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Interactive comment on "Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model" *by* D. Wårlind et al.

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Answers to comments from Anonymous Referee #4

Question 1: The manuscript titled "Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamics vegetation model" is well-suited to the scope of Biogeosciences, and examines an interesting, current topic. However, the novelty and scientific contributions of this article are diminished by the fact that it merely expands on results presented in sections 3.1 and 3.7 of the Biogeosciences article titled "Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model" (Smith et al., 2014).

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Answer: Again, we thank the reviewer for supporting the paper, and agreeing that it fits the scope of Biogeosciences. The reviewer queries the novelty of the manuscript, a comment that puzzled us a lot. Yes, this manuscript is indeed a follow-on from the recent paper by Smith et al., but extends on the findings of that paper in many important aspects. Smith et al, gives detailed description of the new model, and evaluations output on a number of space scales. Most of this evaluation concentrated on groups of site-level observations, and on stylised global-scale experiments. The paper does include one figure showing globally averaged C and N sequestration in the same RCP8.5 simulations that form the basis of the present paper, but there was no detailed analysis of the contrasting regional dynamics that sum up to produce the average global result. The present paper addresses these regional patterns and presents a deep analysis of the underlying interactions between vegetation dynamics, C and N biogeochemistry in response to the changing drivers encapsulated by the RCP8.5 scenario. We also place the findings from our model in the context of other findings in the literature and include factorial experiments to isolate mechanisms underlying responses to individual drivers. These were not included in the earlier paper.

Introduction. Question 2: The description of N dynamics in LPJ-GUESS is necessary and relatively well accomplished. Equally important, however, would be descriptions of the other models to which LPJ-GUESS is compared, and how they represent N dynamics. It would also be good to present here the central findings from these other approaches, and discuss what a forest gap model such as LPJ-GUESS can contribute that existing approaches cannot. In the introduction, the idea is stated that the analysis of C dynamics in forests and savannas benefits from the use of models that include demographic information, but the potential implications for N cycling studies are not fully discussed. This would help frame later discussions regarding differences in predictions generated by LPJ-GUESS relative to other approaches, especially since the findings from previous approaches differ substantially from the ones presented by C-only vs C-N LPJ-GUESS. Answer: The reviewer poses an interesting challenge here: comparing our approach to others especially focussing on differences arising from model struc-

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tural aspects would be an interesting topic. However, it is also an extremely difficult one without running detailed model intercomparisons. From published literature alone it would be difficult to isolate these aspects, since models differ not only in vegetation representation but also in how they incorporate C-N coupling. There is also a more detailed discussion of different C-N model responses already in recent papers that arose from the forest FACE experiments (see FACE experiment baseline paper Walker et al., 2014, and C-N interaction paper Zaehle et al., 2014). Furthermore, to our logic discussing these aspects in a lot of detail before the results are presented would feel strange. Still, in order to take the reviewer's request for more detail into consideration we expand the aspects of demographics and gap dynamics, using examples from savannas: "Scheiter and Higgins (2009) showed the importance of simulating individual trees in savannah ecosystem to be able distinguish between small trees, that are completely consumed in fires, and large trees, that are generally unaffected by fires. A similar result has also been found for simulations with LPJ-GUESS along a climate-transient in sub-Saharan Africa (Arneth et al. 2010b). Especially the effect of tree-tree interaction and self-thinning is important in savannah ecosystems to potentially allow trees to grow taller in the presence of fire than in the absent of fire. What is more, in forest ecosystems, succession between plant functional types can be represented in a realistic manner which is important not only for simulating carbon dynamics after disturbance or when crop-land is re-converted into forest, but also for other exchange processes with the atmosphere that are strongly dependent on vegetation composition (Hickler et al. 2004; Arneth et al., 2008, Lindeskog et al., 2013; Smith et al., 2014)."

