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Reply on RC1

Adrian Gustafson et al.

Author comment on "Nitrogen restricts future sub-arctic treeline advance in an individual-based dynamic vegetation model" by Adrian Gustafson et al., Biogeosciences Discuss., https://doi.org/10.5194/bg-2021-169-AC1, 2021

This manuscript describes a modeling study to understand the climatic and biogeochemical controls on vegetation change in sub-arctic Sweden. The authors parameterized the LPJ-GUESS dynamic vegetation model with the principle plant types found in their study area around Abisko, Sweden. Using a very high resolution local gridded climatology and downscaled GCM output, the authors then ran LPJ-GUESS in a historical and series of future climate scenarios, and in a range of sensitivity tests controlling for different processes including CO_2 *fertilization and nitrogen cycling. The authors conclude that while climate has an overarching control on vegetation composition and position of the treeline, nitrogen availability exerts a very important influence on vegetation dynamics.*

In general, this study is well designed and the methodology and sensitivity tests follow generally accepted protocols for dynamic vegetation modeling experiments. The manuscript is well written and easy to follow. The presentation could be improved, in particular the figures, and I do have a few scientific comments that should be addressed, but overall this manuscript should be suitable for publication in Biogeosciences after moderate revision.

Reply: Thank you for these encouraging words and good suggestions for improvements to the manuscript. Below follow a few discussion points to your questions and point-to-point answers, as well as an updated manuscript with your suggestions incorporated or discussed.

General comments

I would like to see more discussion of the processes that were not included in the model, concentrating on the following:

1. Seed dispersal limitations to vegetation change: A great deal of modeling work has gone in to understanding the role of seed dispersal in limiting plant migration rates, particularly along vertical gradients similar to the principle one at Abisko. The pioneer in this research has been Heike Lischke with her TreeMig Model (Lischke et al., 2006), which has been applied to the Arctic (Epstein et al., 2007), and some representation of dispersal and migration has even been incorporated into a version of LPJ developed in part by your colleagues in Lund (Lehsten et al., 2019). Of course, dispersal limitations are not the *whole story of what limits plant migration (Scherrer et al., 2020). Nevertheless, some further discussion on this topic and additional citations would be welcome in this manuscript, as it is effectively missing at the moment.*

Reply: Thank you for a good comment! As you state, a great deal of research has gone into the study of this topic, where the TreeMIG-model stands out as a pioneering example. Seed dispersal limitations were only briefly touched upon in our Introduction, where we state that latitudinal treelines might be more sensitive to dispersal constraints than elevational treelines (see L49-50), as has been discussed by Rees et al. (2020). LPJ-GUESS assumes the presence of seeds in all grid cells, meaning that simulated species or PFTs can establish once the climate is favourable, as defined by each individual's predefined bioclimatic limits (Smith et al. 2014). While seed dispersal limitations might play a role in constraining larger scale, latitudinal, migration rates, we do not believe that it will play any major role in our case, across distances of the order of tens of metres. This is evidenced by the presence of tree saplings above the current treeline in the Abisko area (Sundqvist et al., 2008) and that some of these stunted mountain birch individuals can be a few decades old (Hofgaard et al., 2009). The latter suggesting that these seedlings have been able to spread and establish above the treeline in historic times, but not develop into mature trees. There should thus not be any constraint on the availability of the birch seeds in the seedbank above the treeline (Truong et al., 2007). According to your suggestion we added a section in the discussion (see L473-487) about this topic.

"LPJ-GUESS assumes the presence of seeds in all gridcells and PFTs may establish when the 20-year running average climate is within PFT-specific bioclimatic limits for establishment. This assumption may overlook potential constraints on plant migration rates such as seed dispersal and reproduction. On larger spatial scales, it is likely that lags in range shifts would arise from these additional constraints (Rees et al., 2020; Brown et al., 2018). Models that account for dispersal limitations generally predict slower latitudinal tree migration than models driven solely by climate (Epstein et al., 2007). However, on smaller spatial scales, the same models predict competitive interactions to be more dominant in determining species migration rates (Scherrer et al., 2020). In a seed transplant study from the Swiss alps, seed viability could not been shown to decline towards the range limits of eight European broadleaved tree species (Kollas et al., 2012; Körner et al., 2016). Similarly, gene flow above the treeline could not be shown to be limited to near-treeline trees in the Abisko region (Truong et al., 2007). Furthermore, tree saplings have been reported to be common up to 100m above the present treeline (Sundqvist et al., 2008; Hofgaard et al., 2009). As environmental conditions improve, these individuals may form the new treeline. Thus, on the scales considered in this study, we do not regard dispersal limitations as a major factor in limiting range shifts of trees."

