Nitrogen restricts future treeline advance in the sub-arctic

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Abstract. Arctic environmental change has induced shifts in high latitude plant community composition and stature with implications for Arctic carbon cycling and energy exchange. Two major components of high latitude ecosystems undergoing change is the advancement of trees into treeless tundra and the increased abundance and size of shrubs. How future changes in key climatic and environmental drivers will affect distributions of major ecosystem types is an active area of research. Dynamic Vegetation Models (DVMs) offer a way to investigate multiple and interacting drivers of vegetation distribution and ecosystem function. We employed the LPJ-GUESS DVM over a subarctic landscape in northern Sweden, Torneträsk. Using a highly resolved climate dataset we downscaled CMIP5 climate data from three Global Climate Models and two 21st century future scenarios (RCP2.6 and RCP8.5) to investigate future impacts of climate change on these ecosystems. We also performed three model experiments where we factorially varied drivers (climate, nitrogen deposition and [CO_2]) to disentangle the effects of each on ecosystem properties and functions. We found that treelines could advance by between 45 and 195 elevational meters in the landscape until the year 2100, depending on the scenario. Temperature was a strong, but not the only, driver of vegetation change. Nitrogen availability was identified as an important modulator of treeline advance. While increased CO_2 fertilisation drove productivity increases it did not result in any range shifts of trees. Treeline advance was realistically simulated without any temperature dependence on growth, but biomass was overestimated. As nitrogen was identified as an important modulator of treeline advance, we support the idea that accurately representing plant-soil interactions in models will be key to future predictions of Arctic vegetation change.

Keywords: Ecosystem model, forest-tundra ecotone, treeline, sub-Arctic, climate change impacts, ecosystem stability, LPJ-GUESS, biogeophysical feedbacks.

1. Introduction

In recent decades, the Arctic has been observed to become greener (Epstein et al., 2012; Bhatt et al., 2010). Causes include an increased growth and abundance of shrubs (Myers-Smith et al., 2011; Elmendorf et al., 2012; Forbes et al., 2010), increased vegetation stature associated with a longer growing season, and poleward advance of the A~~a~~rctic treeline (Bjorkman et al., 2018). Shrubs protruding through the snow and treeline advance will alter surface albedo and energy exchange with potential feedback to the climate system (Chapin et al., 2005; Sturm, 2005; Serreze and Barry, 2011; Zhang et al., 2013; Zhang et al., 2018). Warming and associated changes in high latitude ecosystems have implications for carbon cycling through increased plant productivity and species shifts (Chapin et al., 2005; Zhang et al., 2014), but also increased soil organic matter (SOM) decomposition with subsequent loss of carbon to the atmosphere. Studies of the Arctic carbon balance have shown that the Arctic has been a weak sink in the past (Mcguire et al., 2009; Mcguire et al., 2012; Bruhwiler et al., 2021; Virkkala et al., 2021), although uncertainty is substantial, and it is difficult to determine accurately the strength of this sink. How climate and environmental changes will affect the relative balance between the carbon uptake, i.e. photosynthesis, and release processes, i.e., autotrophic and heterotrophic respiration, will determine whether the Arctic will be a source or a sink of carbon in the future.

Forest-tundra ecotones constitute one of the largest transition zones where abrupt changes in ecosystem functioning occur (Hofgaard et al., 2012). While no generally accepted theory of what drives treeline advance has been put forward, several alternative explanations exist. Firstly, direct effects of rising temperatures have been thoroughly discussed (e.g., Rees et al., 2020; Hofgaard et al., 2019; Körner, 2015; Chapin, 1983). On the global scale, treelines have been found to correlate well with a 6-7°C mean growing season ground temperature (Körner and Paulsen, 2004) and could thus be expected to shift with rising temperatures. A global study of alpine treeline advance in response to warming since 1900 shows that 52% of treelines had advanced while the other half was stationary (47%), with only occasional instances of retreat (1%) (Harsch et al., 2009). Similar patterns have been observed on the circumarctic scale, although latitudinal treelines might be expected to shift more slowly than elevational treelines due to dispersal constraints (Rees et al., 2020). As trees close to the treeline often show ample storage of non-structural carbohydrates (Hoch and Körner, 2012) it has been suggested that a minimum temperature requirement for wood formation, rather than productivity, constrains treeline position (Körner, 2003, 2015; Körner et al., 2016).

Secondly, it has been hypothesised that indirect effects of warming might be equally or more important than direct effects (Sullivan et al., 2015; Chapin, 1983). For example, rising temperatures and subsequently soil temperatures might induce increased nitrogen mineralisation and plant nitrogen uptake (Chapin, 1983). Increased nitrogen uptake could in turn enhance plant productivity and growth (Dusenge et al., 2019). Increased nitrogen uptake as a consequence of increased soil temperatures or nitrogen fertilisation have been shown to increase seedling winter survival among mountain birch (*Betula pubescens ssp. tortuosa*) seedlings (Weih and Karlsson, 1999; Karlsson and Weih, 1996).

Thirdly, experiments of elevated CO_2 often show increased plant productivity and biomass increase, especially in trees (Ainsworth and Long, 2005). Terrestrial biosphere models generally agree with this pattern (Hickler et al., 2008; Smith et al., 2014; Piao et al., 2013). Although difficult to measure in field experiments, treeline position seems unresponsive to increased $[CO_2]$ alone (Holtmeier and Broll, 2007). Whether treelines are responsive to increased productivity through CO_2 fertilisation might yield insights into whether treelines are limited by their productivity, i.e., photosynthesis, or ability to utilise assimilated carbon, i.e., wood formation. However, to what extent increased $[CO_2]$ drives long-term tree and shrub encroachment and growth remains poorly studied.

For treeline migration to occur, it is not only the growth and increased stature of established trees that is important, but also the recruitment and survival of new individuals beyond the existing treeline (Holtmeier and Broll, 2007). Seedlings of treeline species are sometimes observed above the treeline, especially in sheltered microhabitats (Hofgaard et al., 2009; Sundqvist et al., 2008). However, these individuals ~~are~~ often display a stunted growth and can be up to a few decades old, although age declines with elevation (Hofgaard et al., 2009). The suitability of the tundra environment for trees to establish and grow taller will thus be an important factor for the rate of treeline advance (Cairns and Moen, 2004). Interspecific competition and herbivory are known to be important modulators of range shifts of trees (Cairns and Moen, 2004; Van Bogaert et al., 2011; Grau et al., 2012). For instance, the presence of shrubs has been shown to limit tree seedling growth (Weih and Karlsson, 1999; Grau et al., 2012), likely as a consequence of competition with tree seedlings for nitrogen. Comparisons of models incorporating only bioclimatic limits to species distributions and a more ecologically complex model have also revealed interspecific plant competition to be important for range shifts of trees (Scherrer et al., 2020; Epstein et al., 2007). Thus, as a fourth factor, shrub-tree interactions are likely to be important when predicting forest range shifts under future climates. Rising temperatures have been suggested as the dominant driver of increased shrub growth, especially where soil moisture is not limiting (Myers-Smith et al., 2015; Myers-Smith et al., 2018). Furthermore, a changed precipitation regime, especially increased winter snowfall, might promote establishment of trees and shrubs through the insulating effects of snow cover with subsequent increases in seedling winter survival (Hallinger et al., 2010).

