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RESEARCH ARTICLE

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Estimating phenological sensitivity in contemporary vs. historical data sets: Effects of climate resolution and spatial scale

Meredith A. Zettlemoyer | **Jill E. Wilson** | **Megan L. DeMarche**

Department of Plant Biology, University of Georgia, 120 Carlton Street, 2502 Miller Plant Sciences, Athens, Georgia 30602-5004, USA

Correspondence

Meredith A. Zettlemoyer, Department of Plant Biology, University of Georgia, 120 Carlton Street, 2502 Miller Plant Sciences, Athens, Georgia 30602-5004, USA.

Email: meredith.zettlemoyer25@uga.edu

Abstract

Premise: Phenological sensitivity, or the degree to which a species' phenology shifts in response to warming, is an important parameter for comparing and predicting species' responses to climate change. Phenological sensitivity is often measured using herbarium specimens or local studies in natural populations. These approaches differ widely in spatiotemporal scales, yet few studies explicitly consider effects of the geographic extent and resolution of climate data when comparing phenological sensitivities quantified from different data sets for a given species.

Methods: We compared sensitivity of flowering phenology to growing degree days of the alpine plant *Silene acaulis* using two data sets: herbarium specimens and a 6 yr observational study in four populations at Niwot Ridge, Colorado, USA. We investigated differences in phenological sensitivity obtained using variable spatial scales and climate data sources.

Results: Herbarium specimens underestimated phenological sensitivity compared to observational data, even when herbarium samples were limited geographically or to nearby weather station data. However, when observational data were paired with broader-scale climate data, as is typically used in herbarium data sets, estimates of phenological sensitivity were more similar.

Conclusions: This study highlights the potential for variation in data source, geographic scale, and accuracy of macroclimate data to produce very different estimates of phenological responses to climate change. Accurately predicting phenological shifts would benefit from comparisons between methods that estimate climate variables and phenological sensitivity over a variety of spatial scales.

KEYWORDS

alpine, climate change, climate data resolution, growing degree days, herbaria, observational study, phenological sensitivity, phenological shifts, *Silene acaulis*, spatial scale

Phenological shifts are among the most widely documented consequences of climate change (Parmesan, 2006; Thackeray et al., 2016; Cohen et al., 2018). When life-history events such as germination, flowering, reproduction, hibernation, or migration occur earlier or later in relation to their historical occurrence, these phenological shifts can affect fecundity, population persistence, biodiversity, and species interactions (Møller et al., 2008; Willis et al., 2008; Renner and Zohner, 2018; Iler et al., 2021; Kharouba and Wolkovich, 2020). One of the most common ways to measure climate-mediated phenological shifts is to quantify phenological sensitivity, or the change in the timing of a phenological event per unit of environmental change (here defined as a change in phenology per degree of warming [Cleland et al., 2012; Park et al., 2018] or per growing degree day [Jerome et al., 2021]).

Approaches to studying phenological shifts include the use of herbarium specimens (Davis et al., 2015; Willis et al., 2017; Lang et al., 2018; Meineke et al., 2018; Zettlemoyer et al., 2021), observational studies (Iler et al., 2013; Panchen and Gorelick, 2015; Kharouba and Wolkovich, 2020; McDonough MacKenzie et al., 2020), and warming experiments (Bjorkman et al., 2015; Khorsand Rosa et al., 2015; Zettlemoyer et al., 2019; Stuble et al., 2021). These approaches differ widely in spatiotemporal scale and may capture distinct aspects of phenological shifts. For example, herbarium specimens may reflect long-term phenological shifts via either plasticity or evolutionary change and can be biased by geography (collections in accessible locations), temporal scale (collections favored in certain years or seasons and temporal trends in collection efforts [e.g., declining collections since the mid-20th century; Gardner et al., 2014]), and collectors (Davis et al., 2015; Daru et al., 2018). The wide spatial and temporal extent of herbarium data sets may also result in more variability in associated climate data (availability of nearby and historical weather station data), potentially resulting in weaker estimates of phenological sensitivity. At the same time, specimens may be collected close to a weather station, and field observations may or may not be accompanied by locally measured climate data. However, it is not clear whether climate data associated with herbarium specimens are comparable with climate data from field observations.

