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Title: Winter snow and spring temperature have differential effects on vegetation phenology and productivity across Arctic plant communities

Running Title: Winter controls on phenology and productivity

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Abstract

Tundra dominates two thirds of the unglaciated, terrestrial Arctic. Although this region has experienced rapid and widespread changes in vegetation phenology and productivity over the last several decades, the specific climatic drivers responsible for this change remain poorly understood. Here we quantified the effect of winter snowpack and early spring temperature conditions on growing season vegetation phenology (timing of the start, peak, and end of the growing season) and productivity of the dominant tundra vegetation communities of Arctic Alaska. We used daily remotely sensed normalized difference vegetation index (NDVI), and daily snowpack and temperature variables produced by SnowModel and MicroMet, coupled physically based snow and meteorological modeling tools, to (1) determine the most important snowpack and thermal controls on tundra vegetation phenology and productivity and (2) describe the direction of these relationships within each vegetation community. Our results show that soil temperature under the snowpack, snowmelt timing, and air temperature following snowmelt are the most important drivers of growing-season timing and productivity among Arctic vegetation communities. Air temperature after snowmelt was the most important control on timing of season start and end, with warmer conditions contributing to earlier phenology in all vegetation communities. In contrast, the controls on the timing of peak season and productivity also included snowmelt timing and soil temperature under the snowpack, dictated in part by the snow insulating capacity. The results of this novel analysis suggest that while future warming effects on phenology may be consistent across communities of the tundra biome, warming may result in divergent, community-specific productivity responses if coupled with reduced snow insulating capacity that lowers winter soil temperature and potential nutrient cycling in the soil.

Keywords (6-10) NDVI, SnowModel, snowmelt, growing degree days, snow water equivalent, start of season, peak of season, end of season, GS NDVI, Alaska

Introduction

Changes in vegetation phenology and productivity are two of the most critical climate-induced changes occurring in the Arctic. Recently, trends in the timing of vegetation phenological events such as start of season (SOS), peak of season (POS), end of season (EOS), and in growing season plant productivity, have been observed by both remote platforms (Ju & Masek, 2016; Park *et al.*, 2016) and *in situ* studies (Post *et al.*, 2008; Myers-Smith *et al.*, 2019). These changes in vegetation dynamics coincide with decades-long trends of increasing air and soil temperature, particularly in winter, and trends of localized increasing and decreasing precipitation year-round (Overland *et al.*, 2004; Walsh *et al.*, 2011). Plot-based observational and experimental studies of Arctic vegetation demonstrate species-specific response to snow conditions and spring temperature (Molau *et al.*, 2005; Wipf, 2010; Khorsand Rosa *et al.*, 2015; Krab *et al.*, 2018), suggesting it is likely that winter snow and early spring conditions are important controls on the timing of vegetation development and biomass production at the community level. However, despite wide-spread observations of changing snow conditions across the Arctic, and concurrent trends in earlier springs and increasing productivity, the role of snow as a driver of vegetation phenology and productivity at the spatial-scale of vegetation communities is not entirely understood and has been identified as a key field for future investigation (Beamish *et al.*, 2020; Niittynen *et al.*, 2020). In this study we examined the link between winter and spring conditions and vegetation dynamics, and how these relationships vary among tundra vegetation communities of Arctic Alaska.

Trends in phenological transitions and productivity are highly variable across the Arctic, suggesting that the controls are diverse and local (Jia *et al.*, 2006; Macias-Fauria *et al.*, 2017; Wang *et al.*, 2018). Spatial variability in phenological change is evident across northern regions; the growing season is starting earlier throughout much of the Arctic (Karlsen *et al.*, 2009; Zhao *et al.*, 2015), but in some regions the growing season is starting later (Park *et al.*, 2016). Even among regions experiencing an earlier start of the season, the rate of season advancement is not the same (Post *et al.*, 2009; Zhao *et al.*, 2015). There is also important temporal variability, with greater rates of change observed in the decades preceding year 2000 than have been observed in the time since (Park *et al.*, 2016; Bhatt *et al.*, 2017). Trends of vegetation productivity are also spatially diverse; most of the Arctic is characterized by a 'greening' trend, while a few areas show a browning trend (Verbyla, 2008; Ju & Masek, 2016). Just as with changes in phenology, the most rapid greening trends were observed between ca. 1980 and 2000 (Park *et al.*, 2016; Bhatt *et al.*, 2017). Finally, the direction of productivity trends detected from remote sensing data is frequently inconsistent with ground-based observations (Myers-Smith *et al.*, 2020). This notable variability in phenology and productivity in the Arctic suggests local drivers may be more important than previously recognized, and need to be fully explored.

Concurrent with, and possibly responsible for, changes in vegetation phenology and productivity, on-going global climate changes are altering precipitation patterns and temperature regimes with an amplified effect in the Arctic (Kaufman *et al.*, 2009; Serreze *et al.*, 2009; IPCC, 2013). Annual average air temperature has increased across the Arctic region, with the greatest increase in the winter months (Overland *et al.*, 2004; Bintanja & van der Linden, 2013). In contrast, precipitation changes are spatially heterogeneous with localized areas of increased or decreased rain- and snowfall (Walsh *et al.*, 2011; IPCC, 2013; Richter-Menge & Druckenmiller, 2020). These climatic changes are mediated through the Arctic seasonal snowpack in winter and early spring (Callaghan *et al.*, 2011) and play an important role in the growth of Arctic plants. Snowmelt marks the start of the growing season with a release of meltwater that influences soil moisture and nutrient availability throughout the growing season (Jespersen *et al.*, 2018). Snowmelt timing defines when plants first have access to direct sunlight in the spring and controls timing of the growing season and magnitude of peak vegetation greenness in some ecosystems (Grippa *et al.*, 2005; Zeng & Jia, 2013; Pedersen *et al.*, 2018; Assmann *et al.*, 2019). The snow-water equivalent (SWE) of the snowpack at the end of winter also affects the timing of a range of vegetation phenological events (Westergaard-Nielsen *et al.*, 2017).

Arctic plant growth and ecosystem processes are also influenced by specific properties of the seasonal snow cover such as snow depth, density, and thermal conductivity (Bokhorst *et al.*, 2016).

The presence or absence of snow cover influences the surface energy balance (Marks & Dozier, 1992; Groisman *et al.*, 1994; Stiegler *et al.*, 2016), which in turn affects the ground surface thermal regime. Snow cover acts as an efficient insulator during winter (Goodrich, 1982; Sturm *et al.*, 1997; Liston *et al.*, 2002) and keeps soil thermal conditions relatively stable during snow-covered periods (Taras *et al.*, 2002; Sturm *et al.*, 2005; Zhang, 2005). In turn, stable, warm conditions under the snowpack facilitate higher rates of winter soil microbial activity reflected in greater winter nitrogen mineralization and greater winter carbon dioxide emissions (Schimel *et al.*, 2004; Elberling, 2007). In some Arctic vegetation communities deeper winter snow results in greater labile nitrogen supply in the early growing season but not during the winter (DeMarco *et al.*, 2011; Mörsdorf *et al.*, 2019). In both cases, the snow-depth evolution through autumn and winter governs the amount and timing of plant-available nutrients at the end of winter and the following spring in tundra ecosystems (Jones, 1999; Buckeridge & Grogan, 2008). Furthermore, the snowpack insulating capacity protects the vegetation from frost damage (e.g., Bokhorst *et al.*, 2011). However, mid-winter episodic and short-lived warming or rain-on-snow events can change the stratigraphy of the snowpack (i.e., layer thickness and composition of snow types), or introduce ice-layers to the snowpack, and thereby alter the snow insulating properties entirely (Sturm *et al.*, 1997; Liston *et al.*, 2002; Pedersen *et al.*, 2015). Such changes to snowpack properties leave vegetation at risk of exposure to mid-winter freezing, and may allow soil temperatures to decrease as a result of reduced insulation from cold winter air (Inouye, 2000; Semenchuk *et al.*, 2013). Consequently, low soil temperature and vegetation exposure to freezing conditions can alter plant phenology and reduce productivity (Inouye, 2000).

Both snow and air temperature are recognized as important controls on vegetation phenology and productivity in the Arctic, and plot-level studies suggest that the effects of winter and spring conditions on vegetation dynamics vary among functional groups (Wipf & Rixen, 2010) and even species (Krab *et al.*, 2018). In general, higher spring air temperature allows the growing season to start earlier and promotes productivity (Inouye, 2008; Wipf *et al.*, 2009). Specifically, onset of growth is driven by snowmelt timing for shrubs, but is driven by temperature for graminoids (Wipf, 2010; Wipf & Rixen, 2010). In graminoids, plant phenology is relatively inflexible and unresponsive to snow conditions, whereas shrubs can accelerate their phenology in response to a spring with delayed snowmelt (Wipf & Rixen, 2010; Legault & Cusa, 2015). Similar variation exists in productivity. In shrubs, when snowmelt occurs early enough that plants begin growth and lose frost hardiness before the final freezes of the season, frost damage can decrease productivity (Wipf *et al.*, 2009). In contrast, later snowmelt has mixed effects on shrub productivity (Wipf & Rixen, 2010; Krab *et al.*, 2018) largely because dwarf shrubs benefit from a later start to the growing season and deciduous shrubs do not (Christiansen *et al.*, 2018). Finally, like deciduous shrubs, graminoids tend to decrease in productivity following delayed snowmelt (Wipf & Rixen, 2010). These *in situ* studies provide observations of vegetation-specific responses to snow conditions that are lacking from remote sensing observations. As a result, the effect of snow on Arctic vegetation phenology and productivity, and how the role of snow differs among neighboring vegetation communities, remain important outstanding questions.