2. Permafrost effects: While it is mentioned that the study area lies in the permafrost zone, it is not really discussed how changing permafrost dynamics; deepening of the active layer, changes in effective rooting depth, changing water table depth, etc. affects vegetation. At the ultra-high resolution used in the model simulations, it might be important to account for how ground freezing and soil vertical and horizontal movement caused by frost (or lack of it in the future) could affect survival and competition among the various plant functional types simulated. While I appreciate that a full treatment of permafrost dynamics may be beyond the scope of the present study, it would be good to have some further discussion/speculation of how this process could influence the results and conclusions of the modeling work performed here.

Reply: Permafrost aspects are important in the Arctic. Our study area is located within a zone of discontinuous permafrost. In our study domain, the presence of permafrost is limited to wetlands, e.g., the Stordalen area, or at the highest elevations (Callaghan et al., 2013). As we do not include any analysis of wetlands in our study, the only permafrost zones in our study domain are located on the mountains above treeline. Thus, permafrost and treelines in our area are far separated and permafrost effects on the treeline or shrub growth will be of minor importance for our results. Permafrost dynamics may be important for vegetation dynamics at the highest elevations in our historic simulations.

The model simulates the effect of frozen ground and permafrost (where present) on water availability, though the effects of frost horizontal and vertical movement are not taken into account. Such processes could affect survival and competition among the plant functional types, especially in the seedling stage when plants are most vulnerable to mechanical disturbance. These effects could be relevant to treeline dynamics at the high grid resolution of our study, but are not accounted for by our model. We have added a few lines about permafrost dynamics in the results (L279-281; 348-350) and discussion (L 456-463).

L279-281

"Simulated permafrost with an active layer thickness of <1.5 m was present at elevations down to 560 m a.s.l. in a few gridcells, but was always well above the treeline. More shallow permafrost (<1 m) was only present in gridcells at elevations of 940 m a.s.l. and above."

L 346-348

"Permafrost with an active layer thickness of <1.5m disappeared completely from our study domain in all scenarios except the coldest (GFDL-ESM2M-RCP2.6) where it occurred in a few gridcells at elevations of approximately 600 m a.s.l. However, the shallow permafrost (<1m) had disappeared also in this scenario."

L 456-463

"Permafrost was only present at the highest elevations during the historic simulation but had disappeared from the landscape at the end of the century for all except the coldest scenario (GFDL-ESM2M-RCP2.6). The simulated permafrost was however always well above the treeline and did not have a significant impact on the treeline advancement. While some aspects of ground freezing are accounted for in the model, soil vertical and horizontal movement caused by frost, and amelioration of such effects in the warmer future climate are not. Such processes could affect survival and competition among the plant functional types, especially in the seedling stage when plants are most vulnerable to mechanical disturbance. These effects could be relevant to treeline dynamics at the high grid resolution of our study but are not accounted for by our model."

3. Slope and aspect effects: It is mentioned that the study area is hilly or even mountainous; at the resolution of the model, how were slope and aspect handled? Particularly in a high-latitude situation with low sun angle, slope and aspect must be very important in influencing the surface radiation budget, soil temperature, and snowpack dynamics. If slope and aspect were not considered in this study, some explanation of why is required, and similarly to the point above, the authors should include some discussion of the potential effects that this could have on their results. Furthermore, as the resolution of the modeling approaches micrometerological scale, it would be helpful to have some further discussion of how the lakeshore climate may be different from areas further away, e.g., with respect to wind speed and the radiative environment.

Reply: The questions about the influence of slope and aspect will of course be of importance when modelling on this scale. Elevation (i.e. lapse rate) is the main driver of mesoscale temperature variation in our climate dataset. Effects of mountainside aspect are included in the climate dataset by Yang et al. (2011) as local variations to the temperature data alongside the lake effect by Lake Torneträsk. Both surface temperature and radiation are input variables to the model. Any relationships between surface temperature and radiation are not calculated within the model but are implicitly included in the dataset. We have therefore included a statement of these properties of the climate dataset in the methods section (see L 166-167). For a full description of the climate dataset we refer to Yang et al. (2011; 2012). Soil temperature and snowpack dynamics are determined by the pre-calculated surface air temperature and precipitation inputs, and soil properties, with no explicit use of aspect or slope in the model's process descriptions. Effects of wind is not regarded in the model and we do not use wind as input to any parts of the model.

4. Linked to the point above on slope and aspect, I would have liked to see some more discussion of the spatial heterogeneity of the snowpack. Again, at the model resolution and over the spatial domain considered, I would imagine that the formation of snowdrifts and other snowpack variation is important for soil temperature and moisture, plant survival, and N cycling. Numerous studies have demonstrated that wind and slope/aspect have a strong influence on the depth and density of snow in snowdrifts and on the rate and timing of snowmelt. This spatial heterogeneity in snowpack depth and melt rate affects winter surface temperatures and therefore survival of plants at and above the treeline, and growing season soil moisture (there are many studies on this topic but one example is Walker et al., 1999). Again, while a full treatment of snowpack heterogeneity might be beyond the scope of the study, some more discussion of this important process, and how it might influence the region around Abisko specifically, is warranted.

