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## Title

# Summer temperature – but not growing season length – influences growth of a dwarf willow in coastal Arctic tundra

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## Abstract

Arctic climate change is leading to an advance of plant phenology (the timing of life events) with uncertain impacts on tundra ecosystems. Although the lengthening of the growing season is thought to lead to increased plant growth, we have few studies of how plant phenology change is altering tundra plant productivity. Here, we test the correspondence between 14 years of *Salix arctica* phenology data and radial growth. We sampled 38 *Salix arctica* individuals across the landscape on Qikiqtaruk – Herschel Island, Yukon Territory, Canada. We used dendroecology and linear mixed-effect models to test the influence of growing season length and climate variables on growth. We found that summer temperature best explained annual variation in growth. We found no strong evidence that green-up date, earlier leaf senescence date or total growing season length had any direct or lagged effects on growth. Growth was not explained by interannual variation in precipitation, MODIS surface greenness (NDVI), or sea ice concentration. Our results demonstrate that at this site, for the widely-distributed species *S. arctica*, temperature – but not growing season length – influences radial growth. These findings challenge the assumption that advancing phenology and longer growing seasons will increase the productivity of all plant species in Arctic tundra ecosystems.

## Acknowledgements

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## Author Contributions

JB and IMS conceived and designed research. SAB collected the samples and JB conducted lab work, with all authors contributing to the analysis and additional data. The main script was adapted by JB and IMS from code written by SAB. JB and IMS wrote the manuscript, with JJA creating Figure 1. All authors read and approved the manuscript.

## Introduction

The Arctic is warming three to four times faster than the rest of the planet (Meredith et al. 2019) and tundra plant communities are particularly sensitive to that warming (Elmendorf et al. 2015; Bjorkman et al. 2020). Climate change is resulting in a longer snow- and ice-free season, potentially facilitating longer growing seasons (Cleland et al. 2007; Khorsand Rosa et al. 2015; Prevéy et al. 2021; Frei and Henry 2021). Previous research assumes that the altered phenology will correspond directly with increased growth of tundra plants (Myneni et al. 1997; Piao et al. 2007; Ernakovich et al. 2014; Park et al. 2016; Arndt et al. 2019; Kim et al. 2021). Shifts in distribution and abundance (Sturm et al. 2001; Elmendorf et al. 2012a), biomass (Hudson and Henry 2009), and phenology (timing of life events) (Oberbauer et al. 2013) have been observed for species across the tundra. A greening of Arctic ecosystems seen from satellite data has been attributed to an increase in plant productivity with warming (Myers-Smith et al. 2020). Arctic spectral greening trends from vegetation indices, such as the Normalised Differential Vegetation Index (NDVI), are used as proxy metrics of tundra plant phenology (Piao et al. 2007; Zeng et al. 2013; Park et al. 2016). However, remote sensing studies of tundra phenology may not be capturing on-the-ground plant phenological dynamics and may instead be influenced by other land-surface changes such as snowmelt (Helman 2018) particularly in Arctic systems (Arndt et al. 2019; Myers-Smith et al. 2020; Cao et al. 2020).

### *The magnitude of phenology change*

The snow-free season across the Arctic has extended by two to four days per decade of warming (Piao et al. 2007; Barichivich et al. 2013; Park et al. 2016; Myers-Smith et al. 2019). Seasons are starting earlier and finishing earlier or later depending on the location and study metrics investigated (Piao et al. 2007; Zeng et al. 2011, 2013; Keenan and Richardson 2015; Park et al. 2016; Myers-Smith et al. 2019). Both satellite (Myers-Smith et al. 2020) and *in situ* (Oberbauer et al. 2013) studies confirm widespread but variable phenological shifts in the Arctic. Phenology change is primarily accelerated by high temperatures and early snowmelt (Assmann et al. 2019), but these variables may not act in concert at some sites with a deeper snow pack not necessarily melting earlier despite warming (Bjorkman et al. 2015; Kelsey et al. 2020; Rixen et al. 2022). Phenology in both spring and autumn has advanced for *Salix arctica* Pall. (Salicaceae) on Qikiqtaruk - Herschel Island in the Western Canadian Arctic, though autumn only marginally, overall lengthening the growing season by two days per decade (Myers-Smith et al. 2019).

### *Phenology and growth*

Plant phenology is changing throughout the tundra (Myers-Smith et al. 2019; Bjorkman et al. 2020; Prevéy et al. 2021), but the consequences on plant growth remain unclear. Phenology defines the bounds for plant activity, including photosynthesis, and has shifted around the Arctic due to warming (Assmann et al. 2019; Myers-Smith et al. 2020). Two key points in a species' phenology are leaf emergence and leaf senescence: the time between being the entire growing season. Emergence and senescence are both shifting across the Arctic, leading to a longer, earlier growing season at many sites, though changing phenology is not uniform across sites or species (Oberbauer et al. 2013; Assmann et al. 2019; Myers-Smith et al. 2020). Earlier emergence is associated with earlier snowmelt (Assmann et al. 2019; Myers-Smith et al. 2019) and declining sea ice (Post et al. 2009; Bhatt et al. 2010; Kerby and Post 2013), though some studies have identified trends toward later phenology in some species and locations usually aligning with later snowmelt (Wipf and Rixen 2010; Bjorkman et al. 2015). Early senescence through deterministic leaf age (Oberbauer et al. 2013; Keenan and Richardson 2015), nutrient availability (Lim et al. 2007) or photoperiod (Arft et al. 1999) may undermine any growth benefits of earlier emergence. Earlier emergence may also expose individuals to late spring frost events (Wheeler et al. 2015) or other harsh conditions. Whether plants can take advantage of an extended growing season to increase productivity and accumulate biomass is therefore uncertain.

### *Shrub growth and dendroecology*

Dendroecology lets us explore the growth history of shrubs based on the width of rings formed during seasonal woody tissue deposition (Myers-Smith et al. 2015b). Individual annual growth ring chronologies can be compared with environmental variables to reveal the climate sensitivity of growth over time. Through dendroecology, we can directly observe how changing conditions affect shrub growth, validating assumptions and models. Individual growth is a key element in our understanding of shrub expansion throughout the Arctic (Tape et al. 2006; Myers-Smith et al. 2011a, 2019; Elmendorf et al. 2012b; García Criado et al. 2020). Increasing shrub cover and canopy height changes the local environment (Sturm et al. 2005; Way and Lapalme 2021), altering ecosystem processes and species interactions (Myers-Smith et al. 2011a; Ravolainen et al. 2014; DeMarco et al. 2014; Tape et al. 2016, 2018). Shrub encroachment has been linked to warming in studies using dendrochronology (Forbes et al. 2010), remote sensing (Myneni et al. 1997; Myers-Smith et al. 2020), field observations (Hudson and Henry 2009; Myers-Smith et al. 2011b), and experiments (Elmendorf et al. 2012a, 2015; Khorsand Rosa et al. 2015; Frei and Henry 2021). To accurately predict the future structure and function of northern ecosystems, we must understand how plant growth is changing (Myers-Smith et al. 2020), especially the role of phenology as ecological dynamics change under warming (Keenan and Richardson 2015; Myers-Smith et al. 2019; Bjorkman et al. 2020; Samplonius et al. 2020).

### *Implications of changing plant phenology for the carbon cycle*

Arctic vegetation change underpins regional and global feedback loops (Liston et al. 2002; Sturm et al. 2005; Pearson et al. 2013; Grosse et al. 2016) and carbon budgets (Piao et al. 2007; McGuire et al. 2009; Parker et al. 2021). As phenology changes, we expect compositional shifts and increased growth during longer growing seasons (Myneni et al.

1997; Ernakovich et al. 2014; Panchen and Gorelick 2017). Biome-wide shifts in growth rates and community composition could have profound implications for global carbon budgets through biomass accumulation (Piao et al. 2007) and decomposition (DeMarco et al. 2014). Warming drives earlier leaf emergence (Ernakovich et al. 2014; Park et al. 2016), and increased plant growth (Myneni et al. 1997). And thus, studies of satellite-derived spectral greening trends have linked changes in phenology to changes in plant productivity (Myneni et al. 1997; Park et al. 2016; Kim et al. 2021). Accurate Earth-system models depend on our understanding of plant growth-climate relationships and ecosystem-climate feedbacks (Sturm et al. 2005; Loranty and Goetz 2012; Richardson et al. 2013; Pearson et al. 2013; Fisher et al. 2018; Bonan and Doney 2018). Despite them underpinning global models, uncertainty remains in the expected association between phenology and growth of Arctic plants and whether warmer temperatures or longer growing seasons are the primary drivers of increasing tundra plant productivity.

### *Research questions*

In this study, we use dendroecology to test the correspondence between *in situ* phenology observations, environmental factors, and radial growth of *Salix arctica* on Qikiqtaruk - Herschel Island in the Western Canadian Arctic. We test three questions: (1) Do longer growing seasons facilitate greater shrub growth? (2) Of phenological metrics, does leaf emergence date, senescence date, or growing season length best explain shrub growth? (3) Do climatic factors (air temperature, precipitation, sea ice concentration, or snowmelt), or maximum plant productivity (estimated through the spectral Normalised Difference Vegetation Index, NDVI), explain shrub growth better than phenology? We hypothesised that: (1) A longer realised period of growth will increase radial growth; (2) Growing season length will best explain shrub growth, as it encompasses cumulative effects of emergence and senescence change; (3) Phenology (growing season length) will best explain shrub growth as the growing season is short in Arctic systems and predicted to drive vegetation change on Qikiqtaruk (Myers-Smith et al. 2019).

## **Methods**

### *Study site*

We studied *S. arctica* phenology and growth on Qikiqtaruk – Herschel Island, YT, Canada (69.57°N, 138.90°W) (Fig. 1). The island is approximately 100 km$^2$ in area, with soils formed of marine and glacial deposits atop ice-rich permafrost (Burn and Zhang 2009). Qikiqtaruk sits at the northerly extent of tall shrubs, particularly *Salix richardsonii* Hook. (Salicaceae) (Myers-Smith et al. 2011b), which feature heavily in its flora alongside *Eriophorum vaginatum* L. (Cyperaceae) tussock tundra and dwarf shrub heath rich in *S. arctica* (Myers-Smith et al. 2019). At these mid-latitudes of the Arctic, shrubs can be particularly sensitive to climate (Myers-Smith et al. 2015a), and there is ground-based and satellite evidence for rapid shrub expansion in the region (Fraser et al. 2011; Moffat et al. 2016; Myers-Smith et al.

2019).