In this study we explored the linkages between growing season vegetation phenology and productivity and the preceding spring and winter conditions using daily remotely-sensed vegetation greenness and metrics of winter and spring conditions including: potential winter soil microbial activity related to snowpack insulating capacity, water available in the snowpack, the timing of snowmelt, and air temperature in early spring. These variables were evaluated at the spatial (500-m) and temporal (daily) resolution sufficient to resolve the variability in phenology and spatial extent of vegetation communities in Arctic Alaska. Because the vegetation of this region is representative of approximately 70% of Arctic tundra, and more than half of the unglaciated Arctic (Walker *et al.*, 2005), our findings should be broadly applicable across the pan-Arctic region. We addressed the following questions:

(1) Which winter and spring conditions are most important for determining vegetation phenology and productivity across different Arctic vegetation communities?
(2) What is the effect of winter and spring conditions on vegetation phenology and productivity in different Arctic vegetation communities?

Based on past plot-level research results, we hypothesized that the most important drivers of plant phenology and productivity would differ among vegetation communities, with snow conditions emerging as an important control in shrub systems and less important in graminoid systems. Second, we hypothesized that the effect of specific conditions on phenology would be consistent across vegetation communities (e.g., later-persisting snow delaying plant phenology in all vegetation types), but the effect of specific conditions on productivity will vary among vegetation communities (e.g., later-persisting snow decreases productivity of graminiods, but increases productivity of shrubs). Based on our findings, we speculate on the effect of a predicted warmer and more snow-rich winter climate on productivity and phenology of different vegetation communities across the Arctic tundra biome.

Materials and Methods

Site Description

The study region for this work was the North Slope Borough, an area of more than 24 million hectares in northern Alaska extending from the foothills of the Brooks Range to the Beaufort Sea coast (Figure 1). The region is characterized by a dry, polar climate and is underlain by continuous permafrost, except under some lakes and rivers. The northern portion of the study region is composed of the primarily flat topography of the Arctic Coastal Plain. The soil of the coastal plain is typically saturated mineral soil overlain by a thick organic horizon (Nowacki *et al.*, 2003). The dominant vegetation is wet sedge tundra, tussock tundra, and tussock shrub tundra (Boggs *et al.*, 2016). South of this flat coastal plain are the foothills of the Brooks Range, which include rolling hills and exposed ridges overlain by colluvial and eolian deposits. The soil of the foothills ranges from well-drained mineral soil to saturated organics, and the primary vegetation present is sedge and shrub tussock tundra (Nowacki *et al.*, 2003). The most southern portion of our study region is occupied by the Brooks Range mountains. The vegetation of the Brooks Range is primarily alpine tundra with a large proportion of barren or sparsely vegetated land surface (Nowacki *et al.*, 2003).

Our study region is bound by a marine environment in the north and the more continental environment to the south, resulting generally in an increase in mean annual air temperature and total annual precipitation from the coast towards the Brooks Range (Zhang *et al.*, 1996; Shulski & Wendler, 2007; Bieniek *et al.*, 2012). However, throughout the year and among years, air temperature and precipitation patterns across the region vary in complex ways influenced both by the gently rolling hills of the North Slope, and pronounced terrain relief of the mountains in the south, which define temperature and precipitation lapse rates and modify the local wind speed and direction. In addition, the seasonally and inter-annually varying tracks of synoptic-scale weather systems and sea-ice coverage of water bodies surrounding the study region all contribute to high interannual and spatial variability in precipitation (Stuefer *et al.*, 2013, 2020) and air temperature (Overland *et al.*, 2018).

This study focused on six vegetation communities defined by the landcover types reported in the Alaska Vegetation and Wetland Composite (Boggs *et al.*, 2016): Wet Sedge, *Carex aquatilis*, Mesic Sedge-Dwarf Shrub Tundra (hereafter Dwarf Shrub Tundra), Tussock Tundra, Tussock Shrub Tundra, and Birch Ericaceous Low Shrub Tundra (hereafter Low Shrub Tundra) (Table 1). These vegetation classes make up six of the eight most aerially extensive vegetation communities in the North Slope Borough, and cover 62% of the land surface. These communities are also representative of the gradient in vegetation present from the Beaufort Sea coast to the crest of the Brooks Range. The only common landcover types of this region excluded from the analyses are those with sparse vegetation occurring on ridges and mountain slopes. This vegetation landcover dataset has a spatial resolution of 30 m.

Study point selection

We selected 600 points across the North Slope, 100 points within each vegetation community, for our analyses (Figure 1). The sample points are 500-m by 500-m pixels equaling the spatial resolution of the datasets used in this analysis (i.e., Moderate Resolution Imaging Spectroradiometer (MODIS) spectral data). We used a multi-step point-selection process to minimize variation in landcover within our study points and ensure representation of the larger study area. First, we overlaid the MODIS grid on our study region. Within each grid cell, we calculated the percent cover of the dominant vegetation class from the 30-m landcover product and discarded grid cells with less than 90% coverage by the most common vegetation. From the remaining grid cells, we randomly selected 100 cells of each vegetation community of interest.

Vegetation Phenology and Productivity Data

Vegetation phenology and productivity metrics were calculated from the Normalized Difference Vegetation Index (NDVI; Rouse *et al.*, 1973; Tucker, 1979). Daily NDVI values from 2001 to 2017 were derived from the MODIS nadir BRDF-Adjusted Reflectance (NBAR) data product (MCD43A4 Collection 6) at 500-m spatial resolution (Che *et al.*, 2017). Although the MCD43A4 input is smoothed with a 16-day kernel to minimize anisotropic and other high-frequency noise, residual effects of cloud contamination, atmospheric variability, and model error can disturb time series analysis of NDVI data (Atkinson et al. 2012, Che et al. 2017). Therefore, a Savitsky-Golay filter (Savitzky & Golay, 1964) was applied to the NDVI time series to further remove noise.

The resulting smoothed daily NDVI time series was used to calculate the phenological metrics of the timing of SOS, POS, EOS, and average NDVI of the growing season from SOS to EOS ("Growing-Season NDVI", GS NDVI), which provides a unitless estimate of growing season gross primary productivity (Jia *et al.*, 2002; Gu *et al.*, 2013; Guay *et al.*, 2014). The timing of POS was determined as the day of year of the maximum seasonal NDVI value of the smoothed NDVI time series. SOS and EOS were determined as the dates corresponding with the maximum rate of change in NDVI over time in the spring and fall, respectively. The daily rate of change in NDVI was calculated using a 16-day window applied to the smoothed NDVI time series. SOS was identified as the date in the center of the 16-day window with the maximum rate of change on the ascending portion of the annual NDVI curve (where day of year is < POS) and EOS was identified as the date in the center of the 16-day window with the maximum rate of change on the descending portion of the annual NDVI curve (where day of year is > POS). The time-series of phenology (SOS, POS, and EOS) and productivity (GS

NDVI) metrics were processed in each MODIS pixel for each year, and then mosaicked and output to geospatial layer with 500-m resolution.

Winter and Spring Data

To investigate winter and spring controls on vegetation phenology we chose ecologically relevant variables selected to represent (a) the snow-soil interface temperature controlled by the thermal insulating properties of the snowpack, which is presumed to influence winter soil microbial activity and nutrient availability (Active Days), (b) water available from spring snowmelt (snow water equivalent (SWE)), (c) the onset of direct light, access to liquid water, and air temperature above freezing (Snow-free day of year (DOY)), and (d) the thermal conditions during the initial snow-free period (Growing Degree Days (GDD) of June and to peak of season (GDD-to-POS)) (Table 2). June GDD is calculated as the sum of positive (above 0 °C) daily air temperature during the month of June. GDD-to-POS is the sum of positive daily air temperature from 1 January to a community-specific POS date, determined as the average POS for all points in all years in one vegetation community. June GDD were used as an explanatory variable for timing of SOS, and GDD-to-POS were used as an explanatory variable for POS, EOS, and GS NDVI. Active Days are defined as the number of days with snow on the ground, when the ground-snow interface temperature is above -6.0 °C, i.e., when there is presumed soil microbial activity (Taras et al., 2002). Following the methods of Taras et al. (2002) developed on Alaska's North Slope, the ground-snow interface temperature was modeled from daily air temperature, snow depth, and snowpack thermal properties defined by three wind-exposure classes (i.e., exposed, intermediate, and sheltered) specific to a study point's location on the coastal plain or in the uplands (Taras et al., 2002).

These environmental drivers were derived from spatially and temporally explicit air temperature and snow datasets produced by a suite of snow-distribution and snow-evolution modeling tools called SnowModel (Liston & Elder, 2006a), which is broadly applied across the Arctic and globally in any environment experiencing snow (e.g. Liston *et al.*, 2000; Liston & Hiemstra, 2011; Mernild *et al.*, 2017; Pedersen, 2017). The SnowModel simulations were performed at a spatial and temporal resolution identical to the NDVI dataset, i.e. 500-m grid and daily time steps. SnowModel was coupled with a meteorological model called MicroMet (Liston & Elder, 2006b), which spatially distributes meteorological information over the simulation domain and provides inputs needed to drive SnowModel. For this particular application in Arctic Alaska, SnowModel simulations used inputs of air temperature, relative humidity, precipitation, wind speed, and wind direction from NASA's Modern-Era Retrospective Analysis for Research and Applications, version 2 (MERRA-2) gridded atmospheric reanalysis data (Gelaro *et al.*, 2017). The USGS National Elevation Dataset (U.S. Geological Survey, 2019) served as the digital elevation model for these simulations and the North American Land Change Monitoring System (U.S. Geological Survey, 2020) provided the land-cover map. Both invariant datasets were regridded from 30-m to 500-m spatial resolution to match the MODIS grid-cell resolution. Since snow observations are sparse over this study region, we used remotely sensed snow-free day to adjust total winter-precipitation amounts and reproduce realistically modeled snowmelt timing across the study area. Specifically, we assessed our estimate of the pre-melt snowpack SWE in a given location by applying a physically realistic snowmelt rate, and then comparing the modeled to the actual snow-free date for that location and year, determined by remotely sensed imagery (Macander and Swingley, 2017; original in 30-m spatial resolution regridded to 500-m resolution). Discrepancies in the snow-free date estimates were used to determine where pre-melt SWE was too high or too low, i.e., where the SnowModel input of total precipitation required an adjustment.

