

# Large herbivores link plant phenology and abundance in Arctic tundra

Eric Post <sup>a,\*</sup>, R. Conor Higgins<sup>a,b</sup>, Pernille Sporon Bøving <sup>a</sup>, Christian John <sup>c</sup>, Mason Post <sup>d</sup> and Jeffrey T. Kerby <sup>e</sup>

<sup>a</sup>Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA

<sup>b</sup>Yolo County Resource Conservation District, 221 W Court St., Suite 1, Woodland, CA 95695, USA

<sup>c</sup>Marine Science Institute, University of California, Santa Barbara, CA 93106, USA

<sup>d</sup>Brotman Baty Institute, University of Washington, Seattle, WA 98195, USA

<sup>e</sup>Department of Geography, Scott Polar Research Institute, University of Cambridge, Cambridge CB2 1ER, United Kingdom

\*To whom correspondence should be addressed: Email: [post@ucdavis.edu](mailto:post@ucdavis.edu)

Edited By Jiahua Zhang

## Abstract

Plant phenological dynamics have been well studied in relation to abiotic conditions and climate change, but comparatively poorly studied in relation to herbivory. In contrast, plant abundance dynamics have been well studied in relation to abiotic conditions and herbivory, but poorly studied in relation to phenology. Consequently, the contribution of herbivory to plant phenological dynamics and therefrom to plant abundance dynamics remains obscure. We conducted a 9-year herbivore exclusion experiment to investigate whether herbivory might link plant phenological and abundance dynamics in arctic tundra. From 2009 to 2017, we monitored annual green-up timing and abundance of nine plant taxa, including deciduous shrubs, forbs, and graminoids, on plots that were either grazed or experimentally excluded from herbivory by caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*). In 62% of cases, green-up occurred earlier under herbivory, and in 75% of cases abundance was greater under herbivory, compared to green-up and abundance under herbivore exclusion. Moreover, taxa that responded to herbivory with earlier green-up also had comparatively greater abundance later in the growing season. Conversely, taxa that responded to herbivory with delayed green-up exhibited comparatively lower abundance later in the growing season. Hence, well-documented influences of large herbivores on plant abundance and community composition in arctic tundra may relate, at least to some extent, to influences of herbivory on plant phenology. We recommend that ongoing and future assessments of the contribution of herbivores to plant abundance and community responses to climate change, especially in the Arctic, should also consider impacts of herbivores on plant phenology.

**Keywords:** *Betula nana*, community dynamics, herbivory, plant phenology

## Significance Statement

Life-history theory predicts that plant performance, including abundance, should be sensitive to the timing of growth onset. Studies of factors influencing plant performance have long considered both abiotic conditions and herbivory to be important, while studies of the timing of growth onset have focused almost exclusively on abiotic conditions. Hence, whether plant abundance responses to herbivory relate to effects of herbivory on plant phenology remains poorly understood. Here, a 9-year field experiment in arctic tundra reveals associations among herbivory, plant green-up phenology early in the growing season, and plant abundance later in the growing season. Herbivore influences on tundra plant abundance may thus derive at least somewhat from influences on phenology.

## Introduction

Life-history theory predicts that plant performance, including annual growth, abundance, and offspring production, should reflect strategies aimed at optimizing the timing of critical life cycle stages such as the timing of growth onset (1). This is because plants risk tissue losses to both adverse abiotic conditions and herbivory, both of which may subsequently influence abundance, survival, and reproductive success (2). Consequently, both the seasonal timing of growth onset and variation in it (i.e. phenology)

and abundance of plants should be sensitive to abiotic conditions and herbivory (3). Yet plant phenology is studied nearly exclusively in relation to abiotic conditions (4) while plant abundance, diversity, and community dynamics are well studied in relation to both herbivory (5, 6) and weather or climate (7, 8).

Reflecting this disparity, plant phenology has been remarkably well researched in relation to climate change, representing one of the most commonly focused upon biological responses to recent warming (4, 9–11). This is especially evident in the Arctic

