

Impacts of Shrub Coverage for Arctic Ecosystem Carbon Uptake and Storage

Tamara Emmerichs¹, Fabrice Lacroix², Victor Brovkin¹, Sönke Zaehle³, Cheng Gong³, Yu Zhu^{3,4}, Sofie Sjogersten⁵, Carolina Voigt^{6,7}, Klaus Steenberg Larsen⁸, and Eeva-Stiina Tuittila⁹

¹Climate Dynamics, Max Planck Institute for Meteorology, Hamburg, Germany

²Institute of Geography, University of Bern, Bern, Switzerland

³Department Biogeochemical Signals, Max Planck Institute for Biogeochemistry, Jena, Germany

⁴now at: Institute of Plant Science and Microbiology, University of Hamburg, Hamburg, Germany

⁵Faculty of Science, University of Nottingham, Leicestershire, UK

⁶Permafrost Research Section, Alfred-Wegener Institute Helmholtz Centre for Polar and Marine Research, Potsdam, Germany

⁷Department of Earth System Sciences, University of Hamburg, Hamburg, Germany

⁸Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark

⁹School of Forest Sciences, Faculty of Science, Forestry and Technology, University of Eastern Finland, Kuopio, Finland

Correspondence: Tamara Emmerichs (tamara.emmerichs@mpimet.mpg.de)

Abstract. Although shrubs employ ~~distinct water~~ different water and carbon-use strategies compared to trees and are ~~increasingly expanding~~ expanding rapidly across warming tundra and grassland, they ~~remain insufficiently~~ are not adequately represented in global land surface models. ~~Here~~ In this study, we incorporated two ~~shrub types~~ types of shrubs, deciduous and evergreen, into the QUINCY nutrient-enabled terrestrial biosphere model QUINCY, which features a state-of-the-art treatment of soil nutrient dynamics and carbon exchange. We ~~investigate the change in C~~ investigated changes in carbon (C) fluxes and storage due to shrub cover, its response to climate and CO₂ fertilization effect ~~and~~ , as well as the role of nitrogen availability.

With this new implementation, shrubs ~~showed~~ exhibited reasonable seasonal cycle of gross primary production (GPP) at 50 % of the Arctic study sites. The model achieved mean R² values of 0.5 ~~and 0.6~~ on average, when compared with ~~in-situ field~~ measurements and remote sensing products ~~for modeled shrubs~~ , which represents an improvement for evergreen shrubs compared with the old model parametrization. However, ~~at 50 % of the study sites~~ the ~~model underestimated observed GPP~~ due to too strong simulated nitrogen limitation. ~~Compared to needle-leaved evergreen forest the modeled~~ model-measurement agreement is lower at sites with heterogeneous local vegetation, which is not captured by the model hydrology or represented by the shrub plant functional type. The modelled gross primary production of shrubs is similarly distributed ~~with a non-significant~~ compared to needleleaf evergreen forest, with no significant difference in the median. Compared to graminoids ~~the carbon~~ fluxes of shrubs, shrubs' carbon fluxes are 40% higher. Shrubs produce ~~a substantial, though lower, substantial~~ above-ground biomass ~~than needle leaved trees and show phenological patterns that are distinct from those of trees~~. ~~Although~~ , albeit lower than needleleaf trees, and exhibit distinct phenological patterns. While CO₂ fertilization generally benefits all plant types, shrubs appear to ~~maintain a particularly strong growth response~~ have particularly robust growth under elevated CO₂ concentrations.

~~We also demonstrated that the modeled deciduous shrubs reduce their nitrogen sources substantially more than evergreen shrubs, generally resulting in a 50% decrease in gross primary production~~. Providing the plants with unlimited nitrogen ~~and thus~~

doubling doubled gross primary production at most sites and improved the model-measurement agreement by 15 % whereas the modelled deciduous shrubs substantially reduce their nitrogen sources more than evergreen shrubs. A similar effect occurred when initializing nitrogen and carbon contents best were initialized based on permafrost profiles, resulting in partly alleviating which partly alleviated nitrogen limitation in the model. These finding underlines the importance of including Overall, this study demonstrates the impact of evergreen and deciduous shrub PFTs in global land surface models to accurately predict ongoing changes in the Arctic C cycle - vegetation on the Arctic carbon cycle and ongoing changes. It recommends including shrub plant functional types in global Earth system models. However, the strong nitrogen limitation of Arctic shrub productivity when using the standard model parametrizations suggests that the Arctic standard model parameterizations suggests that global models underestimate the Arctic's contribution to global land carbon is underestimated by global models.

30 Copyright statement. TEXT

1 Introduction

The high latitude ecosystems north of 60 degree N are vulnerable to climate change, with this region identified to be. This region is warming at around 3-fold three times the global rate (Giesse et al., 2024). Arctic soils store contain vast amounts of organic carbon (C) in continuously frozen soil layers called permafrost soils. This the permafrost (frozen soil). Under climate warming and the thawing of permafrost, this carbon could be released to the atmosphere as carbon dioxide or methane under climate warming and the thawing of permafrost, inducing a positive climate feedback (Schuur et al., 2015, 2022). With the loop (Schuur et al., 2015, 2022). An increase of atmospheric temperature, prolongation of prolongs the growing season and the deepening of the active layer is causing major deepens the active layer, causing major shifts in vegetation growth and cover shifts in the Arctic (Mekonnen et al. (2021) and references there in), Liu et al. (2025)).

40 Arctic shrub vegetation is short statue (mostly < short-statured (mostly under 2 m tall) and often prostrate and, it can grow beyond the cold limits of trees due to their its adaption to cold environments. Importantly, shrubs show a Shrubs exhibit faster wood production than trees and thus only need a 20-50 % shorter growing seasons, enabling them to complete their growth within a growing season that is 20-50% shorter (Trembl et al., 2019; Körner, 2012), which is a key adaptation to the Arctic conditions, and intense competition for limited light and nutrients beyond the treeline. Shrubs are classified as either evergreen and or deciduous species. Deciduous shrubs grow faster than evergreen species, since their small leaf mass per unit area enables them to intercept more light for a given investment of leaf C than evergreen shrubs (Parker et al., 2021; Mekonnen et al., 2018).

45 Heijmans et al. (2022) Heijmans et al. (2022) found that shrubs are becoming increasingly dominant in the Arctic. Current estimates suggest they comprise about that they comprise approximately 40 % of the Polar Arctic's plant biomass plant biomass in the Polar Arctic (Orndahl et al., 2025). The expansion rate has been estimated to about at around 38 % from 1982-2014 1982 to 2014 and 27 % from 2000-2020 2000 to 2020 in the high-northern latitudes due to increases biomass of, due to increased biomass in existing stands and new establishment (Chen et al., 2020; Andreu-Hayles et al., 2020; Gui et al., 2025). Studies

(Meyer et al., 2021; Elmendorf et al., 2012, e.g.), mainly report an enhanced coverage of tall deciduous shrubs, such as birch, willow~~and alder, which~~, and alder. This process is often termed as 'shrubification'. Recently, ~~the~~ expansion of evergreen dwarf shrubs, which are ecologically ~~different~~ distinct from tall deciduous shrub species, ~~also have~~ has also been observed in the Arctic (Vowles and Björk, 2019). ~~These~~ However, these vegetation changes are, however, spatially heterogeneous and are controlled by a mixture of environmental factors other than temperature, such as changes in soil wetness and plant-plant interactions (García Criado et al., 2025; Martin et al., 2022). ~~Shrubs responding~~ The ability of shrubs to respond more to warming than e.g. graminoids is linked to their ~~ability to grow their woody tissue and thereby increase their capacity to develop woody tissue, thereby increasing the~~ height and width of their canopy (Bret-Harte et al., 2001, 2002).

Changes in ~~the~~ Arctic vegetation cover ~~initiate several feedbacks to the atmosphere by~~ trigger several feedback loops in the atmosphere. These include decreasing the albedo~~and thus rising~~, thereby increasing the surface temperature, and ~~by~~ impacting soil-plant interactions~~through e.g.~~ Examples of this are deepening the active layer, higher ~~mineralization rates and litter quality, which in turn~~ mineralisation rates, and improving litter quality. These changes affect the ecosystem's C balance (Bonfils et al., 2012; Meyer et al., 2021; Mekonnen et al., 2021). ~~Moreover, Arctic vegetation shifts~~ Furthermore, shifts in Arctic vegetation potentially affect permafrost thaw by altering ~~the surface temperature~~ surface temperatures (Heijmans et al., 2022). Buckeridge et al. (2010) conclude that increased nutrient inputs via enhanced litter inputs from smaller shrub species subsequently cause an increase in the growth of tall shrub tundra species.

Field studies show that shrubs ~~have various impacts on~~ impact soil nutrient cycling ~~since in various ways, as~~ they are associated with ~~higher~~ high leaf litter quality and quantity, ~~thus~~. This means they contain more nitrogen, which enhances decomposition rates (~~Martin et al. (2022); Moore et al. (2024)~~ Martin et al. (2022); Moore et al. (2024) and references therein) ~~compared to Boreal~~. This is in contrast to boreal trees. The vertical distribution of soil ~~C~~ carbon (C) is determined by ~~the~~ nutrition allocation, litter quality~~and plants root depth, i.e.~~, and plant root depth; for example, shrubs store more C in deep soils than ~~graminoides~~ (Du et al., 2024). ~~However, the effect of shrub encouragement can not only largely change with climate~~ graminoids (Du et al., 2024). Besides climate, several other factors influence shrub establishment and growth. The acceleration of nutrient cycling, driven by higher soil temperatures~~and~~, greater litter inputs~~and~~, and greater litter turnover, has been found to ~~be a key player for~~ play a key role in vegetation change. However, despite the importance of these processes the impact of nutrient dynamics on shrub growth and C cycling is neglected in most commonly used vegetation models (Miller and Smith, 2012).

The magnitude of the impact of the rapid shrub expansion in Arctic landscapes on the current and future Arctic C balance is uncertain. Given the importance of shrubs in ~~Arctic~~ these landscapes shrub plant functional types (PFTs) must be included in ~~land-biosphere~~ land-biosphere models to more accurately represent C dynamics in the heterogeneous Arctic landscapes. Accordingly, we here employ the QUINCY terrestrial biosphere model ~~QUINCY~~ (QUantifying Interactions between terrestrial Nutrient CYcles and the climate system v1.0) (Thum et al., 2020) which includes the main features of Arctic ecosystems, such as soil C storage, nutrient limitation and vertical ~~discretization for a realistic simulation of~~ discretisation, to realistically simulate C dynamics in the Arctic and physical processes relevant in high latitudes (Lacroix et al., 2022). ~~In contrast to~~ Unlike other major community land models, QUINCY represents vegetation with PFTs based on physiology ~~and not on geography which overcomes~~ rather than geography, overcoming the need for regional PFT definitions~~like boreal trees, thus~~

limiting the need for parameters, such as boreal trees and limiting the number of parameters required to a minimum (Thum et al., 2020). To assess the effects of shrub expansion for on ecosystem C dynamics across the Arctic, we here implemented two shrub PFTs firstly into QUINCY (Sec.2.1, 2.3). With Using this new model configuration, we performed simulations taking that took into account coverage by of three different vegetation types, namely: boreal forest, graminoids and shrubs from 16 Arctic sites, and shrubs. Additionally, we conducted sensitivity simulations with constant CO₂, with nitrogen supply set to levels that do not limit carbon cycling, and with nutrient initialization-initialisation in the permafrost (Sec. 2.2), respectively. By the means of this simulations These simulations were conducted at 16 different Arctic sites. Through these simulations and two observational datasets (Sec. 2.4), we aimed to answer the following research-specific research-specific questions:

- (1) How much carbon do shrubs take up and store and is this in agreement with observations absorb and store, and does this align with observed data? - Section 3.1
- (2) How does the response of C-carbon uptake and storage in shrub-covered ecosystems shrub-covered ecosystems differ from that in boreal forests and graminoid-dominated tundra when subjected to combined climate warming and CO₂ fertilization differ from boreal forest and graminoid-dominated tundra? - Section 3.2 and 3.2.1
- (3) What role does nitrogen cycling play for shrub growth and C storage, in particular in response to increasing particularly in response to increased nitrogen availability from permafrost thaw? - Section 3.3

2 Methods

2.1 QUINCY model

The QUINCY terrestrial biosphere model QUINCY (Thum et al. (2020); qui (2019) simulates the coupled C-carbon, nitrogen (N) and phosphorus (P), as well as water and energy cycles. The model-It represents physical processes relevant to high latitudes, such as snow dynamics, soil freeze-thaw, and adaptive rooting depth-to-layers that are depths to layers in non-frozen layers (Lacroix et al., 2022). The standard version of the model includes 12 different PFTs with flexible parametrizations parameterizations for leaf characteristics, phenology, and other growth and turnover dynamics. This-The concept of PFTs groups all plant species in-into a limited number of classes and thus allows, thus allowing for a much more traceable interpretation of the plant-s interactions (Poulter et al., 2015). The about approximately 40 parameterizations representing the different plant characteristics and functionalities in QUINCY are based on plant trait databases (KATTGE et al.). Here, we have added additional PFTs to simulate Arctic shrubs.

In QUINCY, vegetation consist-consists of structural pools (leaves, sapwood, heartwood, coarse roots, fine roots, and fruit), a fast overturning and a fast overturning, respiring non-structural pool (labile), as well as a seasonal, non-respiring, and non-structural storage pool (reserve). The canopy has-comprises several layers (a multilayer canopy scheme), which-includes-a representation-including separate representations of photosynthesis and canopy conductance for sunlit and shaded leaves separately within every-each layer. Vegetation processes as well as nutrient uptake and availability respond to local environmental conditions on a process-specific time-scale-timescale, dynamically enabling a certain memory effect (Thum et al., 2020). Plants

partition the required C between growth, respiration and storage, ~~with acclimation~~ acclimatising to meteorological conditions
120 and nutrient availability.

The soil is explicitly ~~vertically-discretized in~~ discretized vertically into 15 layers ~~with of~~ increasing thickness down to a
depth of 9.5 m. ~~This applies for~~, ~~and this applies to~~ soil temperature, texture, moisture, and the biogeochemical soil pools.
Soil biogeochemical pools are represented by five organic pools: structural, ~~polymeric~~, polymeric, and woody litter, ~~fast and~~
~~slow-degrading~~, ~~and fast and slow-degrading~~ soil organic matter; as well as solute concentrations of ammonium (NH_4), nitrate
125 (NO_3) and phosphorus (PO_4). Each of these organic pools contains C, N and P (Thum et al., 2020). ~~In particular, the model~~
The model specially accounts for the ~~full~~ nitrogen cycle in ~~the soil~~, soil by simulating nitrogen inputs through symbiotic
(microbial) fixation ~~at higher plants and in higher plants, as well as~~ free-living (~~asymbiotie~~ non-symbiotic) N fixation ~~at in~~ all
parts of the ecosystem. ~~It also accounts for~~ N deposition, and the transformation processes of mineralization, nitrification, and
denitrification, as well as transport between soil layers. N is always accounted for as NO_3^- and NH_4^+ .

