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Phenological Dynamics in a Rapidly Warming Arctic Plant-Herbivore System

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Higgins, Robert Conor

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Phenological Dynamics in a Rapidly Warming Arctic Plant-Herbivore System

By

ROBERT CONOR HIGGINS
THESIS

Submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in

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in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Eric Post, Chair

Justine Smith

Richard Karban

Committee in Charge

2022

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Acknowledgements

UC Davis Land Acknowledgement (modified):

“For thousands of years, this land has been the home of Patwin people. Today, there are three federally recognized Patwin tribes: Cachil DeHe Band of Wintun Indians of the Colusa Indian Community, Kletsel Dehe Wintun Nation, and Yocha Dehe Wintun Nation.

The Patwin people have remained committed to the stewardship of this land over many centuries. It has been cherished and protected, as elders have instructed the young through generations. I am honored and grateful to be here today on their traditional lands.”

I want to start off by acknowledging the lands on which I have had the privilege to study and learn. Much of the off-site learning was done in Davis, California. This place has been my home since 2018, and I am grateful to have learned and benefited from all those that came before me. Data for this thesis was collected in Kangerlussuaq, Kalaallit Nunaat (Greenland). I began working at our study site in 2015, and I came to intimately know the place, from the rocks on the ridge above Aajuitsup Tasia to the plants and animals in the study valley. I am humbled to have had the opportunity to take in the beauty and knowledge provided by the land and people there.

The list of people to thank is extensive, and their contributions—both tangible and intangible—is an even longer list which would be impossible to fully cover in these brief acknowledgements. There are a number of people, however, who should not be left unnamed for their part in helping me to complete this thesis and degree. I would like to start by thanking my advisor, Dr. Eric Post. When I was just a spry, curious undergraduate, you gave me the chance to explore the Arctic and get my hands dirty in my first field assistant position. Little did I know that this would lead to further field positions and eventually a graduate degree. Your candidness and vision helped guide me through this process, and for that I am grateful.

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A long-term project of this nature cannot be completed alone. I would like to thank my committee members, Dr. Justine Smith and Dr. Richard Karban, for their feedback in this process. A thank-you is also due to everyone that contributed to this project, particularly Rebecca Walker, Marleen Eikelenboom, and Bradyn O'Connor with whom I worked in the field. You battled opposing weather, relentless mosquitoes, and my boring stories. Thank you. I would also like to thank Kangerlussuaq International Science Support, the 109th Air National Guard, the Davis R Users' Group, and all the members of the Post lab—past and present—for their thoughts and questions.

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Abstract

Changes in phenology, or the recurring timing of life history events, are one of the most apparent ecological effects of climatic warming. In general, plants have begun to emerge earlier as temperatures have warmed. Warming, however, may not be solely responsible for phenological advance observed in plants—biotic factors such as herbivory may also be involved. This study aimed to understand the effect that the presence and timing of herbivory have on plant phenology. Using 9 years of data from an herbivore exclosure experiment near Kangerlussuaq, Greenland, we investigated whether the timing of plant emergence and flowering, as well as the length of time between those two life stages, differed between plants that were exclosed from or exposed to large herbivores, caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*). Our results indicate that plants exposed to herbivory emerged nearly one day earlier and flowered nearly 1.5 days earlier than plants exclosed from herbivory. Additionally, the length of time between emergence and flowering was nearly one day longer for plants inside of herbivore exclosures. We also analyzed whether plant emergence and flowering phenology, as well as the duration of the emergence phase before flowering, were related to the annual timing of herbivore presence at the study site. Results suggested that emergence and flowering occurred earlier in years when caribou and muskox occurred earlier at the study site. Earlier herbivore presence was also associated with a longer duration between emergence and flowering, though this effect was weaker on plots exposed to herbivory suggesting that herbivory may constrain a lengthening of emergence. Our findings lend support to the notion of phenological escape which suggests that plants avoid or minimize tissue loss and its detrimental fitness consequences by accelerating phenophase progression under exposure to herbivory. This study highlights the importance of better understanding the role of biotic interactions in phenological responses to climate change.

Introduction

The timing of recurring life history events in individual organisms, commonly referred to as phenology, is perhaps the most widely studied and readily observable biological climate change response metric (Walther et al. 2002, Piao et al. 2019). Seasonal variation in abiotic limiting factors such as temperature and precipitation, and their interaction, influences the seasonal and annual timing of the onset of spring life-cycle activity in a wide variety of terrestrial biomes (Cleland et al. 2007, Pau et al. 2011). Relatedly, increases in local temperatures and changes in precipitation regimes associated with global climate change have advanced the timing of springtime events such as the onset of migratory arrival in animals or the onset of plant growth across a range of taxa over the past half century (Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2007). Analysis of observational data for plant species spanning the Northern Hemisphere suggests that a 1°C increase in temperature is expected to elicit a 5-6 day advance in leafing and flowering (Wolkovich et al. 2012), and meta-analyses indicate that species that are better able to track warming with phenological advances should have higher fitness (Cleland et al. 2012). The effect of precipitation, in comparison, tends to be biome-specific and highly dependent upon the timing and form of precipitation (Richardson et al. 2013). In the Arctic, for example, plant emergence phenology is largely affected by snowmelt, which in turn is influenced by snowpack and temperature (Høye et al. 2007, Richardson et al. 2013). Global mean surface temperature is currently 1.09°C greater than the preindustrial average (Gulev et al. 2021), and it is projected to increase by another 1-3°C by the end of the century under an intermediate carbon emissions scenario (Lee et al. 2021). Hence, understanding the implications of continued warming for phenological dynamics and the consequences of phenological shifts remains of paramount importance.

Despite this general warming trend, there is considerable regional variation in rates of warming. In the Northern Hemisphere, warming is occurring twice as fast in the Arctic compared to lower latitudes (Serreze and Francis 2006, Cohen et al. 2014, Post et al. 2019), and as such, higher latitudes have been associated with greater rates of phenological advance across multiple taxa (Parmesan 2007, Post et al. 2018). Meta-analyses suggest an advance of springtime phenology by 0.4-0.5 days/decade for each degree increase in latitude in the northern hemisphere (Post et al. 2018). At one particular site in the High Arctic, median phenological advances for springtime events averaged 14.5 days per decade across several plant and animal species (Hoye et al. 2007), far exceeding an average of 2.3-2.8 days per decade across taxa at a global scale (Parmesan 2007). Even under comparable warming conditions at high-latitude sites, plants at colder sites have been observed to emerge and flower earlier compared to those at warmer sites, suggesting that they may be more sensitive to climatic shifts (Prevéy et al. 2017).

The rate and magnitude of warming in the Arctic are presumed to be more important drivers of plant phenology than biotic interactions such as resource competition, pollinator mutualisms, or exploitation by herbivores (Pau et al. 2011). In other systems, however, herbivory may have a greater impact than temperature or precipitation on the timing of phenological events and plant fitness (Tadey 2020). For instance, in addition to structural damage induced by tissue removal, large herbivores can impact rates and seasonal timing of plant growth through trampling and fertilization (van der Wal et al. 2004, van der Wal and Brooker 2004, Mosbacher et al. 2019). Currently, however, there has been comparatively little research into the effects of herbivory on plant phenological dynamics, and results have shown variable influences. In some cases, herbivory (either by invertebrates or manual clipping) has been associated with delays in flowering (Pilson 2000, Freeman et al. 2003, Lemoine et al. 2017), while other work indicates

that invertebrate herbivory has had no effect on the timing of flowering onset (Zhang et al. 2019). Livestock exclusion in a Tibetan alpine meadow revealed an association between herbivore exclusion and advanced plant greening (Zhu et al. 2016), and muskox (*Ovibos moschatus*) exclusion in the High Arctic resulted in earlier peak aboveground biomass at the community level (Mosbacher et al. 2019). These findings suggest that grazing can delay green-up. Conversely, grazing by American bison in temperate grasslands appears to advance and prolong the timing of spring green-up (Geremia et al. 2019).

Based on the varied results from different studies, it remains unclear what impact herbivory may have on plant phenological dynamics associated with warming. The current study aims to shed further light on this relationship. Moreover, we aim to better understand the relationship by analyzing the impact that herbivore *phenology* has on plant phenology. At our study site, there are two large herbivore species present at varying times throughout the year. Caribou, *Rangifer tarandus*—a migratory species in our study system—travel from their winter range on the coast to their summer calving grounds in and adjacent to the study site in the spring (Thing 1984). Muskoxen, *Ovibos moschatus*—a species that remains resident year-round at the study site—undergo partial migration throughout the local area, and the timing of their peak presence varies from year to year (Post 2019). Because these large herbivores can reduce aboveground abundance of woody plants, promote aboveground growth in graminoids, and supply nutrients for plant growth through fecal and urinary inputs (Post and Klein 1996, Post and Pedersen 2008), we hypothesize that interannual variation in the timing of herbivore presence may influence plant phenology. Most studies investigating the relationship between herbivory and plant phenology to date have overlooked effects of the *timing* of such top-down pressure on plant phenology. We address this knowledge gap by investigating the relationship between the

timing of large herbivore presence and the timing of associated plant emergence and flowering. Specifically, we predict that protection against herbivory by large vertebrates will result in altered plant phenology, and furthermore, that the timing of herbivore pressure will influence the phenology of plants exposed to herbivory.

Methods:

Study Site:

The study site is situated between Greenland's Inland Ice to the east and the Davis Strait to the west, and is located approximately 20 kilometers east of Kangerlussuaq, Greenland (67.11°N, 50.34°W) (Thing 1984, Eikelenboom et al. 2021). The site is a core calving ground for caribou, a species that has been the focus of most of our lab's previous research at the site (Thing 1984, Boving and Post 1997, Post et al. 2003, Post and Pedersen 2008, Post and Forchhammer 2008, Post et al. 2008, Kerby and Post 2013a, Kerby and Post 2013b, Eikelenboom et al. 2021). The study area has a continental climate (Boving and Post 1997), and is characterized by mesic tundra comprising mostly mosses, forbs, graminoids, and deciduous shrubs, with dwarf birch (*Betula nana*) and gray willow (*Salix glauca*) being the most common species at the site (Post et al. 2022). Caribou occur at the site from early spring through the calving season until late June, after which adult females, calves, yearlings, and most adult males migrate out of the site toward a winter range approximately 150 km west. In contrast, muskoxen are present at the site year-round, though their peak presence varies annually (Post 2019). Hence, effects of caribou herbivory relate to activity during the early and mid-parts of the annual plant growing season, while effects of muskoxen relate to activity throughout the year.

Plant Phenology Data Collection:

To measure changes in plant phenology, our research team observed and recorded vascular plant phenology on a daily or near-daily basis each growing season between early or mid-May through June on 27 circular plots (0.5m radius) marked at the center by a metal pin. These plots are located at three separate sites separated by 1 - 2 km, and at each site there are 4

plots located within an 800m² woven wire enclosure (established in mid to late June 2002) and 5 plots located outside of each enclosure totaling 12 exclosed plots and 15 grazed plots altogether (Post and Pedersen 2008). Enclosures prevent grazing by caribou, muskoxen, and arctic hares, but they do not exclude invertebrates or birds. There are no rodents at the study site. Exclosed plots have been monitored since 2003, while grazed plots have been monitored in 2002 and from 2009-17. Data used in this analysis cover the period of overlap between observations on exclosed and grazed plots, 2009-17. Upon each visit, we recorded the genera or species present and the phenophase in which each taxon was observed on that date. Phenophases included emergence (i.e. green-up timing in forbs and graminoids and leaf bud opening in shrubs), flower bud formation, blooming (i.e. flowering), and fruiting. For this study, only emergence and flowering data were used as these phenophases were observed most consistently over the study period and because they typically coincide with the caribou calving season. Additionally, in high latitudes, plant nutritional quality is highest near the onset of emergence (Klein 1990, Albon and Langvatn 1992, Post et al. 2003), so the timing of emergence onset and the duration of emergence may be important to associated herbivores. Approximately 20 different species were present across all sites, but only those species that were most consistently represented (described later) were included in analyses (Table 1).

Table 1 Taxa at the study site near Kangerlussuaq, Greenland (2009-17).

