

Decoupling of permafrost thaw and vegetation growth could mean both ongoing nutrient limitation and an emergent source of N₂O in high latitudes

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Abstract

Biogeochemical cycling in permafrost-affected ecosystems remains associated with large uncertainties, which could impact the Earth's greenhouse gas budget and future climate mitigation policies. In particular, increased nutrient availability following permafrost thaw could perturb biogeochemical cycling in permafrost systems, an effect largely unexplored in global assessments. In this study, we enhance the terrestrial ecosystem model QUINCY, which fully couples carbon (C), nitrogen (N) and phosphorus (P) cycles in vegetation and soil, with processes relevant in high latitudes (e.g., soil freezing and snow dynamics). We use this enhanced model to investigate impacts of increased carbon and nutrient availability from permafrost thawing in comparison to other climate-induced effects and CO₂ fertilization over 1960 to 2019 over a multitude of tundra sites. Our simulation results suggest that vegetation growth in high latitudes is acutely N-limited at our case study sites. Despite this, enhanced availability of nutrients in the deep active layer following permafrost thaw, simulated to be around 0.1 m on average since the 1960s, accounts for only 11 % of the total GPP increase averaged over all sites. Our analysis suggests that the decoupling of the timing of peak vegetative growth (week 27-29 of the year, corresponding to mid-to-late July) and maximum thaw depth (week 34-37, corresponding to mid-to-late August), lead to an incomplete plant use of newly available nutrients at the permafrost front. Due to resulting increased availability of N at the permafrost table, as well as alternating water saturation levels, increases in both nitrification and denitrification enhance N₂O emissions in the simulations. Our model thus suggests a weak (5 mg N m⁻² yr⁻¹) but increasing source of N₂O, which reaches trends of up to +1 mg N m⁻² yr⁻¹ per decade, locally, which is potentially of large importance for the global N₂O budget.

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1. Introduction

Although high-latitude permafrost-affected soils cover over one sixth of the exposed northern hemisphere land surface, large uncertainties remain associated to the past and future perturbation of greenhouse gas fluxes in these regions, which could impact global climate targets (Biskaborn et al., 2019; Bruhwiler et al., 2021; Canadell et al., 2021; Natali et al., 2021; Obu 2021; Schädel et al., 2018; Schuur et al., 2015). On the one hand, increased carbon fixation linked to enhanced vegetation growth in these regions has already been reported over the past few decades, with further drastic changes expected in the future (Canadell et al., 2021; Winkler et al., 2019; Pearson et al., 2013). On the other hand, the warming and thawing of frozen soils expose large organic carbon pools that were stored for thousands of years to aerobic or anaerobic degradation, which in turn potentially increases CO₂ and CH₄ emissions to the atmosphere (Burke et al., 2017; De Vrese and Brovkin, 2021; McGuire et al., 2018; Schädel et al., 2016; Schuur et al., 2015). Additionally, it has been recently suggested that perturbation in permafrost-affected soils could cause a significant source of N₂O to the atmosphere (Voigt et al., 2017; Marushchak et al., 2021), although the spatial and temporal coverage of these measurements remains sparse at the pan-Arctic scale (Voigt et al., 2020).

Since temperatures in Arctic regions have already increased substantially over the historical time period (Ballinger et al., 2020; Screen and Simmonds, 2010), and are projected to further increase in the future (Cai et al., 2021; Previdi et al., 2021), estimating the degree of permafrost thawing and its feedbacks on vegetation and soil carbon stocks is of high importance in the context of quantifying greenhouse gas budgets of high latitudes (Schuur et al., 2015). Potential changes in soil organic matter stocks and its degradation due to temperature changes in the soil have been assessed in the past using Earth System Models (ESMs, e.g., de Vrese et al., 2021; de Vrese and Brovkin, 2021; Koven et al., 2015), although important uncertainties in representing biophysical processes in these regions certainly still exist (Chadburn et al., 2017; Schädel et al., 2018; Yokohata et al., 2020).

The implications that changing climatic conditions and permafrost thaw have for vegetation and microbial dynamics in the high latitudes are still largely enigmatic. In particular, the perturbations that permafrost thaw may impose on nutrient cycles, which in turn affect vegetation growth and soil bacterial activity, are largely unexplored (Beermann et al., 2017; Chadburn et al., 2017). Since Arctic tundra ecosystems with shallow permafrost depths are usually strongly nutrient-limited (Finger et al., 2015; Haag et al., 1974; Natali et al., 2011; Pedersen et al., 2020; Street and Caldararu, 2021), increased nutrient mobilization from permafrost layers could potentially enhance vegetation growth through plant uptake and/or microbial activity. For instance, highly-labile dissolved organic nitrogen (DON) concentrations are reported in permafrost soils (Fouché et al., 2020; Salmon et al., 2016), which could rapidly be degraded to bio-available compounds upon soil thaw. Increased N and P availability have

been demonstrated to impact both plant growth and community composition in a variety of Arctic site-level experiments (Blume-Werry et al., 2019; Natali et al., 2011; Pedersen et al., 2020; Street et al., 2018), as well as in an already collapsed permafrost landscape (Yang et al., 2021). Since plants and microbes compete for sparse nutrients in the shallow active layer of these soils, the fate of nutrients available upon permafrost thaw is dependent on the efficacy of plants to take up nutrients in these newly thawed depths (Voigt et al., 2020), a topic that remains heavily debated in literature (Beermann et al., 2017; Blume-Werry et al., 2019; Finger et al., 2016; Koven et al., 2015; Norby et al., 2019; Pederson et al., 2020; Treat et al., 2016). Both N and P are important constraints for microbial activity in such systems (Salmon et al., 2018; Schaller et al., 2019; Zhang et al., 2014), thus their increasing availability could impact the degradation of organic matter in the deep soil, imposing a potentially important constraint on CO₂ and CH₄ production. Recent measurements have reported evident sources of N₂O to the atmosphere from individual permafrost ecosystems, which could be especially strong when linked with ecosystem disturbances that open nitrogen loss pathways (Voigt et al., 2017; Marushchak et al., 2021; Treat et al., 2016). However, the spatial and temporal coverage of this uncertain source remains sparse (Voigt et al., 2020).

To assess the fate of nutrients originating from permafrost thaw and their impacts on biological productivity and microbial degradation, we enhanced the terrestrial biosphere model QUINCY with additional modules addressing specific bio-physical features important in high latitudes. With these model extensions, we analysed transient simulations over 1960 to 2019 to quantify the impacts that deepening of the active layer depth and increased nutrient availability have on vegetation dynamics and greenhouse gas budgets, with a particular focus on N₂O emissions.

2. Methods

We performed site-level simulations at the pan-Arctic scale over 1901-2019 with the global terrestrial model QUINCY, with the aim of better representing carbon and nutrient (P and N) cycles in high latitude regions. We implemented additional features in both plant and soil modules in QUINCY aiming at a better representation of soil physical processes taking place in cold regions (i.e., soil freezing, snow and inundation), but also including specific conditions for permafrost soils, as well as alterations to vegetation processes as a response to changes in the soil state (i.e., dynamic root depths). Using this extended model version, we performed simulations in order to isolate effects arising from increased nutrient availability following permafrost thaw, other changes in climate and CO₂ fertilization.

2.1 The QUINCY Model

The QUINCY terrestrial biosphere model simulates water and energy exchanges, as well as coupled carbon, nitrogen, and phosphorus cycles in soil and vegetation (Thum et al., 2019). The model has already been applied and validated within a number of studies investigating nutrient cycles in vegetation and soils (Yu et al., 2020; Caldararu et al., 2020; 2021). The model provides improvements compared to other models used in global assessments of the terrestrial biosphere (Canadell et al., 2021) through its state-of-the-art representation of vegetation dynamics (Supplement Text S1) and explicit representation of N and P cycling (Supplement Text S2), which has been identified as one of the major reasons for

disagreements of global terrestrial models with observations in high latitudes (Chadburn et al., 2017). Of particular importance to our study, QUINCY represents production of the nitrogen-containing gases N_2O and N_2 through nitrification and denitrification (Supplement Text S2).

QUINCY discretises both soil physical parameters and biogeochemical pools in the vertical plane, which is highly relevant for permafrost-affected soils, where features and dynamics of the active and permafrost layer strongly differ. The model accounts for 5 pools of soil carbon, i.e., structural, polymeric and woody litter, fast and slow degrading soil organic carbon (SOC), as well as vertically-resolved fine and coarse root biomass.

2.2. Upgraded physical processes for high latitudes: soil freezing, snow dynamics, organic matter effects and inundation

In order to provide a better representation for high-latitude ecosystems, the physical modules in QUINCY were extended to take into account effects of soil freezing and thawing, as well as of snow, on soil layer heat and water exchanges.

We extended the heat budget calculation for every soil layer with latent heat fluxes induced by soil freezing and thawing (Supplement Text S3). Similarly to other studies (Chadburn et al., 2015; Ekici et al., 2014), we assumed that a supercooled liquid water fraction remained present in the soil at freezing temperatures. The implementation of a multi-layer snow module (Supplement Text S4) served to represent the insulating effects of snow coverage, preventing extreme cooling of the soil in the winter, while also delaying liquid water inputs to the soil until the melting season. Here, we used the same 5-layer model structure as described in Ekici et al. (2014), with differences explained in Supplement Text S4.

We also accounted for the lower heat conductivity and higher specific heat capacity observed in soils with high organic contents. Similarly to Burke et al. (2017), we used lower heat conductivity constants for the upper 30 cm of unfrozen soil (Table 1), which is also where the highest soil organic carbon contents are simulated in the model.

We implemented an inundation scheme to reproduce the retention of water over permanently frozen layers, which leads to observed saturated conditions in the Spring/early Summer (Supplement Text S5, Supplement Figure S1, Göckede et al., 2019).

155 Table 1. QUINCY parameters that were changed or introduced for a better representation of high
156 latitude processes.

Soil physics parameters	Original setting	Updated setting
heat conductivity unfrozen organic [$\text{W m}^{-1} \text{K}^{-1}$]	-	1.4
heat conductivity unfrozen mineral [$\text{W m}^{-1} \text{K}^{-1}$]	2.0	2.0
heat conductivity frozen organic [$\text{W m}^{-1} \text{K}^{-1}$]	-	0.8
heat conductivity frozen mineral [$\text{W m}^{-1} \text{K}^{-1}$]	-	1.4
heat capacity unfrozen organic [$\text{J Kg}^{-1} \text{K}^{-1}$]	-	2300
heat capacity unfrozen mineral [$\text{J Kg}^{-1} \text{K}^{-1}$]	2000	2000
heat capacity frozen organic [$\text{J Kg}^{-1} \text{K}^{-1}$]	-	2300
heat capacity frozen mineral [$\text{J Kg}^{-1} \text{K}^{-1}$]	-	2000
Supercooled water to field capacity ratio [-]	-	0.2
Water density [kg m^{-3}]	998	998
Ice density [kg m^{-3}]	-	916.7
Snow parameters		
Albedo VIS & NIR [-]	-	0.6
Snow density [kg m^{-3}]	-	100
Snow heat capacity [$\text{J Kg}^{-1} \text{K}^{-1}$]	-	2200
Snow heat conductivity [$\text{W m}^{-1} \text{K}^{-1}$]	-	0.14
Snow albedo [-]	-	0.8
Minimum threshold for snow to impact soil surface heat budget [m]	-	0.02
Maximum thickness of individual snow layers [m]	-	0.05
Vegetation parameters		
Growth degree day (GDD) threshold [$^{\circ} \text{days}$]	20	30
Senescence temperature [$^{\circ} \text{C}$]	0	2.0

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158 2.3. Upgraded soil biogeochemistry in high latitudes: initialisation and 159 dynamics

160 Biogeochemical features in permafrost soils are unique in that organic material below the
161 permafrost table is largely conserved, meaning that the permafrost stores stabile pools of
162 carbon and nutrients. Achieving an initial vertical state of the soil adequate for the
163 representation of permafrost gradients has been challenging in terrestrial models (Chadburn

et al., 2017). Here, we initialised biogeochemical soil features as closely to observational constraints as possible, and performed a spin-up simulation for the soil active layer to equilibrate to a pre-industrial “non-perturbed” state (Figure 1-a). The soil organic carbon (SOC) was initialised as such to maintain a higher content and reactivity of organic carbon at deeper layers (Figure 1-b-g). In contrast, the standard model assumes exponentially decreasing SOC with depth, thus yielding close to zero contents at permafrost depths. Our approach yielded SOC contents in the top meter of soil ($30 - 90 \text{ kg C m}^{-3}$), which is situated in the range of $50 - 300 \text{ kg C m}^{-3}$ (Hugelius et al., 2012) over the pan-Arctic region. We assumed 5% of soil organic matter to be fast degrading, which is conservative with regard to estimates of up to 10 % (Hugelius et al., 2020; Strauss et al., 2015; Voigt et al., 2020). The initial mole C:N ratio of organic matter was set to 16 (compared to the previous value of 9.5), which is the average values reported for deeper permafrost layers (50 – 100cm) at the Samoylov site (Zubrzycki et al., 2013). It is also in agreement to the averaged DOC to DON ratio of 14.5 derived from measurements for the North American organic permafrost (Fouché et al., 2020). To set initial organic P contents, we used the default organic N:P mole ratio of 55 used in Thum et al. (2019) due to lacking observational constraints. In order to preserve reactive SOC at permafrost depths, our simulations were initialized at negative temperatures to prevent its degradation during the model spin-up. As a result, total organic carbon content decreases below the surface layer, assumed here as the first 30cm, but remains close to constant with further increasing depth, in agreement with observed profiles (Figure 1b-g).