**Competing Interest:** The authors declare no competing interests.

**Received:** February 23, 2024. **Accepted:** September 30, 2024

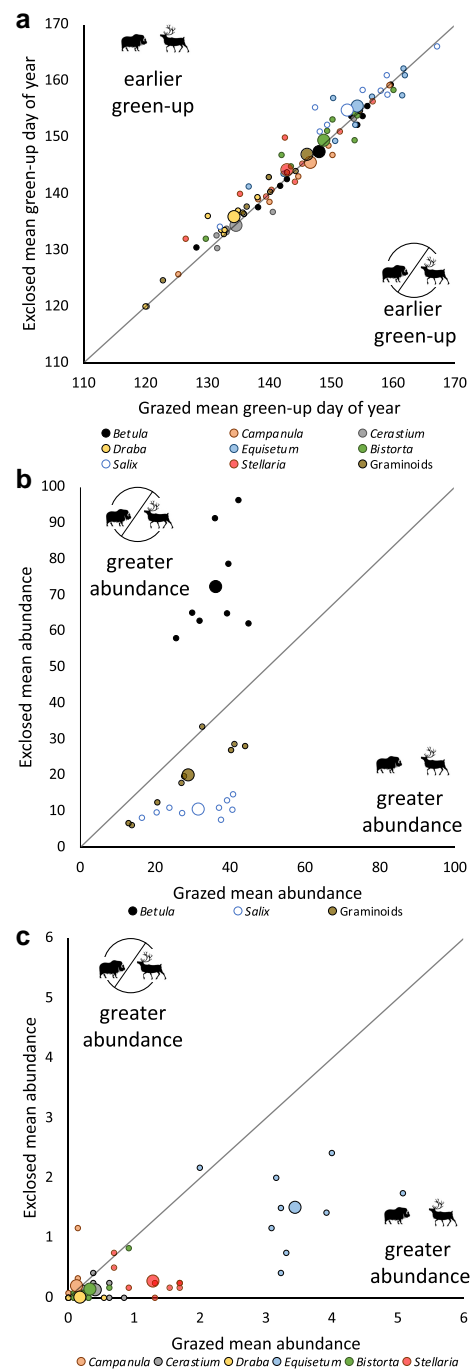
© The Author(s) 2024. Published by Oxford University Press on behalf of National Academy of Sciences. This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs licence (<https://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial reproduction and distribution of the work, in any medium, provided the original work is not altered or transformed in any way, and that the work is properly cited. For commercial re-use, please contact [reprints@oup.com](mailto:reprints@oup.com) for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact [journals.permissions@oup.com](mailto:journals.permissions@oup.com).

(12, 13), where abiotic constraints on the seasonal timing of plant growth are strong (14, 15) and where warming has been rapid and pronounced (16, 17). By comparison, little focus has been placed on plant phenological responses to herbivory (18). Some evidence indicates that large herbivores such as bison (*Bison bison*) can advance plant green-up dynamics by reducing light competition through tissue removal and via promotion of photosynthetic activity by increasing nitrogen content in surviving plant leaf tissue (19). Despite extensive focus on plant phenological responses to warming in the Arctic (20), only two studies have directly examined impacts of herbivory on plant phenology in the region (21, 22). One of those studies, conducted in a High Arctic fen community, revealed that exclusion of muskoxen (*Ovibos moschatus*) advanced the annual timing of peak vegetation biomass (21). The other, conducted in a low arctic shrub-graminoid-forb complex, revealed that exclusion of caribou (*Rangifer tarandus*) and muskoxen delayed the annual onset of plant green-up timing, implying that herbivory accelerated green-up (22). Herbivory by migratory geese that breed in the Arctic, such as snow geese (*Anser caerulescens*) and Pacific black brant (*Branta bernicla nigricans*), can also alter phenological dynamics of ephemeral ponds and plant leaf chemistry in ways consistent with effects on plant phenology (23–25), though these effects have not been tested directly. Consequently, much remains to be understood about the role of herbivory in plant phenological dynamics in the Arctic or elsewhere.

This knowledge gap is notable considering large herbivores, including caribou or reindeer (also *R. tarandus*) and muskoxen in the Arctic, have well-documented effects on plant abundance, diversity, and community composition (26–28). Hence, in the absence of better understanding of herbivore impacts on plant phenology, we currently lack insights into whether or how such impacts might contribute to well-known effects on plant abundance. As well, the lack of studies linking herbivore impacts on plant phenology to herbivore impacts on plant abundance may reflect an assumption that phenological and abundance dynamics are primarily constrained by different factors (29). Addressing this challenge may be especially important in the context of climate change impacts in the far north because the annual timing of plant phenological events is advancing faster in the Arctic than anywhere else on Earth (30–32) and vegetation in the arctic tundra biome is undergoing complex shifts in composition and structure (33). The extent to which these phenomena may be associated, and the potential contribution of herbivory to any such association, is currently unknown but may be informed by studies such as the one presented here.

## Results and discussion

We monitored mean annual green-up dates and annual peak abundances of nine arctic tundra plant taxa from 2009 through 2017 at a study site near Kangerlussuaq, Greenland, on plots inside fenced exclosures designed to prevent herbivory by muskox and caribou and on plots on adjacent, unfenced control areas exposed to herbivory (see “Materials and methods”). Comparison of taxon-specific mean annual green-up dates between exclosed and grazed plots (Figure 1a, small symbols) resulted in calculation of 81 experimental response ratios quantifying the effect of the herbivore exclusion treatment on green-up timing. Of these 81 response ratios, 79 were nonzero (Table S1a). The two zero values resulted from the fact that, in one year of the experiment, mean green-up dates did not differ between exclosed and grazed plots for the forbs *Draba nivalis* and *Stellaria longipes*. Of the nonzero