### Salix arctica *sampling*

As woody perennials, shrubs grow annual rings of wood which record growth over time (Myers-Smith et al. 2015b). Here, we focus on *S. arctica*, a prostrate willow with a circum-Arctic range which reaches as far north as the north coast of Greenland (Argus 2007). We collected 38 shrub samples on a coastal floodplain on the east side of the island in the Ice Creek watershed, a site of known vegetation change (Myers-Smith et al. 2019). The vegetation is dominated by *Salix spp.,* defined by patches of *S. richardsonii*, a canopy-forming willow, with *S. arctica* at ground-level. Sections of 3–5 cm in length were taken from the thickest stem of six to eight individuals at each of five parallel transects on the Qikiqtaruk floodplain in July 2016. Individuals were at least 10 m apart and transects were 50–100 m apart to lower the risk of sampling clones, particularly given the sprawling prostrate growth form of *S. arctica* (Argus 2007).

### *Dendroecological methods*

We sliced thin sections (~ 25 µm) of each sample with a sledge microtome, then photographed (Fig. S1) and measured the rings along four radii per sample using the ObjectJ package (1.04a) for ImageJ (2.0.0-rc-59/1.51j). We visually crossdated samples to check for partly missing rings, then averaged the radii for each individual and crossdated again to check for entirely missing rings between samples.

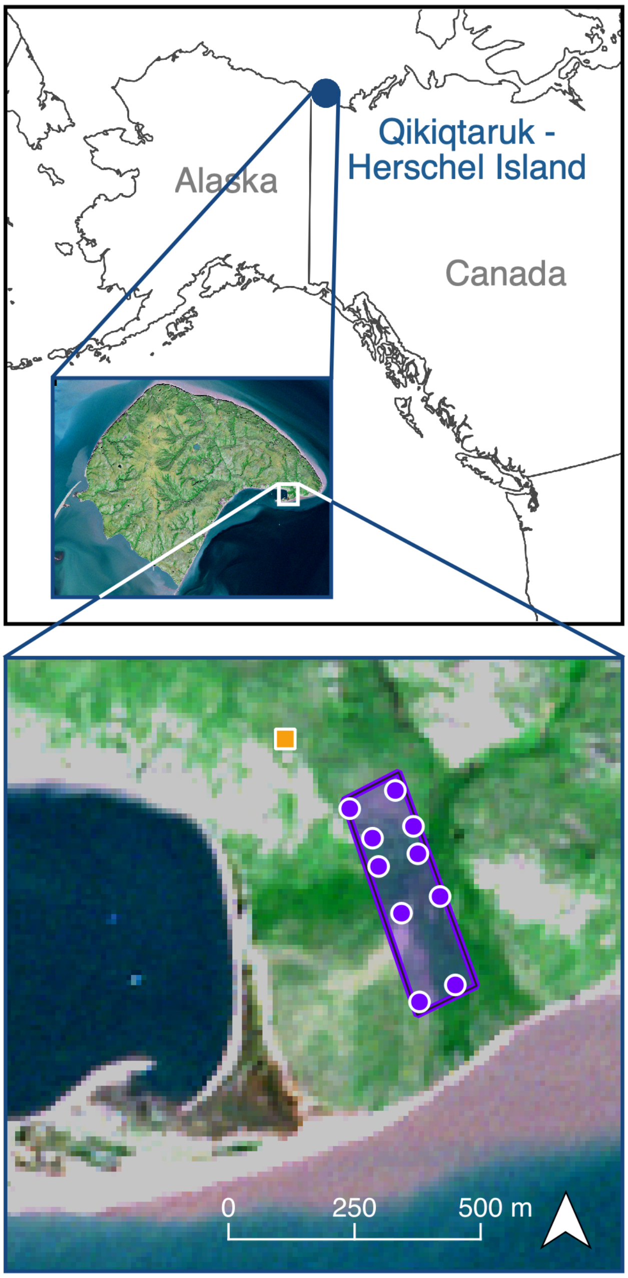

***Fig. 1*** *A Sentinel 2 false-colour map showing the location of Qikiqtaruk within Canada, and the location of the transects on Qikiqtaruk. The purple dots represent the ends of the five transects, and the purple box shows the area within which all samples were taken. The orange square shows the location of the phenology plots*

Individuals with fewer than seven years of growth were removed and we calculated the basal area increments from the ring width data. We then detrended the basal area increment data, fitting a smoothing spline (dplR package for R, $f$ = 0.5, $nyrs$ = 0.67), based on visual assessment of overall and individual trends. Basal area increment data were detrended per a negative exponential fit, also based on visual assessment of trends (Myers-Smith et al. 2015b). We removed the first two years of growth for each individual to account for age-related growth effects, and the data from the year of sampling, as the growth for the season was not completed (Myers-Smith et al. 2015b). To maintain a minimum of four years' growth data after removing the data from 2016 and the first two years, the sample size was reduced to 28 individuals, running from 2002–2015 (Fig. S2). We used detrended basal area increment data as our primary growth data, though detrended ring widths were also tested to verify similarities. For the statistical analysis, all variables were normalised between 1 and -1, so that effect sizes could be compared.

*Phenology data*

Phenological observations have been collected by Yukon Parks Rangers on Qikiqtaruk every 2–3 days from April (snowmelt) until September (senescence) along established transects (~250 m from our study site). The rangers record phenology throughout the growing season (Myers-Smith et al. 2019) in line with ITEX protocol (Prevéy et al. 2021). The phenological dates used in this study are the date of first leaf bud burst (emergence) and the date of first yellowing of leaves (senescence) averaged across the 20 *S. arctica* individuals in the observation transect, collected since 2001. Growing season length (GSL) is calculated as the number of days between emergence and senescence.

*Other environmental data*

We compared growth to seasonal air temperatures and precipitation, snowmelt, sea ice concentration, and productivity. The temperature data came from Environment Canada Qikiqtaruk-Herschel Island weather station (ID 1560) and precipitation data came from the ERA5 gridded dataset produced by Copernicus Climate Change Service and the European Centre for Medium-Range Weather Forecasts (Hersbach et al. 2020). We collated data into seasons (spring: April–May, summer: June–July, autumn: August–September, winter: October–March) including the lagged data for the preceding summer and autumn, as monthly resolution was higher than useful for this study. Snowmelt data are from the Qikiqtaruk phenology dataset, where the date at which transects are free of snow is recorded (Myers-Smith et al. 2019). We used the onset of sea ice melt data (Assmann et al. 2019), determined using the NOAA/NSIDC Climate Data Record (CDR) v3 Passive Microwave Sea Ice Concentrations (Meier et al. 2017). Productivity data are the annual maxima (estimated by smoothing trends in the data with a generalised additive model) of the MODIS MOD13A1v6 NDVI satellite dataset (Myers-Smith et al. 2020).

*Statistical analysis*

To test the relationships between variables we ran linear mixed-effect models, with year, transect, and individual as random effects, and individuals nested within transects. We used mixed models due the hierarchical structure of our data, caused by non-independence of individuals within transects and within years. Shrubs also shared conditions in each year, making them non-independent. The variability among individuals was high, as seen during crossdating, but due to sampling a single species within a relatively small area, similar responses were expected across groups. Thus, we chose not to use random slopes, only random intercepts. We used models with maximum likelihood estimation for AIC comparisons, and models with restricted maximum likelihood estimation for pseudo-$R^2$ and effect size values. Residuals of models were visually assessed for normality with fitted-residual plots, and temporal autocorrelation (first- or second-order) with correlograms (Fig. S3). We did not detect a signal of temporal autocorrelation, and residuals were similar across all models (Fig. S3). We tested the correlation among all environmental and phenological variables and correlation coefficients varied between -0.76 and 0.75 (Fig. S4).

The effect sizes of models were assessed relative to their credible intervals. If the credible intervals for the estimated slope did not cross zero, we considered an effect to be significant. If the credible interval of the model slope sits at zero or fluctuates between overlapping zero and not overlapping zero in different model runs, we consider the effect to be marginally significant. As a secondary analysis presented in the supplementary materials (Table S1, Table S3), we compared models using AIC to see whether the models fit the data better than a null model using the conventional threshold ($\Delta AIC_{null} \geq 2$) (Akaike 1974). We also calculated conditional and marginal pseudo-$R^2$ to test the absolute model fit including and excluding random effects respectively (Nakagawa and Schielzeth 2013). All statistical tests were carried out in R (3.6.3), via RStudio (1.2.1335): Code and data are available at the following GitHub repository: https://github.com/ShrubHub/ShrubRingPhenoHub

## Results

### *Phenology*

We found that growing season length had no effect on *S. arctica* radial growth on an area basis, nor was there a lagged effect from the previous growing season (Table 1, Fig. 2). We found a negative relationship between earlier leaf senescence and growth, though no effect of earlier leaf emergence on growth (Table 1, Fig. 2). Growth was greater in years with an earlier senescence date, though we did not detect a relationship with emergence date, GSL, and previous GSL (Table 1). However, the overall explanatory power of the models was low with no model explaining more than 2.8% of variation (marginal pseudo-$R^2$, Table S1).