Taxon	Cumulative years of emergence data (exclosed, grazed)†	Cumulative years of flowering data (exclosed, grazed)†	Total observations (Exclosed, Grazed)
<i>Betula nana</i> **	9 (9, 9)	9 (9, 9)	201 (101, 100)
<i>Bistorta vivipara</i> *	9 (9, 9)	5 (4, 5)	209 (93, 116)
<i>Calamagrostis</i> sp.	9 (6, 9)	0	45 (22, 23)
<i>Campanula gieseckiana</i> *	9 (9, 9)	3 (3, 2)	214 (99, 115)

<i>Carex sp.</i> **	9 (9, 9)	9 (9, 9)	229 (98, 131)
<i>Cerastium alpinum</i> **	9 (9, 9)	8 (8, 8)	234 (102, 132)
<i>Draba cana</i> **	9 (9, 9)	9 (9, 9)	223 (95, 128)
<i>Equisetum arvense</i> *	9 (9, 9)	1 (1, 1)	117 (49, 68)
<i>Equisetum fluviatile</i> *	8 (8, 8)	0	115 (47, 68)
<i>Festuca brachyphylla</i> *	8 (8, 8)	3 (3, 3)	147 (55, 92)
<i>Kobresia myosuroides</i> **	8 (8, 8)	7 (7, 7)	147 (65, 82)
<i>Luzula sp.</i> **	9 (9, 9)	9 (6, 9)	168 (62, 106)
<i>Poa pratensis</i> **	9 (9, 9)	6 (5, 6)	235 (103, 132)
<i>Potentilla sp.</i>	9 (9, 8)	9 (5, 9)	42 (13, 29)
<i>Pyrola grandiflora</i>	9 (9, 9)	0	40 (13, 27)
<i>Rhododendron sp.</i>	4 (4, 4)	8 (7, 7)	16 (8, 8)
<i>Salix glauca</i> **	9 (9, 9)	7 (6, 6)	188 (97, 91)
<i>Stellaria longipes</i> *	9 (9, 9)	2 (1, 2)	193 (87, 106)
<i>Trisetum sp.</i>	2 (2, 2)	1 (0, 1)	22 (9, 13)
<i>Vaccinium sp.</i>	7 (7, 4)	1 (1, 0)	14 (9, 5)

*Taxa marked with an asterisk were included in emergence analyses.

**Taxa marked with two asterisks were included in emergence, flowering, and emergence duration analyses.

†The number of total years with data for an individual species may be greater than the value for excluded and grazed plots if there are years where there is only data for one plot type. For example, if a species had flowering data on excluded plots in 2010-2015, and it had flowering data on grazed plots in 2011-2015, there would be 7 total years of flowering data, but only 6 years of data for each plot type.

Herbivore Phenology Data Collection:

Observations of caribou and muskoxen were recorded on a daily or near-daily basis during surveys conducted between early to mid-May and late June along fixed routes and from a consistent set of vantage points; numbers of adults and calves of both species were recorded (Eikelenboom et al. 2021). We estimated the annual dates of the onset of arrival and the midpoint of arrival into the study area using daily count data. These were defined, respectively, as the dates on which 5% and 50% of the annual cumulative number of adults was observed. This allowed us to investigate the influence of interannual variation in the timing of early and midseason caribou or muskox presence, and of total large-herbivore presence on plant phenological dynamics in relation to the enclosure treatment as detailed below. To determine the dates of arrival onset and the midpoint of arrival, the annual cumulative animal count for each species was first summed for each sampling period. For analyses using total large-herbivore

presence, the annual cumulative counts for caribou and muskoxen were summed together. Next, we back-calculated the proportion of the yearly cumulative counts observed on each earlier date of that sampling period, and then modeled that data using equation (1) (Post 2019) below to derive estimates of a and b .

$$\Phi = \frac{1}{1+e^{-(a+bX)}} \quad (1)$$

In equation (1), Φ represents the proportion of animals (caribou, muskoxen, or both) observed during the sampling period, and X represents the Julian date on which that proportion was present. The terms a and b quantify the intercept and slope respectively. After obtaining estimates for a and b , equation (1) was solved for X at dates of 5% (onset) and 50% (midpoint) of herbivore presence.

Data selection

We restricted our analyses to a subset of the plant phenology data that included taxa that were consistently represented over the course of the enclosure experiment: *Betula nana*, *Campanula gieseckiana*, *Carex sp.*, *Cerastium alpinum*, *Draba cana*, *Equisetum arvense*, *Equisetum fluviatile*, *Festuca brachyphilla*, *Kobresia myosuroides*, *Luzula sp.*, *Poa pratensis*, *Bistorta vivipara*, and *Salix glauca*, and *Stellaria longpipes*. Taxa were excluded from analyses if they were represented by fewer than 5 years of data for a particular phenophase (emergence or flowering) in either plot type (exclosed or grazed). For example, there were 9 years of emergence data for *Stellaria longpipes*, but only two years for flowering; thus this species was included in emergence analyses, but excluded from flowering analyses. Although there were 5 years of flowering data for *Bistorta vivipara*, it was excluded from flowering analyses because there were fewer than 5 years of data on exclosed plots. Additionally, species with few

observations (<100 over the course of the study) were excluded to prevent excessive influence by an individual plant that may not be generally representative of the species (Table 1).

Analysis of exclosure treatment on plant phenology

We first determined if there were general trends in plant emergence, flowering, or emergence duration (i.e. length of the emergence phenophase, or the time elapsed between emergence and flowering) using linear models. For these models, data were pooled across treatments, plots, and species. The phenological event of interest was the response variable, year and site were included as fixed effects, and species was included as a random intercept.

To examine the effects of the exclosure treatment on emergence and flowering timing, we used linear models with the response variable being the phenological variable of interest: emergence date, flowering date, or emergence duration. Community-level analyses utilized data from all species with sufficient observations and included fixed effects of treatment and site. Year and species were included as random intercepts. Species-level analyses were structured similarly, except the random effect for species was removed and instead, individual models were run for each species.

Analysis of the effect of variation in the timing of large-herbivore presence on plant phenology

Finally, we investigated whether plant phenology was related to variation in the timing of large-herbivore presence at the study site. First, we analyzed the timing of 5% and 50% herbivore presence across the study period. To determine if the timing of herbivore presence shifted over time, a simple linear model was used with the date of animal presence (onset or midpoint of arrival) as the response variable and year as a predictor.

For analyses focusing on effects of herbivore timing on phenology, we used only data from grazed plots. For analyses of effects on emergence timing, only the onset of large herbivore arrival was included because the midpoint of large herbivore arrival occurred after emergence in more than half of all plant observations (Table S1). The emergence model was also rerun with data from either the year of earliest or latest herbivore onset omitted in order to account for effects around the tail of the distribution. For flowering and emergence duration models, however, the dates of the midpoint of herbivore arrival (muskox, caribou, and both) were also investigated along with arrival onset because the midpoint of herbivore presence occurred after emergence in less than half of all flowering observations.

Again, linear mixed models were used for these analyses. The response variable was the Julian date of the phenological variable of interest, and the predictor variable was the date of herbivore arrival onset or the midpoint of arrival. An additional fixed effect was included for site, and for analyses conducted at the plant community level, a random intercept was included for species. AICc scores were then used for model selection: the best model was selected as the most parsimonious with the lowest AICc. A difference in AICc scores of less than two indicates models that fit the data equally well (Anderson 2008). For species-level analyses, the random effect for species was removed and the best model was run individually for each species.

To further investigate the relationship between plant phenology and herbivore timing, we used data from exclosed and grazed plots, pooled across sites, and calculated an annual response ratio corrected for small sample sizes (RR^Δ) for each species and phenophase using equations (2) and (3) below (Lajeunesse 2015).

$$RR = \ln \frac{\textit{Treatment Mean}}{\textit{Control Mean}} \quad (2)$$

$$RR^\Delta = RR + \frac{1}{2} \left[\frac{(SD_T)^2}{N_T \bar{X}_T^2} - \frac{(SD_C)^2}{N_C \bar{X}_C^2} \right] \quad (3)$$

In equation (3), the subscripts T and C refer to treatment and control respectively, SD refers to the standard deviation of the phenological variable under investigation (e.g. emergence date, flowering date, or emergence duration), N refers to the number of samples observed for a species in a given year, and \bar{X} refers to the mean of those samples. A response ratio greater than 0 indicates later plant phenology in exclosed plots compared to grazed plots, and a ratio less than 0 indicates earlier plant phenology in exclosed plots compared to grazed plots.

After calculating corrected response ratios, we used linear regressions similar to those described above to analyze effects of variation in the timing of herbivore presence on differences in plant phenology between grazed and exclosed plots. For each model, RR^Δ was included as the response variable, timing of herbivore presence (muskox, caribou, or total large herbivores) was included as a continuous predictor, and species was included as a random intercept. Models were compared to determine which herbivore species (caribou, muskox, or both) and which date of herbivore presence (5% presence or 50% presence) best fit the data. Because a single annual RR^Δ value was calculated for each plant species, the sample size was small (at most 9 data points per species—one for each year of the study). Hence, models were again compared using AICc to accommodate for small sample sizes. Finally, to determine if results differed by plant species, the best model was rerun individually for each species with the random effect for species removed.

Analyses were conducted in R 4.1.2 using the packages lme4, lmerTest, MuMIn, and emmeans.

Results:

Effect of the herbivore enclosure treatment on plant phenology

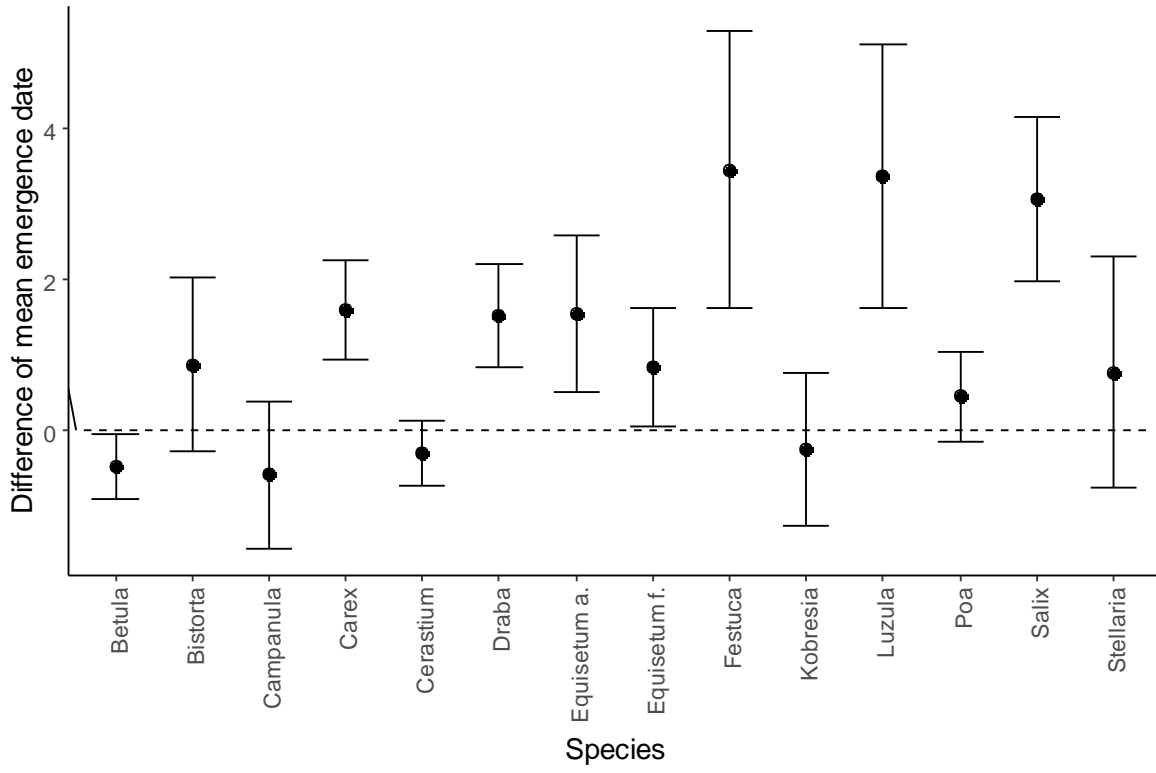
The mean date of plant emergence advanced by approximately 1.80 ± 0.07 days/year ($n = 2612$, $t = -25.70$, $P < 0.01$) over the course of the study when data was pooled across treatments, plots, and plant species. Flowering also advanced by 0.37 ± 0.11 days/year ($n = 898$, $t = -3.45$, $P < 0.01$) when pooled across treatments, plots, and plant species. The duration of the emergence phenophase (time elapsed between emergence and flowering) increased by 1.59 ± 0.10 days/year ($n = 898$, $t = 15.82$, $P < 0.01$) when pooled across treatments, plots, and plant species.