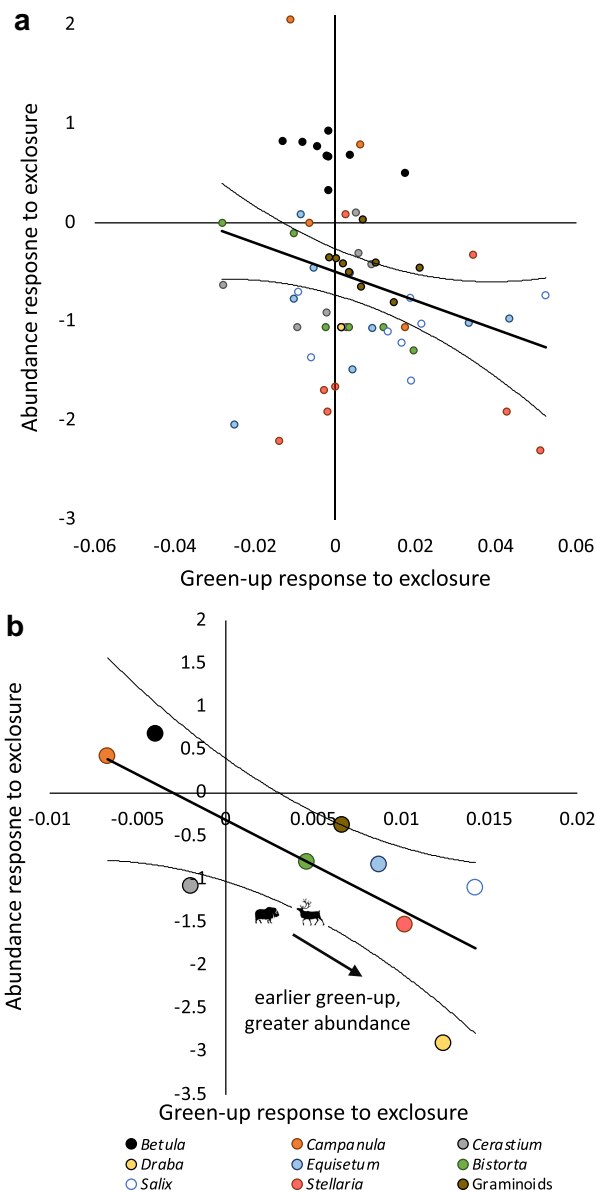
**Fig. 1.** a) Mean annual (for each year from 2009 through 2017; small symbols) and pooled mean (across the entire period 2009–2017; large symbols) green-up timing by nine plant taxa at the study site near Kangerlussuaq, Greenland on plots experimentally exclosed from herbivory by caribou and muskoxen plotted against those means on grazed (control) plots. Values above the diagonal parity line are those for which green-up occurred comparatively earlier under exposure to herbivory and values below the diagonal parity line are those for which green-up occurred comparatively earlier under herbivore exclusion. b and c) Mean annual (for each year from 2009 through 2017; small symbols) and pooled mean (across the entire period 2009–2017; large symbols) abundance (point-frame pin intercepts/0.25 m<sup>2</sup>) of nine plant taxa at the Kangerlussuaq study site on plots experimentally exclosed from herbivory by caribou and muskoxen plotted against those means on grazed (control) plots. Values above the diagonal parity line are those for which abundance was comparatively greater under herbivore exclusion and values below the diagonal parity line are those for which abundance was comparatively greater under exposure to herbivory.

green-up response ratios, 62% were positive and 38% were negative, indicating that in most cases green-up timing occurred earlier under herbivory than under herbivore exclusion (one-sample binomial test  $\chi^2 = -2.03$ ,  $P = 0.043$ ). Comparison of taxon-specific mean annual abundances on excluded and grazed plots (Figure 1b and c, small symbols) resulted in 62 experimental response ratios quantifying the effect of the herbivore exclusion treatment on abundance. Of these, 60 were nonzero (Table S1b). There were fewer abundance response ratios than green-up response ratios due to instances in which taxa were detected on control plots but not treatment plots (14 cases), detected on treatment plots but not control plots (1 case), or not detected on control and treatment plots (4 cases) (reported as “missing” in Table S1b). These disparities might have reflected differential influences of herbivory and herbivore exclusion on abundances of rare vs. common taxa over the course of the experiment (34). The two zero-value abundance response ratios indicate that, in a single year, mean abundances of the forbs *Bistorta viviparum* and *D. nivalis* did not differ between excluded and grazed plots in those cases. Among the 60 nonzero abundance response ratios, 75% were negative and 25% were positive, indicating that in most cases taxon-specific abundance was greater under herbivory than under herbivore exclusion (one-sample binomial test  $\chi^2 = -3.74$ ,  $P < 0.001$ ).

The distributions of positive, negative, or zero-value response ratios varied significantly among the nine focal tundra plant taxa (see “Materials and methods”) for both green-up timing (Likelihood ratio  $\chi^2 = 26.11$ ,  $df = 16$ ,  $P = 0.05$ ) and abundance (Likelihood ratio  $\chi^2 = 45.2$ ,  $df = 16$ ,  $P < 0.001$ ). Two species, the deciduous shrub *Betula nana* and the forb *Campanula gieseckiana*, displayed mostly negative green-up response ratios (Table S1a), indicating that green-up by these two species occurred later under herbivory than under herbivore exclusion (Figure 1a, small symbols). In contrast, three taxa, the forb *D. nivalis*, the deciduous shrub *Salix glauca*, and graminoids, displayed mostly positive green-up response ratios (Table S1a), indicating that green-up by them generally occurred earlier under herbivory than under herbivore exclusion (Figure 1a, small symbols).