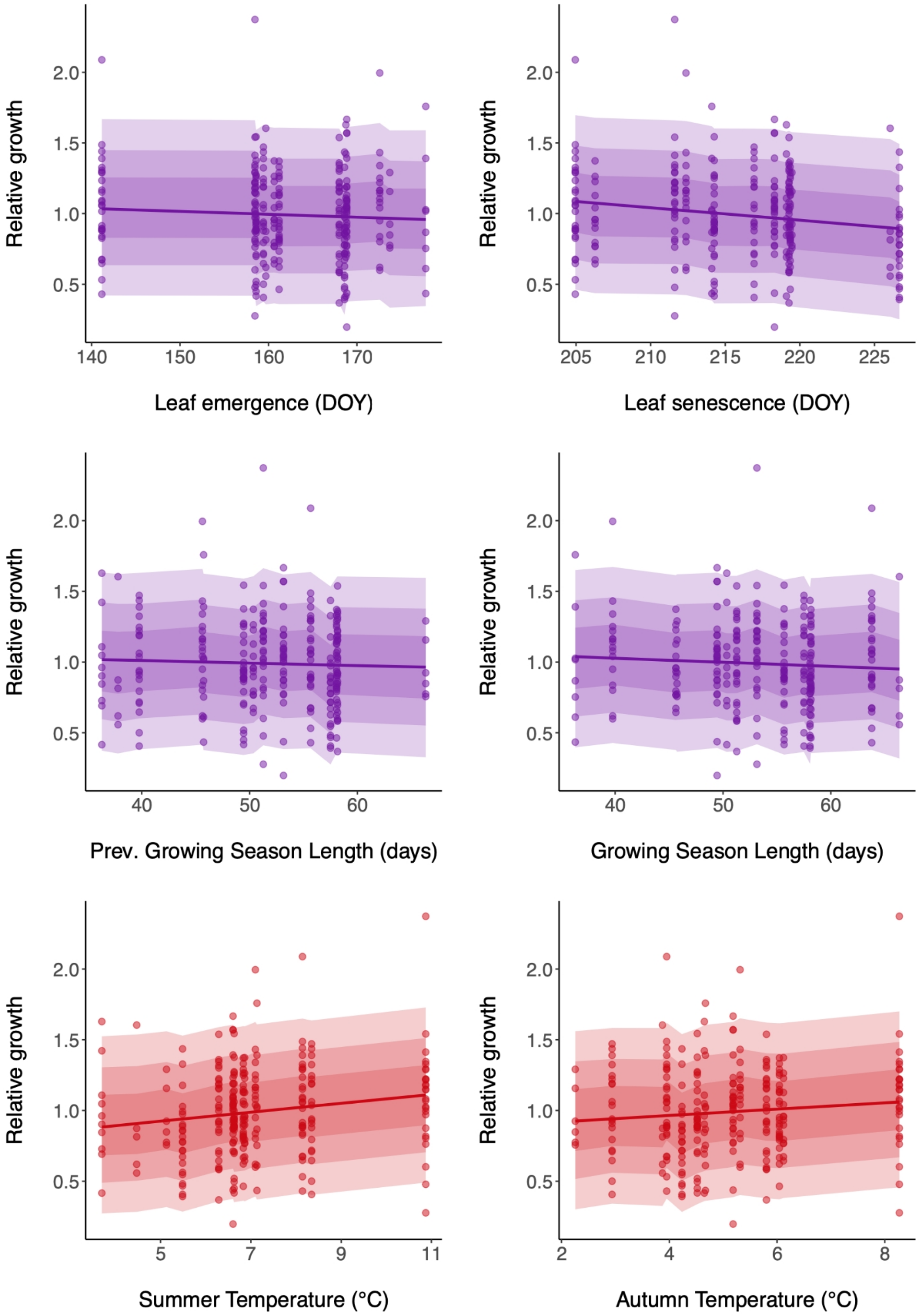

***Fig. 2*** *Growth corresponded weakly with phenological variables and more strongly with some seasonal temperatures. The relationships of growth with both senescence and summer temperature are statistically significant. Scatter plots show four phenological and two temperature variables' relationships to radial growth (basal area increment, indexed) in a given year over the period 2002-2015. Trendlines are predictions from the hierarchical Bayesian models, the shaded areas represent 95%, 80%, and 50% credible intervals of the model estimates*

*Other variables*

Only senescence date and summer temperature explained variation in growth (Fig. 3). Emergence date; current and previous years' growing season length; temperatures from the winter, spring, autumn, and the previous year; all precipitation models; and snowmelt date did not explain variation in growth (Fig. 3). None of the variables tested explained more than 3.2% of variation in annual growth (conditional pseudo-$R^2$, Table S1). Though exact effect sizes differed slightly, the results were similar when models used detrended ring width data or used detrended basal area increment (Table S2, Table S3, Fig. S5, Fig. S6, Fig. S7).

***Table 1****: Statistical results for the hierarchical Bayesian models relating radial growth (basal area increment) to phenology, temperature, precipitation, NDVI, sea ice concentration, and snow-free date (results for ring widths are included in Table S2, Table S3). All models span the period 2002–2015. Asterisk (*) indicates a model where the 95% credible intervals do not overlap zero and which we therefore consider to be significant. Sample depth per year as follows: 2002, n=5; 2003, n=6; 2004, n=8; 2005, n=10; 2006, n=14; 2007, n=16; 2008, n=20; 2009, n=23; 2010, n=25; 2011, n=27; 2012-5, n= 28.*

| **Predictor variable** | **Estimate** | **Standard Error** | **Lower 95% CI** | **Upper 95% CI** | **R-hat** | **Bulk ESS** | **Tail ESS** |
|---|---|---|---|---|---|---|---|
| Leaf emergence | -0.04 | 0.07 | -0.16 | 0.09 | 1.00 | 2422 | 1531 |
| **Leaf senescence*** | **-0.10** | **0.04** | **-0.18** | **-0.01** | **1.00** | **3175** | **2384** |
| Growing season length | -0.05 | 0.06 | -0.18 | 0.07 | 1.00 | 2879 | 2181 |
| Previous growing season length | -0.03 | 0.06 | -0.14 | 0.09 | 1.00 | 2451 | 2102 |
| Previous summer temperature | 0.00 | 0.06 | -0.13 | 0.13 | 1.00 | 2660 | 2297 |
| Previous autumn temperature | 0.09 | 0.05 | -0.01 | 0.19 | 1.00 | 2784 | 2182 |
| Winter temperature | -0.02 | 0.05 | -0.12 | 0.07 | 1.00 | 2848 | 2025 |
| Spring temperature | 0.02 | 0.05 | -0.09 | 0.12 | 1.00 | 1616 | 1401 |
| **Summer temperature*** | **0.12** | **0.05** | **0.02** | **0.23** | **1.00** | **3050** | **2122** |
| Autumn temperature | 0.07 | 0.06 | -0.04 | 0.19 | 1.00 | 2748 | 1687 |
| Previous summer precipitation | -0.03 | 0.06 | -0.15 | 0.09 | 1.00 | 1658 | 1203 |
| Previous autumn precipitation | -0.01 | 0.05 | -0.11 | 0.09 | 1.00 | 2508 | 2317 |
| Winter precipitation | -0.01 | 0.06 | -0.12 | 0.12 | 1.00 | 2879 | 2586 |
| Spring precipitation | -0.01 | 0.04 | -0.10 | 0.08 | 1.00 | 2420 | 1483 |
| Summer precipitation | 0.01 | 0.06 | -0.10 | 0.13 | 1.00 | 1998 | 1616 |
| Autumn precipitation | 0.00 | 0.05 | -0.11 | 0.11 | 1.00 | 1560 | 1664 |
| MODIS NDVI | 0.01 | 0.06 | -0.10 | 0.12 | 1.00 | 2327 | 1660 |
| Minimum sea ice extent | -0.13 | 0.12 | -0.37 | 0.12 | 1.00 | 3460 | 2648 |
| Sea ice melt onset date | -0.09 | 0.06 | -0.22 | 0.03 | 1.00 | 2557 | 1719 |
| Date snow free | -0.05 | 0.07 | -0.19 | 0.10 | 1.00 | 2298 | 2182 |

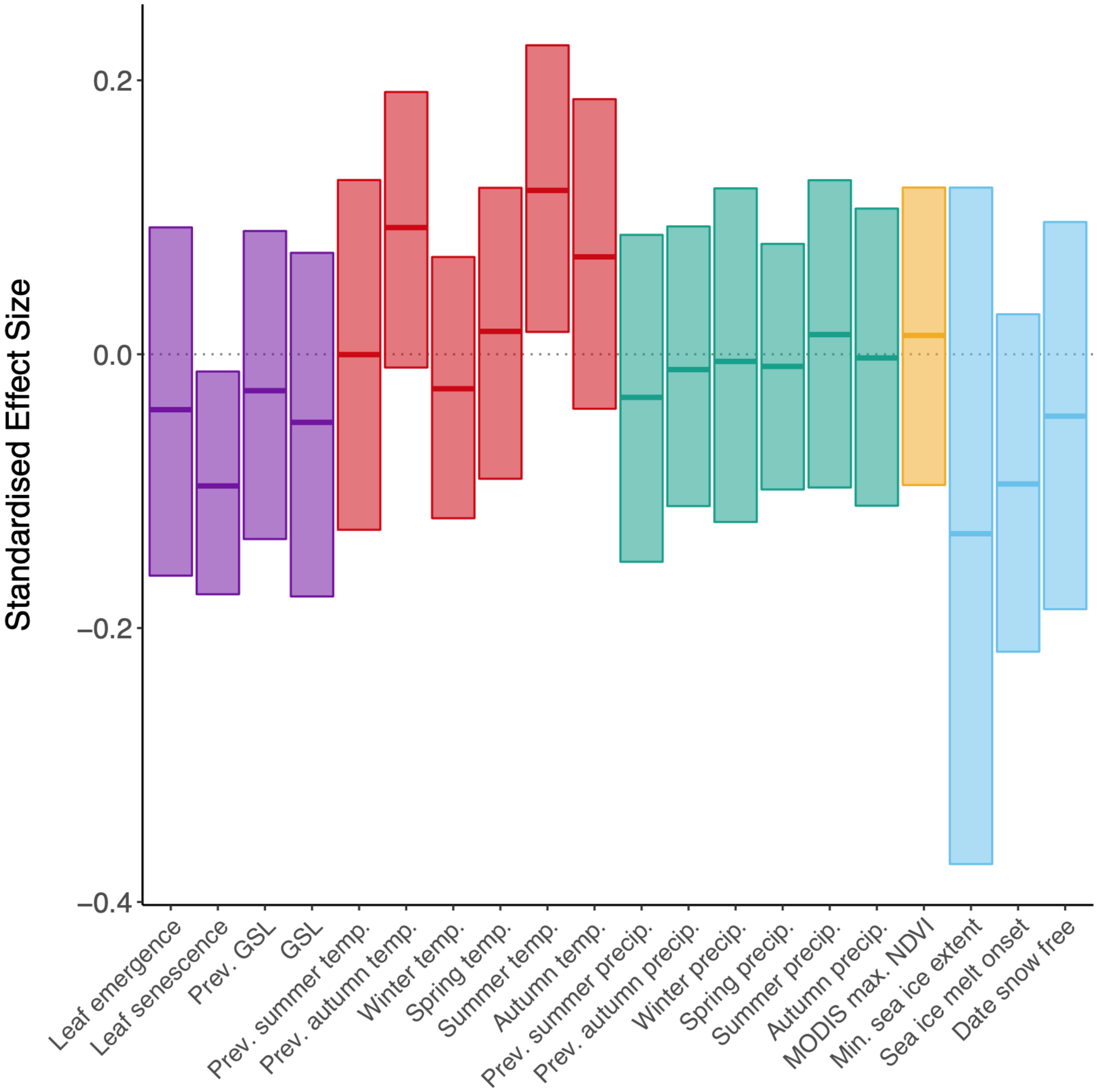

***Fig. 3** Only senescence and summer temperature significantly explained variation in growth, most variables showed no relationship to growth (Table 1). This plot shows standardised effect sizes (slopes) of hierarchical Bayesian models of phenological events (purple), seasonal temperature (red), seasonal precipitation (green), NDVI (yellow), minimum sea ice extent, sea ice concentration, and snowmelt date (all blue) on growth. The centre line is the effect and error bars are 95% credible intervals. For ease of comparison between effect sizes, explanatory variables in this analysis are variance-scaled from -1 to 1*

## Discussion

Through a unique study of long-term *in situ* phenology monitoring and dendroecology, we compared interannual variation in phenology, environmental conditions, and NDVI to interannual variation in radial growth of *S. arctica* on Qikiqtaruk. We found that summer temperatures and senescence – but not leaf emergence or growing season length –

explained variation in radial growth for the widespread Arctic shrub *S. arctica* (Table 1, Fig. 3). Precipitation, sea ice, snowmelt, and NDVI did not correspond with variability in interannual growth in our study. Thus, we did not find support for the hypothesised relationship between phenology and growth. Our results suggest that factors other than phenology, such as temperature, can exert a larger influence on shrub growth in this tundra ecosystem. These findings have implications for how tundra shrub growth is modelled and thus the projection of Arctic carbon budgets.

