNF.

The combination of an invalid hypothesis and an inappropriate model is results that mean nothing and conclusions that mislead. An unwary reader could easily take it at face value that BNF increased by 72 TgN/yr during the deglaciation and an ‘open’ terrestrial nitrogen system was the only, or most likely, way the observed nitrous oxide changes could have occurred. But there is no reliable evidence for either of these assertions.

We have to stress that these statements by the reviewer are not correct. As we show (please compare the figures in the original and the revised manuscript) results for changes in N_2O emissions are similar for low (128 TgN yr^{-1}) and high (523 TgN yr^{-1}) input of reactive N as already discussed above. In addition, we would like to emphasize the distinction between state and change – We do not make statements whether current ecosystems are N limited or not, but are focussing on the *temporal change* as stated on p7,l5 ("To guide further discussion .. for the temporal evolution ..) and on p7,l16-22 ("The question posed in this study is not to what extent different ecosystems are, or have been N, limited. Rather, we ask the question whether BNF and the N cycle adjusted dynamically ...") in the original manuscript. Apparently, we failed to make this point sufficiently clear to the reviewer. As noted above, section "2.3 Working hypotheses" on p6 and 7 is deleted to avoid confusion and misinterpretations. As also noted above, different mechanisms of change are now discussed in the abstract and in section 2 and 4. In addition, we restructured the discussion section and discuss potential changes in N_2O yield per unit N converted early in section 6.1. We state in the conclusion (sect.7): Our model results provide insight into the multi-decadal-to-millennial dynamics of the terrestrial C-N cycling by showing that the ice core terrestrial N_2O emission record could potentially be explained with a rapid adjustment of N cycling to the climate and CO_2-driven acceleration of the C cycle, but they do not exclude the possibility that alternative explanations linked to changes in N_2O yield could be important.

In summary, we aim to present our results in a balanced way and acknowledge the complexity of the C-N cycle. We thank the reviewer for pointing out shortcomings in the presentation of our results, however, we have to reject some of her/his statements and conclusions regarding our results as detailed above. We feel that our additional model runs and the revisions of the manuscript sufficiently address the more fundamental concerns of reviewer #1

The second part of the paper on attribution appears more sensible (issues with the BNF representation in the model not withstanding). This part of the paper might be appropriate for resubmission separately, without the BNF model results. With the two presented together it's difficult to assess the attribution section fairly.

References

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Reply to Reviewer #2

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Interactive comment on Biogeosciences Discuss., https://doi.org/10.5194/bg-2019-118, 2019.

The manuscript of Joos et al combines ice-core derived terrestrial N2O time-series with process-based N2O simulations to derive constraints on terrestrial nitrogen dynamics. The manuscript is well written and easy to read despite a little long and redundant. I suggest to be cautious about points mentioned below before the final acceptance.

Thank you for your general support, the positive recommendation, and for your constructive comments.

We edited the text to reduce redundancy.

One of my concerns is that the conclusion related to biological controls on N acquisition is already pre-included in the assumptions/definitions based on which the model is built. BNF in the manuscript refers to any N inputs, other than atmospheric N deposition, that satisfy ecosystem N demand. With a constant annual N deposition rate, any changes in ecosystem N content and losses are attributable to BNF. Here BNF incorporates both biological and non-biological sources, which might come from weathering, be undiscovered N sources existed in pre-industrial time, or errors from assuming constant N deposition rate.

Thank you for this helpful comment. We adjusted the wording to make clear that the N source in the model includes not only BNF. We generally refer now to 'N source' or 'N input' instead to 'BNF' in the manuscript. Please see also our response to the last comment by the editor given further below. The text in the model description (originally p9, l1; revised p8, l11) is modified to read: .. The remainder determines the total input of reactive N into the ecosystem, implicitly subsuming symbiotic and asymbiotic BNF, and any other potential N sources that may support plant growth, in addition to prescribed N deposition.

Text on p17, l20 (revised p20, l3) is modified to read: Sources of reactive N on land, e.g., from BNF and weathering, may possibly have increased under warming climate and increasing CO_2 over the deglacial period and contributed to meet the N demand of plants, nitrifiers, denitrifiers and cryptogamic covers under more favorable growth conditions.

Text on p18, l13 (revised p20, l14) is added: Similarly, it remains unclear how other smaller sources of reactive N changed over the deglacial period and influenced N_2O emissions.

A second concern is about the adjustments of global inflow of reactive N on multi-decadal to century time scales derived from N2O dynamics. As the authors mentioned, there are multiple-steps and many factors come into play in global N cycle. Different N2O production pathways may evolve through time, alternations of soil organic matter decomposition, stoichiometry and other N loss pathways are likely to shift N2O emissions. These adjustments are likely to occur without significantly alteration of real biological nitrogen fixations. For example, nitrifying and denitrifying microbes may have different temperature sensitivities vs. BNF. Vegetation and microbial evolution are largely unconsidered in this study. There is no strong evidence that N input flux would adjust as quickly as that of N2O emissions.

We agree with the reviewer that a range of factors complicate the link between sources of reactive N and N_2O emissions. We adjusted the formulations in the abstract (see previous comment). Potential changes in the yield factors are discussed on page 19 in the submitted MS. We now discuss these factors early in the MS and acknowledge in section 2, 4 and 6 that the N_2O emission increase may also be explained by the changes mentioned by the reviewer. For example, we add at the end of section 2.1: The amount of N_2O produced per unit of N converted varies with environmental conditions and production pathway. For nitrification and denitrification this yield (or emission) factor depends on substrate availability linked to soil organic matter decomposition and C:N stoichiometry, on oxygen level influenced by soil moisture status, on acidity and temperature (Diem et al., 2017;Davidson et al., 2000;Firestone and Davidson, 1989;Smith, 1997;Phillips et al., 2015;Saggar et al., 2013). In addition, different N_2O production pathways and N loss processes and their relative importance may evolve through time and influence the N_2O yield on local to global scales. Please see also our response to reviewer 1 or the attached MS.

Further, we quantified the influence of variations in yield on N_2O emissions changes in an additional sensitivity simulation discussed in section 5.2 (see reply to next point).

A third concern is related to insights to be learned from this study. Is it necessary to conduct spatially explicit model simulation to test constant vs. dynamic BNF?

The magnitude of N2O emissions can be easily tuned through RN2ODN, whereas the "openness" or 'tightness' of N cycle is, to a large extent, conceptual and not new in literature. The spatial pattern is also within our general understanding of global ecosystems as the model is built upon the contemporary (not paleo-) biogeochemistry and driven by historical climate. I feel the climate sensitivity of N2O emissions are valuable information that worth exploring for models like LPX-Bern.

We are not aware of any publication where the influence of a constant versus a dynamic N source is quantified in deglacial simulations. Therefore, we would like to inform the reader about these model results. The absolute magnitude of N_2O emissions is tunable by adjusting the yield factor. However, model outcomes in terms of deglacial change are not a priori clear and easy to predict as NPP, vegetation growth, soil carbon storage, N remineralisation, N source, N loss fluxes, and yield factors undergo complex changes in space and time over the last 21,000 years as evident in figures 3, 4, 6, 7, and 8.

We are not sure what the reviewer means with "historical climate"; in the context of Earth System modeling the historical period is typically taken from 1800 AD to present. Here, the model was driven with temperature and precipitation output from a transient simulation with the Community Earth System Model over the last 21,000 years and with transient CO_2 and time varying orbital parameters.

In response to this comment, we rewrote section 5.2 (please see the attached MS). We provide now additional context to clarify the implications of the simulations with variable versus constant N source. We added results from an additional sensitivity simulations to quantify the influence of deglacial changes in the N_2O yield factors. The first paragraph of section 5.2 reads now: In this section, we address C-N coupling in LPX-Bern and analyze the spatial patterns for the source of reactive N, soil mineral N, net primary productivity (NPP), and C stocks (Fig. 5) and their changes over the deglaciation (Fig. 6). We quantify two decisive factors for N_2O emission change in the model: (i) changes in the source of reactive N, fueling nitrification and denitrification, and (ii) changes in the N_2O yield per unit N converted.

The paragraph describing the new sensitivity run reads: The N_2O yield factors, i.e., the N_2O produced per unit N converted by denitrification and nitrification, are assumed to vary with temperature and thus in space and time in LPX-Bern v1.4N. In a sensitivity run, these yield factors are set constant with all other settings as in the standard. The deglacial warming leads to a higher N_2O yield in the standard compared to this sensitivity run and 0.44 TgN yr^{-1} of the deglacial increase in land N_2O emissions are attributed to this change in yield (Fig. 7, black line). In other words, changes in the yield factors further amplify the increase in N_2O emissions as driven by the increase in the flow of reactive N in LPX-Bern.

The last paragraph of section 5.2 reads now: In summary, the simulation with constant N source completely fails to reproduce the reconstructed N_2O emissions from the land biosphere. The increase in N_2O yield, as well as in soil and litter C and N turnover rates, under deglacial warming are not sufficient to overcome the effect of N limitation on N_2O emissions in this sensitivity simulation. We note, however, that changes in yield due to processes not incorporated in LPX-Bern could potentially explain the reconstructed increase in N_2O emissions. If the model is allowed to satisfy the demand of N, and thereby implicitly of other elements to support the growth of N fixers, nitrifiers and denitrifiers, and plants, terrestrial N_2O emissions increase as reconstructed.

We acknowledge that other factors than N input may had influenced N_2O emissions and deleted the text on p14,l11 to l18

Specific points:

1. P6L25-30. Does it worth discussion on losses of plant-available vs. plant-unavailable (e.g., through fire and leaching of DON) N and how losses of plantunavailable N alter system dynamics?

Text added as requested. The text on p6,l25-30 has been deleted in response to reviewer 1. We have extended the discussion on fire, DON, and mineral adsorption in the paragraph on p6, l4 (revised p6, l17): On larger scale, N lost by fires will be deposited again and a large part of this N flux is therefore fed again to land ecosystems. In this sense, the fraction of the fire flux not lost to the ocean may be viewed to belong to the internal global land N cycle. N leached as dissolved organic N is typically remineralized downstream and may undergo nitrification and denitrification or be taken up by aquatic organisms. N may also be absorbed by minerals and become unavailable for plants and microbiological assemblages.

2. P10L5. It is unclear when the upper limit of denitrification is used

The statement should refer to nitrification. Text clarified to read: An exception is an adjustment in the upper limit of the fraction of NH_4^+ nitrified per day from 0.1 day^{-1} to 0.09096 day^{-1} at 20^{o}C

Interactive comment on Biogeosciences Discuss., https://doi.org/10.5194/bg-2019-118, 2019.

Reply to Comments by the Editor

Associate Editor Decision: Reconsider after major revisions (05 Jul 2019) by Sönke Zaehle
Comments to the Author:

Dear authors,

many thanks for your comments and also for providing a quantitative response to the criticism raised by the reviewers. The proposed revisions are of a nature that suggest that a suitably revised and reworked manuscript may become acceptable to Biogeosciences. Please make sure that the revised manuscript reflects all points raised by the reviewers, and provides a balanced discussions of these points raised. At this stage, I do not provide detailed comments or a profound assessment, but offer some further guidance for revision with respect to your responses, should you decide to submit a revised version of the manuscript. Please note that a revised manuscript would undergo a full second round of peer-review.

Thank you for your editorial guidance.

(1) The new model version has a much improved estimate of BNF, which makes the results appear more plausible. However, how you have gotten to this result remains unclear from the revisions. I would recommend to detail the changes you have made between the first submission and the revised version (that could be an Appendix), and also offer some key statistics as to how the models differ (e.g. global BNF, NPP, C storage, N leaching and total N gas loss). Since BNF in your model seems to be calibrated by the N immobilisation process, a more in-depth description on how this process works would be appreciated. Somewhere in the model description it reads that the immobilisation process was introduced later into the LPJ-DyN, which is a curious statement, given that N immobilisation is an essential part of the SOM decomposition process, and it is hard to imagine that one can describe a model as prognostic and full representation of the N cycle if this process is not represented.

An appendix is added to the revised manuscript that documents the changes in model parameters and selected model outcomes between LPX-Bern v1.4 and v1.4N as suggested. Please see the appendix in the re-submitted MS for further details.

Thank you for pointing out that our description of how N uptake by N immobilization is accounted for was too brief and not clear. The clause on p8, l14 ”here modified to include N immobilization in soils” is clarified to read: accounting for the uptake of mineral N by N immobilization in soils (Bengtsson et al., 2003;Li et al., 2017;Gütlein et al., 2017) as in Xu-Ri and Prentice (2017).

The text from p8, l13 to p9, l23 in the submitted MS has been restructured and expanded to better explain the approach for the N source, the flux accounting for immobilization, and for model calibration. The paragraph reads now: In LPX, the source of reactive N is implied by maintaining prescribed soil N:C ratios associated with each of the plant functional types, reflecting their different litter chemistries and decomposer assemblages. Due to lower N:C ratios of litter than soil pools, the transfer of mass from litter to soil pools during litter decomposition therefore implies a given amount of N, required to satisfy the soil N:C ratio. The required N is partly satisfied by a flux representing immobilization of mineral N. The remainder determines the total input of reactive N into the ecosystem, implicitly subsuming symbiotic and asymbiotic BNF, and any other potential N sources that may support plant growth, in addition to prescribed N deposition. The amount of N input required to close the N balance of soils and to maintain the soil pools at their high N:C ratios depends on the flux representing

N immobilization. Constant fractions ($frac\_soil\_immob, frac\_litter\_immob$) of the N flux released by soil or litter remineralization are immediately returned to its pool of origin. Hence, the choice of these parameters simultaneously co-determine reactive N input rates and net N mineralization.

We assumed the parameters $frac\_soil\_immob$ and $frac\_litter\_immob$ to be invariant over time and space and calibrated their values (Table A.1) to match a total preindustrial reactive N source of 128 TgN yr^{-1}. This value implicitly includes contributions from symbiotic and asymbiotic BNF, as well as other inputs of reactive N not included in the prescribed N deposition. ..

The wording for "immobilization" is adjusted in the MS (e.g.: "on the flux representing N immobilization"; "account for the uptake of mineral N"; "representation of N uptake by N immobilization")

The model caveat on p20, l30 (revised p21, l1) is expanded by: and a constant fraction of remineralized N is returned immediately to its source soil pool. to read: However, microbial and fungal biomasses are - unlike in microbial-explicit models (Schimel and Weintraub, 2003;Zhu et al., 2017;Allison and Gessner, 2012) - not explicitly modelled and organic matter decomposition does not depend on microbial mass and physiology. Instead, a mass balance approach is applied with C:N stoichiometry prescribed at observation-based PFT-dependent values for litter and soils. A constant fraction of remineralized N is returned immediately to its source soil pool and the N budget is closed by the implied N source flux (Fig. 1). There is also no distinction between different classes of organic matter according to their accessibility to microbial action (Averill and Waring, 2018).

It is surprising that you can tune the model to have a five-fold difference in BNF, but no perceivable difference in C and N cycle trajectories across the LGM to present-day discussion. This fact deserves some discussion (because this is certainly not the case for other N modelling concepts), in particular if the claim is that increased BNF is an important cause of the observed N2O increase.

The following text is added in the model discussion section 6.2: LPX-Bern was applied in an earlier study to simulate climate-N_2O feedbacks under global warming (Stocker et al., 2013) and results for global emissions for the period from 16 to 10 ka BP are presented in Schilt et al. (2014). Recently, model parameters have been updated using a set of modern observational constraints in a Bayesian approach (version v1.4) (Lienert and Joos, 2018b) and here further modified towards a lower N source (version v1.4N) by adjusting the fraction of N remineralized that is returned to the soil pool. Except for the matching of pre-industrial N_2O emission estimates, the model has not been tuned in any way towards matching the ice core reconstruction. These updated versions also account for the uptake of mineral N by N immobilization in soils. Results in terms of deglacial N_2O emission changes are similar between these different versions. Changes in parameter values and selected globally-averaged model results for version v1.4 versus v1.4N are documented in the Appendix Tab. A.1. Appendix Figs. A.1

and A.2 show the spatial patterns for the implied N source, soil mineral N, NPP, total carbon and their changes over the deglaciation. The most striking difference is that the implied N source is a factor of four higher in v1.4 compared to v1.4N. Nevertheless, results for deglacial N_2O emission changes remain basically unchanged between the version v1.4 and v1.4N. The reason is that the relative, percentage changes in the N source flux and in N loss fluxes are similar between the two versions, however, the N_2O yield factors are calibrated in both versions to the same preindustrial N_2O emissions of 5.9 TgN yr^{-1}. The lower N source leads, however, to smaller mineral N concentration. In turn, N limitation of NPP is larger and, hence, NPP and carbon storage are smaller, both in steady state and for deglacial change, in v1.4N than in v1.4.

It is OK to down-tone the hypotheses behind your research criticised by reviewer #1. However, this does not change the fact that in your model, BNF is assumed to occur free of cost and irrespective of an biochemical constraints whenever the decomposition process is limited by N, which, by default increases N cycling and therefore N2O losses whenever productivity increases. It would be beneficial to include a comprehensive discussion of how other hypotheses on how BNF is controlled (as implemented in other global models) would respond to the C and N cycle changes you simulate with the aim to elucidate whether your response is a genuine characteristic of N cycle models, or a feature of your model (for which you can provide of course justification). It would also be important to elucidate on the alternative causes of changes in terrestrial N (given that LPX-Bern does not fully simulate the timing and magnitude of N2O change), in particular relating to the question that the nitrification and denitrification processes appear to be linear with soil moisture (if my reading of Xu-Ri et al. 2008 is correct), which may impair the model's ability to adequately simulate the response of N2O emissions to climate change.

The following text is added in the model discussion section 6.2 on other hypotheses on how BNF is controlled and on alternative causes of changes in terrestrial N: The N source and its changes in LPX are implied by maintaining soil C:N ratio at observed values. This N source thereby accounts for any other source, except explicitly prescribed N deposition (Fig. 1). Carbon costs of N acquisition are not directly considered. Yet, a fraction of 6 % of NPP is directly transferred to a pool with a short overturning time to represent root exudates. The by far largest contribution to the implied N source is thought to come from BNF.

Different approaches to represent BNF are used in different models and their effects on modelled BNF, NPP, carbon stocks, and N_2O emissions are compared in recent studies for modern conditions and future projections (Meyerholt et al., 2016;Wieder et al., 2015a). The simplest approach is a prescribed static map of BNF (Zaehle and Friend, 2010a). Most frequently, empirical models are used describing BNF as a linear function of evapotranspiration (Cleveland et al., 1999) or as an exponential function of NPP (Thornton et al., 2007). More process-oriented models heuristically account for the dependency of symbiotic BNF on N demand by vegetation, soil N status, and light limitations in extratropical regions (Gerber et al., 2010) or on the optimization of plant C investment into resource acquisition (Fisher et al., 2010). Meyerholt et al. (2016) describes asymbiotic BNF as a function of temperature, shading and soil moisture.

The implementation of such different parameterizations in LPX-Bern would likely lead to different estimates for deglacial changes in BNF and N_2O emissions. We may expect that prescribing a constant modern BNF field would lead to approximately constant fluxes for nitrification, denitrification and leaching. In turn, deglacial changes in N_2O emissions would only be due to changes in yield factors and be smaller than modelled in our standard simulation and smaller than reconstructed. A similar result is expected for BNF depending on evapotranspiration, because globally-averaged evapotranspiration changes little over the deglaciation in our standard simulation (Tab. A.1) and global BNF would remain at its modern value. In contrast, some parameterizations would likely yield similar or larger responses than simulated here. A strong increase in BNF is found in global warming simulations for the N-demand (Meyerholt et al., 2016) and the NPP-based (Wieder et al., 2015a) BNF parameterizations. In this latter parameterization, BNF responds immediately to NPP and grows exponentially with NPP, whereas the deglacial increase in BNF of 11 % is smaller than in NPP (13 %) in our standard run (Tab. A.1). Overall, one might expect a similar or even larger increase in BNF and N_2O emissions over the deglaciation when replacing our implicit N source approach with a demand, NPP or cost driven BNF parameterization. However, a corresponding quantitative analysis is beyond the scope of this study.

The N loss in LPX is predominantly driven by local gaseous loss from denitrification, with a much smaller role for fire, leaching, and minor contributions from volatilization of NH_3, and gas release during nitrification (Fig. 1). Denitrification and nitrification are thought to occur at anaerobic and aerobic microsites in the soil, which are challenging to represent. In LPX-Bern the fraction of NH_4^+ available for aerobic nitrification and of NO_3^- available for anaerobic denitrification within a grid cell is assumed to scale linearly with water-filled pore space in the top 50 cm (Xu-Ri and Prentice, 2008). Meyerholt and Zaehle (2018) investigated different algorithms for N loss processes and find variable responses in N loss and in the partitioning of N losses between gaseous and leaching losses under elevated CO_2.

I do not see the need to explicitly refer to rock-based N weathering in this manuscript. The BNF in LPX-Bern is driven by the litter-layer decomposition process (which is largely devoid of weathering material), and does not depend on deeper soil layers N production rate (nor does it reflect the geographic patterns of weathering and lithology). As far as I understand, the essence of BNF in LPX-Bern is asymbiotic, and it would be clearer if that was stated rather than subsuming it with many terms that aren't actually represented in the model.

We agree with the editor that it is unlikely that changes in rock-based weathering are responsible for the increase in N_2O emissions. We still mention the weathering source as a potential N source in section 1 and 2 as it is an integral part of the N cycle and once in section 6, here to address the concern raised by reviewer 2. However, we have deleted the term weathering in the abstract and whenever it occurs in connection with the LPX-Bern model as well as in other places in the MS. We believe that the discussion of the weathering is not central to our MS. The text for the N source in the model description (revised MS p8, l11) reads now: The remainder determines the total input of reactive N into the ecosystem, implicitly subsuming symbiotic and asymbiotic BNF, and any other potential N sources that may support plant growth, in addition to prescribed N deposition. ... This value implicitly includes contributions from symbiotic and asymbiotic BNF, as well as other inputs of reactive N not included in the prescribed N deposition.