Analyses of emergence timing revealed a positive effect of the enclosure treatment at the community level (0.94 ± 0.27 days, $n = 2612$, $t = 3.47$, $P < 0.01$), indicating that species excluded from herbivory emerged nearly one day later than species exposed to herbivory. At the species level, herbivore exclusion significantly delayed emergence for *Carex sp.*: (1.75 ± 0.60 days, $n = 227$, $t = 2.93$, $P < 0.01$), *Draba cana* (1.63 ± 0.59 days, $n = 219$, $t = 2.76$, $P < 0.01$), and *Salix glauca* (2.32 ± 0.72 days, $n = 188$, $t = 3.22$, $P < 0.01$). Emergence timing was also marginally significantly delayed by herbivore exclusion for *Luzula sp.* (2.41 ± 1.29 days, $n = 167$, $t = 1.88$, $P = 0.06$) and *Festuca brachyphylla* (1.84 ± 1.10 days, $n = 147$, $t = 1.67$, $P = 0.10$). When separate functional groups were considered, herbivore exclusion elicited a 1.26 ± 0.42 day difference in emergence timing for graminoids ($n = 923$, $t = 2.98$, $P < 0.01$), but no effect for forbs (0.63 ± 0.48 days, $n = 859$, $t = 1.32$, $P = 0.19$) or shrubs (0.59 ± 0.45 days, $n = 389$, $t = 1.32$, $P = 0.19$). Overall, herbivore exclusion delayed emergence timing for ten of the fourteen species analyzed, though the results were clearest for the three aforementioned species (Figure 1a).

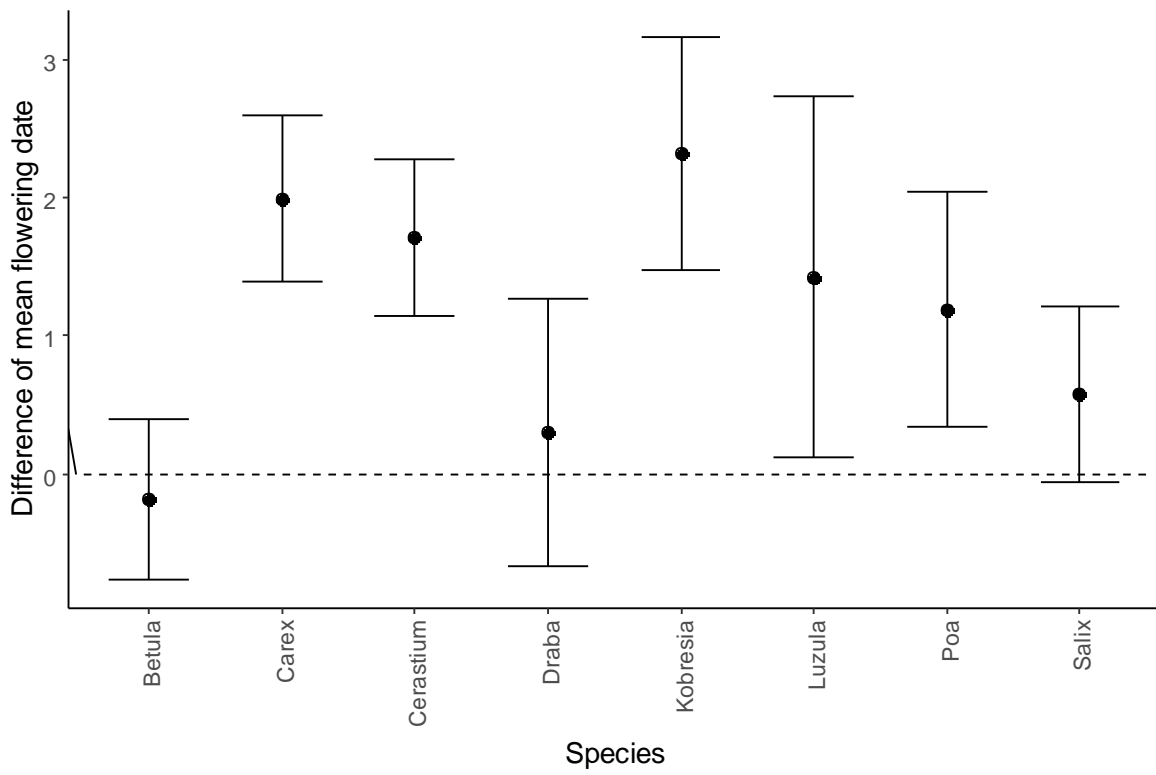
Community flowering was also delayed by herbivore exclusion (1.42 ± 0.35 days, $n = 898$, $t = 4.04$, $P < 0.01$). A modest delay of flowering under herbivore exclusion was evident in seven of eight species analyzed, though it was significant in only two species: *Carex sp.* (2.31 ± 0.47 days, $n = 195$, $t = 4.90$, $P < 0.01$) and *Kobresia myosuroides* (2.31 ± 0.86 days, $n = 86$, $t = 2.69$, $P < 0.01$; Figure 1b). Graminoids were the only functional group with significantly delayed flowering inside of herbivore exclosures (2.13 ± 0.46 days, $n = 387$, $t = 4.62$, $P < 0.01$), though forbs were marginally significantly delayed (1.08 ± 0.60 days, $n = 299$, $t = 1.78$, $P = 0.08$). The exclosure treatment had no effect on shrubs (0.14 ± 0.67 days, $n = 212$, $t = 0.21$, $P = 0.83$).

Analyses also indicated that the duration of the emergence phenophase (i.e. the number of days between emergence and flowering) was prolonged across the community under herbivore exclusion (1.01 ± 0.44 days, $n = 898$, $t = 2.29$, $P = 0.02$). At the species level, emergence was significantly prolonged under herbivore exclusion for *Carex sp.* (1.46 ± 0.55 days, $n = 195$, $t = 2.66$, $P < 0.01$). There also appeared to be a minor negative effect of herbivore exclusion on the duration of emergence for *Salix glauca* (-1.66 ± 0.88 days, $n = 76$, $t = -1.88$, $P = 0.06$) suggesting that leaf bud opening in this species tended to be shorter in exclosed plots compared to grazed ones (Figure 1c). Among functional groups, only graminoids exhibited a significant extension of emergence duration (1.40 ± 0.62 days, $n = 387$, $t = 2.26$, $P = 0.02$), whereas no effect was apparent for forbs (0.64 ± 0.66 days, $n = 299$, $t = 0.96$, $P = 0.34$) or shrubs (-0.04 ± 0.74 days, $n = 212$, $t = -0.05$, $P = 0.96$).

a)



b)



c)

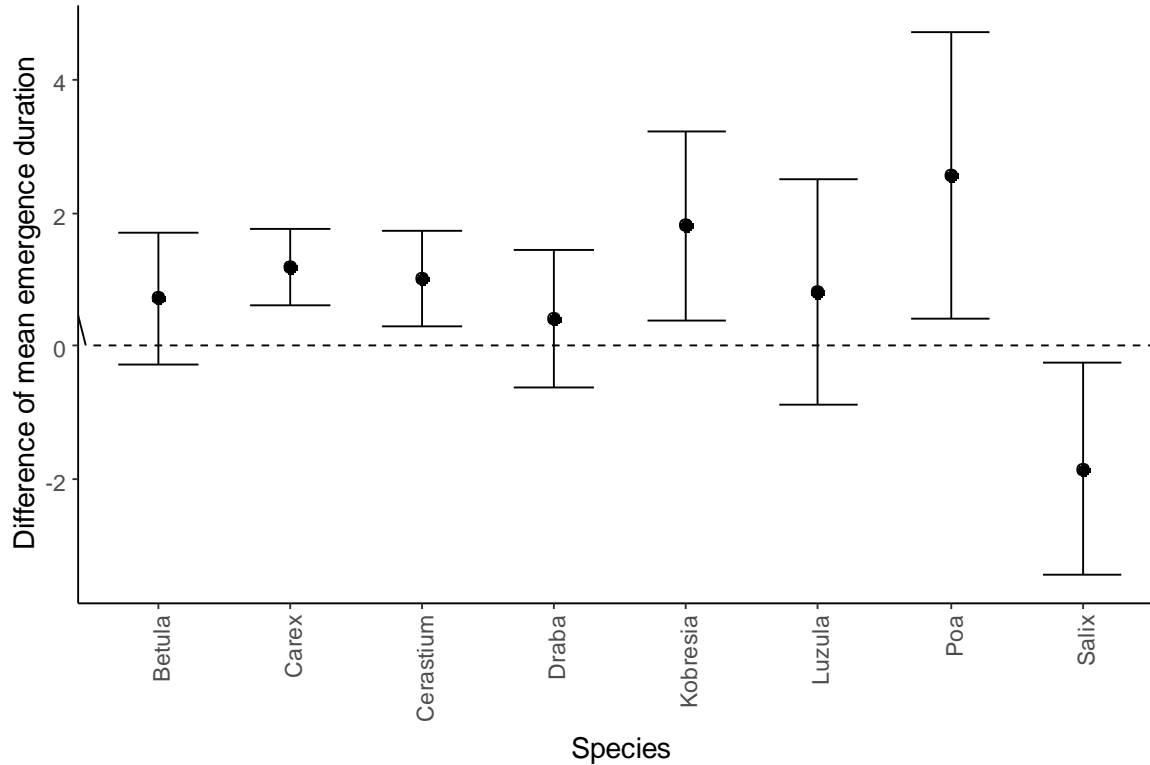


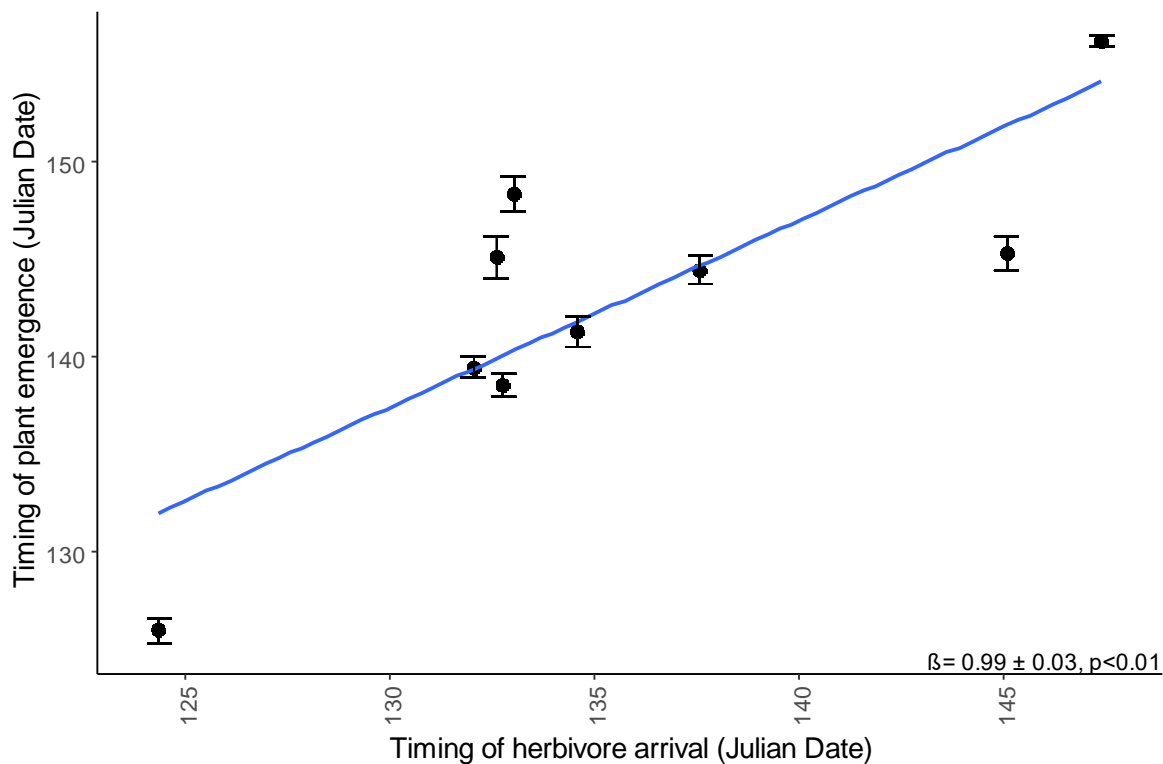
Figure 1: Species level differences (and SE) in mean (a) emergence date, (b) flowering date, and (c) emergence duration between excluded and grazed plots at the Kangerlussuaq, Greenland study site, 2009-17. Values were derived by first calculating each species' annual mean for each phenological variable at each site for both treatments. The annual difference between excluded and grazed means for each species at each site was then calculated, and the mean and SE of these differences across the three sites was then derived. In (a) and (b), values greater than zero (denoted by a dashed line) indicate later phenology in plots excluded from herbivory. In (c), values greater than zero indicate that emergence was prolonged in excluded plots.