### *Phenology*

We found no evidence that earlier leaf emergence and longer growing seasons corresponded with increased radial growth in *S. arctica*, including growth in the following year (Table 1, Fig. 3). Results for preliminary analyses including other willow species from this and other sites have reached similar conclusions (Angers-Blondin 2019). Earlier leaf emergence did not result in greater *S. arctica* growth; however, we did find evidence of greater growth in years with earlier senescence. The biological mechanism linking earlier senescence with enhanced growth is not clear, though early senescence was correlated with warmer summer temperatures (Pearson's product-moment correlation, $df = 263$, $p < 0.001$, $\rho = -0.60$, Fig. S3). Individuals may reach a threshold after intense early growth (Rumpf et al. 2014), allowing for early cessation of growth aboveground. Alternatively, growth and leaf age could be deterministic (Oberbauer et al. 2013; Keenan and Richardson 2015; Semenchuk et al. 2016; Parker et al. 2017), with growth ending at a fixed time after growth begins each year. Our findings are in line with previous evidence that the timing of tundra plant senescence is driven at least in part by non-climatic factors (Arft et al. 1999; Oberbauer et al. 2013). Taken together, our results suggest that shifts to earlier shrub leaf emergence and longer growing seasons are not necessarily driving changes in tundra shrub growth, contrary to interpretations of satellite remote sensing data (Myneni et al. 1997; Zeng et al. 2011, 2013; Arndt et al. 2019) and reviews (Ernakovich et al. 2014).

### *Temperature*

We found that higher summer temperatures increased the radial growth of *S. arctica* at our site. The summer is the peak season for growth and individuals are sensitive to warming in this period (Andreu-Hayles et al. 2020), as observed across the biome (Myers-Smith et al. 2015a; Myers-Smith and Hik 2018) from dendrochronology (Forbes et al. 2010; Blok et al. 2011; Myers-Smith et al. 2011a; Li et al. 2016; Weijers et al. 2018; Le Moullec et al. 2019; Prendin et al. 2022), repeat photography (Sturm et al. 2001; Tape et al. 2006), and experiments (Elmendorf et al. 2012a, 2015; Khorsand Rosa et al. 2015; Frei and Henry 2021). Temperature-growth relationships are heterogeneous across the tundra biome, with relatively low climate sensitivity observed on Qikiqtaruk (Myers-Smith et al. 2015a). Phenological sensitivity to temperature of another dwarf willow species, *Salix polaris* Wahlenb. (Salicaceae), has decreased over time at Bjørnøya, Svalbard (Owczarek et al. 2021). The growth response to early senescence suggests the importance of resource accumulation for growth in the following season. There is accumulating evidence that above-ground phenology may be asynchronous with below-ground root growth (Blume−Werry et al. 2016, 2017; Ögren 2017; Liu et al. 2022), though root phenology itself may not respond to autumn warming (Schwieger et al. 2018). Snow cover insulates shrubs from winter and spring temperatures (Kelsey et al. 2020; Rixen et al. 2022) and Krab et al. (2018) found diverging shrub radial growth responses to winter temperature, spring warming, and snowmelt among species. *Vaccinium vitis−idaea* L. (Ericaceae) grew more with delayed snowmelt with a contrasting reduction in growth in *Empetrum nigrum* L. (Ericaceae). We however found no association between temperatures in the previous year and growth, and no relationship for winter, spring, and autumn temperatures and growth (Table 1, Fig. 3).

### *Hydrology*

We did not find a strong influence of summer precipitation, sea ice or snowmelt on interannual variation in radial growth *S. arctica* in this study. Growth of Arctic shrubs can be moisture-limited (Keuper et al. 2012; Ackerman et al. 2017; Buchwal et al. 2020; Weijers 2022). Moisture sensitivity of growth can depend on temperature (Li et al. 2016), and can vary within (Thompson and Koenig 2018) and between sites (Myers-Smith et al. 2015a). Soils on Qikiqtaruk are frequently saturated, likely reducing the impacts of drought locally (Myers-Smith et al. 2019). We did not detect any influence of precipitation from summer rain, snowmelt, or cloud cover (Table 1, Fig. 3). Decreasing snow cover reduces soil insulation in winter and limits productivity increase under warming and earlier phenology in Alaska (Kelsey et al. 2020). The lack of a precipitation signal detected in our study could be influenced by our use of gridded climate datasets due to a lack of a complete local record for precipitation at this site. Gridded climate datasets poorly capture spatially-variable precipitation, due to the paucity of Arctic meteorological stations and the high spatial variability of precipitation (Macias-Fauria et al. 2014; Myers−Smith and Myers 2018). For sea ice, we found that lower annual minima and earlier melt are weakly associated with increased radial growth of *S. arctica*, although phenology for this species was not found to vary with sea ice extent (Assmann et al. 2019). Sea ice could influence plant growth and phenology through interactions with local climate (Post et al. 2009; Bhatt et al. 2010; Kerby and Post 2013; Macias-Fauria et al. 2017; Assmann et al. 2019) and drought-stress (Forchhammer 2017; Buchwal et al. 2020). We found no relationship between snowmelt date and growth, which is consistent with the primary mechanism of snowmelt controlling phenology and so influencing plant growth (Assmann et al. 2019; Myers-Smith et al. 2019). Taken together, our results suggest that temperature rather than growing season length, precipitation or sea ice dynamics was the primary factor controlling *S. arctica* radial growth on Qikiqtaruk.

*NDVI*

We observed no correlation between NDVI and interannual variation in *S. arctica* radial growth, consistent with results for other shrub species at our site (Myers-Smith et al. 2019). While satellite datasets do not entirely correspond with each other (Guay et al. 2014) and shrub biomass cannot be directly estimated from NDVI alone (Cunliffe et al. 2020), NDVI is easily-scaled, well-studied, and part of a broader picture of complex Arctic tundra vegetation change (Myers-Smith et al. 2020). Arctic shrubification has been linked with satellite-derived Arctic greening trends (Macias-Fauria et al. 2012), and comparing ground observations to spectral greening observed by satellites improves broad-scale interpretation of these trends (Myers-Smith et al. 2020). Correlation of NDVI and shrub growth has been found in some studies (Forbes et al. 2010; Macias-Fauria et al. 2012), but is not universal and varies with site and the time of year (Blok et al. 2011; Brehaut and Danby 2018; Andreu-Hayles et al. 2020). Taken together, these results suggest that satellite spectral greening indices are not capturing all of the variation in plant productivity indicated by shrub radial growth (Angers-Blondin 2019; Berner et al. 2020).

*Study limitations*

While our findings bring together phenology and dendrochronology, two important fields of study of Arctic change, there are limitations. Sampling stem elongation (primary growth) and root collars rather than stems alone would improve the capture of interannual variation in shrub productivity. Primary and secondary (radial) growth can be driven by different controls (Bret-Harte et al. 2002), so study of annual stem increments would more robustly address questions of shrub growth than radial growth alone (Myers-Smith et al. 2015b). Root collars show greater climate sensitivity (Ropars et al. 2017) and less response to individual conditions than stems (Sonesson and Callaghan 1991; Sadras and Denison 2009; Myers-Smith et al. 2015b), yet root collars are challenging to find and excavate in clonal species such as *S. arctica*, and are more destructive to sample. We were not easily able to locate root collars consistently at this site (Angers-Blondin 2019). Innovative techniques such as drone-derived biomass estimates could also help with scaling up to landscape-wide analyses (Cunliffe et al. 2020). Newer approaches to studying tundra plant phenology such as time lapse cameras (a.k.a. phenocams) are overcoming inherent challenges of data collection in the Arctic (Westergaard-Nielsen et al. 2017; Richardson et al. 2018; Parmentier et al. 2021). Local observations of plant phenology and growth can be scaled up using drone and satellite data to bridge scale gaps and form a landscape perspective on tundra productivity change (Riihimäki et al. 2019; Assmann et al. 2019, 2020; Cunliffe et al. 2020). Challenges of scaling and data collection are being met by technological solutions, allowing us to see Arctic change from new angles and more clearly than ever before.

*Future study*

Modern techniques facilitate below-ground monitoring of tundra plant phenology and root growth (Iversen et al. 2015; Sloan et al. 2016; Blume−Werry et al. 2016, 2017), exposing an overlooked dimension of tundra dynamics. An increasing number of studies indicate phenological asynchrony above and below ground at sub-Arctic sites (Ögren 2017; Blume−Werry et al. 2017), with below-ground root growth extending into the late summer and autumn in now-thawed soils. Fungal symbiotes such as mycorrhizae can influence plant growth and carbon exchange in tundra shrubs which could be altering growth-climate interactions (Clemmensen et al. 2006; Compant et al. 2010; Deslippe et al. 2011). Iler et al. (2013) suggest that phenology responses to warming are reaching physiological limits in some Arctic and alpine species, potentially reducing the magnitude of future change. Collins et al. (2021) found that reproductive and vegetative phenologies are affected differently by experimental warming, which could alter ecosystem dynamics via trophic mismatches and resource-allocation (Post and Forchhammer 2008; Clausen and Clausen 2013; Kerby 2015; Wheeler et al. 2015). There has been relatively little investigation of plant senescence and the drivers of the end of the growing season, creating uncertainty in our understanding of plant responses to warming across the growing season. Though further research is required, particularly for Arctic systems (Diepstraten et al. 2018), the increasing scope of monitoring of above- and below-ground plant responses encompassing phenology and growth allows for the investigation of key knowledge gaps about tundra ecosystem responses to global change.