A narrow focus on a single, e.g., summer temperature, or a few driving variables may lead to overestimations of treeline advance in future projections (Hofgaard et al., 2019). Dynamic vegetation models (DVMs) offer a way to investigate the influence of multiple and interacting drivers on vegetation and ecosystem processes. Model predictions may be compared with observations of local treelines and ecotones to validate assumptions embedded in the models, and to interpret causality in observed dynamics and patterns. DVMs also offer a way to extrapolate observable local phenomena to broader scales, such as that of circumarctic shifts in the forest-tundra ecotone and the responsible drivers. Here, we examine a subarctic forest-tundra ecotone that has undergone spatial shifts over recent decades (Callaghan et al., 2013), previously attributed to climate warming. Adopting a DVM incorporating a detailed description of vegetation composition and stature and nitrogen cycle dynamics, we apply the model at high spatial resolution to compare observed and predicted recent treeline dynamics, and project future vegetation change with implications for carbon balance and biogeophysical feedbacks. In addition, we conduct three model experiments to separate and interpret the impact of driving factors (climate, nitrogen deposition, [CO_2]) on vegetation in a forest-tundra ecotone in Sweden's subarctic north.

2. Materials and Methods

2.1 Abisko

Abisko Scientific Research station (ANS; 68°21' N, 18°49' E) has a long record of ecological and climate research. The climate record date~~s~~ back to 1913 and is still ongoing. The research station is situated in a rain shadow and is thus relatively dry despite its proximity to the ocean (Callaghan et al., 2013). The research station is situated in the valley, close to the lake Torneträsk. The forests in the lower parts of the valley cons~~t~~ist mostly of mountain birch *Betula pubescens ssp. czerepanovii* which is also dominant at the treeline. Treeline elevation in the Abisko valley range between 600-800 m above sea level (a.s.l.) (Callaghan et al., 2013). Other tree types in lower parts of the valley are *Sorbus aucuparia*, and *Populus tremula*, along with small populations of *Pinus sylvestris* which are assumed to be refugia species from warmer periods during the Holocene (Berglund et al., 1996). Soils are glaciofluvial till and sediments. A full summary of previous studies and the environment around lake Torneträsk can be found in Callaghan et al. (2013). Our study domain covers an area of approximately 85 km^2 and extends from Mount Njulla in the west to the mountain Nissoncorru in the East (See Fig. 2). In the northern part of our study domain is the lake Torneträsk. The mean annual temperature was -0.5 ± 0.9 °C for the 30-year period 1971-2000 (Fig. 1; Table 2) with January as the coldest month (-10.2 ± 3.5 °C) and July as the warmest month (11.3 ± 1.4 °C). Mean annual precipitation was 323 ± 66 mm for the same reference period. This reference period was chosen as it is the last one in the dataset by Yang et al. (2011).

2.2 Ecosystem model

We used the LPJ-GUESS DVM as the main tool for our study (Smith et al., 2001; Smith et al., 2014; Miller and Smith, 2012). LPJ-GUESS is one of the most ecologically detailed models of its class, suitable for regional and global-scale studies of climate impacts on vegetation, employing an individual- and patch-based representation of vegetation composition and structure. It simulates the dynamics of plant populations and ecosystem carbon, nitrogen, and water exchanges in response to external climate forcing. Biogeophysical processes (e.g. soil hydrology and evapotranspiration) and physiological processes (e.g. photosynthesis, respiration, carbon allocation) are both closely linked and represented mechanistically. The model~~-~~ assumes the presence of seeds in grid cells, meaning that simulated PFTs can establish once the climate is favourable, as defined by each PFT's predefined bioclimatic limits. The competition between neighbouring plant individuals for light, water and nutrients, affecting individual establishment, growth, and mortality, is modelled explicitly. Individuals of the same age co-occurring in a local neighbourhood or patch and belonging to the same plant functional type (PFT; see below) are assumed identical to each other. Decomposition of plant litter and cycling of soil nutrients are represented by a CENTURY-based soil biogeochemistry module, applied at patch scale (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).

For this study we employed LPJ-GUESS version 4.0 (Smith et al. 2014), enhanced with Arctic-specific features (Miller and Smith, 2012; Wania et al., 2009). The combined model incorporates an updated set of arctic PFTs (described below), improved soil physics and a multi-layered dynamic snow scheme, allowing for simulation of permafrost and frozen ground.

Vegetation in the model is represented by cohorts of individuals interacting in local communities or patches and belonging to a number of PFTs that are distinguished by growth form (tree, shrub, herbaceous), life history strategies (shade tolerant or intolerant), and phenology class (evergreen/summergreen). Herbaceous PFTs are represented as a dynamic, aggregate cover of ground layer vegetation in each patch. In this study 11 PFTs were implemented (See Table S2.1 in supplementary material for a description of included PFTs; see Table S2.2 in supplementary material for parameter values associated with each PFT). Out of these, three were tree PFTs, boreal needle-leaved evergreen trees (BNE), boreal shade-intolerant evergreen t~~T~~ree (BINE) and boreal shade-intolerant broad-leaved summergreen tree (IBS). Corresponding tree species present in the Torneträsk region include *Picea abies* (BNE), *Pinus sylvestris* (BINE), *Betula* *pubescens ssp. czerepanovii*, *Populus tremula* and *Sorbus aucuparia* (IBS). Following Wolf et al. (2008), shrub PFTs with different stature were implemented as follows: tall summergreen and evergreen shrubs, corresponding to *Salix spp*. (HSS) and *Juniperus communis* (HSE) and low summergreen and evergreen shrubs. The two latter corresponding to species such as *Betula nana* (LSS) and *Empetrum nigrum* (LSE). We also include two prostrate shrubs and two herbaceous PFTs.

Gridcell vegetation and biogeophysical properties are calculated by averaging over a number of replicate patches, each subject to the same climate forcing. 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. Within each patch, establishment, growth and mortality of individual tree or shrub cohorts are modelled annually (Smith et al., 2001; Smith et al., 2014). Establishment and mortality have both an abiotic (bioclimatic) and biotic (competition-mediated) component. Vegetation dynamics, i.e. changes in the distribution and abundance of different PFTs in grid cells over time, are an emergent outcome of the competition for resources between PFTs within an overall climate envelope determined by bioclimatic limits for establishment and survival. 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. Disturbance i~~wa~~s accounted for by the occasional removal of all vegetation within a patch with an annual probability of one per 300 years, representing random events such as storms, avalanches, insect outbreaks, and wind-throw. The study used three replicate patches within each 50x50m gridcell.

For summergreen PFTs we slightly modified the assumption of a fixed growing degree day (GDD) requirement for establishment, using thawing degree days (TDD; degree days with a 0 °C basis; see Table S2.2) instead.

2.3 Forcing data

2.3.1 Historic period

A highly resolved (50x50m) temperature and radiation dataset using field measurements and a digital elevation model (DEM) by Yang et al. (2011) provided climate input to the model simulations for the historic period (1913-2000). 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 wa~~i~~s 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) (see Fig. S1.1; supplementary materials). For a full description of how this dataset was constructed we refer to Yang et al. (2011) and Yang et al. (2012).

Monthly precipitation input was obtained from the Abisko Scientific Research Station weather records. Precipitation was randomly distributed over each month using probabilities from the CRUNCEP v.7 dataset (Wei et al., 2014). We assumed that local differences in precipitation can be neglected for our study domain and thus the raw station data was used as input to LPJ-GUESS for the historic period. Nitrogen deposition data for the historic and future simulations were extracted from gridcell including Abisko in the dataset produced by Lamarque et al. (2013). Nitrogen deposition was assumed to be distributed equally over the study domain.

