Editor comment

The revised manuscript was re-read by both reviewers, who as before have thoughtful, probing comments and suggestions. Both referees appreciate that you have put a significant amount of effort into revisions, and responded effectively to most of the previous comments. Both recommend only minor revisions. That said, both focus on a common theme: it has to be very clear, in both the title and manuscript, (i) the fact that this is modeling study, (ii) the input variables required to run the model (cf. R2), and (iii) how the model inputs and logic are linked to the conclusions. R1 put this issue succinctly: "I do think readers have a right to read the authors' explanation of how the modelling framework employed (the hierarchy of drivers in particular) led to the main conclusion."

In summary, then, this is a strong manuscript and the reviewers (and I) appreciate your thoughtful responses and revisions made. There remain some minor revisions, mostly related to methodological clarity and being careful about the scope of the inferences as conveyed in the conclusions and title.

Reply:

We would like to thank the editor for his encouraging words and for facilitating the review process. We have answered all the reviewers' comments below. The updated manuscript has a more extensive description of the processes represented in the model. The title is also updated to clarify that this is a modelling study. Furthermore, we have updated the text where any confusion regarding the methodology could arise. Lastly, we have gone through the text to correct spelling errors, grammatical errors and improved clarity.

Reviewer 1 – Christian Körner

This revised version pertains some of the points I had suggested to be adjusted. While valuing such a modelling attempt, it seems imperative that one makes a clear distinction between empirical facts and suggestions derived from a model. The title reads as if N controls treeline in this region, while this is, at best, a suggestion the authors deduce from a model that they configurated in a way that N plays a key role. I accept the point that all models need to assume certain input variables and a certain hierarchy of causalities. I had hoped the authors write a brief paragraph in which they explain the main assumptions that drive this model. These could include that they assume that C is a limiting resource for growth (hence a high priority in the chain of causalities), and because photosynthesis (A) requires N, this is causing growth to be N controlled etc.). Once there are a few sentences of this kind, every reader understands the rationale behind this model and can make up his/her own mind about the results.

Reply: We would like to once again thank Professor Körner for his thoughtful comments on our manuscript.

We have updated the methods section to further clarify how the model represents photosynthesis and growth, see lines 122-132 Furthermore, we have updated the title to clarify that this is a modelling study. However, we do reiterate our early point that the importance of each driving or modulating factor is an emergent outcome of the model and that the model has not been configured to assume nitrogen to be limiting.

L122-132

Canopy fluxes of carbon dioxide and water vapour are calculated by a coupled photosynthesis and stomatal conductance scheme based on the approach of BIOME3 (Haxeltine and Prentice, 1996). Photosynthesis is a function of air temperature, incoming shortwave or photosynthetically active radiation, [CO_2], and water and nutrient availability. Autotrophic respiration has three components - maintenance, growth, and leaf respiration. Tissue maintenance respiration is dependent on soil and air temperature for root and above-ground respiration, respectively, along with a dependency on tissue C:N stoichiometry. All assimilated carbon that is not consumed by autotrophic respiration, less a 10% flux to reproductive organs, is allocated to leaves, fine roots and, for woody PFTs, sapwood, following a set of prescribed allometric relationships for each PFT, resulting in biomass, height and diameter growth (Sitch et al., 2003). Consequently, an individual in the model is assumed to be carbon limited when autotrophic respiration equals or exceeds the amount of carbon assimilated by photosynthesis. Chronically negative carbon balance at the individual level eventually results in plant death.

Since the results contradict what we know from observational data about treeline formation, the discussion would best explain why the authors think the model is still correct. By observational data, I mean the evidence that the treeline position tracks an isotherm globally, irrespective of local soil fertility. One could for instance argue that this correlation has an error term and within that variance, there is space for a nutrient effect. The authors could further argue why the site for which they model future treeline position is special in terms of tree nutrition, thus opening space for what the model outcome suggests. I do think readers have a right to read the authors' explanation of how the modelling framework employed (the hierarchy of drivers in particular) led to the main conclusion. I think this is within the tradition of modelling that model results are discussed with reference empirical data (which can be critisized as well, of course).

Reply: As stated earlier, we do not disagree with the evidence of a global correlation between treeline position and an isotherm of 6-7 ˚C. We also make no claim that treelines should be at higher elevation on more fertile soils. What the study shows is that it is *plausible* in a rapidly changing environment with multiple environmental drivers and lagged ecological and biogeochemical responses for the historically observed correlation between treeline position and temperature to be broken. In our model, this arises as a consequence of nutrient shortage and competition with already established vegetation. The evidence for the global correlation between treelines and an isotherm is strong, but it is by necessity a snapshot in time. As such, it is not necessarily a strong predictor for future treelines. Here we want to highlight the distinction between current or future treeline <u>position</u> and the <u>rate</u> of treeline advancement. We have added a few sentences about this in the discussion, as an attempt to clarify these differences (see lines 427-431; lines 446-448).