The shrub *B. nana* was the only taxon displaying mostly, and in fact exclusively, positive abundance response ratios (Table S1b), indicating that its abundance was greater under herbivore exclusion than under herbivory (Figure 1b, small symbols). Notably, there was no difference in baseline mean abundance of this species on grazed vs. excluded plots at the beginning of the experiment (Figure S2), indicating that the differences reported here developed over the course of herbivore exclusion as the experiment progressed. In contrast, six taxa, including the forbs *Bistorta viviparum*, *Cerastium alpinum*, *Equisetum arvense*, and *S. longipes*; the shrub *S. glauca*; and graminoids all displayed mostly negative abundance response ratios (Table S1b), indicating that for these six taxa abundance was comparatively greater under herbivory than under herbivore exclusion (Figure 1b and c, small symbols). The greater abundance of *B. nana* under herbivore exclusion than under herbivory may have contributed indirectly to lower abundances of these six taxa on excluded plots through competition for space, light, or soil nutrients (e.g. (35–37)). Consistent with this scenario, pairwise associations between plot-scale abundance of each taxon and that of *B. nana* were generally negative under herbivory but not under herbivore exclusion (Figure S3). This suggests that suppression of *B. nana* abundance by herbivory may indirectly promote greater abundances of taxa sensitive to negative effects of competition with *B. nana*.

Annual abundance response ratios were weakly negatively related to annual green-up response ratios (linear model  $R^2 = 0.08$ ,



**Fig. 2.** The magnitude of the response of plant abundance to experimental herbivore exclusion in relation to the magnitude of the response of plant green-up timing to experimental herbivore exclusion. Shown are experimental response ratios (see “Materials and methods”) derived for each of nine plant taxa using a) annual means and b) means for data pooled across the experimental period (2009–2017).

$b = -14.5 \pm 6.50$ ,  $t = -2.23$ ,  $P = 0.03$ ) (Figure 2a). Variation in the magnitude of abundance response ratios pooled across the experimental period (2009–2017) was more strongly and negatively related to variation in pooled green-up response ratios (Figure 2b). Across taxa, 55% of the variation in the magnitude of tundra plant abundance responses to herbivore removal was explained by responses of their green-up timing to herbivore removal (linear model  $R^2 = 0.55$ ,  $b = -104.9 \pm 35.8$ ,  $t = -2.93$ ,  $P = 0.02$ ). This latter relationship indicates that, over the course of the 9-year experiment, earlier green-up timing under herbivory by six taxa (graminoids; the forbs *B. viviparum*, *E. arvense*, *S. longipes*, *D. nivalis*; and the shrub *S. glauca*) was associated with greater abundance under herbivory than under herbivore exclusion later in the growing season (Figure 2b). In contrast, later

green-up under herbivory by two taxa (the shrub *B. nana* and the forb *C. gieseckiana*) was associated with lower abundance under herbivory than under herbivore exclusion later in the growing season (Figure 2b). We emphasize that these relationships are not intended to suggest trends in green-up or abundance within taxa or imply differences in the magnitude or direction of any such trends among species between exclosed and grazed plots over the course of the experiment. Instead, these results merely indicate that the magnitude and direction of taxon-specific mean abundance responses to experimental herbivore exclusion scale with their mean green-up responses over the 9-year experimental period.

In general, plant responses to herbivory, or the risk of it, may be expected to take two forms: short-term physiological responses such as the mobilization of resources to increase growth rate, or longer-term adaptive responses to avoid or minimize loss of tissues early in the life cycle that are critical to productivity later in the life cycle (1). This framework thus predicts that plant growth or abundance should be responsive to strategies employed by plants to cope with, or minimize adverse effects of, herbivory through their growth phenology. Our results appear to provide support for this expectation, but also highlight intriguing taxonomic variation in the nature of such responses that warrants further study. For instance, linked plant phenological and abundance responses to herbivory (or its experimental exclusion) did not, in this study, relate clearly to plant growth form or functional group. Notably, the two deciduous shrub species, *B. nana* and *S. glauca*, displayed opposing green-up and abundance responses to herbivory (Figure 2b). Similarly, responses of low-growing forbs were mixed, with two species (*C. alpinum* and *C. gieseckiana*) exhibiting comparatively later green-up and either lower or greater abundance under herbivory, and four species (*B. viviparum*, *E. arvense*, *S. longipes*, and *D. nivalis*) all displaying comparatively earlier green-up and greater abundance under herbivory.

Hence, both green-up and abundance responses to our experiment were highly variable across tundra plant growth form and functional group. Intriguingly, however, additional evidence suggests that the relative order in which taxa initiate annual growth in this community may contribute to variation in their green-up responses to herbivory or the risk of it. Taxon-specific green-up responses to herbivory were associated nonlinearly with the rank order in which taxa initiate annual growth onset at the study site (Figure S4). Although this relationship is not significant ( $P = 0.16$ ), it suggests that taxa which responded to herbivory with advanced green-up were generally early- and late-emerging taxa (Figure S4). This pattern would appear to be consistent with a strategy of minimizing risk of tissue loss under herbivory by those species most likely to experience greatest exposure to herbivory at the tail ends of the annual progression of green-up across the taxa comprising this community (38). In contrast, taxa for which green-up was comparatively delayed by herbivory were those that initiated growth near the middle of the sequence of emergence from the first to last taxon annually (Figure S3).