Data of soil texture was extracted from the WISE soil dataset (Batjes, 2005) for the Abisko area and assumed to be uniform across the study domain. Callaghan et al (2013) reports that the soils around the Torneträsk areas are mainly glaciofluvial till and sediments. Clay and silt fractions vary between 20-50% in the area (Josefsson, 1990) with higher fractions of clay and silt in the birch forest and a larger sand content in the heaths. In the absence of spatial information on particle size distributions, the soil was prescribed as a sandy loam soil with approximately 43% sand and approximately equal fractions of silt and clay.

2.3.2 Future simulations

Future estimates of vegetation change were simulated for one low (RCP2.6) and one high (RCP8.5) emission scenario. For each emission scenario, climate change projections from three global climate models (GCMs) that had contributed to the CMIP5 GCM ensemble (Taylor et al., 2012) were used to investigate climate effects on vegetation dynamics. The GCMs (MIROC-ESM-CHEM, HadGEM2-AO, GFDL-ESM2M) were selected to represent the largest spread, i.e., highest, lowest and near average, in modelled mean annual temperature for the reference period 2071-2100. Only models that had contributed with simulations for both RCP2.6 and RCP8.5 were used in the selection. Monthly climate data needed as input to LPJ-GUESS (temperature, total precipitation, and shortwave radiation) was extracted for the gridcell including ANS for each GCM.

The historic climate dataset by Yang et al (2011) was extended into the projection period (2001-2100) using the delta change approach, as follows. For each gridcell monthly differences were calculated between the projection climate and the dataset by Yang et al. (2011) for the last 30-year reference period in our historic dataset (1971-2000). For temperature, the difference was derived, while for precipitation and incoming shortwave radiation relative differences between the two datasets were derived. The calculated monthly differences were then either added (temperature) to the GCM outputs, or used to multiply (precipitation, radiation) the GCM outputs from 2001-2100, for each of the climate scenarios used. Forcing data of atmospheric [CO_2] for the two scenarios were collected from the CMIP5 project.

2.4 Model experiments

To investigate the possible drivers of future vegetation change we performed three model experiments. The model was forced with changes to one category of input (driver) variables (climate, [CO_2], nitrogen deposition) at a time for a projection period between the years 2001-2100. A full list of simulations can be found in Table S3 (supplementary materials).

A control scenario with no climate trend (and with [CO_2] and nitrogen deposition held at their respective year 2000 values) was also created. We estimated the effect of the transient climate change, [CO_2] or nitrogen deposition scenarios by subtracting model results for the last decade (2090-2100) in the no-trend scenario from those for the last decade (2090-2100) of the respective transient scenario. To estimate how sensitive the model was to different factors, we performed a Spearman rank correlation for each PFT in 50 m elevational bands over the forest-tundra ecotone. We chose Spearman rank over Pearson since not all correlations were linear.

2.4.1 Climate change

To estimate the sensitivity to climate change the same scenarios as for the future simulations (section 2.3.2) were used while [CO_2] and nitrogen deposition were held constant at their year 2000 value.

Climate anomalies without any trend were created by randomly sampling full years in the last decade (1990-2000) from the climate station data. The climate dataset was then extended using this data. The resulting climate scenario had the same inter-annual variability as the historic dataset and no trend for the years 2001-2100. This scenario was used to investigate any lag-effects on vegetation change. This scenario also provided climate input for the nitrogen and [CO_2] tests described below.

2.4.2 CO_2

For our projection simulations we used five different [CO_2] scenarios from the CMIP5 project. High (RCP8.5), medium (RCP6.0; RCP4.5) and low (RCP2.6) emission scenarios were used.

2.4.3 Nitrogen deposition

Scenarios of nitrogen deposition were collected from the Lamarque et al. (2013) dataset. Since this dataset assumes a decrease of nitrogen deposition after year 2000 we also added four scenarios where nitrogen deposition increased with 2, 5, 7.5 and 10 times the nitrogen deposition relative to the year 2000. These four scenarios were created to test the isolated effect of nitrogen increase without any climate or [CO_2] change. The resulting additional loads of nitrogen in these scenarios were 0.3~~.~~8, 0.9~~.~~7~~5~~, 1.4~~.~~6~~3~~ and 1.~~8.~~9 ~~k~~gN m~~ha~~$^{-2}$~~1~~ yr^{-1} respectively.

2.5 Model evaluation

We evaluated the model against a range of available observations in the Abisko area. Measurements of ecosystem productivity from an eddy covariance (EC) tower were obtained for six non-consecutive years (Olsson et al., 2017). Biomass and biomass change estimates were used to evaluate simulated biomass in the birch forest (Hedenås et al., 2011). Surveys of historic vegetation change above the treeline were collected from Rundqvist et al. (2011). Leaf area index (LAI) and evapotranspiration estimates were obtained from Ovhed and Holmgren (1996).

The two studies by Hedenås et al. (2011) and Rundqvist et al. (2011) documented evaluation measurements within our projection period (year 2010). To compare biomass and vegetation change with these studies we extracted five year multi-model averages around the year 2010 (2008-2012) from our projection simulations (section 2.3.2). These means were used to calculate change in biomass and vegetation in our historic dataset.

To determine the local rates and heterogeneity of treeline migration several~~a number of~~ transects were selected within our study domain (Fig. S1.2; supplementary material). These transects were chosen to represent a large spread in heterogeneity with regard to slope and aspect in the landscape. A subsample of the selected transects~~these~~ were placed close to the transects used by Van Bogaert et al. (2011) and used to evaluate model performance.~~.~~ Results from the model evaluation are summarised in Table 1 and Table S1.1.~~.~~

2.6 Determination of domains in the forest-tundra ecotone

In our analysis we distinguished between forest, treeline and shrub-tundra, defined as follows. Any gridcell containing 30% fractional projective cover or more of trees was classified as forest. This limit has been used by other studies in the area (e.g., Van Bogaert et al., 2011) to determine the birch forest boundary. The treeline was then determined by first selecting gridcells classified as forest. Any gridcell with 4 or more neighbours fulfilling the 30% cover condition criteria was classified as belonging to the forest. The perimeter of the forest was then determined through sorting out gridcells with 4 or 5 neighbours classified as forest. Gridcells with fewer or more neighbors were regarded as tundra or forest, respectively. Gridcells below the treeline were classified as forest in the analysis and gridcells above the treeline were classified as tundra.

2.7 Presentation of results

We present seasonal values for soil and air temperature. These are averages of DJF, MAM, JJA, and SON, referred to as winter, spring, summer and autumn below. For the RCPs average values are presented with the ranges of the different scenarios within each RCP given in parenthesis. We report values of both gross primary production (GPP), which we benchmark the model against, and net primary productivity (NPP) as this is of relevance for the carbon limitation discussion.