Moreover, a short section describing the conceptual differences between models has been added: "TEM is a process-based ecosystem model for monthly estimates of C and N fluxes and pool sizes based on referenced information on climate, soils, vegetation and water availability. FUN determines the C cost for acquiring N for productivity and is driven by nine parameters (NPP, biomass C and N, etc) averaged over five DVM simulations (Fisher et al., 2010a). O-CN is developed from the DVM ORCHIDEE (Krinner et al., 2005) to include N effects on plant and soil processes (Zaehle & Friend, 2010). JSBACH is driven by NPP, leaf are index and climate as input to the model and simulates a background N limitation (Goll et al., 2012).“

Methodology. Question 3: LPJ-GUESS and forcing data are discussed, but there is little description of what is included in each of the four model set-ups used (ALL, CLIM, CO2 and NDEP). Were changes in precipitation and N mineralization included only in the ALL set-up, or in the CLIM one as well? Is the ALL set-up comparable to the CO2 + climate set-up in Smith et al. (2014)? Were there any main differences in the approach used in this paper relative to that used in Smith et al. (2014)? Answer: We expanded the description of the four different model setups: “Four different model setups where used during the study. In ALL, climate change (temperature, precipitation and radiation), CO2 and N deposition conjointly affect simulated processes. In the single factor simulations either climate change (CLIM), atmospheric [CO2] (CO2) and N deposition (NDEP) were varied while values of the other two variables were set to the spin-up protocol.”

Figure 7 of Smith et al. shows globally aggregated results from the ALL simulation of the present study, but the CO2 simulation in Smith et al. was completely different from the one applied in the present study. Here, “CO2” means that only the atmospheric [CO2] scenario was enabled, whereas in Smith et al. the N deposition scenarios was also enabled to allow for a direct comparison with the results from other models presented in Hungate et al 2003.

Results. Question 4: It appears that the main differences in C accumulation over time between the C-only and C-N vegetation classes can be found over Siberia, where the C-N version first overestimates tundra and the C-only version first overestimates forest, relative to Hickler et al. (2006) as discussed in Smith et al. (2014). One of the main findings described in this paper is that the transition from Siberian tundra to forest vegetation occurs preferentially in the C-N model relative to the C-only model, and that this is driven by N mineralization not changes in CO2 or climate, a reasonable conclusion considering the initial vegetation compositions of the C-N and C-only models. How-

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ever, to what extent do these findings merely indicate that the C-N and C-only models suffer from divergent biases in their initial states, which complicate efforts to determine changes over time? Answer: In the first paragraph of the Discussion we try to make it very clear that the C-only and C-N models are simulating a different initial state and that this is one aspect to consider in comparisons of their different results. Both model versions simulate initial (20th century) C pools and vegetation patterns in broad overall agreement with observation-based estimates or results from other models, within the uncertainties (this is covered and discussed in some detail in Smith et al. 2014). Although initial states are different, the models show additional divergence and contrasts in response in the future climate simulations which we discuss and analyse, for example over Siberia. We argue that this provides additional insight on the model behaviour, and plausibly the corresponding dynamics in the real ecosystems it represents, over and above the legacy of different initial conditions. The first paragraph in the Discussion says the following: “Even though two versions of the same model are compared here, with respect to their interactions with a changing environment, a direct comparison between the C-only and C-N version of the model is difficult, due to a number of ecosystem-scale feedbacks that are introduced in the C-N version, causing differences in the equilibrium state after the spin-up in the C-pool sizes (Table A2) and the PFT distribution (Thornton et al. 2009). Large differences in C-pool sizes originate from the equilibrium condition with climate and CO2, both in vegetation and soils. For the N version, the initial state is also in equilibrium with a pre-industrial N-deposition. Since this is not included in the C-only version, the initial states naturally are different. These differences arising from the spin-up procedure are important also for the transient model experiments: If both versions of the model were to start from the same initial condition, the sudden addition of nitrogen to the C-N version when the transient experiment commences would create an artificial offset and/or trend to the simulations. Such a response would render it impossible to separate what is driving the shift in vegetation structure and C sequestration. Either it could be the model converting to equilibrium for the present environmental conditions, or it could be the change in environmental conditions over time.”

Question 5: The initial conditions of the C-only and C:N versions of LPJ-GUESS vary a great deal, especially in terms of litter [Table A2]. For example, C-only has nearly twice as much litter C as C-N, and differences in litter C between C-only and C-N appear as the main difference in the ALL results. Why are these initial conditions so different? How different would your findings be if you ran the C-only and C-N versions from the same initial conditions? Answer: The reviewer is correct in that there are large differences between the initial state of the C-N and C-only version of the model. These are conditions at equilibrium with climate and CO2 both when it comes to vegetation and soils. For the N version, the initial state is also in equilibrium with a pre-industrial N-deposition. As this is not included in the C-only version, the initial states naturally are different. This is important for transient model experiments: If both versions of the model were to start from the same initial condition, then the addition on N to the C-N version would create an artificial sudden offset and/or trend to the simulations. It would thus be impossible to separate what was driving the shift in vegetation structure and C sequestration. Either it could be the model converting to equilibrium for the present environmental conditions, or it could be the change in environmental conditions over time. In order to make this aspect more apparent to the reader we have added more detail on this in the first paragraph of the Discussion.