Due to the changes made to the soil hydrology as a result of soil freezing and inundation (Supplement S5), vertical leaching of biogeochemical compounds past the permafrost front is essentially inhibited in the model. Within the active layer, however, vertical transport of biogeochemical compounds can happen as a result of drainage, diffusion or due to bio-turbation.

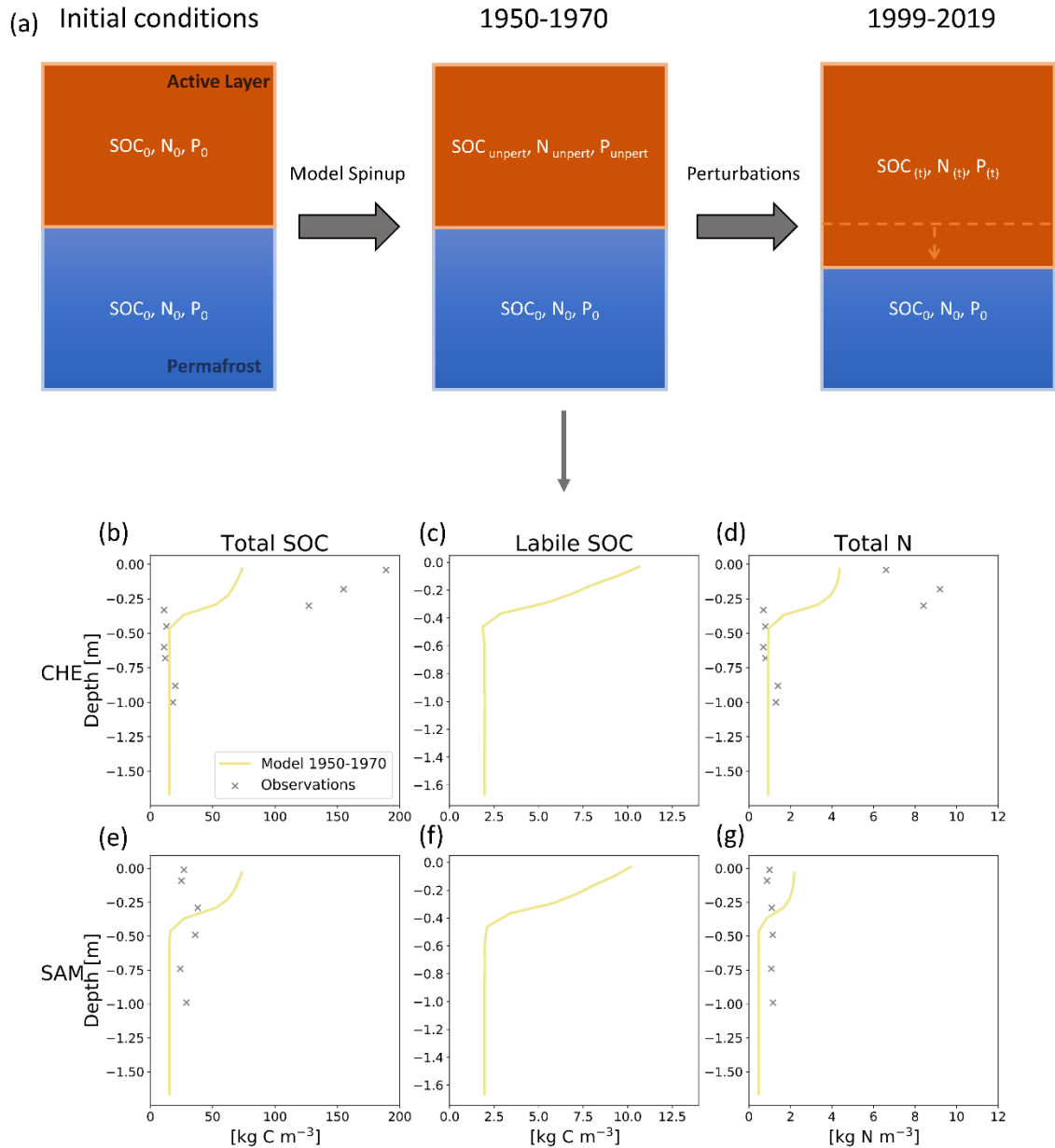


Figure 1. Panel (a) shows a scheme of our initialisation strategies for biogeochemical soil variables for a better representation of the permafrost, with SOC, N and P as simplifications for all soil organic carbon, nitrogen and phosphorus compounds, respectively. Note that in the model, these contents can vary with depth within the active layer, as well as at permafrost depths. Initial conditions show the variables ($\text{SOC}_0, \text{N}_0, \text{P}_0$) prescribed to the model before the spin-up simulations. Spinning-up the model from initialisations leads to an assumed unperturbed state. SOC, N and P remain essentially constant below the permafrost depth during this spin-up period, whereas above-freezing temperatures equilibrates $\text{SOC}_{\text{unpert}}, \text{N}_{\text{unpert}}$ and P_{unpert} in the unfrozen layers above. Changes in atmospheric conditions in the transient simulations trigger changes in biogeochemistry in the active layer that can change in depth (perturbed state) leading to perturbed soil contents $\text{SOC}_{(t)}, \text{N}_{(t)}$ and $\text{P}_{(t)}$. Lower panels b-g show simulated vertical profiles of total SOC (b,e), labile (fast) SOC (c,f) and total nitrogen (d,g) compared to total SOC and total nitrogen observations at the Cherskyi (CHE, top row) and Samoylov (SAM, bottom row) sites, respectively.

2.4. Upgraded vegetation for high latitudes: timing of growth, and frozen-soil dependent root depth

In our model version, the start of the growing season was delayed by snow cover. To account for this, the count of the growing degree-day only began when snow coverage was less than the minimum coverage threshold, defined here as 2 cm snow thickness (Table 1).

Additionally, we developed a module that considers plant roots to be adaptive to the seasonal freezing and thawing of the soil. In this scheme, fine root growth is only possible in unfrozen soil layers at every model time step. Instead of using a fixed root distribution, we prescribed the root distribution used in the standard QUINCY model in the upper 30 cm of the soil, which dictates an exponential decrease of root mass with a decay constant of 5.5, determined for grasses by Jackson et al. (1996). This reflects that most roots in permafrost systems are found in shallow soil depths and do decrease with depth there (Blume-Werry et al., 2019; Finger et al., 2016; Iversen et al., 2014). Below 30 cm, we did not use a weighed profile, meaning that in these unfrozen soil layers, root growth would happen at the same rate in all layers below. A major consequence of the dynamic root scheme is that nutrients stored within permanently frozen layers are unavailable for uptake by the plants. At the same time, recently thawed nutrient pools at the bottom of the active layer only gradually become available for root uptake.

2.5. Simulation Inputs, Forcing and Strategy

We performed model simulations from 1901-2019 for 14 high-latitude tundra sites of continuous permafrost over the Arctic region, represented by the C3 grass plant functional type in the model (Supplement Figure S2, site soil parameters given in Supplement site_info_arctic_grasslands.csv). The model was driven with meteorological data from CRU-JRA (Harris, 2019), which is a reanalysis of incoming solar radiation, surface temperature, humidity, precipitation, surface pressure and surface winds with the goal of forcing land surface models. The dataset is available at a spatial resolution of 0.5x0.5° and a 6-hourly temporal resolution. The atmospheric forcing data for our chosen sites were extracted from the CRU-JRA dataset according to their geographic coordinates, the data was then transformed to half-hourly timestep intervals using a weather generator (Zaehle and Friend, 2010). Furthermore, we used a vertical soil profile resolution of 18 layers, with increasing width down to a depth of 8 m. In our simulations, this set-up proved to be adequate for shallow permafrost table depths of 0.5-1.5m that are the primary focus of our simulations. We note, however, that this maximum depth is likely not sufficient for areas with permafrost table depths of several meters.

We differentiated between effects of (i) atmospheric CO₂ fertilization, (ii) changes arising from perturbation of the climate, and (iii) increased availability of nutrients and carbon from permafrost thaw on carbon cycle processes by conducting several sets of simulations for each pan-Arctic site (Table 2). These simulations were performed after model spin-ups of 300 years, which were driven with atmospheric conditions for 1901-1930, and were subsequently checked for important variable drifts. We conducted the first set of simulations (*climate+withoutpermafrostCNP*, Table 2), considering changes in climate, but initialising

carbon and nutrients contents to exponentially decrease with depth, as in the standard model. By doing this, carbon and nutrient contents at depth are close to zero, thus excluding any potential fertilization effect linked to a deepening active layer. The second set of simulations was again driven by changing climate (*climate*), but this time also considering the release of carbon and nutrient pools from the previously frozen permafrost layers. The third set of simulations additionally considered the impact of increasing atmospheric CO₂ levels to force the dynamics of vegetation and carbon cycle processes (*climate+CO₂*). To isolate the effects of increased nutrients/carbon following permafrost thaw, other climate effects and CO₂ fertilization, differences between scenario runs were computed.

Furthermore, we performed a simulation without the model implementations for the high latitudes described in section 2.2, 2.3 and 2.4 (*withoutHighLat*). To further elucidate the effects of nutrient limitation on vegetation growth, we conducted additional simulations with the same atmospheric conditions as *climate+CO₂*, but fixed soil N and P concentrations at 5-fold their prescribed levels (*withoutNutrientLim*), a value chosen during test simulations with the goal of largely alleviating nutrient limiting conditions.

Table 2. Overview of simulations and their drivers.

Main simulations / Drivers	CO ₂ fertilization	Climate	Permafrost Carbon and Nutrients	Further features
<i>climate+withoutpermafrostCNP</i>		X		
<i>climate</i>		X	X	
<i>Climate + CO₂</i>	X	X	X	
Comparison Simulations				
<i>withoutHighLat</i>	X	X		Without soil freezing, snow dynamics and inundation
<i>withoutNutrientLim</i>	X	X		Constant soil N and P at 5x initialized values

2.6 Case Studies and Validation Datasets

We examined detailed results, including the evolution of biogeochemical fluxes, for the three Siberian tundra sites with underlying continuous permafrost Cherskyi (CHE), Samoylov (SAM), and Chokurdakh (COK), which were chosen due to availability of eddy-covariance based GPP estimates. In the case that data were available, we evaluated modelling output for these sites against observational datasets of soil temperature, soil moisture, Gross Primary Production (GPP), as well as soil nutrients.

The Cherskyi site is located in Northeastern Siberia, in proximity to the Kolyma River. Mean annual temperature is around -11 °C (Göckede et al., 2019). Underneath an organic peat layer of around 20cm, silty loam can be found up to the permafrost table depth of around 60cm.

Vegetation near the site is dominated by tussock-forming species (Kittler et al., 2017). Soil temperature, snow depths, soil moisture and eddy-covariance fluxes for GPP were obtained as described in Kittler et al. (2017) and Göckede et al., (2017). Vertical profiles of soil nitrogen and organic carbon were measured at the site and are provided in Supplement Table S1. Site measurements of biologically available phosphorus was obtained according to Stimmler et al. (in review).

The Samoylov site is a river terrasse situated on an island of the Lena River delta. While the organic layer near the site can be up to 30 cm in thickness, it is typically less than 10 cm on the dry polygon rims due to differing hydrological conditions (Boike et al. 2019). The active layer is found at around 50 cm depth in mid-August, and the permafrost depth extends to over 400m below the surface. Vegetation coverage is dominated by sedges and mosses, dwarf shrubs and forbs (Kutzbach et al., 2004; 2007). We constructed eddy-covariance GPP estimates for 2014 – 2017 based on CO₂ exchange product of Holl et al. (2019), and applying a refined version of the bulk model approach of Runkle et al. (2013, Supplement Text S6). Soil nitrogen and carbon content measurements were taken from Zubrzycki et al. (2013).

Chokurdakh is located near the Indigirka River. The site is subject to continental climate since it is situated 150 km away from the coast. The soil is covered by around 20 cm of organic peat (van der Molen et al, 2017). The vegetation at the site is generally dominated by mosses, graminoids and grasses. We used site-level eddy-covariance GPP estimates as described in van der Molen et al (2007) for the years 2008-2011 (available under FLUXNET2015 dataset, Pastorello et al., 2015).