Effect of herbivore timing on plant phenology

Over the course of the study, the date of arrival onset for caribou and total herbivores (caribou+muskox) advanced ($\beta_{\text{caribou}} = -2.14$, $n = 9$, $t = -2.59$, $P = 0.04$; $\beta_{\text{caribou+muskox}} = -1.87$, $n = 9$, $t = -2.81$, $P = 0.03$), but the date of muskox onset did not ($\beta_{\text{muskox}} = -0.18$, $n = 9$, $t = -0.28$, $P = 0.79$). The date of the midpoint of arrival did not shift over time for caribou, muskox, or total herbivores ($\beta_{\text{caribou}} = -0.44$, $n = 9$, $t = -0.67$, $P = 0.53$; $\beta_{\text{muskox}} = 0.22$, $n = 9$, $t = 0.54$, $P = 0.61$; $\beta_{\text{caribou+muskox}} = -0.40$, $n = 7$, $t = -0.69$, $P = 0.52$).

The best fit model of community-level plant emergence timing vs. the timing of herbivore presence on grazed plots included the date of total herbivore onset (AICc = 10206.4; Table S2). This model indicated a clear positive effect of early season herbivore presence ($\beta = 0.99 \pm 0.03$, $n = 1462$, $t = 31.46$, $P < 0.01$; Figure 2a), suggesting that in years of earlier herbivore presence, community green-up occurred earlier. When accounting for the first date of data collection, the positive association with the annual timing of herbivore onset remained significant ($\beta = 1.00 \pm 0.04$, $n = 1462$, $t = 28.17$, $P < 0.01$). When the model was rerun with data removed from the year of earliest herbivore presence, there was still a positive relationship between herbivore timing and emergence timing ($\beta = 0.68 \pm 0.04$, $n = 1291$, $t = 17.86$, $P < 0.01$). The same was true when data from the year of latest herbivore presence was removed ($\beta = 0.89 \pm 0.04$, $n = 1330$, $t = 22.23$, $P < 0.01$). A positive relationship between emergence date and total herbivore arrival onset was found for all plant species analyzed (Figure 2b).

a)



b)

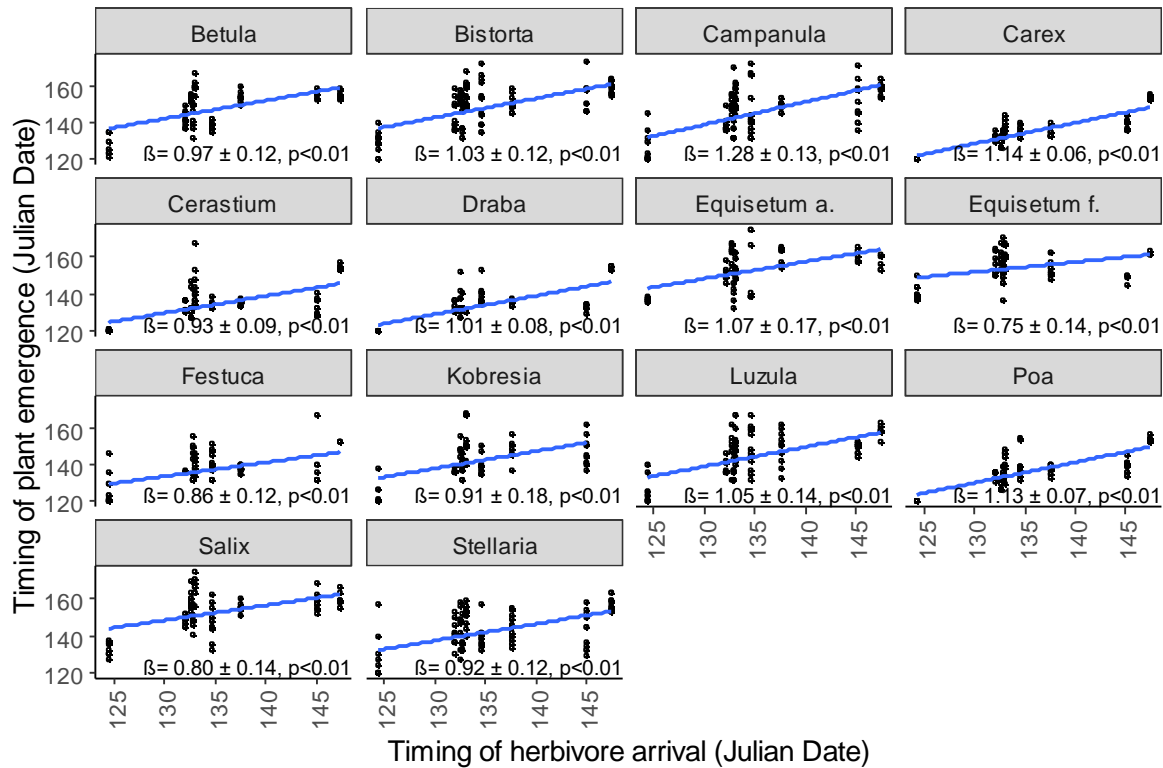
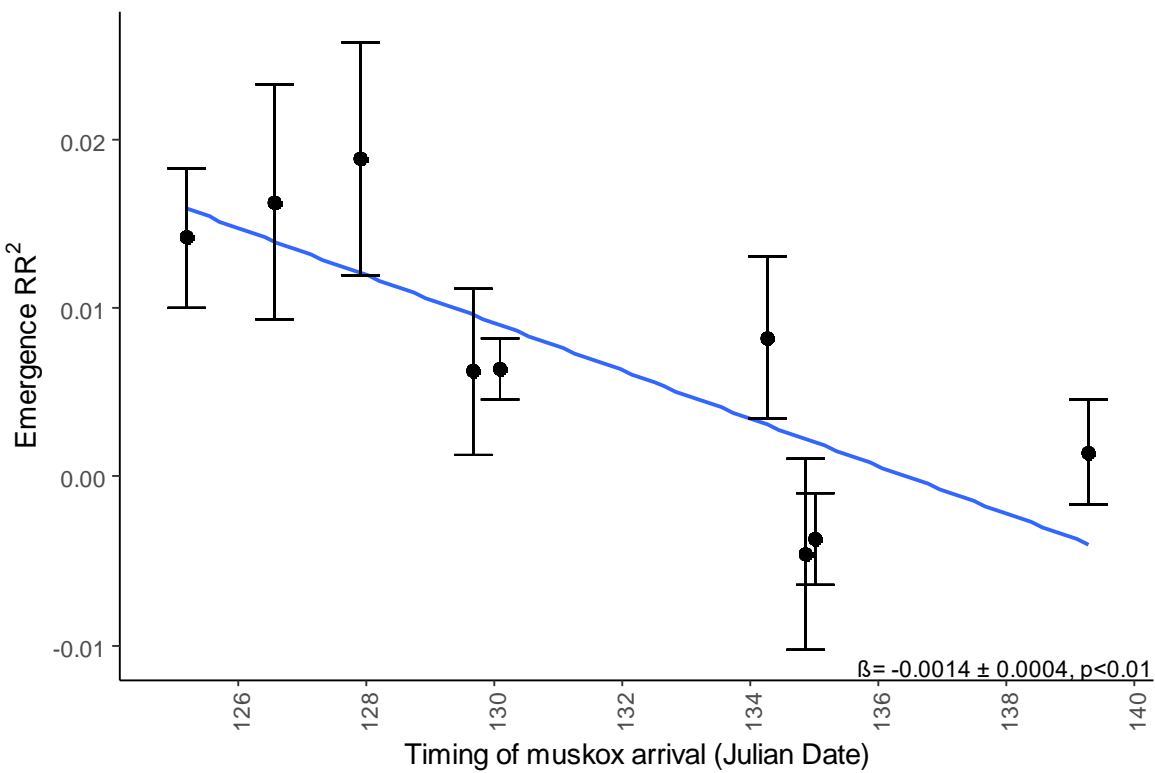


Figure 2: (a) Community-level and (b) species-level emergence timing on grazed plots in relation to the date of total herbivore arrival onset at the Kangerlussuaq, Greenland study site, 2009-17. (a) Annual mean community-level emergence dates (and SE) are compared to the date of total herbivore arrival onset for the same year. (b) Species-specific emergence timing vs. the annual date of total herbivore arrival onset at the study site.

Among models comparing the response ratio of emergence timing (RR^{Δ}) to herbivore timing, the best model included muskox arrival onset ($AIC_c = -607.3$; Table S3). For species pooled across the community, the effect of the enclosure treatment declined with progressively later muskox arrival into the study site (emergence RR^{Δ} vs. date of 5% muskox presence: $\beta = -0.0014 \pm 0.0004$, $n = 123$, $t = -3.87$, $P < 0.01$; Figure 3a). Hence, earlier muskox arrival at the site is associated with a stronger positive effect of the enclosure treatment on community-level emergence timing, indicating earlier community-level emergence under herbivory than under enclosure with earlier muskox arrival. This negative relationship between the enclosure effect

and muskox arrival timing was observed in twelve of fourteen species analyzed, though the result was significant only for *Luzula sp.* ($\beta = -0.0045 \pm 0.0016$, $n = 9$, $t = -2.75$, $P = 0.03$), *Poa pratensis* ($\beta = -0.0015 \pm 0.0005$, $n = 9$, $t = -3.02$, $P = 0.02$), and *Equisetum arvense* ($\beta = -0.0033 \pm 0.0013$, $n = 9$, $t = -2.56$, $P = 0.04$), and marginally significant for *Betula nana* ($\beta = -0.0011 \pm 0.0005$, $n = 9$, $t = -2.03$, $P = 0.08$), and *Bistorta vivipara* ($\beta = -0.0025 \pm 0.0013$, $n = 9$, $t = -1.99$, $P = 0.09$; Figure 3b).

a)



