Manuscript accepted for publication 8 Jul 2020
Arctic, Antarctic, and Alpine Research

Regional variation in green-up timing along a caribou migratory corridor: spatial associations with snowmelt and temperature

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Keywords: Landscape phenology, green-up, snowmelt, climate change, remote sensing

Abstract

Spring green-up in Arctic and alpine systems is predominantly controlled by temperature and snowmelt timing preceding and during the growing season. Variation in the timing of green-up across space is an important aspect of resource variability with which mobile herbivores must contend. Here, we measure the explanatory power of abiotic drivers of green-up in a Low Arctic region of west Greenland, host to a migratory caribou population. We identify inconsistent relationships between green-up and abiotic drivers across space. While green-up timing is most closely related to snowmelt in some areas, in others it is most closely related to spring temperature. The negative correlation between the explanatory power of snowmelt and temperature suggests that at broad scales, where green-up is more constrained by snow cover, such as moist, mountainous coastal areas, it is less constrained by temperature. Where snow is

less persistent through winter, such as cold, dry inland areas, temperature becomes the predominant factor driving green-up. If the principal driver of spring plant growth is inconsistent across a region, long-term trends in resource phenology could vary spatially. For seasonal migrants like caribou, synchronizing migration timing with resource phenology may be complicated by discordant interannual change across drivers of green-up timing.

Introduction

Broad-scale variation in the seasonal timing of plant growth is important for the timing and orientation of migration in ungulates (Albon and Langvatn 1992). Interannual variation in the timing of plant growth is typically related to local abiotic factors such as temperature and snow cover (Cleland et al. 2007, Wipf and Rixen 2010). Within years, spring green-up tends to progress across the landscape, delayed with respect to latitude or elevation in a phenomenon often referred to as the “green wave” (Drent et al. 1978, van der Graaf 2006). Spatiotemporal variation in plant growth may influence the paths selected by migratory herbivores (Merkle et al. 2016, Aikens et al. 2017). Across a landscape, exploitation of plant phenological variability allows mobile consumers to prolong access to high quality, newly emergent forage (Armstrong et al. 2016). Such spatial variation in resource phenology can compound the effect of timing of plant growth on herbivore reproductive success (Post et al. 2008). Thus, it is important to understand the underlying drivers of plant phenology spatial dynamics, and the extent to which these factors explain phenological variation across space and time.

If different factors influence variability in plant phenological dynamics across a region, the timing of plant growth could shift inconsistently over space in response to broad-scale climatic changes. In general, plant growth is limited by the timing of snowmelt in regions with persistent winter snow cover, such as arctic and alpine environments (Wipf and Rixen 2010). Conversely, in the absence of persistent winter snow cover (e.g., in temperate latitudes), other controls, such as photoperiod and temperature, predominate (Körner and Basler 2010, Garonna et al. 2018). In temperate systems, the predominant controls of vegetation phenology may vary within a region depending on topographic and climatic influences (Brown et al. 2019). The extent to which intra-regional variation in the timing of spring plant growth relates to different abiotic conditions in the Arctic is less certain. Here, we seek to uncover drivers of inter- and intra-annual variation in plant phenology in a low-Arctic region that is home to a migratory population of barren-ground caribou (*Rangifer tarandus groenlandicus*). We use satellite-derived measurements of snow cover and green-up timing, in addition to temperature records from two locations at opposing ends of this migratory corridor, to determine the extent to which snow and temperature influence the timing and spread of green-up across the Kangerlussuaq-Sisimiut region of west Greenland.

Methods

Study Site

We analyzed interannual variation in spring green-up timing on the home range of the Kangerlussuaq-Sisimiut caribou herd in southwest Greenland. The population was estimated to be 98,300 in 2010 (Cuyler et al. 2012). The region is bounded by the Davis Strait, Nordre Isortoq Fjord, the Inland Ice, and the Sukkertoppen ice cap (Fig 1a; Thing 1984). Over the course of 2-3 weeks, this herd undergoes a seasonal migration between a winter range located near the village of Sisimiut along the west coast of Greenland and a summer calving range located approximately 150 km inland, east of the village of Kangerlussuaq, near Greenland's Inland Ice. This range was previously described and mapped by Thing (1984). The centroid of the core destination range lies 71 km east of the core departure range. Elevation in the destination range is on average 36 m lower than that in the departure range. Across the region, the mean elevation is 514 m above sea level (Fig 1b, Howat et al. 2014).

The Kangerlussuaq-Sisimiut caribou population is notable for the lack of large predators in the vicinity (Thing 1984); hence, migration in this population is likely to be associated with bottom-up climatic or resource drivers rather than top-down predation pressure. Moderating effects of the maritime climate lead to comparatively mild summers and winters in coastal regions compared to areas nearer Greenland's Inland Ice Sheet, which feature cold winters and comparatively warm, dry summers. However, snow is deeper in the mountainous coastal regions, and less persistent in the windswept areas further inland.

Landscape phenology

The Moderate Resolution Imaging Spectroradiometer (MODIS) collects daily radiometric measurements from two satellite platforms. For this analysis we used two Level-3 products that derive from MODIS measurements, the MOD13Q1 Normalized Difference Vegetation Index (NDVI; Didan 2015) and the MOD10A1 Normalized Difference Snow Index (NDSI; Hall and Riggs 2015). We used the 16-day MOD13Q1, a 250-m NDVI dataset, to investigate seasonal patterns in plant growth from 2001-2018. Interannual variation in satellite-derived landscape phenology in the region is significantly related to detrended ground-based observations of plant phenology (John 2016). The MOD13Q1 raster dataset includes pre-calculated vegetation indices, as well as data quality bands. Vegetation indices are reported as biweekly maximum value composites from daily sampling by the MODIS satellites, alongside the date at which the maximum value was observed ("Composite DOY"). We used the daily MOD10A1, a 500-m grid snow cover dataset, to investigate patterns in snow melt (Hall and Riggs 2015). This dataset includes a snow index, and a Basic QA data quality band. All remote sensing data were quality controlled, mosaicked, and downloaded using Google Earth Engine (Gorelick et al. 2017).