## Conclusions

Our findings demonstrate that plant phenology does not necessarily drive growth in an Arctic shrub, but that warmer temperatures in the summer lead to increased annual radial growth. Interannual variation in precipitation, sea ice, snow cover, and MODIS NDVI for the landscape were not strongly related to growth. Our results indicate that future Arctic warming will likely enhance shrub growth and encroachment (Tape et al. 2006; Myers-Smith et al. 2011a; García Criado et al. 2020), as long as growth is not limited by water or nutrients (Mack et al. 2004; Myers-Smith et al. 2015a; Ackerman et al. 2017), with significant consequences for water, energy, and carbon fluxes (Loranty and Goetz 2012; Pearson et al. 2013; Parker et al. 2021). While questions remain in these complex systems, studying shrub phenology and growth data for other sites and species – and incorporating a below-ground perspective on plant phenology (Iversen et al. 2015) and growth – will paint a clearer panarctic picture of plant responses to rapid Arctic warming (Myers-Smith et al. 2020). Investigating the magnitude and direction of change on-the-ground in tundra ecosystems is necessary to validate assumptions that underpin remote sensing studies (Myers-Smith et al. 2019; Piao et al. 2019; Cunliffe et al. 2020), strengthening our understanding of tundra plant responses to warming. Teasing apart the complex mechanisms between climate change and plant growth in tundra ecosystems is vital to improve projections of how Arctic vegetation change influences global climate.

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## Supplementary materials

Here, we present summary tables of our frequentist mixed-model analysis using basal area increment (Table S1), as well as Bayesian (Table S2) and frequentist (Table S3) analyses using ring width. We also present a thin section image (Fig. S1), sample depth figures (Fig. S2), temporal autocorrelation plots (Fig. S4), and an additional analysis using ring width instead of basal area increment to measure plant growth (Fig. S7).

***Table S1***: *Statistical results for the linear mixed effect models relating radial growth (basal area increment) to phenology, temperature, precipitation, NDVI, sea ice concentration, and snow-free date (results for ring widths are included in Table S3). All models span the period 2002–2015. Asterisk (*) indicates a model for which* $\Delta AIC_{null} \leq -2$. *All* $\Delta AIC_{null} > -2$ *recorded as 0, as differences below 2 are statistically undetectable. Sample depth per year as follows: 2002, n=5; 2003, n=6; 2004, n=8; 2005, n=10; 2006, n=14; 2007, n=16; 2008, n=20; 2009, n=23; 2010, n=25; 2011, n=27; 2012-5, n= 28.*

| **Predictor variable** | **$\Delta AIC_{null}$** | **Pseudo-$R^2$** | | **Effect Size** | |
|---|---|---|---|---|---|
| | | **Marginal** | **Conditional** | **Effect** | **SE** |
| Leaf emergence | 0 | 0.3% | 3.0% | -0.042 | 0.057 |
| **Leaf senescence** | **-4.6*** | **2.8%** | **2.9%** | **-0.097** | **0.035** |
| Growing season length | 0 | 0.4% | 3.1% | -0.052 | 0.057 |
| Previous growing season length | 0 | 0.1% | 2.9% | -0.026 | 0.053 |
| Previous summer temperature | 0 | <0.1% | 3.2% | -0.002 | 0.058 |
| **Previous autumn temperature** | **-2.3*** | **2.0%** | **3.1%** | **0.095** | **0.046** |
| Winter temperature | 0 | 0.2% | 3.1% | -0.023 | 0.042 |
| Spring temperature | 0 | 0.1% | 3.2% | 0.018 | 0.049 |
| **Summer temperature** | **-4.5*** | **2.8%** | **2.8%** | **0.121** | **0.044** |
| Autumn temperature | 0 | 1.0% | 3.0% | 0.071 | 0.051 |
| Previous summer precipitation | 0 | 0.2% | 3.2% | -0.031 | 0.051 |
| Previous autumn precipitation | 0 | <0.1% | 3.0% | -0.011 | 0.049 |
| Winter precipitation | 0 | <0.1% | 3.1% | -0.006 | 0.058 |
| Spring precipitation | 0 | <0.1% | 3.2% | -0.007 | 0.041 |
| Summer precipitation | 0 | <0.1% | 3.2% | 0.016 | 0.053 |
| Autumn precipitation | 0 | <0.1% | 3.2% | -0.006 | 0.050 |
| MODIS NDVI | 0 | <0.1% | 3.0% | 0.121 | 0.090 |
| Minimum sea ice extent | 0 | 0.6% | 2.5% | -0.136 | 0.119 |
| Sea ice melt onset date | 0 | 1.3% | 2.8% | -0.096 | 0.058 |
| Date snow free | 0 | 0.2% | 3.0% | -0.042 | 0.058 |

***Table S2**: Statistical results for the hierarchical Bayesian models relating ring width to phenology, temperature, precipitation, NDVI, sea ice concentration, and snow-free date (Table S3). All models span the period 2002–2015. Asterisk (*) indicates a model where the 95% credible intervals do not overlap zero and which we therefore consider to be significant. Sample depth per year as follows: 2002, n=5; 2003, n=6; 2004, n=8; 2005, n=10; 2006, n=14; 2007, n=16; 2008, n=20; 2009, n=23; 2010, n=25; 2011, n=27; 2012-5, n= 28.*

| **Predictor variable** | **Estimate** | **Standard Error** | **Lower 95% CI** | **Lower 95% CI** | **R-hat** | **Bulk ESS** | **Tail ESS** |
|---|---|---|---|---|---|---|---|
| Leaf emergence | 0.07 | 0.09 | -0.10 | 0.24 | 1.00 | 2722 | 2395 |
| Leaf senescence | -0.04 | 0.07 | -0.19 | 0.10 | 1.00 | 2159 | 1652 |
| Growing season length | -0.13 | 0.09 | -0.30 | 0.04 | 1.00 | 4109 | 2884 |
| Previous growing season length | -0.03 | 0.08 | -0.20 | 0.14 | 1.00 | 2363 | 1965 |
| Previous summer temperature | -0.05 | 0.10 | -0.23 | 0.15 | 1.00 | 3040 | 2239 |
| Previous autumn temperature | 0.08 | 0.08 | -0.08 | 0.24 | 1.00 | 2555 | 2128 |
| Winter temperature | -0.10 | 0.06 | -0.22 | 0.03 | 1.00 | 3345 | 2000 |
| Spring temperature | -0.08 | 0.08 | -0.24 | 0.07 | 1.00 | 2023 | 1366 |
| Summer temperature | 0.13 | 0.09 | -0.04 | 0.30 | 1.00 | 2434 | 1344 |
| Autumn temperature | 0.15 | 0.08 | 0.00 | 0.30 | 1.00 | 4174 | 2441 |
| Previous summer precipitation | -0.12 | 0.08 | -0.26 | 0.04 | 1.00 | 2916 | 1773 |
| Previous autumn precipitation | 0.03 | 0.08 | -0.12 | 0.19 | 1.00 | 2519 | 1515 |
| Winter precipitation | -0.01 | 0.09 | -0.20 | 0.18 | 1.00 | 3655 | 2537 |
| Spring precipitation | -0.04 | 0.06 | -0.16 | 0.09 | 1.00 | 2231 | 2274 |
| Summer precipitation | -0.02 | 0.09 | -0.20 | 0.15 | 1.00 | 2919 | 2401 |
| Autumn precipitation | -0.09 | 0.08 | -0.24 | 0.07 | 1.00 | 2862 | 2114 |
| MODIS NDVI | 0.07 | 0.08 | -0.09 | 0.22 | 1.00 | 2631 | 2098 |
| Minimum sea ice extent | -0.17 | 0.19 | -0.54 | 0.21 | 1.00 | 3762 | 2098 |
| Sea ice melt onset date | -0.13 | 0.09 | -0.31 | 0.06 | 1.00 | 3503 | 2822 |
| Date snow free | 0.04 | 0.11 | -0.18 | 0.26 | 1.00 | 2146 | 1958 |

***Table S3**: Statistical results for the linear mixed effect models relating ring width to phenology, temperature, precipitation, NDVI, sea ice concentration, and snow-free date. All models span the period 2002–2015. Asterisk (*) indicates a model for which $\Delta AIC_{null} \leq -2$. All $\Delta AIC_{null} > -2$ recorded as 0, as differences below 2 are statistically undetectable. Sample depth per year as follows: 2002, n=5; 2003, n=6; 2004, n=8; 2005, n=10; 2006, n=14; 2007, n=16; 2008, n=20; 2009, n=23; 2010, n=25; 2011, n=27; 2012-5, n= 28.*

| **Predictor variable** | **$\Delta$AIC$_{null}$** | **Pseudo-R$^2$** | | **Effect Size** | |
|---|---|---|---|---|---|
| | | **Marginal** | **Conditional** | **Effect** | **SE** |
| Leaf emergence | 0 | 0.4% | 2.7% | 0.072 | 0.084 |
| Leaf senescence | 0 | 0.2% | 2.9% | -0.037 | 0.067 |
| Growing season length | 0 | 1.2% | 2.6% | -0.131 | 0.080 |
| Previous growing season length | 0 | 0.1% | 2.6% | -0.033 | 0.078 |
| Previous summer temperature | 0 | 0.2% | 2.6% | -0.051 | 0.084 |
| Previous autumn temperature | 0 | 0.6% | 2.7% | 0.077 | 0.075 |
| Winter temperature | 0 | 1.5% | 2.6% | -0.098 | 0.054 |
| Spring temperature | 0 | 0.8% | 2.7% | -0.081 | 0.068 |
| Summer temperature | 0 | 1.3% | 2.8% | 0.125 | 0.076 |
| **Autumn temperature** | **-3.1*** | **2.2%** | **2.4%** | **0.155** | **0.065** |
| Previous summer precipitation | 0 | 1.5% | 2.5% | -0.118 | 0.065 |
| Previous autumn precipitation | 0 | 0.1% | 2.8% | 0.023 | 0.071 |
| Winter precipitation | 0 | 0.0% | 2.7% | -0.016 | 0.085 |
| Spring precipitation | 0 | 0.3% | 2.7% | -0.038 | 0.059 |
| Summer precipitation | 0 | 0.0% | 2.8% | -0.022 | 0.078 |
| Autumn precipitation | 0 | 0.8% | 2.7% | -0.087 | 0.069 |
| MODIS NDVI | 0 | 0.4% | 2.4% | 0.068 | 0.073 |
| Minimum sea ice extent | 0 | 0.4% | 2.3% | -0.178 | 0.180 |
| Sea ice melt onset date | 0 | 1.0% | 2.8% | -0.126 | 0.089 |
| Date snow free | 0 | 0.1% | 2.7% | 0.037 | 0.101 |