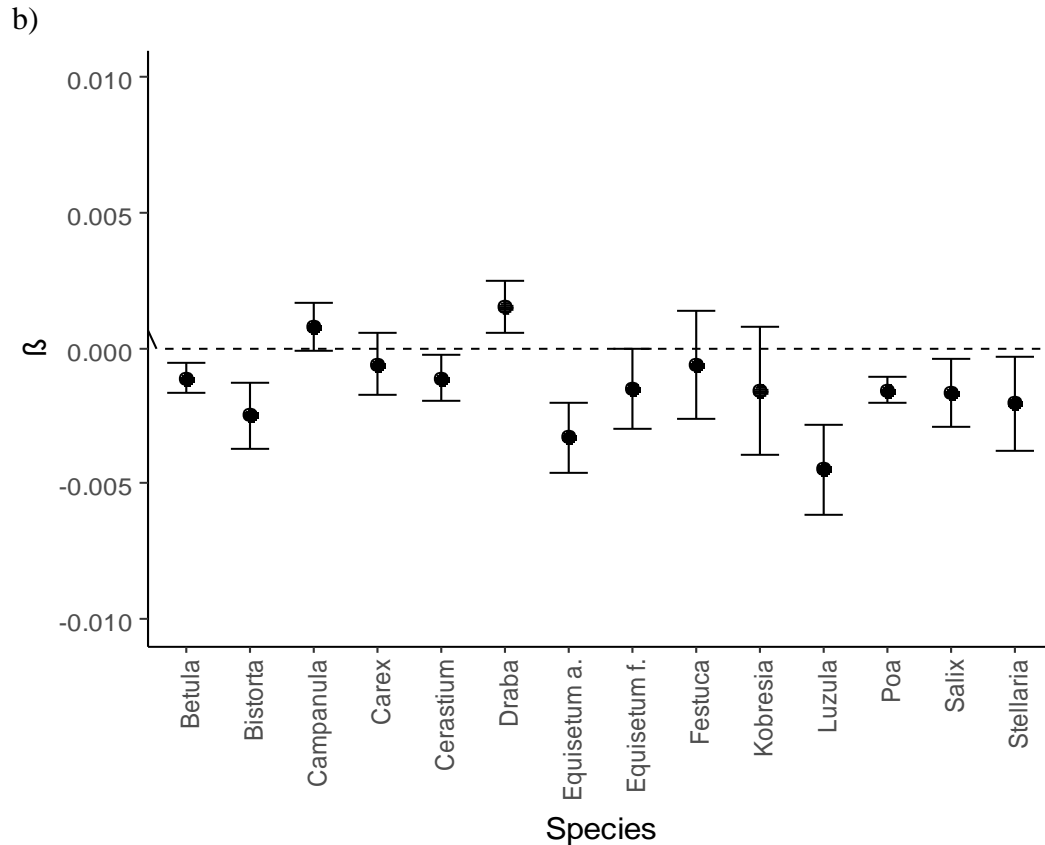
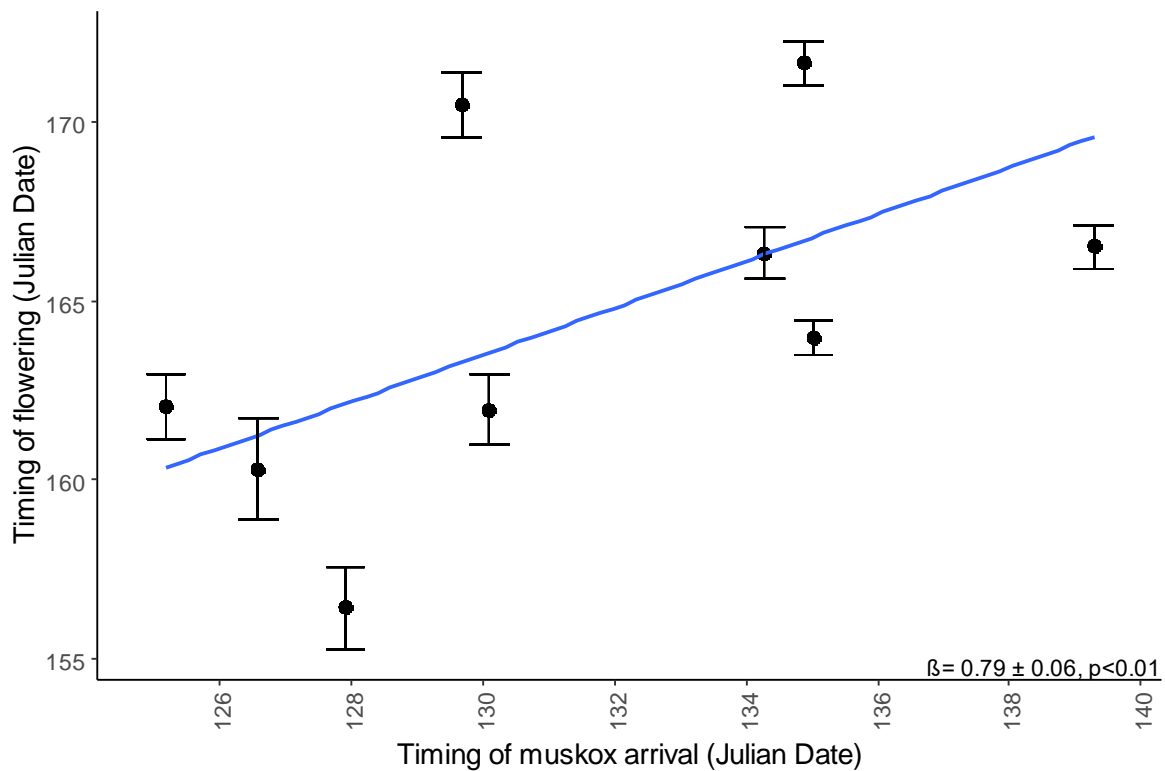


Figure 3: (a) The effect of exclosure treatment on community-level emergence timing, expressed as the response ratio of emergence timing on exclosed vs. grazed plots, plotted against the annual date of onset of muskox arrival at the Kangerlussuaq, Greenland study site, 2009-17. (b) Model-derived slope of emergence RR^{Δ} vs. muskox arrival onset (β) for each species (± 1 SE). Values greater than 0 indicate a positive relationship between the emergence response ratio and muskox arrival onset.

Analyses of the relationships between the timing of flowering on grazed plots and herbivore presence were run separately for the onset of herbivore arrival and the midpoint of herbivore arrival because the two predictor variables were themselves highly correlated (Table S1). The best-fit model among those considering the onset of herbivore arrival included only muskox timing ($AICc = 3551.2$, Table S4). This model indicated a positive relationship between community-level flowering date and muskox onset ($\beta = 0.79 \pm 0.06$, $n = 530$, $t = 12.26$, $P < 0.01$; Figure 4a), and species-specific analyses revealed that this positive relationship occurred for all plant species analyzed except *Poa pratensis* ($\beta = 0.06 \pm 0.34$, $n = 29$, $t = 0.17$, $P = 0.86$; Figure

4b). Among models including the date of midpoint of herbivore presence, the best model included only caribou (AICc = 3492.4, Table S4). This model indicated a positive relationship between flowering date and midseason caribou presence ($\beta = 0.99 \pm 0.07$, $n = 530$, $t = 15.21$, $P < 0.01$), and this positive relationship held for all plant species analyzed except *Poa pratensis* ($\beta = 0.09 \pm 0.23$, $n = 29$, $t = 0.41$, $P = 0.69$).

a)



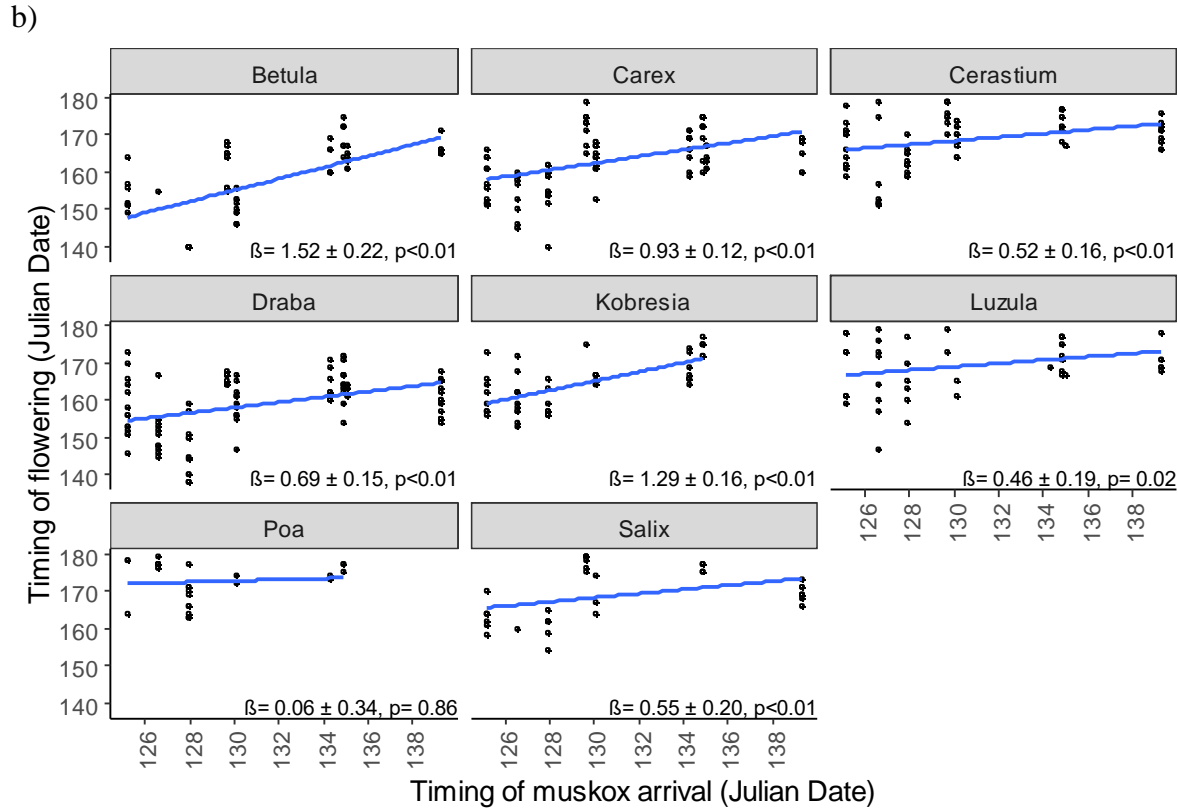


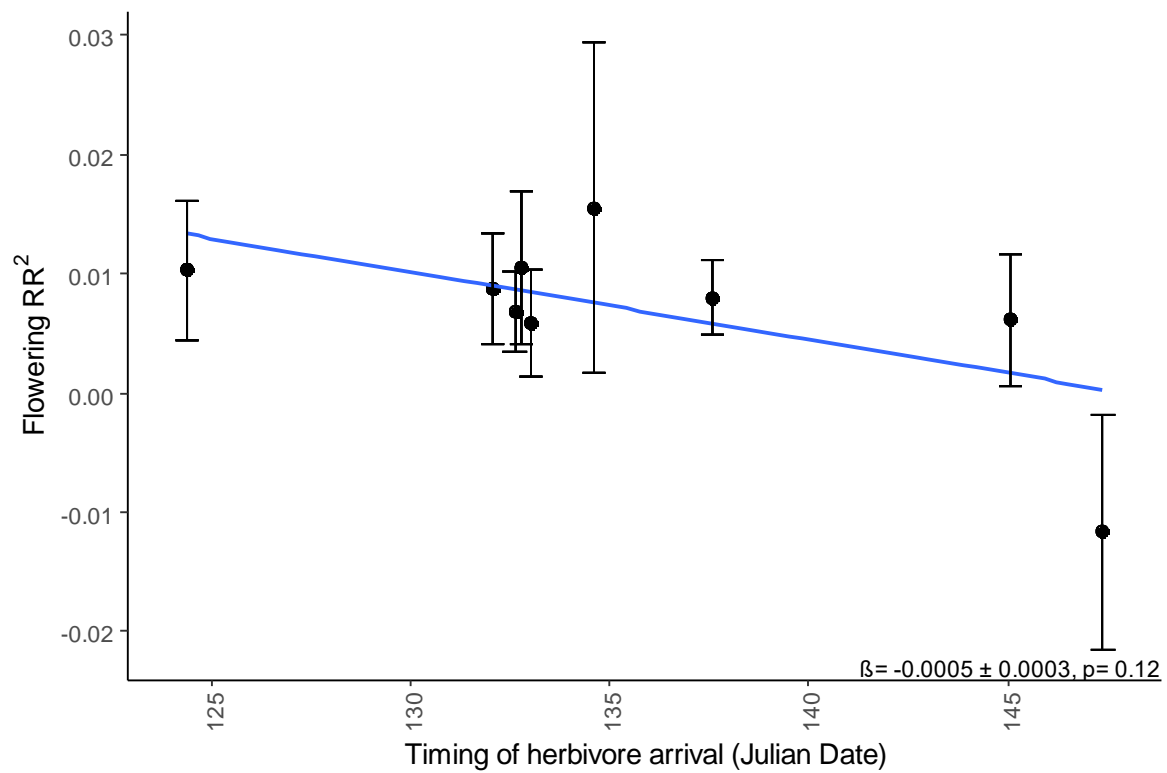
Figure 4: (a) Community-level and (b) species-level flowering timing on grazed plots in relation to the annual date of onset of muskox arrival at the Kangerlussuaq, Greenland study site, 2009-17. Shown in panel (a) are annual mean (± 1 SE) community-level flowering dates plotted against the date of onset of muskox arrival at the study site each year. Shown in panel (b) are species-specific annual flowering dates vs. the dates of onset of arrival of muskoxen at the study site.

Competing models of the enclosure effect on timing of flowering at the community level fit the data equally well (Table S5). Consequently, we selected the model that included the timing of total herbivore onset at the site because it utilized data from both species and thus provided a more holistic view of the impact of herbivory. When considering total herbivore onset, the model indicated a modest, non-significant negative relationship between the enclosure effect on the timing of community-level flowering and the onset of total herbivore arrival into the study site ($\beta = -0.0005 \pm 0.0003$, $n = 49$, $t = -1.60$, $P = 0.12$; Fig. 5a). Similar relationships were disclosed at the species level for *Betula nana* ($\beta = -0.0007 \pm 0.0004$, $n = 8$, $t = -1.76$, $P =$

0.13) and *Kobresia myosuroides* ($\beta = -0.0016 \pm 0.0007$, $n = 6$, $t = -2.42$, $P = 0.07$; Fig 5b).