130 2.2 Site-level simulations setup and forcings

Site-level QUINCY model simulations were conducted for ~~16 sixteen~~ Arctic sites (Fig. ~~??~~, Table ??1 and Table S1) from
1901 to ~~2010 where data measured at~~ 2010. Data on shrubs and GPP estimates were provided by the ABCflux dataset version
2.2 for these sites. In the reference simulation, ~~we represent the vegetation at the 16 sites each site is represented~~ by one
of the two shrub PFTs according to the ~~reported vegetation at the sites (vegetation reported at each site (see Table S1))~~. The
135 simulations include nitrogen dynamics ~~since plants~~, as mineral nitrogen is often known to limit plant growth in the Arctic
are ~~known to be often limited by mineral nitrogen~~ (Mekonnen et al., 2018; Martin et al., 2017; Prager et al., 2017). Different
model configurations were chosen to quantify the differences towards between ecosystems covered by gramomids graminoids
and NE trees at the same sites. A second set of simulations ~~disentangle between~~ disentangles the effects caused by climate
drivers, CO_2 fertilization and nutrient limitation (1).

140 The standard initialization of QUINCY does not account for the elevated ~~contents~~ levels of soil organic C & N characteristic
~~to of~~ permafrost soils. These contents ~~can also not~~ cannot be built up in a standard QUINCY spin-up, ~~as they either, as this~~
would require a ~~paleo-timescale type simulation reproducing (at least)~~ simulation of the type used for paleo-timescales that
reproduces at least the last interglacial and glacial, ~~which periods~~. This is neither practical for our ~~applications, nor do the~~
purposes, nor feasible given the lack of the required model forcing data ~~exist~~. In this study, we therefore ~~changed~~ adapted the
145 initialization procedure by ~~adapting both~~ adjusting the C and N contents, as well as the distribution of the initialization ~~in the~~
~~ease~~, when a site is identified as permafrost based on the definition by and methods in Palmtag et al. (2022). The ~~distribution~~
~~curve in the permafrost is initialized with~~ permafrost distribution curve is initialized using a Weibull function assuming with
a shape parameter of 0.6 (~~instead of 2~~) according to Palmtag et al. (2022). ~~A, and the~~ minimum relative deep permafrost
concentration is set ~~to at~~ 0.3 of ~~surface soil concentrations according to estimated distributions from Palmtag et al. (2022)~~.
150 ~~The soil~~ the surface soil concentration according to the estimated distribution. Soil organic matter is initialized with a single
permafrost content of ~~121000~~ 121,000 gC m⁻² yr⁻¹ for the first 3 m, which is the ~~vertically-integrated average C~~ Estimated by
~~Palmtag et al. (2022)~~. ~~The permafrost~~ vertically integrated average C. Permafrost nitrogen is initialized using a C:N ratio of

~~14 according to Palmtag et al. (2022). We note 14. It should be noted~~ that the applied approach does not account for spatial heterogeneity in permafrost soil ~~contents and distributions for content and distribution during~~ initialization.

155 The meteorological forcing ~~driving the model stems that drives the model is derived~~ from the University of East Anglia Climatic Research Unit Japanese Reanalysis (CRU-JRA; Harris (2019)), which is a reanalysis of incoming solar radiation, surface temperature, humidity, precipitation, surface pressure, and surface winds. ~~The This~~ dataset is available ~~at with~~ a spatial resolution of 0.5×0.5 degrees and at a ~~6-hourly temporal resolution. The data temporal resolution of 6 hours.~~ Data for our selected sites were extracted from the CRU-JRA dataset according to their geographic coordinates (Zaehle and Friend, 2010).

160 Furthermore, the soil is represented by 15 layers, with increasing thickness down to a depth of 9.5 m. The model starts the transient simulations after a spin-up period of 1000 years using ~~repeating cyclic~~ forcing data from 1901-1930. The atmospheric CO₂ concentrations are prescribed according to Friedlingstein et al..

Table 1. Description of the conducted simulations (1901-2010)

Simulation	PFT	Forcing	Nutrients
Shrubs	shrub PFTs	atmospheric CO ₂ forcing according to Friedlingstein et al.	C and N dynamics (CN mode)
Trees	needleleaf evergreen	atmospheric CO ₂ forcing according to Friedlingstein et al.	C and N dynamics (CN mode)
Grass	C ₃ graminoid (TeH)	atmospheric CO ₂ forcing according to Friedlingstein et al.	C and N dynamics (CN mode)
ShrubsNOF	shrub PFTs	constant CO ₂	C and N dynamics (CN mode)
TreesNOF	NE trees	constant CO ₂	C and N dynamics (CN mode)
GrassNOF	C ₃ graminoid	constant CO ₂	C and N dynamics (CN mode)
ShrubsConly	shrub PFTs	atmospheric CO ₂ forcing according to Friedlingstein et al.	C (C-only)
ShrubsNfertC	shrub PFTs	constant CO ₂	C (C-only)
ShrubsPM	shrub PFTs	atmospheric CO ₂ forcing according to Friedlingstein et al.	C and N dynamics (CN mode), addition of permafrost nutrients

2.3 New shrub implementation

We implemented two new shrub PFTs: broadleaved deciduous (BD) and ~~needle-leaved-needleleaf~~ evergreen (NE). ~~As a baseline, the~~ ~~The~~ two shrubs are ~~similarly parametrized as trees but treat based on the respective default parametrization of the woody PFT, but due to the physiological and phenological differences~~ important aspects concerning the initial leaf N, plant allometry, root distribution and ~~turnover times of wood differently. The new parameters are listed in Table 2. According to the physiological and phenological differences to trees (heartwood development, leaf/sapwood ratio, growing, turnover, leaf nitrogen, roots) new parameters were specified differently to the default BD and NE PFT, respectively, wood turnover times are~~

165 ~~specified~~ based on measurement studies and trait databases (e.g. TRY)-, ~~Kattge et al. (2020)). The new parameters are listed in Table 2.~~

170

2.4 Observational data

The ABCfluxnet v2 (~~Virkkala et al., 2025b; Leffler et al., 2026)~~ ~~data~~ ~~data, cited in references~~ Virkkala et al. (2025b); Leffler et al. (2026) ~~was~~ recently compiled to provide a dataset of ~~in-situ in situ~~ Arctic–boreal terrestrial ecosystem CO₂ flux measurements

Table 2. New parameters for NE and BD shrubs replacing the default ~~needle-leaved~~needleleaf evergreen PFT. For simplicity, the latter one is referred to as 'Tree'.

Parameter	BD default (Trees)	BD shrub	NE default (Trees)	NE shrub	TRY database Kattge et al. (2020)
Default leaf nitrogen concentration ($Leaf_N$ in [mgN gDW ⁻¹])	21.34	23.43	12.09	10.11	TRY database Kattge et al. (2020)
Turnover time of the fraction of sapwood that is in branches (τ_{branch} in [years])	10	40	10	30	based on higher sapwood
Turnover time of the fraction of sapwood that is in branches ($\tau_{sapwood}$ in [years])	40	70	40	60	Zhang et al. (2013)
Fraction of sapwood that is in branches, sapwood that is turned to litter ($frac_{sapwood-branch}$)	0.05	0.1	0.05	0.02	Thum et al. (2020)
Parameter in height diameter relationship ($allom_{k1}$)	55	35	55	25	Zhang et al. (2013)
Parameter defining the root distribution ($k_{root,dist}$)	2.0	3.5	2.0	3.5	determined based on calculations
Leaf area to sapwood area ratio (k_{latosa})	4000	3500	4000	3500	Zhang et al. (2013); He et al. (2025)
Coarse root to sapwood mass ratio (k_{crtos})	0.1	0.9	0.1	0.9	Ma et al. (2021)
Weekly air temperature threshold ($t_{air,senesence}$ in [degC])	8.5	0	0	0	Fu et al. (2014)
Maximum GDD requirement ($gdd_{req,max}$ in [degC days])	800	34.8	0	0	Fu et al. (2014) and courtesy to Yu Zhu
Scaling factor in the GDD for dormancy ($k_{gdd,dormance}$ in [days ⁻¹])	0.007	0	0	0	Fu et al. (2014)

175 (Virkkala et al., 2025a). The synthesized GPP is given as cumulative flux densities aggregated at the monthly timescale. In addition to eddy covariance data (EC), this includes fluxes estimated ~~with-using~~using chamber methods to increase data coverage; ~~which were performed-~~These methods were employed during the growing season. We selected sites where ~~the growth of shrubs is reported for more than one point~~shrub growth has been observed at multiple points in time. The 16 study sites are located across the northern USA, Canada, Finland, Norway, Sweden and Siberia, as shown in Figure 1. These sites are

180 in wet, moist or dry tundra, fens, bogs or boreal forests and are vegetated by either a mixture of shrubs, trees and grasses or only shrubs (see Table S1). The measurements were averaged and ~~evaluated-over-used across~~evaluated-over-used across different years to minimize the ~~impacts-impact~~impact of climate variability. ~~First, we compare our model results to the~~The data set includes eddy-covariance (EC) ~~data of the given site (if available) which generally represents measurements, which generally represent~~a 100 m radius footprint of the measurement tower. ~~The chamber data~~For some sites, only chamber data exists (Table S1) ~~can be seen as a~~

185 ~~highest-resolved~~which can be considered the most highly resolved, plot-scale GPP estimate of a specific vegetation/soil unit. To further evaluate the simulated GPP, we also use data extracted from the global MODIS/Terra Level-4 products of MOD17A2H (collection 6) (Running et al., 2015) and MOD17A2HGF (~~collection~~Collection 6.1) (Running and Zhao, 2021) at the site coordinates. Both products provide ~~cumulative 8-day a cumulative eight-day~~composite of GPP values at a spatial resolution of 500

~~m spatial resolution and were interpolated. They estimate GPP by applying m and have been interpolated. GPP is estimated~~by applying a radiation-use efficiency framework that integrates absorbed photosynthetically active radiation (APAR) with the biome-specific radiation conversion efficiency (ϵ), which is constrained by meteorological stress. While the MOD17A2H product contains gaps due to ~~input quality-, the quality of the input data, the~~MOD17A2HGF product reduces data gaps by employing additional temporal gap-filling based on quality control flags. Both products are subject to uncertainties ~~related to input data quality~~relating to the quality of the input data, land cover classification, and model assumptions. With ~~spatially~~

195 ~~and temporally more continuous-a~~GPP time series that is more continuous in space and time, the MOD17A2HGF dataset ~~further introduces interpolation uncertainty-introduces an additional source of uncertainty in the form of interpolation~~, which dampens the signals caused by inter-annual variability ~~of in~~in climate or ecosystem disturbances. Extensive ~~validations-validation~~validation against eddy covariance measurements ~~show that MOD17-series shows that MOD17 series~~products can moderately capture the

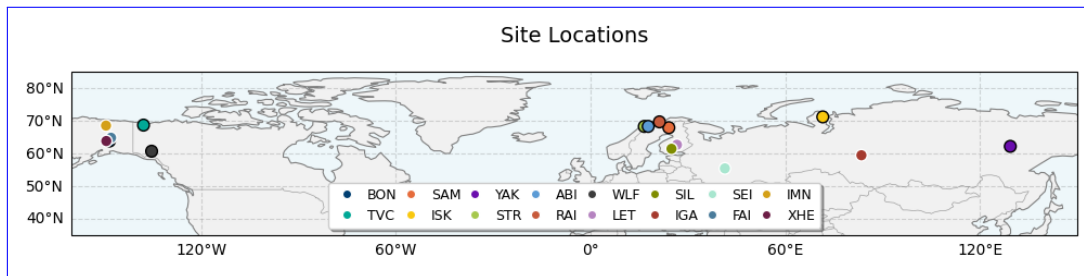


Figure 1. Map of the 16 chosen stations: BON: Bonanza, US; TVC: Trail Valley Creek, CA; SAM: Sammaltunturi fell, FI; ISK: Iskoras, NO; YAK: Yakutsk, RU; STR: Stordalen, SE; ABI: Abisko, SE; RAI: Raisduoddar, NO; XHE: Neon Healy, US; WLF: Wolf Creek, CA; LET: Lettuoso, FI; SIL: Siikaneva, FI; IGA: Igarka, RU; SEI: Seida, RU; FAI: Fairbanks, US; IMN: Imnavait, US. The black edge indicates the needleleaf and the white edge the broad-leaved shrub.

inter-annual interannual and seasonal variability of GPP in GPP, with R^2 over 0.6 across different biomes and climate regimes (Zhu et al., 2018; Tang et al., 2015; Wang et al., 2017). We extracted GPP time series from the datasets for the different sites using the nearest neighbor neighbour approach.

3 Results and Discussion

3.1 Modeled Modelled vegetation productivity versus observations

Comparison of the The modelled shrubs capture a reasonable monthly mean seasonal cycle of modeled and measured GPP show that the CN model configuration agrees well with the GPP measurements at around GPP at half of the sites but leads to an underestimation (R^2 validated sites (six out of twelve, with a 50 % measured seasonal cycle), when compared to the field measurements in Figure 2. Modelling with the new NE shrub PFT improves the mean R^2 (<0.6 , Table S2), Figure 2) at the remaining sites, where the N-limitation may be too strong in the CN model. The C-only model, which allows for unlimited biological N-fixation, improves the model performance by 23 % with regards to the measured GPP data, in particular for NE shrubs (value to 0.46 across nine sites, compared to the default (tree) PFT (see the dashed line in Fig. 2 and Table S2). In contrast, simulations with the BD shrub (7 sites) mostly underestimate the measured seasonal cycle of GPP; the default (tree) PFT therefore agrees better with the measurements (mean $R^2=0.6$) while at three sites (XHE, SIL, IMN sites), the model's GPP estimates fall substantially below observed values. For further evaluation, we compared our model's GPP outputs to GPP MODIS satellite products. MODIS data is widely used for the evaluation of the C to evaluate of the carbon cycle in global terrestrial biosphere models and in the Coupled Model Intercomparison Project (CMIP) models (50 % using use the JSBACH surface scheme) (Hu et al., 2022), showing a high agreement in the high latitudes. Lacroix et al. (2022) reports similar correlations when comparing a permafrost-enabled version of the QUINCY model with MODIS and eddy-covariance data. Here In this study, the MODIS GPP products show a higher correlation towards the model with a with the model, with mean R^2 value of 0.62 and 0.67 (CN and C-only, values of 0.71 for NE shrubs and 0.50 for BD shrubs (Table S2) than compared

220 to the ~~observational data (0.48, 0.57)~~ site measurements. This is generally an improvement for NE shrubs compared to the NE default (tree) PFT ($R^2=0.59$). The MODIS products ~~are generally in line with the observational data but they disagree~~ generally align with field measurements, though they diverge significantly at two sites. At the ISK site (Norway), MODIS and ~~the~~ (CN) model GPP ~~agrees quite well while the observed GPP agree quite well, whereas the GPP measured in the field~~ is much larger. This may be due to ~~by~~ the specifics of ~~the~~ local climate and landscape at the ~~used site coordinates~~. ~~Namely site coordinates~~

225 ~~used. Specially~~, half of the field measurements at the ISK site are taken in wet tundra areas (Pirk et al., 2024) whereas ~~however~~ the model soil hydrology tends to be rather dry (~~Fig. ??~~). ~~A similar uncertainty source exists for the comparison at the SIL site. At the LET (Finland) where most of the measurements happened in a fen ecosystem (reported in dataset as bawld-class) which is not represented in the QUINCY model. At sites with a significant fraction of forest e.g. the LET (Finland) site (Heydel and Tackenberg, 2017) site, which has a significant proportion of forest (e.g. (Heydel and Tackenberg, 2017)) both~~

230 observational datasets show a higher GPP which the model does not reflect because it represents shrubs only (in this simulation). ~~A further~~ ~~Another possible~~ source of the model bias ~~might be~~ is the underestimation of soil moisture at sites with a higher wetness than 25 % ~~like at~~, ~~such as~~ the Stordalen (STR, Sweden) site (Holmes et al., 2022). ~~While we deem the agreement between model and observations inferred from field data measurements (EC measurements if available) and MODIS products to be adequate, the~~ Overall, two out of sixteen sites (Lettuoaso (LET) and Stordalen (STR)) are considered not to be representative

235 ~~of the simulated shrub PFTs due to their heterogeneous ecosystems.~~

~~All in all, the model's performance depends on the model configuration chosen chosen configuration, the evaluated shrub PFT, the shrub PFT type evaluated, local heterogeneity of vegetation coverage, as well as the local meteorological conditions, which may differ from the foreings used in the model. While this comparison is an important benchmark for the model and its new parametrization, it is limited to monthly GPP values. The structural and phenological plant characteristics can be only~~

240 discussed quantitatively in the later analysis of this study due to limited data availability and time constraints.