Best wishes, Sönke

N_2O changes from the Last Glacial Maximum to the preindustrial - part II: terrestrial N_2O emissions constrain carbon-nitrogen interactions

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Abstract. ~~Land ecosystems currently take up a quarter of the human-caused carbon dioxide emissions.~~ Carbon-nitrogen (C-N) interactions regulate N availability for plant growth and for emissions of nitrous oxide (N_2O) as well as the uptake of carbon dioxide. Future projections of these terrestrial greenhouse gas fluxes ~~this carbon sink~~ are strikingly divergent, leading to major uncertainties in projected global warming. ~~This situation partly reflects our insufficient understanding of carbon-nitrogen (C-N) interactions and particularly of the controls on biological N fixation (BNF). It is difficult to infer ecosystem responses for century time scales, relevant for global warming, from the comparatively short instrumental records and laboratory or field experiments.~~ Here we analyse the large increase in terrestrial N_2O emissions ~~of nitrous oxide (N_2O)~~ over the past 21,000 years as reconstructed from ice-core isotopic data and presented in part I of this study. ~~Changing N_2O emissions are interpreted to reflect changes in ecosystem N loss, plant available N, and BNF. The ice-core data reveal a 40 % increase in N_2O emissions over the deglaciation, suggestive of a highly dynamic global N cycle whereby sources of plant-available N adjust to meet plant N demand and loss fluxes.~~ Remarkably, the increase occurred in two steps, each realized over decades and within maximum two centuries, at the onsets of the major deglacial northern hemisphere warming events ~~around 14,600 and 11,700 years ago~~. The data suggest a highly dynamic and responsive global N cycle. The increase may be explained by an increase in the flux of reactive N entering and leaving ecosystems or by an increase in N_2O yield per unit N converted. We applied the LPX-Bern dynamic global vegetation model in deglacial simulations forced with Earth System Model climate data to investigate N_2O emission patterns, mechanisms, and C-N coupling. The N_2O emission changes are mainly attributed to changes in temperature and precipitation and the loss of land due to sea level rise. The reconstructed increase in terrestrial emissions is broadly

reproduced by the model, given the assumption that sources of reactive N~~BNF~~ positively respond~~s~~ to increasing N demand by plants. In contrast, assuming time- and demand-independent N sources ~~levels of BNF~~ in the model to mimic progressive N limitation of plant growth results in N_2O emissions that are incompatible with the reconstruction. Our results appear consistent with suggestions ~~the existence~~ of (a) ~~strong~~ biological controls on ecosystem N acquisition, and (b) flexibility in the coupling of the C and N cycles during periods of rapid environmental change. Alternative mechanisms to explain the reconstructed N_2O emissions include changes in N_2O yield per N lost through gaseous pathways. **[~~301~~297 words]**

1 Introduction

Nitrous oxide (N_2O) is a sensitive proxy of biogeochemical and ecosystem processes on land and in the ocean, and its past atmospheric variations are recorded in ice cores. N_2O is an important greenhouse gas and contributes to ongoing global warming (Stocker et al., 2013). It is also involved in the destruction of stratospheric ozone (Myhre et al., 2013). N_2O is produced primarily by nitrification and denitrification both on land and in the ocean, and photochemically decomposed in the stratosphere (Ciais et al., 2013). Atmospheric N_2O increased from 270 ppb (MacFarling Meure et al., 2006) to around 330 ppb (https://www.esrl.noaa.gov/gmd/) over the industrial period due to human activities including fertilizer application, fossil fuel use and biomass burning (Bouwman et al., 2013;Ciais et al., 2013). Atmospheric N_2O varied naturally between around 180 and 300 ppb over glacial-interglacial cycles (Sowers et al., 2003;Spahni et al., 2005;Schilt et al., 2010). A quantitative explanation of these variations is lacking and this knowledge gap renders projections of the feedbacks between N_2O and climate change uncertain (Stocker et al., 2013;Battaglia and Joos, 2018;Kracher et al., 2016).

Variations in N_2O emission, and thus in tropospheric N_2O content, are closely linked to ecosystem processes governing the cycling of nitrogen (N) and carbon (C) on land and in the ocean (Gruber and Galloway, 2008). N availability to support land plant and phytoplankton growth and terrestrial and marine C storage is governed by the balance of N input and loss fluxes. Reactive N is added by biological nitrogen fixation (BNF) and, on land, by deposition, and weathering. Reactive N is lost from ecosystems through nitrification followed by denitrification, as well as leakage and mineral adsorption. Terrestrial N_2O emissions are a sensitive indicator of the flow of reactive N entering and leaving land ecosystems (Firestone and Davidson, 1989) and reactive N needs to be available for the production of N_2O as well as to support carbon uptake and storage by plants and the land biosphere. ~~Reconstructions of past variations in terrestrial and marine N_2O emissions from ice-core N_2O concentration and isotopic data (Schilt et al., 2014) provide information on the functioning of ecosystems and the coupled C-N cycle. They provide the opportunity to evaluate C-N-climate models, and to test alternative hypotheses for underlying~~

~~ecosystem processes, such as the limitation of plant growth by N limitation and their responses of BNF to climatic and environmental change.~~

The land biosphere sequesters about a quarter of anthropogenic CO_2 emissions and is the largest natural N_2O source (Ciais et al., 2013). Yet key features of the C-N cycle are poorly understood, leading to major uncertainties in global warming projections (Joos et al., 2001;Arora et al., 2013;Friedlingstein et al., 2006;Friedlingstein et al., 2013;Plattner et al., 2008;Zickfeld et al., 2013). The question ~~whether~~ to what extent N availability will limit future land C uptake and N_2O emissions is unresolved. In particular, large uncertainties remain as to what extent ~~BNF~~N sources, net N mineralization, ~~and~~ N uptake, and N loss processes will adjust ~~to support~~and influence plant growth and N_2O emissions under climatic and environmental change (Niu et al., 2016). It is debated how global warming, increasing CO_2, and increased N deposition affect the current land carbon sink (Körner, 2015;Fatichi et al., 2014;Terrer et al., 2016) and how the land carbon sink and greenhouse gas emissions will evolve. Apparently conflicting observations (Davidson et al., 2007;Luo et al., 2004;Reich et al., 2014;Vitousek et al., 2013;Xu-Ri and Prentice, 2008), theories (Zhu et al., 2017;Menge et al., 2017), and model projections (Hungate et al., 2003;Todd-Brown et al., 2013;Wieder et al., 2015b) of the role of N limitation for plant growth and the land C sink (Meyerholt et al., 2016;Zaehle et al., 2014;Walker et al., 2015) represent a major uncertainty in future projections of atmospheric CO_2 and climate (Jones et al., 2013;Joos et al., 2013;Todd-Brown et al., 2013). Results from free-air CO_2 enrichment (FACE) and open-top chamber experiments show that N limitation at least in some ecosystems reduces the response of aboveground biomass growth to elevated CO_2 (McMurtrie et al., 2008;Norby et al., 2010;Terrer et al., 2016) and that soil N and P availability are important controls on this magnitude in ectomycorrhizal and arbuscular mycorrhizal systems, respectively . Increased N immobilization in plant litter, biomass and soil (Luo et al., 2004) and multiple nutrient limitation (Körner, 2015;Vitousek et al., 2010;Elser et al., 2007) have been put forward as explanations of reduced growth responses. ~~A~~ R~~r~~ecent syntheses~~is~~ of the results from CO_2 enrichment experiments suggests that mycorrhizal association exerts an important control on the magnitude of the realized CO_2 fertilization effect (Terrer et al., 2016) and that soil N and P availability are important controls on this magnitude in ectomycorrhizal and arbuscular mycorrhizal systems, respectively (Terrer et al., 2019).

Field and laboratory experiments provide important insights, but extrapolation of such results on the short-term response in ~~BNF and C uptake~~ C and N fluxes to the multi-decadal-to-century time scales, relevant for global warming projections, is uncertain. For example, Reich et al. (2018) found an unexpected reversal of C_3 versus C_4 grass response to elevated CO_2 and shifts in soil N mineralization rates during a 20-year field experiment. These authors concluded that even the best-supported short-term drivers of plant response to global change might not predict long-term results. Additional hindrances to the improvement of our quantitative understanding of C-N cycle coupling are related to large variations in fluxes and inventories on small spatial and temporal scales (Arias-Navarro et al., 2017;Barton et al., 2015) and the diversity of responses across different organisms and ecosystems. Largely missing are long-term observational constraints on the global coupled C and N cycle ~~that might permit us to explore and test alternative hypotheses regarding the degree of N limitation~~ during periods of rapid climate change and increasing atmospheric CO_2.

High-resolution data on the isotopic composition of N_2O from Antarctic ice cores have the potential to provide precise information on past variations in terrestrial and marine N_2O emissions and thus on C-N coupling on time scales from decades to many centuries. A recent ice-core study on the stable isotope composition of N_2O demonstrated the power of this approach (Schilt et al., 2014). The isotopic data showed that both land and oceanic sources increased during the interval from 16 to 10 thousand years before present (ka BP), when ocean circulation and climatic changes strongly affected the global cycling of both CO_2 and N_2O (Schilt et al., 2014). Schilt et al. concluded that natural N_2O emissions will probably increase in response to global warming. In part I of this study (Fischer et al., 2019), this earlier work was extended to reconstruct the evolution in terrestrial versus oceanic emissions of N_2O from the Last Glacial Maximum (LGM; 21 ka BP) to the late preindustrial Holocene using ~~a~~ novel N_2O stable isotope data~~record~~. The ice core data reveal large step-like changes in terrestrial emissions at the onset of warming events, realized over decades and, given the proxy data resolution, last ~~maximum~~ 200 years at maximum. But a detailed process-based investigation of terrestrial N_2O emission changes over the deglaciation, rapid past warming events, and the Holocene warm period, and their links to the flow of N and C in land ecosystems, has not been attempted~~carried out~~ before.

The aim of part II of this study is to improve our understanding of the cycles of N_2O, C and N. ~~We use terrestrial N_2O emissions as a proxy for the flow of reactive N entering and leaving land ecosystems and thus implicitly as a constraint for changes in biological N fixation and soil N availability for plants. In other words, reconstructed terrestrial N_2O emissions are used to shed further light on the N limitation of terrestrial ecosystems, and the land C sink, on a global scale.~~ The unique, new terrestrial N_2O emission record of the past 21 kyr is used to explore ~~and test alternative~~ mechanisms of the functioning of the C-N cycle on land and to quantify terrestrial drivers for atmospheric N_2O concentration changes. Controls on variations in terrestrial emissions are elucidated in the framework of a dynamic global vegetation model. Part I of this study (Fischer et al., 2019) presents the ice core N_2O concentration and isotope data and the reconstruction of global terrestrial and marine N_2O emissions for the past 21,000 years and provides a discussion on the reconstructed marine emissions in the context of past climate and oceanographic changes. ~~In addition, a~~A model-based interpretation of the reconstructed marine N_2O emission changes during past abrupt climate events is given by Joos et al. (2019). Here in part II we focus on the interpretation of the terrestrial N_2O emission record ~~using explicit~~and discuss terrestrial N_2O emissions and C-N responses in transient deglacial simulations within~~in~~ a dynamical vegetation/terrestrial biogeochemistry model.

2 Introduction to N_2O, terrestrial nitrogen and carbon flows ~~and working hypotheses~~

2.1 N_2O budget and production mechanisms

Prather et al. (2015) estimated that the pre-industrial atmospheric lifetime of N_2O was 123 years. Together with the atmospheric N_2O concentration from ice cores, this figure constrains the total net pre-industrial N_2O source to 10.5 ± 1 Tg N yr^{-1}. Marine N_2O emissions were recently estimated by an observation-constrained approach, using water-column and surface N_2O observations as targets, to be 4.6 (± 1 standard deviation range: 3.1 to 6.1) Tg N yr^{-1}. This calculation implies a natural terrestrial N_2O source of 5.9 (4.1 to 7.7) Tg-N yr^{-1} (Battaglia and Joos, 2018), in line with IPCC AR5 estimates of 6.6 (3.3 to 9.0) Tg N yr^{-1}.

N_2O is produced through a variety of pathways both in the ocean and on land and N_2O production is closely linked to the flows of C and N (Wrage et al., 2001;Chapuis-Lardy et al., 2006;Kato et al., 2013;Battaglia and Joos, 2018;Trimmer et al., 2016;Babbin et al., 2015;Gilly et al., 2013;Bange, 2008;Butterbach-Bahl et al., 2013;Firestone and Davidson, 1989). The dominant pathways of net N_2O production are thought to be respiratory denitrification ($NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$) under low oxygen conditions, and autotrophic nitrification ($NH_3 \rightarrow NO_2^- \rightarrow NO_3^-$), mediated by archaea, bacteria and fungi. In addition heterotrophic nitrification, which is the oxidation of organic N to nitrite (NO_2^-) and subsequent reduction to N_2O by incomplete denitrification, was found to be the dominant path in a grassland ecosystem after fertilizer application (Moser et al., 2018). N_2O is produced as a byproduct of nitrification and as an intermediate product during denitrification. N_2O is also produced from nitrite through nitrification, often termed nitrifier-denitrification, through anaerobic ammonium oxidation, chemautotrophic denitrification, abiotic processes or from photoautotrophic organisms in cryptogamic covers (Lenhart et al., 2015;Butterbach-Bahl et al., 2013).

Terrestrial N_2O production and emissions depend sensitively on environmental factors including precipitation, soil temperature, soil moisture, soil texture, soil oxygen concentration or pH, topography as well as on substrate and nutrient availability and on nutrient addition by deposition or fertilizer application (Zhuang et al., 2012;Stehfest and Bouwman, 2006;Wang et al., 2017). Field data- and model-based emission estimates show the highest emissions of N_2O in moist tropical areas, and lower emissions in high latitudes (Stehfest and Bouwman, 2006;Zhuang et al., 2012;Werner et al., 2007;Potter et al., 1996;Xu et al., 2017;Xu-Ri et al., 2012;Wells et al., 2018). Moist soils typically show relatively high N_2O emission (Butterbach-Bahl et al., 2013;Zhuang et al., 2012), but the environmental dependencies of N_2O emission are often complex (Diem et al., 2017;Müller et al., 2015;Schmid et al., 2001a;Matson et al., 2017) and dependent on the production pathway (Kool et al., 2011). Higher N_2O fluxes at high soil water contents have been reported from laboratory and field studies, and linked to increasing denitrification activity in response to reduced oxygen diffusion into the soil (Arias-Navarro et al., 2017). The sensitivity of denitrification to temperature is found to be higher than for CO_2 emissions from soil organic matter decomposition, and a positive feedback of soil warming on N_2O emissions is expected (Butterbach-Bahl et al., 2013). Warming treatment increased measured N_2O emissions in boreal peatlands (Cui et al., 2018). However, responses to warming treatment are found to be highly variable across a range of conditions and ecosystems and it remains unclear whether warming will increase or reduce regional-to-global N_2O emissions (Dijkstra et al., 2012). Positive or neutral responses in N_2O emissions have been found in field experiments under elevated CO_2 in temperate and boreal forests and grasslands (van Groenigen et al., 2011;Dijkstra et al., 2012;Regan et al., 2011;Moser et al., 2018;Zhong et al., 2018). Nitrogen addition by mineral and organic fertilizer causes enhanced N_2O emissions. Emission factors are reported to depend sensitively on soil pH and are typically estimated to be around 0.5 % to 2 % of added N (Charles et al., 2017;Wang et al., 2017), but may vary by more than an order of magnitude.

The amount of N_2O produced per unit of N converted varies with environmental conditions and production pathway. For nitrification and denitrification this yield (or emission) factor depends on substrate availability linked to soil organic matter decomposition and C:N stoichiometry, on oxygen level influenced by soil moisture status and respiration, on acidity and temperature (Diem et al., 2017;Davidson et al., 2000;Firestone and Davidson, 1989;Smith, 1997;Phillips et al., 2015;Saggar et al., 2013). In addition, different N_2O production pathways and N loss processes and their relative importance may evolve through time and influence the N_2O yield on local to global scales.

2.2 C-N-N_2O coupling

The main flow paths of reactive N and its link to N_2O production and C flows on land (Gruber and Galloway, 2008;Butterbach-Bahl et al., 2013;Vitousek et al., 2013;Zähle, 2013;Firestone and Davidson, 1989) are schematically sketched in Fig. 1. These ecosystem flows can be assigned to an internal and an external N cycle. Within an ecosystem (green arrows in Fig. 1), N is primarily taken up in the form of NH_4^+ and NO_3^- by plant roots to support growth, while a large fraction of reactive N is taken up by soil microbes and fungi and is thus immobilized. Organic N is converted back to inorganic N during the mineralization of litter and soil organic matter. Gross N mineralization is thereby modified by the decomposers carbon-use efficiency (Manzoni et al., 2008). Net N mineralization (as in Fig. 1) thus reflects the modified gross N mineralization minus N immobilization. The NO_3^- pool is replenished by nitrification, the conversion of NH_4^+ to NO_3^-. We note the acid-base equilibrium between NH_4^+ and NH_3 in soil water; for simplicity, we generally refer to NH_4^+ only.

Turning to the external cycle, reactive N enters land ecosystems (blue arrows in Fig. 1) through the conversion of dinitrogen (N_2) to organic N and eventually to NH_4^+ by BNF (Cleveland et al., 1999;Vitousek et al., 2013;Zähle, 2013;Sullivan et al., 2014;Xu and Prentice, 2017), through rock weathering (Houlton et al., 2018) and the deposition (Lamarque et al., 2011;Vet et al., 2014;Dentener et al., 2006) of NH_x and NO_y (including sources by lightning). Reactive N is lost from land ecosystems through gaseous losses (including N_2O), leaching of NO_3^- and dissolved organic matter by runoff, and emissions of N compounds by fire (Bouwman et al., 2013;Ciais et al., 2013;Hedin et al., 1995;Hedin et al., 2003). On larger scale, N lost by fires will be deposited again and a large part of this N flux is therefore fed again to land ecosystems. In this sense, the fraction of the fire flux not lost to the ocean may be viewed to belong to the internal global land N cycle. N leached as dissolved organic N is typically remineralized downstream and may undergo nitrification and denitrification or be taken up by aquatic organisms. N may also be absorbed by minerals and become unavailable for plants and microbiological assemblages. ~~In equilibrium~~ Following mass balance, losses of reactive N from ecosystems and changes in N stocks have to be compensated by N inputs, mainly by BNF~~, on decadal to millennial time scales~~.

The external and internal N cycles are coupled. Reactive N in mineral forms serves as substrate for the N loss fluxes (external cycle) as well as a reservoir for plant N uptake (internal cycle). Following mass balance, mineral N concentrations change until the balance of N input by BNF and other sources matches N loss and net ecosystem N uptake (reactive N uptake minus net N mineralization). For example, in a growing ecosystem an increasing amount of N is taken up by plants and converted from inorganic to organic forms. This net ecosystem N uptake tends to deplete reactive N in mineral forms. Correspondingly, N loss fluxes (including N_2O) would decrease and N limitation of plant growth would increase if N sources such as BNF do not adjust to the increasing ecosystem N demand. Whether N limitation increases or not in a growing ecosystem depends therefore critical on the flexibility of N input, hence BNF.

Empirical evidence from N-addition experiments, synthesized by Lue et al. (2011) and Niu et al. (2016), shows that the uptake of N by plants, net primary productivity and biomass as well as NH_x and NO_3^- pools in soils, nitrification, nitrate leaching, denitrification, and N_2O emissions all increase simultaneously with N input. This finding points to a tight coupling between the availability of reactive N for plant growth, nitrification and denitrification fluxes and N_2O. N_2O production on land is predominantly associated with denitrification, and to a smaller extent with nitrification. Large gaseous losses and N_2O emissions are thus indicative of a large N throughput (input and loss), where ecosystem functioning may have adjusted by exploiting energetically costly, but evolutionarily advantageous BNF to compensate for the losses (Batterman et al., 2013;Pons et al., 2007;Vitousek and Hobbie, 2000) or where losses are compensated by N input from weathering or deposition.

In summary of section 2.1 and 2.2, changes in terrestrial N_2O emissions may be linked (i) to changes in the magnitude of reactive N entering and leaving ecosystems, and (ii) to changes in the N_2O yield per unit reactive N converted in land ecosystems.