The difference in initial litter stocks comes from the mid-high latitudes where the N limitation on vegetation growth is the strongest. Here the C-only version has a closed canopy and self-thinning is a reality, whereas for the C-N version the strong N limitation results in the canopy not being closed, resulting in limited self-thinning. In LPJ-GUESS woody litter is only produced from the death of individual trees. So without self-thinning the death rate and woody litter input is much smaller for the C-N version throughout the spin-up. We have explained this better in the manuscript: “The strongest differences between the two model versions are in the sizes of the litter pools. The strong initial N limitation reduces standing biomass to a considerable degree, and prevents closed

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canopy in many regions of the mid-high latitudes. As a consequence, the process of self-thinning is not taking place to a similar degree than in the C-only version, which reduces woody litter"

Question 6: As discussed in Table 1, TEM, O-CN, FUN and JSBACH C-only models sequester less C than C-N versions (1850-2000) but the opposite is predicted over the 1850-2100 time period in these models due to progressive N limitation. LPJ-GUESS has similar findings for the CLIM and CO2 set-ups, but finds that C-N predicts more carbon sequestration than C-only simulations in the ALL simulations. It therefore appears that the increase in C sequestration by the C-N model relative to the C model occurs either as a response to synergistic changes in climate and CO2, or due to the inclusion of N mineralization in the C-N model. Were any model runs conducted with N mineralization alone? Or N mineralization and either CO2 or CLIM? If readers are to consider the conclusion that terrestrial ecosystems will increase C sequestration in response to a changing climate and rising [CO2], and that the potential progressive N limitation has been exaggerated, then findings must be thoroughly analyzed and discussed in relation to limitations in preceding model predictions. Answer: This is an interesting suggestion and would help to identify underlying processes of model-model differences. However, N mineralisation is an output from the soil module, so cannot trivially be turned "on" or "off" independently from other process-calculations. All the different scenarios influence the mineralisation rate differently through soil temperature and moisture (decay rates), litter input and litter quality (N concentration in litter). We have added to the discussion accordingly, since this would be something to keep in mind for future experiments. From this perspective, and as already outlined in the previous version of the manuscript, our result highlights further the large uncertainties regarding the fate of future biospheric carbon sinks. Furthermore, we have added a comment on the large uncertainties within DVMs: "Overall, large uncertainties are associated with the results from DVMs, which should be kept in mind when comparing different models with respect to the net effects of introducing N limitation."

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Discussion. Question 7: Discussion should be provided of results that differ from previous findings. For example, in Smith et al., (2014), the largest differences in NPP between the C-only and C-N models (1996-2002) are observed at sub-tropical latitudes (15-30 S, and 10-40 N). In Warlind et al., estimates of terrestrial C accumulation from the C-only and C-N ALL run (1850-2100) differ most at northern hemisphere high-latitudes. The discussion of trends in C sequestration mainly focus on vegetation, when vegetation C sequestration is relatively unchanged in the C-only (373) and C-N (372) versions of LPJ-GUESS, run with ALL [Table A1]. Conversely, the role of litter is barely described, although this shows the most striking differences in the ALL scenarios of C-only (-23) and C-N (28) [Table A1]. Why does C-only lose litter over time (1850-2100) whereas C-N gains litter C in ALL? Why is the opposite observed in the CO2 model run (193 vs 65)? Answer: We understand the reviewer to be referring to Figure 6 in Smith et al. This figure is showing responses of NPP over forest biomes globally to a step increase in CO2, emulating FACE treatment. The contrasting regional patterns of change in NPP in the present study alluded to by the reviewer are from a simulation in which climate, CO2 and N deposition are changing together and in a gradual way over time (as opposed to a step change). These differences (interactions among drivers, and transient responses to gradual versus step change, explain the apparently contrasting findings. Moreover, NPP differences cannot be directly translated into differences in C sequestration as the aggregate changes in ecosystem C depend on which vegetation and soil pools this additional C ends up in and C residence time there (i.e. depends on allocation and downstream C transfer via phenology, mortality and SOM dynamics). For instance, if C is allocated to tissues with a fast turnover time, such as leaf or fine roots, then overall C sequestration will be smaller than if a sizeable proportion is stored in stems of growing forest.