NDVI data were compiled into annual multidimensional arrays and processed according to the methods described in Bischof et al. (2012). We removed observations that were classified as "Snow/Ice" and "Cloudy" based on the MOD13Q1 quality layer (Didan 2015). NDVI data were stacked into a 365-layer array, according to the Composite DOY for each NDVI observation (along the z dimension), but maintaining relative spatial attributes (x- and y-dimensions). For each pixel in the dataset, the bottom 0.025 quantile of NDVI measurements was used as a winter baseline. The time series was smoothed with a rolling median with a window width of 3 observations. The time series was then scaled so that the top 0.925 quantile of observations was set to 1. Then, for each year, the NDVI time series was fit to a double-logistic curve that features a wintertime baseline, greening upward phase, summer asymptote, and senescing downward phase before returning to the asymptotic wintertime baseline. We derived the timing of peak instantaneous rate of green-up (IRG) from each pixel's NDVI time series to identify a single date representative of the midpoint of the green-up season each year (Bischof et al. 2012, Aikens et al. 2017, Geremia et al. 2019). By projecting this time point for each pixel across space, areas with comparatively large values represent MODIS pixels featuring delayed green-up, and areas with small values represent MODIS pixels featuring earlier green-up.

For snow cover, we retained only “good” and “best” quality NDSI observations based on the Basic QA data quality band from the MOD10A1 dataset. We used a threshold-based approach to differentiate snow-covered and snow-free pixels (Hall et al. 2012), and created daily binary snow images from the MOD10A1 collection. We set snow-covered ($\geq$ 0.2 NDSI) pixels to 1, and snow-free (< 0.2 NDSI) pixels to 0. A double-logistic curve with asymptotes at 1 and 0 was fit to annual binary snow cover time series to identify dates of peak instantaneous rate of snowmelt in an approach analogous to the NDVI curve fitting described above. Because the MOD10A1 dataset contains daily measurements, snowmelt timing was derived from 365 observations (with one observation per day), while green-up timing was derived from 23 observations (with one measurement every 16 days). As opposed to the NDVI curve, the snow cover curve began each year with the wintertime snow-covered state (1) and dropped to the snow-free asymptote (0) during the spring, before returning to snow-covered (1) in the fall or winter. All analyses that draw from both snowmelt and green-up timing data used resampled green-up data in order to match the spatial resolution of snowmelt data.

Associations between abiotic factors and phenological dynamics

Monthly temperature records were acquired from the Danish Meteorological Institute (http://www.dmi.dk) for both Kangerlussuaq and Sisimiut (2001-2018). These villages host the nearest weather stations to the primary spring destination and departure ranges, respectively, of the focal caribou population. Regional monthly temperatures were calculated using the average monthly temperature for each month in both villages. We did not include precipitation in this analysis because a significant gap in precipitation data exists in the Sisimiut records during this period.

At the regional level, mean timing of green-up and snowmelt were used to index broad-scale seasonal patterns each year. Mean regional temperatures for each month leading up to and during the green-up period (January-June) were used as candidate predictors and the timing of green-up for each pixel as response variables in a linear model. Because of multicollinearity among weather stations and months, we used step selection based on Akaike's Information Criterion (AIC) to identify the most parsimonious linear model relating regional green-up timing to monthly temperatures (Burnham and Anderson 2001). A model including only temperature, and one with temperature and snowmelt timing were compared using the corrected Akaike's Information Criterion (AICc) to correct for number of parameters.

At the pixel level, associations between abiotic factors and vegetation green-up timing were assessed by including the mean temperature during the months that were selected using AIC step selection in the regional analysis above. Additional linear models were run using snowmelt timing as a candidate predictor, snowmelt timing and elevation as candidate predictors, and finally snowmelt timing, elevation, and temperature as candidate predictors. Models were compared using AICc adjusted for number of parameters.

Spatial drop-off in predictive capacity was assessed by comparing the AICc of linear models with mean May temperature in Sisimiut and Kangerlussuaq as predictors of green-up for each pixel. In cases where Kangerlussuaq temperature had a lower AICc (ΔAICc < 0), the inland temperature record was a better predictor of interannual variation in green-up timing at the pixel level than the coastal temperature record. When the absolute value of ∆AICc was greater than 2, the difference in predictive capacity between the two weather stations was considered significant (Burnham and Anderson 2001). Longitudinal gradients were analyzed by centering rasters on 0 and converting the UTM coordinate offset to kilometers in order to facilitate interpretation of the results. All statistical analyses and data visualizations were performed using R (R Core Team 2014).

Results

At the regional scale, green-up timing varied considerably among years but did not display significant trends over the duration of the study (2001-2018). Mean monthly temperatures preceding and during the growing season (January through June) emerged as strong predictors of green-up timing at the regional scale (linear regression, $R^2 = 0.84$, $F_{6,11} = 9.36$, $p < 0.001$). Because of multicollinearity among monthly temperatures, we selected the two strongest predictor months, April and May (which were not significantly correlated; Pearson's r = 0.18) for all subsequent analyses. Mean April and May temperatures were weak predictors of snowmelt timing ($R^2 = 0.45$, $F_{2,15} = 6.03$, $p = 0.012$) but strong predictors of green-up timing (Fig 2a, $R^2 = 0.73$, $F_{2,15} = 19.86$, $p < 0.001$). Together with regional snowmelt timing (Fig 2b), April and May temperatures explained 86.3% of variation in green-up timing at the regional scale (linear model, $F_{3,14} = 29.36$, $p < 0.001$), although regional snowmelt and regional May temperature were moderately correlated (Pearson's r = -0.43, p = 0.075).