~~2.3 Working hypotheses~~

~~In a N-limited land ecosystem, N that becomes available through mineralization or deposition is expected to be quickly taken up by plants to support their growth. In turn, the pools of reactive N in soils remain small. As a consequence, N_2O production is expected to be small in ecosystems with severely N-limited biomass growth and a correspondingly “closed” N cycle. On the other hand, in an ecosystem with abundant reactive N supply, mineralized N not used for biomass growth enriches the soil~~

~~pools of reactive N and is eventually converted by nitrification and denitrification and lost from the ecosystem. Thus, N_2O production is expected to be high in such an "open" (or "leaky") system, where plant growth is not or only weakly limited by N availability and where N input by BNF and other sources is high. These two situations are consistent with contrasting setups of the "Hole-in-the-pipe" model (Firestone and Davidson, 1989;Davidson et al., 2000) with low N flow entering and leaving ecosystems and correspondingly low N_2O production in the closed case and high N flow and N_2O production in the open case (Fig. 1). Generally, mid- and high latitude ecosystems are considered to be more generally N limited than tropical ecosystems. Yet the role of BNF in potentially alleviating N limitation, and the trade-offs among N fixation and N use efficiency, soil N uptake, and plant turnover remain unclear (Menge et al., 2017).~~

~~To guide further discussion, we formulate two extreme "end-member" working hypotheses for the temporal evolution of the carbon and nitrogen cycle over the last 21,000 years on the global scale:~~

~~*Hypothesis I* postulates an "open" or "flexible" terrestrial N cycle whereby sources of reactive N on land increased under warming climate and increasing CO_2 over the deglacial period, contributed to meet the increasing N demand of plants under more favorable growth conditions, and, in turn, resulted in a higher flow of N entering and leaving land ecosystems and increased N_2O production from terrestrial ecosystems.~~

~~*Hypothesis II* postulates a "closed" or "inflexible" terrestrial N cycle whereby N sources did not adjust to environmental change, land ecosystems remained or became increasingly N limited over the deglacial period, and consequently terrestrial N_2O production remained small and marine emissions dominated past atmospheric N_2O changes.~~

~~The question posed in this study is not to what extent different ecosystems are, or have been, N limited. Rather, we ask whether BNF and the N cycle adjusted dynamically to (at least partly) meet increasing N demand by plants (hypothesis I) or not (hypothesis II) and address this question by analysing temporal changes in terrestrial N_2O emissions. We note that the ice core record provides a globally integrated signal; spatially differentiated responses are not resolved. Last, but not least, the ice core terrestrial N_2O emission record provides information for time scales of a century or longer – potentially giving sufficient time for ecosystems to adjust.~~

3 Methods

3.1 The LPX-Bern(~~v1.4~~v1.4N) Dynamic Global Vegetation Model

The dynamic global vegetation and land surface process model LPX-Bern ("Land surface Processes and eXchanges" model as implemented at the University of Bern, version 1.4N) (Lienert and Joos, 2018b) is applied here in transient mode over the last 21,000 years (Ruosch et al., 2016). The LPX-Bern model describes dynamical vegetation and terrestrial biogeochemical processes, integrates representations of non-peatland (Gerten et al., 2004;Joos et al., 2004;Sitch et al., 2003) and peatland (Spahni et al., 2013;Wania et al., 2009) ecosystems and their C and N dynamics (Stocker et al., 2013;Xu-Ri and Prentice, 2008;Xu-Ri et al., 2012), and describes the dynamic evolution of wetland and peatland extent (Stocker et al., 2014). The model calculates the release and uptake of the trace gases CO_2, N_2O (Stocker et al., 2013;Xu-Ri and Prentice, 2008;Xu-Ri et al., 2012) and CH_4 (Spahni et al., 2011;Wania et al., 2010;Zürcher et al., 2013).

Vegetation is represented by plant functional types (PFTs) that are in competition for resources (water, light, N) on each grid cell. Here a version with fifteen PFTs is used. Eight generic tree PFTs, and PFTs for C3 and C4-type grasses grow on natural land (excluding peat) and former peat. Two PFTs representing peat mosses and flood-tolerant C3 graminoids as well as three flood-tolerant tropical PFTs grow on peat and wetlands. The model accounts for the dynamic coupling of C and water cycles through photosynthesis and evapotranspiration, which also defines plant water use efficiency (Saurer et al., 2014;Keller et al., 2017). Seven C and N pools per PFT represent leaves, sapwood, heartwood, fine roots, aboveground leaf litter, aboveground woody litter, and belowground litter. Separate soil organic C and N pools receive input from litter of all PFTs. LPX uses a vertically resolved soil hydrology, heat diffusion and an interactive thawing–freezing scheme (Wania et al., 2009).

The LPX-Bern vegetation and soil components interact with a dynamic N-cycle module (Xu-Ri and Prentice, 2008;Xu-Ri et al., 2012), ~~here modified to include~~ accounting for the uptake of mineral N by N immobilization in soils (Bengtsson et al., 2003;Li et al., 2017;Gütlein et al., 2017) as in Xu-Ri and Prentice (2017). The module describes the relevant N and N_2O fluxes and pools for plants and soils as schematically depicted in Fig. 1 and ~~briefly~~ summarized below. ~~For a detailed description, justification, and further references we refer to Xu-Ri and Prentice (2008) and Xu-Ri et al. (2012).~~

In LPX, the source of reactive N is implied by maintaining prescribed soil ~~C:N~~ N:C ratios associated with each of the plant functional types, reflecting their different litter chemistries and decomposer assemblages. Due to lower N:C ratios of litter than soil pools, the transfer of mass from litter to soil pools during litter decomposition therefore implies a given amount of N, required to satisfy the soil N:C ratio. The required N is partly satisfied by a flux representing immobilization of mineral N. The remainder determines the total input of reactive N into the ecosystem, implicitly subsuming symbiotic and asymbiotic BNF, and any other potential N sources that may support plant growth, in addition to prescribed N deposition. The amount of N input required to close the N balance of soils and to maintain the soil pools at their high N:C ratios depends on the flux representing N immobilization. Constant fractions (*frac_soil_immob*, *frac_litter_immob*) of the N flux released by soil or litter remineralization are immediately returned to its pool of origin. Hence, the choice of these parameters simultaneously co-determine reactive N input rates and net N mineralization.

We assumed the parameters *frac_soil_immob* and *frac_litter_immob* to be invariant over time and space and calibrated their values (Tab. A.1) to match a total preindustrial reactive N source of 128 TgN yr^{-1}. This value implicitly includes contributions from symbiotic and asymbiotic BNF, as well as other inputs of reactive N not included in the prescribed N deposition. Estimates of the global BNF for non-agricultural ecosystems are uncertain. They range from 40 to 470 TgN yr^{-1}, with most published estimates around 100 to 150 TgN yr^{-1}. Cleveland et al. (1999) used 100 plot-scale estimates of BNF to estimate global BNF on natural ecosystems to 195 TgN yr^{-1} (range: 100 to 290 Tg N yr^{-1}). Vitousek et al. (2013) suggest a plausible range for preindustrial BNF of 40 to 100 TgN yr^{-1} by computing BNF as the difference from all other global sources and sink fluxes of N. Cleveland et al. (2013) estimate symbiotic BNF to 105 TgN yr^{-1}, based on cost-benefit modelling for N fixation. The same authors estimate asymbiotic N fixation to 22 TgN yr^{-1} by upscaling measurements reported in Cleveland et al. (1999). In contrast, Elbert et al. (2012) estimate asymbiotic N fixation by cryptogamic covers alone to 49 TgN yr^{-1} (27-99 TgN yr^{-1}) by integrating experimental data from 200 studies. In addition, rock weathering is estimated to add 15 (10 to 20) TgN yr^{-1} to land ecosystems (Houlton et al., 2018). Xu-Ri and Prentice, (2017) estimated global N sources to 340 (230–470) TgN yr^{-1} for the parameter settings they adopted within the LPJ-DyN model; this estimate includes contributions from rock weathering and other inputs that are not explicitly prescribed or simulated by LPJ-DyN. Meyerholt et al. (2016) implemented six different BNF formulations in their model to predict modern BNF ranging from 108 to 148 TgN yr^{-1}.

Plant net primary productivity (NPP) and a prescribed constant N:C ratio of new production in different tissues sets the N demand that is satisfied by N uptake from NH_4^+ and NO_3^- pools which in turn depend on net N mineralization fluxes from litter and soil pools and loss fluxes of reactive N (e.g. denitrification, leaching, volatilization) (Fig. 1). In case that available inorganic N (sum of NH_4^+ and NO_3^-) is insufficient to meet the demand, NPP is down-regulated, thereby inducing an effect of N limitation. ~~BNF~~ The implied N source tends to re-establish a balance between the input and the loss of reactive N.

Nitrification is assumed to be proportional to the NH_4^+ soil pool with a temperature dependent rate coefficient. Denitrification is modelled as a two-step process whereby NO_3^- is converted to nitrite (NO_2^-) and NO_2^- is further converted to N_2, following Michaelis-Menten kinetics with dependence on the substrates NO_3^-, NO_2^-, ~~and~~ as well as on labile C availability. Reaction rates are ~~again~~ temperature dependent~~ following *f*~~. NO_3^- leaching depends on soil NO_3^-, available water holding capacity, and daily runoff. Reactive N is also lost from a grid cell by fire, assuming complete loss of N from burned vegetation, and NH_3 volatilization.

N_2O emissions are computed by assuming that fractions of the N fluxes associated with denitrification, nitrification and N leaching are released as N_2O. The calibration of the denitrification and nitrification yield factors is done to satisfy the constraints from the global atmospheric N_2O budget, which suggests global terrestrial emissions to be 5.9 TgN yr^{-1} at pre-industrial (Battaglia and Joos, 2018). Since global terrestrial N_2O emissions depend also on the N loss rates (denitrification and nitrification), we first calibrated the parameters *frac_soil_immob* and *frac_litter_immob*, which co-determine these rates, and then calibrated the yield parameters, given the N loss rates.

For denitrification, the globally-dominant N_2O source path, this fraction is the product of a constant (*RN2ODN*) and a temperature-dependent factor *f*(T). *f* is unity at 22ºC and its value roughly doubles for a temperature increase of 10ºC. The amount of N_2O released per unit N denitrified is therefore higher in warm than in cold regions. ~~The fraction of N_2O production from denitrification has been observed to be in the range of 0.2–4.7 % of the denitrification rate (see references in (Xu-Ri and Prentice, 2008)). Here, t~~The constant *RN2ODN* is set to ~~1.46~~5.418 % of the denitrification rate~~ in order to arrive at pre-industrial (1500 CE) emissions of 5.9 TgN yr^{-1} (Battaglia and Joos, 2018)~~. The corresponding yield fraction~~s~~ for N_2O emissions from nitrification~~s~~ is nominally set to 0.231 % at 22ºC and the same temperature dependence (Smith, 1997) as for denitrification is assumed. ~~and~~ The N_2O yield for the leaching N flux is assumed constant and, for simplicity, set to the nominal value of nitrification (0.231 %). ~~are, in the absence of better information and for simplicity, assumed to be temperature independent and constant across space and time. They are set to 0.05 % and 0.5 % of the respective N fluxes (Stocker et al., 2013).~~

~~The N source by biological N fixation (BNF) is implied by maintaining prescribed soil C:N ratios associated with each of the plant functional types, reflecting their different litter chemistries and decomposer assemblages. N is added to the soil pools when litter is transferred to the soil pools to maintain their high N:C ratios. Sources of reactive N by weathering are implicitly included in the BNF flux.~~

(1999;2013;2013;2012;Houlton et al., 2018;2017;2016)

~~In LPX-Bern, the magnitude of the simulated global N source (BNF and weathering) is partly adjustable by two scaling parameters. These are the fractions of re-mineralized N that is returned to litter and soil by immobilization, respectively. Similarly, global N_2O emission is adjustable by varying *RN2ODN*. The immobilization fractions are set to 0 % for litter and 26.39 % for soil mineralization in the standard setup. This results in a N source flux (Fig. 1) that is higher than the published range (~60 to 340 TgN yr^{-1}) (Vitousek et al., 2013;Cleveland et al., 1999;Xu and Prentice, 2017;Houlton et al., 2018;Cleveland et al., 2013). The extent of immobilization of freshly added N is found to vary between 35 and 95 % from one soil to another with uptake by soil microorganisms~~ (~~, w~~w~~ith a typical turnover of 1-2 months~~)~~, dominating over abiotic processes (Bengtsson et al., 2003).~~

The two-step calibration described above resulted in yield factors that are higher than the range of published estimates. The global mean yield for denitrification, expressed as N_2O per N_2 produced, is 5.6 % and thus higher than the range of estimates (0.2–4.7 %) summarized by Xu-Ri and Prentice (2008). Similarly, the global yield for nitrification (0.26 %) is higher than observation-based estimates (0.01-0.2 %). The mismatches in these estimates for yield may suggest that current best estimates for the N source, N_2O yield, and preindustrial N_2O emissions are not fully consistent. We carried out ~~In two~~ a sensitivity simulation~~s~~ to explore uncertainties:~~,~~ the immobilization fraction~~s are~~ is set to ~~25 % for both soil and litter or to 26.4 % for soil and to 50 % for litter immobilization~~0 % for litter and to 26.39 % for soil mineralization, leading to a preindustrial N source of 523 TgN yr^{-1}. ~~Immobilization lowers the NH$_4^+$ and NO$_3^-$ pools in the model and loss fluxes of reactive N. In turn, less BNF is required to maintain a balance of reactive N. Preindustrial BNF is 310 and 188 TgN yr^{-1} in these two sensitivity simulation~~ This is about a factor of four higher than in the standard setup. Correspondingly, yield factors are about a factor four lower in this sensitivity run than in the standard simulation.

The sensitivity of simulated N$_2$O emission changes over the deglacial period to these parameter choices is relatively small, while the absolute magnitude of the N source has some implications for N stress and thus NPP. The increase in NPP over the deglaciation is larger in simulations with a high compared to a low N source (10.1 versus 5.9 GtC yr^{-1} in the standard). Importantly, the difference in relative changes in modelled global N source is small (16 % versus 10 % in the standard) and the deglacial increase in N$_2$O emissions is only 0.2 TgN yr^{-1} higher in the sensitivity than in the standard run (see Sect. 3.2 and 5), despite the large difference in the implied N source. Thus, related model-based conclusions for N$_2$O emissions are not sensitive to the parameter settings for the yield and the flux representing immobilization.

~~TN$_2$O emissions over the deglaciation are only about 5 % lower than in the standard setup (see Sect. 3.2 and 5).s and within the published range. .~~

3.2 Setup for transient glacial-interglacial simulations

A previously described LPX-Bern model setup for glacial-interglacial simulations is applied (Spahni et al., 2013;Ruosch et al., 2016) and input data are shown in Fig. 2. The evolution of monthly temperature, precipitation, cloud cover, and number of wet days, annual atmospheric CO$_2$ (Joos and Spahni, 2008), orbital insolation changes (Berger, 1978) modulating plant available light, and topography changes through ice-sheet and sea-level changes imposed by ICE-5G (Peltier, 2004) are prescribed. The monthly climate data are obtained by combining monthly values from the observation-based, modern climatology compiled by the Climate Research Unit (CRU) (Mitchell and Jones, 2005) with monthly anomalies for the past 21 kyr from a transient climate simulations over this period (TraCE-21kyr) (Liu et al., 2009;Otto-Bliesner et al., 2014) with the Community Climate System Model, version 3 (CCSM3) maintained by the National Centre for Atmospheric Research (NCAR). Here the LPX-Bern model was run with a spatial resolution of 3.75° longitude × 2.5° latitude and a daily time step was applied in the photosynthesis, water and N-cycle modules. Simulations started from an equilibrated spin-up at 21 ka BP. Annual N deposition from the atmosphere, distributed across days according to precipitation within a year, is prescribed at preindustrial values (Lamarque et al., 2011).

The same model parameter values as determined by Lienert and Joos (2018b) are used, except for the immobilization fractions and N$_2$O yield factors (Tab. A.1). Regarding the N module, the parameters are the same as in a previous studies (Stocker et al., 2013;Schilt et al., 2014) addressing N_2O emissions over the past and under future global warming. An exception is an adjustment in the upper limit of the fraction of NH_4^+ nitrified per day from 0.1 day^{-1} to 0.09096 day^{-1} at 20 °C ~~denitrification~~ and in the yield factors for denitrification, nitrification, and leaching ~~*RN2OND*~~ in response to new observation-constrained estimates of marine N_2O emissions and to a slightly revised estimate of the atmospheric N_2O life time from 120 yr to 123 yr (Prather et al., 2015) as well as the ~~inclusion~~ simple representation of N uptake by N immobilization as discussed above.

Changes in N_2O emissions and other model outcomes are attributed to individual driving factors (temperature, precipitation, CO_2, orbital insolation, and land mask). One driver is kept at its preindustrial state in factorial simulations. BNF was kept at LGM values in an additional factorial run for each land use class and grid cell. In a further simulation, the yield factors for denitrification and nitrification were set to be constant in space and time for each land use class. The difference in results between the standard model setup (baseline) and a factorial run is attributed to the relevant driver. An interaction or synergy term, called "other drivers" is quantified by the difference between the change in N_2O emissions (ΔeN_2O) simulated in the baseline run and the sum of the emission changes attributed to individual drivers: $\Delta eN_2O_{\text{other-drivers}} = \Delta eN_2O_{\text{baseline}} - \Delta eN_2O_{\text{temperature}} - \Delta eN_2O_{\text{precipitation}} - \Delta eN_2O_{CO2}$. The dominant driver is identified as having the largest contribution to ΔeN_2O in the baseline run with the same sign of change. Grid cells that submerge under sea water or emerge from waning ice sheets during the period considered and grid cells with insignificant changes ($|\Delta eN_2O| < 1$ mg N m^{-2} yr^{-1}) are excluded from the spatially-resolved attribution.

The response time scales of LPX are investigated in a further "step-change" sensitivity simulation. Starting from the equilibrated spin-up at 21 ka BP, climatic conditions and atmospheric CO_2 are abruptly changed to conditions for 2.5~~500~~ ka BP. The run is continued for another 1500 years with climate and CO_2 forcing for the period from 2.5~~00~~ ka BP to 1~~000~~ ka BP. The land mask is kept constant at the maximum extent possible for both LGM and late Holocene conditions. A corresponding reference simulation without step change was performed. The simulations, together with the above factorial runs, permit us to address how fast N_2O emissions in the LPX model are able to respond to a sudden warming event, similar to the onset of the B/A and the end of the Younger Dryas.

4 Reconstructed terrestrial N_2O emissions and implications

We start the presentation of results by summarizing the main feature of the terrestrial N_2O emission record (Fig. 3, green line) presented in part I of this study (Fischer et al., 2019). In part I, the global N_2O emissions from land and from the ocean are jointly reconstructed by deconvolving novel ice core data of N_2O and of its isotopic signature, δ15N(N_2O), using an established method and relying on differences in the isotopic signature of land versus marine N_2O emissions. Terrestrial emissions increased between LGM (21 kyr~~a~~ BP) and PI (1500 CE) by about 1.7 TgN yr^{-1}. Terrestrial emissions remained approximately invariant during the Heinrich Stadial I Northern Hemisphere (NH) cold phase (HS1; 17.4 to 14.6 ka BP, (Rasmussen et al., 2014)) until the start of the Bølling/Allerød NH warm period (B/A; 14.6 to 12.8 ka BP). Then, land emissions increased at the start of the B/A, declined again during the Younger Dryas NH cold period (YD, 12.8 to 11.7 ka BP) and peaked at the start of the Preboreal period (PB), followed by a modest increase during the Holocene.

Remarkably, the overall deglacial increase in terrestrial N_2O emissions was mainly realized in two large steps at the onset of the B/A and at the end of the YD, two major northern Hemisphere warming events. The detailed analysis of the ice core N_2O concentration and isotope data (see Fischer et al. (2019)) reveals that global terrestrial N_2O emissions started to rise at the beginning of the warming events. ~~Each step-like increase in terrestrial N_2O emissions was realized within maximum two centuries, and possibly faster, given the temporal resolution of the ice archive.~~ The enclosure process of atmospheric air into firn and ice acts like a low pass filter, smoothing any fast variations in atmospheric N_2O, its isotopic signature, and, correspondingly, in inferred emissions. Fischer et al. conclude that global terrestrial N_2O emissions reacted within maximum 200 years to the large scale climate reorganizations associated with the two major deglacial northern Hemisphere warming events.

Overall, the ice core data show that land ecosystem N_2O emissions responded sensitively to climatic and environmental changes over the deglaciation. The rapid increase in terrestrial N_2O emissions at the onset of the B/A and at the end of the YD and the overall increase in emissions over the past 21,000 years either point (i) to an increase in N_2O yield per unit N converted for emissions to the atmosphere, averaged globally and across all N_2O production pathways, or/and (ii) to an increase in the global flux of converted N. ~~are in line with our working hypothesis I of an increasingly "open" N cycle whereby N input and loss fluxes increased under warming climate and increasing CO_2.~~ Reactive N was available in sufficient amount to support ~~nitrifying and denitrifying organisms and~~ an increase in global terrestrial N_2O emissions during periods where environmental conditions became, on a global scale, more favorable for plant growth and C sequestration (Ciais et al., 2012;Bird et al., 1994;Joos et al., 2004;Jeltsch-Thömmes et al., 2019). ~~This suggests that reactive N was available to support plant growth and to fuel N loss processes.~~

5 Transient simulations of terrestrial N_2O emissions and the C-N cycle over the past 21,000 years

5.1 Simulated changes in global terrestrial N_2O emissions and spatial patterns of change

We next explore governing mechanisms of the deglacial terrestrial N_2O emissions and potential implications for the C-N cycles in the spatially resolved, mechanistic LPX-Bern model. LPX-Bern ~~v1.4~~v1.4N simulates a general increase in global land N_2O emissions over the deglacial period (Fig. 3). The simulated evolution matches the reconstructed change in terrestrial N_2O emissions from the ice core isotopic records relatively well, although modelled changes are smaller and typically less abrupt than reconstructed variations. The model represents the emission variations during the Bølling/Allerød (B/A) and Younger Dryas (YD) periods with peaks in emissions at the onset of the BA (14.6 ka BP) and the preboreal (11.7 ka BP) and an ~~smaller~~

emission peak around 13.5 ka BP and corresponding minima at 14 ka BP and during the YD (12.8 to 11.7 ka BP). Reconstruction and models both show small changes in global terrestrial N_2O emissions over the last 11 ka, the Holocene period. Simulated terrestrial N_2O emissions decreased somewhat between 9 and 8 ka BP, whereas reconstructed emissions slightly increased over the Holocene, leading to a discrepancy between simulated and reconstructed anomalies. Overall, the agreement between proxy reconstruction and model results supports the plausibility of the LPX-Bern model as well as of the underlying TraCE-21kyr climate input data used to force LPX-Bern on these long timescales. On the other hand, ~~the model fails to reproduce the dynamic evolution of terrestrial N_2O emissions during Heinrich Stadial 1 (HS1). T~~the reconstruction suggests relatively constant emissions from the land biosphere during Heinrich Stadial 1 (HS1) and a rapid rise in emissions at the start of the B/A, whereas the model simulates steadily increasing emissions over the second half of the HS1 interval, reflecting the gradual climate warming in the TraCE-21kyr climate input data during HS1 (see discussion below). The model also shows a much slower and a smaller emission increase at the YD/PB transition than reconstructed.