2.7 Analysis strategy

We analysed trends in fluxes and temperatures for the time frame 1960–2019 via linear regression, computing statistical significance through Student's t-tests, and multiplying the yearly trend with the entire analysis timespan. This timeframe was chosen due to the substantial increase in observed temperature past after the 1960s. We also calculated weekly averages for the time period 1950 – 1970, which we assumed to be largely unperturbed, and the perturbed present-day timeframe 1999 – 2019, in order to compare their seasonal dynamics.

In order to estimate the timing and magnitude of N and P limitation on vegetation growth, we used the built-in model output of relative plant P and N demand (Supplement Text S1, Thum et al., 2019). This expresses the ratio between plant P and N demand, which plants already adapt to soil conditions, to soil P and N availability. Thus, these values indicate stronger nutrient limitation the closer to 1 they are.

3 Results

3.1. Validation of soil physics and active layer depths

Simulated seasonal soil temperatures in the model are in good agreement with observed temperatures over a multi-year average when including the model extensions for high-latitude processes (Figure 2). The model reproduces well seasonal temperature fluctuations in the top soil (6-8 cm, Figure 2-a,b) and in the deeper soil (60-64 cm, Figure 2-e,f), where soil temperature remains near the freezing point for an extended time period in the Summer. Our simulations still yield positive summer-time biases of 3 - 6°C for 6-8 cm and 28-32 cm at both Cherskyi and Samoylov sites, while winter soil temperatures are too high at the Samoylov site.

Simulated mean maximum thaw depths of 0.7 m, 0.6 m and 0.6 m adequately reproduce averaged observed maximum thaw depths of 0.5 – 0.7 m, 0.4 – 0.6 m and 0.3 – 0.5 m at Cherskyi, Samoylov and Chokurdakh, respectively (Boike et al., 2019; Göckede et al., 2017; van der Molen et al, 2017). Snow seasonality is reasonably represented, although snow depth is overestimated at Samoylov and underestimated at Cherskyi with respect to observational data (Supplement Figure S3). The model also simulates the timing of saturated and unsaturated conditions accurately (Supplement Figure S1), albeit underestimated in terms of absolute water contents.

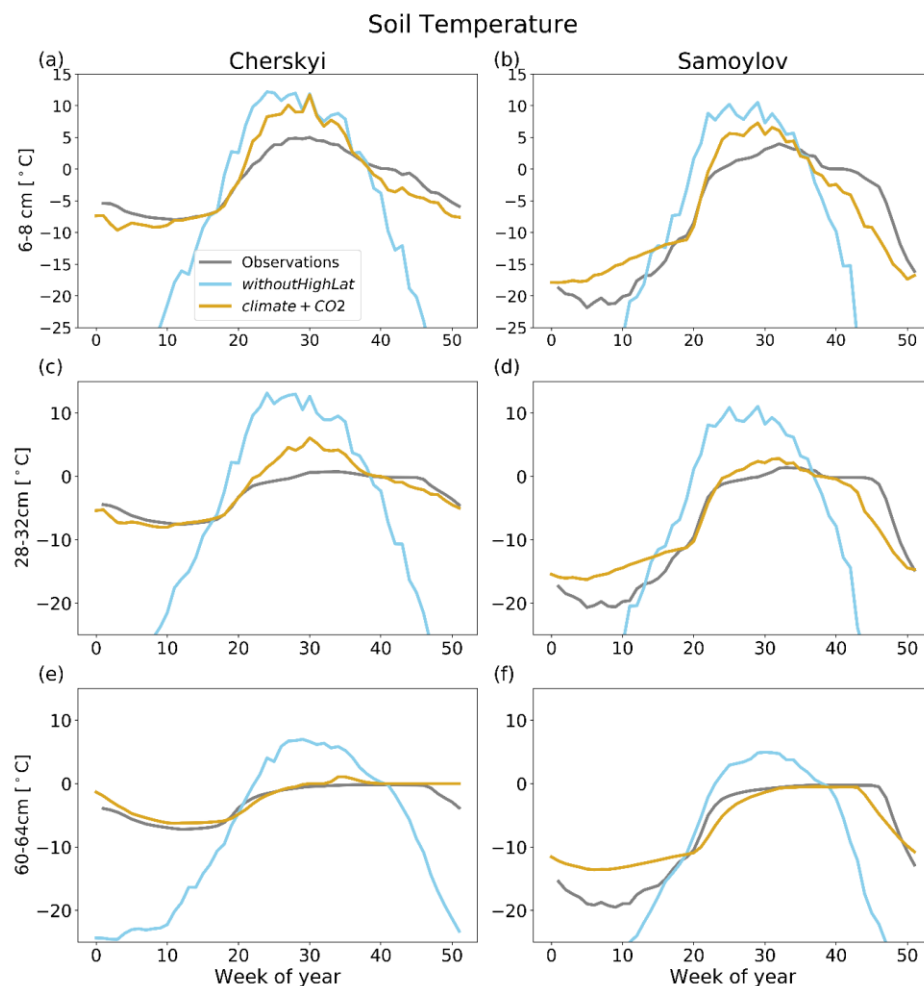


Figure 2. Observed and modelled soil temperature without (*withoutHighLat*) and with (*climate+CO₂*) permafrost-specific implementations at (a,b) 6-8 cm, (c,d) 28-32 cm and (e,f) 60-64 cm depths at Cherskyi (CHE, left panels) and Samoylov (SAM, right panels) sites averaged weekly for years 2015-2019 and 2009-2014 for Cherskyi and Samoylov, respectively.

3.2. Validation and seasonal limitation of GPP

Simulated annual GPP at Cherskyi, Samoylov and Chokurdakh amount to 405, 286 and 303 g C m⁻² yr⁻¹ in the *climate+CO₂* simulation over multiple year means (Figure 3), respectively. In the eddy-covariance derived observations, annual GPP is 321, 134 and 251g C m⁻² yr⁻¹ for the same sites. GPP in *climate+CO₂* is thus slightly overestimated at all sites, with respect to observations. Our model performs well overall in terms of reproducing seasonal variation of site-level GPP over multi-year means (Figure 3-a,c,e). The *climate+CO₂* simulations reproduce peak growth timing and magnitude for Cherskyi and Chokurdakh, but substantially overestimates the peak for Samoylov (Figure 3 a-c). GPP is also overestimated at the end of the growing season in all three cases. Modelled GPP in *climate+CO₂* is substantially lower than in the simulation *withoutNutLim*, in which nutrients do not constrain vegetation growth, leading to better agreement with the observational data. Overall, considering nutrient limitation in *climate+CO₂* reduces the computed annual GPP by over two-fold for all sites.

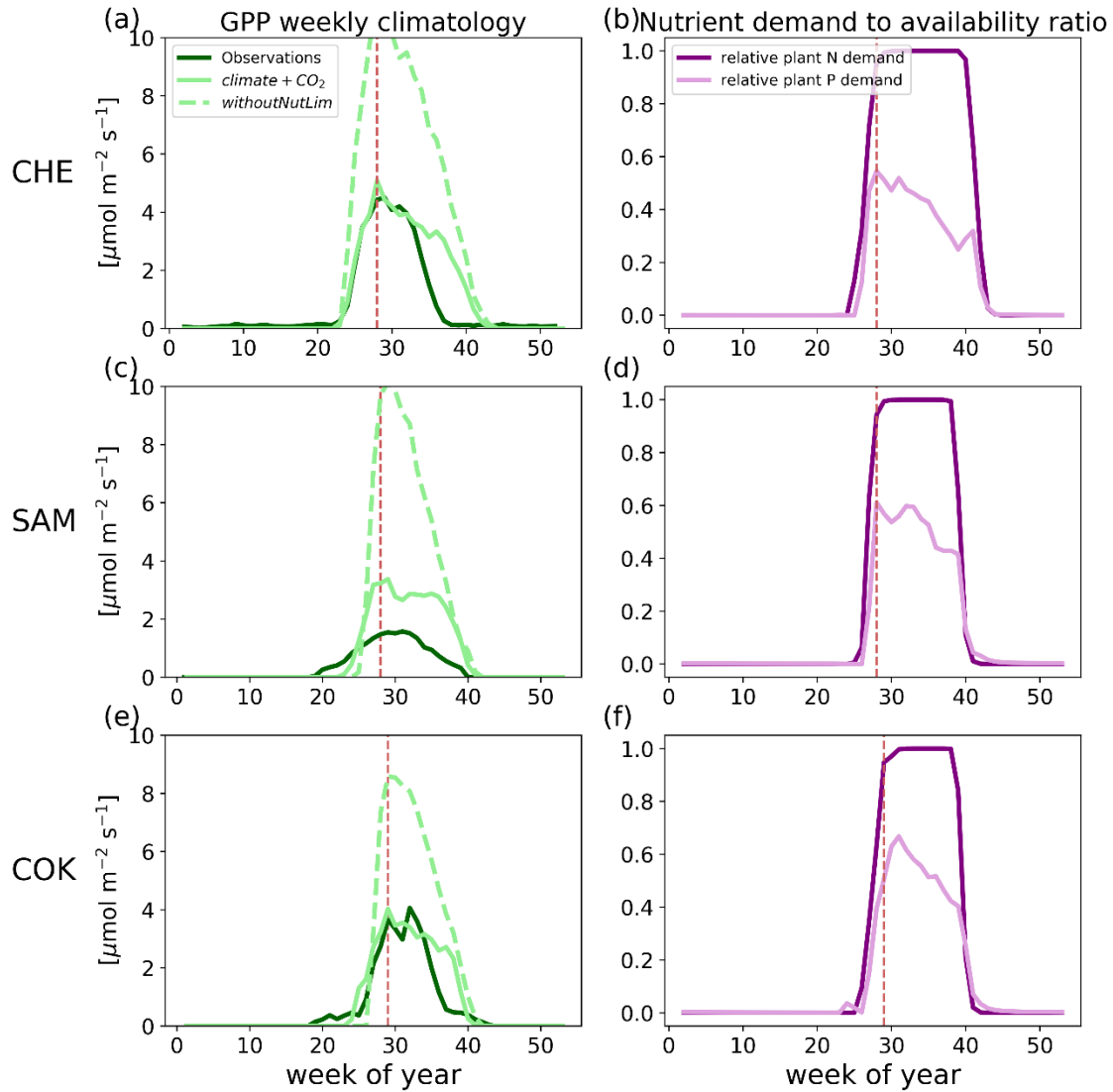


Figure 3. Panels a,c,e show simulated GPP *climate+CO₂* and *withoutNutLim* against observational GPP estimates derived from eddy-covariance flux towers at the Cherskyi (CHE), Samoylov (SAM) and Chokurdakh (COK) sites, averaged over 2015-2019, 2012-2017 and 2008-2010, respectively. Panels b,d,f show the simulated ratio of adapted plant N and P demand to soil N and P availability in the simulation *climate+CO₂* at the same sites (relative plant N demand and relative plant P demand, respectively). The red pointed line indicates the time slice where the simulated relative plant N demand exceeds 0.9.

In all three simulated cases, the seasonal GPP peak is reached in the range of week 27-29 at weekly mean averages of $3.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Samoylov) to $4.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Cherskyi). Accordingly, GPP remains relatively constant for several weeks, then sharply declines in observations. In the model, the initial decline occurs earlier but the end of the season senescence happens at a slower pace.

The model indicates a plant N demand to soil N availability ratio of over 0.9 starting at weeks 27-29. This is concurrent to the start of seasonal GPP decrease in all cases (Figure 3 b,d,f), indicating that soil N availability cannot sustain plant N demand past this point in time. Our

modelling results suggest that GPP decreases past this point in time owe to depletion of soil N.

Furthermore, the simulations show that the GPP peak is earlier than the seasonal thawing maxima (Figure 4-a-c). While the seasonally deepest thaw depth, which also concurs with the time period where N is mineralized in the deeper soil, occurs around week 34-37 in all three case studies, the GPP peak is simulated from week 27-29. In addition to nutrient limitations, soil moisture availability potentially could affect seasonal GPP, due to dry conditions prior soil thaw and after soil freezing. Soil water potential is, however, still high at the time GPP begins to decrease, indicating that soil water is abundant for plant uptake at that point in time, thus drought stress is not the trigger for the reduced carbon uptake in the model (Supplement Figure S1).