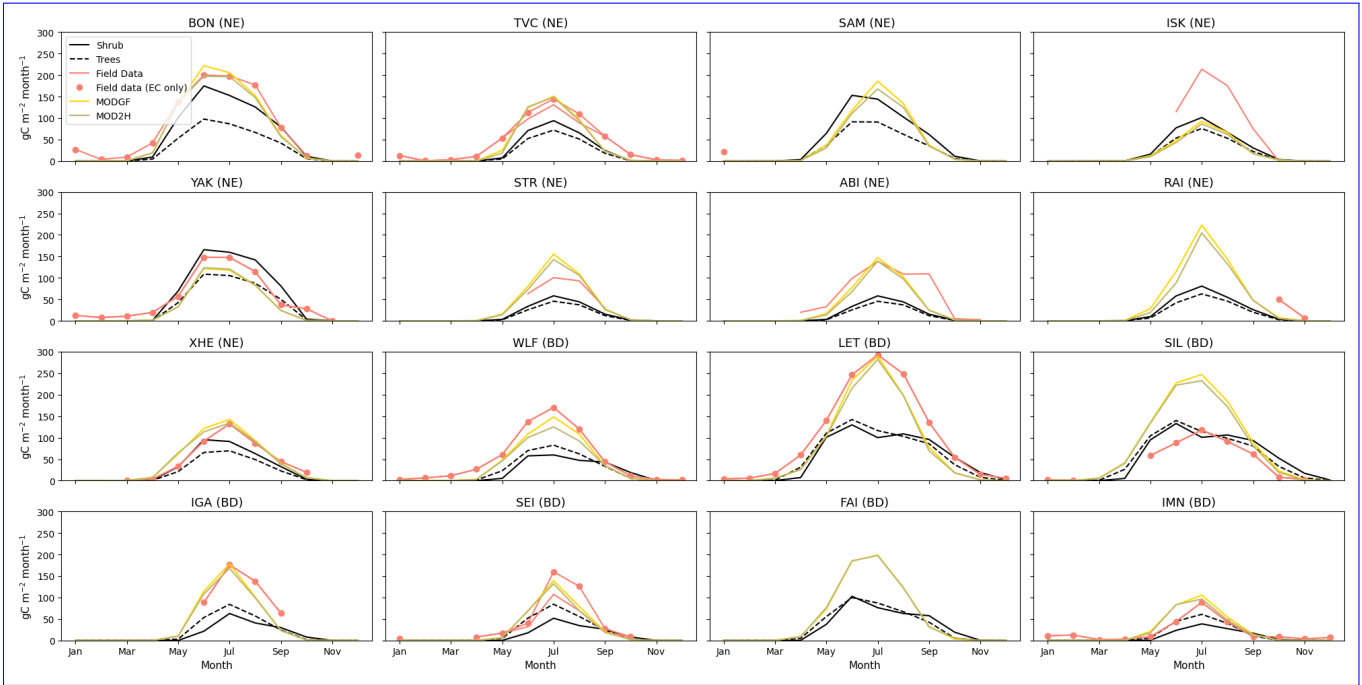


Figure 2. Multi-year mean seasonal cycle of GPP [$\text{gC m}^{-2} \text{ month}^{-1}$] by measurements (field data and MODIS satellite data: [MODGF](#) (MOD17A2HGf) and [MOD2H](#) (MODIS17A2H) and model versions [CN](#) with new shrub PFT, tree PFT and [C-only](#) for graminoid PFT at 16 sites (BON: Bonanza, US; TVC: Trail Valley Creek, CA; SAM: Sammaltunturi fell, FI; ISK: Iskoras, NO; YAK: Yakutsk, RU; STR: Stordalen, SE; ABI: Abisko, SE; RAI: Raisduoddar, NO; XHE: Neon Healy, US; WLF: Wolf Creek, CA; LET: Lettuoso, FI; SIL: Siikaneva, FI; IGA: Igarka, RU; SEI: Seida, RU; FAI: Fairbanks, US; IMN: Imnavait, US) at individual time periods where field data is available. [See Table ?? for the site acronyms.](#)

3.2 Present day C uptake and storage

The simulated (multi-site) average annual GPP flux at [shrubs shrub sites](#) is $371 \text{ gC m}^{-2} \text{ year}^{-1}$, ranging from 132 to $735 \text{ gC m}^{-2} \text{ year}^{-1}$ [among the sites](#) for the time period 1990-2010 (Fig. 3a). These estimates (and their partitioning) are [in line with consistent with the](#) data synthesized by Virkkala et al. (2025a) who report an average (area-upscaled) Arctic GPP of $300 \text{ gC m}^{-2} \text{ year}^{-1}$ for tundra and $416 \text{ gC m}^{-2} \text{ year}^{-1}$ for the [arctic-Arctic](#) permafrost region, [albeit accounting although this accounts](#) for all tundra vegetation species (graminoids, shrubs, mosses, and lichen). The [distribution of annual mean GPP annual GPP for shrubs has a much wider interquantile range than for trees and graminoids, i.e. it is more variable](#) (Fig. 3b) [overlaps with the one by the tree PFT but, in contrast, it is skewed towards higher values which. The distribution is more symmetrical, with shorter tails and a flatter peak and a lower skewness and kurtosis. This](#) shows the better adaptation of shrubs to the cold Arctic climate, as it has been observed [elsewhere](#) (Mekonnen et al., 2021, e.g.). Thus, the median ([without not](#) considering the high values) of ([new](#)) [the new](#) shrub and tree [PFT-PFTs](#) are not significantly different, while the average annual GPP [is increased increases](#) by 16 % due to the implementation of shrubs. [Also Additionally](#), Meyer et al. (2021) report a [substantial substantially](#)

higher GPP at shrubs than at trees ~~simulated at an site when simulating a~~ Canadian site with the CLASSIC model ~~which is in good agreement, which aligns well~~ with the site measurements. ~~Shrubs-Shrub~~ dominance instead of graminoid cover would
255 ~~rise-increase the~~ annual mean and median GPP by 40 %, respectively.

The GPP change of the three PFTs is determined by different N pathways ~~whereas, and~~ the strength of the correlation varies not only across the PFTs ~~but also across the, but also between~~ sites. For ~~instance example~~, the GPP at NE trees and shrubs ~~increases much stronger with-increase much more strongly in response to~~ NH_4^+ uptake than at graminoids ~~while comparing graminoids, whereas comparing graminoids~~ and trees to BD shrubs reveals a similar slope (Fig. S1). Thus, among the
260 shrub species, the model ~~simulate faster growth for deciduous shrubs simulates faster growth~~ in response to NH_4^+ uptake ~~for deciduous shrubs~~, as also reported by (Chen et al., 2020). For all shrubs, the change ~~of in~~ NH_4^+ uptake explained 50-70% of the GPP change compared to trees (see R^2 in Fig. S2). For NE shrubs, N fixation and NH_4^+ net mineralization ~~showed also~~ ~~also showed a~~ significant correlation with the GPP changes (Fig. S2). Most of the ~~GPP-increase-increase in GPP~~ at evergreen shrubs could be additionally explained by higher biological nitrogen fixation (BNF) compared to ~~shrubs, where the default~~
265 ~~PFT. Here~~, the absolute numbers ~~are about approximately~~ half the magnitude of the plant NH_4^+ uptake (Fig. S3). Indeed, Davies-Barnard and Friedlingstein (2020) and Schore et al. (2023) report ~~substantial-substantially~~ higher asymbiotic BNF ~~at shrubs than at trees in shrubs than in trees~~, driven by bacterial activity. The GPP changes ~~at in~~ deciduous shrubs are usually lower than ~~at evergreen shrubs which might in evergreen shrubs, which may~~ explain the low correlation. The GPP differences from graminoids are generally less correlated ~~to with~~ changes in the N uptake pathways.

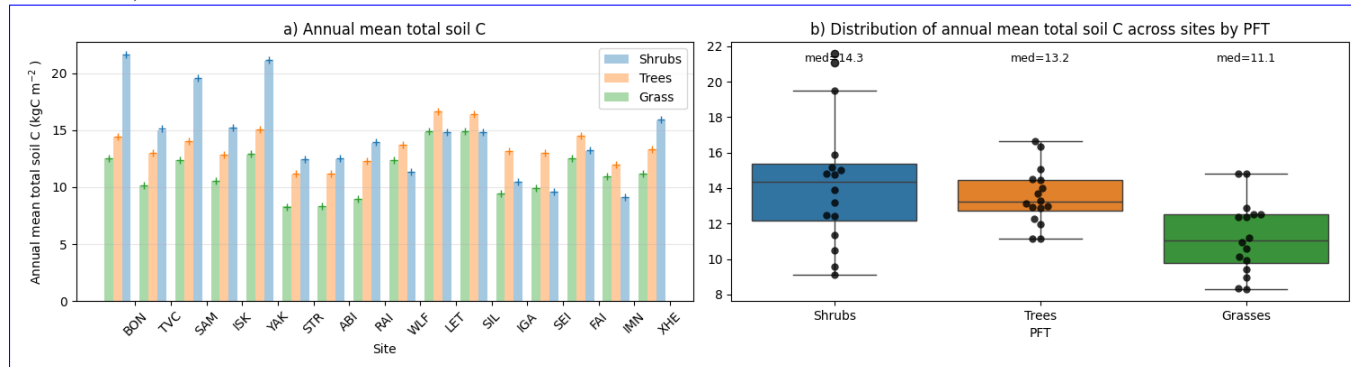
270 The ~~site-averaged-site-averaged~~ foliage (projection) cover of shrubs ~~-(i.e. the percentage coverage of the ground area by leaves from looking down covered by leaves when viewed from above)~~, is very similar to that of trees (4 % higher for shrubs), indicating slightly higher self-thinning in shrubs (Fig.S9).

Shrub cover reduced ~~the~~ carbon-use efficiency (NPP/GPP), at all sites, from 0.64 (~~graminoid graminoids~~) and 0.68 (trees) to 0.63 at NE and 0.57 at BD shrubs, indicating lower efficiency in converting GPP to biomass ~~overall (Fig. S5b)-overall a)~~.
275 This is generally ~~in-line-consistent~~ with satellite estimates of the NPP/GPP ratio ~~reported by Zhang et al. (2013)~~ for the three different vegetation types ~~-In contrast to (needle-leaved)-reported by Zhang et al. (2013). Unlike needleleaf~~ evergreen shrubs, most deciduous shrubs had lower net primary production (NPP) than trees (Fig. S5a) following the growth respiration (Fig. ~~??a). A higher growth respiration would refer to S5b). Higher growth respiration indicates~~ a faster growth rate and higher seasonal leaf turnover (Ge et al., 2017).

280 The new shrub PFTs produced reasonable ~~(aboveground)-total C-varying total aboveground C values, ranging~~ from 0.7 to 2.5 kgC m⁻² (Fig. 4a, site-mean= 1.3 kgC m⁻²) ~~in 1990-2010. Given that the aboveground part of plants contain between 1990 and 2010. Given that~~ approximately 50 % of C ~~in plants is found in the aboveground part~~ (Ma et al., 2018) these values ~~translates~~ ~~translate~~ into biomass estimates ~~in-line-consistent~~ with measurements of 0.4-1.5 kgC m⁻² (Poley et al., 2020; Zhao et al., 2021; Sulman et al., 2021; Orndahl et al., 2025).

285 Most of the simulated C here was stored in the living wood of the shrubs followed by the storage in coarse roots and heartwood (Fig. S4). Shrubs ~~produced-produce~~ less sapwood than trees ~~but show, but have~~ a faster production rate (Fig.S6) ~~which is according to (Tremel et al., 2019, e.g.) explained by narrower and less. According to (Tremel et al., 2019, e.g.) this is due to~~

Figure 3. Simulated multi-year (1990-2010) annual mean GPP [$\text{gC m}^{-2} \text{ year}^{-1}$] per PFT for 16 sites (~~site acronyms are given in the SI-Table ??~~) in the Shrubs, Trees and graminoid (grass) simulations, with the values of two most recent years marked with '+' and (b) the distribution across all sites (BON: Bonanza, US; TVC: Trail Valley Creek, CA; SAM: Sammaltunturi fell, FI; ISK: Iskoras, NO; YAK: Yakutsk, RU; STR: Stordalen, SE; ABI: Abisko, SE; RAI: Raisduoddar, NO; XHE: Neon Healy, US; WLF: Wolf Creek, CA; LET: Lettuoso, FI; SIL: Siikaneva, FI; IGA: Igarka, RU; SEI: Seida, RU; FAI: Fairbanks, US; IMN: Imnavait, US). The first eight bars (BON-RAI) show the results at NE shrubs, the later ones at BD shrubs.

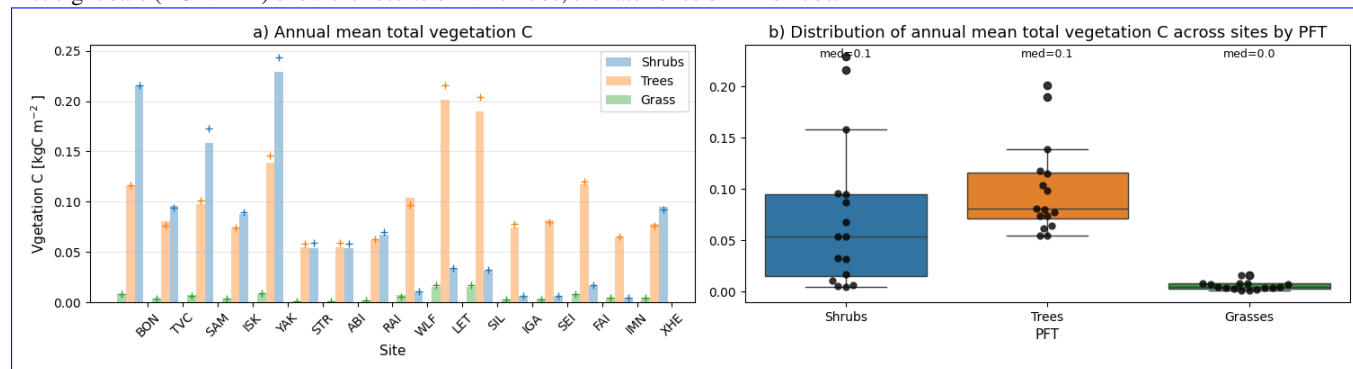


the narrower and fewer xylem cells in shrubs. Therefore, as explained by Parker et al. (2021); Mekonnen et al. (2018) deciduous shrubs grew faster than evergreen species (Figure S7) as explained (Parker et al., 2021; Mekonnen et al., 2018) by, as their small leaf mass per unit area enabling-enabled them deciduous shrubs to intercept more light for a given investment of leaf C than evergreen shrubs. Furthermore, the modeled-modelled shrubs stored more C in coarse roots than trees, so that increasing the coarse root:sapwood ratio is increased by factor 8 which is in agreement by a factor eight. This is consistent with findings by Wang et al. (2016) and a global dataset (including 530 shrub land sites) by Ma et al. (2021). Thus, the total aboveground C storage of shrub vegetation is overall lower than in lower overall than that of trees (at 13 out of 16 sites, Cliff's $\delta=-0.39$). Indeed, Jobbágy and Jackson (2000) report that trees allocate more nutrients aboveground than shrubs and graminoids graminoids.