The changes in global terrestrial N_2O emissions are the result of spatially differentiated responses. LPX-Bern simulates high natural emissions of N_2O in the tropics and low emissions at high latitudes (Fig. 4A). The spatial pattern and the magnitude of emissions are consistent with data-based estimates of natural N_2O emissions from soils (Zhuang et al., 2012;Stehfest and Bouwman, 2006;Potter et al., 1996). At ~~1500~~ 1450 AD, emissions in the tropics can be as high as 250 mgN m^{-2} yr^{-1} and the integrated flux between 20° S and 20° N amounts to 54~~64~~ % of the global emissions, while emissions per unit area are low in high latitudes and northern and southern extra-tropics contribute only a share of 29~~2~~ % and ~~14~~ 17 % to the global terrestrial emissions. In contrast, emissions increased strongly in the northern extra-tropics over the glacial termination (Fig. 4B), while ~~with~~ the integrated change in emissions is negligible in the tropical belt. ~~being half as large for the tropics than for the northern extra-tropics~~. Large increases per unit area are simulated over the termination in mid- and low-latitudes on the North and South American continents, in the southern boreal zone in Eurasia and in parts of eastern Asia, India, Indonesia and Africa. N_2O emissions decreased in a few regions, namely in Africa around 15°S and in northern Australia (Fig. 4B). Loss of tropical land due to rising sea level and the addition of land emerging from waning ice sheets (Peltier, 2004) are important drivers of modelled terrestrial N_2O emissions between 15~~4~~ and 8 ka BP. The net loss of terrestrial N_2O emissions by land area changes was dominated by the submergence of the high-productivity *Sunda* and *Sahul Shelf* regions. This loss offsets about one-third of the G-IG increase in global terrestrial N_2O emissions (Fig. 3). Changes in the land extent caused by changes in sea level represent~~is~~ an important factor for past global terrestrial N_2O emissions.

The patterns of change in terrestrial N_2O emissions (Fig. 4C), as well as spatial and seasonal patterns in precipitation and temperature, are complex for the Holocene period. Despite small changes in global terrestrial N_2O emissions during the Holocene, LPX-Bern simulated large regional shifts in source strength, linked to changes in temperature and precipitation. This includes for example a decrease in N_2O emissions from 11 to 0.5 ka BP in boreal Asia, in the sub-Sahara region in Africa and in parts of the conterminous United States of America (USA)~~, including Alaska,~~ and an increase in emissions in tropical Africa, parts of Australia and Latin America as well as in ~~Canada or Scandinavia~~western Europe.

5.2 Biological Nitrogen Fixation and carbon-nitrogen coupling

In this section, we address C-N coupling in LPX-Bern and analyze the spatial patterns for the source of reactive N, soil mineral N, net primary productivity (NPP), and C stocks (Fig. 5) and their changes over the deglaciation (Fig. 6). We quantify two decisive factors for N_2O emission change in the model: (i) changes in the source of reactive N, fueling nitrification and denitrification, and (ii) changes in the N_2O yield per unit N converted.

We first address C and N fluxes for the preindustrial mean state (Fig. 5), before turning to deglacial change. The N source (Fig. 5A) is typically smaller than 0.5 gN m^{-2} yr^{-1} in northern mid and high latitudes and around 1 gN m^{-2} yr^{-1} in tropical rainforest and in Central America, comparable to observational estimates (Sullivan et al., 2014;Wurzburger and Hedin, 2016a, b). An N source in the range of 2 to 6 gN m^{-2} yr^{-1} is simulated in many semi-arid regions, including southern Africa, the sub-Sahara region, India, northern Australia, and in the southern parts of North America. Soil mineral N (Fig. 5B) is typically below 0.5 gN m^{-2} in tropical forests and around 1 gN m^{-2} in temperate and boreal forests and tundra regions, while higher values of up to and more than 10 gN m^{-2} are simulated in exatratropical semi-arid and arid regions. Annually integrated NPP (Fig. 5C) is largest in the tropics, while large carbon stocks (Fig. 5D) are simulated in tropical forests and in the northern boreal zone. We note that the patterns of these C and N fluxes and stocks are all different, pointing to spatially distinct relationships between these four variables.

The N_2O yield factors, i.e., the N_2O produced per unit N converted by denitrification and nitrification, are assumed to vary with temperature and thus in space and time in LPX-Bern v1.4N. In a sensitivity run, these yield factors are set constant with all other settings as in the standard. The deglacial warming leads to a higher N_2O yield in the standard compared to this sensitivity run and 0.44 TgN yr^{-1} of the deglacial increase in land N_2O emissions are attributed to this change in yield (Fig. 7, black line). In other words, changes in the yield factors further amplify the increase in N_2O emissions as driven by the increase in the flow of reactive N in LPX-Bern.

~~At the LGM and in both model setups, two thirds of the simulated global input and loss of reactive N on land and two thirds of net primary productivity (NPP) occur within the tropics, while about 55 % of the global C inventory in surface soils (2 m) and vegetation is simulated to be stored in the tropics. The higher percentage storage in extratropical C compared to N and C fluxes is explained by a slower turnover time of organic C in the cooler extratropical compared to the warmer tropical regions.~~ Turning to changes in the sources of reactive N, the simulated N source increased by 12 % from 113 TgN yr^{-1} at the LGM to 128 TgN yr^{-1} at 0.5 ka BP in the standard setup. B~~B~~iological nitrogen fixation (BNF) is assumed to adjust dynamically to an increase in N demand and partly alleviating N limitation of plant growth in LPX-Bern. It is implicitly assumed that limitation by other nutrients does not affect the cycling of N and C through ecosystems on multi-decadal to century time scales and that nutrient input into ecosystems by deposition, and weathering (plus BNF for N) is large enough to support plant growth. These assumptions are controversial (Hungate et al., 2003;Luo et al., 2004;Körner, 2015;Wieder et al., 2015b;Vitousek et al., 2010;Fatichi et al., 2014). Our novel ice core isotope reconstruction of terrestrial N_2O emissions allows us to critically evaluate this assumption in a quantitative way on the multi-decadal to centennial time scales as relevant for the anthropogenic perturbation. To this end, we implement an N cycle representation leading to strong long-term nutrient limitation in the model. This is achieved by fixing the rate of the variable N source ~~BNF~~ to its glacial value in each grid cell and land use class and by keeping these rates of ~~BNF~~ N source constant in a sensitivity simulation over the past 21 kyr. ~~The simulation with constant BNF completely fails to reproduce the reconstructed N_2O emissions from the land biosphere.~~ This more strongly N-limited simulation yields not an increase, as reconstructed, but a decrease in global terrestrial N_2O emissions (Fig. 3, black line). The decrease in global land N_2O emissions is ~~due~~ related to the loss of land in response to sea level rise (-0.11 TgN yr^{-1}, ~~while~~and a small decrease in N_2O emissions on remaining land (-0.088 TgN yr^{-1}) ~~changes little~~ in this sensitivity simulation.

The comparison of changes in C and N fluxes and stocks ~~results~~ between the simulations with variable and ~~without~~ constant N source~~limitation~~ provides~~yields~~ also further insight into the N and C coupling (Fig. ~~5 and~~ 6). The ~~N-limited model~~setup with constant N source leads to~~yields~~ smaller ~~-~~changes in the N cycle, a small deglacial decrease (-1.2 PgC yr^{-1}) ~~er~~ instead of an increase (5.9 PgC yr^{-1}) in global ~~net primary productivity~~NPP, and a ~~reduced in~~decrease in ~~vegetation growth and~~ terrestrial C stocks of 47 PgC ~~than~~ compared to an increase of 482 PgC simulated in the standard setup. ~~The sSimulated BNF increased by 16 % from 451 TgN yr^{-1} at the LGM to 523 TgN yr^{-1} at 0.5 ka BP in the standard setup. BNF~~

The N source increases i~~o~~n ~~most~~ many land regions in the standard setup, but remains~~ed~~ by design almost constant on non-flooded land in the ~~N limited~~ simulation with constant N source per land use class ~~-~~(Fig. 6A,B). ~~Over this period~~In the standard ~~and on non-flooded land~~, ~~BNF~~ the N source ~~increased~~ decreased ~~in the standard setup~~over the deglaciation by ~~56~~ 7 TgN yr^{-1} in the tropics, due to land loss and a decrease in parts of Africa, while the~~. The~~ N source ~~, and~~ increased by 1~~5~~6 and 4~~17~~ TgN yr^{-1} in the northern and southern extratropics, respectively. Corresponding changes are simulated for nitrification and denitrification in the standard setup, whereas changes in nitrification and denitrification remain small on non-flooded land in the N-limited run.

In response to the increased N input, the availability of reactive N ~~-~~remained roughly constant or increased in most land areas in the standard run, despite increased storage of N in plant and soil organic matter and accelerated nitrification and denitrification (Fig. 6C). ~~(except~~ A decrease in mineral N is simulated in the standard in regions ~~in parts of mid-latitude Eurasia~~ where also C stocks decreased or changed little including parts of mid-latitude Eurasia, Africa, Australia and of the southern US~~)~~. In contrast soil reactive N concentrations decreased in many extratropical regions in the ~~N-limited~~ simulation with constant N source (Fig. 6D) ~~as more N became progressively locked into vegetation and soil C~~. Globally integrated, soil mineral N decreased by 19 % over the deglaciation in the run with constant N source, compared to a negligible change in the standard setup.

These differences in BNF (including ~~plus~~ abiotic input) and the N cycle between the run with constant N source ~~N-limited~~ and the standard case have profound impacts, not only for the emission of N_2O, but also for NPP (Fig. 6E,F) and C sequestration (Fig. 6G,H). Global NPP increased over the deglaciation by 13~~21~~ % in the standard case, compared to a decrease by 3~~11~~ % in the ~~N-limited~~ run with constant N source~~from the LGM to PI~~. LPX-Bern predicts that most of the NPP increase is realized in the northern extratropics.~~,~~ T~~while integrated NPP even decreased in the tropics in response to a shrinking land area in both model setups~~he NPP increase in the extratropics is almost twice as large in the standard than in the sensitivity run. As a result of the generally higher NPP ~~on remaining land in the standard setup compared to the N-limited setup~~, the deglacial change in C storage ~~at 0.5 ka BP~~ is in the standard about ~~700~~ 402 PgC larger in the extratropics and about ~~32~~ 127 PgC ~~higher~~ larger ~~than in the LGM~~ in the tropics than in the run with constant N source.~~extratropical and tropical regions, respectively.~~

In summary, ~~-~~the simulation with constant N source completely fails to reproduce the reconstructed N_2O emissions from the land biosphere. ~~no increases in global N loss and N_2O emissions from soils over the G-IG transition (Fig. 3A) are simulated in the N-limited model setup which is in clear contradiction to the ice core derived terrestrial N_2O emission record.~~ The increase in N_2O yield, as well as in soil and litter C and N turnover rates, under deglacial warming are not sufficient to overcome the effect of N limitation on N_2O emissions in this sensitivity simulation. We note, however, that changes in yield due to processes not incorporated in LPX-Bern could potentially explain the reconstructed increase in N_2O emissions. ~~Only i~~If the model is allowed to satisfy the demand of N, and thereby implicitly of other elements to support the growth of N fixers, nitrifiers and denitrifiers, and plants, terrestrial N_2O emissions increase as reconstructed.~~. The combined ice core andIn the standard modeldeglacial simulation, results suggest that the global terrestrial N cycle operated in an increasingly "open" mode as in our working hypothesis I, where excess N, not used for biomass production, is lost to the environment and replaced again, e.g. through BNF, deposition and weathering.~~ ~~In contrast, the emergence of an "inflexible" N cycle (hypothesis II), as expected under progressive N limitation, did not materialize over the past 21,000 years. We emphasize that the ice core N_2O concentration and isotope data represent globally integrated emissions and do not permit interferences on regionally differentiated responses, including possible nutrient limitation in specific regions.~~

5.3 Attribution of simulated terrestrial N_2O emissions to climatic and environmental drivers

The complex spatio-temporal changes in land N_2O emissions are attributed to climatic and environmental drivers (Fig. 7 to 10). This attribution helps us to better understand the simulated changes and data-model mismatches. ~~to elucidate why the model fails to simulate the reconstructed changes in terrestrial N_2O emissions during the Heinrich Stadial 1 (17.4 to 14.6 ka BP).~~ Globally, deglacial warming is the most important factor in the model contributing 1.4 TgN yr^{-1} to the overall emission increase, followed by ~~increasing atmospheric CO_2 (~0.4 TgN yr^{-1}), and~~ changes in precipitation (0.7~~25~~ TgN yr^{-1}, Fig. 7).

Changes due to increasing atmospheric CO_2 and o~~O~~rbitally driven changes in photosynthetically active radiation slightly offset the emission increase, while~~ and~~ non-linear interactions among the different drivers contribute to the global increase~~ slightly offset the emission increase~~. The change in land extent due to ice sheet melting and sea level rise leads to a reduction in terrestrial N_2O emissions (–0.5~~7~~ TgN yr^{-1}). As described in the previous section, a substantial part of the increase attributed to temperature is due to a temperature driven change in the yield factor of nitrification and denitrification (Fig. 7, red and black lines).

Turning to HS1 and the transition to the B/A, ~~the simulated increase in N_2O emissions during this period is only about a quarter smaller when atmospheric CO_2 is kept at the PI value than in the standard setup (Fig. 7). This means that~~ the majority of the simulated emission increase is in response to changes in physical climate, i.e., changes in temperature and precipitation (Fig. 7). In other words, the simulated rise in land N_2O emissions, which occurred earlier in the simulation than the ice core reconstruction, is not ~~primarily~~ driven by CO_2 fertilization and an associated ~~increase~~ change in N ecosystem flows, but by the prescribed climate change from TraCE-21kyr. ~~We note, however, that the small initial rise during the first part of HS1 is attributed to changes in CO_2.~~ It is not clear whether the model's failure to represent the reconstructed emission changes during the HS1 period and at the onset of the BA in the standard simulation is due to deficiency in the response of the LPX-Bern to early deglacial climate change, or to deficiencies in the climate input data, or a combination of the two.

Individual drivers exert regionally distinct influences and these may vary between different periods. Here, we attribute the spatial changes to changes in temperature, precipitation, CO_2 and their non-linear interactions for the glacial termination and the Holocene using factorial simulations (Fig. 8) and by examining the temperature and precipitation changes of the TraCE-21kyr input data (Fig. 9). Generally, attributed changes in emissions find their counterpart in underlying changes in individual drivers, but sometimes non-linear interactions and non-additivity of individual responses hamper the attribution to individual drivers.

Changes in temperature over the termination caused emissions to rise substantially in Eurasia, in the conterminous USA as well as in Argentina and southern Brazil and in eastern Australia (Fig. 8A). On the other hand, regional cooling in parts of the Amazon region and in parts of Africa ~~eastern Asia~~and India caused emissions to fall in this period. The pattern of change in N_2O emissions attributed to changes in temperature (Fig. 8B) is very different for the Holocene compared to the termination. The summer (June, July, August) cooling also found in climate data (Wanner et al., 2008) and simulated over the Holocene period in boreal Eurasia and the western part of North America results in a decrease in N_2O emissions over large parts of Eurasia and North America. The slight summer warming in eastern Canada and Scandinavia in the model has little impact on simulated emissions. An increase in terrestrial emissions is simulated in tropical Africa and Latin America, including the Amazon region, in response to changing temperatures.

The attribution of emissions to changes in precipitation (Fig. 8C,D) reveals some well-expressed dipole patterns, partly indicative of spatial shifts in precipitation regions (Fig. 9C). Attributed emission changes reflect corresponding changes in precipitation with generally increasing emissions under increasing precipitation. ~~As expected, i~~Increasing CO$_2$ exerts a generally positive influence on simulated emissions in tropical regions, except in semi-arid regions including eastern Africa and Brazil which dominate the globally integrated signal~~, in particular in the tropical belt~~ (Fig. 8E,F). Non-linear interactions between the three drivers can be significant regionally and either enhance or reduce simulated emission changes (Fig. 8G,H). The temperature-attributed decrease in emissions over the termination at around 15^{o} S to 20^{o} S in Africa (Fig. 8A) is not linked to a corresponding change in seasonal or annual temperatures. This particular attribution as well as the attribution of negative emission changes to increasing CO$_2$ in this region (Fig. 8E,F) most likely reflect non-linear interactions between precipitation, temperature and CO$_2$.

Figure 10 further illustrates which driver exerts the largest influence on simulated regional emission changes in a given grid cell. Over the termination, changing temperature is the dominant influence on the simulated emission changes in mid- and high-latitude Eurasia and North America, while changes in precipitation dominate emission changes south of the Sahara, in India and large parts of Australia, where temperatures were already rather high. ~~Increasing CO$_2$ exerts a dominant control in tropical Latin America, Africa and in Indonesia over the termination.~~ Over the Holocene, temperature is the dominant driver in northern Eurasia, while changes in precipitation dominate the emission response in Africa. Changes in CO$_2$ generally play a secondary role.

5.4 The time scales of response to a step change in climate and CO$_2$

Next, we investigate potential causes of the relatively slow N$_2$O increase during past abrupt NH warming events in the standard simulation compared to the ice core reconstruction. To this end, we assess on which time scales N$_2$O emissions adjust in LPX-Bern after a sudden change in environmental conditions. The question is whether LPX-Bern can simulate an equally fast response in N$_2$O emissions as reconstructed from the ice core data for the abrupt warming events at the onset of the B/A and the end of the YD or whether the intrinsic response time scales of the model are too long to match reconstructed emissions. We construct an extreme~~ bounding~~ case for rapid warming events by switching climate (and CO$_2$) instantaneously, step-like from LGM to late Holocene conditions in LPX-Bern (Fig. 11A).

LPX-Bern shows a fast response, followed by a relatively small century scale adjustment (Fig 11). About 80 % of the final response in global N$_2$O emissions to the step change is realized within 40 years and about 90% within a century, while it takes about 700 years to reach a near equilibrium (Fig. 11B). Taking the atmospheric lifetime of N$_2$O of more than 100 years into account, such a fast multi-decadal increase in N$_2$O emissions would cause a century scale increase in atmospheric N$_2$O concentrations, similar to what is seen in the ice core record. The adjustments in global ~~BNF,~~ nitrification and denitrification fluxes evolve similar as for N$_2$O emissions with the main increase in these fluxes again realized within about 40 years (not shown). The global N source peaks 20 years after the step (not shown). Then, it decreases again to reach a new steady state value, which is about 20 % higher than before the step. In contrast, the model's global N–leaching flux decreases ~~immediately~~ within about a decade (by about ~~10-15~~20 % relative to LGM) after the step, followed by a ~~century-scale~~slight increasing trend over the next 1500 years~~e to approach late Holocene conditions around 1000 years after the step~~. This transient evolution~~decrease and recovery~~ in modelled N leakage is indicative of a corresponding evolution of soil NO_3^- availability. Modelled global NPP (Figure 11C) increases immediately after the step and about three quarters of the NPP change are realized in the first year after the step. Then it takes again about 700 years to reach the new equilibrium.

The fast initial response is explained as follows. NPP responds immediately to the change in environmental conditions. The associated enhanced plant N uptake depletes soil NO_3^- leading to the ~~initial~~ decrease in N leakage, while warming accelerates soil decomposition and the release of NH_4^+. The newly assimilated C and N is allocated to leaves, sapwood and hardwood and roots, before released to litter and ~~relatively fast overturning~~labil soil organic matter overturning~~s~~ on time scales from years to decades. These annual-to-decadal vegetation and litter turnover time scales govern the initial response time of ~~BNF~~N source, nitrification, denitrification and N_2O emissions. The century-scale response is linked to the equilibration time scales of C and N in the slowly overturning soil pools as well as to the poleward expansion of vegetation. Finally, there is a small remaining offset between the reference run and the near equilibrium of the step simulation which is linked to remaining peat in the step-simulation formed under LGM conditions, but absent in the reference simulation.

In conclusion, this sensitivity experiment demonstrates that N_2O emissions in the LPX-Bern model are indeed able to adjust within decades to less than a century to abrupt warming events, given prescribed forcing is changing fast enough. We conclude that the exact timing of simulated N_2O emissions at the onset of the B/A and the end of the YD depends sensitively on the climate forcing data prescribed in~~to~~ the LPX-Bern model.

6 Discussion

6.1 Reconstructed terrestrial N_2O emissions and implications for the C-N cycle

Terrestrial N_2O emissions show a 40 % increase from the Last Glacial Maximum to the late preindustrial period ~~(~~(Fischer et al., 2019)~~)~~. Most of the deglacial increase was realized in two large steps, linked to rapid, decadal-scale and widespread northern hemisphere warming and to shifts in the Intertropical Convergence Zone (ITCZ) and precipitation patterns. ~~This increase occurred in two major~~Each steps~~, each~~ was realized within maximum 200 years. and thus on a time scale similar to that of the ongoing anthropogenic climate perturbation.

It has remained somewhat unclear whether warming will increase or reduce regional to global scale N_2O emissions, as responses to warming treatment are found to be highly variable across a range of conditions and ecosystems (Dijkstra et al., 2012). The ice-core record shows that past warming events, such as those at the onset of the B/A and the end of the YD, strongly promoted N_2O emissions globally. This suggests, as noted earlier (Schilt et al., 2014) and as projected (Stocker et al., 2013), that terrestrial N_2O emissions from natural land will likely increase further as climate warms, implying the existence of a positive climate feedback linked to the terrestrial N cycle (Xu-Ri et al., 2012).