3. Results

3.1 Historic vegetation shifts

The dominating PFT in the forest and at the treeline was IBS which constituted 90% of the total LAI (Fig. 2a-3a). The only other tree PFT present in the forest was BINE, which comprised a minor fraction of total LAI. However, in the lower (warmer) parts of the landscape BINE comprised up to 20% of total LAI in a few gridcells. Forest understory was mixed but consisted mostly of tall and low evergreen shrubs and grasses. Shrub tundra vegetation above the treeline was more mixed but LSE dominated with 51% of total LAI. Grasses comprised an additional 25% of total LAI and IBS was present close to the treeline where it comprised up to 5% of LAI in some gridcells. NPP for IBS in the forest increased from 96 gC m^{-2} yr^{-1} to 180 gC m^{-2} yr^{-1} over our historic period (1913-2000). Corresponding values at the treeline did not increase but were stagnant at around 60 gC m^{-2} yr^{-1}. Above the treeline, IBS showed very low NPP values (<15 gC m^{-2} yr^{-1}), while NPP for the dominant shrub (LSE) doubled from 20 gC m^{-2} yr^{-1} to 40 gC m^{-2} yr^{-1}.

Between the start and end of our historic (1913-2000) simulation the landscape scale treeline shifted upwards 67 elevational meters on average, corresponding to a rate of 0.83 m yr^{-1}. However, during the 20th century both a period (1913-

1940) with more rapid warming (0.8°C) and faster tree migration rate (1.23 m yr^{-1}) as well as a period (1940-1980) with a cooling trend (-0.3°C) and stationary treeline occurred (Fig. 5). Between 1913-2000, the lower boundary of the treeline shifted upwards 2 meters, while treeline upper boundaries shifted upwards 123 m. These shifts corresponded to rates of 0.03 and 1.54 m yr^{-1}, respectively. Similar rates were also found in the transects established to test the heterogeneity of treeline migration (Fig. S1.2; Table S1.1; supplementary materials) where the average migration rate was 0.87 (0.54 - 1.25) m yr^{-1}.

During the 1913-2000 period, annual air temperature at the simulated treeline warmed from -2.0°C to -0.8°C. Warming occurred throughout the year but was strongest in winter and spring where temperatures increased by 3.0°C and 1.4°C, respectively. In contrast, both summer and autumn temperatures warmed by only 0.6°C. The resulting winter, spring, summer, and autumn air temperatures at the treeline in 1990-2000 were -8.7°C, 3.3°C, 8.8°C, and -0.1°C, respectively. The increases in air temperatures were also reflected in soil temperature increases of a similar magnitude, by 2.1°C from -0.8°C to 1.3°C. Winter soil temperature increased with 3.7°C from -5.6°C in 1913 to -1.9°C in 2000. The warmer soil temperatures resulted in a 4.8% increase in annual net nitrogen mineralisation rate in the treeline soils over the same period. In absolute numbers, nitrogen mineralisation increased from 1.29 gN m^{-2} to 1.36 gN m^{-2}. Combined with an increased nitrogen deposition load from 0.06~~5~~ ~~k~~g~~-~~N m~~ha~~$^{-2}$~~^{1}~~ in 1913 to 0.2~~.~~0 ~~k~~g~~-~~N m~~ha~~$^{-2}$~~^{1}~~ in 2000 and an increased nitrogen fixation from 0.1~~.~~3~~5~~ ~~k~~g~~-~~N m~~ha~~$^{-2}$~~^{1}~~ to 0.1~~.~~8~~76~~ ~~k~~g~~-~~N m~~ha~~$^{-2}$~~^{1}~~, plant available nitrogen increased by 15.9%. 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 (active layer thickness <1 m) was only present in gridcells at elevations of 940 m a.s.l. and above.

3.2 Projected vegetation shifts

During the 100 year projection period (2001-2100) treelines advanced between 45 (HadGEM2-AO-RCP2.6) and 195 (GFDL-ESM2M-RCP8.5) elevational meters in the different scenarios, corresponding to rates of 0.45 and 1.95 elevational meters yr^{-1}. Total LAI increased in the entire ecotone in both RCP2.6 and RCP8.5 compared to the historic (1990-2000) values (Fig. 3b-c). The increase was more pronounced in RCP8.5, which also saw a large increase in low evergreen shrubs (LSE) at the end of the century (2090-2100). While the forest was still dominated by IBS, evergreen trees (BNE and BINE) increased and together comprised approximately 15% of total LAI. The fraction of evergreen trees in the forest correlated well with the degree of warming in each scenario. Forest ~~productivity (~~GPP~~)~~ was mainly driven by tree PFTs and increased by 50% (12% - 99%) for RCP2.6 and 177% (98% - 270%) for RCP8.5. Above the treeline, low shrubs (LSS and LSE) contributed most to annual GPP increases, which increased by 33% (-12% - 67%) and 239% (105% - 370%) in RCP2.6 and RCP8.5, respectively. Forest NPP, wherein IBS was always dominant, increased from 200 gC m^{-2} y^{-1} in year 2000 to 300 (220 – 375) gC m^{-2} yr^{-1} and 490 (380 - 610) gC m^{-2} yr^{-1} 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^{-2} yr^{-1} to 80 (74 - 90) gC m^{-2} yr^{-1} and 104 (80 - 116) gC m^{-2} yr^{-1} for RCP2.6 and RCP8.5. Above the treeline NPP remained low (<25 gC m^{-2} yr^{-1}) 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^{-2} yr^{-1} and 130 (81 – 180) gC m^{-2} yr^{-1}. ~~-~~The productivity increase translated into a biomass C increase of the same magnitude in both the forest and above the treeline.

The average summer air temperature at the treeline between the last decade in the historic and projection periods increased by 0.3°C and 6.7°C for the coldest (GFDL-ESM2M-RCP2.6) and warmest (MIROC-ESM2M-RCP8.5) GCM scenario, respectively. The advance of the 6°C JJA soil temperature isoline was more rapid than the treeline advance (Fig. 4). In the two warmest scenarios (MIROC-ESM2M-RCP8.5 and HadGEM2-AO-RCP8.5) summer soil temperatures exceeded 6°C in the whole study domain. Treeline elevations in these scenarios only reached 745 and 660 m a.s.l., respectively. Treelines advanced almost twice as fast in RCP8.5 compared to RCP2.6, 1.55 (1.10 - 1.96) m yr^{-1} and 0.84 (0.44 - 1.16) m yr^{-1}, respectively.

3.3 Model experiments

A slight treeline advance at the end of the projection period (2090-2100) of approximately 11 elevational meters was seen in the control simulation where all drivers were held constant. This revealed a lag from the historical period, likely resulting from smaller trees that had established in the historic period that matured during the projection period.

3.3.1 Climate change

Treeline advance occurred in all climate change scenarios although the rate was not uniform throughout the projection period (Fig. 5). When driven by climate change alone, migration rates were faster than the projection simulations where nitrogen deposition and CO_2 were also changed (section 3.2). Treeline advance in climate change only scenarios ranged between 60 elevational meters (HadGEM2-AO-RCP2.6) to 245 elevational meters (MIROC-ESM-CHEM-RCP8.5) over the 100 year projection period.

Tree productivity was strongly enhanced by air temperature over the whole study domain (Fig. 6a). Other climate factors such as precipitation and net shortwave radiation also correlated with productivity, however, these correlations were weaker (Fig. S1.5; S1.6; supplementary materials). Annual precipitation increased in all climate change scenarios (Table 2). In the lower parts of the valley, the increased precipitation did not result in any increased soil moisture during summer as losses through evapotranspiration driven by temperature exceeded the additional input. Spring and autumn soil moisture increased in the forest, mainly because of earlier snowmelt and thawing ground in spring and a relatively weaker evapotranspiration in autumn. Above the treeline, soil moisture increased as the lower temperatures and LAI did not drive evapotranspiration as strongly as in the lower parts of the valley and the increased rain thus outweighed the slightly increased evapotranspiration.