While the distribution of annual mean vegetation carbon at shrub sites overlaps with that of trees (Fig. 4a), the (multi-site) mean-biomass-mean biomass at sites with shrub coverage is 17 % lower than the mean tree biomass as, as indicated by the lower carbon use efficiency of shrubs (Fig. S5b) indicated. The shrub distribution has a much larger inter-quartile range and more-skewness-interquartile range and is more skewed towards higher values than trees which pointed tree distribution, which points to the higher variability of shrubs. The total vegetation C of graminoid-graminoids is significantly lower (effect size: Cliff's $\delta=1.0$) than in both woody PFTs when considering distribution, median and range, as also found by Lett et al. (2004). Graminoids store relatively more C in fine root-roots and the labile pool (almost 40%), but the size of the wood and the woody plants have significantly larger wood and coarse root storage in woody plants is significantly larger.

The higher fraction of coarse root C stored by shrubs (Fig. ??a) determines the increase in total soil C, namely towards (Fig. 7a), reaching 14.3 kgC m⁻² compared to the other PFTs (vs. 13.2 for trees and 11.1 kgC m⁻² multi-site annual mean at trees and graminoids for graminoids) at 81 % of the stations. This small (6 %) increase of in soil C due to shrub coverage compared to trees is in line with observation studies reporting more below consistent with observational studies reporting

Figure 4. Multi-year (1990-2010) annual mean total vegetation C , values of two most recent years marked with '+' and (b) distribution of multi-year annual mean total soil C per PFT in [kgC m⁻²] at all sites (BON: Bonanza, US; TVC: Trail Valley Creek, CA; SAM: Sammaltunturi fell, FI; ISK: Iskoras, NO; YAK: Yakutsk, RU; STR: Stordalen, SE; ABI: Abisko, SE; RAI: Raisduoddar, NO; XHE: Neon Healy, US; WLF: Wolf Creek, CA; LET: Lettuoso, FI; SIL: Siikaneva, FI; IGA: Igarka, RU; SEI: Seida, RU; FAI: Fairbanks, US; IMN: Imnavait, US). The first eight bars (BON-RAI) show the results of NE shrubs, the later ones of BD shrubs.



greater belowground than aboveground C with shrub vegetation coverage (Ma et al., 2021). ~~We note~~ It should be noted that the soil type is a primary ~~control factor~~ that can explain increases as well as both increases and decreases in soil organic contents content, as a meta-analysis ~~by Li et al. (2016) found at of~~ different shrub species globally found globally (Li et al., 2016). Parker et al. (2021) even report a substantial C loss by shrub expansion ~~which is in line~~, which is consistent with other studies. At a landscape scale, Zhao et al. (2023) found an increase ~~of in~~ soil organic carbon with shrub expansion in the Arctic. Our ~~model~~ modelling study shows that, evergreen shrubs ~~have the tendency tend~~ to conserve more C than deciduous shrubs (first 8-eight bars in Figs. 4) ~~as is also~~, as reported by Mekonnen et al. (2018). In comparison with graminoids, soil C ~~is increased~~ increases by 18 % as substantially more C is stored in coarse roots ~~Since of shrubs~~. ~~However, since~~ the model does not yet consider the long-term C storage in permafrost soils yet, the impact on soil C is only discussed briefly here. Given that shrubs exhibit higher root nutrient absorption rates than trees ~~as supported by Chen et al. (2020), who analyzed 170 root samples from Arctic shrubs, and as corroborated by our simulations (Fig. S7)~~ significant impacts on nitrogen cycling can also be expected (Martin et al., 2022). Overall, we ~~show here demonstrate~~ that the newly modeled-modelled shrubs produce reasonable C fluxes and storage whereas they reproduce while reproducing important physiological processes (e.g. wood formation ,and root allocation) different from that differ from those of trees.

3.2.1 Transient changes in uptake and storage

Our transient simulations from ~~1901-2010~~ 1901 to 2010 show an average ~~change in annual GPP~~ annual GPP change of 60 g m⁻² yr⁻¹ for shrubs, ~~strongly increasing with a significant increase~~ since 1960 (Fig. 5a). ~~In comparison, the GPP increase, the~~ increase in GPP over time for trees and graminoids is 30-50 % weaker.

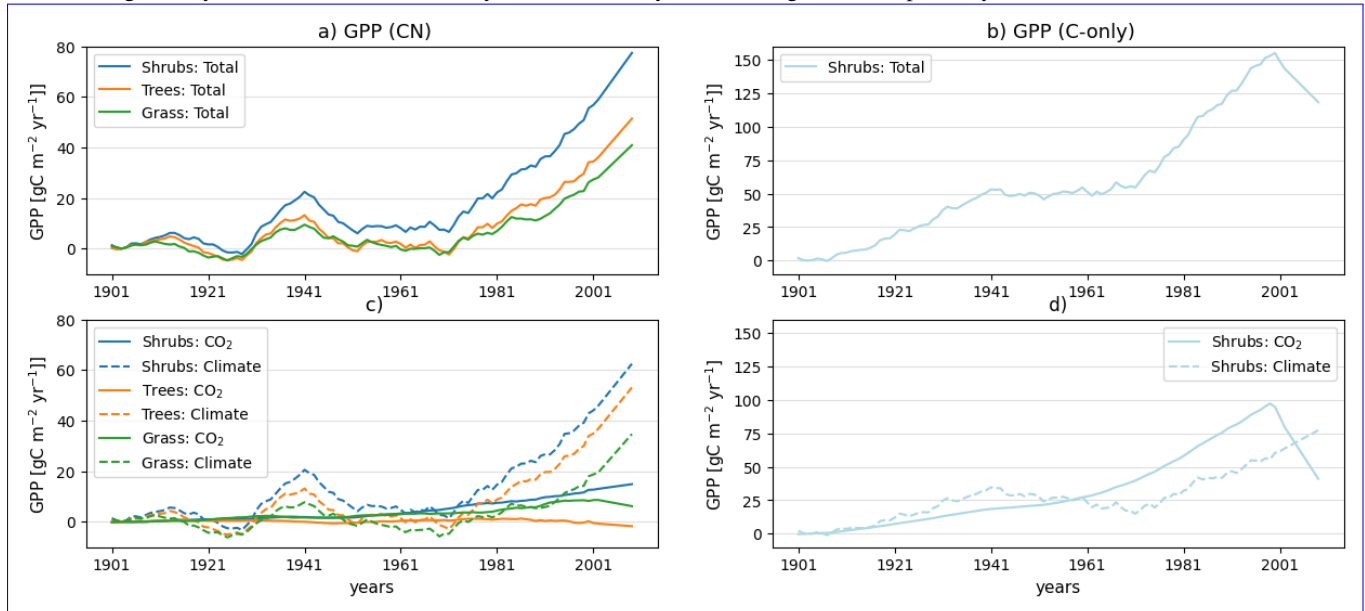
We deduct from the *Shrubs* and *ShrubsNof* simulations the CO₂ fertilization effect on shrub GPP across the study sites, with a steep rise in the CO₂ effect on GPP since the 1960s (Fig. 5c) following increased atmospheric CO₂ concentrations (Fig. ??) (ipc, 2022). This effect is ~~larger for more pronounced at~~ sites where nitrogen dynamics have ~~no a~~ low impact. For ~~instance example~~, at YAK (Yakutsk, Russia), where ~~no difference is simulated there is no difference~~ between C-only and CN simulations, we found an GPP increase of up to 40 gC m⁻² yr⁻¹, caused by CO₂ fertilization alone. Most shrub-dominated sites are strongly nitrogen-limited, which ~~causes the results in a small average~~ CO₂-fertilization effect ~~to be small on average~~ (Fig.5a) across all sites ~~for 1960-2010. This estimate is in line with the~~ between 1960 and 2010. This estimate aligns with the ~~results of the~~ QUINCY model study ~~results for~~ the high-Arctic tundra by Lacroix et al. (2022), as well as with a number of field N fertilization experiments ~~with involving~~ tundra and mixed shrub coverage (DeMarco et al., 2014; Shaver et al., 2001).

For NE trees, positive changes in GPP outweigh negative changes at only a few sites over time ~~leading to an overall small,~~ leading to a small overall change (Fig.5a). ~~This is~~ consistent with their lower N uptake compared to shrubs. Thus, the newly ~~modeled shrubs show a modelled shrubs demonstrate~~ higher growing potential (N uptake ~~, and~~ GPP) under increased CO₂ in comparison to NE trees (default parameters). The CO₂-fertilization effect (on GPP) is higher the less nitrogen-limited the sites are ~~nitrogen-limited~~ (e.g. the YAK site ~~, in~~ Russia). Indeed ~~shrubs have been found to,~~ it has been found that shrubs deepen their roots in response to increasing CO₂ (Mekonnen et al., 2021).

After 1960, the climate effect clearly becomes ~~dominating dominant~~ due to the strong significant temperature increase in the Arctic ~~e.g. reported, as reported, for example,~~ by Wei et al. (2018). The multi-site average GPP increases until 45 gC m⁻² yr⁻¹ at shrub-dominated sites relative to 1901-1910, which is about approximately 12 % of the absolute GPP. ~~For trees, the foliage projection cover rise similarly over time as for~~ The foliage projection cover of trees rises over time, similarly to that of shrubs (Fig.3). ~~while the GPP at graminoids show approximately.~~ In contrast, the GPP of graminoids shows only half of the increase. Until 1960, the climate impact of all three PFTs ~~exhibits exhibited~~ a 20-year cycle, driven by variations in dominant climate factors. ~~Overall, among~~ Among all three PFTs, shrubs respond most to climate effects in the model, e.g. ~~increasing temperature (since 1960). This feature is reported as to increasing temperature since 1960. This feature has been cited as a~~ reason for the shrub expansion in the Arctic, as described in Mekonnen et al. (2021, e.g.,).

~~Unsurprisingly~~ As expected, alleviating N limitation in the (*ShrubsOnly*, *ShrubsNof*) simulations ~~result resulted~~ in a substantially higher CO₂ fertilization effect (on average 58 gC ~~m2-m-2~~ year⁻¹, Fig. 5b). This can be explained by the change in (plant) biological nitrogen fixation (BNF) ~~during in plants during an~~ unlimited N supply. BNF ~~rises with increasing increases~~ with temperature (Yu and Zhuang, 2020) and the model formulation used here favors elevated CO₂ (Meyerholt et al., 2016). Thus, ~~here BNF increases with rising CO₂ BNF increases~~ by 5 % yr⁻¹ with rising CO₂ (Fig. S11), ~~so that meaning that by~~ 2010 the CO₂ fertilized C-only simulation ~~reached had~~ 30 % more BNF than the non-fertilized simulation. BNF is ~~known~~ an important N source for plants, whereas the contribution of symbiotic (bacteria) and free-living ~~parts organism~~ is uncertain (Davies-Barnard et al., 2020). In our C-only model used here plant BNF is unlimited. Thus, a simulation ~~estimate twice the~~ that is twice the size of the observations in the Arctic (see Meyerholt et al. (2016)) compensates ~~for missing N sources (like~~ symbiotic BNF, ~~the absence of other N sources, such as symbiotic BNF~~ (gray line in Fig. S11).

Figure 5. Multi sites average 15-years rolling mean total changes (a,b) and CO₂ fertilization and climate effect (c,d) in GPP relative to 1901-1911 [gC m⁻² yr⁻¹] carried out with the N dynamic and C-only model configuration, respectively.



360 The ~~climate effect on~~ effect of climate on the total vegetation C (Fig.S10) is similar ~~as for GPP~~ to that on GPP, with a sharp increase around 1970 to a change of 0.2 kgC m⁻² (8% of the ~~absolute~~ at shrubs. In fact, many studies like Elmendorf et al. (2012) ~~report the boost~~ total amount). Indeed, numerous studies, such as Elmendorf et al. (2012), have reported an increase in Arctic ecosystem productivity due to climate warming. The CO₂ fertilization ~~, however, is minor at~~ has a minor effect on shrubs and graminoids ~~while it-, and~~ even leads to a reduction in tree vegetation C of about 5 %. Comparing ~~the~~ CN and C-only simulations ~~of shrubs reveal for shrubs reveals~~ the same climate effect, as the climate forcing is the same, but a much higher CO₂ fertilization effect occurred in the C-only simulation (0.5 kg m⁻², 25 %) ~~occurred in the C-only simulation~~. Norby et al. (2010) and McCarthy et al. (2010) confirm that local N availability ~~strongly drives~~ influences the strength and the sign of the CO₂ fertilization effect at-on Arctic trees. ~~The change~~ Changes in vegetation C also ~~reflects to the foliage~~ affect the foliage projection cover of trees and shrubs. CO₂ fertilization has no significant impact on ~~modeled-modelled~~ shrub foliage projection cover (Fig. S9). For trees, however, we see a decrease in ~~foilage-foliage~~ cover when accounting for CO₂ fertilization over the last 20 simulation years (Fig. S9, orange compared to coral line) which ~~translates into a results in~~ higher self-thinning and thus ~~a reduction of fewer~~ trees per leaf ~~areas~~ area. ~~Graminoids similarly to shrubs~~ area. Similar to shrubs, graminoids show only a modest response to CO₂ fertilization ~~response as also seen for GPP~~ (Fig.5a).