Reply: Our version of the model does not include any formulation of snowdrift or wind compaction. The simulated spatial heterogeneity of the snowpack in the model is thus minimal (<1%) for the winter (DJF) months. Snow trapping processes or any potential snow-shrub feedbacks (Sturm et al., 2001) are therefore not included in our simulations. These processes are undoubtedly important for soil temperatures and subsequently mineralisation of soil organic matter. The model accounts for snow insulation effects on soil temperature, but do not have any representation of frost damage, which might affect seedling survival and be ameliorated by an insulating snow cover. As the model does not account for heterogeneity over the landscape in the compaction and drifting of snow, this might lead to an overestimation of winter soil temperatures above the treeline, where high winds and low roughness tend to deplete snow cover, and an underestimation of winter soil temperatures in the forest, where the opposite is true. We have extended the discussion to include these feedbacks (see L 443-450).

"Furthermore, our model does not include any wind related processes such as wind mediated snow transport or compaction. Thus, our simulations result in a homogenous snowpack during the winter months with no differentiation in sheltering or frost damage that may result from different snow and ice properties. Sheltered locations in the landscape are known to promote survival of tree saplings (Sundqvist et al., 2008). For N cycling this may also mean that suggested snow-shrub feedbacks (Sturm et al., 2001; Sturm, 2005) are not possible to capture with the current version of our model. While overall rates of advance were captured, local variations arising from physical barriers such as steep slopes, stony patches or anthropogenic disturbances were consequently not possible to capture as these processes are not implemented in the model."

Any explicit representation of physical barriers, e.g., stones, or processes such as snowdrift resulting from topography are also not included in our simulations. We have updated the manuscript to clarify that these processes are not included in the discussion section (see L 446-447). The analysis of the transects are intended as a way of clarifying how these barriers in the landscape influence our simulated treeline advance.

5. Given the overall importance of N cycling for the results of this study, it would be helpful to have an overview of the N module in LPJ-GUESS. In particular, I would like to *understand how biological N fixation is represented and if certain PFTs (e.g., something representing Alnus spp.) can be advantaged in nitrogen poor settings because they are capable of enhanced N fixation especially with warmer temperatures.*

Reply: A more detailed description of the N cycle in LPJ-GUESS have been included in the manuscript (see L 125-128). Full details and equations, which are too extensive to repeat in the present paper, are presented in the cited paper by Smith et al. (2014).

"Biological N fixation is represented by an empirical relationship between annual evapotranspiration and nitrogen fixation (Cleveland et al., 1999) and occurs differently within each patch. Additional inputs of nitrogen to the system occur through nitrogen deposition or fertilisation. Nitrogen is lost from the system through leaching, gaseous emissions from soils and wildfires. For a full description of the nitrogen cycle in LPJ-GUESS, see Smith et al. (2014)."

Specific comments

Line 148

It is mentioned that three replicate patches in each gridcell are used for LPJ-GUESS. It is worth going in to a little more detail here to justify this choice of the number of replicate patches. As I understand, each patch in LPJ-GUESS is meant to represent an area of 0.1 ha. With a 50m grid (cells of 0.25 ha), three replicates effectively makes an explicit representation of the entire gridcell, no?

Reply: The replicate patches are intended to give an estimation of landscape-scale heterogeneity within a gridcell or stand that might arise from spatial variation in stochastic processes and histories in the model (e.g. stochastic establishment, mortality and patch destroying disturbance events). No assumptions are made about how the patches are distributed within a wider area, they are merely a statistical sample of equally possible disturbance/demographic histories across the landscape of a grid cell. We have adjusted the text to improve clarity on lines 147-148.

"No assumptions are made about how the patches are distributed within a gridcell, they are a statistical sample of equally possible disturbance/demographic histories across the landscape of a gridcell."

Line 153

Further to my general comment above, please explain how slope and aspect are incorporated into this gridded climatology.

Reply: We have added a clarification of how the dataset was constructed. In general, the field measurements were set up in forms of transects with temperature loggers. These transects were selected to cover variations in mesoscale climate patterns that arise from elevation (i.e., lapse rate), and local variations (aspect and lake effects). See lines 161-168.

