

Biogeosciences Discuss., author comment AC2  
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## Reply on RC2

Adrian Gustafson et al.

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Author comment on "Nitrogen restricts future sub-arctic treeline advance in an individual-based dynamic vegetation model" by Adrian Gustafson et al., Biogeosciences Discuss.,  
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*Gustafson et al. aim at modelling future treeline position in northern Sweden and the causes that control potential shifts. I am familiar with the associated theory and the region. Using environmental data and biological response functions, a digital vegetation model is applied (with the treeline forming species of this region, Betula pubescens ssp.).*

We would like to thank Professor Körner for his comments on our manuscript and for giving us the opportunity to clarify a few aspects of our narrative.

*Such a model has a predefined response hierarchy, that is, assumptions on both, the relative importance of drivers and the direction of causality. These assumptions, though absolutely central, are not mentioned upfront, but they become obvious as one reads the text.*

All models are simplifications of reality and have assumptions underpinning the processes and parameters included in the model. One of the motivations of this study and the use of such a high-resolution grid was to test some of the assumptions built into the model. The scale used in the study enables comparison to experimental and observational data, which is more difficult to do when, as is typical, the model output represents the average over a large spatial scale. The Abisko region has been thoroughly studied with diverse observational datasets, providing an ideal laboratory for benchmarking a model. A modelling study complements empirical approaches in interpreting the causalities in observed dynamics of treeline advance and vegetation shifts. Lastly, the study aims to simulate future vegetation shifts in the area, something only a model can do.

*One of the key assumptions is that these trees are C limited and that photosynthesis, A f (T, PFD, CO<sub>2</sub>) drives growth. Starting with such assumptions, the inevitable outcome is that CO<sub>2</sub> matters for growth, although it may not matter for treeline position, depending in other assumptions. Yet, in my view this is dressing the horse from the tail. It became obvious in recent decades that outside horticulture and agro-conditions, growth controls A via phloem downloading on demand for C, and this demand is set by meristem activity and other sinks. Not surprisingly manipulating C supply in the field neither rose growth or productivity in alpine vegetation, nor in treeline trees (there were transitory effects on young, isolated Larix individuals in exceptionally warm summers, that did not affect final biomass data, pine was never affected). None of these works are cited (the only reference to CO<sub>2</sub> experiments is the differential response of two upper montane understorey shrubs).*

*I do respect the skills of the authors to parameterize and handle such a complex set of algorithms, but the underlaying rationale reflects our understanding of causalities in the 1980s. I am quite aware that starting with modelling growth rises other issues, but several teams have no engaged (Simone Fatichi, Andrew Friend, several papers) and even the dendro-community is now moving forward in that direction (read e.g. Jan Tumajer et al. *Frontiers in Plant Sciences* 28 Jan 2021). They are still unable to handle resource supply as modulating factors.*

LPJ-GUESS includes representations of several processes that can interact to drive or constrain changes in vegetation composition and ecosystem functioning, and moreover these vary over time in response to the evolving ecosystem state. An example is the treeline and productivity changes investigated in our study. Specifically, the following are tested:

- Climatic – We simulate the influence of historic and future climate (temperature, precipitation and solar radiation) change through a range of scenarios extracted from the CMIP5 project (Taylor et al., 2012).
- Nutrient limitation – This is tested in different nitrogen deposition scenarios (see section 2.4.3 in the manuscript) where we vary the nitrogen load in our projection simulations.
- Productivity – We mainly test the influence of productivity on vegetation shifts through our CO<sub>2</sub>-fertilisation experiment (see section 2.4.2 in the manuscript).
- Ecological – A prerequisite for treeline advance is the establishment and growth of trees above the current treeline. Tree seedlings will have to compete with existing vegetation during their establishment (Grau et al., 2012; Lett and Dorrepaal, 2018). Our model includes a representation of interspecific competition for light, soil water and nutrients.

Productivity does not drive treeline advance – we agree with this, in fact it is an outcome of our study, demonstrating that emergent dynamics can not necessarily be trivially predicted from the inputs and modelled processes. Specifically, in our CO<sub>2</sub>-only experiment, the treeline did not advance despite increased GPP (Photosynthesis) (See Sec. 3.3.2 & Fig. 5b). If anything, this indicates that the lack of a correlation between tree productivity and treeline advance in the real world could have more than one mechanistic interpretation. There is no scientific consensus yet that meristem activity universally explains treeline position. Indeed it would be strange if evolution were not ‘smart’ enough to make maximal use of available resources to drive fitness.