Attempts to link changes in plant demography, including abundance, to drivers of phenological dynamics have been generally inconclusive (29, 39, 40). This may be at least somewhat attributable to the likelihood that drivers of variation in plant abundance may differ in the magnitude and direction of their effects from drivers of variation in plant phenology. For instance, in arctic tundra plant communities, warming commonly elicits earlier spring growth (41–45), but it may increase or reduce abundance (20, 46–48). Similarly, herbivory itself can increase or reduce plant abundance depending to some extent on plant growth form (2,

26, 28, 35, 49, 50). Our results indicate that even minor effects of herbivore removal on plant emergence phenology may contribute to pronounced effects of herbivore removal on abundance. Moreover, the nature of this relationship suggests that advancement of emergence timing under exposure to herbivory translates into greater relative abundance later in the growing season, consistent with predictions of the induced response framework (51). In contrast, delayed emergence timing in response to herbivory apparently contributes to reduced relative abundance, possibly as a consequence of increased competition for limiting resources (52). Relatedly, a consideration that our simple experimental approach lacks the power to resolve is whether effects of herbivory on phenology are indirect and mediated by effects on abundance. For instance, dwarf birch is the most common species on our plots (34) and the reduction or constraint of its abundance by herbivory may indirectly facilitate phenological escape (i.e. earlier green-up) by under-canopy forbs and graminoids (53, 54), possibly through alleviation of shading effects on light competition (55) or soil surface temperature (56). Additional, possibly more complex, experimentation may be needed to address that hypothesis. Nonetheless, our results suggest that the contribution of green-up timing or emergence phenology to plant abundance and community compositional dynamics in arctic tundra warrants further study, especially in the context of interactions between herbivory and climate change.

## Materials and methods

### Study site, experimental design, and plant phenology and abundance monitoring

The study site is located ~20 km east of the village of Kangerlussuaq, Greenland. In June 2002, we initiated a long-term experiment designed to investigate effects of herbivory by caribou and muskoxen on tundra plant abundance, diversity, and community composition. We erected three circular, 800 m<sup>2</sup> exclosures constructed of woven wire fencing and steel t-posts to exclude caribou and muskoxen. Adjacent to each exclosure, we identified a paired control area that remained unfenced and thus open to herbivore access and grazing. The three pairs of exclosure/grazed controls were separated by several hundred meters within an area ranging from ~67°6'28"N, 50°21'6"W to 67°6'53"N, 50°19'51"W.

In May 2003, we initiated annual monitoring of taxon-specific plant phenological dynamics inside all three exclosures by recording phenophases of all vascular plants present on four permanently marked plots in each of the three exclosures ( $n = 12$  herbivore-exclosed plots) on a daily or near-daily basis. This effort resulted in yearly records of annual timing of growth initiation (i.e. basal tissue greening in graminoids, leaf emergence in forbs, and leaf bud opening in deciduous shrubs; hereafter “green-up”), flower set, and blooming for nine vascular plant taxa under herbivore exclusion: dwarf birch (*B. nana*), gray willow (*S. glauca*), draba (*Draba* sp.), harebell (*C. gieseckiana*), horsetail (*E. arvense*), longstalk starwort (*S. longipes*), alpine chickweed (*C. alpinum*), alpine bistort (*Bistorta vivipara*), and graminoids (sedges and grasses) (22). In May 2009, we added five permanently marked plots outside of each of the three exclosures, on the adjacent grazed control areas, and initiated monitoring of the same phenophases of all vascular plants occurring on those plots ( $n = 15$  grazed plots). This effort resulted in annual records of seasonal green-up, flower set, and blooming for the same nine taxa on plots exposed to herbivory. Phenological observations commenced in early to mid-May each year and progressed through late June annually (Figure S1). The period of



observation was determined by our initial interest in monitoring plant phenology during the annual period when female caribou were present at the site for calving (57) and remained consistent as our research interests expanded (Figure S1). Although muskoxen are present in the area year-round, their seasonal occurrence at the site begins to increase and peak around early May (22, 38). Female caribou migrate into the area annually in early May for calving in late May through early June, before migrating out again in late June (58). The exclosures were removed at the end of the growing season in 2017. Data used here span 2009 through 2017, the period of overlap of phenological monitoring on exclosed and grazed plots. Because we were interested in assessing the role of herbivory in linking vascular plant green-up timing to abundance, we focused our analyses on the subset of phenology data comprising taxon-specific green-up dates.