The increasing terrestrial N_2O emissions imply either an increase in N_2O yield per unit N converted, averaged globally and across all N_2O production pathways, or an increase in the global flux of converted N or a combination of these factors. Regarding yield, u~~U~~ncertainties in the interpretation of the terrestrial N_2O emission record are linked to uncertainties in the ratio between N_2O produced to N converted~~ during nitrification and denitrification~~. This yield factor is known to vary with environmental conditions and across N_2O production pathways, though quantitative experimental evidence is often not unequivocal (Diem et al., 2017;Davidson et al., 2000;Firestone and Davidson, 1989;Saggar et al., 2013;Butterbach-Bahl et al., 2002). For nitrification, the ratio of N_2O/NO_3^- produced increases with increasing acidity and decreasing oxygen (Firestone and Davidson, 1989) and increasing temperature (Smith, 1997). For denitrification, the production ratio of N_2O/N_2 yield increases with increasing NO_3^- availability, increasing oxygen concentration, decreasing decomposable carbon, decreasing pH and decreasing temperature. Changes in precipitation may have altered the N_2O yield over the deglaciation. Higher soil water content and associated anoxic conditions generally favor the conversion of N_2O to N_2 and results in a low yield of N_2O (Weier et al., 1993), though dependencies of yield on water filled pore space are sometimes complex (Diem et al., 2017) and soil texture and drainage affect water filled pore space and yield (Bouwman et al., 2002). Yield is low under low NO_3^- availability (Diem et al., 2017) and generally found to increase when NO_3^- becomes more available (Weier et al., 1993). This relation, when considered in isolation, implies increasing N_2O emissions to be indicative of increasing NO_3^- availability. ~~Thus, the known dependency of yield on NO_3^- availability is not in conflict with the idea implicit in working hypothesis 1 that reactive N became more available with increasing N_2O emissions.~~ The ratio of N_2O to N_2 emitted generally- decreases with increasing temperature (Firestone and Davidson, 1989). On the other hand, the warming over the glacial termination is also expected to accelerate organic matter turnover and thus ~~C~~ availability of decomposable C which would tend to lower this ratio (Firestone and Davidson, 1989). Further, experimental studies on grasslands yield both higher and lower ratio of N_2 to N_2O under elevated CO_2 compared to ambient CO_2 (Zhong et al., 2018;Baggs et al., 2003). In addition, different N_2O production pathways and their relative importance may evolve through time and changes in soil organic matter decomposition pathways and in the stoichiometry of plant-derived material may affect yield. Given this complexity, we are not in the position to evaluate whether the N_2O yield factor for the combined N ~~loss~~conversion processes increased or decreased over the deglaciation on the global scale. ~~An increase would imply that the relative change in the flow of N through ecosystems was lower than the relative change in N_2O emissions~~Changes in globally-averaged yield may possibly explain the reconstructed terrestrial N_2O emission increase. ~~In contrast, a decrease in yield would indicate that the relative change in ecosystem N through flow was even larger than the relative increase in terrestrial N_2O emissions from the Last Glacial Maximum to the preindustrial period. Changes in N supply,~~

~~e.g. by BNF, would scale accordingly. In any case, changes in yield factor cannot plausibly reconcile our N_2O emission reconstruction with working hypothesis II of a closed N cycle. As noted by Bouwman et al. (2002), N_2O losses will be low at low flow rates, regardless of the yield factor.~~

Regarding the flow of reactive N, t~~T~~he reactive N lost from ecosystems must be replaced if ecosystem N pools are not to be depleted. This mass balance consideration suggests that the total input flux of N ~~from BNF increased~~changed hand in hand with ~~N_2O emissions and~~ related loss fluxes over the deglacial period and sufficiently to support changes in ecosystem N storage. An alternative to a balanced N input and output flux would be that N losses are fueled by existing reservoirs of reactive N. Large nitrate deposits ("caliche") are currently found in the hyperarid Atacama desert (Ericksen, 1981;Tapia et al., 2018). But such large deposits are very unusual, and require several hundred thousand of years to accumulate (Michalski et al., 2004). Microorganisms require readily decomposable carbon substrate for the denitrification of nitrate, otherwise nitrate may accumulate under the absence of substrate availability (Weier et al., 1993). Carbon substrate availability for denitrifiers might have increased at the onset of the B/A and at the end of the YD when climate warmed, precipitation pattern shifted and organic matter remineralization accelerated in many regions. This in turn could have led to the conversion of nitrate that had potentially accumulated previously. This would lead to a depletion of this nitrate pool and, in turn, one would expect a decrease in N_2O emissions. ~~However, s~~Such a scenario appears ~~unlikely~~in conflict with the reconstruction, given that reconstructed N_2O emissions remained high during the early B/A and even slightly increased throughout the Holocene.

Terrestrial N_2O emissions result primarily from nitrification and denitrification (Firestone and Davidson, 1989). A requirement for these processes to take place is the availability of ammonium and nitrate, as consumed by nitrifiers, denitrifiers and plants alike. ~~Reactive nitrogen (N) lost from ecosystems must be replaced by BNF, weathering and deposition to avoid ecosystem depletion of reactive N in the long term.~~ Variation in reactive N availability among diverse land classes are found to correspond to variations in N_2O emissions (Davidson et al., 2000). In addition, cryptogamic covers fix large amounts of N and contribute substantially to global N_2O emissions (Elbert et al., 2012). ~~According to the hole-in-the-pipe concept (Firestone and Davidson, 1989), N_2O emissions are directly indicative of the flow of N entering and leaving ecosystems.~~ The ice core data show that reactive N must have been available in sufficient quantity to support ~~N uptake by nitrifiers and denitrifiers and~~ increasing terrestrial N_2O production over the deglacial period. ~~The increasing N_2O emissions imply an increasing flow of reactive N through land ecosystems on the global scale. In other words, the ice core data support our working hypothesis I of an increasingly "open" or "leaky" (Niu et al., 2016) global terrestrial N cycle whereby~~ S~~s~~ources of reactive N on land, e.g., from BNF and weathering, may possibly have increased under warming climate and increasing CO_2 over the deglacial period and contributed to meet the N demand of plants, nitrifiers~~, and~~ denitrifiers and cryptogamic covers under more favorable growth conditions. At the same time, the ice core reconstructions do not suggest that ~~seem to falsify - on century time scales - working hypothesis II, postulating that~~ reactive N for the production of N_2O ~~(and implicitly for plant growth)~~ remained scarce and that

~~, while~~ marine emissions dominated past atmospheric N_2O variations. ~~The consistently high terrestrial N_2O emissions reconstructed for the last 7,000 years, a period when atmospheric CO_2 rose by 20 ppm (Elsig et al., 2009), appear also to be in conflict with the idea that reactive N becomes increasingly limiting under increasing CO_2.~~

~~Wieder et al. (2015b) proposed to downscale the carbon (C) uptake as projected by CMIP5 models for the 21st century to account for a postulated N limitation. This proposal was based on the assumption that the global inflow of reactive N to ecosystems is limited and static (Hungate et al., 2003) and consequently N availability is not sufficient to support the C sink projected by the CMIP5 models. The ice-core data, however, do not support the assumption of a strongly N-limited future land C sink (Hungate et al., 2003;Wieder et al., 2015b). Rather, they point to a dynamic global N cycle whereby, at a global scale, N losses from soil inorganic N pools are replaced by adjustments of biotic or abiotic sources. The ice core data and the inferred rapid increase in terrestrial emissions at the onset of the B/A and the end of the YD suggest that such adjustment processes take place on multi-decadal to century time scales.~~ The magnitude of possible adjustments in the N source is unclear. Wang and Houlton (2009) modelled an increase in N fixation under increasing CO_2 and temperature. Yet their modelled increase in BNF was too small to meet projected N demand in global warming scenarios; the authors therefore proposed to downscale future C uptake in the warming projections of C4MIP models. However, this conclusion is based on an assumed optimum temperature for BNF of around 25ºC, an assumption that has been challenged by Liao et al. (2017) who found the abundance of N-fixing trees to increase monotonically with temperature by analyzing more than 125,000 forest plots in the USA and Mexico. ~~Taken together, the ice core and forest plot data do not support downscaling of C uptake in the CMIP4 and CMIP5 projections.~~ More work is needed to improve projections of BNF under ~~global warming~~past and future environmental change, considering also the cost of BNF (Shi et al., 2018) and relying on data-based and model approaches (Fisher et al., 2012). Similarly, it remains unclear how other smaller sources of reactive N changed over the deglacial period and influenced N_2O emissions.

~~The reactive N lost from ecosystems must be replaced if ecosystem N pools are not to be depleted. This mass balance consideration suggests that the total input flux of N from BNF (Cleveland et al., 1999;Vitousek et al., 2013;Zähle, 2013;Sullivan et al., 2014), rock weathering (Houlton et al., 2018), and deposition (Lamarque et al., 2011;Vet et al., 2014;Dentener et al., 2006) increased hand in hand with N_2O emissions and related loss fluxes over the deglacial period. An alternative to a balanced N input and output flux would be that N losses are fueled by existing reservoirs of reactive N. Large nitrate deposits (“caliche”) are currently found in the hyperarid Atacama desert (Ericksen, 1981;Tapia et al., 2018). But such large deposits are very unusual, and require several hundred thousand of years to accumulate (Michalski et al., 2004) . Microorganisms require readily decomposable carbon substrate for the denitrification of nitrate, otherwise nitrate may accumulate under the absence of substrate availability (Weier et al., 1993). Carbon substrate availability for denitrifiers might have increased at the onset of the B/A and at the end of the YD when climate warmed, precipitation pattern shifted and organic matter remineralization accelerated in many regions. This in turn could have led to the conversion of nitrate that had potentially~~

~~accumulated previously. However, such a scenario appears unlikely, given that N_2O emissions remained high during the early B/A and throughout the Holocene.~~

~~It has remained somewhat unclear whether warming will increase or reduce regional to global scale N_2O emissions, as responses to warming treatment are found to be highly variable across a range of conditions and ecosystems (Dijkstra et al., 2012). The ice-core record shows that past warming events, such as those at the onset of the B/A and the end of the YD, strongly promoted N_2O emissions globally. This suggests, as noted earlier (Schilt et al., 2014) and as projected (Stocker et al., 2013), that terrestrial N_2O emissions from natural land will likely increase further as climate warms, implying the existence of a positive climate feedback linked to the terrestrial N cycle (Xu-Ri et al., 2012).~~

~~Uncertainties in the interpretation of the terrestrial N_2O emission record are linked to uncertainties in the ratio between N_2O produced to N converted during nitrification and denitrification. This yield factor is known to vary with environmental conditions (Diem et al., 2017;Davidson et al., 2000;Firestone and Davidson, 1989). For nitrification, the ratio of N_2O/NO_3^- produced increases with increasing acidity and decreasing oxygen (Firestone and Davidson, 1989). For denitrification, the production ratio of N_2O/N_2 yield increases with increasing NO_3^- availability, increasing oxygen concentration, decreasing decomposable carbon, decreasing pH and decreasing temperature. Changes in precipitation may have altered the N_2O yield over the deglaciation. Higher soil water content and associated anoxic conditions generally favor the conversion of N_2O to N_2 and results in a low yield of N_2O (Weier et al., 1993), though dependencies of yield on water filled pore space are sometimes complex (Diem et al., 2017) and soil texture and drainage affect water filled pore space and yield (Bouwman et al., 2002). Yield is low under low NO_3^- availability (Diem et al., 2017) and generally found to increase when NO_3^- becomes more available (Weier et al., 1993). This relation, when considered in isolation, implies increasing N_2O emissions to be indicative of increasing NO_3^- availability. Thus, the known dependency of yield on NO_3^- availability is not in conflict with the idea implicit in working hypothesis 1 that reactive N became more available with increasing N_2O emissions. The ratio of N_2O to N_2 emitted generally decreases with increasing temperature (Firestone and Davidson, 1989). On the other hand, the warming over the glacial termination is also expected to accelerate organic matter turnover and thus C availability which would tend to lower this ratio. Further, experimental studies on grasslands yield both higher and lower ratio of N_2 to N_2O under elevated CO_2 compared to ambient CO_2 (Zhong et al., 2018;Baggs et al., 2003). Given this complexity, we are not in the position to evaluate whether the N_2O yield factor for the combined N loss processes increased or decreased over the deglaciation on the global scale. An increase would imply that the relative change in the flow of N through ecosystems was lower than the relative change in N_2O emissions. In contrast, a decrease in yield would indicate that the relative change in ecosystem N through flow was even larger than the relative increase in terrestrial N_2O emissions from the Last Glacial Maximum to the preindustrial period. Changes in N supply, e.g. by BNF, would scale accordingly. In any case, changes in yield factor cannot plausibly reconcile our N_2O emission reconstruction with working hypothesis II of a closed N cycle. As noted by Bouwman et al. (2002), N_2O losses will be low at low flow rates, regardless of the yield factor.~~

The ice-core data and emission estimates represent global values with century-scale resolution. They do not permit us to discriminate regional variations, nor interannual to decadal changes. ~~We do not exclude the possibility that responses were regionally differentiated during the deglacial, and that our hypothesis II and progressive N limitation may have been realized in some regions or during short periods, as found in comparably short field experiments (Luo et al., 2004).~~ In particular, N-limitation is considered to be common in high-latitude regions. But this does not exclude a decadal-to-century scale increase in ~~BNF~~ N sources under changing environmental conditions. Sufficient N and other nutrients were available to support the northward expansion of boreal forest during the deglaciation. Indeed, it has been hypothesized that an increase in BNF may become cost-effective under more severe N limitation in mid and high latitudes (Menge et al., 2017). Field data support a role of~~for~~ BNF in supporting forest growth in particular for early successional forests. Experimental evidence comes from chronosequence studies in the Amazon region and in Panama (Batterman et al., 2013;Gehring et al., 2005), from forest clay and sand box studies in Brazil and in the USA (Davidson et al., 2018;Bormann et al., 2002) as well as from forest inventory data covering tropical-to-temperate climatic conditions (Liao et al., 2017). Regional changes may have contributed to the deglacial N$_2$O emission increase.

~~In summary, the reconstruction of terrestrial N$_2$O emissions from ice-core data support working hypothesis I. The data show a deglacial increase in N$_2$O emissions. This increase occurred in two major steps, each realized within maximum 200 years. and thus on a time scale similar to that of the ongoing anthropogenic climate perturbation. The increase in N$_2$O emissions implies an increased input of N by BNF and other sources in land ecosystem, an increased flow of N entering and leaving ecosystems, and a global N cycle that adjusted dynamically to meet increased N demand under more favorable growth conditions. We emphasize that this conclusion does not depend on a specific land biosphere model, but emerges from the ice core terrestrial N$_2$O emission record.~~

6.2 Simulating deglacial terrestrial N$_2$O emission changes with LPX-Bern

We applied the LPX-Bern dynamic global vegetation model to investigate regional N$_2$O emissions patterns, governing mechanisms, and C-N coupling in simulations over the past 21,000 years. The model~~ was forced with climate anomalies from the TraCE-21kyr simulation that used the Community Earth System Model (Liu et al., 2009;Otto-Bliesner et al., 2014), ice core CO$_2$ data, and reconstructions of sea-level and ice-sheet extent. The model was applied in an earlier study to simulate climate-N$_2$O feedbacks under global warming (Stocker et al., 2013) and results for global emissions for the period from 16 to 10 ka BP are presented in Schilt et al. (2014). Recently, model parameters have been updated using a set of modern observational constraints in a Bayesian approach~~ (Lienert and Joos, 2018b)~~. The updated version also includes immobilization of N released during remineralization. Results for deglacial N$_2$O emissions remain basically unchanged between the previous (Stocker et al., 2013;Schilt et al., 2014) and the updated model version. We also note that the model has not been tuned in any way towards matching the ice core reconstruction.~~

~~LPX-Bern~~ represents the cycling of N and C in soils and plants in a simplified way. C and N is stored in PFT-specific plant and litter pools and a fast and a slow overturning soil pool in each grid cell. This chain of pools represents a spectrum of overturning time scales on each grid cell. LPX-Bern, being a spatially explicit model, reacts differently in different regions to changes in climatic and environmental drivers (Fig. 4,8). However, microbial and fungal biomasses are - unlike in microbial-explicit models (Schimel and Weintraub, 2003;Zhu et al., 2017;Allison and Gessner, 2012)~~)~~ - not explicitly modelled and organic matter decomposition does not depend on microbial mass and physiology. Instead, a mass balance approach is applied with C:N stoichiometry ~~is fixed within a single pool~~prescribed at observation-based PFT-dependent values for litter and soils. A constant fraction of remineralized N is returned immediately to its source soil pool and the N budget is closed by the implied N source flux (Fig. 1). There is also no distinction between different classes of organic matter according to their accessibility to microbial action (Averill and Waring, 2018). ~~(2018)Further, BNF is treated in a simplified way and the cost of nitrogen acquisition are not considered (Fisher et al., 2010). (Xu-Ri and Prentice, 2008)Only net N_2O production during denitrification is considered, while gross production and consumption of N_2O during denitrification (Schmid et al., 2001b) are not explicitly modelled.~~ Potential N_2O release by lichens and bryophytes is also not modelled (Porada et al., 2017). Only net N_2O production during denitrification is considered, while gross production and consumption of N_2O during denitrification (Schmid et al., 2001b) are not explicitly modelled. In future work, N_2O may be treated as an intermediate product of denitrification to explicitly simulate N_2O consumption as well as the related ratio of N_2O to N_2 emissions, i.e., the yield factor.

~~Nevertheless, the results provide a first estimate of past regional N_2O emission changes and their drivers.~~

Uncertainties in modelled N_2O emissions are also associated with uncertainties in the representation of N sources and N loss processes. The N source and its changes in LPX are implied by maintaining soil C:N ratio at observed PFT-dependent values. This N source thereby accounts for any other source, except explicitly prescribed N deposition (Fig. 1). Carbon costs of N acquisition are not directly considered. Yet, a fraction of 6 % of NPP is directly transferred to a pool with a short overturning time to represent root exudates. The by far largest contribution to the implied N source is thought to come from BNF.

Different approaches to represent BNF are used in different models and their effects on modelled BNF, NPP, carbon stocks, and N_2O emissions are compared in recent studies for modern conditions and future projections (Meyerholt et al., 2016;Wieder et al., 2015a). The simplest approach is a prescribed static map of BNF (Zaehle and Friend, 2010a). Most frequently, empirical models are used describing BNF as a linear function of evapotranspiration (Cleveland et al., 1999) or as an exponential function of NPP (Thornton et al., 2007). More process-oriented models heuristically account for the dependency of symbiotic BNF on N demand by vegetation, soil N status, and light limitations in extratropical regions (Gerber et al., 2010) or on the optimization of plant C investment into resource acquisition (Fisher et al., 2010). Meyerholt et al. (2016) describes asymbiotic BNF as a function of temperature, shading and soil moisture.

The implementation of such different parameterizations in LPX-Bern would likely lead to different estimates for deglacial changes in BNF and N_2O emissions. We may expect that prescribing a constant modern BNF field would lead to approximately constant fluxes for nitrification, denitrification and leaching. In turn, deglacial changes in N_2O emissions would only be due to changes in yield factors and be smaller than modelled in our standard simulation and smaller than reconstructed. A similar result is expected for BNF depending on evapotranspiration, because globally-averaged evapotranspiration changes little over the deglaciation in our standard simulation (Tab. A.1) and global BNF would remain at its modern value. In contrast, some parameterizations would likely yield similar or larger responses than simulated here. A strong increase in BNF is found in global warming simulations for the N-demand (Meyerholt et al., 2016) and the NPP-based (Wieder et al., 2015a) BNF parameterizations. In this latter parameterization, BNF responds immediately to NPP and grows exponentially with NPP, whereas the deglacial increase in BNF of 11 % is smaller than in NPP (13 %) in our standard run (Tab. A.1). Overall, one might expect a similar or even larger increase in BNF and N_2O emissions over the deglaciation when replacing our implicit N source approach with a demand, NPP or cost driven BNF parameterization. However, a corresponding quantitative analysis is beyond the scope of this study.

The N loss in LPX is predominantly driven by local gaseous loss from denitrification, with a much smaller role for fire, leaching, and minor contributions from volatilization of NH_3, and gas release during nitrification (Fig. 1). Denitrification and nitrification are thought to occur at anaerobic and aerobic microsites in the soil, which are challenging to represent. In LPX-Bern the fraction of NH_4^+ available for aerobic nitrification and of NO_3^- available for anaerobic denitrification within a grid cell is assumed to scale linearly with water-filled pore space in the top 50 cm (Xu-Ri and Prentice, 2008). Meyerholt and Zaehle (2018) investigated different algorithms for N loss processes and find variable responses in N loss and in the partitioning of N losses between gaseous and leaching losses under elevated CO_2.