Our simulation results are not inconsistent with the observation of ample carbon storage in trees close to the treeline (Hoch and Körner, 2012), which indicates that trees close to the treelines do not suffer from carbon shortage. To further highlight this, we have added results for NPP to the results (L266-269; L301-306) and discussion (L404-407) sections of the manuscript. We do acknowledge (Table 1) that the simulated over-estimation of biomass is a limitation of the model and an area where potential improvements can be made. While a few factors (e.g., herbivory from both mammals and insects, mainly *Epirrita autumnata*) may reconcile the model results with the observations, they cannot fully explain our over-estimation of biomass. Recognising this, and in line with the comments by the reviewer, we put forward temperature limitations on xylogenesis (wood formation) as a potential area for model improvements in the future, as has also been done by others (e.g., Friend et al., 2019; Leuzinger et al., 2013; Pugh et al., 2016) - see our Discussion (see L425-438). This will be of importance for future projections of boreal and Arctic carbon budget estimations and could potentially alter the simulated treeline advance in our Abisko domain. Lastly, our modelled treeline advance is not only constrained by tree physiological factors (e.g., xylogenesis or photosynthesis), but also by ecological factors (e.g., interspecific plant competition and soil nutrient cycling). The importance of including ecological processes in model studies of treeline rather than solely considering bioclimatic limits to treeline advance has also been emphasised by others

(e.g., Scherrer et al., 2020). The model does however include hard limits to vegetation distribution through the bioclimatic envelope of each PFT. We have added a few sentences in the methods to clarify this (see L153-156).

We note that more mechanistic treatments of migration and the spread of seeds could also play a role, as could altered disturbance patterns, type and intensity, as was also pointed out by reviewer #1.

Added texts in the manuscript:

Line 153-156:

The bioclimatic envelope is a hard limit to vegetation distribution, intended to represent the physiological niche of a PFT. Furthermore, the climate envelope is a proxy for physiological processes such as meristem activity that may set species ranges, but also for climatic stressors such as tissue freezing.

Line 266-269:

NPP for IBS in the forest increased from 96 gC m<sup>-2</sup> yr<sup>-1</sup> to 180 gC m<sup>-2</sup> yr<sup>-1</sup> over our historic period (1913-2000). Corresponding values at the treeline did not increase but were stagnant at around 60 gC m<sup>-2</sup> yr<sup>-1</sup>. Above the treeline, IBS showed very low NPP values (<15 gC m<sup>-2</sup> yr<sup>-1</sup>), while NPP for the dominant shrub (LSE) doubled from 20 gC m<sup>-2</sup> yr<sup>-1</sup> to 40 gC m<sup>-2</sup> yr<sup>-1</sup>.

Line 301-306:

Forest NPP, wherein IBS was always dominant, increased from 200 gC m<sup>-2</sup> yr<sup>-1</sup> in year 2000 to 300 (220 – 375) gC m<sup>-2</sup> yr<sup>-1</sup> and 490 (380 - 610) gC m<sup>-2</sup> yr<sup>-1</sup> for RCP 2.6 and RCP 8.5, respectively, over the projection period. NPP for the same period for IBS at the treeline increased slightly from 60 gC m<sup>-2</sup> yr<sup>-1</sup> to 80 (74 - 90) gC m<sup>-2</sup> yr<sup>-1</sup> and 104 (80 - 116) gC m<sup>-2</sup> yr<sup>-1</sup> for RCP2.6 and RCP8.5. Above the treeline NPP remained low (<25 gC m<sup>-2</sup> yr<sup>-1</sup>) for IBS in all scenarios and always had a lower NPP than the most productive shrub PFT (LSE). NPP for this shrub was 49 (24 - 64) gC m<sup>-2</sup> yr<sup>-1</sup> and 130 (81 – 180) gC m<sup>-2</sup> yr<sup>-1</sup>.

Line 404-407:

Furthermore, although NPP for IBS was lower at the treeline than in the forest, it was never close to zero. Such a pattern, which was seen above the treeline, would have indicated a stagnant growth, and that the productivity and carbon costs of maintaining a larger biomass would have cancelled each other out.

Line 441 – 454:

IBS at the treeline had a positive carbon balance (NPP) and was thus not directly limited by its productivity in our simulations. This is consistent with observations of ample carbon storage in treeline trees globally (Hoch and Körner, 2012). The modelled treeline is thus not set by productivity directly but rather by competition, as other PFTs become more productive above the treeline. Whether the treeline is set by productivity constraints or by cold temperature limits on wood formation and meristematic activity has been a subject of some discussion (Körner, 2015, 2003; Körner et al., 2016; Fatichi et al., 2019; Pugh et al., 2016). DVMs have traditionally assumed photosynthesis to be constraining for growth, and thus species distributions. On the other hand, trees close to the treeline have not shown any shortage of carbon for growth (Hoch and Körner, 2012). Furthermore, enhancement of photosynthesis through added CO<sub>2</sub> has also not always resulted in

increased tree growth close to the treelines (Dawes et al., 2013), and wood formation is slow around 5°C, leading to a hypothesis of reversed control of plant productivity and range distributions of trees (Körner, 2015). Lately, ecological interactions as a component in the control of treeline position, rather than just considering hard limits to species distributions, has been a subject of more attention in modelling studies (See for ex., Scherrer et al., 2020). These studies add an extra dimension to the discussion as they do not only consider plant physiology but also broadly accepted ecological concepts such as realised versus fundamental niches.