Observational studies—whether documenting phenology in single or several populations (e.g., Iler et al., 2013; Hall et al., 2018) or using geographically extensive remote sensing (Piao et al., 2019)—similarly capture phenological trends over time or in response to climate. Observational studies also generally collect a range of potential phenological metrics (e.g., first flower, peak flower, and flowering duration) that may not be comparable with metrics derived from herbarium specimens, which may reflect flowering at any time across the flowering season (Miller et al., 2021). Many observational studies and warming experiments span a shorter time period or a more limited geographic extent than herbarium studies. These biases can result in mismatched estimates of phenological sensitivity across data sets. For example, warming experiments underestimate phenological shifts, compared to observational studies (Wolkovich et al., 2012), and herbarium studies' estimates of flowering time are days later, on average, than field studies (Davis et al., 2015; Ramirez-Parada et al., 2022). Such differences in metric or scale can limit comparisons between data sets, leading to a need to determine what measurements we can use to synthesize historical and contemporary phenological records (Miller et al., 2021). Given that there may be intraspecific variation in phenological sensitivity, accurate models of phenological shifts would benefit from a combination of methods that estimate phenological sensitivity over a variety of spatial scales and climate data sources (Wolkovich et al., 2012; Stuble et al., 2021).

To assess the comparability of spatial and climate data between observational and historical phenological records, we leveraged a 6-year observational study and herbarium specimens to quantify flowering phenology over time and in response to climate for the alpine plant *Silene acaulis*. Alpine species' flowering phenology is highly sensitive to climate change (Kimball et al., 2014; Smith et al., 2012; Suonan et al., 2019), and alpine environments are experiencing rapid rates of climate change (Losapio et al., 2021). Flowering phenology of *S. acaulis* has been shown to advance strongly with growing degree days (GDD) in a local observational study using microclimate data at Niwot Ridge, Colorado, USA (Hall et al., 2018; DeMarche, 2021). Here, we compare the phenological sensitivity of *S. acaulis* as calculated from herbarium specimens versus observational data, using a range of geographic and climate data scales. We ask: (1) Does flowering phenology shift over time and in response to GDD in herbarium specimens? (2) Do herbarium specimens and direct observational data sets produce similar estimates of phenological sensitivity? (3) How does varying the spatial scales of sampling in herbarium data sets or the source of climate data affect estimates of phenological sensitivity? We predicted that estimates of phenological sensitivity between data sets should be most similar when analyses use similar spatial scales (e.g., limiting the spatial extent of herbarium specimens) or climate data sources (e.g., using broad-scale weather station data in the observational study).

MATERIALS AND METHODS

Study system

Silene acaulis (L.) Jacq. (Caryophyllaceae) is a long-lived, gynodioecious cushion plant common to arctic and alpine tundra habitats throughout the Northern Hemisphere (Morris and Doak, 1998). Individuals of *S. acaulis* flower in early summer after snowmelt, continue to flower for 1–2 wk, and are primarily fly- and bee-pollinated (Hall et al., 2018).

Herbarium specimens

We examined 1120 specimens that had at least one open flower at the time of collection from digitized specimens obtained from 40 herbaria spanning 1872–2021 (Figure 1A, B; Appendix S1). Buds and fruits are often indistinguishable on specimens, so we were unable to quantify other phenological stages. We restricted specimens to the USA and Canada because North American populations represent a single well-supported phylogenetic lineage (Gussarova et al., 2015), whereas European populations comprise a species complex with varying taxonomic resolution. We removed any specimens from New Hampshire and Newfoundland/Labrador ($N = 41$) because they were only collected and recorded in those areas prior to 1900. For specimens with recorded coordinate data, we included the longitude and latitude reported on the specimen label. For specimens without recorded coordinate data, we georeferenced latitude and longitude based on the most detailed locality information available. We excluded specimens for which recorded locality information was insufficient to determine latitude and longitude (e.g., only the county reported or locality name no longer in use).