3.3 Role of nitrogen availability

375 Here, we compare the C-only (*ShrubsConly*) and CN ~~simulations~~ (*Shrubs*) simulations, i.e. simulations ~~with nitrogen supply~~ in which the nitrogen supply is maintained at levels that do not constrain plant growth versus an explicit simulation of nitrogen

input and output processes ~~and, as well as~~ the limitation of plant growth due to nitrogen availability. Accounting for nitrogen limitation significantly reduced the GPP at all sites in shrub cover simulations (Fig. 2, 7 Figs. 6b and Fig. S8), most significantly ~~at notably for~~ deciduous shrubs. These reductions ~~range-ranged~~ from 3 gC month⁻¹ m⁻² (2 %, not significant) for the evergreen shrub at the YAK site (~~Russia~~) ~~in Russia~~ to 150 gC month⁻¹ m⁻² (75 %) for the deciduous shrub at the IGA site in Russia (Fig. 6a). We demonstrate that the magnitude of GPP change (Fig. 6b) depends on the ~~growing-season-length-length of the growing season~~ (Fig. 6a), which impacts the ~~ecosystem's nitrogen supply-nitrogen supply to the ecosystem~~ through net N mineralization, fixation (not shown) and uptake (Fig. 6c). At sites with deciduous shrubs and a ~~3-months-three-month~~ growing season only (at the ~~sites~~ SEI, IMN, IGA ~~sites~~; whereas SEI and IGA shrubs behave very similar), these main N sources declined in the CN simulations, leading to a ~~strong-reduction-of-significant decrease in~~ GPP (Fig. 6b). ~~Shrubs-In contrast, shrubs~~ at other sites, e.g. at the WLF site (~~Canada~~) ~~in Canada~~, showed at least an increase ~~of N-uptake-under the CN-configuration-in N uptake~~ at the start of the growing season ~~under the CN configuration~~. When both N uptake terms and the use of N storage ~~rise increase~~ (at the sites YAK, STR, ~~ABI~~ ~~whereas and ABI~~, where the shrubs at STR and ABI ~~shrubs behave very similar~~) ~~behave similarly~~, the reduction in GPP is only slight (Fig. 6b, c). ~~Overall,~~ we demonstrated that ~~nitrogen supply strongly limits~~ most simulated shrubs ~~are strongly limited by nitrogen supply,~~, which is consistent with other studies e.g. Street and Caldararu (2022). Other than ~~modelled~~ evergreen shrubs, the ~~modeled~~ deciduous shrubs have a higher N demand and respond more rapidly to N additions ~~as also reported for al-pine,~~ ~~as has been reported for alpine~~ shrubs by Zhou et al. (2023). ~~However, our results suggest~~ The C-only model, which allows for unlimited biological N fixation, performs better than measurements (Table S2). This suggests that the N dynamics in the model may be overly restrictive. ~~Supporting this hypothesis, we extracted 89 measurements of the C/N ratio at Betula nana leaves and 36 measurements of the C/N ratio at Betula glandulosa leaves were extracted from the TRY database (Kattge et al., 2020). The C/N ratio estimated by the C-only configuration at seven stations (with deciduous species) is 24.0 (median), which is consistent with the measured median values (26.06±2.0, and could be improved by 22.56±2.1). However, the median value of the CN model (29.06) instead overestimates the measured C/N ratio (i.e. it underestimates the leaf N concentration), thus supporting our hypothesis of overly too strong N limitation in the CN model. We recommend to improve the model by refining key processes such as BNF, to better reflect Arctic conditions.~~

~~The initialization of~~ ~~Initializing~~ N and C in the permafrost (simulation: *ShrubsPM*) increased the soil C pool by 10-60 kgC m⁻² (Fig. 7a, 4-18 %) ~~towards a,~~ ~~towards~~ better agreement with the permafrost C estimates of 20-150 kgC m⁻² (0-3 m) ~~by (Hugelius et al., 2014),~~ where the majority of the soil C is stored ~~in the model~~ (Hugelius et al., 2014). It also ~~improves improved the~~ total soil N ~~contents-content~~ from 1.5 kgN m⁻² to 7.4 kgN m⁻² (Fig. S13). Palmtag et al. (2022) report estimates of around 5 kgN m⁻², when extrapolated to our ~~modeled-modelled~~ soil depths of 9 m using the same vertical distribution.

~~The higher~~ ~~Higher~~ soil N levels, originating from the improved soil initialization, stimulated primary productivity, ~~which in turn increased vegetation.~~ This increases the C storage in the coarse root, sapwood and ~~heart-wood-heartwood~~ pools of the plants. ~~As a result~~ ~~Consequently~~, total vegetation C ~~rose-increased~~ by 1 kgC m⁻² (93 %) on average (Fig. S12).

For most of the sites with NE shrubs, the effects of ~~the~~ enhanced soil N supply (Fig. ??) ~~are strongly-S8) are clearly~~ reflected in the annual GPP, which increased by 73-290 gC m⁻² yr⁻¹ compared to the standard model simulations (*Shrubs*). The additional nutrients ~~lead-led~~ to a significant increase ~~of the leaf-to-root-in the leaf-to-root~~ mass ratio (Fig. S14), ~~clearly~~

Figure 6. Multi-year (1990-2010) average seasonal cycle of (a) growing season length, (b) GPP change (*Shrubs-ShrubsConly*), (c) change of N uptake and net mineralization, including NH_4^+ and NO_3^- (*Shrubs-ShrubsConly*) at particular stations.

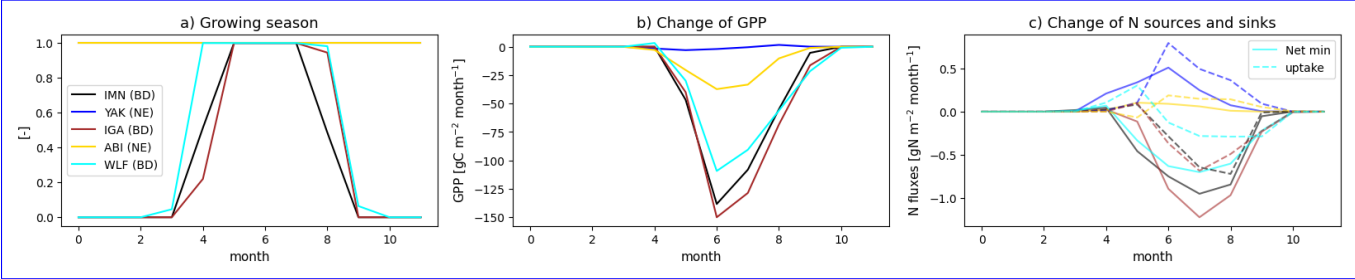
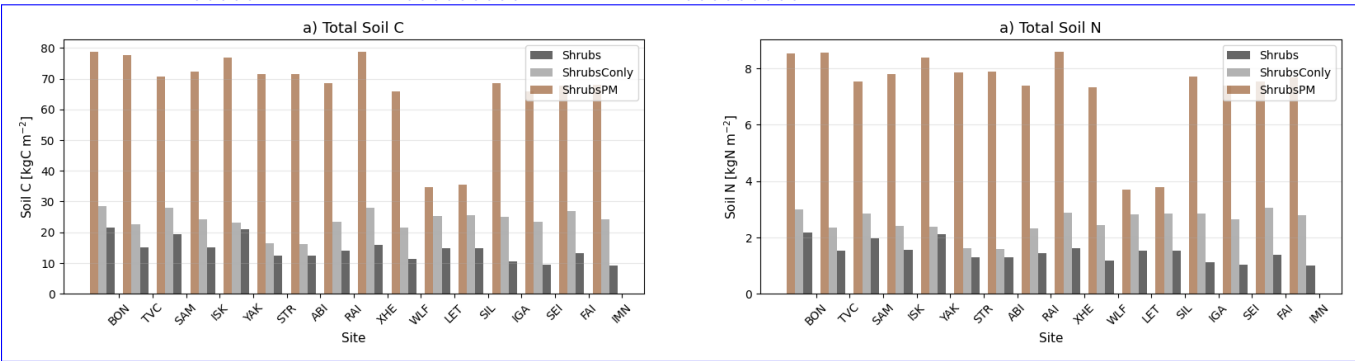


Figure 7. Multi-year (1990-2010) average total soil C (left) and total soil nitrogen (right) at the 16 different sites estimated by the three simulations: *ShrubsShrubs*, *ShrubsConlyShrubsConly* and *ShrubsbPMShrubsbPM*.



indicating a which indicates significant alleviation of nitrogen limitation, a pattern. This pattern has been widely reported for other vegetation types, thus causing and causes the shrubs to allocate more growth into to aboveground biomass than roots; the to roots. The latter is needed to take up more nutrients. In contrast, GPP for BD shrubs is less strongly affected (Fig. ??S8), and the leaf and fine root C ratios leaf-to-root mass ratio at BD shrub sites are also not significantly changed do not change significantly (Fig. ??S14b). This feature highlights the contrasting nitrogen sensitivities and acquisition strategies of NE and BD shrubs. In fact, Martin et al. (2022) reports Indeed, Martin et al. (2022) report a rapid increase of GPP and leaf:root mass ratio at in GPP and leaf-to-root mass ratio in NE shrubs with higher N availability while whereas BD shrubs only show a slight response to more increased N due to the conservative economics and higher respiration efficiency (Street and Caldaru, 2022).

415 The change in GPP due to the PM initialization varies significantly over time. From the initialization the GPP difference rapidly increases by $10 \text{ gC m}^{-2} \text{ yr}^{-1}$ to a level which is more or less constant until 1960. With increasing CO_2 the GPP difference increases by $30 \text{ gC m}^{-2} \text{ yr}^{-1}$ until 2010.

420

4 Conclusions

We ~~implemented~~incorporated broadleaf deciduous and ~~needle-leaved~~needleleaf evergreen shrubs into the QUINCY nutrient-
425 enabling terrestrial biosphere model ~~QUINCY using empirically-based parameters to improve using empirically based parameters~~
~~to enhance~~ the representation of Arctic ~~C-carbon~~ cycle processes. We simulated ~~the growth of~~ shrub, tree and ~~graminoid-growth~~
~~graminoids separately~~ at 16 Pan-Arctic sites separately to assess the impact of Arctic shrub cover on ~~C-carbon~~ uptake and stor-
age. We found that:

- ~~Modeling shrubs using empirically-based~~Modelling shrubs using empirically based parameters enabled a reasonable
430 simulation of gross primary production, achieving R^2 values of 0.5 ~~-0.6~~on average when compared with field data
and MODIS satellite observations, ~~while accurately capturing~~. This approach also accurately captured well-known
physiological processes that are distinct from those of trees.
- At the same simulated sites, shrubs ~~exhibit larger~~exhibited greater growth than NE ~~forest~~forests and graminoids, leading
to ~~mean GPP increase~~a mean increase in GPP of 16% or 40%, respectively.
- Climate-induced effects ~~dominate~~dominated over other driving factors when simulating enhanced shrub growth from
435 ~~1901-2010. This~~1901 to 2010. The results imply that this is due to the ~~nitrogen-limitation~~nitrogen limitation, which was
strengthened ~~with by~~ CO₂ fertilization ~~but weakened in~~, but weakened by a warmer climate ~~that~~. This enhanced nitrogen
fixation and soil ~~N~~nitrogen turnover.
- The initialization of soil nitrogen concentrations, parametrized from observation products, enhanced shrub growth, espe-
440 cially at NE sites, improving the model-measurement comparison by 15 %. It also affected the increased C uptake over
1901-2010.

Overall, ~~we show our results demonstrate~~ that explicitly presenting shrubs ~~enhances simulated C~~is important to capture
vegetation heterogeneity in the Arctic and significantly changes simulated carbon uptake and storage, ~~underlining~~. This
underlines the importance of including evergreen and deciduous shrub ~~PFTs~~plant functional types (PFTs) in global land
445 surface models to accurately predict ongoing changes in the Arctic C cycle. ~~Given the strong influence of~~In the light of the
significant impact of nitrogen limitation on ecosystem C fluxes as revealed here, we recommend improved constraints on the
soil N cycle ~~under low temperatures and their changes in~~in low-temperature conditions and its changes in a warming climate.
We also call for additional measurements needed to parametrize the PFT-specific traits, such as the ~~allocation of biomass~~
biomass allocation to roots, ~~that influence the efficiency of shrubs~~which influence shrubs' efficiency in accessing soil nitrogen
450 (Martin et al., 2022) and are likely to become increasingly important with permafrost thaw.

Code and data availability.

The code is temporary available at <https://nextcloud.bgc-jena.mpg.de/s/eJjWSzMonLfLKTj> for the review phase. Later, ~~there will be a provided with a~~ we provide a tag of the code version. The model output is available here: (Emmerichs, 2026).

455 *Author contributions.* TE developed the shrub implementation, conducted the simulations and wrote the main of the manuscript. FL importantly contributed to the concept of the manuscript, prepared the site-level model forcings and developed the permafrost initialization. VB and FL extensively reviewed the manuscript. YZ prepared the MODIS satellite products for the model evaluation. SZ and CG did the most recent improvements of the nitrogen dynamics in QUINCY. SS, CV, KSL, EST have conducted the field measurements at Stordalen, Trail Valley Creek, Abisko and Siikaneva, respectively. All authors contributed to the review of the manuscript.

460 *Acknowledgements.* TE was funded by the European Research Council under the European Union's Horizon 2020 research and innovation program as part of the Q-Arctic project (grant agreement No 951288) and by the German Research Foundation as part of the CLICCS Clusters of Excellence (DFG EXC 2037). FL received support from Swiss National Science Foundation (grant no. PZ00P2 216442). YZ was supported by the MoLiCarb project (Deutsche Forschungsgemeinschaft DFG, Project Nr. ~~514539694~~-514539694). SZ and CG were supported by the European Union's Horizon 2020 research and innovation programme under grant agreement N 101003536 (ESM-2025). CV acknowledges funding from the European Research Council Starting Grant COLDSPOT (no. 101163177). The authors acknowledge the
465 availability of the ABCfluxnet dataset. Especially, we thank Claire Treat, Lona van Delden, Joshua Hashemi to allow using the GPP data from the Siikaneva2 chambers and Sean Carey, Erin Nicholls, Graham Clark for the tower data at Wolfs Creek.

Competing interests. The authors declare no potential conflict of interests.