Line 457-465:

... elevation than observed by Hedenås et al. (2011). The mean annual biomass carbon increase in the same dataset is, although highly variable, on average  $2.5 \text{ gC m}^{-2} \text{ yr}^{-1}$  between 1997 and 2010. As simulated GPP and LAI were within the range of observations in the area (Rundqvist et al., 2011; Ovhed and Holmgren, 1996; Olsson et al., 2017), this indicates a coupling between photosynthesis and growth in the model that is stronger than observed. Terrestrial biosphere models often overestimate biomass in high latitudes (Pugh et al., 2016; Leuzinger et al., 2013) and potentially lack processes that likely limit growth close to low temperature boundaries. Examples of such processes are carbon costs of nitrogen acquisition (Shi et al., 2016), including costs for mycorrhizal interactions (Vowles et al., 2018), and temperature limits on growth increment (Friend et al., 2019), i.e., decoupling of growth and photosynthesis. However, data on carbon allocation and its temperature dependence is scarce (Fatichi et al., 2019).

*With these concerns, the results of the modelling reflects the assumptions. If one assumes soil fertility matters for treeline trees and selects N to represent these nutrients, the outcome is that N matters.*

Dynamic vegetation models (DVMs) are designed to test multiple and interactive driving factors and processes under different environmental conditions. LPJ-GUESS (Smith et al., 2001; Smith et al., 2014), does not build on the assumption of any single driving or modulating factor. The importance of each driver is an emergent outcome of the simulated dynamics in response to variation in the drivers, and the evolving state of the system (e.g. soil N availability, plant community structure) which also modify the processes. Thus we respectfully disagree with the statement "*the results of the modelling reflects the assumptions*". While this is true by definition for any model, the point the reviewer is making, that the simulated treeline dynamics could be trivially pre-empted, knowing the input to the model and the process formulations used, is not correct.

*If soil fertility were controlling treeline position there should not be a global treeline isotherm and treeline should be at higher elevation on good soils and at lower elevations on poor soils, not what we see in the field (e.g. soils developing on young glacial deposits versus treelines on geologically old, weathered, low latitude mountains.*

The reviewer's comment states that, given our conclusions, local variations in soil fertility would give rise to differences in treeline elevation and that no such pattern is seen in global treeline records. This would be true if no recognition of temperature as a controlling factor were made. We do not dispute the importance of temperature as an overall control on treeline position, but stand by our conclusion, consistent with physiological, demographic, and ecological principles and assumptions around which there is broad scientific consensus, that nitrogen limitation will constrain rates of future treeline advance in this area.

The global correlation between treelines and the 6.7°C isotherm (6-7°C in arctic/boreal regions; Körner and Paulsen, 2004) is not disputed in this study. In fact, results from our historic simulations corroborate this, at least for this region since the position of the

simulated treeline correlates well with an isotherm close to this limit (Fig S1.4; supplementary materials). The lag arises in our future projections of treeline advance when the isotherm displacement is more rapid than the treeline advance in most scenarios (Fig 4). We traced this effect to N-limitation in the soils as we see a faster treeline migration in our climate change only simulations compared to the future projections when N-deposition is decreasing.

*Experiments by Hoch (2013) revealed that there is no compensatory effect of nutrient addition to low temperature constraints of growth. There is also no direct link between tree vigor and treeline position. Trees at treelines in Bolivia and Tibet at close to 5000 m elevation hardly grow (minute tree ring width), because they are clearly moisture and thus, nutrient limited.*

The model simulates induced treeline advance when only nitrogen deposition increased (Fig 5c). This was a result of an increased allocation to above-ground biomass with a subsequent advantage in the light competition. The reviewer refers to the study by Hoch (2012) as evidence against such an effect. However, the Hoch study was performed in a fully factorial design with seedlings grown in phytotrons with controlled environment at 6 °C or 12 °C and half of the seedlings fertilised. The cold temperature seedlings showed no response to added fertiliser, while warm temperature seedlings showed a strong biomass increase with fertilisation. We would argue that such a controlled climate study may not mimic the role of nitrogen effects in a full ecosystem setting.

*I hope these comments are useful for revisiting the rationales underpinned in this model. I read the other report in copernicus, thanks for providing it. It seems to address additional facets of treeline formation, but does not touch upon the more fundamental bias regarding the assumptions that drive the model output.*

We would like again to thank Professor Körner for his comments. We would also argue that our study makes a meaningful contribution to the treeline literature, and hope that our findings will stimulate further experimental and modelling studies of treeline advance and associated feedbacks to climate.

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