Increased tree productivity in the forest resulted in an increased LAI of 18-90%, which in absolute terms was equivalent to an increased LAI of 0.3-1.5 m^2 m^{-2}. BNE appeared in the forest and dominated in a few gridcells. In most places BNE constituted approximately 5% of total LAI. Tall shrub (HSE and HSS) productivity and LAI increased in the forest, however, the increase was negatively correlated with temperature, i.e., increase was highest in the coldest climate change scenarios. Above the treeline, tall shrubs showed the opposite pattern, increasing by 8-50% to finally constitute 10-36% of total LAI.

Higher soil moisture content in spring and autumn favoured trees in the whole ecotone, while forest understory suffered from earlier onset of the growing season with subsequent flushing of the leaf and light shading from taller competitors.

Although soil moisture in summers decreased in the forest, LAI and biomass carbon of summergreen shrubs were positively correlated with soil moisture. A higher soil moisture during summers in the wetter GCM scenarios~~GCMs~~ promoted summergreen shrubs over evergreen shrubs in the whole ecotone. As an example, vegetation composition on the tundra above the treeline differed between the two GCMs GFDL-ESM2M and MIROC-ESM-CHEM under RCP8.5, where the warmer GCM showed a 52% biomass C increase in the tall evergreen shrub, HSE. The intermediately warmed scenario (GFDL-ESM2M-RCP8.5) showed a more mixed increase of biomass carbon in HSE (20%) and HSS (24%). While annual temperature differed with 3.9°C between the two scenarios, average annual precipitation only differed by 6.2 mm, yielding a much (26%) lower JJA soil moisture in the warmest scenario (MIROC-ESM-CHEM-RCP8.5) compared to the colder (GFDL-ESM2M-RCP8.5). A relatively higher soil moisture and subsequently lower water stress allow for taller plants to establish.

Radiation correlated positively with the growth of tree PFTs, with spring and autumn radiation found to be especially important for height and biomass increase (Fig. S1.7; supplementary materials). Increased radiation provided a competitive advantage for taller trees and shrubs to shade out lower shrubs and grasses in the forest. Shrubs above the treeline were also favoured by increased light.

Net nitrogen mineralisation, i.e., the difference between microbial nitrogen mineralisation and immobilisation, at the treeline showed great variation between different climate change scenarios, ranging from a 4% decrease in one scenario (GFDL-ESM2M-RCP8.5) to a 79% increase in the strongest warming scenario (MIROC-ESM-CHEM- RCP8.5). In absolute terms, the latter increase corresponds to an increase from 1.35 gN m^{-2} yr^{-1} at the end of our historic period (1990-2000) to 2,43 g N m^{-2} yr^{-1} at the end of the century (2090-2100). This is comparable to the nitrogen load in the 7.5x increased nitrogen deposition scenario. Interestingly, despite very different plant available nitrogen and warming, the two scenarios displayed a similar resulting (2090-2100) treeline elevation (Fig. 5a).

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.

3.3.2 CO_2

Productivity increase in most PFTs correlated well with a [CO_2] increase (Fig. 6b). Total GPP averaged over the forest increased between 2-10% depending on the [CO_2] scenario, with the largest increase in RCP8.5 and smallest in RCP2.6. The CO_2 fertilisation effect was not uniform within the landscape, but stronger towards the forest edge with increases from 2% to 18% from the weakest to the strongest [CO_2] scenario. IBS NPP increased uniformly over the forest with 2.5-8.4% but decreased above the treeline. Thus, the productivity of the two dominant PFTs (IBS in the forest and LSE above the treeline) was reinforced in their respective domains. The increased productivity translated into a 1-5% increase in tree LAI in the forest while low shrub LAI increased with 24-77%. Likewise, increase in leaf area of low shrubs was largest on the tundra under elevated [CO_2], which saw a 15-40% LAI increase in the low and high [CO_2] scenario respectively. Above the treeline, the productivity of grasses and low shrubs responded strongly to the CO_2 fertilisation with a 350% increase in GPP for grasses and 150% increase for low shrubs. The additional litter fall produced by the increased leaf mass did not lead to any increase in N mineralisation. However, immobilisation of nitrogen through increased uptake by microbes increased with 2-6% between the lowest and highest [CO_2] scenarios, yielding a net reduction of plant available nitrogen. Furthermore, the productivity increase did not drive any range shift of the forest, i.e., the treeline remained stationary in all [CO_2] scenarios (Fig. 5b).

3.3.3 Nitrogen deposition

Productivity of woody PFTs was in general positively correlated with nitrogen concentration in the different nitrogen deposition scenarios. In contrast, productivity of grasses was negatively correlated (Fig. 6c) as they suffered in the light competition with the trees. Annual GPP of trees (especially IBS) was positively correlated throughout the whole ecotone, however, the increase in GPP was larger towards the forest boundaries than in the lower parts the forest when nitrogen was added. Nitrogen stressed plants in the model allocate more carbon to their roots at the expense of foliar cover when they suffer a productivity reduction. In the two scenarios with decreasing nitrogen deposition (RCP2.6; RCP8.5) there was an overall reduction in LAI in both the tundra and the forest of a magnitude 6-10%. The largest reduction was seen in tree PFTs, which have the largest biomass and consequently could be assumed to have the highest nitrogen demand, followed by tall shrubs. Low shrubs and grasses did however increase their LAI in the forest when nitrogen input decreased resulting from a decreased light competition from trees. Above the treeline, LAI of low shrubs and grasses PFTs also decreased with less nitrogen input.

In all scenarios with increasing nitrogen deposition there was an advancement of the treeline in the order of 10-85 elevational meters with smallest (2x nitrogen deposition) having the smallest change in treeline elevation and vice versa for largest input (10x nitrogen deposition) scenario (Fig. 5c). In the scenarios where nitrogen input was constant or decreasing, the treeline remained stationary.

4. Discussion

In our simulations, rates of treeline advance were faster under climate change-only scenarios than when all drivers were changing. This revealed nitrogen as a modulating environmental variable, as nitrogen deposition was prescribed to decrease in both the RCP2.6 and RCP8.5 scenarios. In contrast to previous modelling studies of treeline advance (e.g., Paulsen and Körner, 2014), we include not only temperature dependence on vegetation change, but also the full nitrogen cycle and CO_2 fertilisation effects (Smith et al., 2014). Increased nitrogen deposition induced treeline advance, further illustrating the importance of nitrogen dynamics in our results. In the elevated [CO_2] scenarios, higher productivity in all plants was induced, but productivity enhancements alone did not lead to significant treeline advance. 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. However, enhancement of productivity in combination with an allocation shift to the plant canopies, enabled by a greater nitrogen uptake, favoured taller plants over their shorter neighbours in the competition for light within the model. Field experiments with nitrogen fertilisation have shown that mountain birch at the treeline displays additional growth after nitrogen additions (Sveinbjörnsson et al., 1992). Furthermore, fertilisation with nitrogen improved birch seedling survival above the treeline (Grau et al., 2012), and is thus likely important for establishment and growth of new individuals to form a new treeline. ~~This pattern is in line with the hypothesis that productivity increase alone does not drive range shifts of trees (Körner, 2015).~~ As has also been pointed out by others (Hofgaard et al., 2019; Van Bogaert et al., 2011), considering climate change or temperature alone in projections of treeline advance could potentially result in overestimations of vegetation change. Our results clearly indicate the importance of nitrogen cycling when predicting future Arctic vegetation shifts.