At the local (pixel) scale, spring green-up timing was positively associated with elevation, indicating green-up occurred later at higher elevations (Fig 3a; β = 1.48 days/100m elevation, R^2 = 0.063, $F_{1,195066} = 1.3_{x10}^{4}$, $p < 0.001$). This pattern was consistent for all years of the study (2001-2018; see Fig S1). A regular inland-to-coastal progression of green-up emerged (Fig S2), which opposed the direction of spring migration by the local caribou population (Thing 1984). Green-up timing was also associated with snowmelt timing across the dataset (Fig 3b; slope = 0.53 days/day snowmelt, $R^2 = 0.38$, $F_{1,192792} = 1.20_{x10}^{5}$, $p < 0.001$), a relationship that was maintained each year (see Fig S3). Snowmelt was somewhat delayed with respect to elevation, but the two variables were sufficiently unrelated that both could be used together as predictors (Pearson's $r = 0.32$, $p < 0.001$, variance inflation factor = 1.097). Inclusion of both terms in a linear model explained 39% of variation in green-up timing across the duration of the study ($F_{1,192791} = 6.15_{x10}^{4}$, $p < 0.001$).

May temperatures in both villages were better predictors of inland green-up timing than of green-up timing nearer the coast (Fig S4). The predictive power (R^2) of temperature on green-up timing was inversely related to that of snowmelt timing on green-up timing ($p < 0.001$). Accordingly, we detected a consistent pattern across the landscape in the relative proportion of variance in green-up timing that was better predicted by temperature vs. snowmelt timing (Fig 4). May temperature in Kangerlussuaq was a consistently better predictor of green-up timing than May temperature in Sisimiut, especially for areas farther inland (Fig S5).

The regional balance of green-up (measured as the slope of a linear model of green-up vs. longitude; see Fig S2) was not significantly affected by the difference in May temperature between Kangerlussuaq and Sisimiut ($p > 0.05$). Instead, while temperature was more predictive of inland green-up timing than coastal green-up timing ($R^2 = 0.024$, $F_{1,10944}=273$, $p < 0.001$), snowmelt timing, which was not strongly related to temperature, was a more important predictor for green-up timing near the coast than it was farther inland ($R^2 = 0.012$, $F_{1,10944}=138$, $p < 0.001$).

Discussion

Across years, mean regional spring green-up timing was broadly related to regional spring temperature and snowmelt timing, but the relationship between green-up and abiotic variables was less consistent at finer scales. At the local scale, green-up was delayed with respect to increasing elevation, a pattern which held across all years of the study. Green-up was also generally delayed with respect to later snowmelt across years. However, this pattern was not consistently evident, and temperature was an equal or more important predictor in some parts of the Kangerlussuaq-Sisimiut region. In the western and southern portions of the region, the primary winter range used by caribou, interannual variation in green-up timing was most closely related to snowmelt timing. These areas tend to be mountainous and have increased precipitation, but milder winter temperatures due to the maritime influence of the Davis Strait. Conversely, toward the northern and inland part of the region, the core of the caribou summer calving range, interannual variation in green-up timing was most closely related to spring temperature. The comparatively reduced precipitation and colder winter temperatures are likely associated with proximity to the Inland Ice sheet.

Our results reveal a complex relationship between green-up and snowmelt timing at the local and regional level. Across years, while green-up consistently followed snowmelt regionally, the slope of that relationship was less than 1, indicating that green-up occurs more immediately after snowmelt in years with later snowmelt (Fig 2b). This relationship was manifest as a window after snowmelt but preceding peak green-up that lasted as little as 20 days in years with delayed snowmelt (2001) and as much as 44 days in years with early snowmelt (2013).

In a Bayesian analysis of effects of temperature, snowmelt, and sea ice on plant phenology dates across four Mid- and High-Arctic sites in North America, the mean effect of snowmelt on plant phenology was estimated to be 0.45 days of plant phenological advance per day of snowmelt advance (Assmann et al. 2019). These relationships presumably reflect the added constraints of temperature, photoperiod, and their interactions on plant phenology (Assmann et al. 2019).

Within years and across space, the slope of the relationship between green-up and snowmelt was similarly less than 1, but there were numerous cases where green-up preceded snowmelt (Fig 3b). This was likely due to the method by which we calculated snowmelt timing. Rather than using the first snow-free day of the year, we used a curve-fitting technique to derive the end of the snowy season. Therefore, brief snow-free conditions followed by a period of snow cover could extend the duration of the snowy season while promoting initiation of plant growth. In areas with less persistent snow cover, such as the northeast inland area occupied by caribou during the summer calving season, limitations imposed by snow cover are alleviated and broad-scale green-up appears to respond more strongly to temperature. The warm foehn winds characteristic of west Greenland can thaw entire landscapes (Thing 1984), and may explain a great deal of the residual variation in local green-up timing presented here. A future analysis of the effect of foehn winds could improve our understanding of early-season plant growth and its importance for herbivore ecology.