Annual peak growing season abundances of the same nine taxa were assessed in late July or early August each year (Figure S1) using nondestructive point-frame sampling on a separate but proximal set of permanently marked plots inside ( $n = 12$ ) and outside ( $n = 13$ ) of the same exclosures from 2009 through 2017. Point-frame sampling was conducted using a 0.25 m<sup>2</sup> clear Plexiglas tabletop frame on four adjustable legs. A consistent orientation of the frame during each sampling event was ensured by anchoring the legs in four hollow aluminum pegs set into the ground at the corners of each plot at the cardinal directions. The Plexiglas tabletop frame was drilled with 20, randomly located holes. During sampling, a steel welding pin was lowered through each hole in succession and each contact of the tip of the pin was recorded to species, genus, or functional group according to the nine taxa listed above. This effort resulted in a grand total of 23,356 pin intercepts distributed across the focal taxa as follows: *Betula* = 12,053, *Salix* = 4,829, graminoids = 5,551, *Equisetum* = 566, *Stellaria* = 180, *Cerastium* = 63, *Bistorta* = 55, *Campanula* = 37, and *Draba* = 22. We recorded phenological observations on plots separate from those on which abundances were recorded to avoid the potential, however unlikely, for altering phenology through contact with plants (59).

## Analytical approach

Data on both green-up timing (22) and annual abundances (60–62) of the focal taxa have been analysed previously in relation to the exclosure treatment. Here, we used both sets of data to assess whether the abundance responses of the focal taxa to the exclosure treatment scale with their green-up responses to that treatment. To achieve this, we calculated experimental response ratios of both the green-up response and the abundance response of each taxon to the exclosure treatment both annually for each year from 2009 through 2017 and over the pooled period 2009–2017. This was done using the following formula:

$$RR_i = \ln\left(\frac{\mu_{Ti}}{\mu_{Ci}}\right). \quad (1)$$

In which  $RR_i$  is the experimental response ratio for taxon  $i$ ,  $\mu_{Ti}$  is the treatment mean green-up date or abundance for taxon  $i$  for a given year in the case of annual response ratios or for the period 2009–2017 in the case of pooled response ratios, and  $\mu_{Ci}$  is the control mean green-up date or abundance for taxon  $i$  for a given year in the case of annual response ratios or for the period 2009–2017 in the case of pooled response ratios. Thus,  $RR < 0$  when green-up is later on grazed compared to exclosed plots or when abundance is greater on grazed than on exclosed plots. The magnitude of green-up response ratios varied interannually (Table S2), indicating

variation in the extent to which the phenology of spring growth onset was altered by the herbivore exclosure treatment over the course of the experiment. For instance, delay of green-up by the exclosure treatment was negligible or absent in 2014, when spring growth onset of some taxa even occurred slightly earlier inside exclosures than outside (Table S2). A previous, related analysis of these data revealed that interannual variation in the response of community-level green-up timing to the exclosure treatment declined with later springtime arrival of large herbivores at the site, and this association was stronger for muskoxen than for caribou (22). Notably, muskoxen moved into the site later in 2014 than in any other year, perhaps contributing to the anomalous green-up response to the exclosure treatment that year.

To test whether plant abundance responses to herbivory were related to their phenological responses to herbivory, we analyzed variation in taxon-specific abundance response ratios as a function of variation among taxon-specific green-up response ratios. We did this both for taxon-specific response ratios calculated using annual means as well as for taxon-specific response ratios calculated using means pooled for 2009–2017. In each approach, we used a simple linear model with the former as the dependent variable and the latter as the predictor variable. This was intended to determine whether, and in which direction, the abundance responses of the focal taxa to herbivore removal scaled with their green-up responses to herbivore removal. Although herbivore exclusion is the experimental treatment in this study, we describe the results of the response ratio analyses largely in terms of responses to herbivory. We employ this approach to lend interpretability to our results in the context of the contextual framework described in the “Introduction”.

## Acknowledgments

We thank Mads Forchhammer for critical input on experimental design and inspiration for this study, the staff at Kangerlussuaq International Science Support for assistance with project development and logistical arrangements, and Mark Hebblewhite, Ben Lee, and two anonymous reviewers for constructive comments on the manuscript.

## Supplementary Material

Supplementary material is available at PNAS Nexus online.

## Funding

We gratefully acknowledge support from the U.S National Science Foundation (NSF) under grants 0124031, 0217259, 0732168, 0713994, 1107381, and 1525636, and the National Geographic Society to E.P.; and from the European Union’s Horizon 2020 Research and Innovation Program under the Marie Skłodowska-Curie grant (754513), and the Aarhus University Research Foundation to J.T.K.

## Author Contributions

E.P., R.C.H., P.S.B., C.J., M.P., and J.T.K. conceptualization, investigation, and writing—review & editing; E.P., P.S.B., and J.T.K. methodology; E.P. and R.C.H. analysis; E.P., R.C.H., and J.T.K. data curation; E.P. writing—original draft preparation, supervision, and project administration; E.P., R.C.H., and P.S.B. visualization; E.P. and J.T.K. funding acquisition.

## Preprint

A draft of this manuscript was posted on a preprint server: (<https://doi.org/10.1101/2024.02.23.581818>).

## Data Availability

Data on plant green-up dates and abundances are available at the Arctic Data Center (63, 64).