We agree that modelling studies should evaluate the model's performance against available evidence. The paper discusses both long-term (e.g. treeline positions inferred from pollen records; lines 454-462) and short-term (rates of advance during the last 100 years; lines 452-453 + Table 1) treeline positions and rates of advance. Drivers or modulators for treeline advance that are discussed include the carbon limitation hypothesis (lines 474-487), permafrost effects (lines 520-528), physical barriers (lines 505-513), competitive effects on vegetation dynamics (lines 541-552) and nutrient cycling (lines 425-451).

<u>Lines 427-431</u>

During our historic simulations, the treeline correlated well with a soil temperature isotherm close to the globally observed 6-7°C isotherm. However, in our projection period the correlation between the treeline position and the isotherm weakened, revealing a fading or potential lag of the treeline-climate equilibrium that became stronger with increased warming. Future rates of treeline advance were thus constrained by factors other than temperature in our simulations.

Lines 446-448
Historically, treeline positions show a strong correlation with the 6-7°C isotherm (Körner and Paulsen, 2004). These records are, however, a snapshot in time and are not necessarily a strong predictor of future treeline, with other factors (as for nitrogen in our results) potentially breaking the link to temperature.

I am aware of the common jargon, but still find it needs more caution when the word 'test' is employed. We tested N deposition..., we tested CO2 effects... would better read: we performed test runs with the model to explore its sensitivity to...

Reply: We have updated the text and believe we are expressing ourselves accurately in the few instances where we use the word "tests".

On meristems: these are just one of the components it needs to build a tree. Mycorrhiza is another one. LPG assumes A drives meristems. Fine, why not say so? Others found it is the other way round. This is merely an issue of open debate and the need of an attempt to justify why the authors think A drives meristems (sensu growth).

Reply: It is not photosynthesis (A) but NPP that drives growth in LPJ-GUESS, where it is assumed that all NPP except for a 10% deduction for reproduction drives plant growth. We are aware that this assumption is subject to discussion, and we discuss this on lines 474-487. We have also clarified this assumption on lines 130-131.

Lines 130-131
… Consequently, an individual in the model is assumed to be carbon limited when autotrophic respiration equals or exceeds the amount of carbon assimilated by photosynthesis …

On plant competition: sure this matters, in the seedling stage. So if there are good reasons to assume a recruitment limitation, a few words would be welcome on whether the model assumes a dominance of symmetric (soil-root) or asymmetric (light, LAI) competition, and for which life stage such interactions are assumed to be critical. A seed limitation can be excluded in mountain birch, given the billions of light weight seeds produced ever autumn. What matters is (a) the seedling establishment process within the aerodynamic boundary layer close to the ground and (b) the emergence of saplings from that layer. These are two entirely different steps in establishing a young tree.

Reply: We have revised the model description section in methods substantially, and now describe in some detail how the model represents these processes, see lines 135-138. We have also added detail in the Discussion to clarify how various assumptions influence the simulated treeline dynamics (see lines 440-442)

Lines 135-138

Competition for light and nutrients is assumed to be asymmetric, i.e., individuals with taller canopies or larger root systems will be advantaged in the capture of resources under scarcity. Water uptake is divided equally among individuals according to the water availability and the fraction of each PFT's roots occupying each soil layer.

Lines 440-442
For treeline advance to occur, trees need to invade the space already occupied by other vegetation. As the model assumes asymmetric competition for nutrients, newly established seedlings have a disadvantage compared to incumbent vegetation, further slowing down the modelled rate of treeline advance.

Bioclimatic envelope: it would be good to read which thermal envelope the model assumes if any. I mean, all organisms have a thermal limit somewhere and mountain birch is no exception. Whatever envelope the model employs and how this envelope is assumed to act upon trees should be explained (it could be an influence on A, on respiration, on meristems, on freezing tolerance, on microbial soil activity... or a combination of all; we simply need to be told, how the range limit is defined in this LPG variant).

Reply: We have added information in the model description section in methods to describe how the bioclimatic envelope sets the hard limits to PFT ranges in the model (see lines 174-175). Specific PFT parameters can be found in Supplementary Table S2.2.

Lines 174-175
The parameters are intended to capture broader climatic properties of each gridcell. A detailed description of each bioclimatic parameter and its respective values can be found in Supplementary Table S2.2

In summary, this papers requires more explicit statements on the drivers of tree responses assumed. It cannot be left to the reader to find this out in the LPG script.

Reply: We appreciate the thoughtful comments from Professor Körner. We hope that the additional model detail and interpretation in the manuscript, as outlined above, make it clear and understandable for readers.

Reviewer 2 – Anonymous

Review of

Nitrogen restricts future treeline advance in the sub-arctic

By Adrian Gustafson, et al.

In their revised manuscript, the authors have generally done a good job of responding to the detailed and critical reviewer comments.

I still have a few open issues with the manuscript, that should be able to be addressed with minor revisions.

Line numbers refer to the clean copy of the revised manuscript.

Reply: We would like to thank the reviewer for the thoughtful comments and for once again taking the time to scrutinise our paper.

Line 126
So, biological nitrogen fixation does not depend on the plant species/functional type assemblage that is present? That is to say, there are no plant types/species that are more likely to be associated with biological N fixation than others? I guess not in this model, but it would be good to add that precision here.