Random Forest modeling

Analysis of Random Forest regression-trees (Breiman, 2001), an extension of the decision-tree algorithm for continuous response variables, was used to identify the most important drivers of vegetation phenology and productivity and describe the relationship between winter and spring conditions and vegetation response. Our analyses were completed using the *randomForest* package (Liaw & Wiener, 2002) in R (R Core Team). We limited the number of variables we investigated *a priori* by focusing on the winter and spring conditions presumed to have the greatest ecological importance: Active Days, Snow-free DOY, SWE, and GDD. We conducted a Random Forest regression of 500 trees on each of our six vegetation communities. All explanatory variables (Active Days, SWE, Snow-free DOY, and GDD) were tested against each phenology and productivity metric (SOS, POS, EOS, and GS NDVI) at each split in every regression tree.

Random Forest analyses were used to evaluate our study questions: (1) which of the explanatory variables (Active Days, SWE, Snow-free DOY, and GDD) are the most important drivers of vegetation phenology and productivity, and (2) what is the relationship between Active Days, SWE, Snow-free DOY, and GDD and vegetation phenology and productivity? We addressed the first question using variable-importance rankings determined by node purity, a relative measure of how a given explanatory variable contributes to increasing homogeneity of the regression tree-nodes when used as a split. A greater node purity indicates that the given variable is more important in determining the response. To address the second question we constructed partial dependence plots to determine the relationship between each explanatory variable and vegetation response variable while holding all other explanatory variables constant.

Results

SOS, POS, EOS, and GS NDVI varied by vegetation community across the study region, and among study years (SI Figure 1). Mean SOS, POS, and EOS differed among communities ($p < 0.001$) with a ca. 10 day range (Figure 2). The earliest mean SOS, POS, and EOS occurred in Low Shrub Tundra on 21 June, 23 July, and 23 August (DOY 172, 204, and 235) respectively. The latest mean SOS, POS, and EOS occurred in Wet Sedge on 1 July, 2 August, 1 September (DOY 182, 214, and 244), respectively. The greatest mean GS NDVI was observed in the Low Shrub Tundra community (0.69) and the lowest was observed in Wet Sedge (0.53). Most explanatory variables (Active Days, SWE, and GDD) showed variability among vegetation communities (Table 3). The mean number of Active Days varied between 39 in *Carex aquatilis* to over 61 in Low Shrub Tundra; mean SWE varied from 0.21 m in *Carex aquatilis* and Wet Sedge to 0.27 m in Tussock Shrub Tundra and Low Shrub Tundra. Mean June GDD varied between 179.4 in *Carex aquatilis* to 273.0 in Low Shrub Tundra and mean GDD-to-POS varied between 510.6 and 610.5 between these same communities. In contrast, the mean Snow-free

DOY was similar among vegetation types, with the earliest mean Snow-free DOY at 27 May (DOY 147) in Low Shrub Tundra and the latest mean Snow-free DOY at 31 May (DOY 151) in Wet Sedge and Tussock Shrub Tundra.

The Random Forest analyses indicated that winter and spring conditions explained a similar amount of variation in SOS, POS, and GS NDVI, and slightly less variation in EOS (Table 4). However, the amount of variation explained by winter and spring conditions varied considerably among vegetation communities. For both phenology (SOS, POS, and EOS) and productivity (GS NDVI), winter and spring conditions explained the greatest amount of variation within Low Shrub Tundra, followed by Dwarf Shrub Tundra and *Carex aquatilis*, and the lowest amount of variation in Tussock Tundra, Tussock Shrub Tundra, and Wet Sedge (Table 4).

Start of Season (SOS)

Active Days, SWE, Snow-free DOY, and GDD explained between 40.6% and 78.6% of the variation in SOS (Table 4). The highest percentage of variation in SOS was explained in Low Shrub Tundra, with the lowest percentage of variation explained in Tussock Shrub Tundra. Within these models, June GDD was the most important driver of SOS in all vegetation communities (Figure 3), and greater June GDD contributed to an earlier SOS in all communities except Dwarf Shrub Tundra where we observed no clear trend (Figure 4). The effect of June GDD on SOS appeared to saturate such that greater GDD was only beneficial in advancing SOS up to a certain point (approx. 250 GDD) after which greater GDD did not contribute to earlier SOS. This pattern may indicate that the ~10% of data showing no relationship between SOS and GDD were the cases where SOS occurred early in June, thus lessening the effect of June GDD on SOS. The analysis revealed that Active Days and Snow-free DOY also contributed to the model's explanatory power in some vegetation communities with greater Active Days contributing to an earlier SOS, and delayed Snow-free DOY contributing to a later SOS (SI Figure 2).

Peak of Season (POS)

Active Days, SWE, Snow-free DOY, and GDD-to-POS explained between 45.6% and 80.8% of variation in POS, with the highest percentage of variation explained in Low Shrub Tundra, and the lowest percent explained in Wet Sedge (Table 4). The most important control varied among vegetation communities, but the direction of the relationship between the winter explanatory variable and the response phenology variable was consistent among vegetation communities (Figure 4). Snow-free DOY was the most important in Wet Sedge, Dwarf Shrub Tundra, and Low Shrub Tundra, with an earlier Snow-free DOY corresponding to an earlier POS. GDD was the most important control in *Carex aquatilis* and Tussock Shrub Tundra, with more GDD corresponding to an earlier POS. Active Days was the most important control in Tussock Tundra and revealed a complex relationship with POS, but greater Active Days corresponded with an earlier POS for the majority of points (Figure 4; SI Figure 3).

End of Season (EOS)

Active Days, SWE, Snow-free DOY, and GDD-to-POS explained between 26.3% and 66.7% of variation in EOS, with the lowest percent explained in Tussock Shrub Tundra and the highest percentage of variation explained in Low Shrub Tundra (Table 4). The most important control was GDD-to-POS in all vegetation communities (Figure 3). In all communities, more GDD corresponded with an earlier EOS until approximately 700 GDD (Figure 4, SI Figure 4). Above 700 GDD, the relationship reversed so that more GDD corresponded with a later EOS, but this reversal was driven by 10% or less of the data in most vegetation communities (Figure 4).

Productivity (GS NDVI)

Active Days, SWE, Snow-free DOY, and GDD-to-POS explained between 27.0% and 68.5% of the variation in GS NDVI (Table 4). The lowest percentage of variation was explained in Tussock Shrub Tundra and like for phenology, the greatest percentage of variation was explained in Low Shrub Tundra. GDD-to-POS was the most important control of GS NDVI in *Carex aquatilis*, Tussock Shrub Tundra, and Low Shrub Tundra, with Active Days as the most important for Wet Sedge, Dwarf Shrub Tundra, and Tussock Tundra (Figure 3). In all vegetation communities where Active Days was the most important control, more Active Days corresponded with a greater GS NDVI (Figure 4). In the communities where GDD was most important, more GDD led to higher GS NDVI in some communities, with no visible trend in others (Figure 4; SI Figure 5).

Discussion

Winter and spring conditions are important drivers of vegetation phenology and productivity across Arctic vegetation communities, but our results show the specific drivers differ among vegetation communities. Spring temperature (GDD) is the primary control on start and end of season in all vegetation communities. In contrast, POS and productivity are more closely related to snow conditions; POS is controlled by snowmelt timing and vegetation productivity by winter soil temperature under the snowpack (Active Days), in addition to GDD. Taken together our results suggest that future climate-induced changes to winter snowpack and spring temperature will manifest in variable responses among tundra vegetation communities. More GDD may shift timing of the start and end of the growing season earlier in all communities, whereas productivity changes will depend on temperature and snow insulating capacity. This heterogeneity of vegetation responses highlights the complex nature of vegetation-snow interactions in Arctic tundra, and suggests that neighboring tundra vegetation communities may exhibit contrasting responses to climate change as they respond to different specific climatic drivers.

Controls of Vegetation Phenology

GDD was the most important driver of the timing of growing season start and end in every tundra vegetation community we examined. This result was consistent with our hypothesis that the effect of winter and spring conditions on phenology would be the same across vegetation communities, but contradictory to our hypothesis that most important drivers of plant phenology would differ among communities. The variation in timing of SOS and EOS in response to GDD conditions was significant (~5-7 days) given that the growing season in this region is less than 10 weeks long. GDD is a widely accepted metric for predicting vegetation phenology in Arctic and alpine regions (Arft *et al.*, 1999; Molau *et al.*, 2005; Khorsand Rosa *et al.*, 2015), although many studies also highlight the importance of snowmelt timing in the start of the season (Wipf, 2010; Khorsand Rosa *et al.*, 2015). Our results suggest that because more GDD contribute to an earlier start and end to the growing season in every vegetation community, warmer conditions are unlikely to extend the growing season in these communities. This finding corroborates Arctic plot-scale field studies indicating warming does not lengthen the growing season but can shift it earlier (Starr *et al.*, 2000; Khorsand Rosa *et al.*, 2015 but see May *et al.*, 2020), and complements remote sensing observations that show no or little trend of lengthening growing season in much of the Arctic (Gamon *et al.*, 2013; Zhao *et al.*, 2015; Gonsamo *et al.*, 2018). The absence of a change in growing season length for Arctic plants in response to warming is likely due to the accumulation of water deficit due greater evapotranspiration during the warmer spring, a phenomenon which has been recently observed in many ecosystems, including those typically thought to be temperature-limited (Angert *et al.*, 2005; Buermann *et al.*, 2018; Gonsamo *et al.*, 2019). Such a shift in timing of the growing season may have implications for ecological function such as synchrony of plant-pollinator (Kudo & Cooper, 2019) or plant-herbivore interactions (Nolet *et al.*, 2020), which can in turn influence plant traits and ecosystem nutrient cycling (Beard *et al.*, 2019).