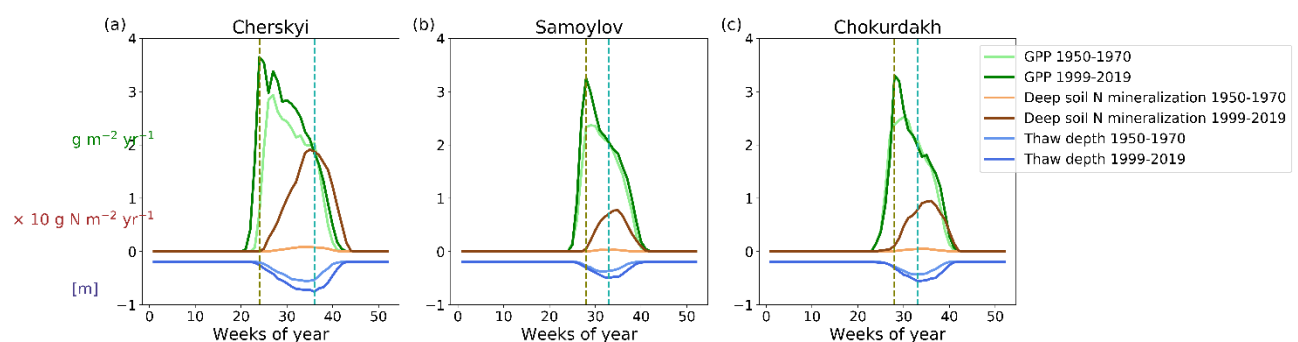


Figure 4. Seasonal evolution of GPP, deep-soil (50–100 cm) N mineralization, and unfrozen soil depths averaged over 1950 – 1970 and 1999 – 2019 in the *climate+CO₂* simulation. Pointed olive green and pointed light blue lines indicate the timing of the GPP peak and of maximum soil thaw, respectively.

3.3. Perturbation of active layer depth and deep-soil nutrient availability

Our observation-based forcing dataset prescribes rising atmospheric CO₂ levels, from 312 ppm in 1960 to 409 ppm in 2019, as well as atmospheric 2m temperatures, rising from 2.5, 2.2, and 2.0 °C over 1960 – 2019 for the Cherskyi, Samoylov and Chokurdakh sites, respectively (Figure 7-a,d,h). The perturbation of heat exchange between atmosphere and soil surface is also reflected through warming rates in simulated upper-soil temperatures (30cm), which show increases of 0.8, 1.5 and 1.2 °C at the same sites. The warming even impacts the depth of the permanently frozen layer in our simulations, with the active layer depth increasing by 0.19 m, 0.15 m and 0.13 m over 1960 – 2019 (Figure 5 b,f,j). The soil also starts thawing one (Samoylov and Chokurdakh) or two (Cherskyi) weeks earlier in the year (Figure 4-a-c). Based on soil organic carbon contents averaged for the period 1950-1970 in *climate+CO₂*, these increases in active layer depth would expose 2.2 – 3.1 kg C m⁻² yr⁻¹ to potential degradation over 1960 –2019 (low value for Chokurdakh, high value for Cherskyi), of which 0.3 to 0.4 kg C m⁻² yr⁻¹ is fast-degrading. This fast-degrading organic C is largely responsible for the simulated increase in heterotrophic respiration of 38 – 60 g C m⁻³ yr⁻¹ in deep soil depths of 50 – 100 cm (low value for Samoylov, high value for Cherskyi). The top

layer of this vertical range is exposed to above-zero temperatures for only 2 – 6 weeks of the year (low value for Chokurdakh, high value for Cherskyi) over 1999 – 2019 on average.

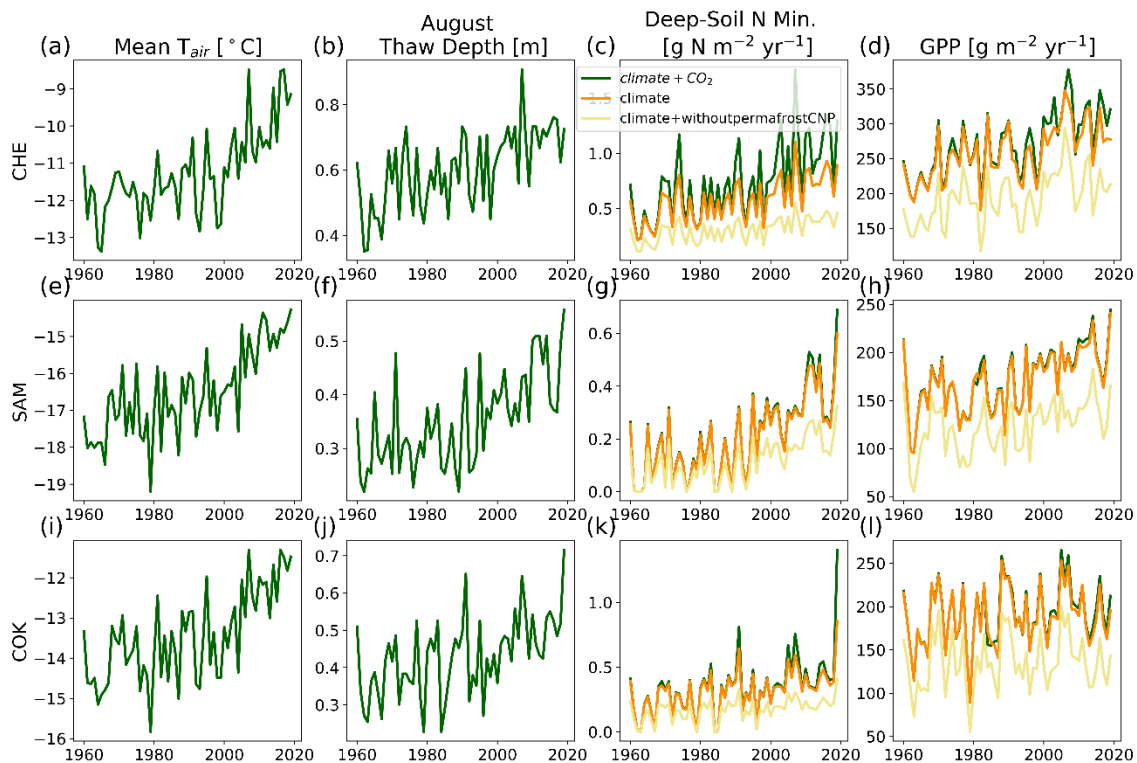


Figure 5. Temporal evolution of annual mean air surface temperature (left column), simulated average August thaw depth (middle left), simulated annual N mineralization from 50-100cm (Deep-Soil N Min., middle right) and simulated annual GPP (right column). Deep-Soil Min. and GPP are shown for simulations considering CO₂ fertilization and climate perturbations (*climate + CO₂*), as climate perturbations alone (*climate*) and climate perturbations without our permafrost nutrient initialisations (*climate+withoutpermafrostCNP*) at the Cherskyi (CHE), Samoylov (SAM) and Chokurdakh (COK) sites.

Simulated soil thaw also exposes organic P and N to degradation and potential use by vegetation. Increases in active layer depth over the simulation time span increase organic P and N mineralization by 0.4 – 1.2 g N m⁻² yr⁻¹ and 0.02 - 0.06 g P m⁻² yr⁻¹ in the deep soil, aggregated over the 1960 – 2019 period. In the case of N, this means a steep 2-to-3-fold increase with respect to 1950 – 1970 organic N mineralization levels, which were close to zero (Figure 4, Figure 5c-k). In the case of P, thawing into deeper layers also increases the net transformation of mineral-bound P to biologically-available P by 0.25 – 0.33 g P m⁻² yr⁻¹.

As a result of the deepening of the active layer, annual mean root carbon content undergoes a strong relative increase at depths of 50 cm (+3 g C m⁻², or +152 % in relative terms). Overall, however, the root carbon distribution only experiences minor changes in our simulations when comparing the beginning of the 1960s with present day conditions, with around 85 % of roots still simulated in the upper 20cm of the soil (Figure 6a-c) for 1999-2019. Since root

growth and nutrient uptake is inhibited by the frozen layer depth in the model, root growth past 50cm is also limited to 2 – 6 weeks during the year. Increased root growth at depth is responsible for increasing plant nutrient uptake in the deep soil by $0.2 - 0.6 \text{ g N m}^{-2} \text{ yr}^{-1}$ and $0.08 - 0.09 \text{ g P m}^{-2} \text{ yr}^{-1}$ (Figure 6-e-g). These results suggest that around 30 – 60% of increased biologically-available P and N inputs are removed from the deep soil through plant uptake over the entire year, dependently on the site.

Due to the incomplete use of increased nutrients in the deep soil, our model simulates a vertical gradient in nutrient availability increasing towards the permafrost front for 1999 – 2019 (Supplement Figure S5). The simulated results are broadly consistent with observational biologically-available P measurements (Supplement Figure S5-d, Stimmler et al., in review), which suggest biologically-available P contents in the range of 7 to 41 g m^{-3} (including P weakly bound to minerals) at Cherskyi, and a tendency of increasing nutrient availability near the permafrost layer (Supplement Figure S5).

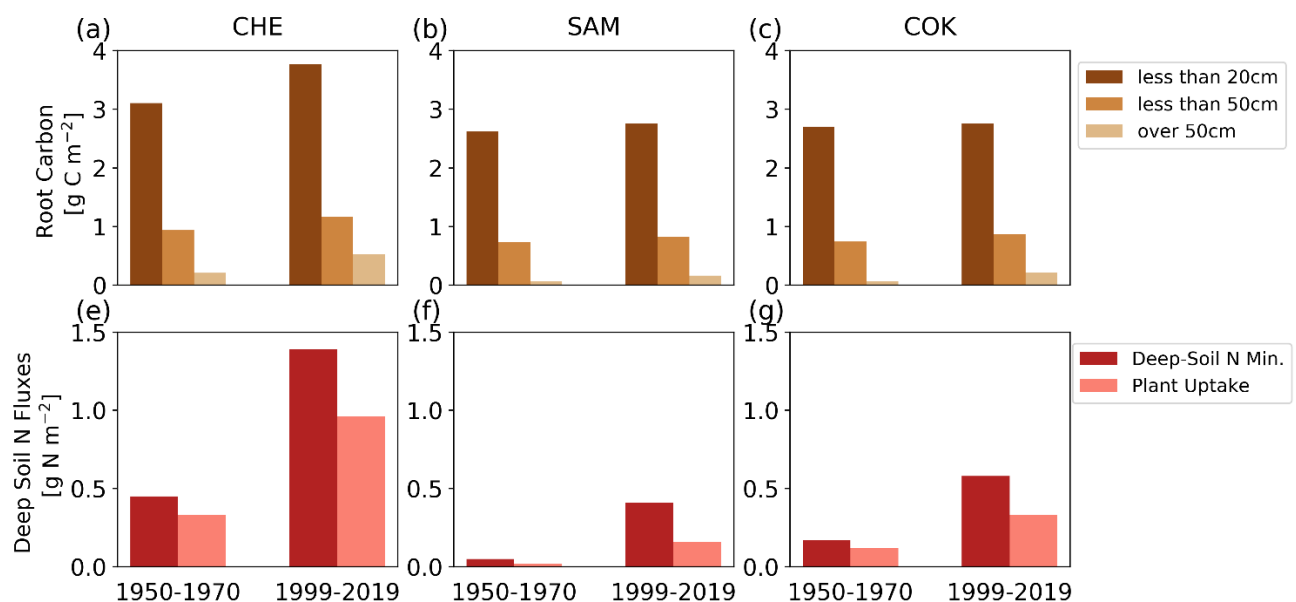


Figure 6. Panels a-c show mean root carbon and panels d-f show annual mean deep-soil (50 – 100cm) N mineralization (Deep-Soil N Min.) and plant N uptake (Plant Uptake) at Cherskyi (CHE), Samoylov (SAM) and Chokurdakh (COK), averaged over 1950-1970 and 1999-2019.

3.4. Effect of increased nutrient mobilization from the permafrost on GPP compared to other perturbations

Our simulations indicate an increase in GPP for all case-study sites over 1960 – 2019 in the *climate+CO₂* simulation, thus a result of all perturbations (Figure 5, Figure 8). At the Cherskyi, Samoylov and Chokurdakh sites, GPP trends arising from both increasing atmospheric CO₂ levels and changes of climate account for an increase in GPP of 106, 68 and $37 \text{ g C m}^{-2} \text{ yr}^{-1}$ aggregated over the entire 1960-2019 timespan, respectively. These changes represent increases of 46%, 36% and 20% with respect to 1950-1970 mean levels, respectively.

Increased nutrient availability from the thawing of permafrost thereby contributes increases of 17 and 13 $\text{g C m}^{-2} \text{ yr}^{-1}$ at the Cherskyi and Samoylov sites, whereas Chokurdakh does not show a statistically significant trend as response to increased nutrient availability originating from permafrost layers. Other climate-induced changes account for increases in the GPP of 67, 51 and 26 $\text{g C m}^{-2} \text{ yr}^{-1}$. Alone, CO_2 fertilization accounts for rising the GPP by only 22, 4 and 11 $\text{g C m}^{-2} \text{ yr}^{-1}$. Climate-induced effects (combined permafrost nutrients and carbon, and other climate effects) thus account for over 70% of the total GPP change in all cases.

Accounting for all perturbations (*climate+CO₂*), GPP is also more strongly enhanced earlier in the season, despite the increase in nutrient availability in deeper layers later in the season. For instance, GPP is enhanced by +64 % for Cherskyi and +95 % for Samoylov during weeks 20-30 of the year, whereas the increase during weeks 30-40 is only of 11% for Cherskyi, and 13 % for Samoylov.