References

- Quincy Model, <https://git.bgc-jena.mpg.de/quincy/quincy-model-releases>, <https://doi.org/10.17871/quincy-model-2019>, 2019.
- 470 Emissions Trends and Drivers., IPCC, 2022: Climate Change 2022: Mitigation of Climate Change. Contribution of Working Group III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, <https://doi.org/10.1017/9781009157926.004>, 2022.
- Andreu-Hayles, L., Gaglioti, B. V., Berner, L. T., Levesque, M., Anchukaitis, K. J., Goetz, S. J., and D'Arrigo, R.: A narrow window of summer temperatures associated with shrub growth in Arctic Alaska, *Environmental Research Letters*, 15, 105012, <https://doi.org/10.1088/1748-9326/ab897f>, publisher: IOP Publishing, 2020.
- 475 Bonfils, C. J. W., Phillips, T. J., Lawrence, D. M., Cameron-Smith, P., Riley, W. J., and Subin, Z. M.: On the influence of shrub height and expansion on northern high latitude climate, *Environmental Research Letters*, 7, 015503, <https://doi.org/10.1088/1748-9326/7/1/015503>, publisher: IOP Publishing, 2012.
- Bret-Harte, M. S., Shaver, G. R., Zoerner, J. P., Johnstone, J. F., Wagner, J. L., Chavez, A. S., Gunkelman, R. F., Lippert, S. C., and Laundre, J. A.: Developmental Plasticity Allows *Betula nana* to Dominate Tundra Subjected to an Altered Environment, *Ecology*, 82, 18–32, <https://doi.org/10.2307/2680083>, publisher: Ecological Society of America, 2001.
- 480 Bret-Harte, M. S., Shaver, G. R., and Chapin III, F. S.: Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change, *Journal of Ecology*, 90, 251–267, <https://doi.org/10.1046/j.1365-2745.2001.00657.x>, eprint: <https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1046/j.1365-2745.2001.00657.x>, 2002.
- Buckeridge, K. M., Zufelt, E., Chu, H., and Grogan, P.: Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks, *Plant and Soil*, 330, 407–421, <https://doi.org/10.1007/s11104-009-0214-8>, 2010.
- 485 Chen, W., Tape, K. D., Euskirchen, E. S., Liang, S., Matos, A., Greenberg, J., and Fraterrigo, J. M.: Impacts of Arctic Shrubs on Root Traits and Belowground Nutrient Cycles Across a Northern Alaskan Climate Gradient, *Frontiers in Plant Science*, 11, <https://doi.org/10.3389/fpls.2020.588098>, publisher: Frontiers, 2020.
- Davies-Barnard, T. and Friedlingstein, P.: The Global Distribution of Biological Nitrogen Fixation in Terrestrial Natural Ecosystems, *Global Biogeochemical Cycles*, 34, e2019GB006387, <https://doi.org/10.1029/2019GB006387>, publisher: John Wiley & Sons, Ltd, 2020.
- 490 Davies-Barnard, T., Meyerholt, J., Zaehle, S., Friedlingstein, P., Brovkin, V., Fan, Y., Fisher, R. A., Jones, C. D., Lee, H., Peano, D., Smith, B., Wårlind, D., and Wiltshire, A. J.: Nitrogen cycling in CMIP6 land surface models: progress and limitations, *Biogeosciences*, 17, 5129–5148, <https://doi.org/10.5194/bg-17-5129-2020>, publisher: Copernicus GmbH, 2020.
- DeMarco, J., Mack, M. C., and Bret-Harte, M. S.: Effects of arctic shrub expansion on biophysical vs. biogeochemical drivers of litter decomposition, *Ecology*, 95, 1861–1875, <https://doi.org/10.1890/13-2221.1>, publisher: John Wiley & Sons, Ltd, 2014.
- 495 Du, Z., Zheng, H., Penuelas, J., Sardans, J., Deng, D., Cai, X., Gao, D., Nie, S., He, Y., Lü, X., and Li, M.-H.: Shrub encroachment leads to accumulation of C, N, and P in grassland soils and alters C:N:P stoichiometry: A meta-analysis, *Science of The Total Environment*, 951, 175534, <https://doi.org/10.1016/j.scitotenv.2024.175534>, 2024.
- Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Dorrepaal, E., Elumeeva, T. G., Gill, M., Gould, W. A., Harte, J., Hik, D. S., Hofgaard, A., Johnson, D. R., Johnstone, J. F., Jónsdóttir, I. S., Jorgenson, J. C., Klanderud, K., Klein, J. A., Koh, S., Kudo, G., Lara, M., Lévesque, E., Magnússon, B., May, J. L., Mercado-Dí'az, J. A., Michelsen, A., Molau, U., Myers-Smith, I. H., Oberbauer, S. F., Onipchenko, V. G., Rixen, C., Martin Schmidt, N., Shaver, G. R., Spasojevic, M. J., Porhallsdottir, P. E., Tolvanen, A., Troxler, T., Tweedie, C. E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P. J.,

- Welker, J. M., and Wipf, S.: Plot-scale evidence of tundra vegetation change and links to recent summer warming, *Nature Climate Change*, 2, 453–457, <https://doi.org/10.1038/nclimate1465>, publisher: Nature Publishing Group, 2012.
- Emmerichs, T.: Data from the study 'Impacts of Shrub Coverage for Arctic Ecosystem Carbon Uptake and Storage', <https://doi.org/10.17617/3.BOEHLH>, 2026.
- Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Gregor, L., Hauck, J., Le Quere, C., Luijkx, I. T., Olsen, A., Peters, G. P., Peters, W., Pongratz, J., Schwingshackl, C., Sitch, S., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S. R., Alkama, R., Arneeth, A., Arora, V. K., Bates, N. R., Becker, M., Bellouin, N., Bittig, H. C., Bopp, L., Chevallier, F., Chini, L. P., Cronin, M., Evans, W., Falk, S., Feely, R. A., Gasser, T., Gehlen, M., Gkritzalis, T., Gloege, L., Grassi, G., Gruber, N., and Gürses, ö.: Global Carbon Budget 2022, *Earth System Science Data*, 14, <https://doi.org/10.5194/essd-14-4811-2022>.
- Fu, Y., Piao, S., Zhao, H., Jeong, S., Wang, X., Vitasse, Y., Ciais, P., and Janssens, I.: Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at northern middle and high latitude, *Global Change Biology*, 20, <https://doi.org/10.1111/gcb.12610>, 2014.
- García Criado, M., Myers-Smith, I. H., Björkman, A. D., Elmendorf, S. C., Normand, S., Aastrup, P., Aerts, R., Alatalo, J. M., Baeten, L., Björk, R. G., Björkman, M. P., Boulanger-Lapointe, N., Butler, E. E., Cooper, E. J., Cornelissen, J. H. C., Daskalova, G. N., Fadrique, B., Forbes, B. C., Henry, G. H. R., Hollister, R. D., Høye, T. T., Jacobsen, I. B. D., Jägerbrand, A. K., Jónsdóttir, I. S., Kaarlejärvi, E., Khitun, O., Klanderud, K., Kolari, T. H. M., Lang, S. I., Lecomte, N., Lenoir, J., Macek, P., Messier, J., Michelsen, A., Molau, U., Muscarella, R., Nielsen, M.-L., Petit Bon, M., Post, E., Raundrup, K., Rinnan, R., Rixen, C., Ryde, I., Serra-Diaz, J. M., Schaepman-Strub, G., Schmidt, N. M., Schrod, F., Sjögersten, S., Steinbauer, M. J., Stewart, L., Strandberg, B., Tolvanen, A., Tweedie, C. E., and Vellend, M.: Plant diversity dynamics over space and time in a warming Arctic, *Nature*, 642, 653–661, <https://doi.org/10.1038/s41586-025-08946-8>, publisher: Nature Publishing Group, 2025.
- Ge, L., Lafleur, P. M., and Humphreys, E. R.: Respiration from Soil and Ground Cover Vegetation Under Tundra Shrubs, *Arctic, Antarctic, and Alpine Research*, 49, 537–550, <https://doi.org/10.1657/AAAR0016-064>, 2017.
- Giesse, C., Notz, D., and Baehr, J.: The Shifting Distribution of Arctic Daily Temperatures Under Global Warming, *Earth's Future*, 12, e2024EF004961, <https://doi.org/10.1029/2024EF004961>, _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1029/2024EF004961>, 2024.
- Gui, Y., Wang, K., Huntingford, C., Wei, S., Li, X., Myneni, R. B., and Piao, S.: Vegetation greenness in 2024, *Nature Reviews Earth & Environment*, 6, 255–257, <https://doi.org/10.1038/s43017-025-00656-z>, publisher: Nature Publishing Group, 2025.
- Harris, I. C.: CRU JRA v1.1: A forcings dataset of gridded land surface blend of climatic research unit (CRU) and Japanese reanalysis (JRA) data; Jan.1901—Dec.2017, 2019.
- He, P., Ye, Q., Yu, K., Wang, H., Xu, H., Yin, Q., Yue, M., Liang, X., Wang, W., You, Z., Zhong, Y., and Liu, H.: Growing-Season Precipitation Is a Key Driver of Plant Leaf Area to Sapwood Area Ratio at the Global Scale, *Plant, Cell & Environment*, 48, 746–755, <https://doi.org/10.1111/pce.15169>, _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/pce.15169>, 2025.
- Heijmans, M. M. P. D., Magnusson, R. I., Lara, M. J., Frost, G. V., Myers-Smith, I. H., van Huissteden, J., Jorgenson, M. T., Fedorov, A. N., Epstein, H. E., Lawrence, D. M., and Limpens, J.: Tundra vegetation change and impacts on permafrost, *Nature Reviews Earth & Environment*, 3, 68–84, <https://doi.org/10.1038/s43017-021-00233-0>, publisher: Nature Publishing Group, 2022.
- Heydel, F. and Tackenberg, O.: How are the phenologies of ripening and seed release affected by species' ecology and evolution?, *Oikos*, 126, 738–747, <https://doi.org/10.1111/oik.03442>, _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/oik.03442>, 2017.
- Holmes, M. E., Crill, P. M., Burnett, W. C., McCalley, C. K., Wilson, R. M., Frolking, S., Chang, K.-Y., Riley, W. J., Varner, R. K., Hodgkins, S. B., Coordinators, I. P., Team, I. F., McNichol, A. P., Saleska, S. R., Rich, V. I., and Chanton, J. P.: Carbon Accumu-

- lation, Flux, and Fate in Stordalen Mire, a Permafrost Peatland in Transition, *Global Biogeochemical Cycles*, 36, e2021GB007113, <https://doi.org/https://doi.org/10.1029/2021GB007113>, e2021GB007113 2021GB007113, 2022.
- Hu, Q., Li, T., Deng, X., Wu, T., Zhai, P., Huang, D., Fan, X., Zhu, Y., Lin, Y., Xiao, X., Chen, X., Zhao, X., Wang, L., and Qin, Z.:
545 Intercomparison of global terrestrial carbon fluxes estimated by MODIS and Earth system models, *Science of The Total Environment*,
810, 152231, <https://doi.org/https://doi.org/10.1016/j.scitotenv.2021.152231>, 2022.
- Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C.-L., Schirrmeister, L., Grosse, G., Michaelson, G. J., Koven,
C. D., O'Donnell, J. A., Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J., and Kuhry, P.: Estimated stocks of circumpolar permafrost
carbon with quantified uncertainty ranges and identified data gaps, *Biogeosciences*, 11, 6573–6593, <https://doi.org/10.5194/bg-11-6573->
550 2014, publisher: Copernicus GmbH, 2014.
- Jobbágy, E. G. and Jackson, R. B.: The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and
Vegetation, *Ecological Applications*, 10, 423–436, [https://doi.org/10.1890/1051-0761\(2000\)010\[0423:TVDOSO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2), _eprint:
<https://onlinelibrary.wiley.com/doi/pdf/10.1890/1051-0761%282000%29010%5B0423%3ATVDOSO%5D2.0.CO%3B2>, 2000.
- KATTGE, J., DÍAZ, S., LAVOREL, S., PRENTICE, I. C., LEADLEY, P., BÖNISCH, G., GARNIER, E., WESTOBY, M., REICH, P. B.,
555 WRIGHT, I. J., CORNELISSEN, J. H. C., VIOLLE, C., HARRISON, S. P., Van BODEGOM, P. M., REICHSTEIN, M., ENQUIST, B. J.,
SOUDZILOVSKAIA, N. A., ACKERLY, D. D., ANAND, M., ATKIN, O., BAHN, M., BAKER, T. R., BALDOCCHI, D., BEKKER,
R., BLANCO, C. C., BLONDER, B., BOND, W. J., BRADSTOCK, R., BUNKER, D. E., CASANOVES, F., CAVENDER-BARES, J.,
CHAMBERS, J. Q., CHAPIN III, F. S., CHAVE, J., COOMES, D., CORNWELL, W. K., CRAINE, J. M., DOBRIN, B. H., DUARTE, L.,
DURKA, W., ELSER, J., ESSER, G., ESTIARTE, M., FAGAN, W. F., FANG, J., FERNANDEZ-MENDEZ, F., FIDELIS, A., FINEGAN,
560 B., FLORES, O., FORD, H., FRANK, D., FRESCHET, G. T., FYLLAS, N. M., GALLAGHER, R. V., GREEN, W. A., GUTIERREZ,
A. G., HICKLER, T., HIGGINS, S. I., HODGSON, J. G., JALILI, A., JANSEN, S., JOLY, C. A., KERKHOFF, A. J., KIRKUP, D.,
KITAJIMA, K., KLEYER, M., KLOTZ, S., KNOPS, J. M. H., KRAMER, K., KÜHN, I., KUROKAWA, H., LAUGHLIN, D., LEE,
T. D., LEISHMAN, M., LENS, F., LENZ, T., LEWIS, S. L., LLOYD, J., LLUSIÀ, J., LOUAULT, F., MA, S., MAHECHA, M. D.,
MANNING, P., MASSAD, T., MEDLYN, B. E., MESSIER, J., MOLES, A. T., MÜLLER, S. C., NADROWSKI, K., NAEEM, S., NI-
565 INEMETS, Ü., NOELLERT, S., NÜSKE, A., OGAYA, R., OLEKSYN, J., ONIPCHENKO, V. G., ONODA, Y., ORDONEZ, J., OVER-
BECK, G., OZINGA, W. A., PATINO, S., PAULA, S., PAUSAS, J. G., PEÑUELAS, J., PHILLIPS, O. L., PILLAR, V., POORTER,
H., POORTER, L., POSCHLOD, P., PRINZING, A., PROULX, R., RAMMIG, A., REINSCH, S., REU, B., SACK, L., SALGADO-
NEGRET, B., SARDANS, J., SHIODERA, S., SHIPLEY, B., SIEFERT, A., SOSINSKI, E., SOUSSANA, J.-F., SWAINE, E., SWEN-
SON, N., THOMPSON, K., THORNTON, P., WALDRAM, M., WEIHER, E., WHITE, M., WHITE, S., WRIGHT, S. J., YGUEL,
570 B., ZAEHLE, S., ZANNE, A. E., and WIRTH, C.: TRY – a global database of plant traits, *Global Change Biology*, 17, 2905–2935,
<https://doi.org/https://doi.org/10.1111/j.1365-2486.2011.02451.x>.
- Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A.
T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C. C., Aleixo, I., Ali, H., Amiaud, B., Ammer,
C., Amoroso, M. M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D. M. G., Ashman, T.-L., Asmara, D. H., Asner, G. P.,
575 Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W. J., Bakker, J. P., Baldocchi, D.,
Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D. R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M.,
Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar,
L., Berdugo-Lattke, M. L., Berenguer, E., Bergamin, R., Bergmann, J., Bergmann Carlucci, M., Berner, L., Bernhardt-Römermann, M.,
Bigler, C., Bjorkman, A. D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K. T., Boeckx, P., Bohlman,