In contrast to the GDD drivers of SOS and EOS, POS was related to snow conditions of the preceding winter and spring in many vegetation communities. In particular, the timing of POS was driven by snowmelt timing in Wet Sedge, Dwarf Shrub Tundra, and Low Shrub Tundra, and by Active Days in Tussock Tundra. The importance of snowmelt timing on Arctic phenology is demonstrated by many field-based, plot-scale studies (Walker *et al.*, 1999; Molau *et al.*, 2005; Inouye, 2008; Khorsand Rosa *et al.*, 2015) that suggest Arctic plants shorten or prolong their ‘prefloration timing’ in response to snowmelt timing (Wipf & Rixen, 2010; Legault & Cusa, 2015). The species whose phenological development is most sensitive to snowmelt timing are those that begin seasonal growth directly following snowmelt in the spring (Dunne et al., 2003; Wipf, 2010). Dwarf shrubs are known to capitalize on early snowmelt (Starr & Oberbauer, 2003; Wipf, 2010), therefore the relationship between POS and snowmelt timing that we observed in Low Shrub Tundra and Dwarf Shrub Tundra may be related to the prevalence of dwarf shrub species in these communities. Shifts in the timing of

POS can have implications for ecosystem productivity as an earlier POS means the period of maximum photosynthetic capacity coincides with the highest annual insolation near the summer solstice. POS can vary independently from the start and end of the growing season, for example POS occurs in late spring in arid climates to maximize water availability (Rotenberg & Yakir, 2007), and recent evidence suggests POS is occurring earlier in the season in the Northern Hemisphere (Xu *et al.*, 2016; Gonsamo *et al.*, 2018).

Our study assesses the relative importance of temperature versus snow conditions on Arctic vegetation phenology, a distinction which is critical for disentangling the drivers behind observed phenology trends and for anticipating future conditions. The few previous studies that assessed the relative importance of these drivers primarily focused on Arctic shrubs at the plot level, and suggested a complex relationship between the timing of snowmelt and spring temperature. For example, delayed snowmelt, as a result of deeper snowpack, counteracted the season advancement from long-term climate warming in the high-Arctic tundra of Ellesmere Island (Bjorkman *et al.*, 2015). In contrast, in an experimental setting in similar vegetation, higher spring soil temperatures advanced green-up more than early snowmelt (Krab *et al.*, 2018). Finally, sedges and dwarf shrubs in interior Alaska responded to both snowmelt and warming but at different stages; early phenophases (i.e., budburst) were driven primarily by the timing of snowmelt and later phenophases (i.e., total greening) were related to accumulated temperature (Wipf, 2010). Our study found that SOS timing was driven by GDD, but the discrepancy between our finding and previous field observations may be related to the exact phenophases represented by our observations of SOS. NDVI, the vegetation metric we used to measure SOS, is an amalgamated signal of many different species and can only be used to assess phenological change when there is no remaining snow cover. Therefore, our assessment of SOS is likely later in the phenological development, for example after budburst. However, evidence from previous work indicates that remote sensing and snow modeling tools can effectively be used to identify temperature versus snow drivers of phenology and productivity (Westergaard-Nielsen et al., 2017; Pedersen et al., 2018) and disentangle the ways that snow affects vegetation growth (Wang et al., 2018). Attention to specifying the aspect of snow (e.g., water content or insulating capacity) being investigated in future snow-vegetation research will lead to a more nuanced knowledge of Arctic vegetation response to climate change.

Controls of Vegetation Productivity

Controls on productivity differed among communities, and were closely associated with snow in addition to GDD, both consistent with our hypotheses. While relationships between winter conditions and vegetation productivity have been observed previously both by plot-level and remote sensing studies (Walker *et al.*, 1993; Grippa *et al.*, 2005; Wipf & Rixen, 2010; Krab *et al.*, 2018), our study suggests these relationships are dependent on vegetation community. We found that greater Active Days contributed to increased productivity in all vegetation communities (SI Figure 5), and was the most important driver in Wet Sedge, Dwarf Shrub Tundra, and Tussock Tundra. In all other communities, GDD was the most important driver. Active Days are expected to influence nutrient cycling and availability (Schimel *et al.*, 2004; Welker *et al.*, 2005; Borner *et al.*, 2008), therefore the contrasting drivers of productivity among vegetation communities may reflect ability of species to respond to enhanced nutrient cycling (Seastedt & Vaccaro, 2001). Evergreen shrubs, in particular, are more able to take advantage of the increase in nutrients available at the winter-spring transition because they begin photosynthesizing under the snowpack (Starr & Oberbauer, 2003). But an increase in snow may be detrimental to other plants; some tussock-forming sedges experience negative effects of a prolonged snow-covered season that results in lower summer season productivity (Bell & Bliss, 1979). Our results suggest that such species-specific differences are manifested in differences among vegetation communities, highlighting that the productivity response to future climate change may differ among vegetation communities as they are responding to different drivers.

Our study is one of the first to investigate the relative importance of drivers of Arctic vegetation phenology and productivity, how they vary among different vegetation communities, and employs higher temporal resolution data than most previous works. Therefore, this work provides important context for the plethora of recent studies investigating trends in Arctic vegetation phenology and productivity. For example, a previous NDVI trend study in the Arctic demonstrated a relationship between declining sea ice, air temperature, and NDVI, and suggested that snow may be an important intermediary step in this process (Bhatt *et al.*, 2017). Our results contribute greater nuance to this link by suggesting that snow, specifically the effect on winter soil temperature under the snowpack, is indeed the strongest driver of vegetation phenology and productivity in some vegetation communities, while spring GDD is the strongest driver of productivity in others. As both GDD and higher winter soil temperature due to greater snow insulating capacity are related to increased productivity, these may be the mechanisms responsible for some of the greening trends already observed in the Arctic. However, if future projected warming during winter results in precipitation falling as rain instead of snow (Krasting *et al.*, 2013; Bintanja & Andry, 2017), the response among vegetation communities may diverge because communities responding to GDD may continue to green while those responsive to soil thermal conditions, which are dependent on the insulating capacity of the snowpack, may not. Such variation in drivers among neighboring vegetation communities is a critical component of untangling the drivers of vegetation change, and anticipating future effects on vegetation in Arctic regions.

Future Implications

Northern Alaska is expected to be warmer with more winter snowfall in the future (Krasting et al., 2013) and recent studies suggest that this transition may already be underway (Overland et al., 2018; Stuefer et al., 2020). Our results suggest the projected warming will produce more GDD after snowmelt and shift the start and end of the growing season earlier in the year in all communities without lengthening the season (Figure 5a). In contrast, changes to productivity will come through warming in some vegetation communities, and changes to the snowpack in others. Assuming that future winters remain cold enough to allow the predicted increases in snowfall to accumulate on the ground, increased accumulation will improve insulating capacity of the snowpack. Greater insulation will produce relatively higher winter soil temperature (i.e., more Active Days), and greater future plant productivity (Figure 4, Figure 5a), up to the point where air and soil temperature become decoupled by the snowpack (>80 cm snowpack for Alaska's North Slope (Taras et al., 2002)).

However, these vegetation responses are likely dependent on physical properties of the future snowpack. The insulating effect of the snowpack is a product of several snow properties (layer thickness, the snow types, and their related thermal conductivity (Sturm et al. 1997)) that may change in response to mid-winter melting of the snowpack. Mid-winter melting can also produce an ice-layer on top, within, or below the snowpack. Depending on how physical snowpack properties respond to a warmer and more snow-rich climate and/or more frequent mid-winter melt events, a decrease in Active Days, and subsequent decline in productivity may be equally likely in a warming scenario (Figure 5b). As such, speculative trends of uniform changes across tundra vegetation only persist as long as greater heat (more GDD) coincides with increased winter snowfall and snow accumulation. If, in contrast, continued warming results in some winter precipitation falling as rain (Krasting *et al.*, 2013; Bintanja & Andry, 2017), the response among vegetation communities may diverge. In sum, a future Arctic with higher temperatures but lower snowpack insulating capacity may see similar phenological change among vegetation communities, but diverging productivity responses as productivity declines in some communities despite warming.

Limitations

A limiting factor of our study is that the spatial resolution of the NDVI data (500-m) constrains our analyses and defines the spatial resolution of our results. We acknowledge that processes driving the relationships between winter conditions and vegetation response in some communities are occurring on spatial scales not resolved by our 500-m datasets. For example, we did not see evidence that a deeper snowpack drives greater productivity specifically in shrub-dominated communities, despite previous research suggesting a positive feedback where greater snow accumulation promotes winter-time nutrient cycling, which then increases shrub growth (Sturm *et al.*, 2005). The lack of evidence of such a relationship in this study may indicate that in some communities these vegetation dynamics play out at spatial scales smaller than those represented in our data. We intentionally designed our study despite this limitation because the daily resolution allowed us to obtain the most accurate metrics of phenology currently available, and this was balanced against the level of spatial detail. Furthermore, this study intentionally spans the entire Arctic Alaska region in an effort to make these results broadly applicable to pan-Arctic tundra landscapes. However, future work that aims to investigate snow as driver of vegetation dynamics on a more local scale should use snow datasets (e.g., produced by SnowModel) of spatial extent and resolution that capture snow (re-) distribution across the landscape and resolve differences in snow accumulation and -melt patterns between vegetation communities of interest.