Climate data

For each herbarium specimen, we downloaded daily maximum and minimum temperatures from the closest weather station (within a 50-km radius of the specimen's

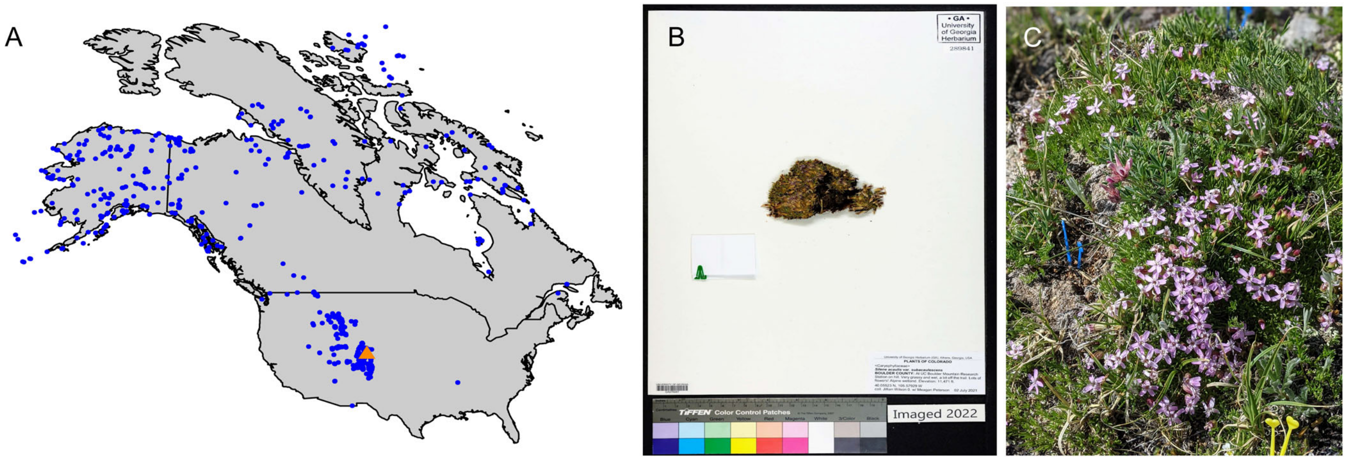

FIGURE 1 (A) Map of *Silene acaulis* specimens included in this study (blue dots), from across the species' North American range. Orange triangle indicates Niwot Ridge, Colorado, USA. (B) Flowering herbarium specimen and (C) individual *S. acaulis* in the field at Niwot Ridge. Photo credits: (B) J. Wilson, (C) M. Zettlemoyer.

collection location) with data for the calendar year of collection, using the package rnoaa in R (Chamberlain et al., 2021; R Core Team, 2021; Appendix S2). Although a 50-km radius may encompass great spatial and climatic variability, thresholds below this level resulted in fewer than half of herbarium specimens with associated climate data and primarily excluded older or geographically remote specimens. We calculated growing degree days (GDD; Gordon and Bootsma, 1993) for every specimen as heat accumulation (summed degrees Celsius) from 1 April to 15 June, with a baseline temperature of 2°C, based on previous evidence that this measure of seasonal GDD is a strong predictor of flowering phenology in *S. acaulis* (M. Zettlemoyer et al., unpublished data). We used historical weather station data because GDD requires historical daily temperature records. We were able to estimate GDD for 57% (620/1079) of the herbarium specimens.