~~The model allows us to investigate alternative working hypotheses in a consistent model framework. It remains to be seen whether other models incorporating the cycling of N and C (e.g., (Zaehle et al., 2014;Averill and Waring, 2018;Thornton et al., 2007;Fisher et al., 2010) and~~ ~~N_2O~~ ~~emissions~~ (Zhu et al., 2016;Saikawa et al., 2013;Tian et al., 2015;Xu et al., 2017;Huang and Gerber, 2015;Zaehle and Friend, 2010a;Olin et al., 2015;Goll et al., 2017) ~~are able to represent the reconstructed terrestrial~~ ~~N_2O~~ ~~emissions over the past 21,000 years. The setup of our deglacial simulation could be used to compare and evaluate models, e.g., in the framework of the model intercomparison initiated by the Global Carbon Project (Tian et al., 2018).~~

~~The model~~LPX-Bern was applied in an earlier study to simulate climate-N_2O feedbacks under global warming (Stocker et al., 2013) and results for global emissions for the period from 16 to 10 ka BP are presented in Schilt et al. (2014). Recently, model parameters have been updated using a set of modern observational constraints in a Bayesian approach (version v1.4) (Lienert and Joos, 2018a) and here further modified towards a lower N source (version v1.4N) by adjusting the fraction of N remineralized that is returned to the soil pool. Except for the matching of pre-industrial N_2O emission estimates, the model has not been tuned in any way towards matching the ice core reconstruction. These updated versions also account for the uptake of mineral N by N immobilization in soils~~includes immobilization of N released during remineralization.~~ Results in terms of deglacial N_2O emission changes are similar between these different versions. Changes in parameter values and selected globally-averaged model results for version v1.4 versus v1.4N are documented in the Appendix Tab. A.1. Appendix Figs. A.1 and A.2 show the spatial patterns for the implied N source, soil mineral N, NPP, total carbon and their changes over the deglaciation. The most striking difference is that the implied N source is a factor of four higher in v1.4 compared to v1.4N. Nevertheless, r~~R~~esults for deglacial N_2O emission changes~~s~~ remain basically unchanged between the version v1.4 and v1.4N~~previous (Stocker et al., 2013;Schilt et al., 2014) and the updated model version~~. The reason is that the relative, percentage changes in the N source flux and in N loss fluxes are similar between the two versions, howerver, the N_2O yield factors are calibrated in both versions to the same preindustrial N_2O emissions of 5.9 TgN yr^{-1}. ~~.~~ The lower N source leads, however, to smaller mineral N concentration. In turn, N limitation of NPP is larger and, hence, NPP and carbon storage are smaller, both in steady state and for deglacial change, in v1.4N than in v1.4.~~We also note that the model has not been tuned in any way towards matching the ice core reconstruction.~~

LPX-Bern forced by TraCE-21kyr output represents the reconstructed emissions reasonably well, while differences between reconstructed and simulated global land N_2O emission remain. The modelled deglacial increase in global N_2O emissions is at the lower bound of the reconstructed range. This may be related to the model's C cycle and/or to the model formulation for denitrification and other shortcomings discussed above. LPX-Bern is known for a relatively low sensitivity to increasing CO_2 and simulates a modest increase in NPP and the terrestrial carbon sink over the industrial period (Lienert and Joos, 2018a). A larger deglacial increase in NPP would tend to increase the implied N source in the model and potentially increase nitrification, denitrification and N_2O emissions. Further, denitrification processes are assumed to respond to the relevant substrate concentration following Michaelis–Menten kinetics (Xu-Ri and Prentice, 2008). This limits N conversion rates and N_2O production at high substrate concentrations, whereas a recent synthesis of N fertilization experiments (Niu et al., 2016) points towards an exponential relationship between N load and N_2O emissions. ~~N_2O emissions are simulated to increase during Heinrich Stadial 1 (17.4 to 14.6 kaBP) in contrast to the reconstruction that shows stable emissions during this period. Most of this modelled increase is attributed to the prescribed changes in climate. It is unclear whether this early increase reflects deficiencies in the climate input data or in the LPX-Bern model.~~ Regarding the time scales of response, r~~R~~esults of a sensitivity simulation~~, where environmental conditions are changed step-like,~~ demonstrate that LPX-Bern is able to represent abrupt, multi-decadal scale change in global terrestrial N_2O emissions as ~~implied by the ice core reconstructions~~reconstructed for past ~~the~~ rapid warming events.~~, given climate forcing is prescribed to remain sufficiently long at LGM conditions and to change fast during the warming event. The sensitivity simulation reveals a decadal adjustment time scale for the majority of the N_2O emission response, followed by a smaller century-scale adjustment.~~ Further, factorial simulations demonstrate ~~Deglacial changes in N_2O emissions reflect~~ a complex interplay of different driving factors for deglacial N_2O emissions with considerable synergistic or antagonistic interactions related to changes in temperature, precipitation, and CO_2. ~~Globally averaged, and in mid- and high latitudes, the changes are predominantly driven by changes in temperature. Regional changes in precipitation exert the largest control in semi-arid regions, while increasing CO_2 leads to the largest relative responses in some tropical regions, where changes in precipitation and temperature were modest.~~

~~The model suggests that increases in N_2O emissions per unit land area were largest in low and mid-latitude regions, but the integrated change in emissions is larger for the northern mid- and high latitudes than for the tropical belt. Flooding of shelf regions, mainly around the maritime continent, led to a considerable reduction of tropical N_2O sources during the deglaciation.~~ Remarkably, a~~A~~bout a third of the simulated global increase in terrestrial N_2O emissions over the past 21,000 was counteracted by land loss due to flooding of previously exposed shelf regions. ~~. We conclude that past sea-level variations causing the flooding and emergence of shelves were an important factor for the evolution of terrestrial N_2O emissions over glacial-interglacial time scales.~~

We applied LPX-Bern to analyse the consequences of alternative C-N cycle hypotheses ~~in a quantitative manner and in a self-consistent, spatially and temporally resolved setting~~. In the model's standard setup, the N cycle responds dynamically to changes in environmental conditions; the N source increases under increasing ecosystem N demand. ~~The results of the standard deglacial run are in line with working hypothesis I of an increasingly open terrestrial N cycle. Modelled sources of reactive N changed little or increased in most regions under warming climate and increasing CO_2 over the deglacial period.~~ This additional N source contributed to meet the rising N demand of plants simulated under more favorable growth conditions and resulted in a higher flow of N through land ecosystems and increased N_2O production from terrestrial ecosystems as well as increased carbon storage on land. The increase in N_2O emissions, linked to this increase in N source, is further amplified by an increase in the yield of N_2O per N converted by nitrification and denitrification.

~~The availability of inorganic N in soils increased in many mid and high-latitude regions and remained high in the tropics.~~

In an alternative deglacial simulation, the sources of reactive N were prescribed at the level simulated for the Last Glacial Maximum. In this case, the ~~results~~ model yields a decrease in N_2O emissions, in clear conflict~~correspond to working hypothesis II but do not agree~~ with the ice core ~~record~~data. The increase in N_2O emissions attributable to the increase in the model's N_2O yield factors for denitrification and nitrification under deglacial warming as well as the positive response of soil and litter turnover rates to increasing temperatures are not sufficient to offset the decrease in N_2O emissions in this run with constant N source. ~~The terrestrial C cycle is simulated to become progressively N limited over the deglacial period. The availability of inorganic N decreased in many regions. Consequently, simulated terrestrial N_2O emissions decreased and t~~The simulated ~~increase in the~~ terrestrial C inventory ~~amounted~~ decreased ~~to 169 PgC~~over the deglaciation in this simulation, again~~,~~ in conflict with data-based reconstructions (Lindgren et al., 2018;Jeltsch-Thömmes et al., 2019) that suggest a growing land biosphere carbon inventory as also predicted in the standard setup.~~much smaller than the 901 PgC simulated in the standard setup, which is similar to terrestrial carbon storage increases simulated by models that do not account for N limitation (Prentice et al., 2011;Joos et al., 2004).~~

~~In the standard setup, the simulated soil C inventories and their deglacial changes are consistent comparable with a recent measurement-based reconstruction for the northern extratropics by Lindgren et al. (2018). These authors reconstruct current C stocks in peat and mineral soils (above 3 m) of 1630 GtCPgC on land that was permafrost during the LGM, while LPX-Bern v1.4v1.4N simulates 1420 953 GtCPgC in peat and mineral soils (incl. litter; above 2 m) north of 30° N. The reconstructed deglacial increase is 420 GtCPgC, compared to 770 497 GtCPgC simulated by LPX-Bern in soil and litter north of 30° N. Current northern extratropical peat C stocks (and deglacial C changes) simulated by LPX-Bern v1.4v1.4N are with 380 150 GtCPgC comparable tomuch smaller than a recent estimate of ~430 GtCPgC (Loisel et al., 2014). We note that the peat, vegetation, and soil module was not adjusted when switching from version v1.4 with a N source of 523 TgN to the current version with a source of 128 TgN. Correspondingly, N limitation is stronger in the current version and peat, vegetation and carbon stocks biased low. The simulated LGM-to-Holocene change in total organic carbon stocks on land of 901 372 GtCPgC is also comparable toat the lower end of the estimate by Jeltsch-Thömmes et al. (2018). These authors constrain the deglacial increase in land carbon inventory to 850 GtCPgC (median estimate; 450 to 1250 GtCPgC ±1σ range) by using reconstructed changes in atmospheric δ^{13}C, marine δ^{13}C, deep Pacific carbonate ion concentration, and atmospheric CO$_2$ as observational targets.~~

Within the current setup of LPX-Bern, acknowledging its limitations, a growing N source appears necessary to simulate increasing N$_2$O emissions over the last deglaciation. It would be interesting to see~~remains to be seen~~ whether other models incorporating the cycling of N and C (e.g., (Zaehle et al., 2014;Averill and Waring, 2018;Thornton et al., 2007;Fisher et al., 2010) and N$_2$O emissions (Zhu et al., 2016;Saikawa et al., 2013;Tian et al., 2015;Xu et al., 2017;Huang and Gerber, 2015;Zaehle and Friend, 2010b;Olin et al., 2015;Goll et al., 2017) reveal similar or alternative mechanisms and whether these models are able to represent the reconstructed terrestrial N$_2$O emissions over the past 21,000 years. The setup of our deglacial simulation could be used to compare and evaluate models, e.g., in the framework of the model intercomparison initiated by the Global Carbon Project (Tian et al., 2018).

7 Conclusions

Part I (Fischer et al., 2019) and II of this study present three novel elements to gain insights into the functioning of the global carbon-nitrogen cycle: First, a record of the N$_2$O isotopic history over the past 21,000 years, complementing the existing records over parts of the termination (Schilt et al., 2014); second, the first reconstructions of marine and terrestrial N$_2$O emissions from the Last Glacial Maximum (LGM) to the preindustrial period as obtained by deconvolving the N$_2$O and isotope ice core records using a robust, established method; third, the application of a dynamic global vegetation model to simulate deglacial terrestrial N_2O emissions ~~under nitrogen and non-nitrogen limited conditions~~ and to attribute deglacial N_2O emissions changes to different regions and governing processes. Our ~~study~~ model results provide~~s~~ insight into the multi-decadal-to-millennial dynamics of the terrestrial C-N cycling by showing that the ice core terrestrial N_2O emission record ~~is~~ could potentially be explained with a rapid adjustment of N cycling to the climate and CO_2-driven acceleration of the C cycle, but they do not exclude the possibility that alternative explanations linked to changes in N_2O yield could be important.

The records provide the opportunity to evaluate models that simulate biological nitrogen fixation and nitrogen cycling (e.g. (Meyerholt et al., 2016;Nevison et al., 2016;Thornton et al., 2007;Xu and Prentice, 2017;Wieder et al., 2015a) and feedbacks between climate change, land carbon, and terrestrial greenhouse gas emissions (Arneth et al., 2010;Stocker et al., 2013;Tian et al., 2018) for improved projections. Here, we evaluated LPX-Bern and found that the model is able to simulate the evolution in global terrestrial N_2O emissions over the past 21,000 years in reasonable agreement with the ice core emission data. This adds confidence to projections of the climate-N_2O feedbacks with this model (Stocker et al., 2013). Model results for regional changes and specific processes and forcings await confirmation by other studies.

~~We explored two alternative working hypotheses of an increasingly “open” versus an “inflexible” global terrestrial nitrogen cycle on multi-decadal to century time scales. Reconstructed changes in terrestrial N_2O emissions are interpreted to reflect changes in the nitrogen flow through land ecosystems (Firestone and Davidson, 1989) and to be indicative of the availability of reactive N to support the growth of plants and other organisms on the global scale.~~ The ice core data presented in part I reveal a highly dynamic terrestrial nitrogen cycle ~~where sources of reactive N adjusted on multi-decadal time scales to meet increasing N demand to support plant growth and to fuel ecosystem loss fluxes of reactive N~~. Remarkably, substantial changes in global terrestrial N_2O emissions were realized within maximum 200 years, and possibly faster, in response to past northern Hemisphere warming events. Reconstructed N_2O emissions changed by up to 1 TgN yr^{-1} and within less than two centuries at the onset of the NH warming events around 14.6 and 11.7 ka BP. These time scales are relevant for 21st century climate projections and much longer than accessible in typical laboratory or field experiments. Taken at face value, these results suggest that the nitrogen cycle and N_2O emissions will also adjust on the global scale in the coming centuries ~~towards meeting N demand to support additional carbon uptake by plants under increasing temperature and CO_2.~~

The ice-core data and the N_2O emission reconstruction in combination with models provide a new window to integrate across systems and relevant time scales to improve our understanding of the coupled C-N cycle in the Earth system. The results may help to put emerging results from observational field and laboratory studies into the context of decadal-to-century scale environmental and climate change.

Appendix: Difference between LPX-Bern v1.4 and LPX-Bern v1.4N

A few parameters of the nitrogen module of LPX-Bern are updated for this study compared to the previous version (v1.4) (Lienert and Joos, 2018a). These updated parameter values are set to obtain a preindustrial implied N source of 128 TgN yr^{-1} and land biosphere N_2O emissions of 5.9 TgN yr^{-1}. The difference in parameter values and in key model outcomes between the version v1.4N, used here, and version (v1.4) are summarized in Tab. A.1. The parameter *frac_soil_immob* governing the fraction of the C and N flux from gross soil organic matter remineralization which is transferred back to the soil organic matter pool is adjusted to a higher value. This yields a smaller simulated BNF and smaller simulated N loss fluxes in v1.4N compared to v1.4. In turn, the parameters governing the yield in N_2O emissions per unit N converted by nitrification (*RN2ON)*, denitrification (*RN2ODN)*, and leaching (*RN2ONL)* are re-calibrated in order to get preindustrial N_2O emissions from the land biosphere of 5.9 TgN yr^{-1} as in v1.4 and as suggested by observational estimates. In v1.4, the yield factor from nitrification is assumed constant. In v1.4N the same temperature dependency as for the yield for denitrification is assumed. We note that corresponding results and figures for version v1.4 are given in the manuscript published in Biogeosciences Discussion (https://www.biogeosciences-discuss.net/bg-2019-118/).

Table A.1: Differences between LPX-Bern version v1.4N used in this study and the previous version v1.4. Model results represent global average values. Percentage changes are given in parentheses and are relative to preindustrial.

	v1.4N	v1.4
model parameters		
frac_soil_immob, fraction of soil remineralization N flux converted back to soil N (%)	60	26.39
frac_soil_immob, fraction of litter remineralization N flux converted back to soil N (%)	0	0
RN2ODN, N_2O yield factor for denitrification at 22°C (%)	5.41	1.46
RN2ON, N_2O yield factor for nitrification at 22°C (%)	0.231	0.05
RN2OL, N_2O yield factor for N leaching (%)	0.231	0.5
f(T), function for the temperature dependency of the N_2O yield for nitrification (T in Kelvin)	*f*(T)= exp[270 · (1/68.02 - 1/(Tsoil+46.02))]	1.0
model results: preindustrial		
Implied N source (TgN yr^{-1})	128	523
Nitrification (TgN yr^{-1})	271	817
Denitrification (TgN yr^{-1})	89.6	405
N leaching (TgN yr^{-1})	16.9	77.1
N_2O emissions (TgN yr^{-1})	5.90	5.90
Net primary productivity (PgC yr^{-1})	50.7	58.5
Total C inventory (PgC yr^{-1})	2260	3190
Transpiration and interception (mm yr^{-1})	380	375
model results: deglacial change (0.5 kyr BP minus 21 kyr BP)		
ΔImplied N source (TgN yr^{-1})	12.0 (9 %)	71.3 (14 %)
ΔNitrification (TgN yr^{-1})	27.8 (12 %)	115 (14 %)
ΔDenitrification (TgN yr^{-1})	10.3 (12 %)	61.6 (15 %)
ΔN leaching (TgN yr^{-1})	-4.1 (-24 %)	-4.4 (-6 %)
ΔN_2O emissions (TgN yr^{-1})	0.96 (16 %)	1.13 (24 %)
ΔNet primary productivity (PgC yr^{-1})	5.9 (12 %)	10.1 (24 %)
ΔTotal C inventory (PgC yr^{-1})	482 (21 %)	1062 (42 %)
ΔTranspiration and interception (mm yr^{-1})	-2.5 (- 1 %)	-5.8 (-2 %)

Competing Interests

The authors declare that they have no conflict of interest.

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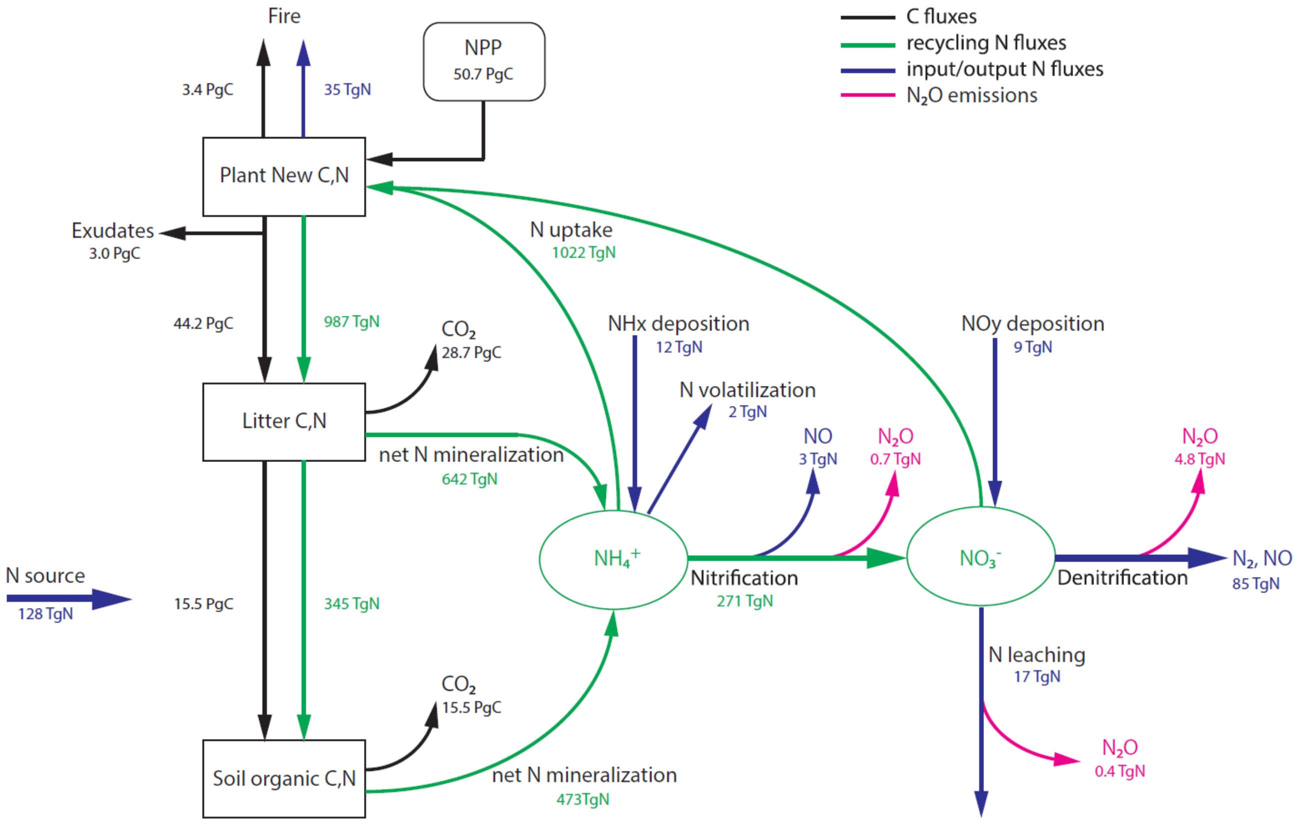

Figure 1: Terrestrial C and N cycles. Simple schematic of global annual C fluxes (black), recycling (green) and input/output (blue) N fluxes, and N_2O emissions (magenta) from nitrification and denitrification processes. Fluxes are illustrated with a quantitative budget from the LPX-Bern(~~v1.4~~v1.4N) model for pre-industrial conditions (~~1500~~ 1450 AD~~CE~~) Plant net primary productivity (NPP) sets the N demand that is satisfied by N uptake from ammonium (NH_4^+) and nitrate (NO_3^-). N enters the ecosystem mainly through biological N fixation (BNF) by plant symbiotic and free-living microorganisms in the soil.