When the midpoint of herbivore presence was considered, there was no relationship between the enclosure effect on timing of community-level flowering and herbivore timing ($\beta = -0.0006 \pm 0.0005$, $n = 49$, $t = -1.15$, $P = 0.26$). Similar non-significant relationships were observed at the species level for *Carex sp.* ($\beta = -0.0012 \pm 0.0009$, $n = 9$, $t = -1.46$, $P = 0.18$) and *Kobresia myosuroides* ($\beta = -0.0018 \pm 0.0009$, $n = 6$, $t = -1.95$, $P = 0.12$)

a)



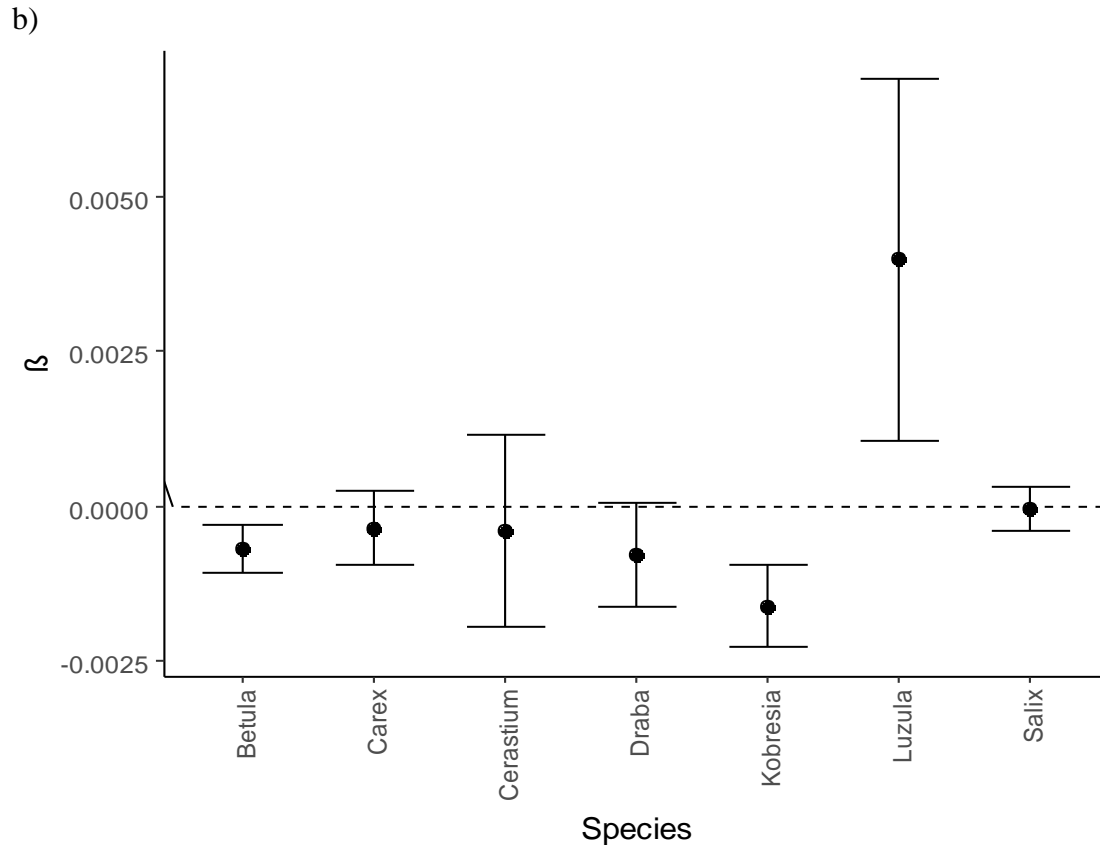
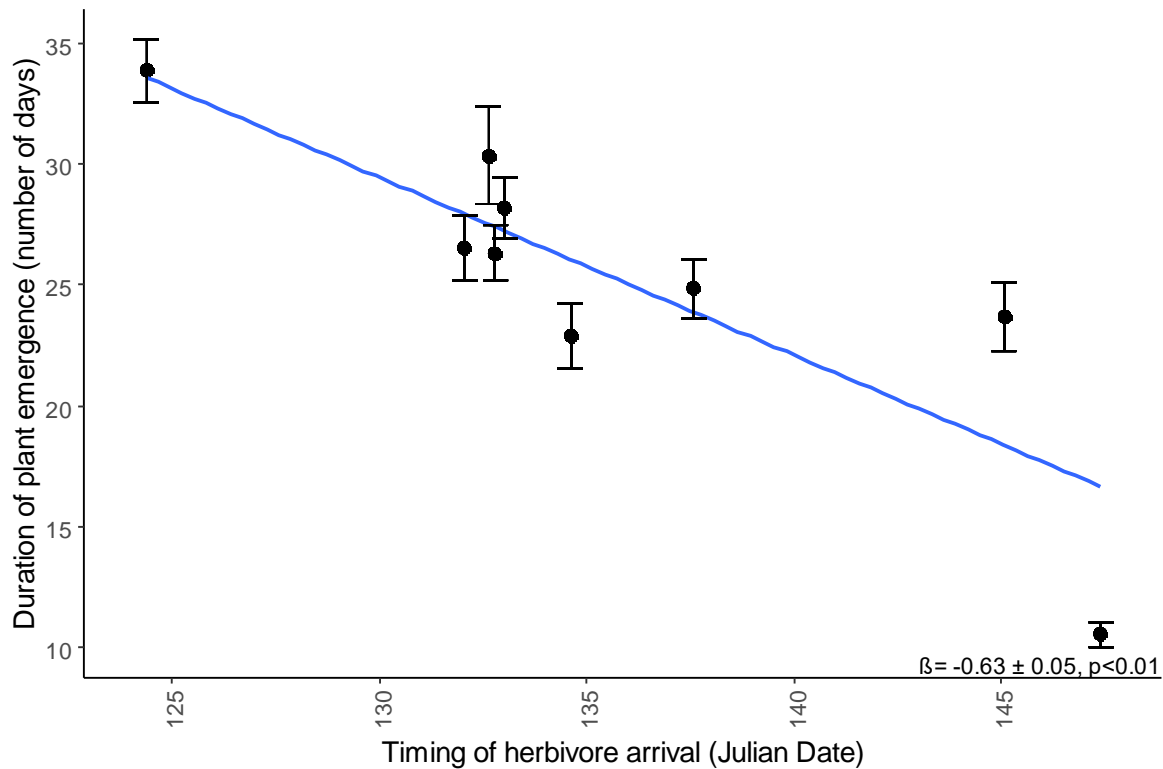


Figure 5: (a) The effect of the exclosure treatment on community-level flowering timing, expressed as the response ratio of flowering timing on exclosed vs. grazed plots, plotted against the annual date of onset of total herbivore arrival at the Kangerlussuaq, Greenland study site, 2009-17. (b) Model-derived slope of flowering RR^A vs. total herbivore arrival onset (β) for each species (± 1 SE). Values greater than 0 indicate a positive relationship between the flowering response ratio and herbivore onset.

The best fit model of community-level emergence duration included the annual date of total herbivore onset of arrival at the study site ($AICc = 3644.2$, Table S6), and indicated a significant negative relationship between emergence duration and herbivore onset ($\beta = -0.63 \pm 0.05$, $n = 530$, $t = -11.59$, $P < 0.01$; Figure 6a). Hence, emergence was prolonged at the community level in years when herbivore timing occurred earlier. At the species level, this negative relationship was observed for all species analyzed as well, though the effect was minor for *Betula nana* ($\beta = -0.14 \pm 0.08$, $n = 69$, $t = -1.88$, $P = 0.06$; Figure 6b). When the midpoint of herbivore arrival was considered, the best model included only muskox ($AICc = 3747.9$, Table

S6), and the model revealed a significant positive relationship between emergence duration and the midpoint of muskox arrival ($\beta = 0.45 \pm 0.12$, $n = 530$, $t = 3.81$, $P < 0.01$). At the species level, a relationship was observed for only *Carex sp.* ($\beta = 1.06 \pm 0.27$, $n = 111$, $t = 3.91$, $P < 0.01$) and *Cerastium alpinum* ($\beta = 0.71 \pm 0.28$, $n = 75$, $t = 2.54$, $P = 0.01$), and a minor effect was observed for *Draba cana* ($\beta = 0.58 \pm 0.30$, $n = 109$, $t = 1.94$, $P = 0.06$)

a)



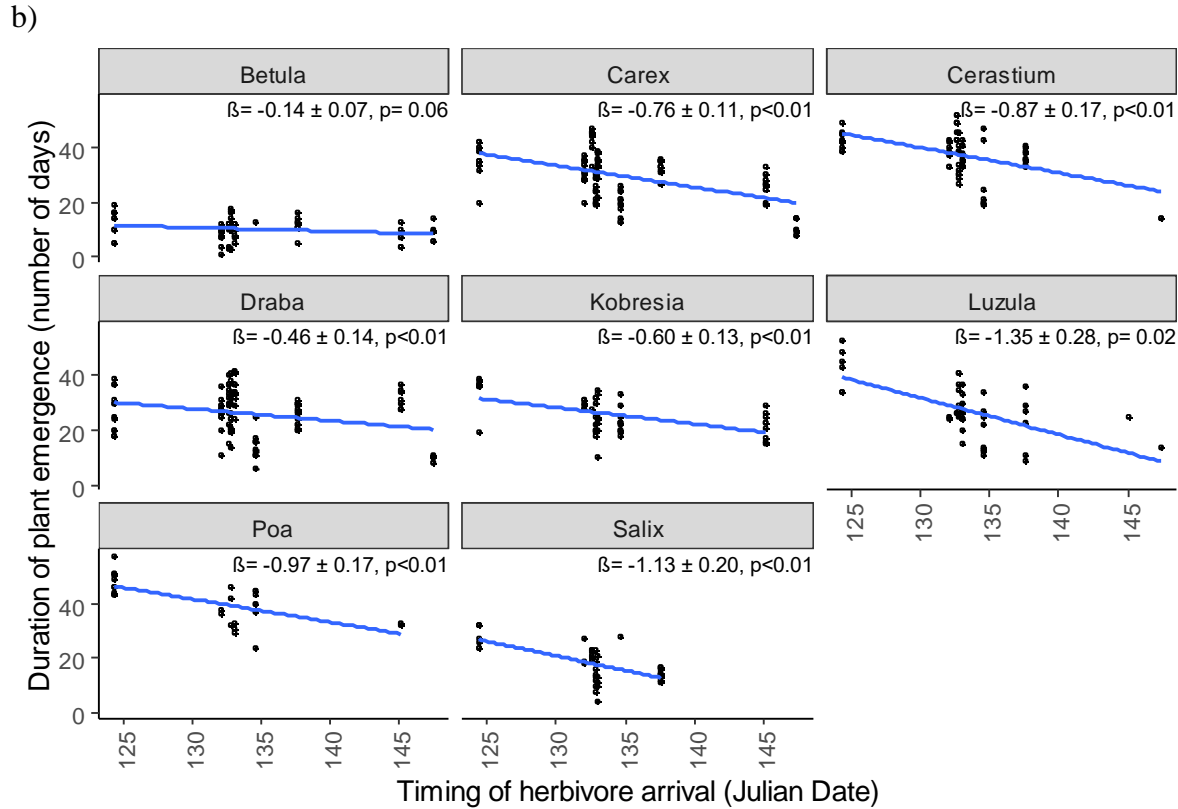
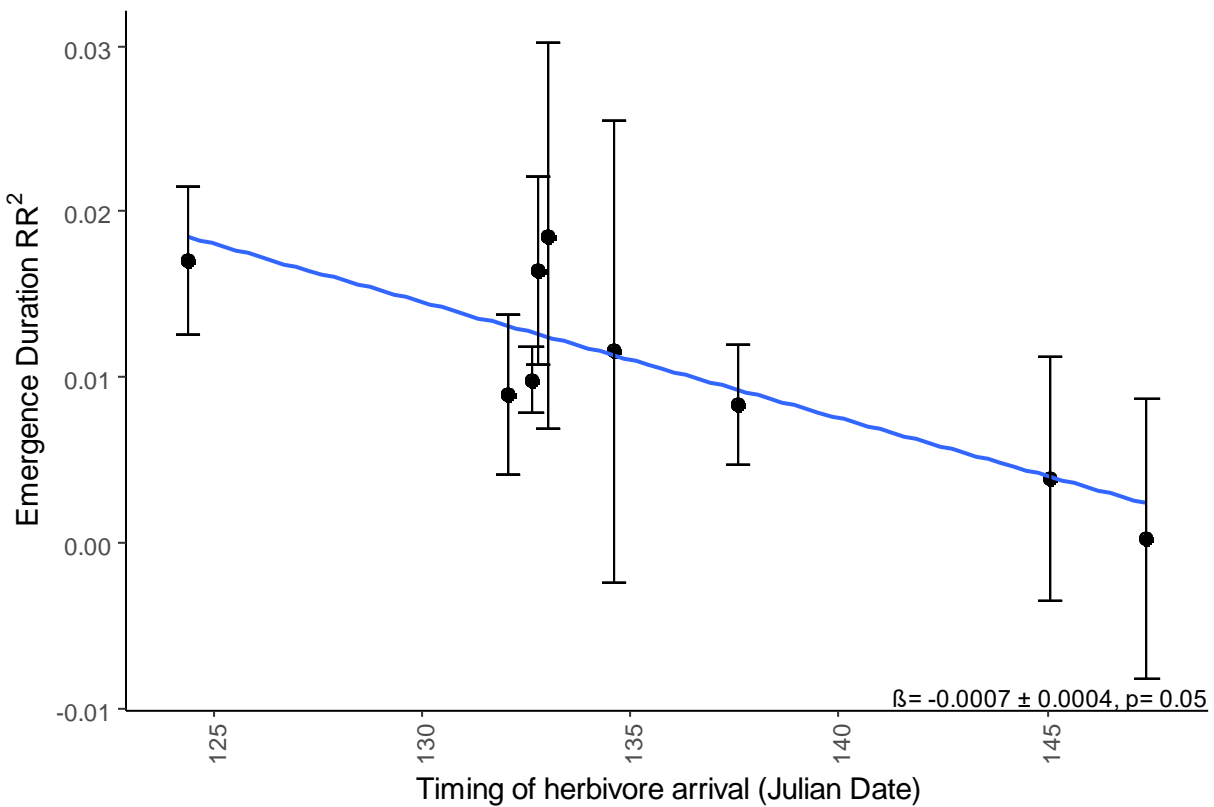