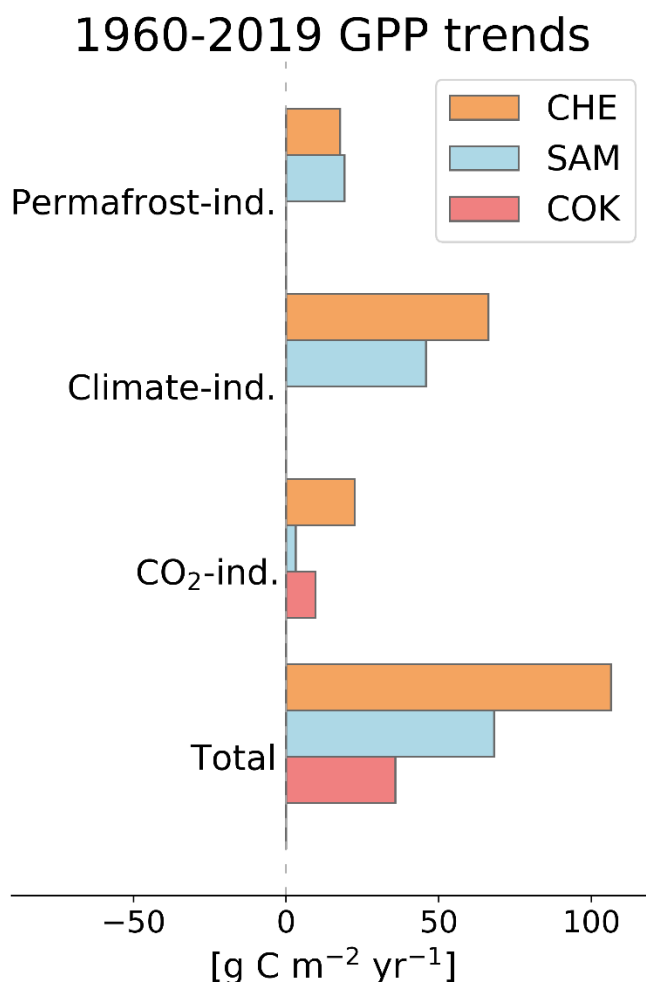


Figure 7. Statistically significant trends in site GPP induced by increased permafrost nutrient availability (Permafrost nutrient-ind.), other climate-induced perturbations (climate-ind.), CO_2 -fertilization (CO_2 -ind.) and total changes (Total).

3.4. Implications for N loss pathways and N₂O Emissions

Since newly-mineralized N from previously frozen organic soil layers is not completely removed from the deep-soil through plant uptake (Figure 6), thereby contributing to increase solute N at the permafrost front (Supplement Figure S7), deep-soil loss pathways of biologically-available nitrogen (i.e., nitrification, denitrification, and transport) are opened at all three sites in the *CO₂ + climate* simulation (Figure 8d-f). Increased nitrification and denitrification fluxes at Cherskyi, which increase by 0.72 and 1.23 g N m⁻² yr⁻¹, are larger than the increased 50-100 cm vegetative uptake at the site (Figure 8d). Vegetative uptake is however larger than nitrification and denitrification fluxes at Chokurdakh and Samoylov (Figure 8e-f), where simulated thaw depths are slightly shallower (Figure 4b,c). These increases in nitrification and denitrification increased N₂O fluxes of 4, 2 and 1 mg N m⁻² yr⁻¹ of N₂O to the atmosphere for Cherskyi, Samoylov and Chokurdakh (Figure 8a-c), respectively. These increases lead to present-day fluxes of 11, 4 and 5 mg N m⁻² yr⁻¹ of N₂O for 1999-2019, which suggests an increase of around 42 – 68 % over all sites over 1960-2019. Our simulation results furthermore show peaks in emissions at the beginning of the growing season, and a larger peak at the end of the growing season at all sites (Supplement Figure S6). Overall, the months of August and September account for 32 – 54 % of total yearly N₂O emissions over 1999-2019. We simulate large interannual variability of N₂O fluxes, with standard deviations of 3 – 9 mg N m⁻² yr⁻¹ of N₂O after detrending. The year-to-year magnitude of the N₂O fluxes shows significant correlation with surface air temperature (2m) of 0.39 (Cherskyi) to 0.54 (Chokurdakh).

Baseline N₂O emissions, as well as their increase over 1960 – 2019 is generally higher in *CO₂+climate* than in *climate+withoutpermafrostCNP*, which does not consider increased N availability via the mobilization of permafrost pools (Figure 8-a-c).

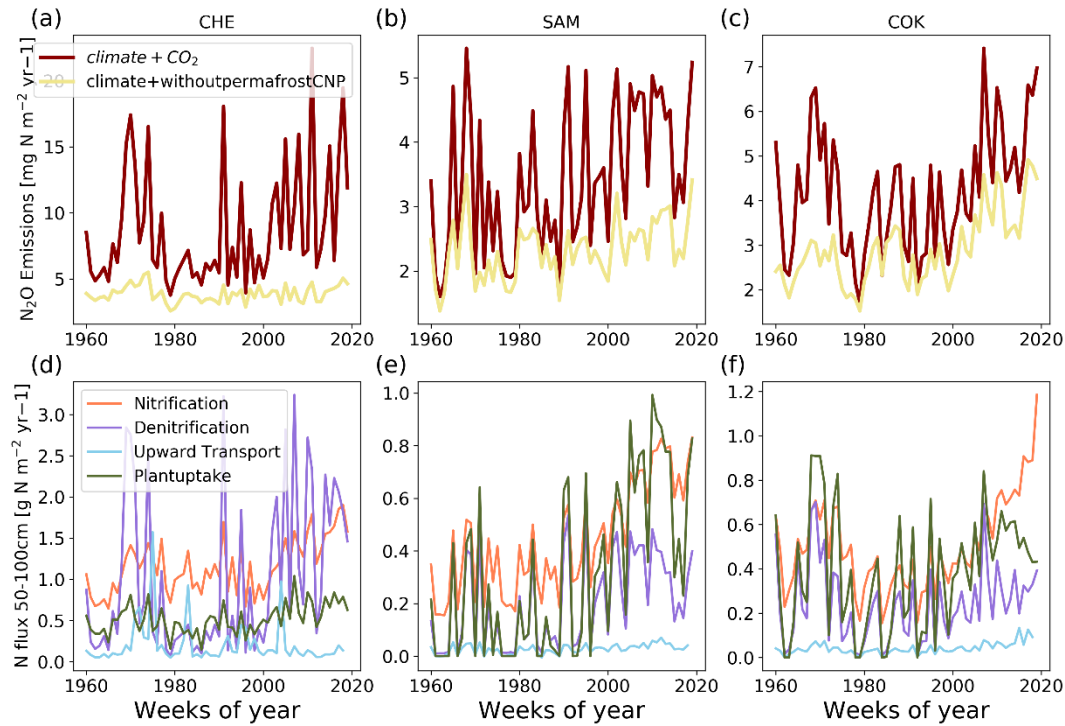


Figure 8. Evolution of N₂O emissions (a-c) and (d-f) nitrification, denitrification, upward transport and plant N uptake between 50 – 100cm over 1960-2019 at Cherskyi, Samoylov and Chokurdakh sites.

3.5. Extrapolation to pan-arctic scale

At the 14 Arctic grassland sites at pan-arctic scale, the CRU-JRA dataset prescribes averaged increases in atmospheric temperature of 2.1 °C over 1960 – 2019, whereas precipitation does not show a significant trend. Similarly to the cases studies, soil temperatures at 30cm depth increase by 1.9 °C over all sites on average. This perturbation in the soil heat budget leads to an averaged increase in active layer depth of 0.14 m. The mean increase in GPP across all sites amounts to 67 g m⁻² yr⁻¹ (+24%) considering all perturbations over 1960-2019 (Figure 9, 10a), ranging from increases of 9 g m⁻² yr⁻¹ (Zackenberg, DK-ZA) to 107 g m⁻² yr⁻¹ (Inuvik, CA-INK). Of this averaged GPP increase, 52 g m⁻² yr⁻¹ (79%) is caused by climate-induced changes only, contributing more than half of the total GPP changes. Changes in permafrost nutrients account for on average 7 g m⁻² yr⁻¹, thus contributing to 11 % of the total GPP change. The simulation *withoutNutLim*, in which nutrient-limiting conditions are largely alleviated, hindcasts a GPP increase of 142 g m⁻² yr⁻¹ averaged over all sites over 1960-2019, thus around 112 % higher than simulations considering nutrient limitation. Overall, the effects of both increases in GPP and total ecosystem respiration largely even out at the pan-Arctic scale over the historical time period, although the net ecosystem exchange (NEE) slightly increases by 16 g m² yr⁻¹ over the site average (Figure 10b).

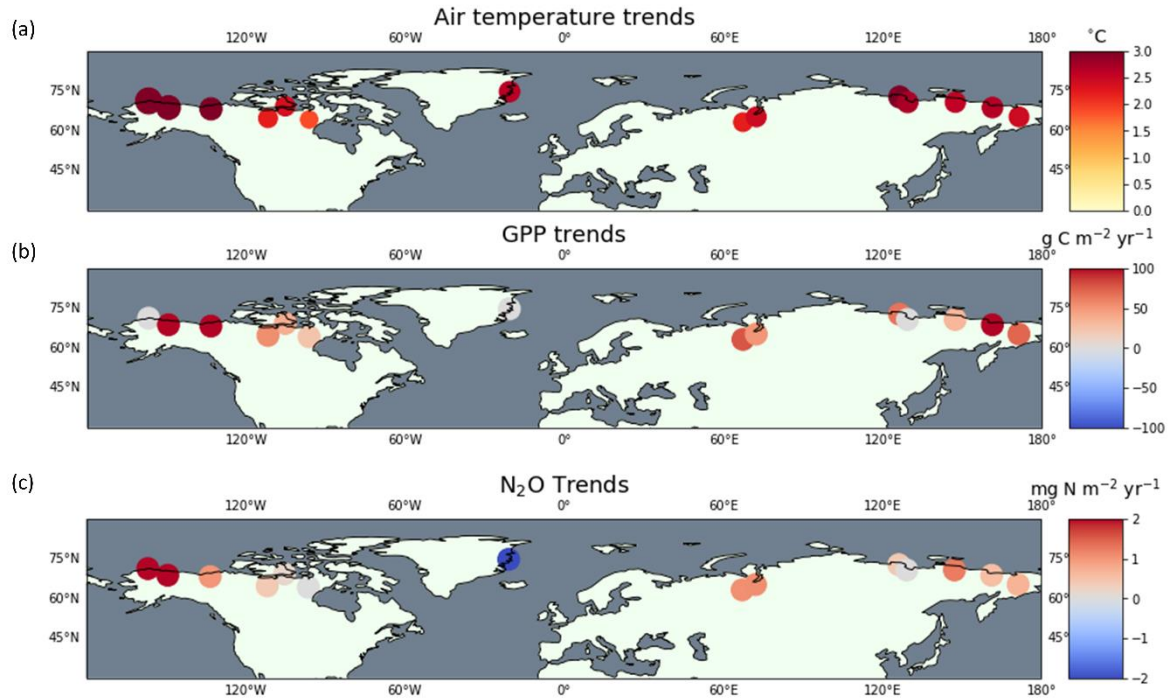


Figure 9. Simulated pan-arctic scale trends in (a) annual mean air temperature [K], (b) annual GPP (*climate+CO₂*) [g m⁻² yr⁻¹] and (d) annual N₂O emissions [mg m⁻² yr⁻¹].

Additionally, we compute a pan-Arctic site average N₂O emissions increase of 1.2 mg N m⁻² yr⁻¹ over 1960-2019 (Figure 9-c, Figure 10-c). This suggests an increase of around one fifth with regard to the present-day flux of 5 mg N m⁻² yr⁻¹, averaged at the pan-arctic scale. The change in the N₂O flux over the time period shows strong variability from site to site (Figure 9-c). A maximum of increase in N₂O emission of 4 mg N m⁻² yr⁻¹ is simulated at the site CA-CBY, whereas a substantial reduction in N₂O emissions (-5 mg N m⁻² yr⁻¹) is simulated at DK-ZAK.