Summary and Conclusions

The heterogeneity of vegetation responses revealed in this study highlights the complex nature of vegetation-snow interactions in Arctic tundra. We found that Arctic vegetation phenology, specifically timing of the start and end of the growing season, are primarily driven by Growing Degree Days such that the growing season starts and ends earlier in warmer years. Peak of season timing does not follow this trend, rather later snowmelt postpones peak of season timing in some communities. Productivity is strongly responsive to the insulating effect of snow; particularly the productivity in Wet Sedge, Dwarf Shrub Tundra, and Tussock Tundra increases in response to more days of winter soil microbial activity (Active Days), whereas in Tussock Shrub Tundra, Low Shrub Tundra, and *Carex aquatilis*, productivity increases as a result of more Growing Degree Days. Because we identified snow characteristics as critical drivers of Arctic phenology and productivity, future studies should include snow information at resolutions matching vegetation community distributions, e.g., as demonstrated possible herein by using SnowModel. Our research highlights the importance of integrating and defining the multi-facetted effects of snow in combination with air and soil temperature, such as the mediating effect of snowpack insulation on vegetation productivity, in order to understand the diverse response to climate change among neighboring vegetation communities within the Arctic tundra biome.

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Works Cited

Angert A, Biraud S, Bonfils C et al. (2005) Drier summers cancel out the CO2 uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 10823–10827.

Arft AM, Walker MD, Gurevitch J et al. (1999) Responses of Tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. *Ecological Monographs*, **69**, 491–511.

Assmann JJ, Myers-Smith IH, Phillimore AB et al. (2019) Local snow melt and temperature—but not regional sea ice—explain variation in spring phenology in coastal Arctic tundra. *Global Change Biology*, **25**, 2258–2274.

Beamish A, Raynolds MK, Epstein H et al. (2020) Recent trends and remaining challenges for optical remote sensing of Arctic tundra vegetation: A review and outlook. *Remote Sensing of Environment*, **246**, 111872.

Beard KH, Kelsey KC, Leffler AJ, Welker JM (2019) The Missing Angle: Ecosystem Consequences of Phenological Mismatch. *Trends in Ecology and Evolution*, **34**, 885–888.

Bell KL, Bliss LC (1979) Autecology of Kobresia bellardii: why winter snow accumulation limits local distribution. *Ecological Monographs*, **49**, 377–402.

Bhatt US, Walker DA, Raynolds MK et al. (2017) Changing seasonality of panarctic tundra vegetation in relationship to climatic variables. *Environmental Research Letters*, **12**.

Bieniek PA, Bhatt US, Thoman RL et al. (2012) Climate divisions for Alaska based on objective methods. *Journal of Applied Meteorology and Climatology*, **51**, 1276–1289.

Bintanja R, Andry O (2017) Towards a rain-dominated Arctic. *Nature Climate Change*, **7**, 263–267.

Bintanja R, van der Linden EC (2013) The changing seasonal climate in the Arctic. *Scientific Reports*, **3**, 1–8.

Bjorkman AD, Elmendorf SC, Beamish AL, Vellend M, Henry GHR (2015) Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology*, **21**, 4651–4661.

Boggs K, Flagstad L, Boucher T, Kuo T, Fehringer D, Guyer S, Aisu M (2016) Vegetation Map and Classification: Northern, Western, and Interior Alaska. 1–96.

Bokhorst S, Bjerke JW, Street LE, Callaghan T V., Phoenix GK (2011) Impacts of multiple extreme winter warming events on sub-Arctic heathland: Phenology, reproduction, growth, and CO_2 flux responses. *Global Change Biology*, **17**, 2817–2830.

Bokhorst S, Pedersen SH, Brucker L et al. (2016) Changing Arctic snow cover: A review of recent developments and assessment of future needs for observations, modelling, and impacts. *Ambio*, **45**, 516–537.

Borner AP, Kielland K, Walker MD (2008) Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan Arctic tundra. *Arctic, Antarctic, and Alpine Research*, **40**, 27–38.

Breiman L (2001) Random forests. *Machine Learning*, **45**, 5–32.

Buckeridge KM, Grogan P (2008) Deepened snow alters soil microbial nutrient limitations in arctic birch hummock tundra. *Applied Soil Ecology*, **39**, 210–222.

Buermann W, Forkel M, O'Sullivan M et al. (2018) Widespread seasonal compensation effects of spring warming on northern plant productivity. *Nature*, **562**, 110–114.

Callaghan T V., Johansson M, Brown RD et al. (2011) Multiple effects of changes in arctic snow cover. *Ambio*, **40**, 32–45.

Christiansen CT, Lafreniére MJ, Henry GHR, Grogan P (2018) Long-term deepened snow promotes tundra evergreen shrub growth and summertime ecosystem net CO_2 gain but reduces soil carbon and nutrient pools. *Global Change Biology*, **24**, 3508–3525.

DeMarco J, Mack MC, Bret-Harte MS (2011) The Effects of Snow, Soil Microenvironment, and Soil Organic Matter Quality on N Availability in Three Alaskan Arctic Plant Communities. *Ecosystems*, **14**, 804–817.

Dunne JA, Harte J, Taylor KJ (2003) Subalpine meadow flowering phenology responses to climate change: Integrating experimental and gradient methods. *Ecological Monographs*, **73**, 69–86.

Elberling B (2007) Annual soil CO2 effluxes in the High Arctic: The role of snow thickness and vegetation type. *Soil Biology and Biochemistry*, **39**, 646–654.

Gamon JA, Huemmrich KF, Stone RS, Tweedie CE (2013) Spatial and temporal variation in primary productivity (NDVI) of coastal Alaskan tundra: Decreased vegetation growth following earlier snowmelt. *Remote Sensing of Environment*, **129**, 144–153.

Gelaro R, McCarty W, Suárez MJ et al. (2017) The modern-era retrospective analysis for research and applications, version 2 (MERRA-2). *Journal of Climate*, **30**, 5419–5454.

Gonsamo A, Chen JM, Ooi YW (2018) Peak season plant activity shift towards spring is reflected by increasing carbon uptake by extratropical ecosystems. *Global Change Biology*, **24**, 2117–2128.

Gonsamo A, Ter-Mikaelian MT, Chen JM, Chen J (2019) Does earlier and increased spring plant growth lead to reduced summer soil moisture and plant growth on landscapes typical of tundra-taiga interface? *Remote Sensing*, **11**.

Goodrich LE (1982) The influence of snow cover on the ground thermal regime. *Canadian Geotechnical Journal*, **19**, 421–432.

Grippa M, Kergoat L, Le Toan T, Mognard NM, Delbart N, L'Hermitte J, Vicente-Serrano SM (2005) The impact of snow depth and snowmelt on the vegetation variability over central Siberia. *Geophysical Research Letters*, **32**, 1–4.

Groisman PY, Karl TR, Knight RW (1994) Observed impact of snow cover on the heat balance and the rise of continental spring temperatures. *Science (New York, N.Y.)*, **263**, 198–200.

Gu Y, Wylie BK, Bliss NB (2013) Mapping grassland productivity with 250-m eMODIS NDVI and SSURGO database over the Greater Platte River Basin, USA. *Ecological Indicators*, **24**, 31–36.

Guay KC, Beck PSA, Berner LT, Goetz SJ, Baccini A, Buermann W (2014) Vegetation productivity patterns at high northern latitudes: A multi-sensor satellite data assessment. *Global Change Biology*, **20**, 3147–3158.

Inouye DW (2000) The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, **3**, 457–463.

Inouye DW (2008) Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers. *Ecology*, **2**, 353–362.

IPCC (2013) Climate change 2013: the physical science basis. In: *Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), pp. 1–1535. Cambridge University Press, Cambridge, UK.

Jespersen RG, Leffler AJ, Oberbauer SF, Welker JM (2018) Arctic plant ecophysiology and water source utilization in response to altered snow: isotopic (δ18O and δ2H) evidence for meltwater subsidies to deciduous shrubs. *Oecologia*, **187**, 1009–1023.

Jia GJ, Epstein HE, Walker DA (2002) Spatial characteristics of AVHRR-NDVI along latitudinal transects in northern Alaska. *Journal of Vegetation Science*, **13**, 315–326.

Jia GJ, Epstein HE, Walker DA (2006) Spatial heterogeneity of tundra vegetation response to recent temperature changes. *Global Change Biology*, **12**, 42–55.

Jones HG (1999) The ecology of snow-covered systems: A brief overview of nutrient cycling and life in the cold. *Hydrological Processes*, **13**, 2135–2147.

Ju J, Masek JG (2016) The vegetation greenness trend in Canada and US Alaska from 1984-2012 Landsat data. *Remote Sensing of Environment*, **176**, 1–16.

Karlsen SR, Hegda KA, Wielgolaski FE, Tolvanen A, Tømmervik H, Poikolainen J, Kubin E (2009) Growing-season trends in Fennoscandia 1982-2006, determined from satellite and phenology data. *Climate Research*, **39**, 275–286.

Kaufman DS, Schneider DP, McKay NP et al. (2009) Recent warming reverses long-term arctic cooling. *Science (New York, N.Y.)*, **325**, 1236–9.

Khorsand Rosa R, Oberbauer SF, Starr G, Parker La Puma I, Pop E, Ahlquist L, Baldwin T (2015) Plant phenological responses to a long-term experimental extension of growing season and soil warming in the tussock tundra of Alaska. *Global Change Biology*, **21**, 4520–4532.

Krab EJ, Roennefarth J, Becher M et al. (2018) Winter warming effects on tundra shrub performance are species-specific and dependent on spring conditions. *Journal of Ecology*, **106**, 599–612.