Figure 6: (a) Community-level and (b) species-level emergence duration on grazed plots in relation to the annual date of total herbivore arrival onset at the Kangerlussuaq, Greenland study site, 2009-17. (a) Annual mean community-level emergence duration (and SE) are compared to the date of total herbivore onset for the same year. (b) Species-specific emergence duration vs. the annual date of total herbivore presence at the study site.

Caribou and total herbivore arrival onset models analyzing the enclosure effect on community-level emergence duration fit the data equally well. Again, the model with total herbivore arrival onset was selected because it utilized data from both species, thus providing a broader assessment of the impact of herbivory (AICc = -234.1, Table S7). This model revealed a minor negative relation to the annual onset of total herbivore arrival at the site ($\beta = -0.0007 \pm 0.0004$, $n = 49$, $t = -1.98$, $P = 0.05$; Figure 7a). This suggests that community-level emergence is prolonged by enclosure from herbivory in years when herbivores arrive earlier at the study site. In other words, even though early arrival of herbivores tends to prolong emergence on grazed plots, this extension of the green-up period is still shorter than that on plots excluded from

herbivory. At the species level, this association was significant only for *Betula nana* ($\beta = -0.0016 \pm 0.0005$, $n = 8$, $t = -2.73$, $P = 0.03$, Figure 7b), suggesting that the community-level pattern was driven primarily by this species. All models utilizing the midpoint of herbivore arrival fit the data equally well, so the model including total herbivore arrival midpoint was selected because it used the most herbivore data (AICc = -232.9; Tables S7). There was no relationship between the exclosure effect and the midpoint of total herbivore arrival ($\beta = -0.0008 \pm 0.0006$, $n = 49$, $t = -1.27$, $P = 0.21$). At the species level, there was a significant negative relationship for *Luzula sp.* ($\beta = -0.0079 \pm 0.0016$, $n = 5$, $t = -4.96$, $P = 0.02$), a minor negative relationship for *Betula nana* ($\beta = -0.0025 \pm 0.0012$, $n = 8$, $t = -2.04$, $P = 0.09$), and a minor positive relationship for *Draba cana* ($\beta = 0.0017 \pm 0.0009$, $n = 9$, $t = 1.96$, $P = 0.09$)

a)



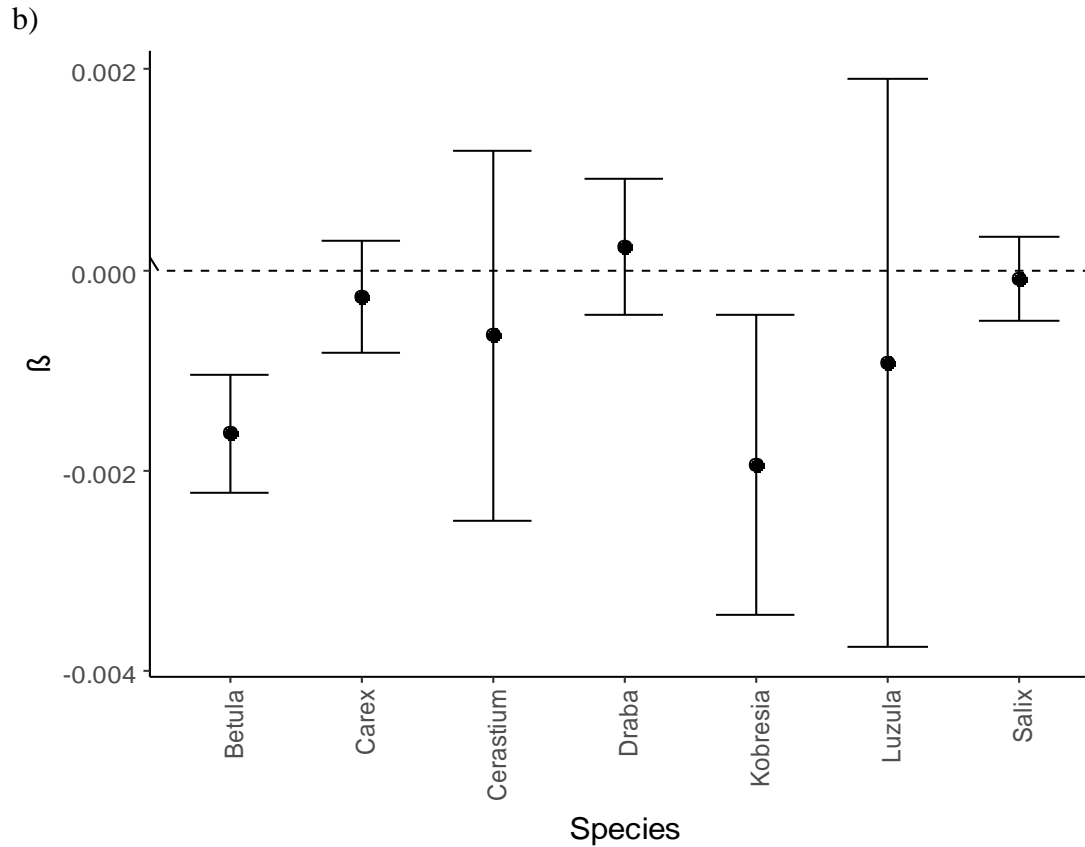


Figure 7: (a) The effect of exclosure treatment on community-level emergence duration, expressed as the response ratio of emergence duration on exclosed vs. grazed plots, plotted against the annual date of onset of total herbivore arrival at the Kangerlussuaq, Greenland study site, 2009-17. (b) Model-derived slope of emergence duration RR^A vs. total herbivore arrival onset (β) for each species (± 1 SE). Values greater than 0 indicate a positive relationship between the emergence duration response ratio and herbivore onset.

Discussion

Over the course of this study, plant community-level emergence and flowering advanced by 1.80 ± 0.07 days/year and 0.37 ± 0.11 days/year respectively across both grazed and exclosed plots, while the annual duration of emergence increased by 1.59 ± 0.10 days/year. These results lend support to previous findings at our study site indicating an advance of the midpoint of community-level emergence by approximately 1.6 days/year from 2002-2011 and 2002-2013 (Kerby and Post 2013, Post et al. 2016). This advance has been previously linked to an indirect effect of sea ice decline in the Arctic (Kerby and Post 2013, Post et al. 2016), so considering that Northern Hemisphere sea ice has continued to decline in the past decade (Post et al. 2019), it is likely still associated with the advance our results indicated. The present analyses, however, were intended to illuminate whether large herbivore presence and timing of arrival into the study site influenced plant phenological dynamics in addition to effects of changing abiotic conditions.

Our results indicated that emergence and flowering occurred earlier under exposure to herbivory than under herbivore exclusion. According to the phenological escape hypothesis, advancement of vulnerable phenophases by plants exposed to herbivory may confer fitness advantages by reducing the risk of tissue loss that might otherwise reduce reproductive success (Feeny 1977, Agrawal 2000). Empirical tests of this hypothesis are limited, however, particularly in relation to herbivory by large vertebrate herbivores. In one common garden experiment, *Solidago velutina* plants taken from sites with introduced elk, *Cervus canadensis nelson*, flowered earlier than those taken from elk-free sites, suggesting that advanced flowering may be selected for under pressure from herbivory (Smith et al. 2015). At our site, plant community emergence occurred nearly one day earlier on average when exposed to herbivore pressure, and flowering occurred more than one day earlier. Though directional shifts such as

this may be selected for if plants with advanced phenology are able to reduce seed or flower loss, shifting is also dependent upon the relative abundance and timing of associated herbivores (Pilson 2000). Hence, an additional aim of this study was to better understand the relationship between the seasonal timing of herbivory and plant phenology.

The timing of grazing can impact plant community productivity, particularly if the rate of plant seasonal development and growth progresses nonlinearly (Staver et al. 2021). One study of native pasture management in Australia demonstrated that withholding grazing until plants reached an optimal growth stage resulted in a greater density of perennial grasses (Nie and Zollinger 2012). We found that the timing of herbivore presence is positively associated with both emergence timing and flowering timing. Hence, while changing background abiotic conditions appear to be driving an advance in plant emergence timing at the study site (Kerby and Post 2013, Post et al. 2016), herbivory and herbivore arrival phenology have both apparently hastened this advance on grazed plots. When the onset of herbivore arrival into the study site (i.e. the annual date of 5% herbivore presence) was relatively early, plant emergence and flowering occurred earlier on grazed plots. Moreover, the negative relationship between the treatment response ratios (RR^A) and the timing of herbivore presence suggested that in years of earlier herbivore arrival timing, plant phenological advance was more pronounced under herbivory than under herbivore exclosure. Together, these findings lend additional support to the phenological escape hypothesis.

In addition to the date of emergence and flowering, we investigated whether the duration of emergence was related to herbivory. Time can be viewed as a limited resource which organisms use for different developmental stages: while an individual is allocating time to one phenophase, it is not allocating that time to another (Post 2019). Hence, the allocation of time to

different developmental phases may indicate developmental priorities. Resource availability and the presence of abiotic and biotic stressors such as herbivory may influence how time is allocated (Rathcke and Lacey 1985, Elzinga et al. 2007, Post 2019). Our results indicated that the plant community on plots exposed to herbivory tended to experience a shorter annual period of emergence by approximately one day compared to that on plots exclosed from herbivores. Though earlier onset of herbivore arrival at the study site was associated with an extension of emergence duration under herbivory, response ratio analyses indicated that this extension was less on grazed plots than on exclosed plots. Hence, while changing abiotic conditions are associated with a longer growing season (Post et al. 2019), this latter finding suggests that an earlier herbivore presence is constraining a lengthening of the emergence phenophase. Because prolonged exposure to herbivory can result in greater risk of destruction or loss of plant tissue (Maschinski 2001), plants that develop earlier and more rapidly may minimize damage compared to those with static, delayed, or slower development.

The plant species included in the present study were representative of three functional groups: graminoids, forbs, and deciduous shrubs. Graminoids and deciduous shrubs are the primary forage for muskoxen, with graminoids composing most of the winter diet and willow most of the summer diet (Thing et al. 1987, Forchhammer and Boomsma 1995). Graminoids also constitute the largest portion of caribou summer diet at the study site, while shrubs and forbs are consumed to a lesser extent (Thing 1984). Our results indicate that only graminoids exhibited a significantly earlier emergence and flowering under herbivory compared to under herbivore exclosure, and it was the only functional group with significantly shorter emergence in grazed plots. Moreover, the only genus that exhibited comparatively advanced phenology (emergence and flowering) *and* shortened emergence under herbivory, *Carex sp.*, is a graminoid

that is preferred forage of both muskoxen (Mulder 1999) and caribou (Thing 1984). Given that graminoids are preferred by both large herbivore species at the study site, the relatively advanced phenology associated with herbivore exposure may be further evidence of phenological escape.