The difference in litter stocks and its changes over the study period for the C-N and C-only version are mainly due to the already explained differences in forested area of mid-high latitudes. In order to clarify this better, we have added to the discussion how with climate change the decomposition rate of litter is enhanced. In essence, for the C-only version, where the litter already comes from a closed canopy with self-thinning active, the increase in litter input is more than cancelled out by the increase in decomposition rates. By contrast, in the C-N version the increase in litter input is larger than the increase in litter decomposition. For the CO2 simulations there is no increase in decomposition rates in the mid-high latitudes and the C-only version has a higher increase in litter production as it does not experience any N limitation on C assimilation: “The strongest differences between the two model versions are in the sizes of the litter pools. The strong initial N limitation reduces standing biomass to a considerable degree, and prevents closed canopy in many regions of the mid-high latitudes. As a consequence, the process of self-thinning is not taking place to a similar degree than in the C-only version, which reduces woody litter.” “Especially in the mid-high latitudes the increase in woody vegetation has large impact on the C sequestrated. In response to the future projected changes in climate and CO2, woody vegetation in these regions becomes sufficiently dense for the process of self-thinning to be more prominent in the growth dynamics of the ecosystem, leading to notably enhanced litter input. This increased litter input can be observed in figure A1 as the sudden increase in litter C accumulated around year 2030, which more than compensates for warming-induced respiratory C loss through decomposition.”

Question 8: In general, it seems that LPJ-GUESS has a greater difference in C sequestration between the C-only vs C-N versions than other similar models, and this could be interesting to discuss. It would also be interesting to compare predictions of future vegetation (2000-2100) by C-only and C-N LPJ-GUESS to those predicted by other groups. For example, is the substantial increase in Asian LAI seen in the C-only version also predicted by others, or do they predict LAI to remain near 0? Answer: According to Table 1 and Figure 1 it is only FUN that has a smaller absolute difference in C sequestration between the C-only and C-N versions compared to LPJ-GUESS. Both in the Results and Discussions section we compare and discuss the different model results when it comes to total C sequestration. None of the papers we are comparing to have shown vegetation and soil C sequestration separately, so we cannot do a direct

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comparison in this respect.

Question 9: Many of the differences between C-only and C-N LPJ-GUESS pertain to non-forested regions, or regions which are non-forested for at least a portion of the time in one of the model runs. How well does a forest gap model such as LPJ-GUESS simulate non-forested regions? Which assumptions are made? Is this something that needs to be addressed, or discussed as a potential limitation? Which advantages does LPJ-GUESS offer over other models in representing forest N dynamics? Answer: LPJ-GUESS has been applied and benchmarked for most major biomes and generally performs comparably to other DGVMs. This includes non-forest ecosystems such as savannah and grassland (e.g. Hely et al. 2006). The time and speed of the transition from grassland to forest will have a large affect on the C sequestration. So introducing C-N interactions, which affect the competitive balance between trees and grasses, will in turn influence C sequestration. The advantages of an explicit treatment of stand structure and demography, as in the gap model approach, in grassland/savannah regions have been shown in studies with other models, which we now refer to relevant literature on (page 3 and 4; Scheiter and Higgins 2009, Arneth et al. 2010b). For the case of forests there are numerous studies arguing that demography and stand structure are critical for an adequate representation of successional and biomass dynamics, e.g. the cited papers by Purves & Pacala, Fisher et al. and Wolf et al. on page 3. This is also an issue we highlighted in Smith et al. (2014).