Krasting JP, Broccoli AJ, Dixon KW, Lanzante JR (2013) Future changes in northern hemisphere snowfall. *Journal of Climate*, **26**, 7813–7828.

Kudo G, Cooper EJ (2019) When spring ephemerals fail to meet pollinators: Mechanism of phenological mismatch and its impact on plant reproduction. *Proceedings of the Royal Society B: Biological Sciences*, **286**.

Legault G, Cusa M (2015) Temperature and delayed snowmelt jointly affect the vegetative and reproductive phenologies of four sub-Arctic plants. *Polar Biology*, **38**, 1701–1711.

Liaw A, Wiener M (2002) Classification and Regression by randomForest. *R News*, **2/3**, 18–22.

Liston GE, Elder K (2006a) A distributed snow-evolution modeling system (SnowModel). *Journal of Hydrometeorology*, **7**, 1259–1276.

Liston GE, Elder K (2006b) A meteorological distribution system for high-resolution terrestrial modeling (MicroMet). *Journal of Hydrometeorology*, **7**, 217–234.

Liston GE, Hiemstra CA (2011) The changing cryosphere: Pan-Arctic snow trends (1979-2009). *Journal of Climate*, **24**, 5691–5712.

Liston GE, Winther J-G, Bruland O, Elvehøy H, Sand K, Karlöf L (2000) Snow and blue-ice distribution patterns on the coastal Antarctic Ice Sheet. *Antarctic Science*, **12**, 69–79.

Liston GE, Mcfadden JP, Sturm M, Pielke RA (2002) Modelled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs. *Global Change Biology*, **8**, 17–32.

Macias-Fauria M, Karlsen SR, Forbes BC (2017) Disentangling the coupling between sea ice and tundra productivity in Svalbard. *Scientific Reports*, **7**, 1–10.

Marks D, Dozier J (1992) Climate and energy exchange at the snow surface in the Alpine Region of the Sierra Nevada: 2. Snow cover energy balance. *Water Resources Research*, **28**, 3043–3054.

May JL, Hollister RD, Betway KR et al. (2020) NDVI Changes Show Warming Increases the Length of the Green Season at Tundra Communities in Northern Alaska: A Fine-Scale Analysis. *Frontiers in Plant Science*, **11**, 1–12.

Mernild SH, Liston GE, Hiemstra CA, Malmros JK, Yde JC, McPhee J (2017) The Andes Cordillera. Part I: snow distribution, properties, and trends (1979–2014). *International Journal of Climatology*, **37**, 1680–1698.

Molau U, Nordenhäll U, Eriksen B (2005) Onset of flowering and climate variability in an alpine landscape: A 10-year study from Swedish Lapland. *American Journal of Botany*, **92**, 422–431.

Mörsdorf MA, Baggesen NS, Yoccoz NG, Michelsen A, Elberling B, Ambus PL, Cooper EJ (2019)

Deepened winter snow significantly influences the availability and forms of nitrogen taken up by plants in High Arctic tundra. *Soil Biology and Biochemistry*, **135**, 222–234.

Myers-Smith IH, Grabowski MM, Thomas HJD et al. (2019) Eighteen years of ecological monitoring reveals multiple lines of evidence for tundra vegetation change. *Ecological Monographs*, **0**, e01351.

Myers-Smith IH, Kerby JT, Phoenix GK et al. (2020) Complexity revealed in the greening of the Arctic. *Nature Climate Change*, **10**, 106–117.

Niittynen P, Heikkinen RK, Luoto M (2020) Decreasing snow cover alters functional composition and diversity of Arctic tundra. *Proceedings of the National Academy of Sciences*, **117**, 202001254.

Nolet BA, Schreven KHT, Boom MP, Lameris TK (2020) Contrasting effects of the onset of spring on reproductive success of Arctic-nesting geese. *Auk*, **137**, 1–9.

Nowacki GJ, Spencer P, Fleming M, Brock T, Jorgenson T (2003) *Unified Ecoregions of Alaska: 2001*.

Overland JE, Spillane MC, Percival DB, Wang M, Mofjeld HO (2004) Seasonal and regional variation of pan-Arctic surface air temperature over the instrumental record. *Journal of Climate*, **17**, 3263–3282.

Overland JE, Wang M, Ballinger TJ (2018) Recent increased warming of the Alaskan marine Arctic due to midlatitude linkages. *Advances in Atmospheric Sciences*, **35**, 75–84.

Park T, Ganguly S, Tømmervik H et al. (2016) Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environmental Research Letters*, **11**, 84001.

Pedersen SH (2017) *Scaling-up climate change effects in Greenland*. Aarhus University.

Pedersen SH, Liston GE, Tamstorf MP, Westergaard-Nielsen A, Schmidt NM (2015) Quantifying episodic snowmelt events in arctic ecosystems. *Ecosystems*, **18**, 839–856.

Pedersen SH, Liston GE, Tamstorf MP, Abermann J, Lund M, Schmidt NM (2018) Quantifying snow controls on vegetation greenness. *Ecosphere*, **9**.

Post ES, Pedersen C, Wilmers CC, Forchhammer MC (2008) Phenological sequences reveal aggregate life history response to climatic warming. *Ecology*, **89**, 363–370.

Post E, Forchhammer MC, Bret-Harte MS et al. (2009) Ecological dynamics across the arctic associated with recent climate change. *Science*, **325**, 1355–1358.

Richter-Menge J, Druckenmiller ML (2020) The Arctic [in "The State of the Climate in 2019]. *Bulletin of the American Meterological Society*, **101**, S263–S265.

Rotenberg E, Yakir D (2007) Contribution of Semi-Arid Forests to the Climate System. *Science*, **316**, 451–454.

Rouse JW, Hass RH, Schell JA, Deering DW (1973) Monitoring vegetation systems in the great plains with ERTS. *Third Earth Resource Technology Satellite Symposium*, 309–317.

Savitzky A, Golay MJE (1964) Smoothing and differentiation fo data by simplified least squares procedures. *Analytical chemistry*, **36**, 1627–1639.

Schimel JP, Bilbrough CJ, Welker JM (2004) Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, **36**, 217–227.

Seastedt T, Vaccaro L (2001) Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, **33**, 100–106.

Semenchuk PR, Elberling B, Cooper EJ (2013) Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic Svalbard. *Ecology and Evolution*, **3**, 2586–2599.

Serreze MC, Barrett AP, Stroeve JC, Kindig DN, Holland MM (2009) The emergence of surface-based Arctic amplification. *Cryosphere*, **3**, 11–19.

Shulski M, Wendler G (2007) *The Climate of Alaska*. University of Alaska Press, Faribanks, AK.

Starr G, Oberbauer SF (2003) Photosynthesis of arctic evergreens under snow: Implications for tundra ecosystem carbon balance. *Ecology*, **84**, 1415–1420.

Starr G, Oberbauer SF, Pop EW (2000) Effects of lengthened growing season and soil warming on the phenology and physiology of Polygonum bistorta. *Global Change Biology*, **6**, 357–369.

Stiegler C, Lund M, Røjle Christensen T, Mastepanov M, Lindroth A (2016) Two years with extreme and little snowfall: Effects on energy partitioning and surface energy exchange in a high-Arctic tundra ecosystem. *Cryosphere*, **10**, 1395–1413.

Stuefer S, Kane DL, Liston GE (2013) In situ snow water equivalent observations in the US arctic. *Hydrology Research*, **44**, 21–34.

Stuefer SL, Kane DL, Dean KM (2020) Snow Water Equivalent Measurements in Remote Arctic Alaska Watersheds. *Water Resources Research*, **56**, 1–12.

Sturm M, Holmgren J, König M, Morris K (1997) The thermal conductivity of seasonal snow. *Journal of Glaciology*, **43**, 26–41.

Sturm M, Schimel J, Michaelson G et al. (2005) Winter biological processes could help convert arctic tundra to shrubland. *BioScience*, **55**, 17–26.

Taras B, Sturm M, Liston GE (2002) Snow-ground interface temperatures in the Kuparuk River Basin, Arctic Alaska: Measurements and model. *Journal of Hydrometeorology*, **3**, 377–394.

Tucker CJ (1979) Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, **8**, 127–150.

U.S. Geological Survey (2019) The National Map.

U.S. Geological Survey (2020) 2010 Land Cover of North America at 30 meters.

Verbyla D (2008) The greening and browning of Alaska based on 1982-2003 satellite data. *Global Ecology and Biogeography*, **17**, 547–555.

Walker ADA, Halfpenny JC, Walker MD, Wessman CA (1993) Long-term Studies of Snow-Vegetation Interactions. *BioScience*, **43**, 287–301.

Walker MD, Walker DA, Welker JM et al. (1999) Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrological Processes*, **13**, 2315–2330.

Walker DA, Raynolds MK, Daniëls FJA et al. (2005) The Circumpolar Arctic vegetation map. *Journal of Vegetation Science*, **16**, 267–282.

Walsh JE, Overland JE, Groisman PY, Rudolf B (2011) Ongoing climate change in the arctic. *Ambio*, **40**, 6–16.

Wang X, Wang T, Guo H et al. (2018) Disentangling the mechanisms behind winter snow impact on vegetation activity in northern ecosystems. *Global Change Biology*, **24**, 1651–1662.

Welker JM, Fahnestock JT, Sullivan PF, Chimner RA (2005) Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska. *Oikos*, **109**, 167–177.

Westergaard-Nielsen A, Lund M, Pedersen SH, Schmidt NM, Klosterman S, Abermann J, Hansen BU (2017) Transitions in high-Arctic vegetation growth patterns and ecosystem productivity tracked with automated cameras from 2000 to 2013. *Ambio*, **46**, 39–52.