Though we aimed to capture the first date of each phenophase for all species, there were years when plants were already emergent upon arrival to the study site. As described earlier, steps were taken to account for the timing of annual sampling, and the direction of trends remained the same after doing so. Hence, emergence data utilized in this study were conservative and may actually underestimate the effect of grazing on plant phenology. The present study utilized only one derived herbivore timing date per year (e.g. the date of onset of herbivore arrival or the midpoint of arrival), but multiple corresponding plant phenological dates. Future analyses could benefit by incorporating a Bayesian framework to account for differences in the number of corresponding herbivore and plant data points. Nonlinear models could be considered as well; because frost can damage early-emerging plants, plant phenology cannot advance indefinitely (Iler et al. 2013). Data on the date of snowmelt would be useful to incorporate into models, especially if grazing affects snowmelt through trampling and foraging, though previous work in Zackenberg, Greenland has demonstrated that exclosures do not affect snowmelt dates (Mosbacher et al. 2019). Moreover, future work should aim to include mutualistic influences (e.g. pollinators) since mutualist interactions and antagonistic pressures (e.g. herbivory) may present opposing pressure on plant timing (Elzinga et al. 2007).

The effect of herbivory on plant community composition and biomass is already well-documented at our study site (Post and Pedersen 2008, Post et al. 2021, Post et al. 2022). This is the first time, however, that we have related plant phenology to the presence and timing of herbivore pressure. In addition to tolerating and resisting damage, plants can respond to

herbivory by avoidance (Agrawal 2000), but such studies are limited, and many focus on herbivory by invertebrates. The findings of this study indicate that earlier plant emergence and flowering is associated with herbivore presence and timing. Our results emphasize the importance of further research into the role of herbivory on plant phenology, especially with the current backdrop of climatically induced phenological advance.

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Appendix:

Supplementary Table S1: Herbivore timing descriptive statistics and cross-correlations at the study site in Kangerlussuaq, Greenland 2009-17. Animal timing was compared to the date of emergence observations to assess whether it was appropriate to include animal timing as a predictor of emergence timing in models. Of all plant observations included in analyses, emergence occurred after the back-calculated date of muskox arrival onset in 1179/1462 cases. 966/1462 emergence observations are after the date of caribou onset, and 1007/1462 observations are after total herbivore onset. 295/1462 emergence observations occurred after the midpoint of muskox arrival, 154/1462 observations occurred after the midpoint of caribou arrival, and 167/1462 observations occurred after the midpoint of total herbivore arrival. Because the majority of emergence observations occurred before the midpoint of herbivore arrival, the date of midpoint of arrival was not included in emergence analyses. All 530 flowering observations occurred after the date of muskox, caribou, and total herbivore arrival onset. 475/530 flowering observations are after the date of the midpoint of muskox arrival, 439/530 are after the midpoint of caribou arrival, and 441/530 are after the midpoint of total herbivore arrival. Hence, the dates of both the onset and midpoint of herbivore arrival were utilized for flowering and emergence duration analyses.

Year	First muskox observation	First caribou observation	Date of 5% muskox presence	Date of 5% caribou presence	Date of 5% total herbivore presence	First plant emergence observation
2009	132	132	135	148	147	153
2010	132	132	127	136	135	132
2011	128	126	134	151	145	128
2012	132	131	125	134	133	132
2013	132	125	135	133	133	130
2014	134	133	139	137	138	133
2015	119	116	130	134	133	127
2016	120	119	128	123	124	120
2017	136	136	130	133	132	130

Herbivore timing cross-correlations at the study site in Kangerlussuaq, Greenland 2009-17.

Variable	Caribou 5% presence	Muskox 5% presence	Total herbivore 5% presence	Caribou 50% presence	Muskox 50% presence
Caribou 5% presence	-				
Muskox 5% presence	0.50	-			
Total herbivore 5% presence	0.98	0.56	-		

Caribou 50% presence	0.77	0.65	0.70	-	
Muskox 50% presence	0.27	0.72	0.26	0.56	-
Total herbivore 50% presence	0.77	0.66	0.71	0.99	0.61

Supplementary Table S2: Comparison of models of community-level plant emergence timing vs. the timing of herbivore presence. Models were structured as follows: Emergence date ~ Predictor variable (see below) + Site + (1|species). Data included only species in grazed plots at the study site in Kangerlussuaq, Greenland 2009-17.

Species	Predictor variables	AICc score	R^2 value (marginal, conditional)
Caribou	5% presence	10617.3	0.25, 0.59
Muskox	5% presence	10314.4	0.15, 0.49
Total herbivores	5% presence	10206.4	0.28, 0.62

Supplementary Table S3: Comparison of models of emergence RR^{Δ} vs. herbivore timing at the study site in Kangerlussuaq, Greenland 2009-17. Models were structured as follows: $RR^{\Delta}_{\text{emergence}} \sim$ Predictor variable (see below) + (1|species).

Species	Predictor variables	AICc score	R^2 value (marginal, conditional)
Caribou	5% presence	-596.6	0.04, 0.05
Muskox	5% presence	-607.3	0.11, 0.13
Total herbivores	5% presence	-598.6	0.05, 0.06

Supplementary Table S4: Comparison of models of community-level plant flower timing vs. the timing of herbivore presence. Models were structured as follows: Flowering date ~ Predictor variable (see below) + Site + (1|species). Data included only species in grazed plots at the study site in Kangerlussuaq, Greenland 2009-17.

Species	Predictor variables	AICc score	R^2 value (marginal, conditional)
Caribou	5% presence	3592.2	0.14, 0.47
Muskox	5% presence	3551.2	0.18, 0.51
Total herbivores	5% presence	3594.3	0.14, 0.47
Caribou	50% presence	3492.4	0.22, 0.58
Muskox	50% presence	3647.3	0.08, 0.38

Total herbivores	50% presence	3524.3	0.20, 0.55
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Supplementary Table S5: Comparison of models of flowering RR^{Δ} vs. herbivore timing at the study site in Kangerlussuaq, Greenland 2009-17. Models were structured as follows: $RR^{\Delta}_{\text{flowering}} \sim \text{Predictor variable (see below)} + (1|\text{species})$.

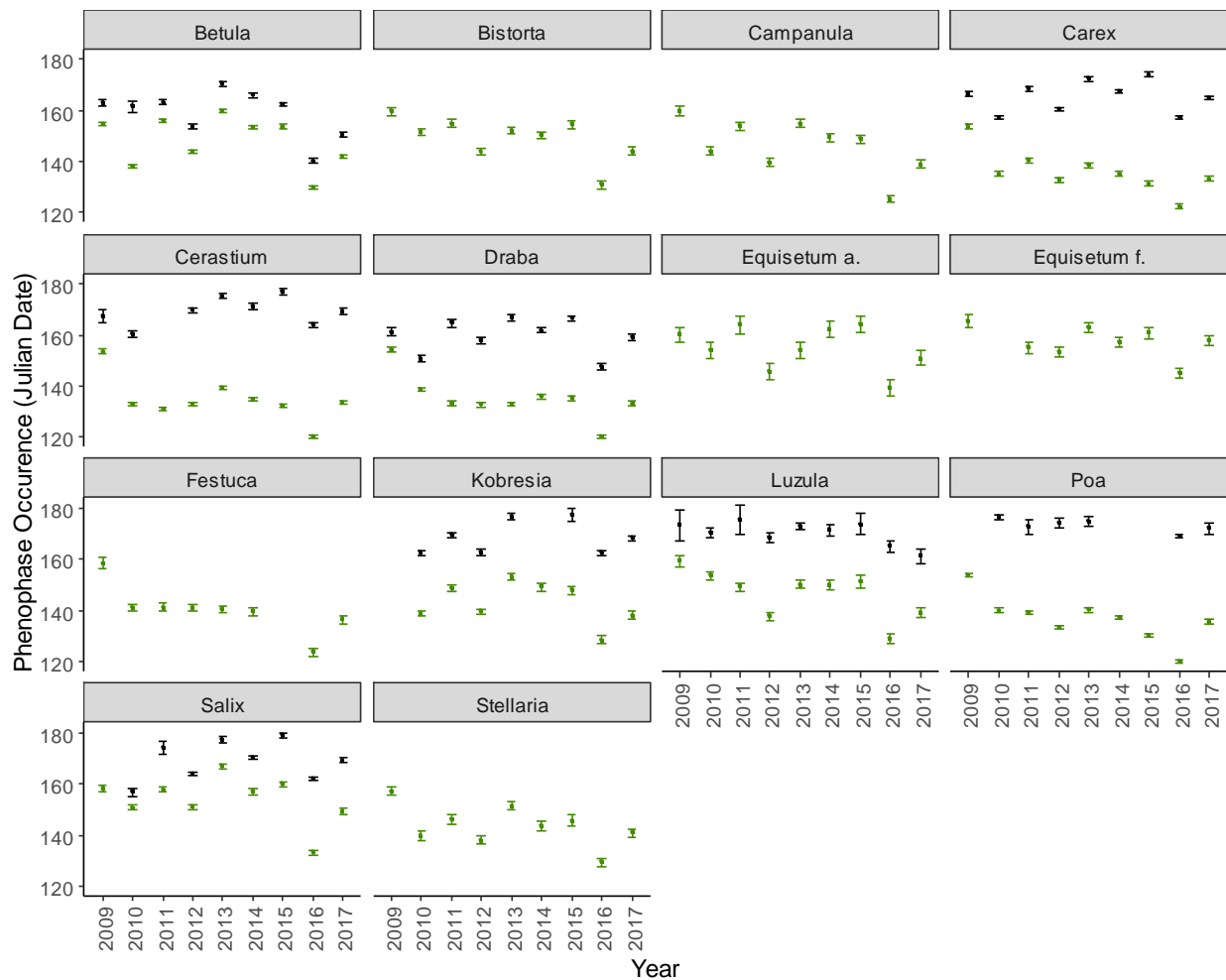
Species	Predictor variables	AICc score	R^2 value (marginal ,conditional)
Caribou	5% presence	-241.3	0.04, 0.19
Muskox	5% presence	-241.8	0.03, 0.17
Total herbivores	5% presence	-242.2	0.05, 0.20
Caribou	50% presence	-241.6	0.02, 0.17
Muskox	50% presence	-241.3	0.00, 0.15
Total herbivores	50% presence	-241.9	0.02, 0.17

Supplementary Table S6: Comparison of models of community-level plant emergence duration vs. the timing of herbivore presence. Models were structured as follows: Emergence duration \sim Predictor variable (see below) + Site + (1|species). Data included only species in grazed plots at the Kangerlussuaq study site, 2009-17.

Species	Predictor variables	AICc score	R^2 value (marginal ,conditional)
Caribou	5% presence	3664.3	0.09, 0.64
Muskox	5% presence	3760.8	0.01, 0.58
Total herbivores	5% presence	3644.2	0.10, 0.65
Caribou	50% presence	3761.0	0.01, 0.58
Muskox	50% presence	3747.9	0.02, 0.60
Total herbivores	50% presence	3761.2	0.01, 0.58

Supplementary Table S7: Comparison of models of emergence duration RR^{Δ} vs. herbivore arrival onset at the study site in Kangerlussuaq, Greenland 2009-17. Models were structured as follows: $RR^{\Delta}_{\text{emergence_duration}} \sim \text{Predictor variable (see below)} + (1|\text{species})$. Though AICc values of caribou and total herbivore onset are similar, total herbivore onset was selected as the best fit model because it incorporates more data.

Species	Predictor variables	AICc score	R ² value (marginal ,conditional)
Caribou	5% presence	-233.9	0.07, 0.26
Muskox	5% presence	-231.7	0.01, 0.18
Total herbivores	5% presence	-234.1	0.06, 0.26
Caribou	50% presence	-232.6	0.03, 0.21
Muskox	50% presence	-232.5	0.01, 0.08
Total herbivores	50% presence	-232.9	0.03, 0.21



Supplementary Figure S1: Yearly mean emergence date and SE of each species for which emergence analyses were conducted (green). Yearly mean flowering date and SE of each species for which flowering analyses were conducted (black). The duration of the emergence phenophase is the vertical distance between the emergence date and the flowering date. These mean values are derived from grazed and exclosed data pooled together. Data encompasses the years of the exclosure experiment near Kangerlussuaq, Greenland from 2009-2017.