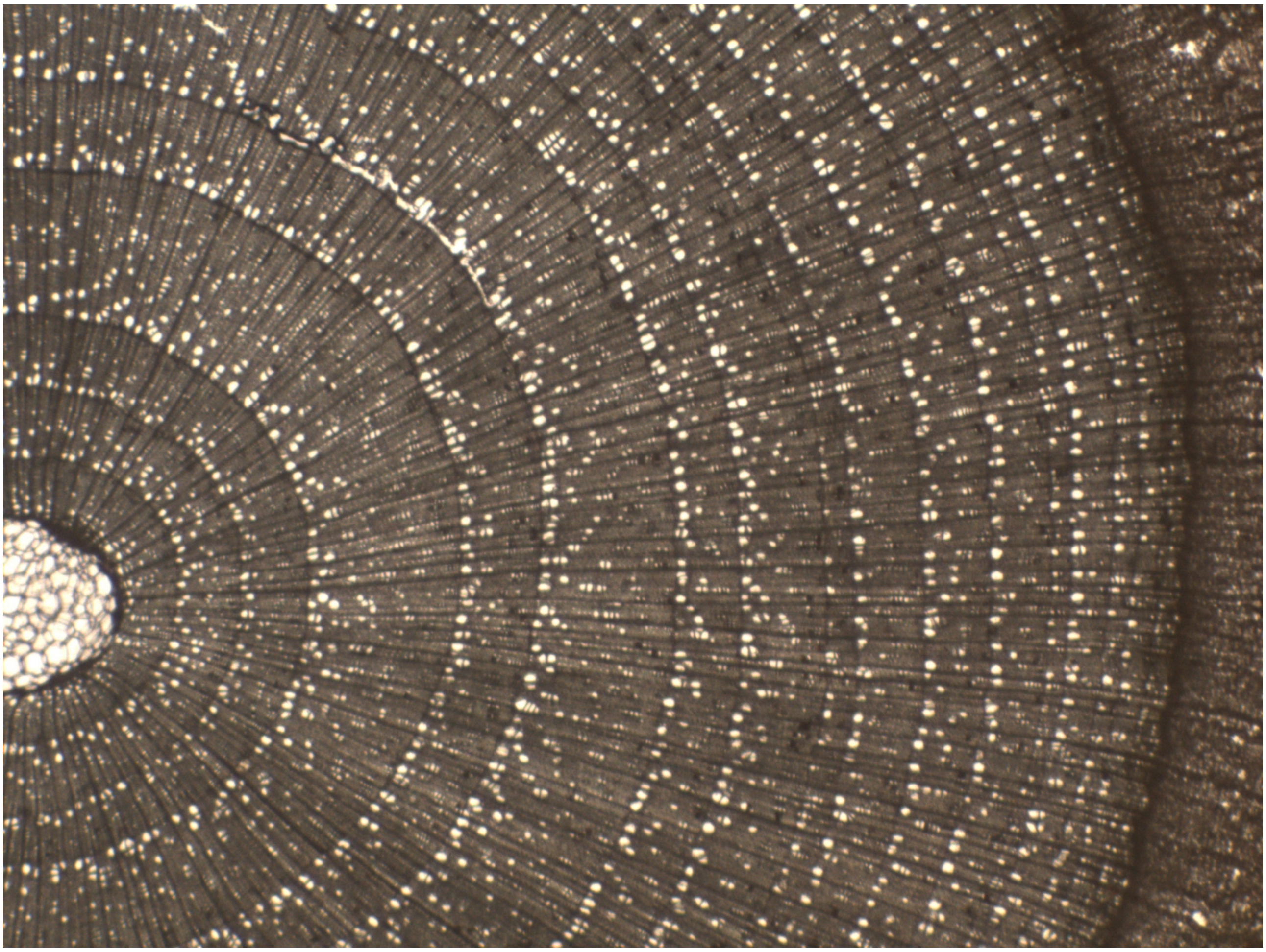


***Fig. S1** An example of one of the four thin section radii of* S. arctica *as used in this study. This stem came from transect 5, and was 18 years old when it was sampled. The rings can be made out clearly, with the outer ones being the youngest and those with wider rings and a larger surface area being deposited in years of higher growth*

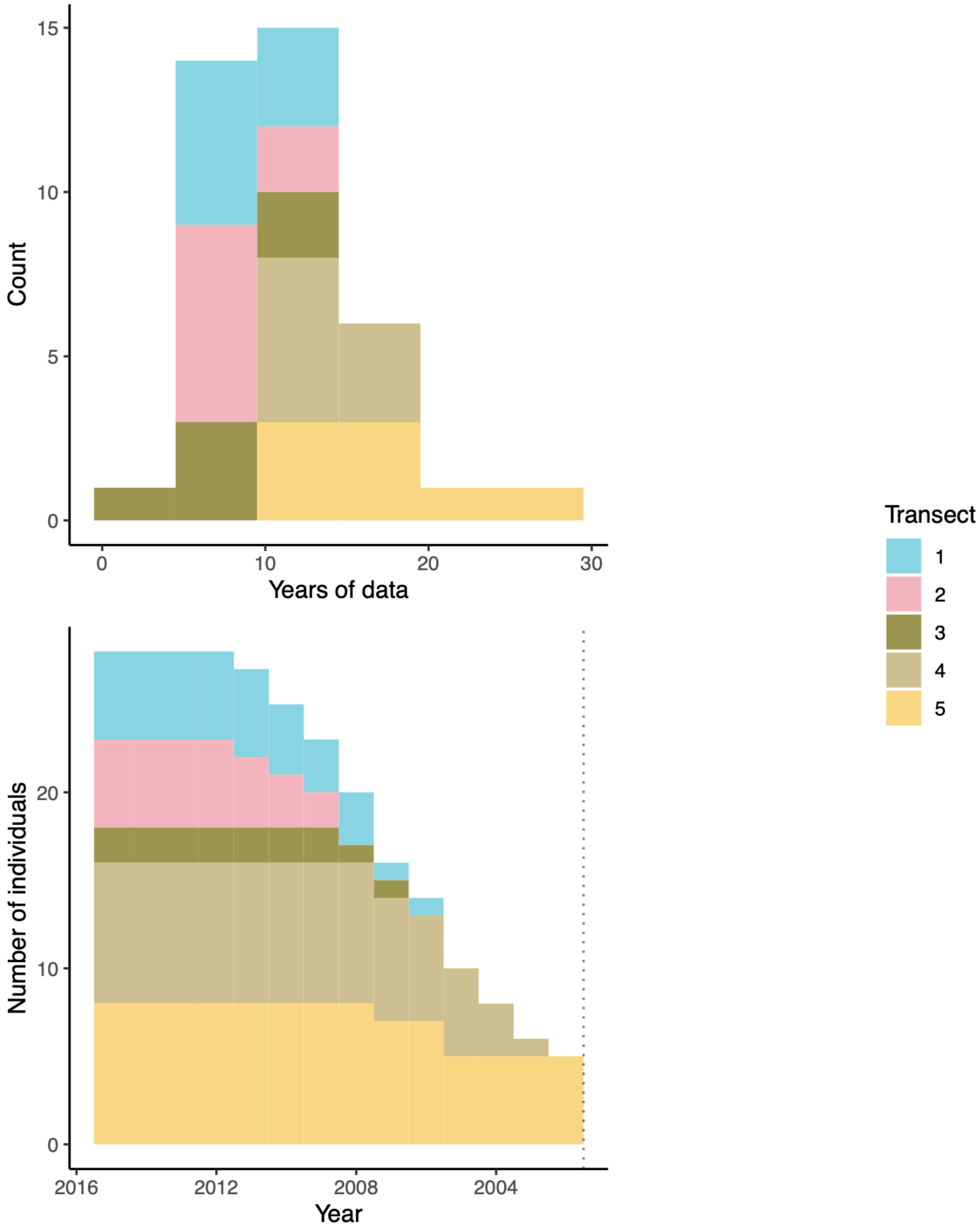
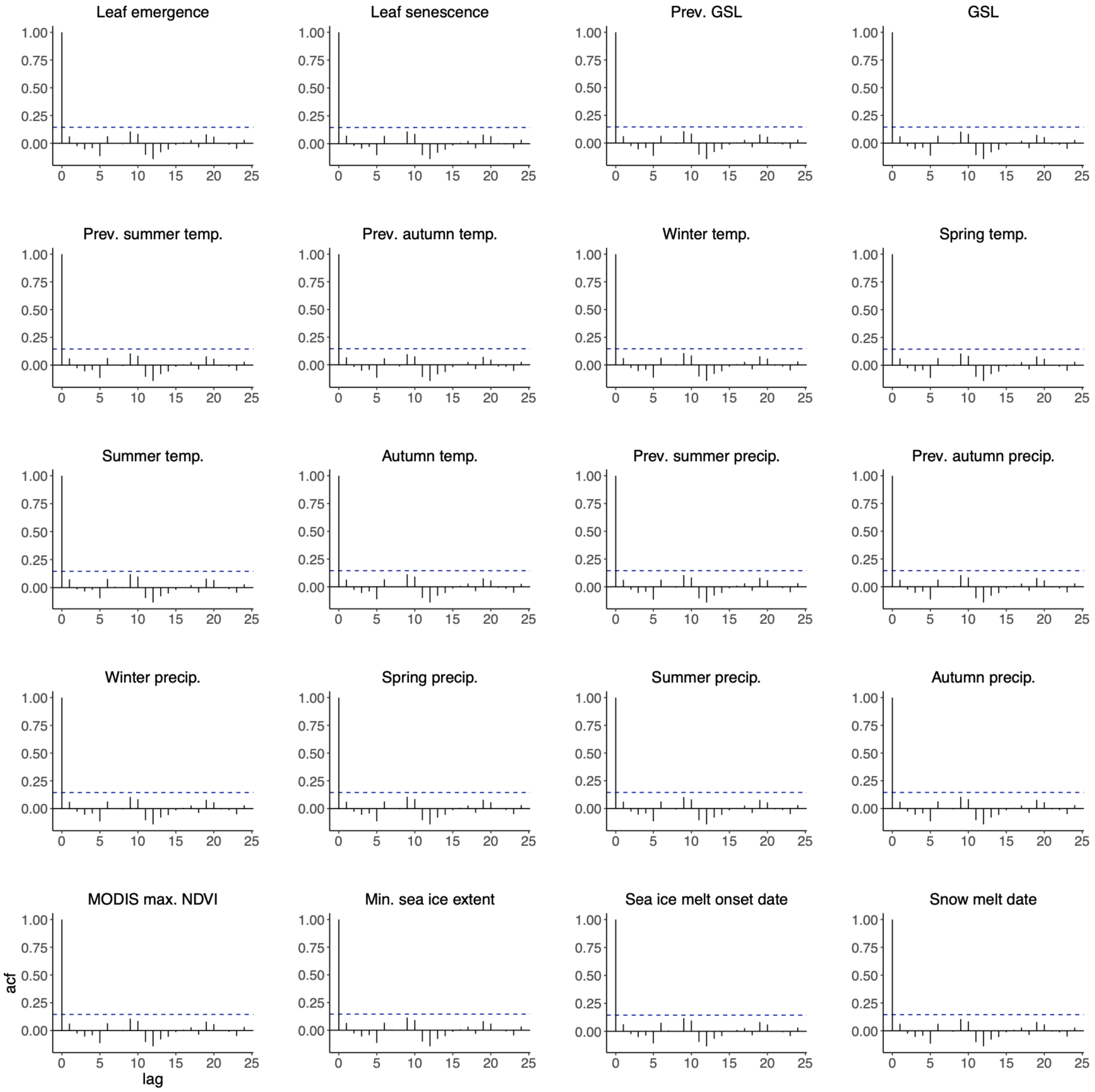
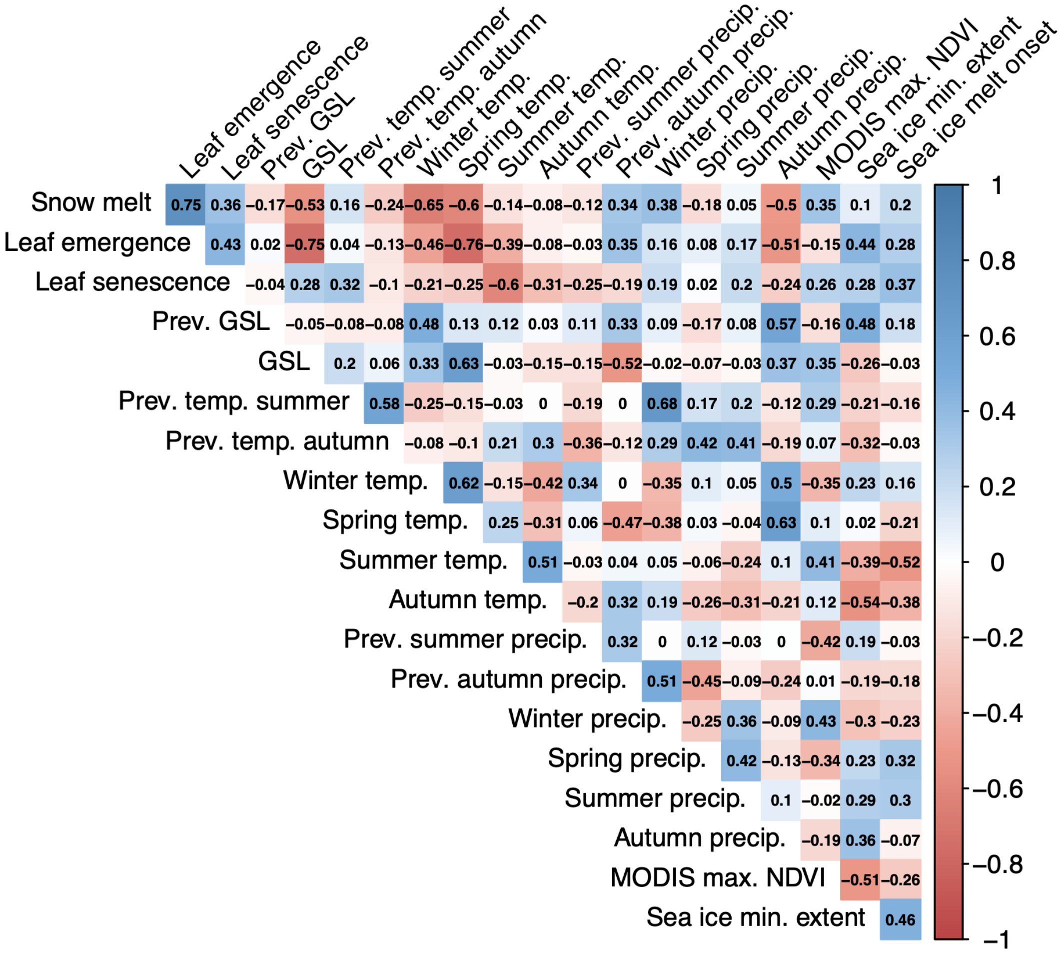