Pettorelli et al. (2005) used a site-based approach to investigate the drivers of variation in the timing of plant growth and the effect of such variation on reindeer body mass in Norway. Similar to the findings presented here, in that study warm springs led to earlier plant growth, and deep snow and high altitude were associated with delayed plant growth (Pettorelli et al. 2005). However, whereas timing of spring plant growth occurred earlier near the coast in Norway (Pettorelli et al. 2005), we found a later onset of spring green-up near the coast compared to green-up timing farther inland (Fig S2). We expect this is due to combined effects of the lower elevations of inland Greenland (Fig 1b), and the persistent snow cover that is characteristic of coastal southwest Greenland. While snow depth, snow persistence and surface temperature are all related both directly and through feedbacks (Xu and Dirmeyer 2011), air temperature can only begin to act on plant phenology once sufficient insulating snow has melted away. Therefore, temperature could emerge as an important factor controlling plant growth in years with comparatively low snow cover near the coast.

The spatial variability in predominant drivers of landscape phenology documented here is relevant to the migratory ecology of the local caribou population. The presence of an inland-to-coast progression of spring green-up presumably complicates tracking by caribou of green-up from their coastal winter range toward their inland summer calving range. However, migratory arrival timing by caribou in this population at the summer range is highly correlated with local emergence phenology of some key forage species at their calving grounds, including the forbs *Campanula* sp. and *Stellaria longipes*, and the shrub *Betula nana* (Post 2019). Rather than relating to departure timing itself or generalized phenological conditions on the departure range, caribou springtime migratory arrival on calving grounds may be influenced by additional proximal factors – such as insect harassment, snow cover, and variation in plant growth along the way – that govern the pace of migration through effects on body condition (Gurarie et al. 2019).

In-situ validation measurements are chronically lacking from studies of remotely-sensed greening and phenology data (Myers-Smith et al. 2020). In other Arctic sites, MODIS vegetation indices have been shown to broadly relate to the phenology of polar willow (Karlsen et al. 2014). Here, we used time series NDVI from the MOD13Q1 satellite to derive green-up timing across space. This green-up metric was strongly correlated to detrended interannual variation in plant community emergence timing at a study site within the region (John 2016). While no such ground validation of snowmelt exists for the area, MODIS products have been used elsewhere in the Arctic to model snowpack depletion (Homan et al. 2011). Evidence suggests that while the MOD10A1 albedo product exhibits more high-frequency variability than in-situ albedo measurements, it generally tracks seasonal patterns in ground-validated albedo (Stroeve et al. 2006).

We have identified a spatial disparity in predominant drivers of landscape green-up timing that operates on a scale relevant to migratory herbivores. Because green-up is limited by different factors across the Kangerlussuaq-Sisimiut region, ongoing climatic change could dampen or exacerbate intra-regional differences in landscape phenology. Future investigations in landscape phenology and herbivore migration should consider the multiple factors influencing plant growth, and recognize that the magnitude of abiotic effects on plant growth may not be consistent across space. Future work should also seek to identify where and how transitions between dominant abiotic processes emerge. Specifically, by targeting sites at the interface between snow-dominated and temperature-dominated green-up patterns, factorial snowmelt and temperature manipulations may shed light on the unique and interactive effects of these drivers on fine-scale green-up. Aerial photogrammetric measurements of these manipulations could help bridge the gap between plot-scale and satellite-scale observations.

Data availability

All data used in this analysis are publicly available through National Aeronautics and Space Administration (NASA), National Snow and Ice Data Center (NSIDC), and the Greenland Ice Mapping Project (GIMP) and were accessed using Google Earth Engine. Code for accessing, processing, and analyzing the data will be made available on a public Github repository upon acceptance of the manuscript for publication.

Acknowledgements

The authors thank R. Conor Higgins and two anonymous reviewers for helpful comments on an earlier version of this manuscript. Financial support was provided by US National Science Foundation grant PLR1525636 to EP.

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Figures

Fig 1. The Kangerlussuaq-Sisimiut region of west Greenland (indicated by the orange polygon on inset) is bounded on all sides by the Davis Strait, Nordre Isortoq Fjord, the Inland Ice, and the Sukkertoppen ice cap (starting at the west, clockwise). Two villages in the region, Kangerlussuaq and Sisimiut, are designated by an orange inverted triangle and circle, respectively. Data in the satellite image (A) were generated using a median composite of all June imagery collected by Landsat 8 (2013-2018; Image product courtesy of the U.S. Geological Survey). Elevation across the region (B) is variable, with inland terrain lying closer to sea level, while coastal and southern areas are more mountainous.