Specific comments. Question 10: Page 162: If global C:N ratios rise, then doesn't this indicate greater N stress, rather than greater "N saturation"? Answer: Increasing global C:N ratio arises paradoxically via the release from N stress in mid-high latitudes where biomass, litter and soils have a higher baseline C:N ratio, hence increasing the global C:N ratios. Have made this clearer in manuscript: "These shifts for the C-N version can also be seen in the increase of global C:N ratios of both vegetation and soils (Table A3) as mid-high latitude vegetation and soils have higher baseline C:N ratios compared to the global averages"

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Question 11: Page 163: Is it realistic for northern Siberia and northern Canada to be dominated by evergreen vegetation in 2000, or even by 2100? Would you need to include other environmental constraints on plant distributions? Answer: The northern extent of evergreen vegetation is more or less correctly located by LPJ-GUESS in figure 2 in Smith et al. for the period 1961-1990. Smith et al. obtained these results with CRU TS 3.0 climate forcing, whereas this study is forced with MPI-ESM-LR, which is bias corrected to match CRU TS 3.0 1961 to 1990 climatologies. With this setup we obtain similar northern extents of evergreen forests as Smith et al. for the 1961 to 1990 period. By the end of the 21st century the area dominated be needle leaved vegetation has moved further north both for the C-only and C-N version of LPJ-GUESS (light blue area in figures 3 and 4). This pattern is in the C-N simulation not quite as pronounced as for the C-only. In Siberia this is with a mixture of both summer- (Larix) and evergreen needle leaved plant functional types. Larch species are shade-intolerant pioneer trees with poor competitive strength relative to evergreen species such as spruce in milder boreal climates where both can coexist. It is hard to know whether this shift from larch to evergreen coniferous forest in response to 100 years of warming is realistic or not.

Question 12: Page 164: What advantage, specifically, does the use of LPJ-GUESS offer over LPJ for this specific project? This paragraph most likely belongs in the introduction rather than in the discussion. Answer: While LPJ and LPJ-GUESS share a common early development history, and retain broadly the same representations of carbon physiology and biogeochemistry they must be considered as two different models having some very distinct features, particularly after the introduction of N cycling in LPJ-GUESS. Therefore there is no clear basis, nor do we see any strong justification, for a discussion of the advantages of LPJ-GUESS over this specific model in the present paper. We do refer to the general advantages of an explicit description of stand and landscape structure in models like LPJ-GUESS, compared to DGVMs more typically lacking such detail: “Only a few DVMs explicitly represent differences in age/size structure among individuals within a PFT and canopy structural variation in time as a result of birth, death and growth of individuals (so called demographics) (Moorcroft et

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al., 2001, Smith et al., 2001, 2014, Fisher et al., 2010b). It has been suggested that the representation of demographics is a precondition for the accurate representation of the C dynamics and climate feedbacks in forest and savannah ecosystems (Purves & Pacala, 2008, Fisher et al., 2010b, Wolf et al., 2011). Scheiter and Higgins (2009) showed the importance of simulating individual trees in savannah ecosystem to be able distinguish between small trees, that are completely consumed in fires, and large trees, that are generally unaffected by fires. A similar result has also been found for simulations with LPJ-GUESS along a climate-transient in sub-Saharan Africa (Arneth et al. 2010b). Especially the effect of tree-tree interaction and self-thinning is important in savannah ecosystems to potentially allow trees to grow taller in the presence of fire than in the absent of fire."

Question 13: It could be nice to have more information about assumptions and limitations of your approach, especially as they relate to LPJ-GUESS simulations over non-forested regions Answer: With LPJ-GUESS there is not any specific assumption related to non-forested regions. All modelled regions are driven by climate, atmospheric [CO2] and N deposition. With these conditions all PFTs, with their specific characteristics, have to compete for resources. Table B1 in Smith et al. describes the different PFTs characteristics.

Question 14: Fig. A1E and Fig. A1E: it is difficult to correctly identify dashed from dot-dashed lines when they are very close together. Answer: Thanks, that is true. Figure A1 has been updated to make E and F clearer.

Question 15: In Table 1, results are compared to O-CN, not ORCHIDEE. Answer: Thanks, table 1 and figure 1 has been corrected.