## References

- Harper JL. 1977. *Population biology of plants*. London: Academic Press. p. 892.
- Strauss SY, Agrawal AA. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol Evol*. 14:179–185.
- Silvertown J, Franco M, Harper JL. 1997. *Plant life histories: ecology, phylogeny and evolution*. Cambridge, UK: Cambridge University Press.
- Schwartz MD. 2003. *Phenology: an integrative environmental science*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Stowe KA, Marquis RJ, Hochwender CG, Simms EL. 2000. The evolutionary ecology of tolerance to consumer damage. *Annu Rev Ecol Syst*. 31:565–595.
- Milchunas DG, Noy-Meir I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*. 99:113–130.
- Elmendorf SC, et al. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat Clim Chang*. 2:453–457.
- Van der Putten WH, Macel M, Visser ME. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philos Trans R Soc B-Biol Sci*. 365:2025–2034.
- Vitasse Y, et al. 2022. The great acceleration of plant phenological shifts. *Nat Clim Chang*. 12:300–302.
- Scheffers BR, et al. 2016. The broad footprint of climate change from genes to biomes to people. *Science*. 354:aaf7671.
- Piao SL, et al. 2019. Plant phenology and global climate change: current progresses and challenges. *Glob Chang Biol*. 25:1922–1940.
- Prevéy JS, et al. 2022. The tundra phenology database: more than two decades of tundra phenology responses to climate change. *Arctic Science*. 8:1026–1039.
- Collins CG, et al. 2021. Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nat Commun*. 12:3442.
- Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology*. 76:694–711.
- Shaver GR, Kummerow J. 1992. Phenology, resource allocation, and growth of Arctic vascular plants. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J, editors. *Arctic ecosystems in a changing climate*. New York: Academic Press. p. 193–238.
- Box JE, et al. 2019. Key indicators of Arctic climate change: 1971–2017. *Environ Res Lett*. 14:045010.
- Rantanen M, et al. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. *Commun Earth Environ*. 3:168.
- Rasmussen NL, Yang LH. 2023. Timing of a plant-herbivore interaction alters plant growth and reproduction. *Ecology*. 104:e3854.
- Geremia C, et al. 2019. Migrating bison engineer the green wave. *Proc Natl Acad Sci U S A*. 116:25707–25713.
- Elmendorf SC, et al. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecol Lett*. 15:164–175.
- Mosbacher JB, Michelsen A, Stelvig M, Hjernstad-Sollerud H, Schmidt NM. 2019. Muskoxen modify plant abundance, phenology, and nitrogen dynamics in a high Arctic fen. *Ecosystems*. 22:1095–1107.
- Higgins RC. 2022. *Phenological dynamics in a rapidly warming Arctic plant-herbivore system*. [M.S. Thesis]. Davis: University of California. p. 51.
- Park JS. 2017. A race against time: habitat alteration by snow geese prunes the seasonal sequence of mosquito emergence in a subarctic brackish landscape. *Polar Biol*. 40:553–561.
- Beard KH, et al. 2019. Migratory goose arrival time plays a larger role in influencing forage quality than advancing springs in an Arctic coastal wetland. *PLoS One*. 14:e0213037.
- Choi RT, et al. 2020. Early goose arrival increases soil nitrogen availability more than an advancing spring in coastal Western Alaska. *Ecosystems*. 23:1309–1324.
- Olofsson J, Post E. 2018. Effects of large herbivores on tundra vegetation in a changing climate and implications for rewilding. *Philos Trans R Soc B-Biol Sci*. 373:20170437.
- Frank DA, McNaughton SJ, Tracy BF. 1998. The ecology of Earth's grazing ecosystems. *Bioscience*. 48:513–521.
- Post E, et al. 2023. Large herbivore diversity slows sea ice-associated decline in Arctic tundra diversity. *Science*. 380:1282–1286.
- Iler AM, CaraDonna PJ, Forrest JRK, Post E. 2021. Demographic consequences of phenological shifts in response to climate change. *Annu Rev Ecol Syst*. 52:221–245.
- Oberbauer SF, et al. 2013. Phenological response of tundra plants to background climate variation tested using the International Tundra Experiment (ITEX). *Philos Trans R Soc Ser B*. 368:20120481.
- Høye TT, Post E, Meltofte H, Schmidt NM, Forchhammer MC. 2007. Rapid advancement of spring in the high Arctic. *Curr Biol*. 17:R449–R451.
- Post E, Steinman BA, Mann ME. 2018. Acceleration of phenological advance and warming with latitude over the past century. *Sci Rep*. 8:3927.
- Myers-Smith IH, et al. 2020. Complexity revealed in the greening of the Arctic. *Nat Clim Chang*. 10:106–117.
- Post E, Pedersen C, Watts DA. 2022. Large herbivores facilitate the persistence of rare taxa under tundra warming. *Sci Rep*. 12:1292.
- Kaarlejärvi E, Eskelinen A, Olofsson J. 2017. Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nat Commun*. 8:419.
- Bjorkman AD, et al. 2018. Plant functional trait change across a warming tundra biome. *Nature*. 562:57–62.
- Eskelinen A, Harpole WS, Jessen MT, Virtanen R, Hautier Y. 2022. Light competition drives herbivore and nutrient effects on plant diversity. *Nature*. 611:301.
- Post E. 2019. *Time in ecology: a theoretical framework, monographs in population biology*. Princeton (NJ): Princeton University Press.
- Fremelin KM, McLaren JR, DeSandoli L, Turkington R. 2011. The effects of fertilization and herbivory on the phenology of the understory vegetation of the boreal forest in Northwestern Canada. *Arct Antarct Alp Res*. 43:389–396.
- Kimball S, Angert AL, Huxman TE, Venable DL. 2010. Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Glob Chang Biol*. 16:1555–1565.
- Post E, Pedersen C, Wilmers CC, Forchhammer MC. 2008. Phenological sequences reveal aggregate life history response to climatic warming. *Ecology*. 89:363–370.
- Bokhorst S, Bjerke JW, Street LE, Callaghan TV, Phoenix GK. 2011. Impacts of multiple extreme winter warming events on