A. B.

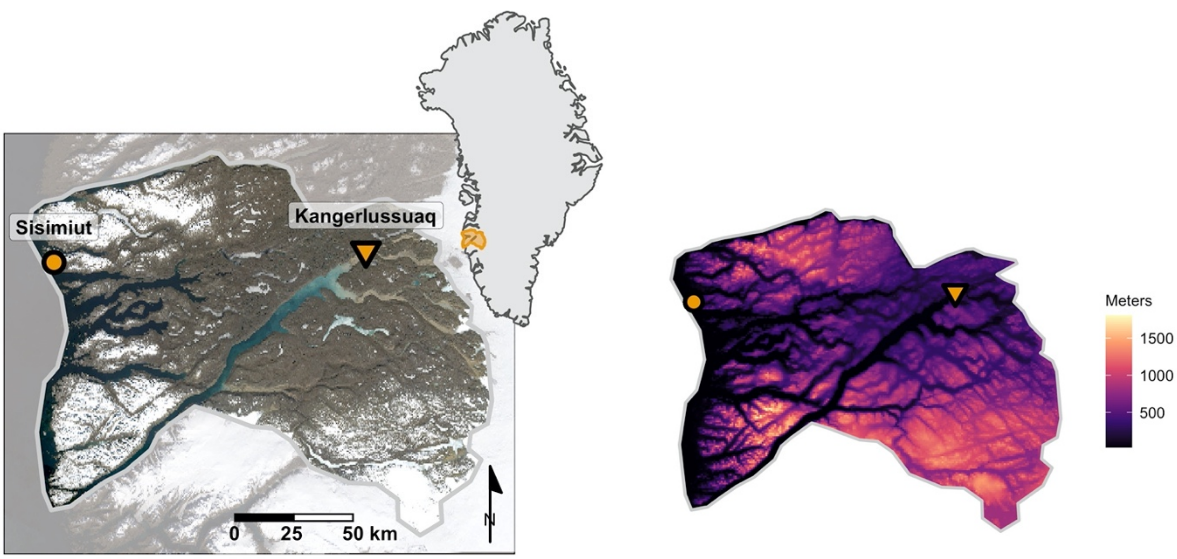


Fig 2. In the Kangerlussuaq-Sisimiut region (2001-2018), the timing of spring plant growth occurs earlier in years with warm springs and early snowmelt. The mean regional temperature during May (in A) is the strongest single month temperature predictor of mean regional green-up timing (β = -3.05 ± 0.58, R^2 = 0.63, $F_{1,16}$ = 27.38, $p < 0.05$). Mean April temperature (not shown) is also significantly associated with regional green-up (April β = -1.13 ± 0.46, $p < 0.05$ as a standalone predictor; when including both April and May as predictors, R^2 = 0.73, $F_{2,15}$ = 19.86, $p < 0.001$). Spring green-up timing always follows snowmelt timing at the regional level (B; β = 0.598 ± 0.12, R^2 = 0.60, $F_{1,16}$ = 23.93, $p < 0.001$; black line indicates the 1:1 relationship).

A. B.

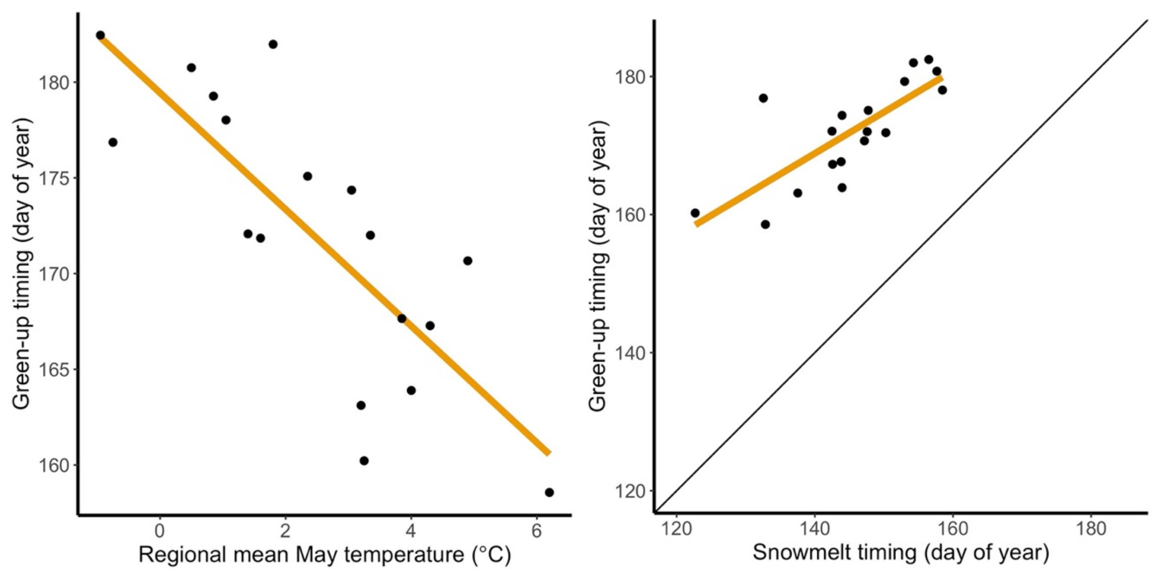


Fig 3. Across the Kangerlussuaq-Sisimiut region (2001-2018), spring green-up timing is delayed with increasing elevation (A) and delayed snowmelt timing (B) at the pixel level. Orange lines are linear regressions with spring green-up timing in response to either of the abiotic predictors (in A, β = 1.48 days/100m elevation; in B, β = 0.53 days/day snowmelt). Black line in B is the 1:1 relationship.