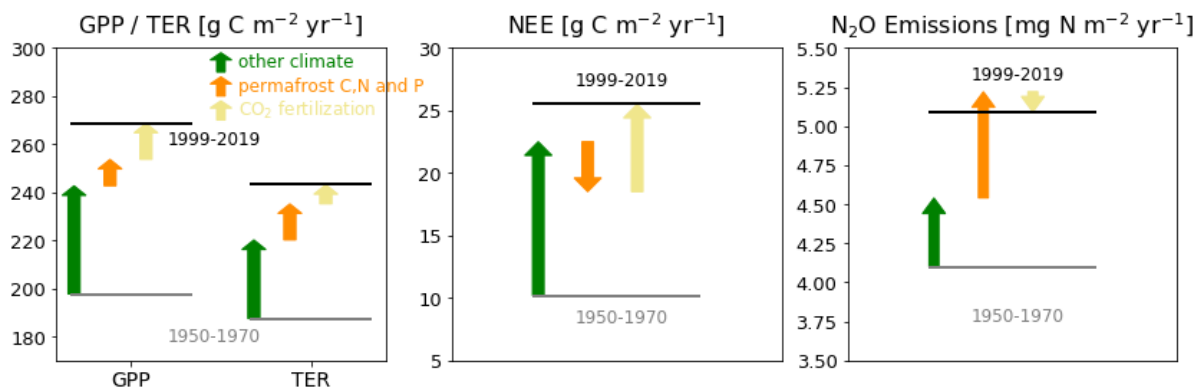


Figure 10. Simulated response of GPP and total ecosystem respiration (TER, panel a), NEE (panel b) and N₂O emissions (panel c) to climate effects other than increased permafrost nutrients and carbon (other climate, green), permafrost nutrients and carbon (permafrost C,N and P, orange) and CO₂ fertilization (khaki), all averaged over all sites.

4 Discussion

4.1. Modelling the terrestrial biosphere of high-latitudes in QUINCY

Estimating human-caused changes in greenhouse gas exchanges over time is presently strongly dependent on global land surface models (Canadell et al., 2021; Friedlingstein et al., 2021). The representation of biophysical processes in high latitudes is, however, still associated with strong limitations (Chadburn et al., 2017; Schädel et al., 2016). Through the full vertical discretization of both physical and biogeochemical variables, the QUINCY model extended with permafrost-relevant processes permits the analysis of changes associated with vertical permafrost thaw and their impact on vegetation and soil dynamics, while also taking into account a full representation of C, N and cycles. Through the representation of N and P cycles, our model also alleviates an important uncertainty found in terrestrial land surface models for the high latitudes (Chadburn et al., 2017). Our model representation of roots, whose growth distribution is formulated to be dependent on thaw depth, and soil biogeochemistry initialization for permafrost profiles, offers a robust framework in order to assess impacts of changing soil conditions on vegetation and microbial dynamics. In terms of assessing nutrient inputs from the thawing permafrost and their impacts for the ecosystem, only strongly simplified impacts of nitrogen inputs from the permafrost have been assessed using bucket-type approaches (Beermann et al., 2017).

The model presented here still, however, has important limitations in its biophysical representation of high-latitude permafrost ecosystems. Strong simplifications are made in both physical soil processes, as well as vegetation dynamics. Our parametrizations we implemented here are of first order, with certain schemes found in other models offering more complex solutions. For instance, we assume fixed snow constants for snow density, specific heat conductivity and heat capacity, which are partly computed dynamically in other models (Chadburn et al., 2015; Guimberteau et al., 2018). In our model, soil heat conductivity and specific heat capacity do not change dynamically as a response to soil water content and soil organic matter, which could lead to certain bias in soil temperatures. A further source of uncertainty arises from the handling of species composition in the model. Assuming homogenous grassland coverage could cause bias in GPP, for instance as shown at the Samoylov site, where GPP is reported to be majorly affected by mosses (Holl et al., 2019). Such bias could potentially be reduced by improving the representation of Arctic plant functional types in global vegetation models (Sulman et al., 2021). Our model, furthermore, does represent spatial heterogeneity linked with the polygonal tundra landscape, found at many sites, and thus our results should be interpreted as the bulk mean of the spatial fluxes with a strong degree of local uncertainty.

4.2 Changes in vegetation growth from increasing atmospheric CO₂ levels, changes in climate and increased nutrient availability from the permafrost

Over the past century, Arctic regions have been subject to disproportionate warming due to climate change (e.g., Serreze and Berry, 2011), which is reflected in our forcing data. Our model shows various types of responses to perturbations of the Earth system (i.e., atmospheric CO₂ levels, climate and soil conditions). Primarily, vegetation growth is impacted

more strongly by changes in climate than the effects of atmospheric CO₂ fertilization alone. Our computed GPP increase of around 25 % for the 1960-2019 period is broadly consistent with increases in greenness of around 10 % per decade since the 1980s derived from satellite estimates (Winkler et al., 2019). Although it should also be noted that both our modelled and the satellite-derived results show strong variability at the local scale. Our results also suggest a trend towards a slightly earlier start and peak of the growing season. This feature is in agreement with Park et al. (2019), who report a historical trend in start and peak of vegetation growth of 1 day per decade derived from satellite imagery, with our simulations showing a two weeks earlier growing season peak of GPP at Cherskyi, and one week earlier peak at Samoylov and Chokurdakh over the 1960 to 2019 period.

Our model suggests that increased nutrient input from permafrost thaw is only responsible for 11 % of the total GPP change over 1960 – 2019. This is confirmed by stronger total increases in GPP in the early growing season than in the later summer. Thus, other climate factors, such as earlier growing season, as well as faster cycling of upper-soil organic matter due to higher temperature, are simulated as more important factors than increased nutrient availability due to deep-thawing later in the season for the 1960 – 2019 time span. With increased soil thaw in the future, increased nutrient supply and longer time-scales for mixing nutrients to the upper soil could still mean stronger trends for the GPP of ecosystems with shallow permafrost table depths.

4.3 Increased deep-soil nutrient availability and vegetation uptake

Ecosystems in the Arctic tundra are reported to be strongly nutrient-limited during the growing season (Schimmel et al., 1996; Schuur et al., 2016; Martin et al., 2021), owing to shallow active layers meaning a limited nutrient pool accessible for plant roots and lower mineralization rates due to thermal constraints. In accordance to this, nutrients added to the active layer in fertilization experiments have been shown to strongly enhance vegetation growth (Natali et al., 2011; Pedersen et al., 2020; Street et al., 2018). In our simulations, historical increases in permafrost organic matter mineralization led to the release of additional N to the active layer, especially in late summer. This fertilization effects is, however, only responsible for 10-15% of the total GPP increase in our case studies and at the pan-Arctic scale. The relatively weak effect of this increased nutrient supply firstly owes to the timing of simulated peak vegetation growth, which occurs 4-8 weeks earlier than the timing of maximum permafrost thaw, when new nutrients in the deep active soil are mineralized to biologically available forms. In relation to the temporal mismatch of vegetation growth and deep-soil thaw, conditions only allow for root growth in the deep soil for several weeks in the late summer, greatly limiting the build-up of root mass at depth in the model. Due to this temporal and spatial decoupling, plants only use around 30-60% of increased N to the active layer in our case studies, opening other loss pathways (i.e., outgassing, transport). Treat et al. (2016) also suggest a mismatch between the growth season and increased N availability due to deep-soil thaw while tracking N with stable isotopes at the local scale.

Few studies have assessed seasonal dynamics in plant uptake in relation to the seasonality of soil thaw. In our model, the vast majority (> 85%) of roots are simulated in the top 20-30cm of the tundra ecosystems, which is in accordance to observed vertical root profiles (Blume

Werry et al., 2019; Iversen et al., 2015; Keuper et al., 2020). Since the vegetation is already in senescence by the time the seasonal thaw maximum is reached, the vegetation's investment into root growth is low in the model. However, it remains unclear if these relatively small root fractions in the deep-soil (<5% of total root mass) could lead to disproportionate uptake of nutrients in the deeper soil. In the case of *Eriophorum vaginatum*, adapted uptake in the late summer could give the species a competitive advantage in the case of active layer deepening (Blume-Werry et al., 2019). Uptake of deep-soil N in late autumn has also been demonstrated for *Salix arctica* by Pederson et al. (2020) through the use of stable isotopes, but overall, the magnitude that a competitive advantage of individual species exhibits at the ecosystem scale still remains enigmatic.

Due to the almost exclusive root growth in the upper 30 cm, timescales at which nutrients reach the upper soil versus the rate at which they are used by microbes in the deep active layer are key to understanding the fate of nutrients originating from the permafrost thaw (e.g., Marushchak et al., 2021). Finger et al. (2016), in turn, postulate in their analysis of nitrogen availability over permafrost thaw gradients that vegetation uses additional nitrogen made available through permafrost thaw over time-scales of years to centuries, which could open loss pathways for nitrogen (Treat et al., 2016; Voigt et al., 2020). While our model may provide a plausible first-order representation of organic matter degradation and the fate of nutrient mineralized nutrients originating from permafrost soil layers, it certainly entails uncertainties which affect simulated degradation and composition of permafrost organic matter, and plant uptake dynamics in the soil.

4.4 Implications for nutrient outfluxes

Due to the incomplete use of deep active layer nutrients by plants, our model shows accumulation of both biologically-available P and N at the near the permafrost table. Ultimately, three loss pathways are plausible for nutrients that are not taken up by the vegetation. Either they are mixed into the active soil layer, exported laterally, or in the case of nitrogen, used microbially for denitrification and outgassed as either N₂O or N₂ (Treat et al., 2016; Voigt et al., 2020).

Our model suggests that the importance of different nitrogen fluxes in the deep active layer could be dependent on the seasonal thaw depth, with Cherskyi having the least effective vegetative uptake in relation to increased N mineralization in combination with deepest seasonal thaw depth. It is plausible that deeper thaw depths could limit accessibility of roots to the deepest part of the active layer, which could lead to larger increases in N₂O and N₂ gas fluxes to the atmosphere due to less efficient plant use of new N.

Since lateral exports eliminate biogeochemical compounds from permafrost systems, it could affect the potential use of nutrients originating from permafrost thaw by plants and microbes (Treat et al., 2016). Lateral water and biogeochemical exports from the permafrost are, however, still poorly constrained (Lacroix et al., 2020; 2021; Terhaar et al., 2021), and thus difficult to assess in our model-based study.

4.5. High latitudes as a weak, but emergent source of N₂O gas

N₂O is a strongly potent greenhouse gas and its global budget could impact the change of the global climate in the future (Tian et al., 2020). The magnitude of N₂O emissions from high latitudes has, however, been largely disregarded due to low active layer nutrient contents in these regions (Marushchak et al., 2021). Recent studies that have measured N₂O fluxes at site-level, have, however reported weak emissions per area in permafrost ecosystems, that could add up to an important component of the global N₂O budget (Voigt et al., 2017; Marushchak et al., 2021). Our model results regarding N₂O emissions are of particular importance, since they show that, while N₂O emissions were close-to-zero in simulations that did not consider an additional N source from the deep soil, they are likely increasing due to permafrost thaw and increased N availability in the deep soil. The overall magnitude of our present-day N₂O emission estimate at the pan-Arctic scale (5 mg N m⁻² yr⁻¹) is over two-fold lower than the reported estimate if 11 mg N m⁻² yr⁻¹ of Voigt et al. (2020).

Our model simulates increasing N₂O emissions, which could further increase with enhanced N availability following thaw of permafrost. The high year-to-year variability in the simulated annual N₂O emission magnitudes is likely related to elevated temperatures and thaw of new layers in given years, which provides a new source of nitrogen that is incompletely used by plants. It is, however, also likely that the simulated changing soil hydrological conditions, and thus changes in soil aeration that are needed for N₂O formation, impact the magnitude of the fluxes. Indeed, short aerobic periods are a requisite for nitrification, whereas longer anaerobic timespans are needed for denitrification (Voigt et al., 2020), both of which are simulated at our case studies (Supplement Figure S1).

5 Conclusions

Our model results show that nutrient release from permafrost thaw since the 1960s leads to a fertilization effect on plant growth and vegetation C uptake. Due to spatial and temporal decoupling of vegetation growth and permafrost thaw, this fertilization effect is, however, low in comparison to other climate-caused perturbations. Since enhanced deep-soil N and P sources are used incompletely by vegetation, other nutrient loss pathways are opened. This is of particular importance with respect to N₂O emissions from high latitudes. Through the mismatch of peak vegetation growth and deep-soil thaw, our results could explain for a present-day N₂O source reported in recent local-scale studies despite generally low N availability in permafrost soils (Voigt et al., 2020; Marushchak et al., 2021). Our results also suggest that N₂O emissions from high latitudes may have increased to add up to a considerable source to the atmosphere in recent decades. Since thawing of permafrost is projected to substantially increase over the next century, thus potentially increasing mobilization of nitrogen in deeper parts of the soil with potentially poor access for plant roots, our results call for increased efforts to improve the understanding of nutrient fates upon permafrost thawing and to improve N₂O measurements at the pan-Arctic scale, especially in the non-growing season.

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7. Data Availability Statement and Conflict of Interests

Model code and model results will be made publicly available during the review process and are available upon request to the corresponding author until then. All authors declare no conflict of interests.