***Fig. S2*** *Sample depth plots showing the age distribution of the samples from different transects and the number of samples representing different years across the different sample transects. The oldest samples (up to 28 years) were taken from transect 5 and the youngest (from 3 years) from transect 3 (indicated by colour). The number of total samples is lower in the second plot as it shows the data after processing where some have been removed for having too few years' data. The dotted line indicates the cutoff point for the data used in this study*



706 ***Fig. S3*** *Autocorrelation plots for each environmental and phenological variable used in the overall analyses (using*

707 *basal area increment). We found no strong temporal autocorrelation for any of the variables tested*



|  | Leaf emergence | Leaf senescence | Prev. GSL | GSL | Prev. temp. summer | Prev. temp. autumn | Winter temp. | Spring temp. | Summer temp. | Autumn temp. | Prev. summer precip. | Prev. autumn precip. | Winter precip. | Spring precip. | Summer precip. | Autumn precip. | MODIS max. NDVI | Sea ice min. extent | Sea ice melt onset |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Snow melt | 0.75 | 0.36 | −0.17 | −0.53 | 0.16 | −0.24 | −0.65 | −0.6 | −0.14 | −0.08 | −0.12 | 0.34 | 0.38 | −0.18 | 0.05 | −0.5 | 0.35 | 0.1 | 0.2 |
| Leaf emergence |  | 0.43 | 0.02 | −0.75 | 0.04 | −0.13 | −0.46 | −0.76 | −0.39 | −0.08 | −0.03 | 0.35 | 0.16 | 0.08 | 0.17 | −0.51 | −0.15 | 0.44 | 0.28 |
| Leaf senescence |  |  | −0.04 | 0.28 | 0.32 | −0.1 | −0.21 | −0.25 | −0.6 | −0.31 | −0.25 | −0.19 | 0.19 | 0.02 | 0.2 | −0.24 | 0.26 | 0.28 | 0.37 |
| Prev. GSL |  |  |  | −0.05 | −0.08 | −0.08 | 0.48 | 0.13 | 0.12 | 0.03 | 0.11 | 0.33 | 0.09 | −0.17 | 0.08 | 0.57 | −0.16 | 0.48 | 0.18 |
| GSL |  |  |  |  | 0.2 | 0.06 | 0.33 | 0.63 | −0.03 | −0.15 | −0.15 | −0.52 | −0.02 | −0.07 | −0.03 | 0.37 | 0.35 | −0.26 | −0.03 |
| Prev. temp. summer |  |  |  |  |  | 0.58 | −0.25 | −0.15 | −0.03 | 0 | −0.19 | 0 | 0.68 | 0.17 | 0.2 | −0.12 | 0.29 | −0.21 | −0.16 |
| Prev. temp. autumn |  |  |  |  |  |  | −0.08 | −0.1 | 0.21 | 0.3 | −0.36 | −0.12 | 0.29 | 0.42 | 0.41 | −0.19 | 0.07 | −0.32 | −0.03 |
| Winter temp. |  |  |  |  |  |  |  | 0.62 | −0.15 | −0.42 | 0.34 | 0 | −0.35 | 0.1 | 0.05 | 0.5 | −0.35 | 0.23 | 0.16 |
| Spring temp. |  |  |  |  |  |  |  |  | 0.25 | −0.31 | 0.06 | −0.47 | −0.38 | 0.03 | −0.04 | 0.63 | 0.1 | 0.02 | −0.21 |
| Summer temp. |  |  |  |  |  |  |  |  |  | 0.51 | −0.03 | 0.04 | 0.05 | −0.06 | −0.24 | 0.1 | 0.41 | −0.39 | −0.52 |
| Autumn temp. |  |  |  |  |  |  |  |  |  |  | −0.2 | 0.32 | 0.19 | −0.26 | −0.31 | −0.21 | 0.12 | −0.54 | −0.38 |
| Prev. summer precip. |  |  |  |  |  |  |  |  |  |  |  | 0.32 | 0 | 0.12 | −0.03 | 0 | −0.42 | 0.19 | −0.03 |
| Prev. autumn precip. |  |  |  |  |  |  |  |  |  |  |  |  | 0.51 | −0.45 | −0.09 | −0.24 | 0.01 | −0.19 | −0.18 |
| Winter precip. |  |  |  |  |  |  |  |  |  |  |  |  |  | −0.25 | 0.36 | −0.09 | 0.43 | −0.3 | −0.23 |
| Spring precip. |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.42 | −0.13 | −0.34 | 0.23 | 0.32 |
| Summer precip. |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.1 | −0.02 | 0.29 | 0.3 |
| Autumn precip. |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | −0.19 | 0.36 | −0.07 |
| MODIS max. NDVI |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | −0.51 | −0.26 |
| Sea ice min. extent |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | 0.46 |

***Fig. S4*** *Correlation plots for each environmental and phenological variable used in the overall analyses. Correlation coefficients varied between -0.76 and 0.75*