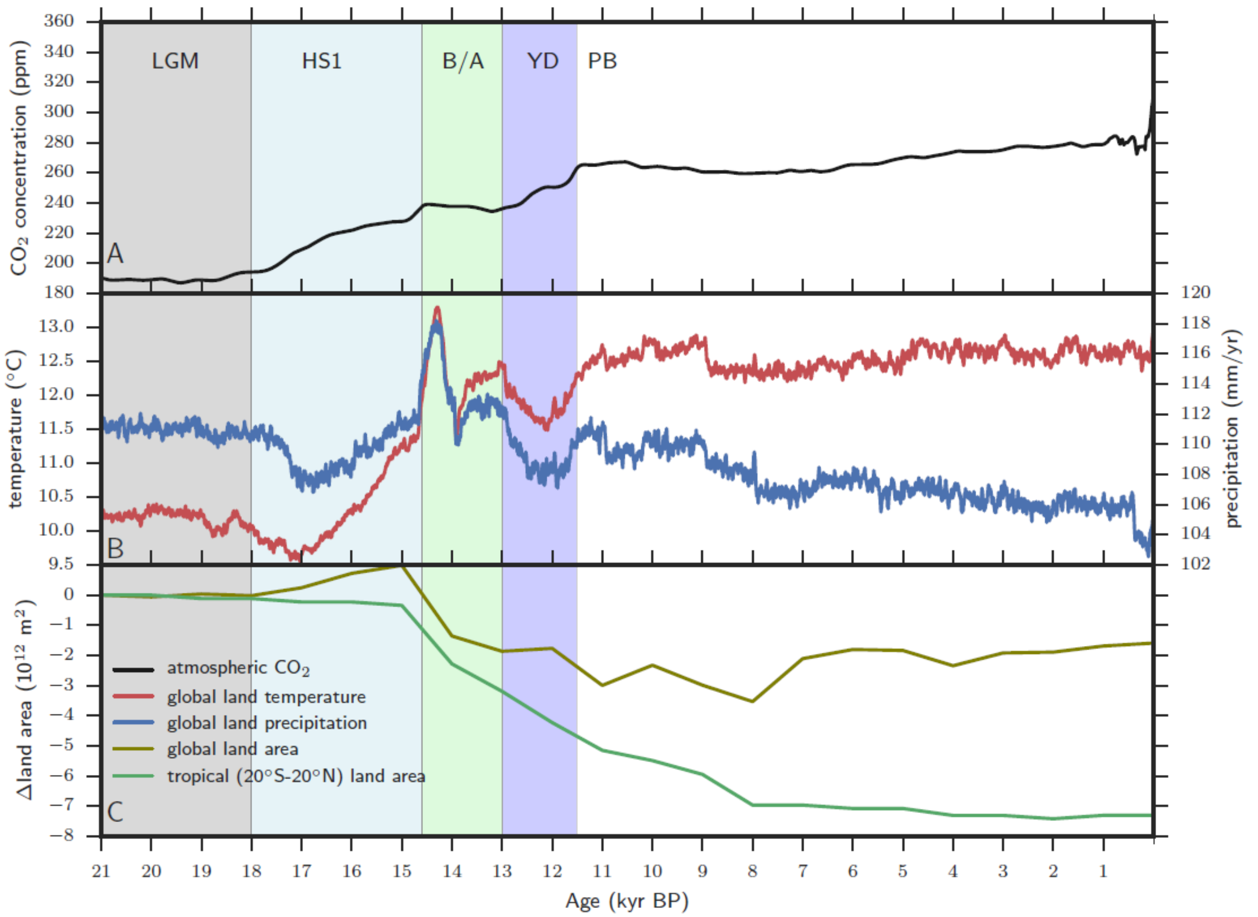

Figure 2: Aggregated LPX-Bern(~~v1.4~~v1.4N) input data. (A) Evolution of atmospheric CO$_2$, (B) temperature and precipitation, and (C) of changes in tropical and global land as available for plant growth relative to 21 ka BP (bottom). Temperature and precipitation represent mean values over global land areas that were not flooded and not ice-covered at 21 ka PB and at 0.5 ka BP.

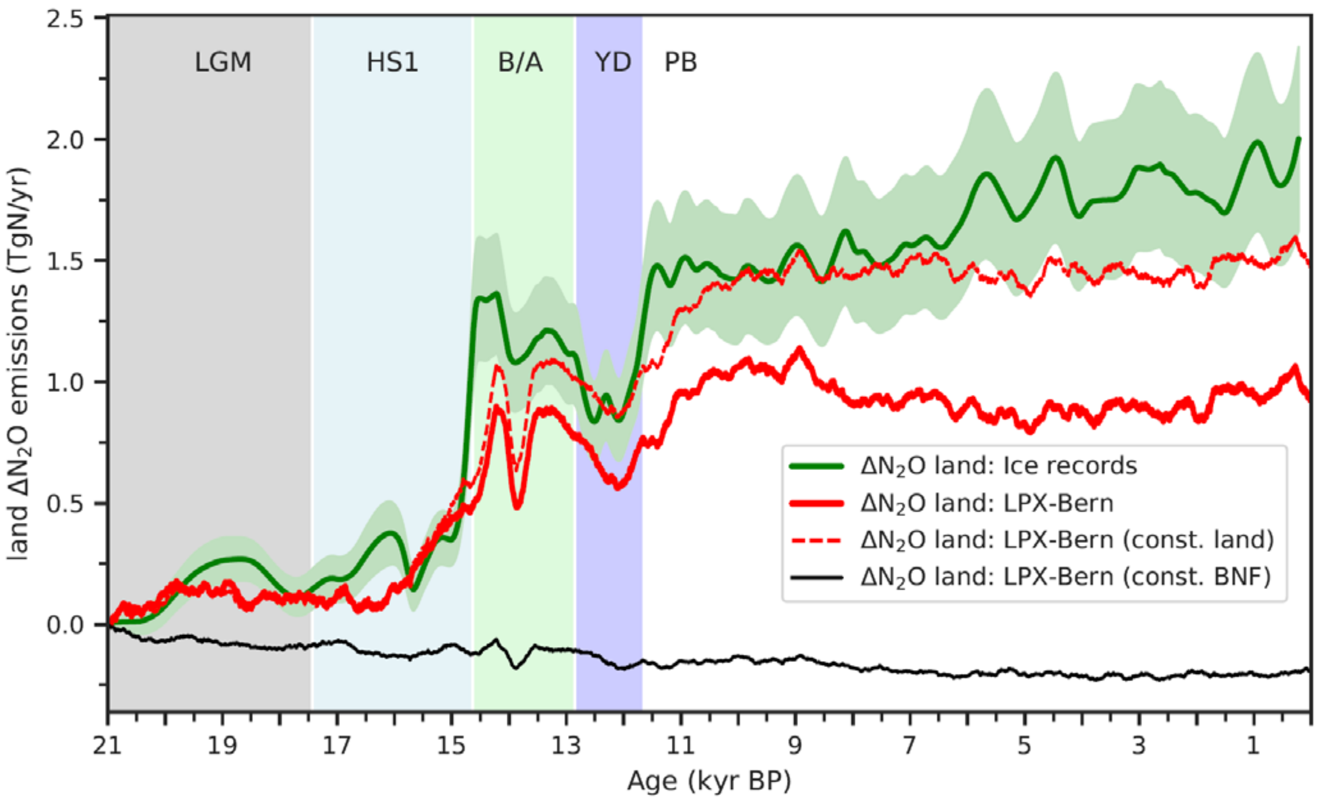

Figure 3: Changes in global terrestrial emissions of N_2O. Reconstructed changes in global land N_2O emissions are shown by the solid green line together with an uncertainty estimate (±1 standard deviation; shaded area). Reconstructed changes are calculated with an atmospheric two-box model (Schilt et al., 2014) from ice records of N_2O concentration and $\delta^{15}N(N_2O)$. Reconstructed changes are compared to LPX-Bern(~~v1.4~~v1.4N) for the baseline simulation (red line), a constant land area simulation (thin dashed red line), and a simulation with biological nitrogen fixation kept constant at Last Glacial Maximum values (thin black line).

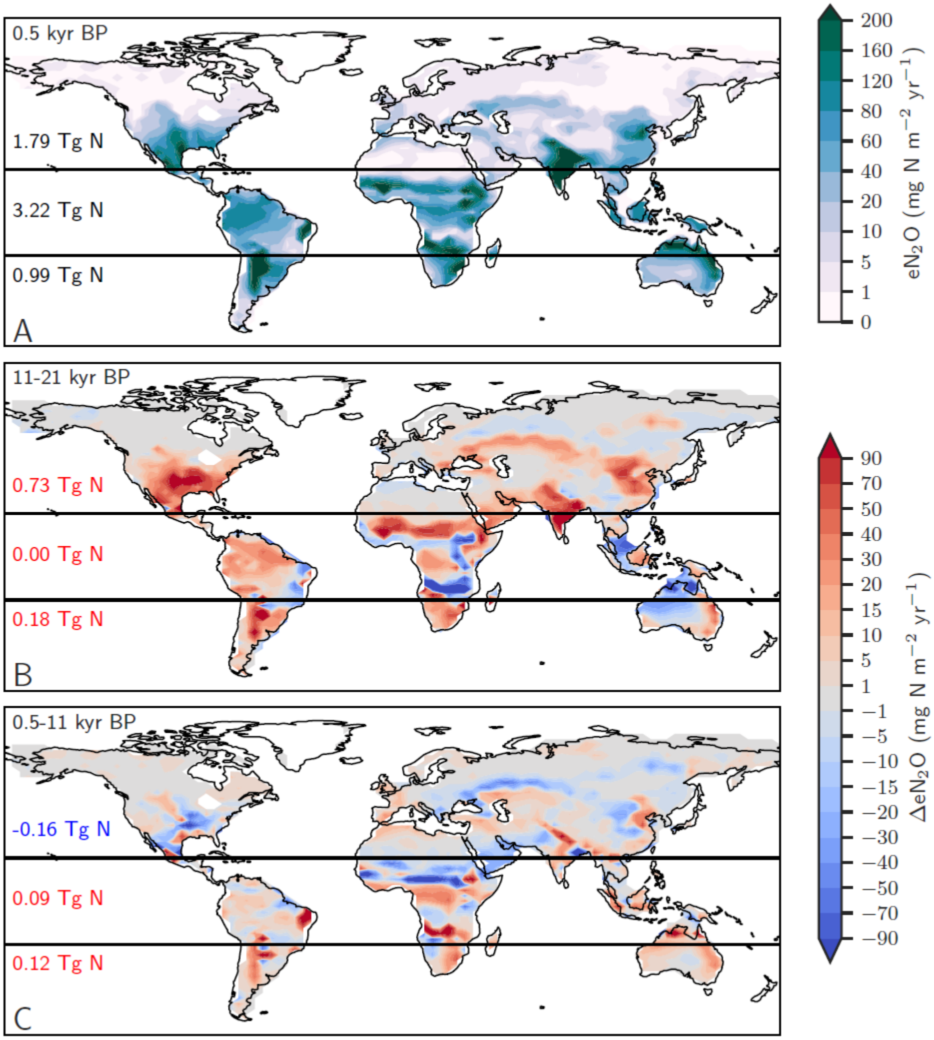

Figure 4: Preindustrial patterns (A) and changes in terrestrial N_2O emissions for the last glacial termination (B; 11 ka BP minus 21 ka BP) and the Holocene (C; 0.5 ka BP minus 11 ka BP) as simulated with the LPX-Bern(~~v1.4~~v1.4N). Numbers indicate integrated values for three latitudinal bands (90° S–20° S; 20°S–20° N; 20°N–90° N).

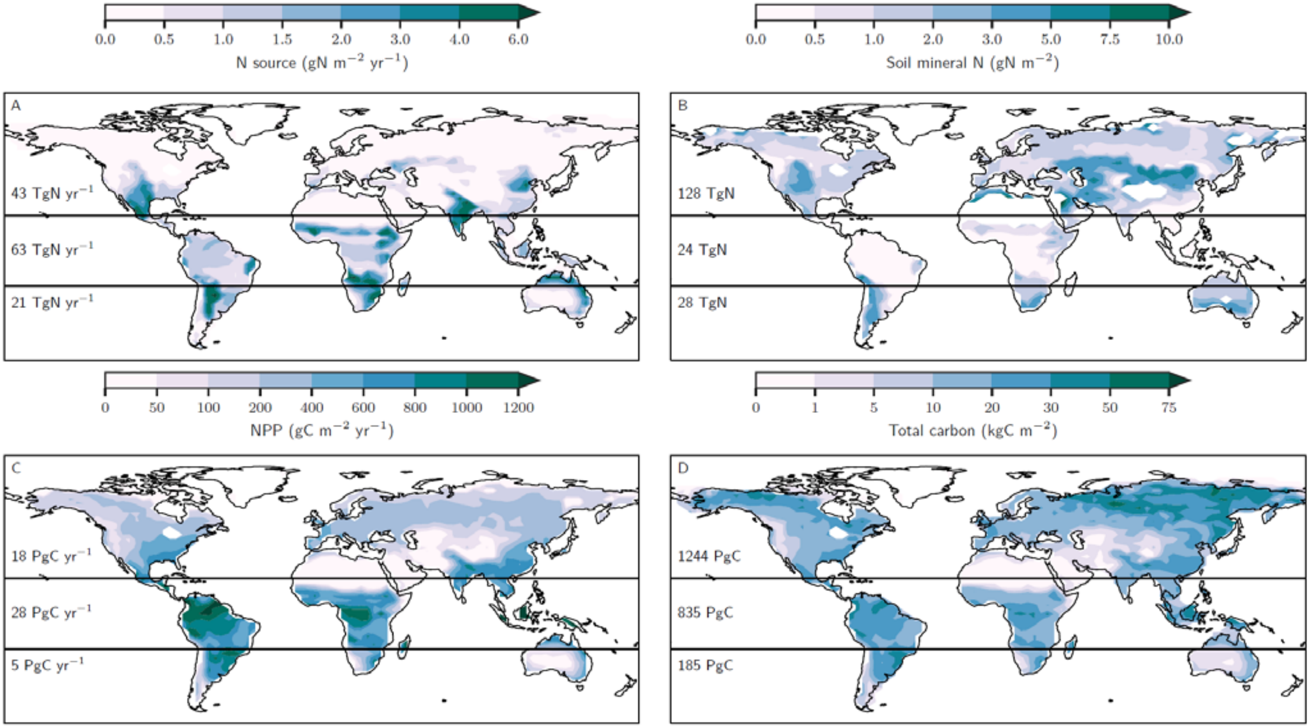

Figure 5: Preindustrial patterns of the input flux of new nitrogen (N) into ecosystems (A), the bioavailable concentration of N in the form of ammonium and nitrate in soils (B) net primary productivity (C) and total carbon in the land biosphere (D) as simulated by LPX-Bern(~~v1.4~~v1.4N). The N source in (A) ~~represents ecosystem input by biological nitrogen fixation and weathering and~~ does not include the prescribed N deposition. Deserts with high mineral nitrogen concentrations are masked for clarity in (B). Numbers indicate integrated values for three latitudinal bands (90° S–20° S; 20° S–20° N; 20° N–90° N).

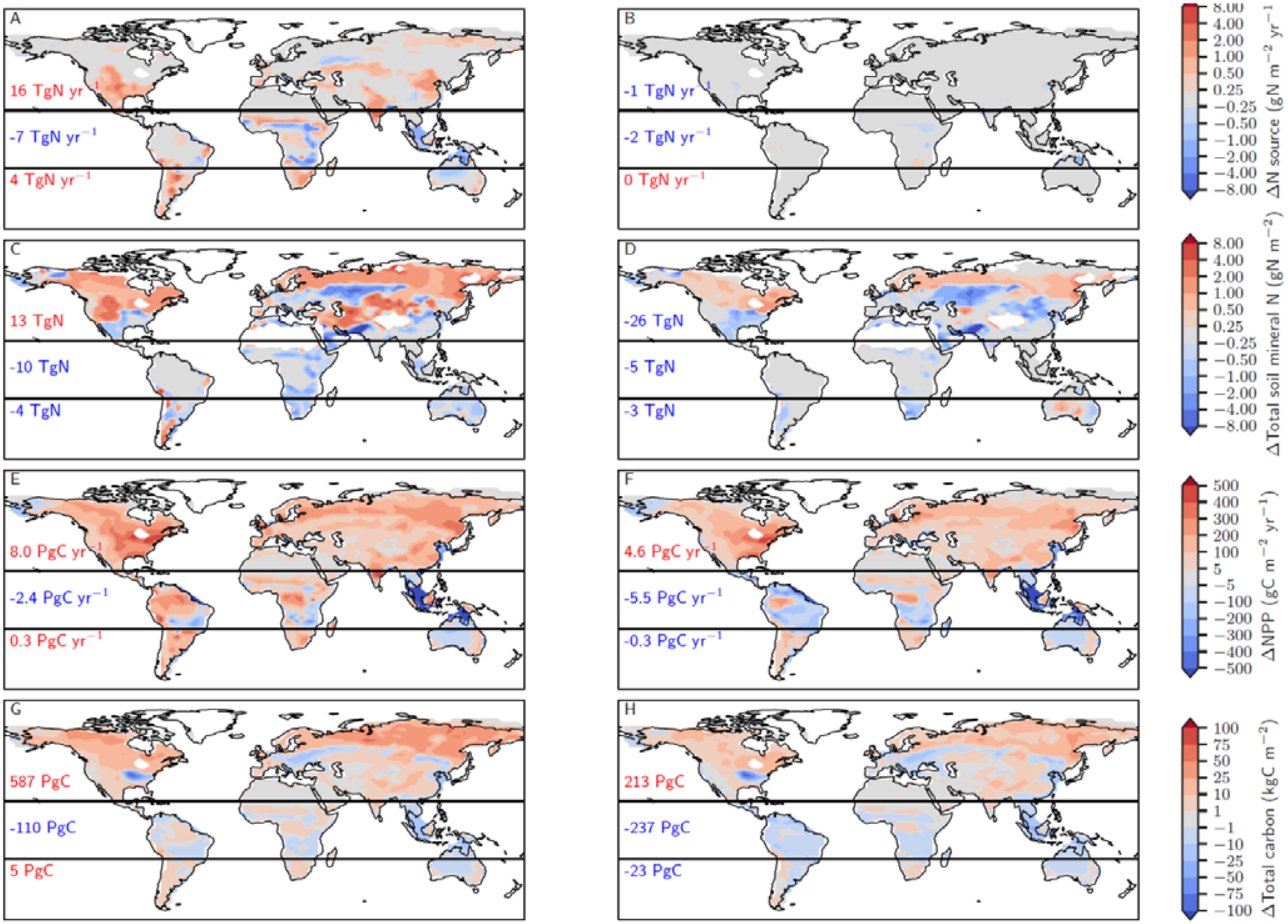

Figure 6: Biological nitrogen fixation adjusts to plant demand (left) versus time-invariant ~~nitrogen fixation~~N source (right). The figures shows simulated deglacial changes (0.5 ka BP minus 21 ka BP) for the standard setup of LPX-Bern(~~v1.4~~v1.4N) (left column) and a setup where the nitrogen source flux is kept constant at values simulated for the Last Glacial Maximum (right column) for the same variables shown in Fig. 5. Note that a decreasing ~~BNF~~ N source is shown in panel B for land areas lost due to deglacial sea level rise and in some tropical cells where mineral soils with relatively high ~~BNF~~ N source are replaced by peat with relatively low ~~BNF~~N source.

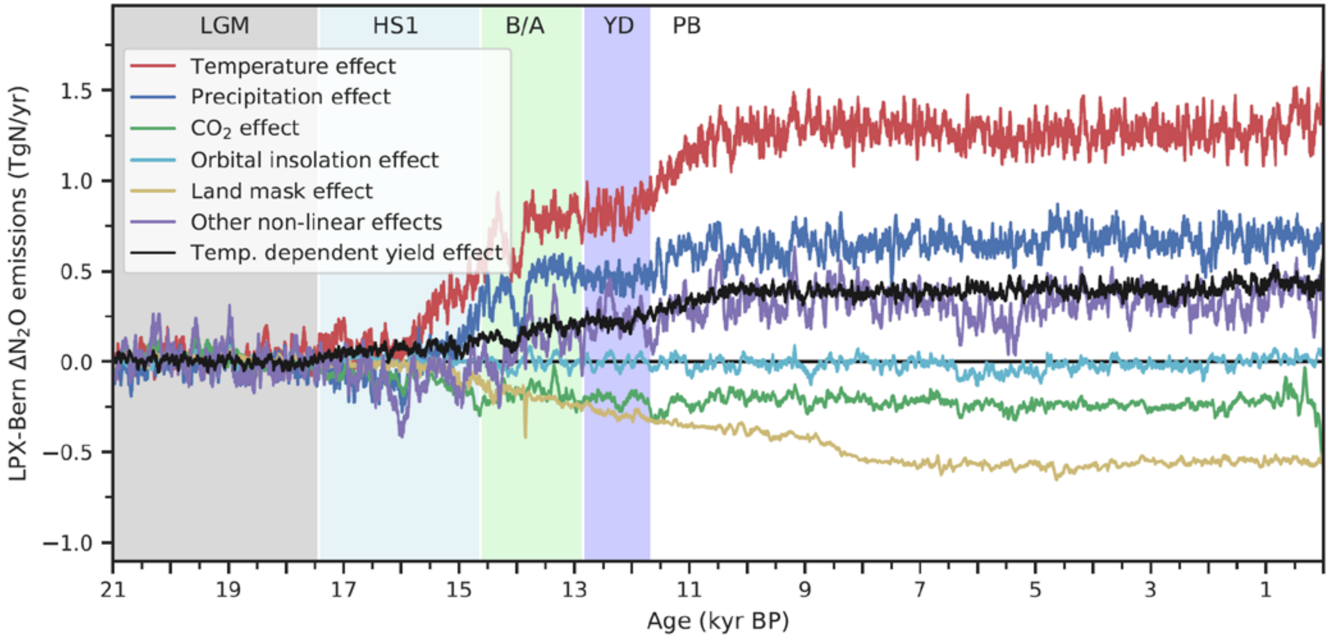

Figure 7: Attribution of simulated global terrestrial N$_2$O emission changes to individual drivers. Results are from LPX-Bern(~~v1.4~~v1.4N) for the standard and factorial simulations, where an individual driver (temperature (red), precipitation (blue), atmospheric CO$_2$ (green), orbital parameters affecting photosynthetic active radiation (blue), land mask accounting for sea level changes) is kept at preindustrial level. The violet curve (Other non-linear effect) is the difference between simulated emissions in the standard setup and the sum of all these attributed emissions; it reflects the effect of non-linear interactions between different drivers. In addition, the black curve indicates the change in N$_2$O emissions attributed to variations in the N$_2$O yield factor for nitrification and denitrification.