The treelines in our projection simulations advanced at similar rates to those experienced during the historic period, resulting in a displacement of 45-195 elevational meters over the 100 year projection period. Some estimates based on lake sediments in the Torneträsk region from the Holocene thermal maximum, when summer temperatures could have been about 2.5°C warmer than present (Kullman and Kjällgren, 2006), indicate potential treeline elevations approximately 500m above present in the area in a warmer climate, although these elevations are likely overestimated (Kullman, 2010). Macrofossil records from lakes in the area indicate that birch was present 300-400 meters above the current treeline (Barnekow, 1999). Furthermore, pine might have occurred approximately 100-150 meters above its present distribution (Berglund et al., 1996). IBS emerged as the dominant forest and treeline PFT in both our historic and projection simulations, but with larger fractions of evergreen trees (BNE and BINE) at the end of the century (2090-2100). Mountain birch, represented by IBS in our model, has historically dominated this area, even during warmer periods of the Holocene (Berglund et al., 1996), but with larger populations of pine (BINE) and spruce (BNE) than present. Both pine and spruce have been found in high elevation lake pollen sediments, and can thus be assumed to have grown in higher parts of the ecotone during warmer periods (Kullman, 2010). Treeline advance for the historic period in our simulations is broadly consistent with observational studies from the Abisko region (Van Bogaert et al., 2011). Temperature was a strong driver of tree productivity and growth in the whole ecotone. During our historic period rates of treeline advance followed periods of stronger warming. However, other factors such as precipitation indirectly influenced treeline advance through changes in vegetation composition and nitrogen mineralisation. This was illustrated by the comparison of the GCMs GFDL-ESM2M and MIROC-ESM-CHEM under RCP8.5, where the more intermediately warmed but wetter scenario had very similar resulting treeline elevation as the warmer scenario. While simulated treeline position was too low compared to the treeline elevation reported by Callaghan et al. (2013), the correlation with the globally observed 6-7°C ground temperature isoline (Körner and Paulsen, 2004) throughout the historic period gives confidence in the model results. However, during our projection period the correlation between the treeline position and the 6-7°C isoline weakened, revealing a fading or potential lag of the treeline-climate equilibrium that became stronger with increased warming.

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_2 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.

The model overestimated biomass carbon densities in the forest but captured historic rates of biomass carbon increase. The overestimation was more severe closer to the forest boundaries as the model showed a weaker negative correlation between biomass carbon and 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 gC m^{-2} 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). Additionally, the overestimation in our study can be partly attributed to lack of herbivory in the model. Outbreaks of the moth *Epirrita autumnata* are known to limit productivity and reduce biomass of mountain birch in the area in certain years (Olsson et al., 2017), however, this is likely not enough to explain our biomass carbon overestimation. ~~Simulated productivity and LAI were within the range of observations in the area (Rundqvist et al., 2011; Ovhed and Holmgren, 1996; Olsson et al., 2017).~~ Since growth and biomass increment in the model do not include a direct temperature dependence, nor any decoupling of growth and productivity, we do not regard these mechanisms as necessary to accurately predict treeline dynamics. However, they might be important to accurately predict forest biomass towards their low temperature boundaries.

To assess the modelled heterogeneity of treeline advance, we established a number of transects close to observation points in the landscape. Average treeline advance in the transects showed a somewhat faster and more homogenous migration than reported (Van Bogaert et al., 2011). The model does not include historic anthropogenic disturbances, topographic barriers, or insect herbivory, all of which have been documented as important for the heterogeneity of the treeline advance rates and placement in the landscape (Van Bogaert et al., 2011; Emanuelsson, 1987). 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. 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

A longer growing season favoured tree PFTs in the whole ecotone, which escaped early-season desiccation due to milder winters and earlier spring thaw. 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 (Holtmeier and Broll, 2007). These effects could be relevant to treeline dynamics at the high grid resolution of our study but are not accounted for by our model.

Higher summer soil moisture in the more precipitation rich climate scenarios shifted the ratio of summergreen to evergreen shrubs in favour of the summergreen shrubs, in line with observations (Elmendorf et al., 2012). Conversely, drier scenarios yielded an increased abundance of evergreen shrubs, similar to what has been observed in drier parts of the tundra heath in the Abisko region (Scharn et al., 2021). Within RCP8.5, the warmest (MIROC-ESM-CHEM-RCP8.5) and coldest (GFDL-ESM2M-RCP8.5) scenario gave rise to very similar treeline positions at the end of the projection period (2090-2100). The colder scenario had both higher soil moisture and a greater abundance of summergreen shrubs. Higher soil moisture promoted a larger carbon allocation to the canopy, and thus favoured the taller IBS tree PFT over tall shrubs (HSS). Increased shrub abundance and nutrient cycling have been shown to have potentially non-linear effects on shrub growth and ecosystem carbon cycling (Buckeridge et al., 2009; Hicks et al., 2019), and some observations indicate that changes in the ratio of summergreen to evergreen shrubs, or an increased abundance of trees, might have far-reaching consequences for soil carbon loss (Parker et al., 2018; Clemmensen et al., 2021). Thus, our results indicate that any future change in soil moisture conditions could play an important role in the competitive outcome of shrubs in the forest-tundra ecotone and for its carbon balance.

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 be shown to decline towards the range limits of eight European broadleaved tree species~~s~~ (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.

Above the treeline low evergreen shrubs (LSE) dominated the vegetation in both our historic and projection simulations. The productivity of shrubs and grasses was greatly enhanced by CO_2 fertilisation in our [CO_2] model experiment, and a large proportion of tundra productivity increases in our projection simulations could be attributed to rising [CO_2]. Physiological effects of elevated CO_2 on Arctic and alpine tundra productivity and growth are understudied. Free Air CO_2 Enrichment (FACE) experiments are generally considered the best method for quantifying long-term ecosystem effects of elevated CO_2 but are extremely costly and therefore limited in number and distribution. A majority of FACE experiments have been implemented in temperate forests and grasslands, yielding limited evidence of relevance to boreal and tundra ecosystems (Hickler et al., 2008). One FACE experiment situated in a forest-tundra ecotone in the Swiss Alps showed differing responses to elevated CO_2 among shrub species where *Vaccinium myrtillys* showed 11% increased shoot growth while *Empetrum nigrum* was unresponsive and the response of *V. gaultherioides* depended on the forest type in which it was growing (Dawes et al., 2013). Our model results indicated that shrubs are carbon limited and shrub productivity and growth consequently are responsive to CO_2 fertilisation.

5. Conclusions

In this study we identified nitrogen cycling and availability as an important modulator of treeline advance. Internal cycling of nutrients in soils is the main source of nutrients for Arctic plants (Chapin, 1983). The model performed well regarding rates of shrub increase and treeline advance but overestimated biomass carbon in the forest. Treeline migration rates were realistically simulated although the model did not represent temperature limitations on tree growth. While a decoupling between productivity and growth in the model could potentially have improved estimates of biomass carbon, it was not needed to correctly predict treeline elevation. Instead, our results point to the importance of indirect effects of rising temperatures on tree range shifts, especially with regards to nutrient cycling. Furthermore, soil moisture strongly influenced vegetation composition within the model with implications for treeline advance. How models represent nutrient uptake and cycling, as well as a better empirical understanding of processes that determine tree and shrub growth will be key to better predictions of Arctic vegetation change and carbon and nitrogen cycling. Models are a valuable aid in judging the relevance of these processes on the pan-Arctic scale.