Observational study

We used a 6 yr observational data set of flowering phenology for *S. acaulis* at the Niwot Ridge Long-term Ecological Research site in Colorado, USA (3574 m a.s.l.) (DeMarche, 2021). Dates of first and peak flower were recorded for 657 individuals across four plots ($N = 77–212$/plot; Figure 1C) from 2016 to 2021. The number of open flowers on each plant was recorded every 2–3 d throughout the growing season, and individual-level flowering phenology was summarized by fitting curves to the proportion of open flowers on each census day and extracting the day of first flower and peak flower for each individual (Hall et al., 2018).

Local soil surface temperature was recorded every 2–4 h using multiple temperature sensors in each plot (2008–20: Thermochron iButtons; 2020–21: Onset HOBO pendants; $N = 3–8$/plot). We summarized local temperature data to calculate GDD for each plot and year using the same formula as for weather station data. To control for differences in climate data (i.e., local vs. weather station measurements), we also downloaded local weather station data to calculate GDD, following the same approach we used for herbarium specimens (Appendix S3).

Statistical analyses

To examine whether flowering shifts over time in herbarium specimens, we used a linear model examining the effects of collection year on flowering time (collection day of year; $N = 1079$ specimens). We included latitude and longitude to control for spatial variation in flowering phenology. Because *S. acaulis* is limited to high-elevation or high-latitude tundra environments, elevation was collinear with latitude ($r = -0.90$, $P < 0.0001$) and was removed from analyses.

To examine whether flowering time shifts in response to warming in the herbarium data set, we used a linear model with flowering time as the response variable and GDD, latitude, and longitude as predictor variables ($N = 620$ specimens). To explore the effect of geographic scale on estimates of phenological sensitivity, we also refit this model using (1) only specimens from Colorado ($N = 189$ specimens) and (2) only specimens from counties neighboring Niwot Ridge (i.e., Boulder, Gilpin, Clear Creek, Grand, Jackson, and Larimer counties, thus more closely mirroring the spatial scale of the observational data set; $N = 24$ specimens). We were unable to examine specimens from Niwot Ridge alone, due to limited specimens ($N = 2$). To explore the effect of climate data resolution on estimates of phenological sensitivity, we also refit this model using only specimens for which climate data were obtained from weather stations within 4 km of a specimen's collection location (mirroring the spatial scale of weather station data collected for the observational data set from Niwot Ridge (see below; $N = 82$ specimens; Appendix S2).

To examine shifts in flowering time in the observational data set, we included day of first flower (day of year) as the response variable and GDD (measured at the site level from temperature loggers) as the predictor variable ($N = 1589$ observations). We included plot (SN1–4) as a fixed effect to control for local variation in phenological responses. To explore the effect of climate data resolution on estimates of phenological sensitivity, we refit models using GDD calculated from (1) the closest weather station (matching methods above; these stations were all within 4 km of Niwot Ridge) and (2) weather stations ~13 km away (i.e., approximately the average distance to weather stations in the herbarium data set; Appendix S2). We also fit similar models with day of peak flower as the response variable because peak flowering may be more comparable to herbarium data sets (Davis et al., 2015).

We estimated phenological sensitivity as the slope of flowering day to GDD (number of days shifted per GDD), calculated from the linear models described above (following Park et al., 2018; Zettlemoyer et al., 2021).

RESULTS

Day of collection of flowering individuals, a proxy for flowering time, has advanced by −0.052 ± 0.020 d/yr ($F_{1, 1071} = 6.52$, $P = 0.01$; Appendix S4; Figure 2). Flowering shifted earlier with warming in both data sets (Figure 3), although the magnitude of response varies (Figure 4). In the herbarium data set, flowering advanced by −0.012 ± 0.004 d/GDD ($F_{1,616} = 7.21$, $P = 0.007$; Appendix S4; Figure 3A) whereas in the observational data set, first flowering advanced by −0.098 ± 0.003 d/GDD ($F_{1,1584} = 1128.02$, $P < 0.0001$; Appendix S5; Figure 3E; results for peak flowering are qualitatively similar; Appendix S6). GDD increased over time in the observational data set, but not in the herbarium data set (Appendix S7).