Reply: This assumption is correct; no PFT has intrinsically greater biological N fixation ability in the model. We have clarified this on lines 143-145. In addition, very few species in the study area form root association with N-fixing microbes and those *Alnus spp* and *Fabaceae* species that can be found are never dominant in the local plant communities.

Lines 143-145
LPJ-GUESS does not currently incorporate PFT-specific nitrogen fixation, which for instance may be associated with species that form root nodules, such as *Alnu*s spp.

Lines 139-146
Could you please put the content of this into a table? I find it quite irritating to constantly be looking back in the text to try to find the acronyms describing the plant functional type and species names. The authors did not accept my suggestion to spell out the plant names in the color bar on Figure 2, but they did put the abbreviations into the caption. Nevertheless, it would be much easier to read if there was a simple table in to accompany the text with the plant name and abbreviation.

Reply: The information about each PFT and their target species is provided in Supplementary Table S2.1. Plant functional types do not necessarily represent a single species, but rather a group of species with similar functional and physiognomic traits. However, a PFT may have a target species which the modeller had in mind when parameterising the PFT. In the case of IBS, mountain birch (*Betula pubescens ssp. czerepanovii*) which forms the treeline in our study region was the target species. This PFT may also include species such as rowan (*Sorbus aucuparia),* which is also a species growing in the forest-tundra ecotone in the area, but of less significance.

Line 159
There appears to have been some misunderstanding of my comment about the replicate patches. While the authors now provide some additional information on the meaning of the replicate patch, they still do not explain/justify how/why they chose to use three patches per gridcell. Why not four patches, or 10, or two? Please add a simple explanation here.

Reply: We apologise for the misunderstanding. We have added a motivation for the 3 patches on lines 178-179.

Lines 178-179
We judged this number sufficient to obtain a stable representation of vegetation dynamics given the relative area of each gridcell and replicate patches (0.1 ha).

Line 162
Just below the section header here, please briefly summarize all of the input variables required to run

LPJ-GUESS. This information is too difficult to find as it is scattered throughout the following paragraphs. Picking through the text I could infer that LPJ-GUESS is driven by monthly mean temperature, precipitation, and solar radiation, and soil texture. Is solar radiation downwelling shortwave only? In what units? What about longwave fluxes? What about slope and aspect? Minimum and maximum temperature or diurnal temperature range, or only the mean? How many soil layers, and to what depth? Coarse fragments or only texture fractions? Alternatively, you could provide a table with this information.

Reply: We have added information about inputs to the requested section, see lines 184-187. However, for clarity we only include variables that are used within the model, and thus exclude variables that are not used, e.g., long wave radiation fluxes, slope and aspect, etc. We also included a sentence in the model description about the number of soil layers, see line 150.

Line 150
The soil scheme includes 15 equally distributed soil layers constituting a total soil depth of 1.5 meters.

Lines 184-187
The input variables used as forcing in LPJ-GUESS simulations are monthly 2m air temperature (°C), precipitation (mm), and incoming shortwave radiation (W m^{-2}) as well as annual atmospheric [CO_2] (ppm), soil texture (mineral fractions only), and nitrogen deposition (kg N ha^{-1} $month^{-1}$). Monthly air temperature and shortwave radiation are interpolated to a daily time-step while precipitation is randomly distributed over the month using monthly wet-days.

Line 174
I also infer here that a wet-day probability is also required input to LPJ-GUESS. How was CRUNCEP downscaled to the appropriate resolution? How was the wet-day probability handled for the future climate runs? Please add wet day probability to the information above.

Reply: The reviewer's assumption is correct. The wet-day probability is used to randomly distribute monthly precipitation over the days in the month. This input was retrieved from the CRUNCEP dataset and used in its 'raw' form. The observational precipitation dataset from Abisko had a monthly resolution and did thus not provide any additional information for adjusting any bias in the number of wet days per months. For our projection simulations we assumed the historic 1971-2000 wet-day climatology to be constant also in the future. As the number of wet days per month was relatively high (often >20 days per month), we do not believe that this assumption had a significant influence on our results. We added a clarification of this on lines 218-219.

Lines 218-219
The number of wet-days per month was assumed not to change in the future scenario simulations, so we used the 1971-2000 climatology for this period.

Figure 2
Figure 2 is much improved but I cannot see the location of the Abisko station marked on the map even though this is promised in the response to reviewers. Also, why have you made

these maps so tiny? Biogeosciences is not a tabloid journal, and you should have nothing to hide. I recommend increasing the size of each of the four maps in this figure by 100%. These are key results and deserve to be easier to scrutinize. Also, could you please add a scale bar in meters or km?

Reply: We have added the Abisko station and a scale bar to the map. Furthermore, we have increased the size of the plots.

Figure 3
Could you please put the color bar in the same order as the way it is presented in Figure 2? Yes, I know this is a little thing, but irritating nevertheless.

Reply: Done

Figure S1.4
You could plot Lake Tornetrask on these maps in blue as it is done in Figure 2. Much easier to read.

Reply: Done