Wipf S (2010) Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology*, **207**, 53–66.

Wipf S, Rixen C (2010) A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Research*, **29**, 95–109.

Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: Plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, **94**, 105–121.

Xu C, Liu H, Williams AP, Yin Y, Wu X (2016) Trends toward an earlier peak of the growing season in Northern Hemisphere mid-latitudes. *Global change biology*, **22**, 2852–2860.

Zeng H, Jia G (2013) Impacts of snow cover on vegetation phenology in the arctic from satellite data. *Advances in Atmospheric Sciences*, **30**, 1421–1432.

Zhang T (2005) Influence of the seasonal snow cover on the ground thermal regime: an overview. *Reviews of Geophysics*, **43**.

Zhang T, Osterkamp TE, Stamnes K (1996) Some characteristics of the climate in northern Alaska, U.S.A. *Arctic and Alpine Research*, **28**, 509–518.

Zhao J, Zhang H, Zhang Z, Guo X, Li X, Chen C (2015) Spatial and temporal changes in vegetation phenology at middle and high latitudes of the northern hemisphere over the past three decades. *Remote Sensing*, **7**, 10973–10995.

Figure 1. Map of the study region. Icons indicate the location of the study points within northern Alaska. Shading indicates elevation in meters above sea level.

Figure 2. Mean and range of start, peak, and end of season as day of year (DOY), and Growing Season NDVI for each vegetation type from 2001 to 2017. Colors correspond with vegetation community. Dots represent the mean, the bars represent the standard deviation, and the width of the shape represents the distribution of the data. *Abbreviations: SOS – Start of season; POS – Peak of season; EOS – End of season; GS NDVI – Growing Season NDVI.*

Figure 3. Ranking of predictor variable importance within vegetation community. Dot size represents the importance of each explanatory variable on the response variables of vegetation phenology or productivity relative to the most important variable. The most important variables are opaque. Importance was determined by node purity from Random Forest analyses. Colors correspond with vegetation community. *Abbreviations: SOS – Start of season; POS – Peak of season; EOS – End of season; GS NDVI – Growing Season NDVI; AD – Active Days; SF DOY – Snow-free day of year; SWE – Snow water equivalence; GDD – Growing degree days.*

Figure 4. Partial Dependence plots showing the modeled effect of the most important predictor variables (determined by node purity) on the date of start of season (SOS), peak of season (POS), end of season (EOS) and Growing Season NDVI (GS NDVI), while holding all other variables at their mean. Colors correspond with vegetation community. Growing degree days (GDD) refer to June GDD for SOS plots and GDD-to-POS for POS, EOS, and GS NDVI plots. *Abbreviations: AD – Active days; SF DOY– Snow-free DOY.*

Figure 5. Scenarios of future temperature and snow properties and the anticipated effects on tundra vegetation phenology and productivity. Panels lay out the relationship of winter temperature and snowfall to changes in vegetation phenology and productivity under a) current conditions, the years 2001 to 2017 as presented in this analysis; b) future climate warming in spring and winter with winter temperature consistently below freezing; and c) future warming in spring and winter with occasional

melt events during winter.

Tables

Table 1. Description of vegetation types, summarized from the Alaska Vegetation and Wetland Composite (Boggs *et al.*, 2016).

Vegetation Type	Surface water (% cover)	Sedge (% cover)	Shrubs < 20 cm (% cover)	Shrubs 20-130 cm (% cover)	Shrubs >130 cm (% cover)	Soil environment*	Common species
Wet Sedge	0-10	20	< 25			Acidic or non-acidic; saturated during summer; active layer is organic.	*Carex aquatilis, Eriophorum angustifolium, Salix fuscescens, S. pulchra, Andromeda polifolia, Betula nana, Vaccinium uliginosum.*
Carex aquatilis	present	present		present		Polygonal ground.	*Carex aquatilis, Eriophorum angustifolium Betula nana, Salix pulchra, Rhododendron tomentosum, Vaccinium vitis-idaea, V. uliginosum, Empetrum nigrum.*
Dwarf Shrub Tundra		> 25	> 25	> 25		Surface is mesic but may be saturated below 15 cm depth.	*Eriophorum angustifolium, Carex aquatilis, C. bigelowii, C. macrochaeta, Salix pulchra, S. richardsonii, S. reticulate, Dryas spp., Betula nana, Rhododendron lapponicum, Vaccinium uliginosum.*
Tussock Tundra		> 35	present	present	<25	Old, poorly drained. Shallow organic layer underlain by mesic, silty mineral soil.	*Eriophorum vaginatum, Betula nana, Salix pulchra, Rhododendron tomentosum, Vaccinium vitis-idaea, V. uliginosum, Empetrum nigrum.*
Tussock Shrub		> 35	present	present	>25	Old, poorly drained. Shallow organic layer	*Eriophorum vaginatum, Betula nana, Salix pulchra, Rhododendron tomentosum,*

Tundra				underlain by mesic, silty mineral soil.	*Vaccinium vitis-idaea, V. uliginosum, Empetrum nigrum.*
Low Shrub Tundra	< 35	> 25 or most common	< 25	Mesic and mineral, well-decomposed organic layer (5-30 cm thick).	*Betula nana, Salix barclayi, S. pulchra, Vaccinium uliginosum, Rhododendron tomentosum.*

* All vegetation communities underlain by permafrost.

Table 2. Definitions of winter and spring climate conditions determined for each year of the study at each study point.

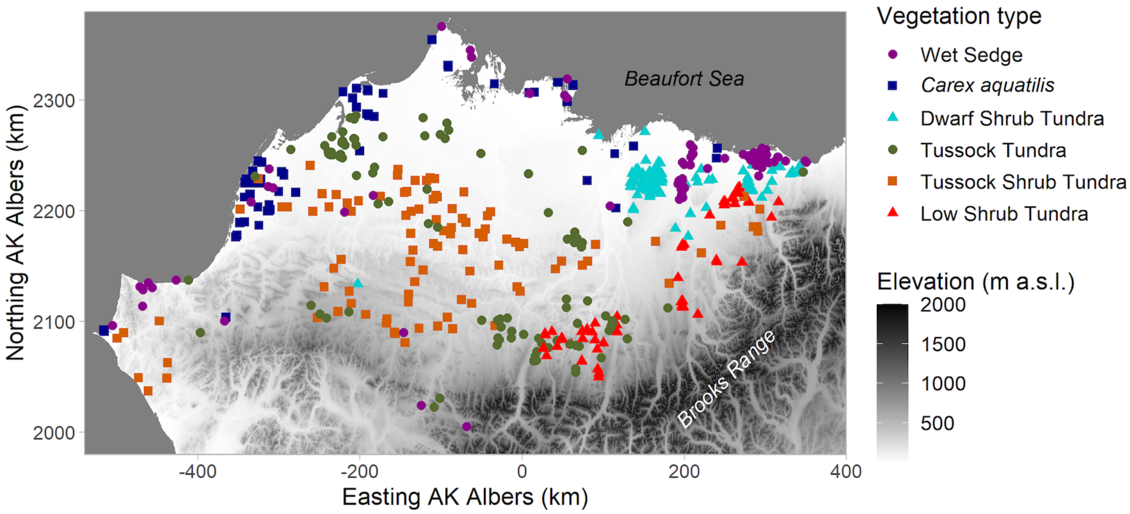
Winter/spring condition	Unit	Definition
Active Days	Days	Number of days per winter with snow on the ground and the soil-snow interface temperature above -6.0°C, where there is presumed soil microbial activity (Taras et al., 2002).
SWE	m	End-of-winter snow water equivalent (SWE) of the snowpack before snowmelt begins.
Snow-free Day of Year	DOY	First day of year (DOY) in spring when there is no remaining snow on the ground.
June GDD	° C	Growing degree days (GDD) calculated as the sum of the air temperature of all days with an average temperature above 0 °C during the month of June.
GDD-to-POS	° C	Growing degree days (GDD) calculated as the sum of the air temperature of all days with an average temperature above 0 °C from 1 January to the date of average peak of season (POS) from 2001 to 2017 for a given vegetation community.

Table 3. Mean and standard deviation (std. dev.) of modeled Active Days, Snow Water Equivalent (SWE), Snow-free day of year (DOY), and growing degree days (GDD) in each vegetation type from 2001 to 2017.

	Active Days		SWE (m)		Snow-free DOY		June GDD		GDD-to-POS	
Vegetation Type	**mean**	**std. dev.**	**mean**	**std. dev.**	**mean**	**std. dev.**	**mean**	**std. dev.**	**mean**	**std. dev.**
Wet Sedge	40.7	10.0	0.21	0.06	150	6.8	180.5	56.9	510.6	106.0
Carex aquatilis	39.3	7.9	0.21	0.06	151	7.3	179.4	59.3	469.9	115.6
Dwarf Shrub Tundra	44.0	12.7	0.24	0.06	150	5.8	208.6	48.0	543.6	87.4
Tussock Tundra	49.2	16.5	0.26	0.06	150	6.2	245.3	54.8	592.1	102.2
Tussock Shrub Tundra	48.4	15.8	0.27	0.07	151	6.2	255.0	50.2	587.2	94.5
Low Shrub Tundra	61.2	14.1	0.27	0.06	147	5.4	273.0	48.4	610.5	83.5

Table 4. Percent variation explained by Random Forests in each vegetation type for start of season (SOS), peak of season (POS), end of season (EOS), and Time-integrated NDVI (TINDVI).