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Supplementary Information

Supplement Text

S.1 Vegetation growth in QUINCY

Vegetation growth in QUINCY is calculated as the minimum of source (i.e., photosynthesis, derived at half-hourly timestep with a state-of-the art coupled photosynthesis-stomatal model accounting for a vertically resolved canopy) and sink limitation (growth of new tissue constrained by plant labile N and P, as well as vegetation temperature and moisture). Short-term fluctuation (days) between source and sink limitations are buffered through labile carbon and nutrient pools. Vegetation nutrient uptake is driven by available C for growth and tissue stoichiometry, where dynamic plant stoichiometry enables for adaptation of plants to low nutrient levels (Caldararu et al., 2020). Nutrient uptake is limited by several factors, including fine root biomass and solute nutrient concentrations of the respective soil layer.

S.2 Nutrient Cycling in QUINCY

The model includes a comprehensive representation of nitrogen fluxes in the soil, including the production of the nitrogen gases such as N₂O and N₂ through nitrification and denitrification as a function of solute NH₄⁺ and NO₃⁻, labile soil organic carbon, soil temperature and moisture, which affects the fraction of the soil that is aerated. Thereby, NH₄⁺ that is available upon organic matter degradation can be transformed to NO₃⁻ via nitrification under aerobic conditions. The process also releases a small fraction of N₂O. NO₃⁻ can be further used for microbial metabolic activities under anaerobic conditions, producing the gases N₂O and N₂. The model does not consider intermediate forms of nitrogen in both nitrification and denitrification processes.

QUINCY also incorporates a full representation of the phosphorus cycle, in particular simulating exchanges of primary, solute, absorbed and occluded phosphorus in the soil (Thum et al., 2019; Yu et al., 2020). Phosphorus sorption capacity depends on mineral and organic material in each soils layer and is affected by soil temperature and moisture.

S.3 QUINCY extensions for high latitudes: Soil Freezing

The soil module in QUINCY previously considered surface exchange through net radiation balance R_{net} , latent heat from evapotranspiration $H_{latent,evapotrans}$, and vertical heat transfer G as a result of heat conductance through the soil. For this study, we extended the soil layer heat balance, which is solved implicitly in the model. Thus, the update of soil layer temperatures at every model timestep, takes into account the freezing and melting of soil water, and its impact on latent heat. For the surface exchange this extends the budget to:

$$(1) C_s \frac{\partial T_s}{\partial t} = R_{net} + H_{sensible} + H_{latent,evapotrans} + H_{latent,freezethaw} + G$$

With T_s being the surface soil temperature, C_s the volumetric heat capacity of the layer adjusted for soil layer width in J m⁻² K⁻¹. R_{net} is the net radiation with positive values meaning a flux towards the soil in J m⁻² s⁻¹. $H_{sensible}$ is the heat flux from sensible heat exchange with

the atmosphere, $H_{latent, evapotrans}$ is the evapotranspiration flux, and $H_{latent, freezethaw}$ is the latent heat flux from freezing and thawing of soil, all in $J\ m^{-2}\ s^{-1}$.

The heat budget in the sub-surface soil is governed by the vertical soil ground heat flux G and latent heat fluxes. Temperatures in the subsurface soil T_s were computed through conductive transfer with heat conductivity constant λ_s ($J\ K^{-1}\ s^{-1}$) and corrected for latent heat fluxes due to evapotranspiration and freezing/thawing of soil in every layer:

$$(2) C_s \frac{\partial T_{soil}}{\partial t} = \frac{\partial}{\partial z} \left(-\lambda_s \frac{\partial T}{\partial z} \right) + H_{latent, evapotrans} + H_{latent, freezethaw}$$

Where ∂z was the difference between the center points of the soil layers in m.

We considered $H_{latent, freezethaw}$ from the fusion phase change (freezing/melting) of water change both for the surface heat budget, as well as for the subsurface soil layers. In similarity to implementations in JSBACH3 (Ekici et al., 2014), we considered a threshold of supercooled water that cannot undergo a phase change to ice. We defined this threshold as $1/5^{th}$ of the soil layer field capacity as a result of analysed soil moisture observed at the Cherskyi site (Supplement Figure S1). After subtracting this supercooled water volume, the potentially available for freezing in every soil layer is therefore given as:

$$(3) V_{w, available} = \frac{\partial (V_{w, soil} - V_{w, supercooled})}{\partial t}$$

In the model, we use water volumes per area with unit $m^3\ m^{-2}$. The supercooled water fraction was estimated to be 0.2 of the saturated capacity of the soil (Supplement Figure S1). Pragmatically, however, this supercooled liquid water needed to be kept at levels above the permanent wilting point at depths at less than 20 cm in order for vegetative organs to survive the winter.

If the temperature of the soil layer decreased below the freezing point and liquid water susceptible to freezing ($V_{w, available}$) is still present in the soil, the amount of liquid water that froze was derived by first computing the heat difference ΔH of the soil layer temperature, after accounting for the ground heat flux to the layer, and the freezing point temperature. If the cooling given by ΔH is larger in magnitude than cooling needed to freeze the entirety of soil water susceptible to freezing $V_{w, available}$, F_{freeze} ($m\ s^{-1}$) is equal to $V_{w, available}$ and the rest the heat deficit reduces the soil layer temperature after accounting for the latent heat flux from freezing (Equation 9):

$$(4) F_{freeze} = \frac{\partial V_{w, available}}{\partial t}$$

If the cooling determined by ΔH is insufficient to freeze all the water of a soil layer, the amount of water that freezes was calculated as following in every individual soil layer:

$$(5) F_{freeze} = \frac{\Delta H}{L_{fV,w}}$$

With $L_{fV,w}$ being the volumetric latent heat of water in $J\ m^{-2}$. In this case temperature remains at the freezing point (273.15 °K), and liquid water content is reduced by the freezing flux F_{freeze} .

If ice is present in a soil layer, and the temperature resulting from Equation (2) would exceed the freezing point after accounting for the groundheat flux G_s , ΔH is calculated as the heat excess past freezing point. If ΔH is larger in magnitude than the heat required to melt soil layer water content V_{ice} , the amount of ice that is melted is given by V_{ice} given as a negative flux F_{freeze} :

$$(6) F_{freeze} = - \frac{V_{ice}}{\partial t}$$

If ΔH is not large enough in magnitude to melt soil layer ice content m_{ice} , the amount of ice that is melted is calculated as:

$$(7) F_{freeze} = - \frac{\Delta H}{L_{fV,w}}$$

After determining F_{freeze} , soil layer water content V_w , soil layer ice content V_{ice} and soil layer temperature T_{soil} are updated:

$$(8) \frac{\partial V_w}{\partial t} = F_{freeze}$$

$$(9) \frac{\partial V_{ice}}{\partial t} = -F_{freeze}$$

$$(10) \Delta T_s = \frac{\Delta H + L_{fV,w} * F_{freeze}}{C_s * h_s}$$

With h_s being the width of the soil layer in m.

S.4 QUINCY extensions for high latitudes: Snow dynamics

We represented snow dynamics in a 5-layer scheme, for which we considered flows of heat and water within and between the snow layers. We assumed a minimum snow depth threshold of 2 cm, at which the snow coverage of an individual layer starts to affect soil

surface energy fluxes. From 2 cm to 5 cm snow depth, we compute a fraction at which the snow affects the surface heat exchange from nil to one, the rest of the surface heat exchange is driven by bare soil surface heat exchange. The snow layers were constrained to a maximum height of 5 cm, except for the top layer, which can exceed this threshold infinitely. The snow surface heat exchange was solved implicitly, as for the soil:

$$(10) \quad C_{Snow} \frac{\partial T_{Snow,surf}}{\partial t} = R_{net,snow} + H_{sensible,snow} + H_{latent,snowevaporation} + H_{latent,snowmelt} + G_{snow}$$

C_{Snow} is the volumetric heat capacity of snow scaled to the snow layer height $J m^{-2}$, T_{snow} being the snow surface layer temperature, $R_{net,snow}$ the net radiation flux to the snow, $H_{sensible,snow}$ the sensible heat flux to the snow, $H_{latent,snowevaporation}$ the latent heat flux from snow sublimation, $H_{latent,snowmelt}$ the latent heat flux from snow melting, and G_{snow} is the vertical heat flux, all in $J m^{-2} s^{-1}$. The snow surface layer was determined dynamically at every timestep, being the top snow layer where the snow height threshold of 2 cm was exceeded. Snow was thereby assumed to reflect radiation with the albedo constant of 0.6 for both NIR and VIS.

We assumed that the transfer of heat through snow layers was driven by conductivity, with specific heat conductivity and specific heat constants given in Table 1. The transfer of heat between snow layers was assumed to be dominated from fluxes as a result of conductance, for which we assumed a single constant (Table 1). Snow layer temperatures below the snow surface layer were computed as a result of the heat transfer and the single heat capacity used for every layer (Table 1).

$$(11) \quad C_{snow} \frac{\partial T_{snow}}{\partial t} = \frac{\partial}{\partial z} \left(-\lambda_{snow} \frac{\partial T_{snow}}{\partial z} \right) + H_{latent,snow}$$

Heat exchange between snow and soil was considered through conductivity between the bottom snow layer and the first soil layer. Thus, the heat exchange there was computed as the flux between the bottom snow layer and the top soil layer, using the heat conductivity constant of snow.

For temperatures at and above freezing point, we assumed phase change of snow to liquid water and calculated the latent heat flux originating from the phase change. This was done exactly as for the soil latent heat flux from thawing, but without a supercooled liquid water fraction. We also did not represent water re-freezing with the snow column, thus liquid water infiltrated the soil, or was re-routed to the surface runoff flux in the case that the soil was already saturated, directly after melting.

S.5 QUINCY extensions for high latitudes: Inundation

Soil freezing disturbs water flows in the soil, effectively inhibiting vertical transfer of water past frozen soil depths and thus retaining moisture in the top soil (Walvoord and Kurylyk, 2016). We considered the physical inhibition of flow through frozen layers once their ice water mass reached field capacity. We furthermore represented inundation above the permafrost layers. Since there were generally no downward flows past the permafrost layer depth, water accumulates above the permafrost layer in the spring thaw season (Supplement Figure S1).

Drainage of the deepest soil layer was set to nil if it was frozen, causing water to eventually accumulate in soil layers above saturated frozen layers. In soil layers above the permafrost layers, liquid water accumulates in periods of large fluxes of water to the soil (e.g., snow melt), causing saturated conditions through the whole soil column as found in observations in spring/early summer (Supplement Figure S1). Liquid water from snow melt was added to the top soil layer, without considering refreezing within the snow column.

S.6 Construction of GPP product for the Samoylov site

For the site on Samoylov Island, we used the dataset of net eddy covariance CO₂ fluxes which was made publicly available by Holl et al. 2019b and further processed it to obtain partitioned CO₂ fluxes, namely separate half-hourly time series of gross primary production (GPP) and total ecosystem respiration (TER) for the months from May up to and including September. We used a refined version of the bulk model approach presented by Runkle et al. 2013 by fitting a combined photosynthesis-respiration model to consecutive subsets of flux data from within 2-day windows in order to obtain parameter time series instead of fixed NEE model parameters over the course of a vegetation period. We then linearly interpolated the resulting parameter time series with two days resolution to one-day steps and approximated the course of a smooth parameter curve with the same temporal resolution using an infinite impulse response lowpass filter with a cutoff frequency of 90 days from the Matlab v9.7 Signal Processing Toolbox. A similar method has been applied by Holl et al. 2019a who could also show good agreement with bulk model parameter estimates from manual chamber measurements which were interspersed throughout an eddy covariance observation period. To estimate half-hourly TER and GPP flux time series, we used half-hourly observations of air temperature and photosynthetically active radiation to drive the previously determined daily model versions. We filled remaining gaps using a wider range of half-hourly observations of meteorological and soil variables and artificial neural network ensembles following Holl et al. 2020. This approach uses multilayer perceptrons with a single hidden layer and includes an input selection algorithm as well as a complexity reduction routine to minimize the number of hidden layer nodes.

Supplement Figures

Supplement Figure S1

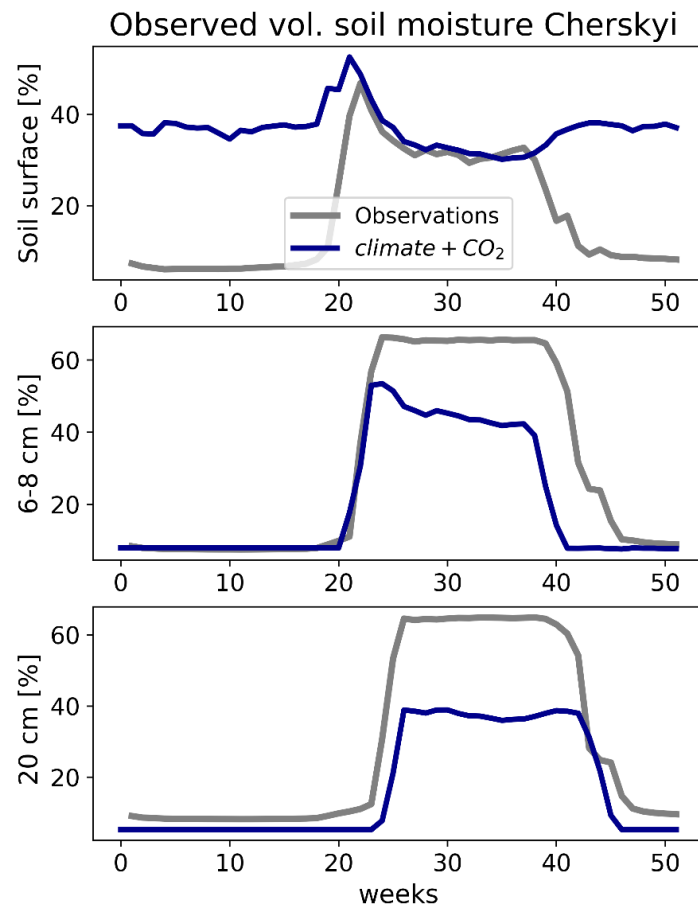


Figure S1. Relative soil moisture averaged over 2015-2019 at the Cherskyi site derived from our model simulations (blue) and observations (grey).