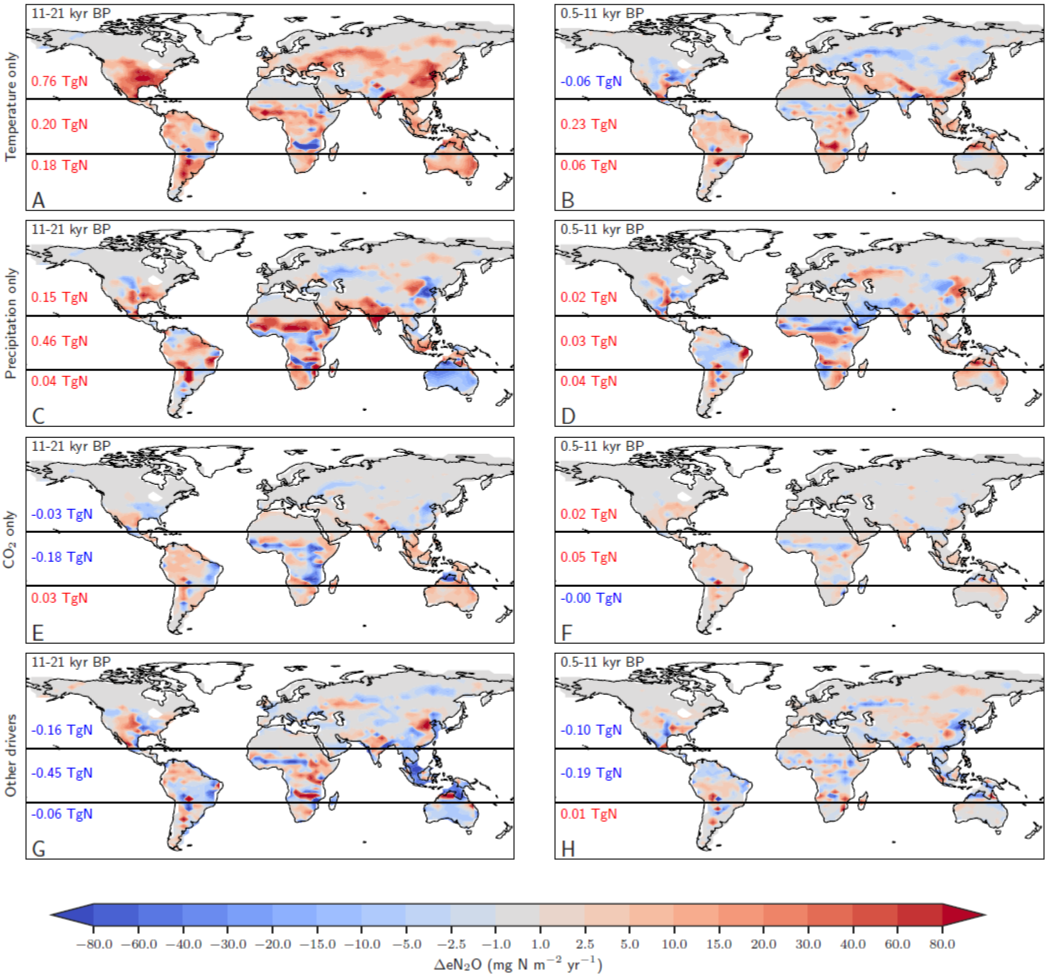

Figure 8: Attribution of simulated global terrestrial N_2O emission changes to individual drivers for the last glacial termination (11 ka BP minus 21 ka BP; left) and the Holocene (0.5 ka BP minus 11 ka BP; right). Changes are attributed to changes in temperature~~precipitation~~ (A,B), precipitation~~temperature~~ (C, D), atmospheric CO_2 (E,F) and to non-linear interactions among the drivers plus the small effect due to changes in incident solar radiation (G,H).

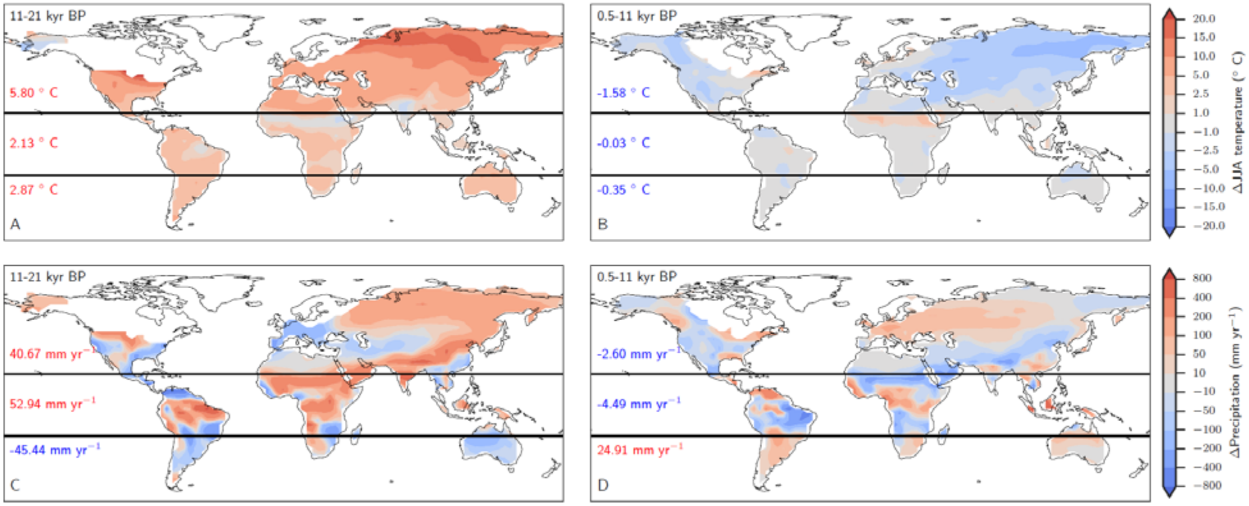

Figure 9: Changes in northern hemisphere summer temperature (June, July, August, panels A and B) and annual precipitation (C,D) as simulated by CCSM3 and prescribed to LPX-Bern(~~v1.4~~v1.4N) for the glacial termination (A,C) and the Holocene (B,D)

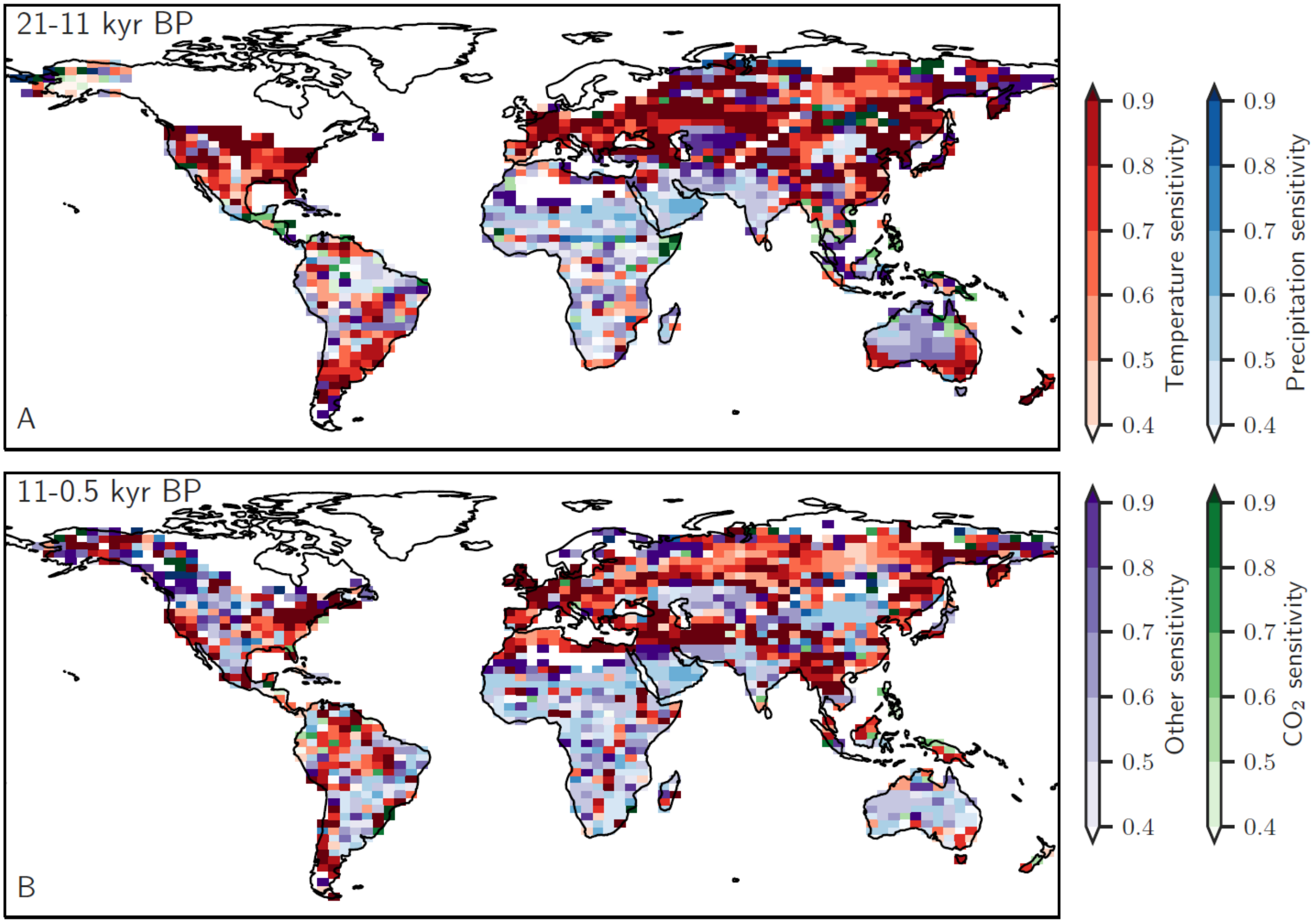

Figure 10: The dominant drivers for changes in terrestrial N_2O emissions over (A) the glacial termination and (B) the Holocene are temperature (red), precipitation (blue), CO_2 (green), and other non-linear effects in LPX-Bern(~~v1.4~~v1.4N) to these driver combinations (violet). The color shading indicates the fraction of the total emission change attributed to the dominant driver typically explaining between 40 and 90 %. Areas with minimal changes are masked.

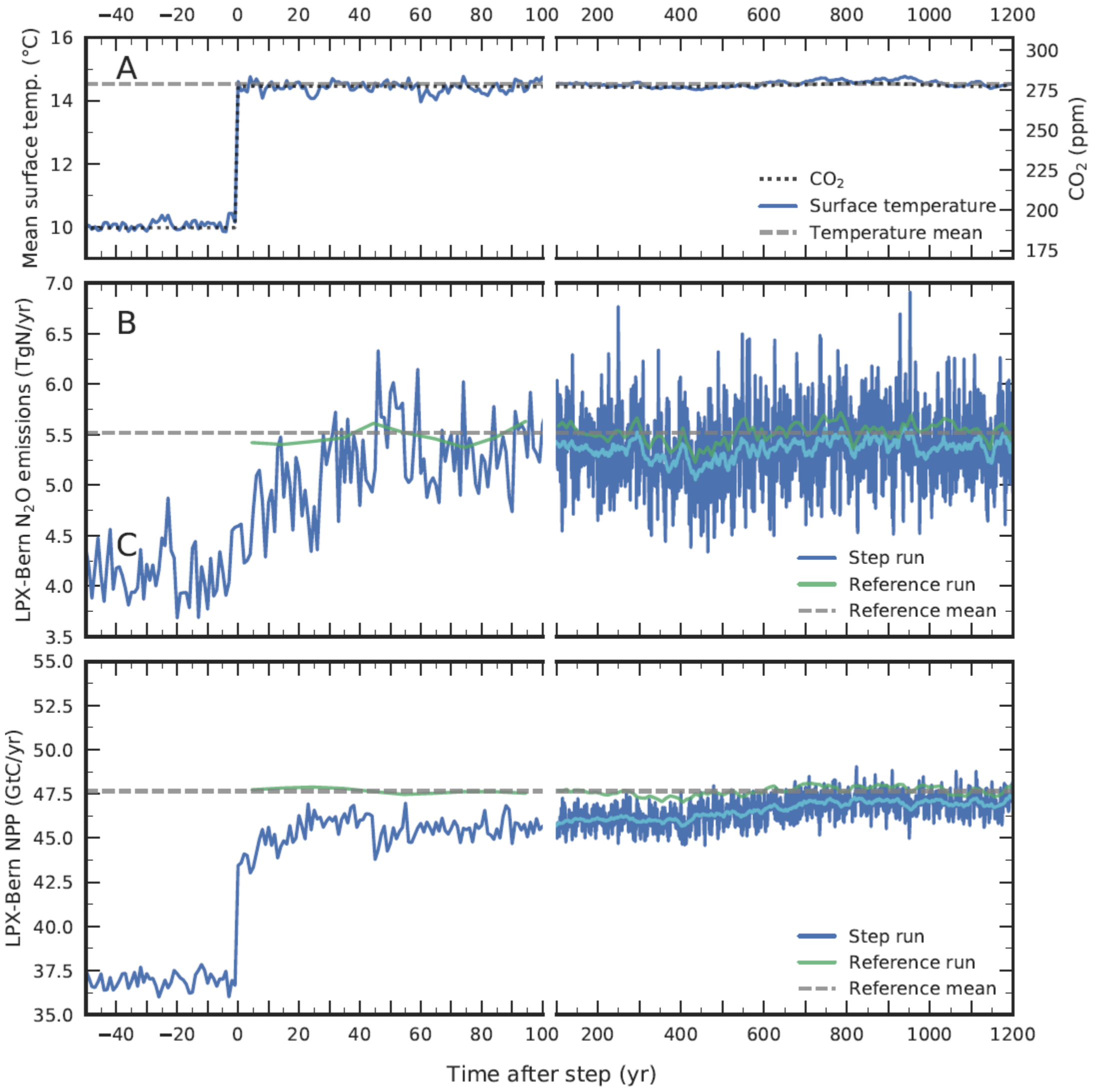

Figure 11: Response to a step-like change in (A) environmental conditions for globally averaged terrestrial (B) ~~-~~N_2O emissions and (C) NPP. Atmospheric CO_2 (dotted line in (A)) and climate is prescribed to suddenly change from Last Glacial Maximum conditions to late Holocene conditions in a sensitivity simulation with LPX-Bern(~~v1.4~~v1.4N) ("step run", blue lines). Annual values for the step run are shown in dark blue and smoothed (31-yr average) values in light blue for the step run and in dark green for a corresponding reference run. The dashed horizontal lines represent averages from the reference run over the model period 0 to 1200 years. Surface air temperature in (A) represents the average over the model's land area. Note the change in the time axis scaling at year 100.

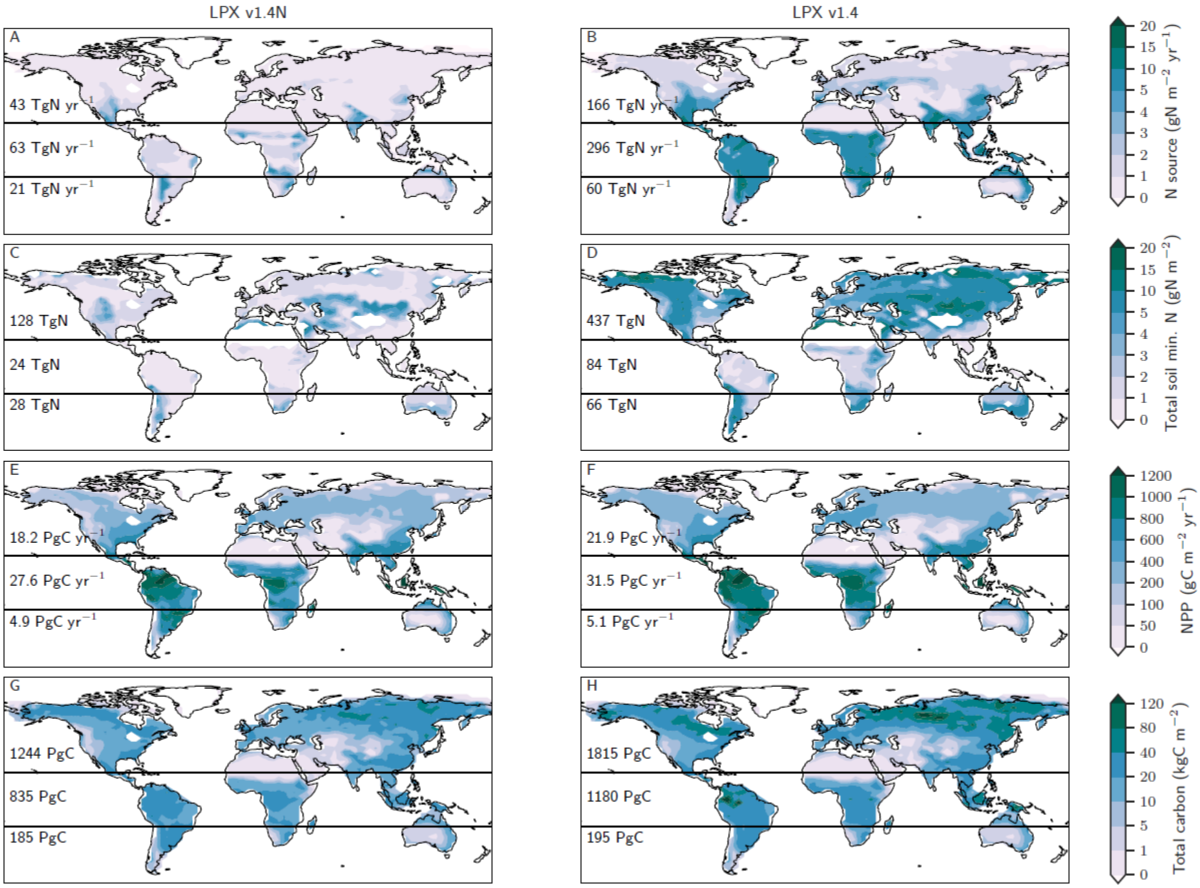

Figure A.1: Comparison of model version LPX-Bern v1.4N (left) versus version v1.4 (right) for the preindustrial (0.5 ka BP) patterns in the implied N source (A, B), bioavailable concentrations of ammonium and nitrate in soils (C,D), net primary productivity (E,F), and total carbon (G,H)

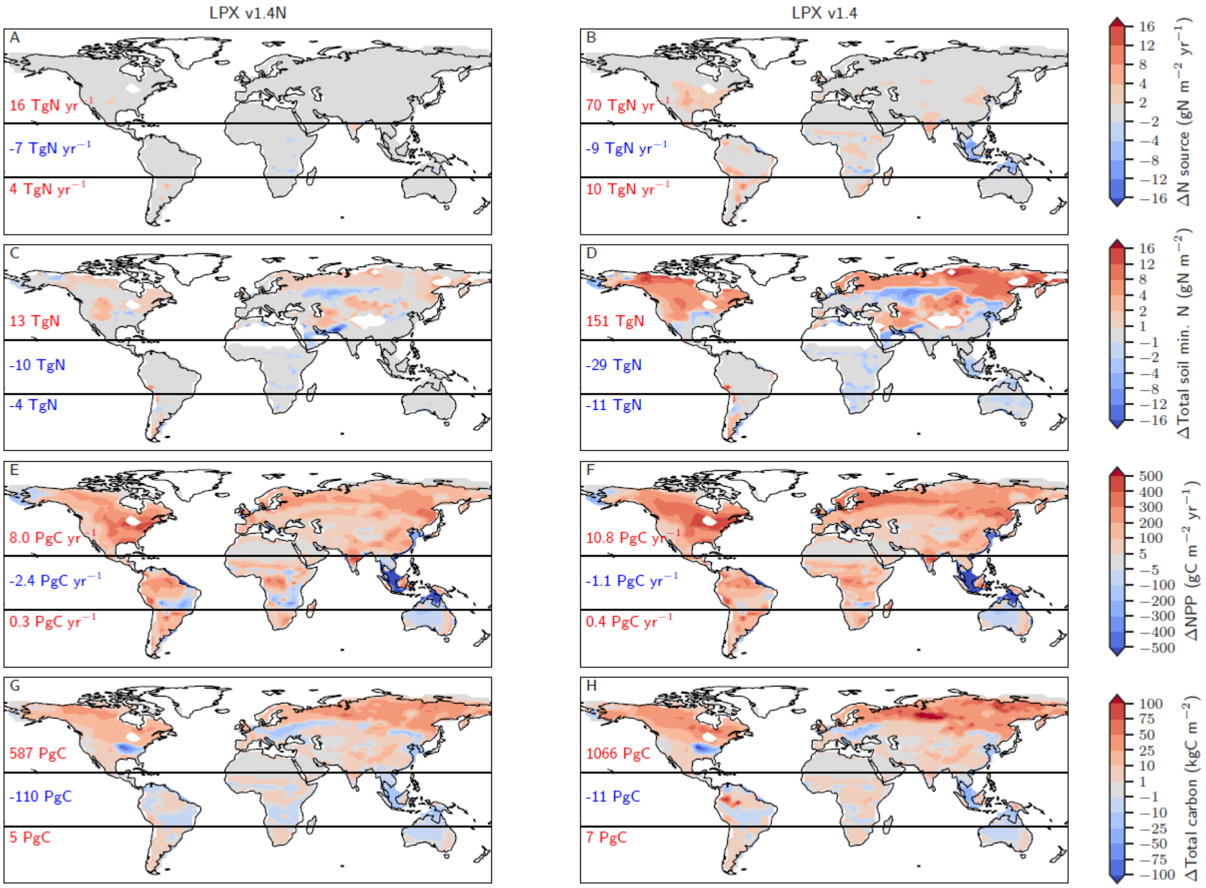

Figure A.2: Comparison of model version LPX-Bern v1.4N (left) versus version v1.4 (right) for simulated deglacial changes (0.5 ka BP minus 21 ka BP) in the implied N source (A, B), bioavailable concentrations of ammonium and nitrate in soils (C,D), net primary productivity (E,F), and total carbon (G,H)

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