Vegetation Type	SOS	POS	EOS	GS NDVI
Wet Sedge	40.6	45.6	34.3	47.7
Carex aquatilis	57.5	50.6	41.8	56.9
Dwarf Shrub Tundra	61.7	65.7	43.1	61.1
Tussock Tundra	43.0	51.2	32.9	55.4
Tussock Shrub Tundra	43.9	49.0	26.3	27.0
Low Shrub Tundra	78.6	80.8	66.7	68.5



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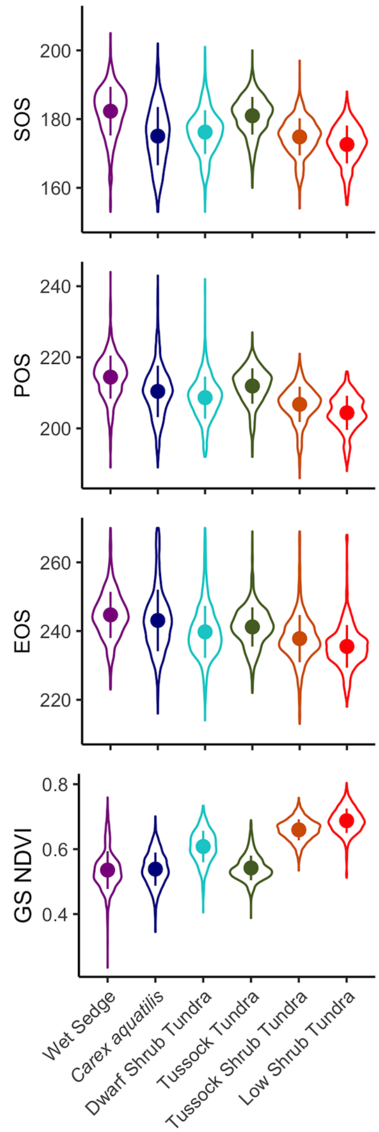

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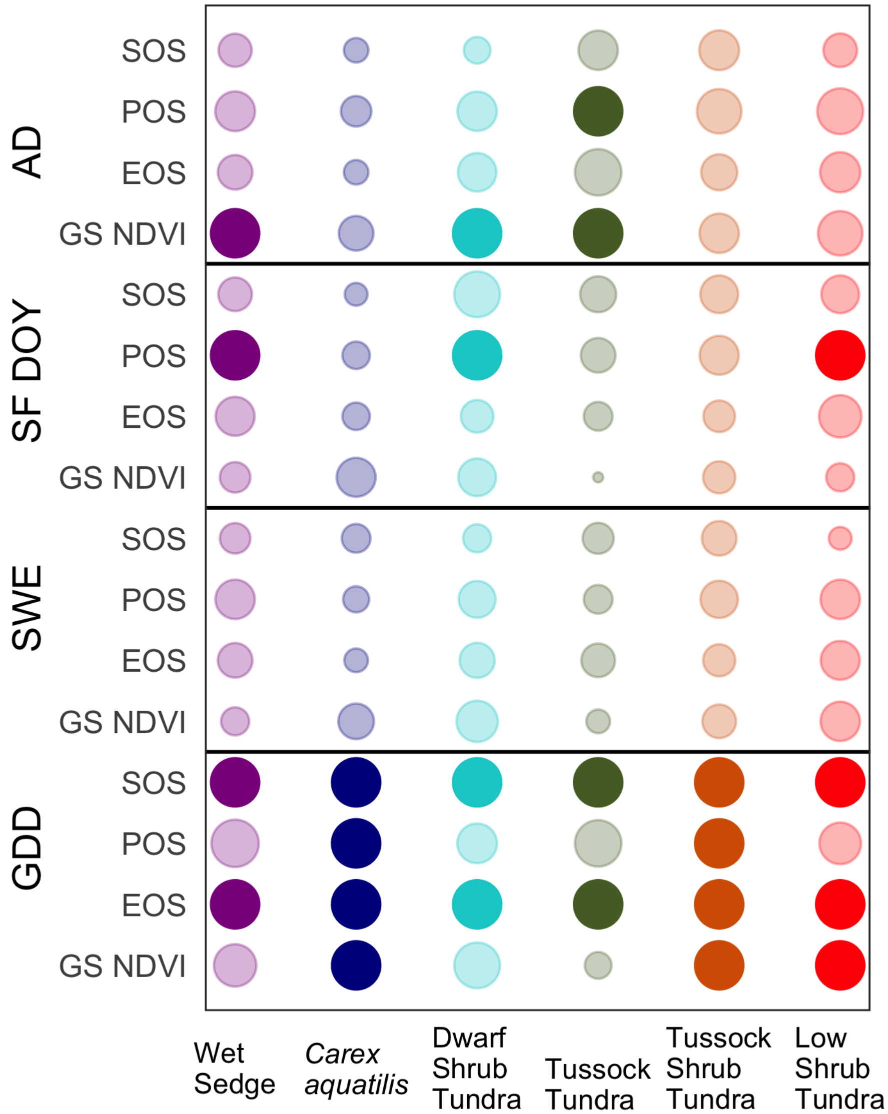

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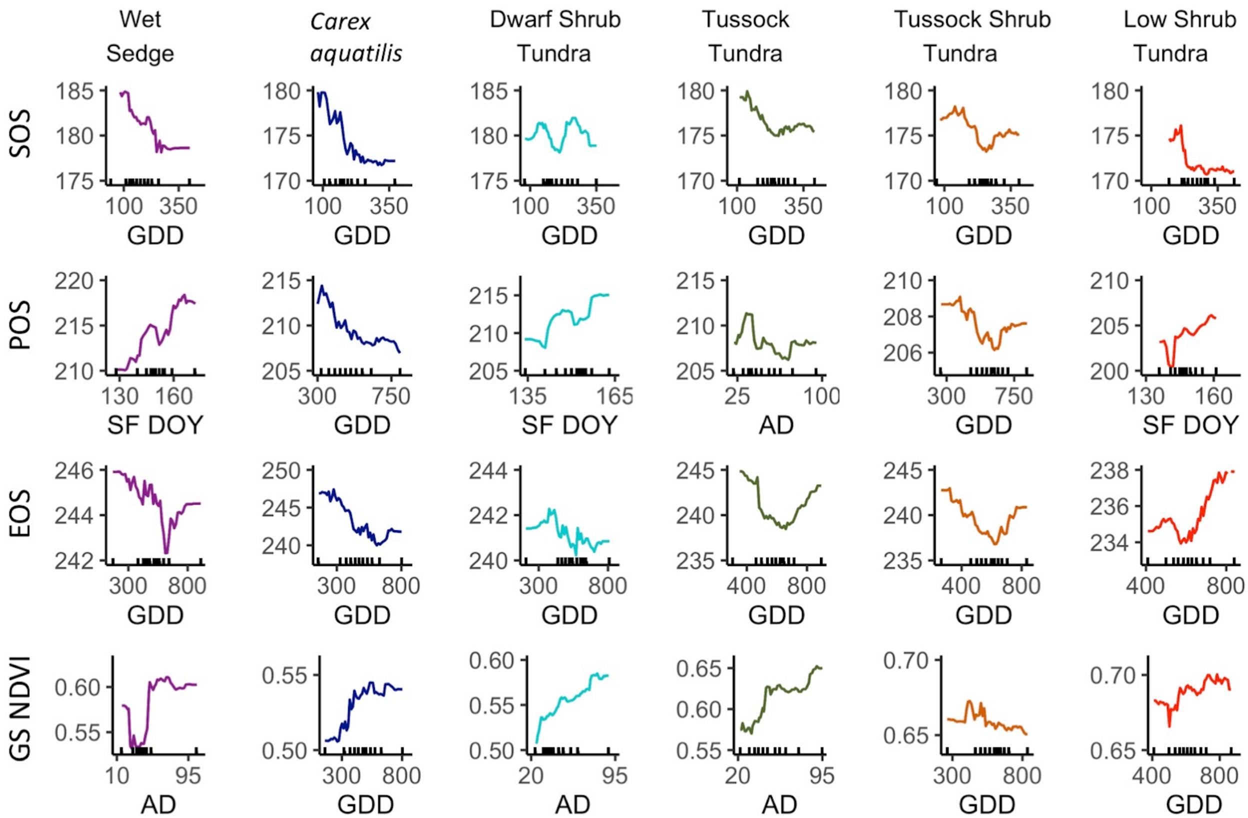

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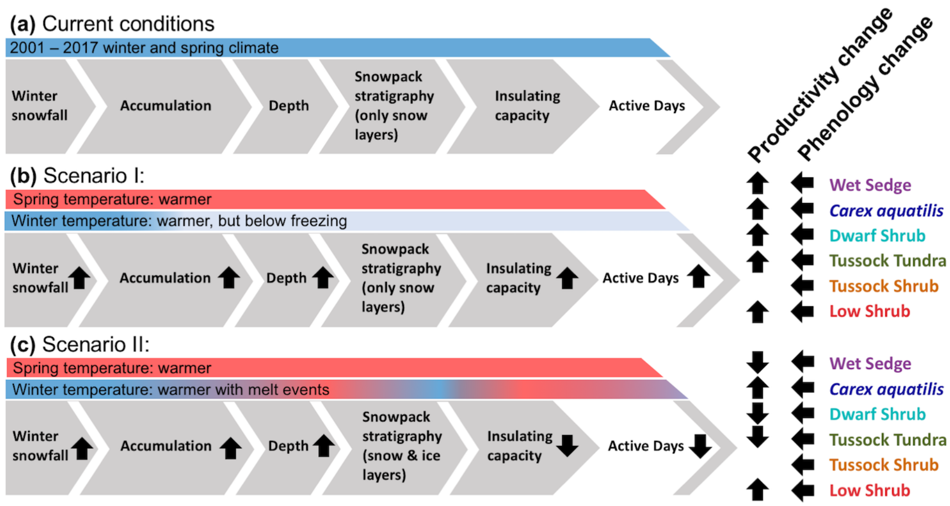

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