Supplement Figure S2

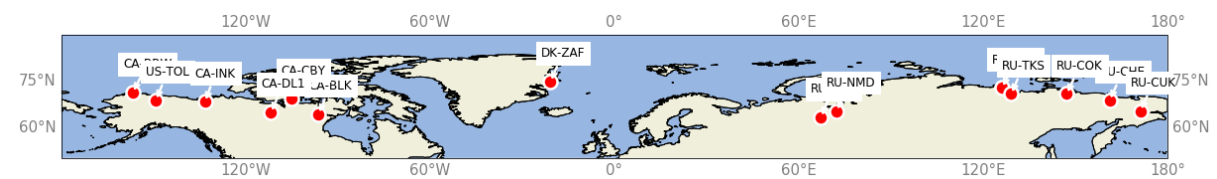


Figure S2. 15 grassland sites chosen across the Pan-Arctic region with Fluxnet identifications (Pallandt et al., 2021).

Supplement Figure S3

Snow depth

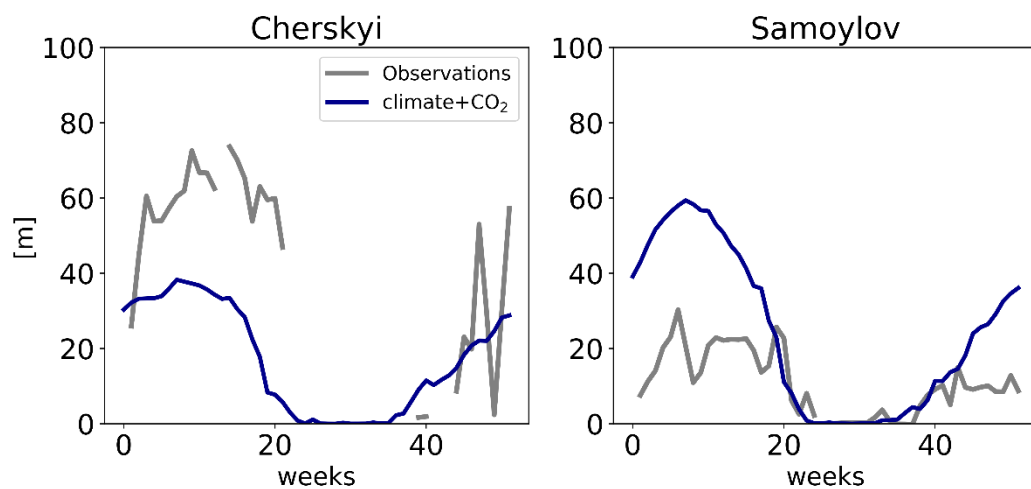


Figure S3. Observed snow depths at Cherskyi and Samoylov over 2015-2019 and 2009-2015, respectively.

Supplement Figure S4

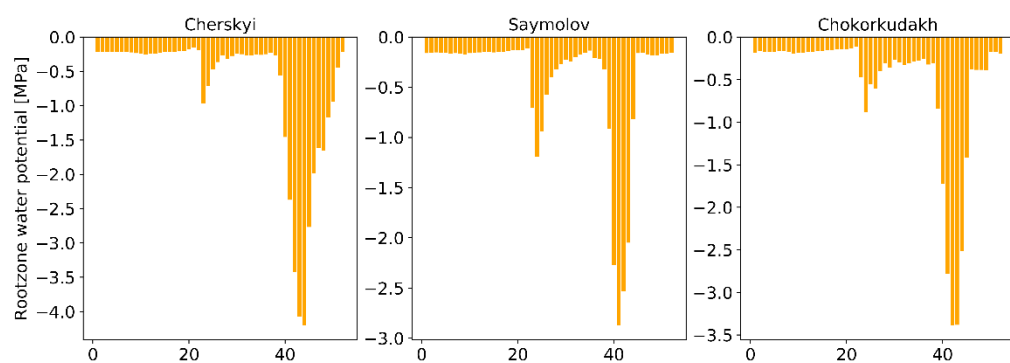
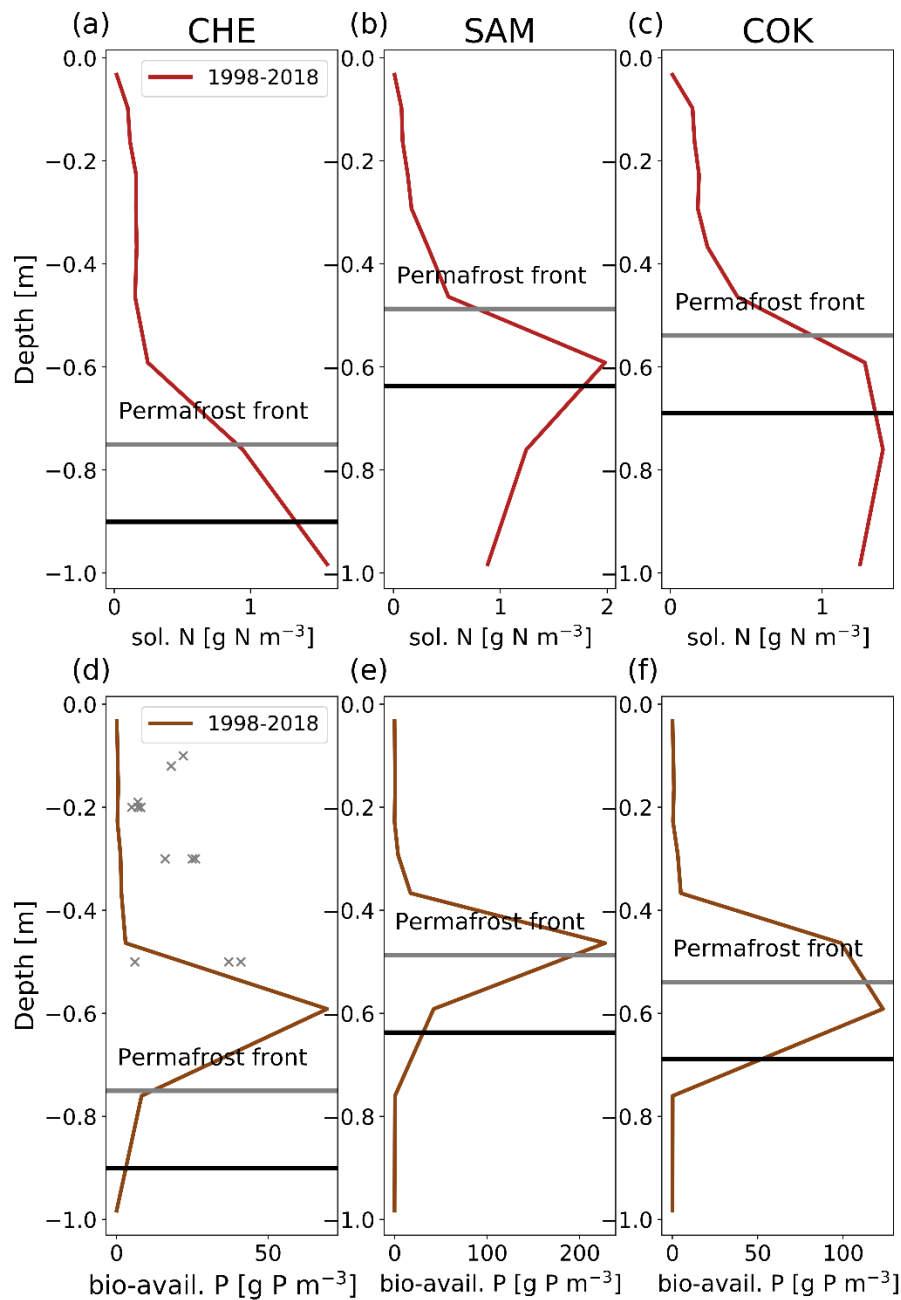


Figure S4. Rootzone water potential [MPa] at Cherskyi, Samoylov and Chokorkudakh sites.

Supplement Figure S5



Supplement S5. Annual mean vertical profiles of (panels a,b,c) inorganic nitrogen (sol. N), meaning solute $\text{NH}_4^+ + \text{NO}_3^-$, and biologically available (solute and weakly bound to mineral) phosphorus (panels d,e,f) at Cherskyi (CHE), Samoylov (SAM) and Chokurdakh (COK) sites averaged over 1999-2019 in simulation *climate+CO₂*. Crosses in panel (d) are observed biologically available P at Cherskyi (Stimmler et al., in review).

Supplement Figure S6

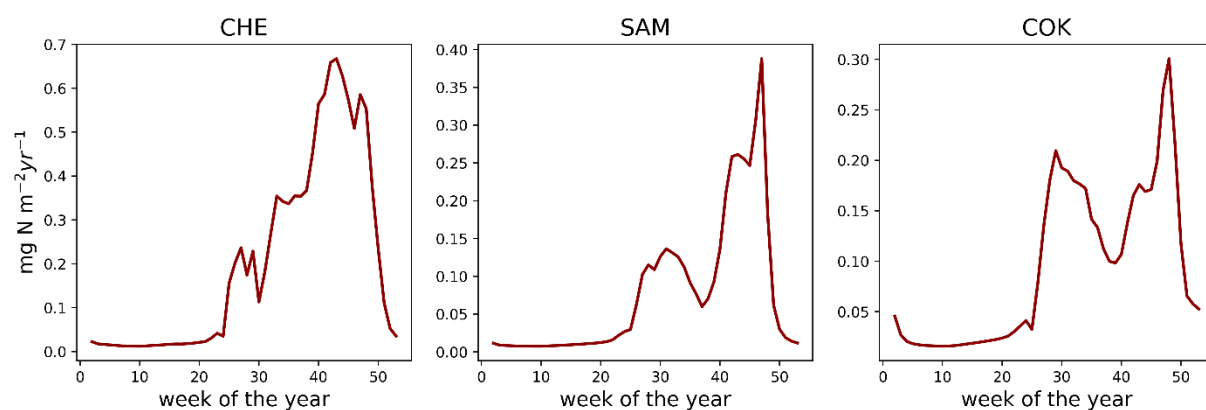


Figure S6 Simulated weekly N_2O emissions averaged over 1999-2019 at (a) Cherskyi, (b) Samoylov and (c) Chokurdakh.

Supplement Tables

Supplement Table S1: Soil bulk weight, N and C ratios of soil samples collected at Cherskyi.

Depths	Bulk weight [mg]	N [%]	C [%]
01, 3 - 5 cm	21,24	1,33	37,89
02, 18 cm	22,38	1,84	31,00
03, 30 cm	20,51	1,68	25,35
04, 33 cm	33,17	0,14	2,09
05, 45 cm	33,53	0,17	2,51
06, 60 cm	35,53	0,14	2,12
07, 68 cm	74,11	0,17	2,41
08, 88 cm	74,73	0,28	4,05
09, 100 cm	80,27	0,26	3,61
10, 113 cm	80,64	0,27	3,49
11, 120cm	79,99	0,16	1,79
12, 138cm	81,81	0,15	1,74
13, 165cm	83,01	0,16	1,87
14, 180cm	80,71	0,14	1,58
15, 200cm	80,92	0,17	2,13
16, 227cm	81,98	0,11	1,20
17, 255cm	81,33	0,15	1,69
18, 287cm	82,49	0,17	2,07
19, 295cm	82,17	0,11	1,28
20, 318cm	81,68	0,19	2,16
21, 338cm	81,22	0,15	1,58
22, 360cm	82,21	0,07	0,60
23, 380cm	83,07	0,15	1,65
24, 395cm	105,42	0,18	2,09
25, 405cm	104,63	0,07	0,65
26, 418cm	109,02	0,11	1,37
27, 465cm	107,32	0,06	0,72
28, 475cm	99,65	0,15	1,72
29, 495cm	111,83	0,07	0,63
30, 505cm	111,80	0,08	0,75

Supplementary Information: References

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