Question 16: Fig. 3 and Fig. 4 are difficult to interpret. A single legend for each plot, with full descriptions of the relevant acronyms, would be helpful. These figures are labelled as showing vegetation shift from 2000-2100, but the x axis is from 1850-2100, so they could be mislabelled Answer: Both figure 3 and 4 have now a full set of legends. And we have also made it clearer in the text that the major biome shift happens during the 21st century, which is the reason we chosen to depicted the biome shift for this period instead of the full period: "Figure 3. Major biome shift for the C-only version from year 2000 to 2100 using three broad biome classifications; grass (G), broadleaf (B), and needleleaf (N) dominated. Shifts are denoted in the central panel as biome to biome, e.g. shift from grass to broadleaf dominated is denoted as “GtoB”. “No” is implying no major shift of biome over the period. The panels labelled a-f show changes of leaf area index [m2 m-2] over the simulated simulation period for gridcells in the eight regions from Figure 2. BNE = boreal needleleaved evergreen tree; BINE = boreal shade-intolerant needleleaved evergreen tree; BNS = boreal needleleaved summergreen tree; TeBS = temperate broadleaved summergreen tree; IBS = temperate shade-intolerant broadleaved summergreen tree; TeBE = temperate broadleaved evergreen tree; TrBE = tropical broadleaved evergreen tree; TrIBE = tropical shade-intolerant broadleaved evergreen tree; TrBR = tropical broadleaved raingreen tree; C3G = C3 (cool) grass; C4G = C4(warm) grass." "Figure 4. Major biome shift for the C-N version from year 2000 to 2100, applying the same classification and approach as in Figure 3. Like in Figure 3, the global map is accompanied by detailed time-trends for a number of regions identified in Figure 2."

Technical corrections. Question 17: Tables and figures outside the appendix should not be listed as A1,A2 etc. Answer: Tables and figures are named with a single number in the paper and with an A before the numbers in the appendix.

Question 18: Page 156: change “snow lie” to “’snowpack”, and “porportion” to “proportion”. Answer: These corrections have been done.

Question 19: The manuscript would benefit from the application of spelling and grammar checks Answer: The manuscript has gone through a thorough spelling and grammar check.

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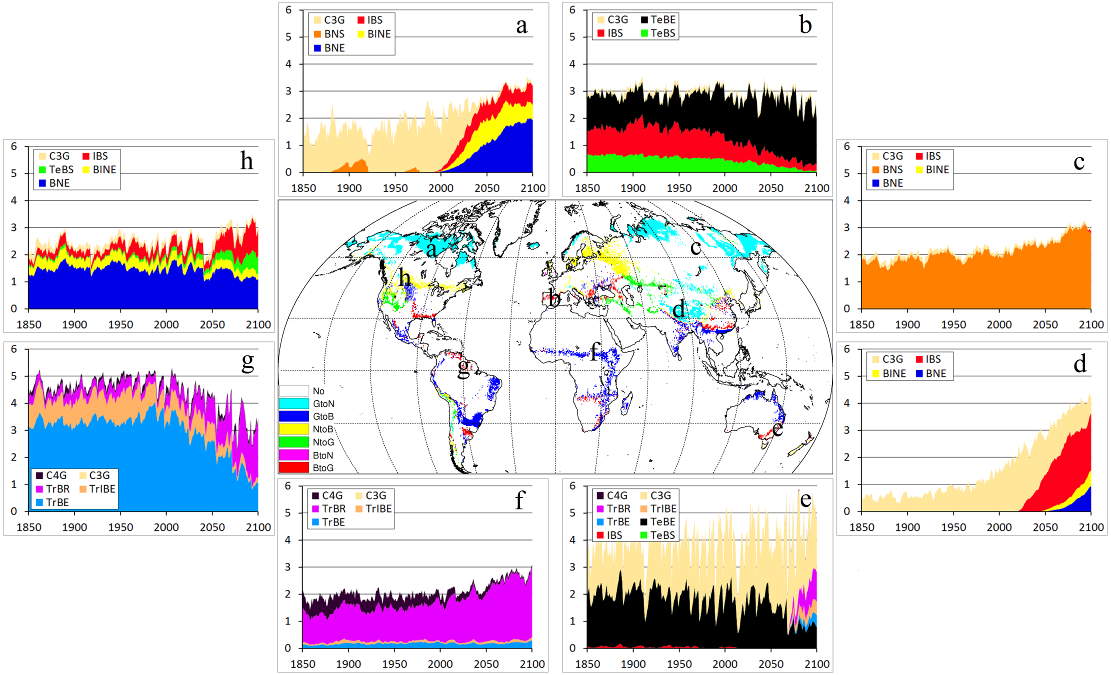