"The field measurements were conducted in form of transects that captured mesoscale climatic variations, i.e., lapse rates. In addition, the transects were placed to capture microclimatic effects of the nearby lake Torneträsk and variations in radiation stemming from mountainside aspect. The temperature in the lower parts of the Abisko valley in the resulting dataset was influenced by the lake with milder winters and less yearly variability. At higher elevation, the temperature was more variable over the year and the local scale variations were more dependent on the different solar angles between seasons and mountainside aspect (Yang et al., 2011; Yang et al., 2012)"

Line 157 and Fig S1.1

From looking at the figure I don't really see how temperature is "more variable" with increase in elevation. Perhaps some descriptive statistics would be more useful here

Reply: We acknowledge that the statement about climate variability is not evident from the figure. It is however a feature of the climate dataset described closer in Yang et al. (2012). We have updated the figure with larger elevational bands for clarity and values written out in the figure. In addition, we have added a panel with the standard deviation for each elevational band and month. This panel may be interpreted as the magnitude of the local effect at each elevational band and month.

Line 167-169

Soil edaphic controls on vegetation are an important part of treeline and subarctic biogeography; it is even mentioned on this line. So why not make any attempt to account for spatial variation in soils? Although the spatial resolution is still a bit coarse, why not use the pedometrics-based Soilgrids250 (Hengl et al., 2017) instead of simply prescribing the same soils everywhere? Could you have done some sensitivity tests to quantify the model response of vegetation distribution and treeline to different soil physical properties?

Reply: We agree that soil factors are undoubtedly important also for soil nutrient cycling and storage. We assumed a uniform soil texture within our study domain sourced from our standard soil dataset (Batjes, 2005) as input to the model. We came to this decision after we had contacted the Swedish Geological Survey (SGU), which we judged as the best source of more detailed soil data or surveys. A more detailed survey of soil texture for this area was however non-existent. The dataset by Hengl et al. (2017)is indeed impressive and includes a few processes known to create variations in soil texture over the landscape. However, we would argue that a dataset with higher resolution is not necessarily a more reliable or accurate dataset. Furthermore, the variations in soil textures within our study domain are not larger than approximately 3% for the clay or sand fractions. Such small variations in soil texture would not generate any significant changes to the landscape heterogeneity. We did some sensitivity tests in a sub-section of our domain during the preparation phase of the simulations. While some factors such as soil organic carbon content was affected, more drastic variations in soil texture are needed to affect vegetation distribution or treeline dynamics to any large degree. We have not included these sensitivity tests in our results. We have added a sentence in the discussion (L451-454) about this limitation in soil texture heterogeneity in our model input.

"High-resolution, local observations of vertically-resolved soil texture and soil organic matter content (see, e.g. Hengl et al. (2017) for an example compiled using machine-learning) have the potential to improve the spatial variability of modelled soil temperatures and nutrient cycling in our study domain. We will investigate this uncertainty in future studies."

Line 418

Where are these transects? Call out the supplementary figure here or even better refer to an overview map (see comment below). How were the locations and orientations of these transects chosen?

Reply: The figure has been referenced in the text on line 235. We also include a short sentence in the methods section (see L 235-237) and figure caption (supplementary materials) about how these transects were selected.

Comments on presentation

I would appreciate seeing an overview map or aerial photo of the study area showing topography and the location of the lake, any rivers, and settlements, roads, etc. I would also like to see at least an inset map showing the location of the study area within Europe and Sweden.

Reply: We have provided an inset map of Sweden and the location of Abisko in figure 2. In this figure we added contour lines to mark the landscape topography. We also marked the lake and the location of the Abisko scientific station (ANS) in this figure. We thank the reviewer for these suggestions which we believe improves the maps a lot. We do not include settlements, roads and rivers as our simulations are not affected by these features.

Fig. 2

What is the white area in these maps? Why are the colors used for the PFTs in Fig. 2a not the same as those used in Fig. 3? Please harmonize. Please add a scale bar to these figures, and perhaps one or two longitude and latitude tick marks/labels. As many readers look only at the figures, or the figures first, it would be helpful to spell out the PFT names in the figure legend here instead of making the reader refer back to an additional table or text to decode these.

Reply: We have updated the figure and figure caption in accordance with these suggestions.

Fig. 3

Harmonize the colors with Fig. 2a

Reply: We have updated the figure with harmonized colors as in figure 2.

Fig. S1.1

The figure caption appears to be cut off

Reply: Fixed.

Supplement S1 Table 1

What is reported in the column "Reported (van Bogart et al. 2011)"? What are these units of?

Reply: These are estimated treeline migration in elevational meters reported by van Bogart et al (2011). We have updated this table to clarify this.

Fig. S1.4

What is the gray scape in plotted in the background of the map? What is the white area?

Reply: The gray scape in this figure is the landscape relief and the white area is Lake Torneträsk. We have clarified this in the figure caption.

Fig. S1.6e

What is the principle control on annual shortwave radiation? Is it cloud cover? This could also be discussed in the main text.

Reply: The principal control of the annual shortwave radiation within the global climate models (GCMs) is cloud cover. However, we use the monthly bias adjusted shortwave radiation-output from the GCMs as input to our model. The annual values are averages of the monthly output provided by the GCMs. We have updated the figure caption to clarify this.

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