6. Author contributions

AG designed the experiments with contributions from PM and SO. AG also performed necessary model code developments and carried out model simulations and data analysis. RGB and BS contributed greatly with comments on the manuscript, scientific advice, and input throughout the study. AG prepared the manuscript with contributions from all co-authors.

7. Competing interests

The authors declare that they have no conflict of interest.

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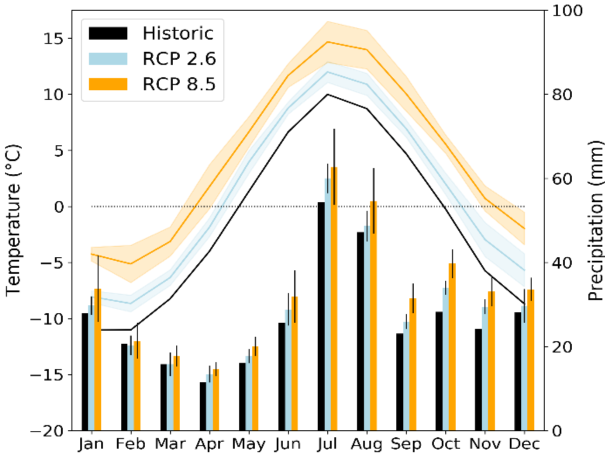

Figure 1. Historic (1971-2000) and projected (2071-2100) temperature (left) and precipitation (right) variability in Abisko. The shaded areas (temperature) and black bars (precipitation) mark ±1 standard deviation uncertainty in the three CMIP5 multi-model mean for RCP2.6 and RCP8.5 respectively.

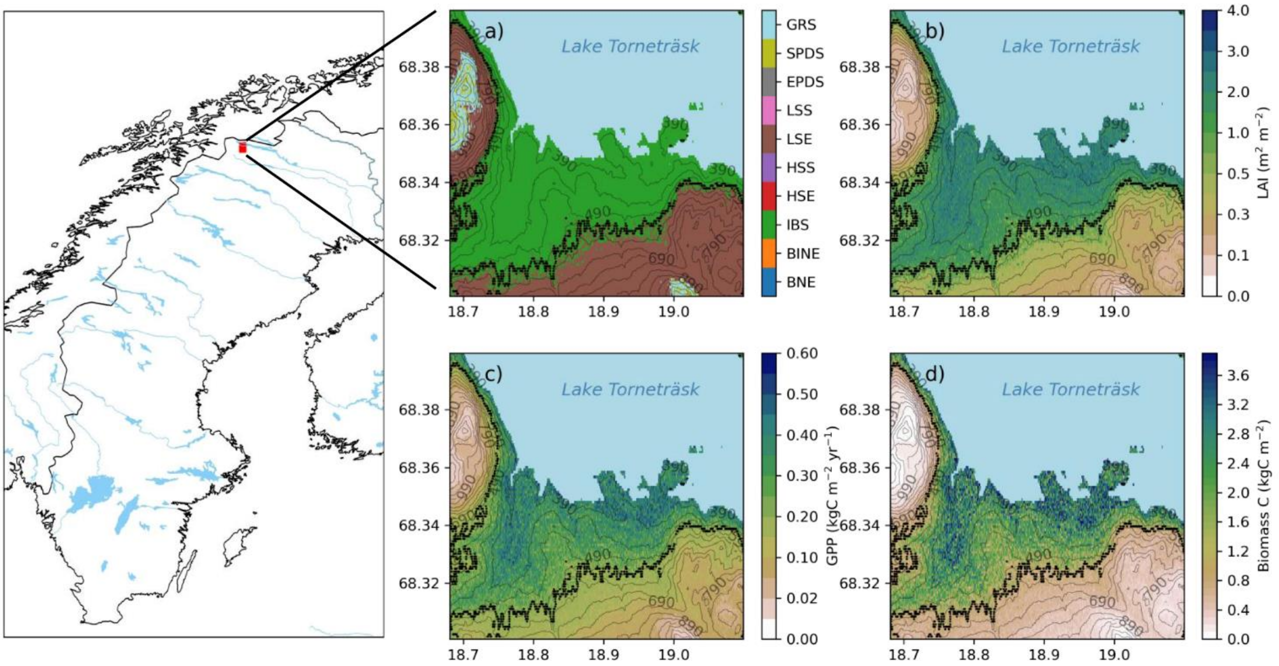

Figure 2. Map of Sweden and Scandinavia with a red square marking the study area. Panels on the right show the study area in more detail and the modelled forest-tundra ecotone for the historic period (1990-2000). a) Dominant PFT (BNE – Boreal needle leaved evergreen tree; BINE – Boreal shade-intolerant needle leaved tree; IBS – Boreal shade-intolerant broadleaved tree; HSE – Tall evergreen shrub; HSS – Tall summergreen shrub; LSE – Low evergreen shrub; LSS – Low summergreen shrub; EPDS – Evergreen prostrate dwarf shrub; SPDS – Summergreen prostrate dwarf shrub; GRS - grasses) in the ecotone and total ecosystem b) LAI (m^{2} m^{-2}) c) productivity (GPP; kgC m^{-2} yr^{-1}) and d) plant biomass carbon density (kgC m^{-2}). The black line in panels a-d shows the modelled treeline position. Numbers on the contour lines mark elevation in meters above sea level. Data source for map: Natural Earth

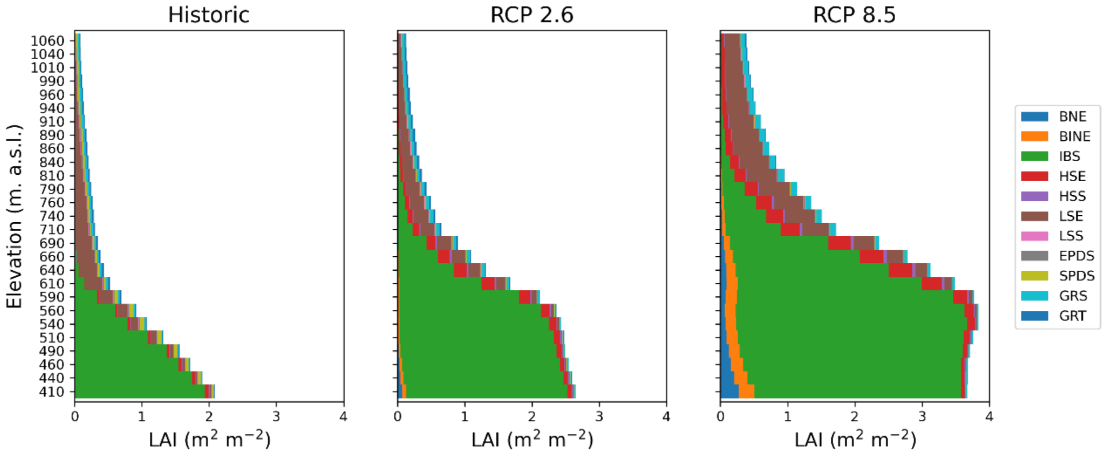

Figure 3. Leaf area index (LAI) in the forest-tundra ecotone for a) historic (1990-2000) and at the end of the century (2090-2100) for b) RCP2.6 and c) RCP8.5 respectively. Each bar represents an approximate 50 elevational meter band in the ecotone.