580 S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C. C. F., Bordin, K., Boughton, E. H., Boukili, V., Bowman, D. M. J. S., Bravo, S., Brendel, M. R., Broadley, M. R., Brown, K. A., Bruelheide, H., Brumlich, F., Bruun, H. H., Bruy, D., Buchanan, S. W., Bucher, S. F., Buchmann, N., Buitenwerf, R., Bunker, D. E., Bürger, J., Burrascano, S., Burslem, D. F. R. P., Butterfield, B. J., Byun, C., Marques, M., Scalon, M. C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J. J., Campy, C., Campetella, G., Campos, J. A., Cano-Arboleda, L., Canullo, R., Carbone, M., Carvalho, F., Casanoves, F., Castagnyrol, B., Catford, J. A., Cavender-Bares, J., Cerabolini, B. E. L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F. S., Chelli, S., Chen, S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C. G., Conti, L., Coomes, D., Cornelissen, J. H. C., Cornwell, W. K., Corona, P., Coyea, M., Craine, J., Craven, D., Crowsigt, J. P. G. M., Cseceserits, A., Cufar, K., Cuntz, M., da Silva, A. C., Dahlin, K. M., Dainese, M., Dalke, I., Dalle Fratte, M., Dang-Le, A. T., Danihelka, J., Dannoura, M., Dawson, S., de Beer, A. J., De Frutos, A., De Long, J. R., Dechant, B., Delagrang, S., Delpierre, N., Derroire, G., Dias, A. S., Diaz-Toribio, M. H., Dimitrakopoulos, P. G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R. L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M. B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T. F., Fagan, W. F., Fagúndez, J., Falster, D. S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T. J., Flynn, D. F. B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G. T., Fry, E. L., Fyllas, N. M., Mazzochini, G. G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J. L., de Gasper, A. L., Gea-Izquierdo, G., Gibson, D., Gillison, A. N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M., Goldberg, E., Gödel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J. L., González-Melo, A., González-Robles, A., Graae, B. J., Granda, E., Graves, S., Green, W. A., Gregor, T., Gross, N., Guerin, G. R., Günther, A., Gutiérrez, A. G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S. P., Hattingh, W., Hawes, J. E., He, T., He, P., Heberling, J. M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A. L., Hiron, A., Hock, M., Hogan, J. A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K. A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C. M., Izquierdo, J., Jackson, R. B., Jackson, B., Jactel, H., Jagodzinski, A. M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J. R. P., Jiang, G.-F., Johansen, J. L., Johnson, D., Jokela, E. J., Joly, C. A., Jordan, G. J., Joseph, G. S., Junaedi, D., Junker, R. R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M. I., Kinlock, N. L., Kissling, W. D., Kitajima, K., Kitzberger, T., Kjeller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J. M. H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N. J. B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D. J., Laughlin, D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P. C., le Roux, E., Lee, T., Lens, F., Lewis, S. L., Lhotsky, B., Li, Y., Li, X., Lichstein, J. W., Liebergesell, M., Lim, J. Y., Lin, Y.-S., Linares, J. C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusia, J., Lohbeck, M., Lopez-Garcia, A., Lopez-Gonzalez, G., Lososova, Z., Louault, F., Lukacs, B. A., Lukes, P., Luo, Y., Lussu, M., Ma, S., Maciel Rabelo Pereira, C., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A. C. M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Maskova, T., Mason, K., Mason, N., Massad, T. J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M. L., McCulloh, K., McFadden, I. R., McGill, B. J., McPartland, M. Y., Medeiros, J. S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F. P. L., Mencuccini, M., Meredieu, C., Messier, J., Meszaros, I., Metsaranta, J., Michaletz, S. T., Michelaki, C., Migalina, S., Milla, R., Miller, J. E. D., Minden, V., Ming, R., Mokany, K., Moles, A. T., Molnár V. A., Molofsky, J., Molz, M., Montgomery, R. A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A. S., Mori, S., Morris, D., Morrison,

- J., Mucina, L., Mueller, S., Muir, C. D., Müller, S. C., Munoz, F., Myers-Smith, I. H., Myster, R. W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A. S., Neuschulz, E. L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H.,
620 Nouvellon, Y., Novakovskiy, A., Network, T. N., Nystuen, K. O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., öllerer, K., Olson, M. E., Onipchenko, V., Onoda, Y., Onstein, R. E., Ordonez, J. C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G. E., Ozinga, W. A., Pahl, A. T., Paine, C. E. T., Pakeman, R. J., Papageorgiou, A. C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J. G., Peco, B., Penuelas, J., Perea, A., Peri, P. L., Petisco-Souza, A. C., Petraglia, A., Petritan, A. M., Phillips, O. L., Pierce, S., Pillar, V. D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmouth, A., Poschlod, P.,
625 Potvin, C., Pounds, D., Powell, A. S., Power, S. A., Prinzing, A., Puglielli, G., Pysek, P., Raavel, V., Rammig, A., Ransijn, J., Ray, C. A., Reich, P. B., Reichstein, M., Reid, D. E. B., Rejou-Mechain, M., de Dios, V. R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M. C., Riviera, F., Robert, E. M. R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A. V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J. A., Rosenfield, M. F., Rossi, C., Roy, D. B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S. B., Rusch, G. M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A. C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J. V., Schowanek, S. D., Schrader, J., Schrod, F., Schuldt, B., Schurr, F., Selaya Garvizu, G., Semchenko, M., Seymour, C., Sfair, J. C., Sharpe, J. M., Sheppard, C. S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T. A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N. G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M. V., Sosinski Jr, E. E., Soudzilovskaia, N. A., Souza, A. F., Spasojevic, M., Sperandii, M. G., Stan, A. B., Stegen, J., Steinbauer, K., Stephan, J. G., Sterck, F.,
630 Stojanovic, D. B., Strydom, T., Suarez, M. L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauougourdeau, S., Tavsanoğlu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P. E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M. G., Tng, D. Y. P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J. M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J. L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P. M., van Breugel, M., Van Cleemput, E., van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M. T., van Kleunen, M., Van Meerbeek, K., Vanderwel, M., Vanselow, K. A., Vårhammar, A., Varone, L., Vasquez Valderrama, M. Y., Vassilev, K., Vellend, M., Veneklaas, E. J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A. P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J. T., Wei, L., Weigelt, P., Weiher, E., Wells, A. W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P. J., Whitten, M., Williams, M., Winkler, D. E., Winter, K., Womack, C., Wright, I. J.,
640 Wright, S. J., Wright, J., Pinho, B. X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K. J., Zanne, A. E., Zeleny, D., Zhao, Y.-P., Zheng, J., Zheng, J., Zieminska, K., Zirbel, C. R., Zizka, G., Zo-Bi, I. C., Zotz, G., and Wirth, C.: TRY plant trait database – enhanced coverage and open access, *Global Change Biology*, 26, 119–188, <https://doi.org/https://doi.org/10.1111/gcb.14904>, 2020.
- Körner, C.: *Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits* Springer, Basel, Google Scholar, pp. 141–173,
650 2012.
- Lacroix, F., Zaehle, S., Caldararu, S., Schaller, J., Stimmer, P., Holl, D., Kutzbach, L., and Göckede, M.: Mismatch of N release from the permafrost and vegetative uptake opens pathways of increasing nitrous oxide emissions in the high Arctic, *Global Change Biology*, 28, 5973–5990, <https://doi.org/10.1111/gcb.16345>, _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.16345>, 2022.
- Leffler, A. J., Serrone, A., Bolek, A., Rocha, A. V., Korrensalo, A., Vähä, A., Tremblay, A., Barr, A., Salazar, A., Sabrekov, A. F., Rasanen, A., Mavrovic, A., Roy, A., Panov, A. V., Townsend-Small, A., Niyazova, A., Prokushkin, A., Jonsson, A., Lindroth, A., and . . . Harazono,
655

- Y.: ABCFlux v2: Arctic-Boreal CO₂ and CH₄ In-situ Flux and Environmental Data (Version 1), ORNL Distributed Active Archive Center, <https://doi.org/10.3334/ORNLDAAAC/2448>, accessed: 2026-02-25, 2026.
- Lett, M. S., Knapp, A. K., Briggs, J. M., and Blair, J. M.: Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland, *Canadian Journal of Botany*, 82, 1363–1370, <https://doi.org/10.1139/b04-088>, publisher: NRC Research Press, 2004.
- Li, H., Shen, H., Chen, L., Liu, T., Hu, H., Zhao, X., Zhou, L., Zhang, P., and Fang, J.: Effects of shrub encroachment on soil organic carbon in global grasslands, *Scientific Reports*, 6, 28974, <https://doi.org/10.1038/srep28974>, publisher: Nature Publishing Group, 2016.
- Liu, D., Zhang, C., Ogaya, R., Acil, N., Pugh, T. A. M., Domene, X., Zhang, X., Fang, Y., Yang, X., Essl, F., Dullinger, S., and Peñuelas, J.: World-wide impacts of climate change and nitrogen deposition on vegetation structure, composition, and functioning of shrublands, *New Phytologist*, 247, 1117–1128, <https://doi.org/10.1111/nph.70235>, [eprint: https://nph.onlinelibrary.wiley.com/doi/pdf/10.1111/nph.70235](https://nph.onlinelibrary.wiley.com/doi/pdf/10.1111/nph.70235), 2025.
- Ma, H., Mo, L., Crowther, T. W., Maynard, D. S., van den Hoogen, J., Stocker, B. D., Terrer, C., and Zohner, C. M.: The global distribution and environmental drivers of aboveground versus belowground plant biomass, *Nature Ecology & Evolution*, 5, 1110–1122, <https://doi.org/10.1038/s41559-021-01485-1>, publisher: Nature Publishing Group, 2021.
- Ma, S., He, F., Tian, D., Zou, D., Yan, Z., Yang, Y., Zhou, T., Huang, K., Shen, H., and Fang, J.: Variations and determinants of carbon content in plants: a global synthesis, *Biogeosciences*, 15, 693–702, <https://doi.org/10.5194/bg-15-693-2018>, 2018.
- Martin, A. C., Jeffers, E. S., Petrokofsky, G., Myers-Smith, I., and Macias-Fauria, M.: Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach, *Environmental Research Letters*, 12, 085007, <https://doi.org/10.1088/1748-9326/aa7989>, publisher: IOP Publishing, 2017.
- Martin, A. C., Macias-Fauria, M., Bonsall, M. B., Forbes, B. C., Zetterberg, P., and Jeffers, E. S.: Common mechanisms explain nitrogen-dependent growth of Arctic shrubs over three decades despite heterogeneous trends and declines in soil nitrogen availability, *New Phytologist*, 233, 670–686, <https://doi.org/10.1111/nph.17529>, [eprint: https://nph.onlinelibrary.wiley.com/doi/pdf/10.1111/nph.17529](https://nph.onlinelibrary.wiley.com/doi/pdf/10.1111/nph.17529), 2022.
- McCarthy, H. R., Oren, R., Johnsen, K. H., Gallet-Budynek, A., Pritchard, S. G., Cook, C. W., LaDeau, S. L., Jackson, R. B., and Finzi, A. C.: Re-assessment of plant carbon dynamics at the Duke free-air CO₂ enrichment site: interactions of atmospheric [CO₂] with nitrogen and water availability over stand development, *New Phytologist*, 185, 514–528, <https://doi.org/10.1111/j.1469-8137.2009.03078.x>, 2010.
- Mekonnen, Z. A., Riley, W. J., and Grant, R. F.: Accelerated Nutrient Cycling and Increased Light Competition Will Lead to 21st Century Shrub Expansion in North American Arctic Tundra, *Journal of Geophysical Research: Biogeosciences*, 123, 1683–1701, <https://doi.org/10.1029/2017JG004319>, [eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1029/2017JG004319](https://onlinelibrary.wiley.com/doi/pdf/10.1029/2017JG004319), 2018.
- Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C., and Grant, R. F.: Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance, *Environmental Research Letters*, 16, 053001, <https://doi.org/10.1088/1748-9326/abf28b>, publisher: IOP Publishing, 2021.
- Meyer, G., Humphreys, E. R., Melton, J. R., Cannon, A. J., and Lafleur, P. M.: Simulating shrubs and their energy and carbon dioxide fluxes in Canada's Low Arctic with the Canadian Land Surface Scheme Including Biogeochemical Cycles (CLASSIC), *Biogeosciences*, 18, 3263–3283, <https://doi.org/10.5194/bg-18-3263-2021>, 2021.
- Meyerholt, J., Zaehle, S., and Smith, M. J.: Variability of projected terrestrial biosphere responses to elevated levels of atmospheric CO₂ due to uncertainty in biological nitrogen fixation, *Biogeosciences*, 13, 1491–1518, <https://doi.org/10.5194/bg-13-1491-2016>, 2016.

695 Miller, P. A. and Smith, B.: Modelling Tundra Vegetation Response to Recent Arctic Warming, *AMBIO*, 41, 281–291,
<https://doi.org/10.1007/s13280-012-0306-1>, 2012.

Moore, E. R., Pouyat, R. V., and Trammell, T. L. E.: Soil nitrogen cycling in forests invaded by the shrub *Rosa multiflora*: importance of soil
moisture and invasion density, *Biogeochemistry*, 167, 301–319, <https://doi.org/10.1007/s10533-024-01133-3>, 2024.

Norby, R. J., Warren, J. M., Iversen, C. M., Medlyn, B. E., and McMurtrie, R. E.: CO₂ enhancement of forest pro-
ductivity constrained by limited nitrogen availability, *Proceedings of the National Academy of Sciences*, 107, 19 368–19 373,
700 <https://doi.org/10.1073/pnas.1006463107>, 2010.

Orndahl, K. M., Berner, L. T., Macander, M. J., Arndal, M. F., Alexander, H. D., Humphreys, E. R., Loranty, M. M., Ludwig, S. M., Nyman,
J., Juutinen, S., Aurela, M., Mikola, J., Mack, M. C., Rose, M., Vankoughnett, M. R., Iversen, C. M., Kumar, J., Salmon, V. G., Yang,
D., Grogan, P., Danby, R. K., Scott, N. A., Olofsson, J., Siewert, M. B., Deschamps, L., Maire, V., Lévesque, E., Gauthier, G., Boudreau,
S., Gaspard, A., Bret-Harte, M. S., Raynolds, M. K., Walker, D. A., Michelsen, A., Kumpula, T., Villoslada, M., Yläne, H., Luoto, M.,
705 Virtanen, T., Greaves, H. E., Forbes, B. C., Heim, R. J., Hölzel, N., Epstein, H., Bunn, A. G., Holmes, R. M., Natali, S. M., Virkkala,
A.-M., and Goetz, S. J.: Next generation Arctic vegetation maps: Aboveground plant biomass and woody dominance mapped at 30 m
resolution across the tundra biome, *Remote Sensing of Environment*, 323, 114 717, <https://doi.org/10.1016/j.rse.2025.114717>, 2025.

Palmtag, J., Obu, J., Kuhry, P., Siewert, M., Weiss, N., and Hugelius, G.: A high spatial resolution soil carbon and nitrogen dataset for the
northern permafrost region., <https://doi.org/https://doi.org/10.17043/palmtag-2022-spatial-1>, 2022.

710 Parker, T. C., Thurston, A. M., Raundrup, K., Subke, J.-A., Wookey, P. A., and Hartley, I. P.: Shrub expansion in the Arctic may induce large-
scale carbon losses due to changes in plant-soil interactions, *Plant and Soil*, 463, 643–651, <https://doi.org/10.1007/s11104-021-04919-8>,
2021.

Pirk, N., Aalstad, K., Mannerfelt, E. S., Clayer, F., de Wit, H., Christiansen, C. T., Althuisen, I., Lee, H., and Westermann, S.: Disag-
gregating the Carbon Exchange of Degrading Permafrost Peatlands Using Bayesian Deep Learning, *Geophysical Research Letters*, 51,
715 e2024GL109 283, <https://doi.org/https://doi.org/10.1029/2024GL109283>, 2024.

Poley, L. G., Laskin, D. N., and McDermid, G. J.: Quantifying Aboveground Biomass of Shrubs Using Spectral and Structural Metrics
Derived from UAS Imagery, *Remote Sensing*, 12, 2199, <https://doi.org/10.3390/rs12142199>, number: 14 Publisher: Multidisciplinary
Digital Publishing Institute, 2020.

Poulter, B., MacBean, N., Hartley, A., Khlystova, I., Arino, O., Betts, R., Bontemps, S., Boettcher, M., Brockmann, C., Defourny, P., Hage-
720 mann, S., Herold, M., Kirches, G., Lamarche, C., Lederer, D., Ottlé, C., Peters, M., and Peylin, P.: Plant functional type classification for
earth system models: results from the European Space Agency’s Land Cover Climate Change Initiative, *Geoscientific Model Development*,
8, 2315–2328, <https://doi.org/10.5194/gmd-8-2315-2015>, 2015.