Fig. 1. Figure 3

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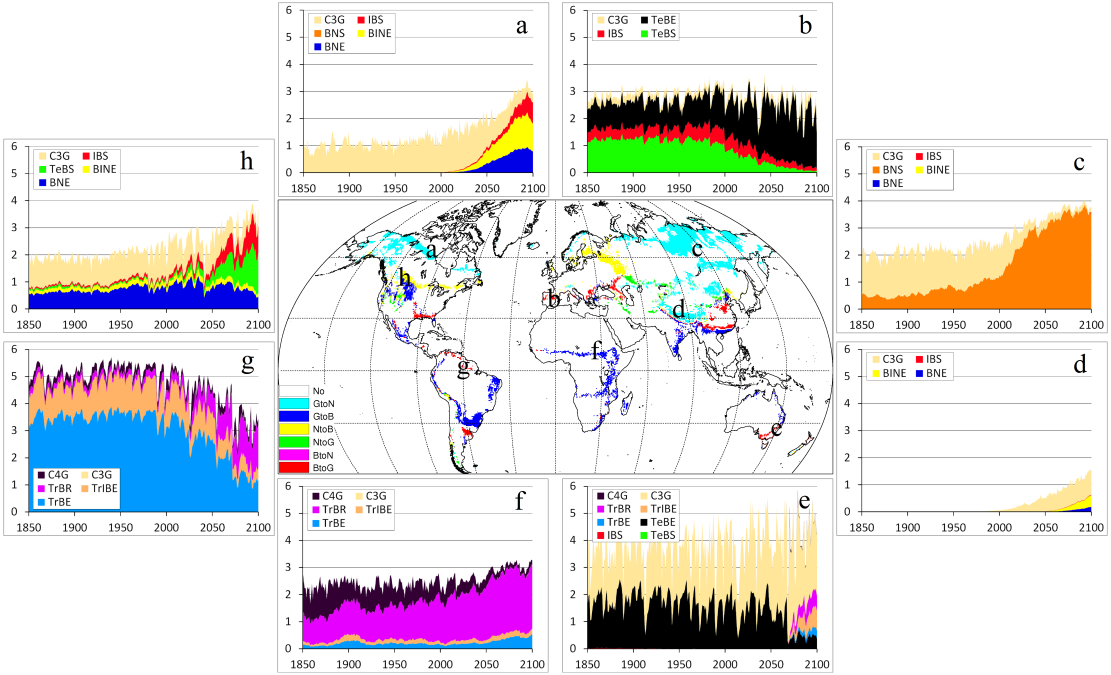

Fig. 2. Figure 4

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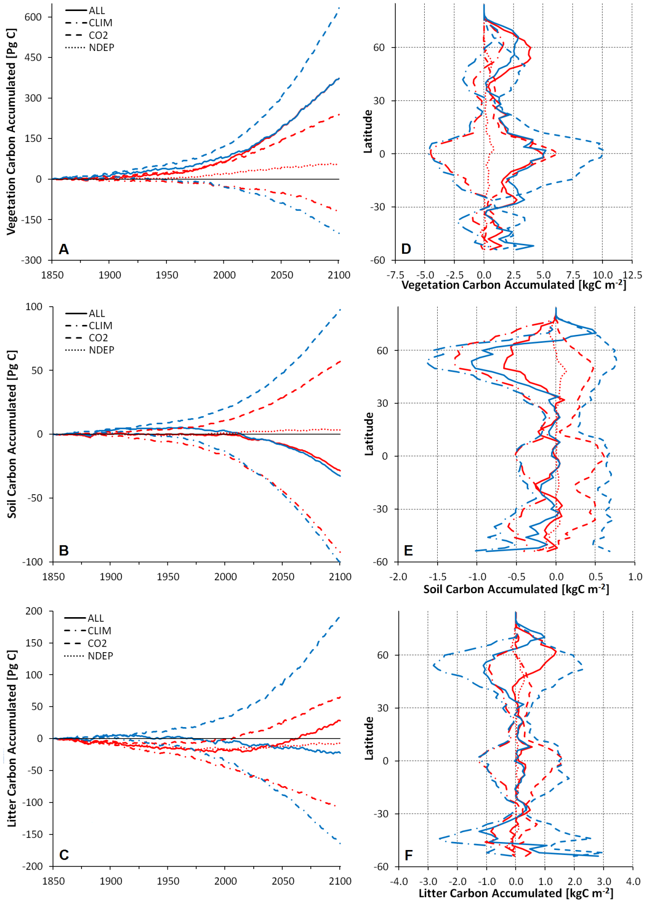

Fig. 3. Figure A1