A. B.

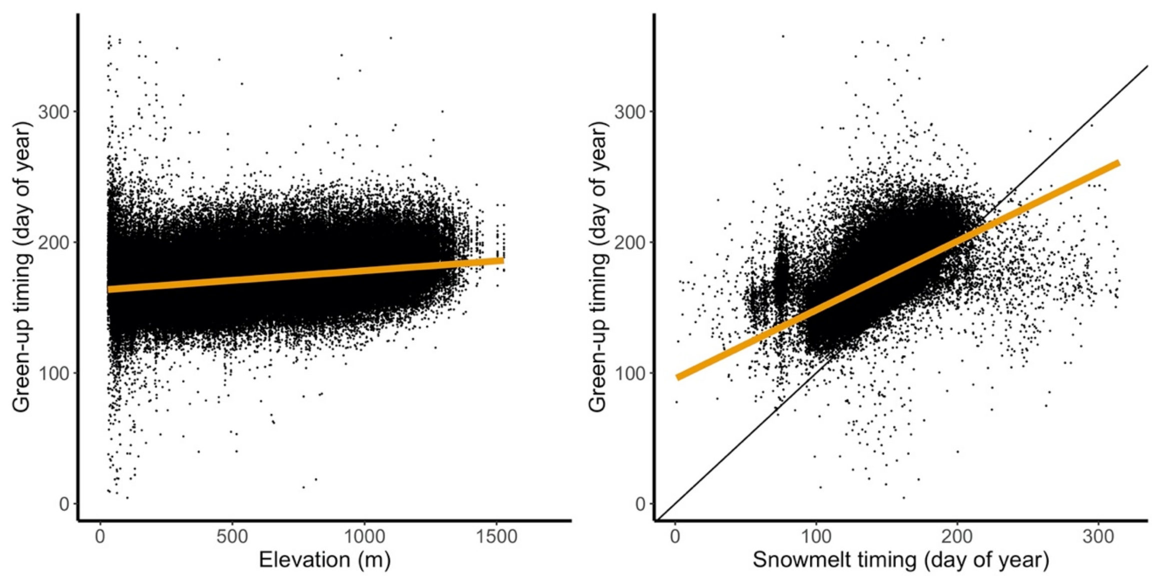
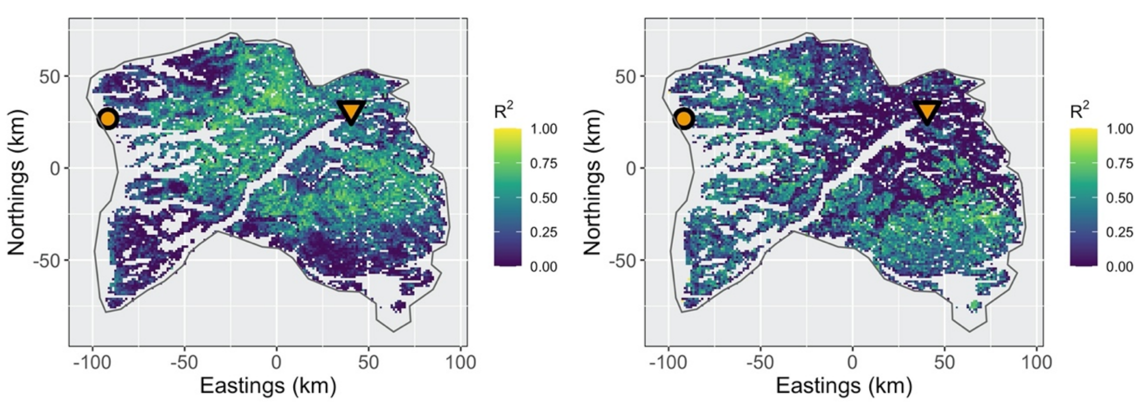


Fig 4. Proportion of interannual variance in green-up timing explained by temperature (A) and snowmelt (B) across the Kangerlussuaq-Sisimiut region (2001-2018). In general, temperature and snowmelt are inversely predictive of green-up timing ($p < 0.001$); areas exhibiting a strong relationship between temperature and green-up timing tend to exhibit a weak relationship between snowmelt timing and green-up timing, and vice versa. Weather stations are denoted with an orange circle (Sisimiut) and triangle (Kangerlussuaq).

A. **B.**



Supplementary figures

Fig S1. Green-up timing regressed against elevation for all MOD13Q1 pixels in the Kangerlussuaq-Sisimiut region, 2001-2018. A positive relationship emerges every year, with delayed green-up at higher elevations.