Prager, C. M., Naeem, S., Boelman, N. T., Eitel, J. U. H., Greaves, H. E., Heskell, M. A., Magney, T. S., Menge, D. N., Vierling, L. A.,
and Griffin, K. L.: A gradient of nutrient enrichment reveals nonlinear impacts of fertilization on Arctic plant diversity and ecosystem
725 function, *Ecology and Evolution*, 7, 2449–2460, <https://doi.org/10.1002/ece3.2863>, 2017.

Running, S. and Zhao, M.: MODIS/Terra Gross Primary Productivity Gap-Filled 8-Day L4 Global 500m SIN Grid V061.,
<https://doi.org/10.5067/MODIS/MOD17A2HGF.061>, 2021.

Running, S., Mu, Q., and Zhao, M.: MOD17A2H MODIS/Terra Gross Primary Productivity 8-Day L4 Global 500m SIN Grid V006.,
<https://doi.org/10.5067/MODIS/MOD17A2H.006>, 2015.

- 730 Schore, A. I. G., Fraterrigo, J. M., Salmon, V. G., Yang, D., and Lara, M. J.: Nitrogen fixing shrubs advance the pace of tall-shrub expansion in low-Arctic tundra, *Communications Earth & Environment*, 4, 421, <https://doi.org/10.1038/s43247-023-01098-5>, publisher: Nature Publishing Group, 2023.
- Schuur, E. A., Abbott, B. W., Commene, R., Ernakovich, J., Euskirchen, E., Hugelius, G., Grosse, G., Jones, M., Koven, C., Leshyk, V., Lawrence, D., Lorant, M. M., Mauritz, M., Olefeldt, D., Natali, S., Rodenhizer, H., Salmon, V., Schädel, C., Strauss, J., Treat, C., and
- 735 Turetsky, M.: Permafrost and Climate Change: Carbon Cycle Feedbacks From the Warming Arctic, *Annual Review of Environment and Resources*, 47, 343–371, <https://doi.org/10.1146/annurev-environ-012220-011847>, 2022.
- Schuur, E. a. G., McGuire, A. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., Hugelius, G., Koven, C. D., Kuhry, P., Lawrence, D. M., Natali, S. M., Olefeldt, D., Romanovsky, V. E., Schaefer, K., Turetsky, M. R., Treat, C. C., and Vonk, J. E.: Climate change and the permafrost carbon feedback, *Nature*, 520, 171–179, <https://doi.org/10.1038/nature14338>, publisher: Nature Publishing Group, 2015.
- 740 Shaver, G. R., Bret-Harte, M. S., Jones, M. H., Johnstone, J., Gough, L., Laundre, J., and Chapin III, F. S.: SPECIES COMPOSITION INTERACTS WITH FERTILIZER TO CONTROL LONG-TERM CHANGE IN TUNDRA PRODUCTIVITY, *Ecology*, 82, 3163–3181, [https://doi.org/https://doi.org/10.1890/0012-9658\(2001\)082\[3163:SCIWFT\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2), 2001.
- Street, L. E. and Caldararu, S.: Why are Arctic shrubs becoming more nitrogen limited?, *New Phytologist*, 233, 585–587, <https://doi.org/https://doi.org/10.1111/nph.17841>, 2022.
- 745 Sulman, B. N., Salmon, V. G., Iversen, C. M., Breen, A. L., Yuan, F., and Thornton, P. E.: Integrating Arctic Plant Functional Types in a Land Surface Model Using Above- and Belowground Field Observations, *Journal of Advances in Modeling Earth Systems*, 13, e2020MS002396, <https://doi.org/10.1029/2020MS002396>, _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1029/2020MS002396>, 2021.
- Tang, X., Li, H., Huang, N., Li, X., Xu, X., Ding, Z., and Xie, J.: A comprehensive assessment of MODIS-derived GPP for forest ecosystems using the site-level FLUXNET database, *Environmental Earth Sciences*, 74, 5907–5918, 2015.
- 750 Thum, T., Nabel, J. E. M. S., Tsuruta, A., Aalto, T., Dlugokencky, E. J., Liski, J., Luijkx, I. T., Markkanen, T., Pongratz, J., Yoshida, Y., and Zaehle, S.: Evaluating two soil carbon models within the global land surface model JSBACH using surface and spaceborne observations of atmospheric CO₂, *Biogeosciences*, 17, 5721–5743, <https://doi.org/10.5194/bg-17-5721-2020>, publisher: Copernicus GmbH, 2020.
- Treml, V., Hejda, T., and Kašpar, J.: Differences in growth between shrubs and trees: How does the stature of woody plants influence their ability to thrive in cold regions?, *Agricultural and Forest Meteorology*, 271, 54–63, <https://doi.org/10.1016/j.agrformet.2019.02.036>, 2019.
- 755 Virkkala, A.-M., Rogers, B., Watts, J., Arndt, K., Potter, S., Wargowsky, I., Schuur, E., See, C., Mauritz, M., Boike, J., Bret-Harte, M., Burke, E., Burrell, A., Chae, N., Chatterjee, A., Chevallier, F., Christensen, T. R., Commene, R., Dolman, H. A., and Natali, S.: Wildfires offset the increasing but spatially heterogeneous Arctic–boreal CO₂ uptake, *Nature Climate Change*, 15, 188–195, <https://doi.org/10.1038/s41558-024-02234-5>, 2025a.
- 760 Virkkala, A.-M., Wargowsky, I., Vogt, J., Kuhn, M. A., Madaan, S., O’Keefe, R., Windholz, T., Arndt, K. A., Rogers, B. M., Watts, J. D., Kent, K., Göckede, M., Olefeldt, D., Rocher-Ros, G., Schuur, E. A. G., Bastviken, D., Aalstad, K., Aho, K., Ala-Könni, J., Alcock, H., Althuisen, I., Arp, C. D., Asanuma, J., Attermeyer, K., Aurela, M., Balathandayuthabani, S., Barr, A., Barret, M., Batkhisig, O., Biasi, C., Björkman, M. P., Black, A., Blanc-Betes, E., Bodmer, P., Boike, J., Bolek, A., Bouchard, F., Bussmann, I., Cabrol, L., Canfora, E., Carey, S., Castro-Morales, K., Chae, N., Christen, A., Christensen, T. R., Christiansen, C. T., Chu, H., Clark, G., Clayey, F., Crill, P., Cunada, C.,
- 765 Davidson, S. J., Dean, J. F., Dengel, S., Detto, M., Dieleman, C., Domine, F., Dyukarev, E., Edgar, C., Elberling, B., Emmerton, C. A., Euskirchen, E., Falvo, G., Friborg, T., Garneau, M., Giamberini, M., Glagolev, M. V., Gonzalez-Meler, M. A., Granath, G., Guðmundsson, J., Happonen, K., Harazono, Y., Harris, L., Hashemi, J., Hasson, N., Heerah, J., Heffernan, L., Helbig, M., Helgason, W., Heliasz, M.,

- Henry, G., Hensgens, G., Hiyama, T., Hock, M., Holl, D., Holmes, B., Holst, J., Holst, T., Hould-Gosselin, G., Humphreys, E., Hung, J., Huotari, J., Ikawa, H., Ilyasov, D. V., Ishikawa, M., Iwahana, G., Iwata, H., Jackowicz-Korczynski, M. A., Jansen, J., Järveoja, J., Jassey, V. E. J., Jensen, R., Jentsch, K., Jespersen, R. G., Johannesson, C.-F., Jones, C. P., Jonsson, A., Jung, J. Y., Juutinen, S., Kane, E., Karlsson, J., Karsanaev, S., Kasak, K., Kelly, J., Kempton, K., Klaus, M., Kling, G. W., Kljun, N., Knutson, J., Kobayashi, H., Kochendorfer, J., Kohonen, K.-M., Kolari, P., Korkiakoski, M., Korrensalo, A., Kortelainen, P., Koster, E., Koster, K., Kotani, A., Krishnan, P., Kurbatova, J., Kutzbach, L., Kwon, M. J., Kyzivat, E. D., Lagroix, J., Langhorst, T., Lapshina, E., Larmola, T., Larsen, K. S., Laurion, I., Ledman, J., Lee, H., Leffler, A. J., Lesack, L., Lindroth, A., Lipson, D., Lohila, A., López-Blanco, E., St. Louis, V. L., Lundin, E., Luoto, M., Machimura, T., Magnani, M., Malhotra, A., Maljanen, M., Mammarella, I., Männistö, E., Marchesini, L. B., Marsh, P., Martkainen, P. J., Marushchak, M. E., Mastepanov, M., Mavrovic, A., Maximov, T., Minions, C., Montemayor, M., Morishita, T., Murphy, P., Nadeau, D. F., Nicholls, E., Nilsson, M. B., Niyazova, A., Nordén, J., Noumonvi, K. D., Nykanen, H., Oechel, W., Ojala, A., Okadera, T., Pal, S., Panov, A. V., Papakyriakou, T., Papale, D., Park, S.-J., Parmentier, F.-J. W., Pastorello, G., Peacock, M., Peichl, M., Petrov, R., St. Pierre, K., Pirk, N., Plein, J., Preskienis, V., Prokushkin, A., Pumpanen, J., Rains, H. A., Rakos, N., Räsänen, A., Rautakoski, H., Rinnan, R., Rinne, J., Rocha, A., Roulet, N., Roy, A., Rutgersson, A., Sabrekov, A. F., Sachs, T., Sahlée, E., Salazar, A., Sawakuchi, H. O., Schulze, C., Seco, R., Sepulveda-Jauregui, A., Serikova, S., Serrone, A., Silvennoinen, H. M., Sjogersten, S., Skeeter, J., Snöäl, J., Sobek, S., Sonnentag, O., Stanley, E. H., Strack, M., Strom, L., Sullivan, P., Sullivan, R., Sytiuk, A., Tagesson, T., Taillardat, P., Talbot, J., Tank, S. E., Tenuta, M., Terenteva, I., Thalasso, F., Thibault, A., Thorgeirsson, H., Garcia Tigreros, F., Torn, M., Townsend-Small, A., Treat, C., Tremblay, A., Trotta, C., Tuittila, E.-S., Turetsky, M., Ueyama, M., Umair, M., Vähä, A., van Delden, L., van Hardenbroek, M., Varlagin, A., Varner, R. K., Veretennikova, E., Vesala, T., Virtanen, T., Voigt, C., Vonk, J. E., Wagner, R., Walter Anthony, K., Wang, Q., Watanabe, M., Webb, H., Welker, J. M., Westergaard-Nielsen, A., Westermann, S., White, J. R., Wille, C., Williamson, S. N., Zolkos, S., Zona, D., and Natali, S. M.: ABCFlux v2: Arctic–boreal CO₂ and CH₄ monthly flux observations and ancillary information across terrestrial and freshwater ecosystems, *Earth System Science Data Discussions*, 2025, 1–86, <https://doi.org/10.5194/essd-2025-585>, 2025b.
- Vowles, T. and Björk, R. G.: Implications of evergreen shrub expansion in the Arctic, *Journal of Ecology*, 107, 650–655, <https://doi.org/10.1111/1365-2745.13081>, eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/1365-2745.13081>, 2019.
- Wang, L., Zhu, H., Lin, A., Zou, L., Qin, W., and Du, Q.: Evaluation of the latest MODIS GPP products across multiple biomes using global eddy covariance flux data, *Remote Sensing*, 9, 418, 2017.
- Wang, P., Heijmans, M. M., Mommer, L., van Ruijven, J., Maximov, T. C., and Berendse, F.: Belowground plant biomass allocation in tundra ecosystems and its relationship with temperature, *Environmental Research Letters*, 11, 055 003, 2016.
- Wei, T., Li, J., Rong, X., Dong, W., Wu, B., and Ding, M.: Arctic climate changes based on historical simulations (1900–2013) with the CAMS-CSM, *Journal of Meteorological Research*, 32, 881–895, <https://doi.org/https://doi.org/10.1007/s13351-018-7188-5>, 2018.
- Yu, T. and Zhuang, Q.: Modeling biological nitrogen fixation in global natural terrestrial ecosystems, *Biogeosciences*, 17, 3643–3657, <https://doi.org/10.5194/bg-17-3643-2020>, publisher: Copernicus GmbH, 2020.
- Zachle, S. and Friend, A. D.: Carbon and nitrogen cycle dynamics in the OCN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates, *Global Biogeochemical Cycles*, 24, <https://doi.org/10.1029/2009GB003521>, eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1029/2009GB003521>, 2010.
- Zhang, W., Miller, P. A., Smith, B., Wania, R., Koenigk, T., and Döscher, R.: Tundra shrubification and tree-line advance amplify arctic climate warming: results from an individual-based dynamic vegetation model, *Environmental Research Letters*, 8, 034 023, <https://doi.org/10.1088/1748-9326/8/3/034023>, publisher: IOP Publishing, 2013.

- 805 Zhao, Y., Liu, X., Wang, Y., Zheng, Z., Zheng, S., Zhao, D., and Bai, Y.: UAV-based individual shrub aboveground biomass estimation calibrated against terrestrial LiDAR in a shrub-encroached grassland, *International Journal of Applied Earth Observation and Geoinformation*, 101, 102 358, <https://doi.org/10.1016/j.jag.2021.102358>, 2021.
- Zhao, Y., Wang, H., Ma, Y., Li, Z., Mi, W., and Cao, Z.: Spatial estimation of soil carbon and nitrogen in a grassland shrubland transition, *Ecological Indicators*, 153, 110 384, <https://doi.org/10.1016/j.ecolind.2023.110384>, 2023.
- 810 Zhou, Y., Sha, M., Jin, H., Wang, L., Zhang, J., Xu, Z., Tan, B., Chen, L., Wang, L., Liu, S., Xiao, J., You, C., Huang, Y., Chen, Y., and Liu, Y.: The expansion of evergreen and deciduous shrubs changed the chemical characteristics and biological community of alpine meadows soil, *European Journal of Soil Biology*, 117, 103 505, <https://doi.org/https://doi.org/10.1016/j.ejsobi.2023.103505>, 2023.
- Zhu, X., Pei, Y., Zheng, Z., Dong, J., Zhang, Y., Wang, J., Chen, L., Doughty, R. B., Zhang, G., and Xiao, X.: Underestimates of grassland gross primary production in MODIS standard products, *Remote Sensing*, 10, 1771, 2018.
- 815 ~~List of the study sites with coordinates and soil forcing specifying the clay, silt and sand soil proportion, the bulk density (bd) of organic matter kg m⁻³, the available water content (awc), the ph value, usda taxonomy class, nwr taxonomy class and the initial phosphorus pools (labile, slow, occluded and primary) in the soil g m⁻². The initial soil depth for phosphorus is 0.5 m.~~
- ~~Map of the 16 chosen stations.~~
- 820 ~~List of the study sites reporting the site reference, dominant vegetation, available data points, used flux method and time period.~~
- ~~R² values between different model versions and observation data (ABCfluxnet data and the mean of the MODIS products) for the available time span of the ABCfluxnet data. If available we use only the EC measurements from the ABCflux data. NaN mark data with too small data size.~~
- 825 ~~Multi-year (2000-2010) mean seasonal cycle of the standard derivation of GPP derived from two MODIS satellite products (MOD17A2HGF and MOD17A2H).~~