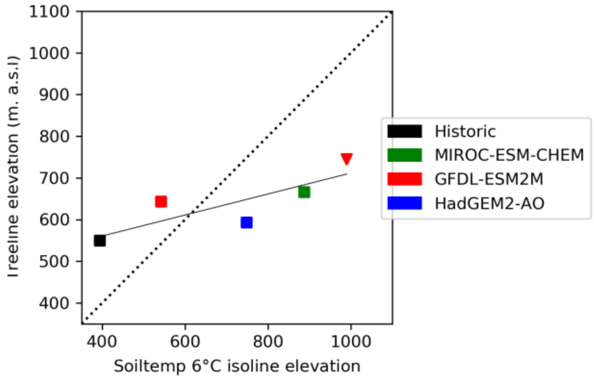

Figure 4. JJA 6°C soil temperature isoline correlation with average treeline elevation. Square markers represent RCP2.6 while triangles represent RCP8.5. In the two warmest scenarios (HadGEM2-AO-RCP8.5 and MIROC-ESM-CHEM-RCP8.5), the 6°C soil temperatures exceed 6°C in the whole landscape. The dotted line represents the 1:1 relationship between treeline and isoline placement while the full line displays the treeline-soil temperature regression.

Table 1. Model evaluation and benchmarking results.

Parameter	Unit	Domain	Time Interval	Model value	Estimated value	Reference
GPP (Average)	gC m^{-2} yr^{-1}	Birch forest	2007-2014	410 ± 64	440 ± 54	Olsson et al., 2017
Carbon density	tC ha-1	Birch forest	2010	21.8 ± 10	4.39 ± 3.46	Hedenås et al., 2011
Carbon density change	%	Birch forest	1997-2010	25	19	
LAI	m^2 m^{-2}	Forest canopy	1988-1989	1.65 ± 0.66	~2.0	Ovhed & Holmgren, 1996
		Understory		0.17 ± 0.12	~0.5	
Densification	%	Shrub tundra	1976-2010	+87 ± 15	+50-80	Rundqvist et al., 2011
Treeline elevation (min)	m. a.s.l.	Treeline	2010	444	~600	Callaghan et al., 2013
Treeline elevation (mean)				564	-	
Treeline elevation (max)				723	~800	
Treeline elevation change (mean)	Elevational meters	Treeline	1912-2009	80	24	van Boogart et al., 2011
Treeline elevation change (max)				123	145	
Treeline migration rate (mean)	m yr-1	Treeline	1912-2009	+0.85	+0.6	van Boogart et al., 2011
Treeline migration rate (max)				+1.18	+1.1	

Table 2. Seasonal temperature and precipitation for historic and scenario simulations.

		1971-2000	2071-2100					
		Yang et al., 2011	GFDL-ESM2M		HadGEM2-AO		MIROC-ESM-CHEM	
	Season	Historic	RCP2.6	RCP8.5	RCP2.6	RCP8.5	RCP2.6	RCP8.5
Temperature (°C)	Winter (DJF)	-9.8	-8.2	-5.4	-8.1	-4.4	-7.4	-3.1
	Spring (MAM	-2.1	-1.3	1.0	0.4	4.11	0.7	4.8
	Summer (JJA)	9.9	10.9	13.2	11.9	14.4	13.1	13.4
	Autumn (SON)	0.1	1.1	4.2	2.3	9.1	3.2	7.2
	Annual (mean)	-0.5	0.6	3.3	1.6	5.0	2.4	6.6
Precipitation (MM)	Winter (DJF)	75	80	85	75	80	70	95
	Spring (MAM	45	40	45	40	45	50	55
	Summer (JJA)	125	130	130	130	150	135	145
	Autumn (SON)	75	90	95	85	95	95	110
	Annual (sum)	325	340	355	335	370	350	405

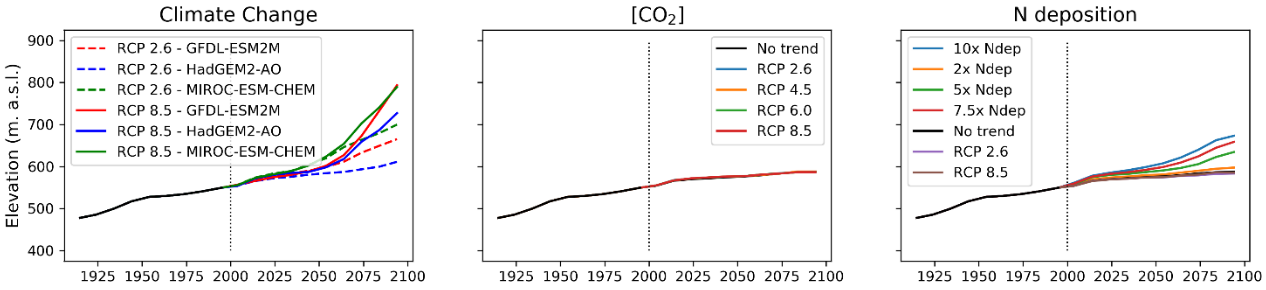

Figure 5. Shifts in average treeline elevation over the simulation period for the three experiments a) climate change b) CO_2 fertilisation and c) nitrogen deposition. Start of projection simulations are marked with a vertical dotted line in all panels. No-trend scenario in panel b-c represent a scenario where climate, CO_2 and nitrogen deposition are kept constant (without trend) relative to year 2000. Black line before year 2000 represents our historic simulation.

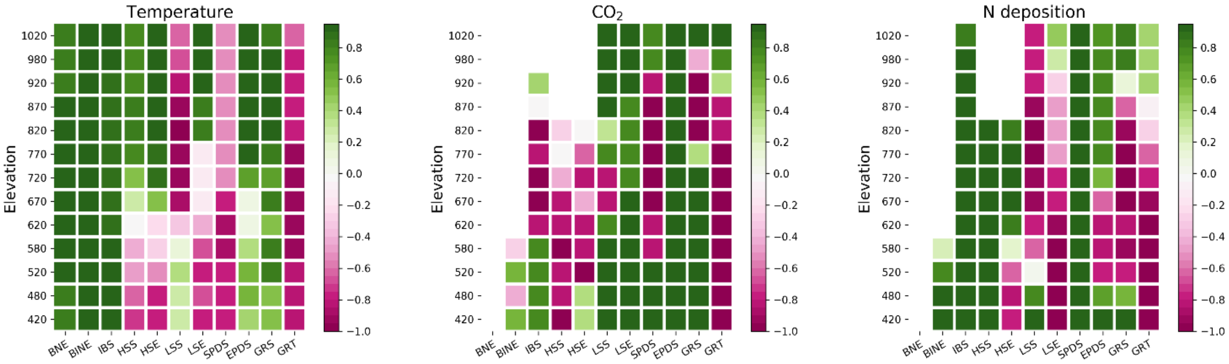

Figure 6. Correlation (Spearman rank) between annual GPP for each PFT and a) average end of century (2090-2100) temperature anomalies in the climate change experiment, b) CO_2 scenario and c) nitrogen deposition scenario. Each box represent a 50 elevational meter band in the ecotone for a given PFT.