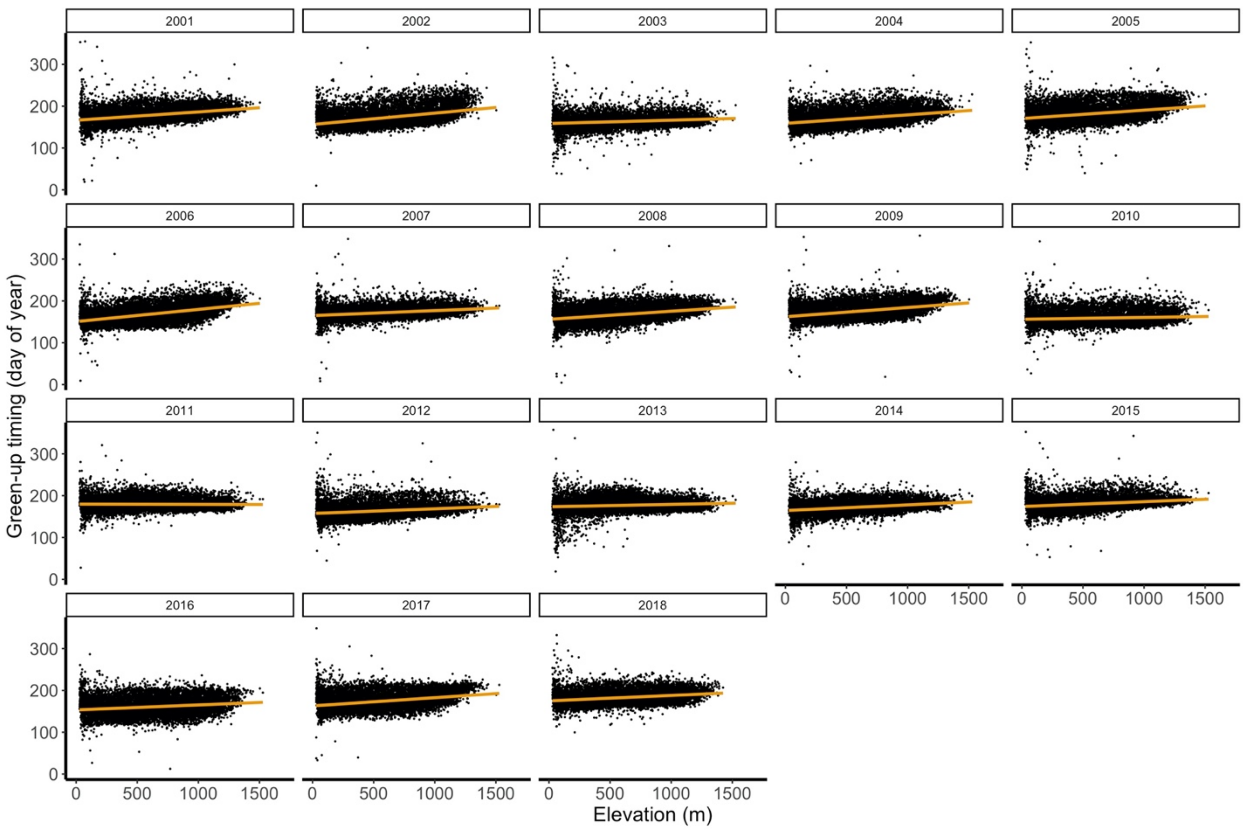


Fig S2. Green-up timing regressed against longitude for all MOD13Q1 pixels in the Kangerlussuaq-Sisimiut region, 2001-2018. A negative relationship emerges every year, with advanced green-up toward the eastern extent of the region.

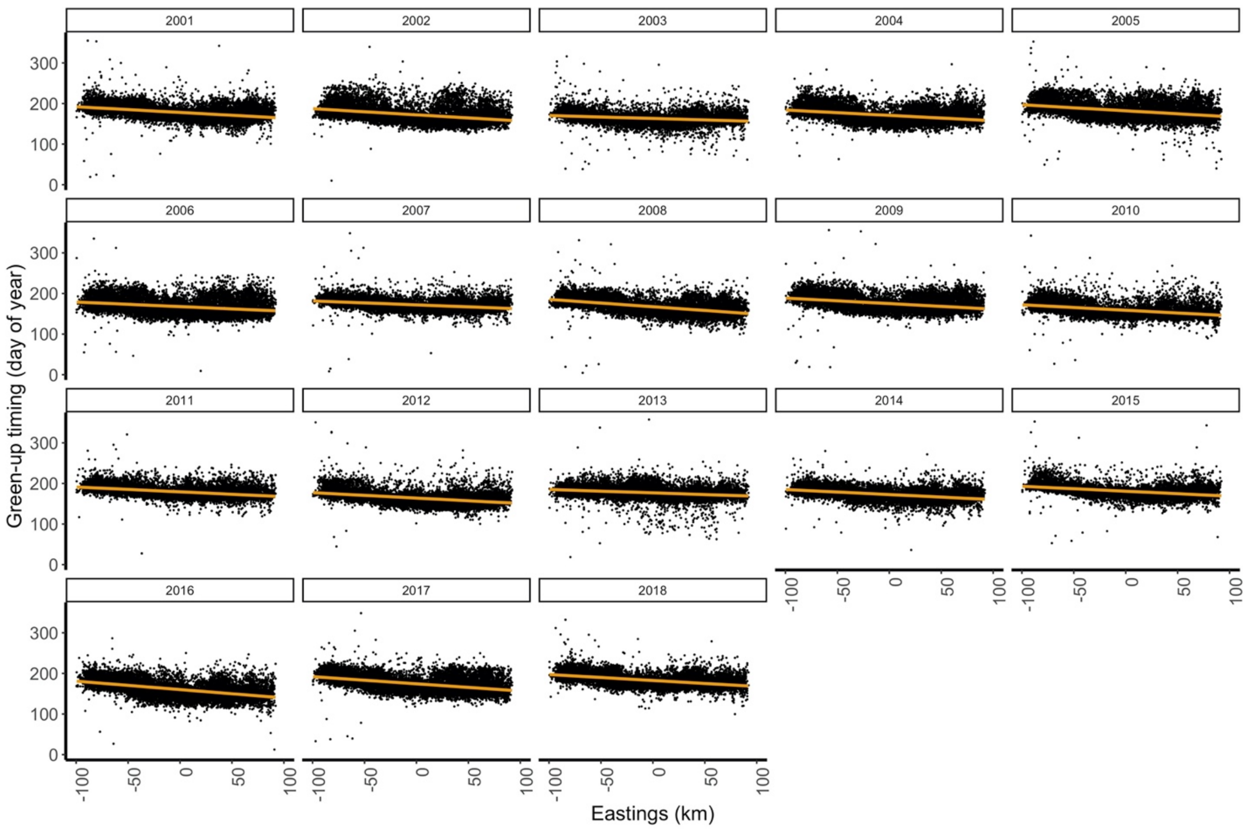


Fig S3. Green-up timing regressed against snowmelt timing for all MOD13Q1 pixels in the Kangerlussuaq-Sisimiut region, 2001-2018. A positive relationship emerges every year, with delayed green-up occurring in areas with delayed snowmelt. The black line in each plot indicates the 1:1 relationship between green-up and snowmelt timing.