- sub-Arctic heathland: phenology, reproduction, growth, and CO<sub>2</sub> flux responses. *Glob Chang Biol.* 17:2817–2830.
- 43 Zeng HQ, Jia GS, Forbes BC. 2013. Shifts in Arctic phenology in response to climate and anthropogenic factors as detected from multiple satellite time series. *Environ Res Lett.* 8:035036.
- 44 Björkman AD, Elmendorf SC, Beamish AL, Vellend M, Henry GHR. 2015. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Glob Chang Biol.* 21:4651–4661.
- 45 Prevéy J, et al. 2017. Greater temperature sensitivity of plant phenology at colder sites: implications for convergence across northern latitudes. *Glob Chang Biol.* 23:2660–2671.
- 46 Arft AM, et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol Monogr.* 69:491–511.
- 47 Walker MD, et al. 2006. Plant community responses to experimental warming across the tundra biome. *Proc Natl Acad Sci U S A.* 103:1342–1346.
- 48 Kremers KS, Hollister RD, Oberbauer SF. 2015. Diminished response of Arctic plants to warming over time. *PLoS One.* 10:e0116586.
- 49 te Beest M, Sitters J, Menard CB, Olofsson J. 2016. Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. *Environ Res Lett.* 11:125013.
- 50 Christie KS, et al. 2015. The role of vertebrate herbivores in regulating shrub expansion in the Arctic: a synthesis. *Bioscience.* 65:1123–1133.
- 51 Agrawal AA. 1998. Induced responses to herbivory and increased plant performance. *Science.* 279:1201–1202.
- 52 Wolkovich EM, Cleland EE. 2011. The phenology of plant invasions: a community ecology perspective. *Front Ecol Environ.* 9:287–294.
- 53 Lee BR, Yancy AJ, Heberling JM. 2024. Phenological escape and its importance for understory plant species in temperate forests. *Int J Plant Sci.* 185:321–333
- 54 Lee BR, et al. 2022. Wildflower phenological escape differs by continent and spring temperature. *Nat Commun.* 13:7157.
- 55 Eskelinen A, et al. 2023. Herbivory and nutrients shape grassland soil seed banks. *Nat Commun.* 14:3949.
- 56 Aalto J, le Roux PC, Luoto M. 2013. Vegetation mediates soil temperature and moisture in Arctic-alpine environments. *Arct Antarct Alp Res.* 45:429–439.
- 57 Post E, Bøving PS, Pedersen C, MacArthur MA. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. *Can J Zool.* 81:1709–1714.
- 58 Thing H. 1984. Feeding ecology of the West Greenland caribou (*Rangifer tarandus*) in the Sisimiut-Kangerlussuaq region. *Danish Rev Game Biol.* 12:1–53.
- 59 Hik DS, Brown M, Dabros A, Weir J, Cahill JF. 2003. Prevalence and predictability of handling effects in field studies: results from field experiments and a meta-analysis. *Am J Bot.* 90:270–277.
- 60 Pedersen C, Post E. 2008. Interactions between herbivory and warming in aboveground biomass production of Arctic vegetation. *BMC Ecol.* 8:17.
- 61 Post E, Pedersen C. 2008. Opposing plant community responses to warming with and without herbivores. *Proc Natl Acad Sci U S A.* 105:12353–12358.
- 62 Post E, Cahoon SMP, Kerby JT, Pedersen C, Sullivan PF. 2021. Herbivory and warming interact in opposing patterns of covariation between Arctic shrub species at large and local scales. *Proc Natl Acad Sci U S A.* 118:e2015158118.
- 63 Post E, Kerby J, Pedersen C. 2024. *Observed plant species emergence dates on grazed and exclosed plots at the Kangerlussuaq, Greenland study site 2009 through 2017.* Arctic Data Center. urn:uuid:7370857f-af43-4a1f-947f-48b75211fc3a.
- 64 E. Post. 2022. *Tundra taxa annual abundances under experimental herbivore exclosure and warming near Kangerlussuaq, Greenland, 2003–2017.* Arctic Data Center. <https://doi.org/10.18739/A2CR5ND85>