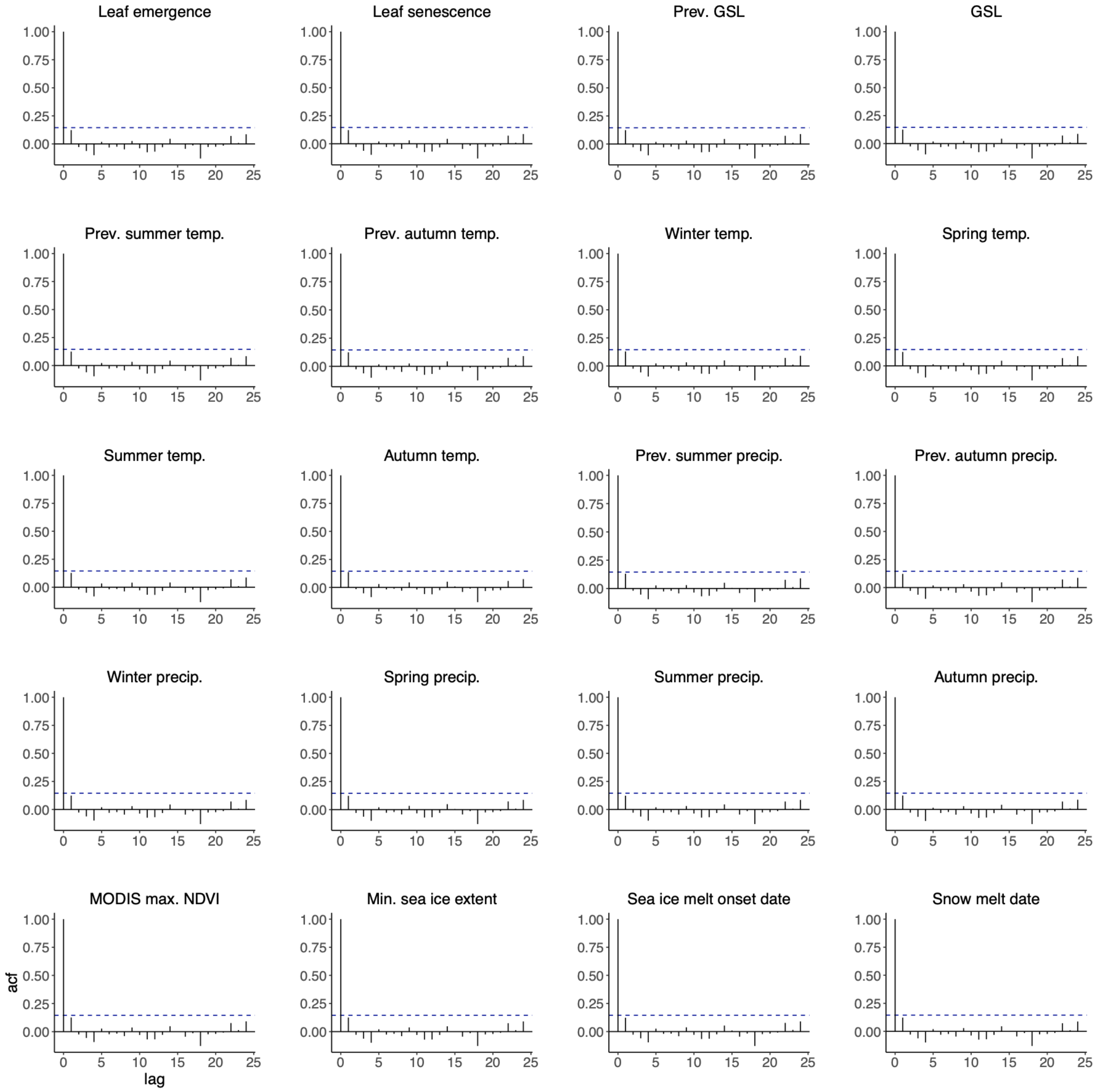


***Fig. S5*** *Autocorrelation plots for each variable used in the overall analyses (using ring width). We found no strong temporal autocorrelation for any of the variables tested*

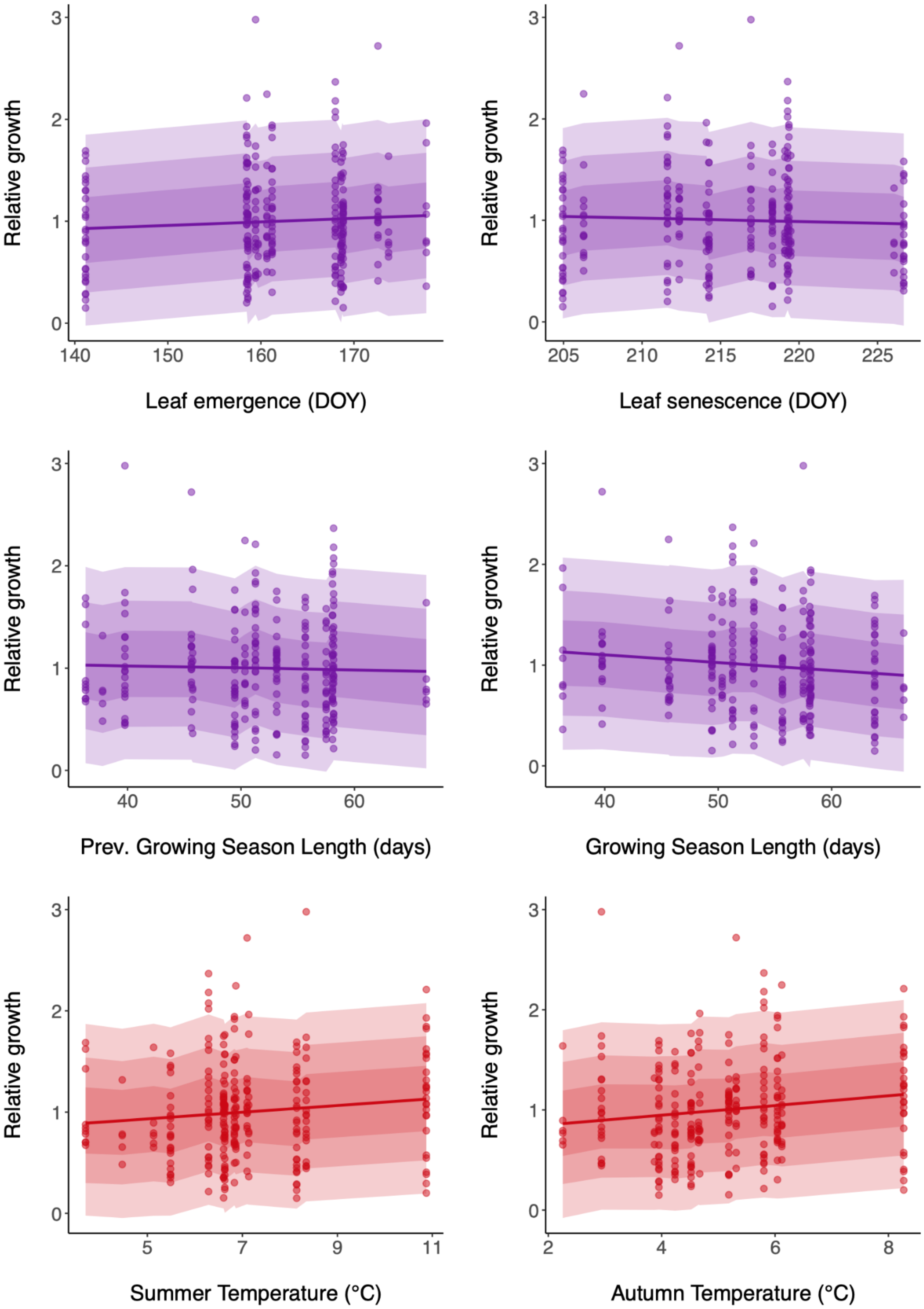


***Fig. S6*** *Annual ring width growth data corresponded weakly with phenological variables and more strongly with summer and autumn temperatures. The relationship with autumn temperature is statistically significant. Scatter plots show four phenological and two temperature variables' relationships to radial growth (ring width, indexed) in a given year over the period 2002-2015. Trendlines are predictions from the hierarchical Bayesian models, the shaded areas represent 95%, 80%, and 50% credible intervals of the model estimates*

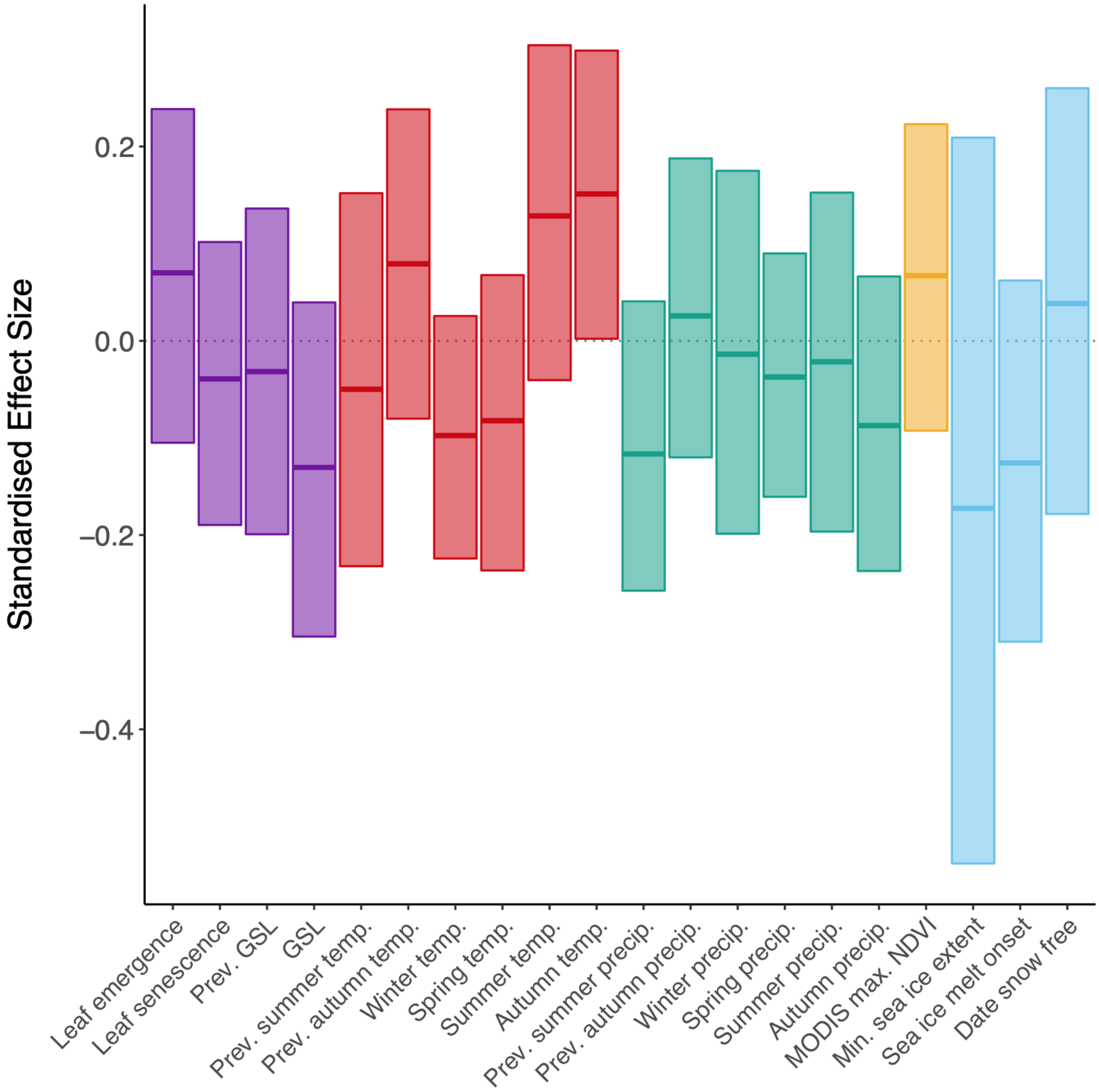


***Fig. S7*** *In the analysis of annual ring widths, no variables tested had a strong, direct relationship to growth, autumnal temperature was marginally significant, with a credible interval at or just overlapping zero (Table S2). This plot shows standardised effect sizes (slopes) of hierarchical Bayesian models of phenological events (purple), seasonal temperature (red), seasonal precipitation (green), NDVI (yellow), minimum sea ice extent, sea ice concentration, and snowmelt date (all blue), on growth. The centre line is the effect and error bars are 95% credible intervals. For ease of comparison between effect sizes, explanatory variables in this analysis are variance-scaled from -1 to 1*