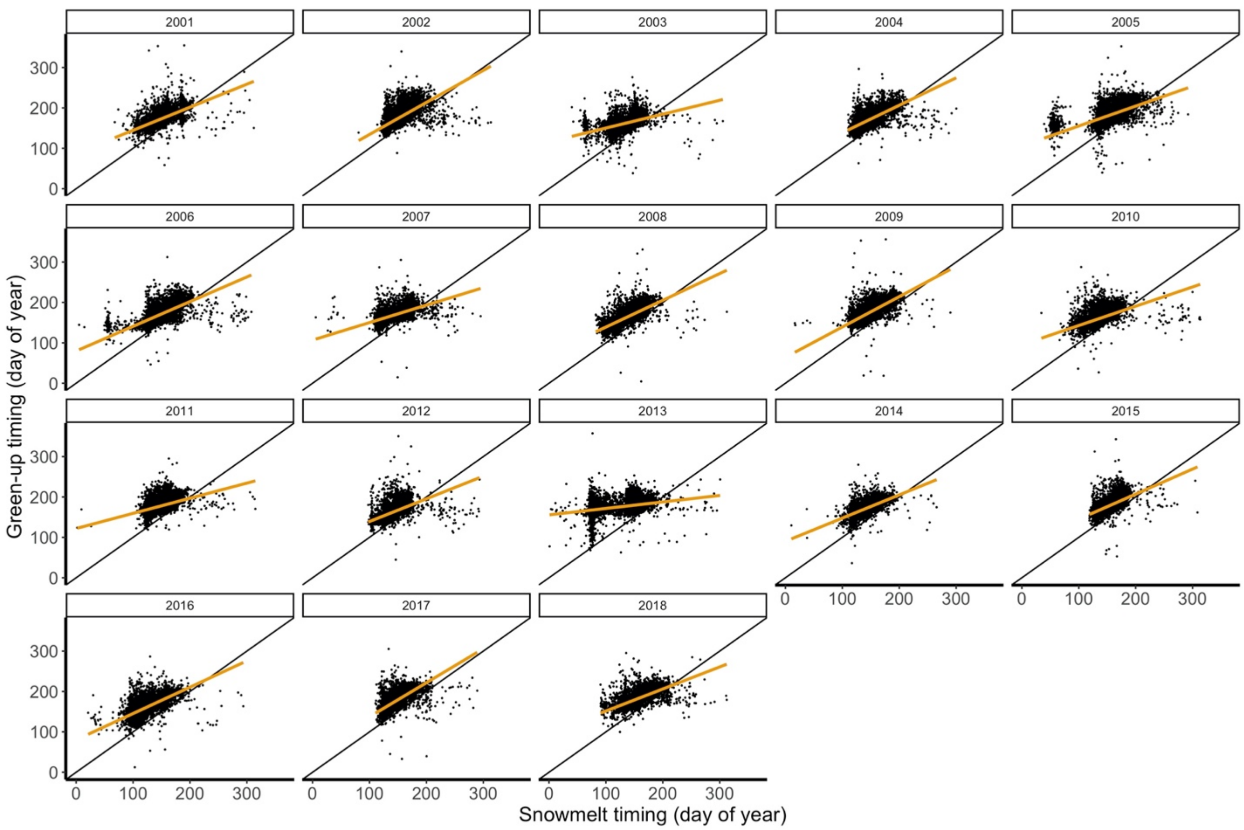


Fig S4. Explanatory power of May temperature at two weather stations for interannual variation in green-up timing across the Kangerlussuaq-Sisimiut region (2001-2018). For both Kangerlussuaq and Sisimiut, temperature explains a greater proportion of interannual variation in green-up timing toward the inland end of the region, nearer the Inland Ice Sheet. Weather stations denoted with an orange circle (Sisimiut) and triangle (Kangerlussuaq).

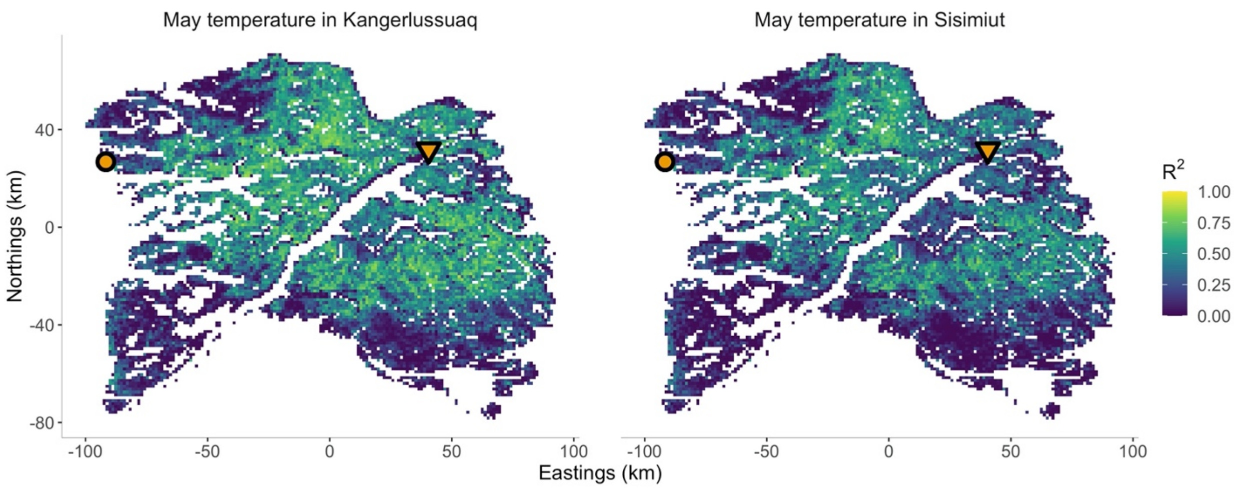


Fig S5. AICc comparison between May temperature in Kangerlussuaq and Sisimiut as predictors of interannual variation in spring green-up timing at the satellite pixel level. When ΔAICc = 0, mean May temperature in Kangerlussuaq and mean May temperature in Sisimiut were equally effective predictors of phenology; when ΔAICc is positive, mean May temperature in Sisimiut was a better predictor of phenology than mean May temperature in Kangerlussuaq; and when ΔAICc is negative mean May temperature in Kangerlussuaq was a better predictor of phenology than mean May temperature in Sisimiut. Solid orange line: linear relationship between ΔAICc and latitude, $\beta = -0.013$, $p < 0.001$. Solid black line: ΔAICc = 0; dashed lines: ΔAICc = ± 2.