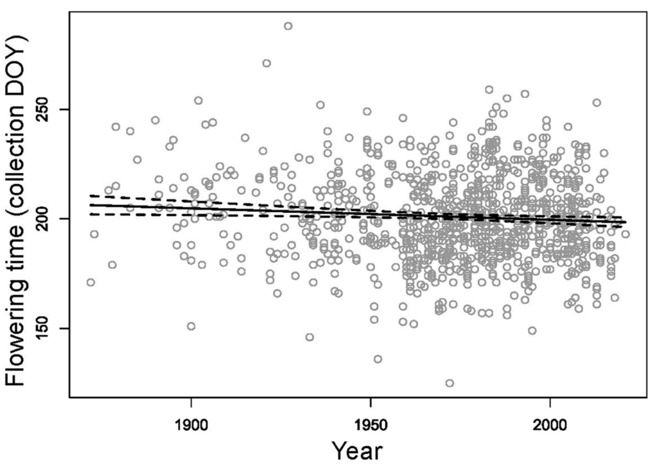

FIGURE 2 Collection dates for *Silene acaulis* (day of year [DOY], a proxy for flowering time) across the years represented in the (full) herbarium data set. Gray circles represent observed data; solid line represents the estimated slope of phenology over time after controlling for latitude and longitude; dashed lines represent 95% confidence intervals.

Narrowing the spatial scale of herbarium specimens resulted in stronger estimates of phenological sensitivity (e.g., greater advances in flowering per degree warming; Figure 4A). However, even spatially limited herbarium data results in weaker sensitivity estimates than the site-level observational data set (Figure 4A).

Altering the source of climate data used to estimate GDD had mixed effects on estimates of phenological sensitivity (Figure 4B). We obtained similar estimates of phenological sensitivity from observational data sets when using either locally measured microclimate data or macroclimate data from nearby weather stations (0–3.98 km away; −0.10 ± 0.004 d/GDD; $F_{1,1584} = 819.07$, $P < 0.0001$; Appendix S5; Figure 3F). However, using weather station data from farther away results in sensitivity more similar to that estimated from the herbarium data set (−0.016 ± 0.003 d/GDD; $F_{1,1584} = 28.19$, $P < 0.0001$; Appendix S5; Figure 3G). For this analysis, we used climate data from weather stations ~13 km away, similar to the average weather station distance in the herbarium data set. Interestingly, limiting our herbarium analysis to specimens with nearby weather stations (<4 km away) did not result in sensitivity estimates closer to observational estimates. We also did not detect significant advances in flowering time in this analysis, potentially due to low sample size (Appendices S4, S8, S9; Figure 3D).

DISCUSSION

We estimate qualitatively similar patterns of response in flowering phenology to GDD, but very different quantitative sensitivities between herbarium and observational data sets of the alpine plant *Silene acaulis*, with herbarium data sets consistently underestimating phenological shifts in comparison to observational data. By varying the spatial extent and source of climate data across analyses, we found support for geographic scale and, less consistently, for climate data resolution having an important influence on estimates of phenological sensitivity. These results highlight the importance of carefully considering these methodological factors in quantitative comparisons or syntheses of phenological responses to climate change.

Differences in spatial scale within and among data sets affected estimates of phenological sensitivity, with greater advancements in flowering phenology with GDD detected from larger to narrower geographic samples (USA and Canada < Colorado < Niwot Area < observational study). However, the differences in sensitivity estimates within the herbarium data set were not statistically different, potentially due to necessarily smaller sample sizes with limited geographic scale.

Further, even limiting the herbarium data set to neighboring counties around Niwot Ridge underestimated phenological sensitivity in comparison to the observational

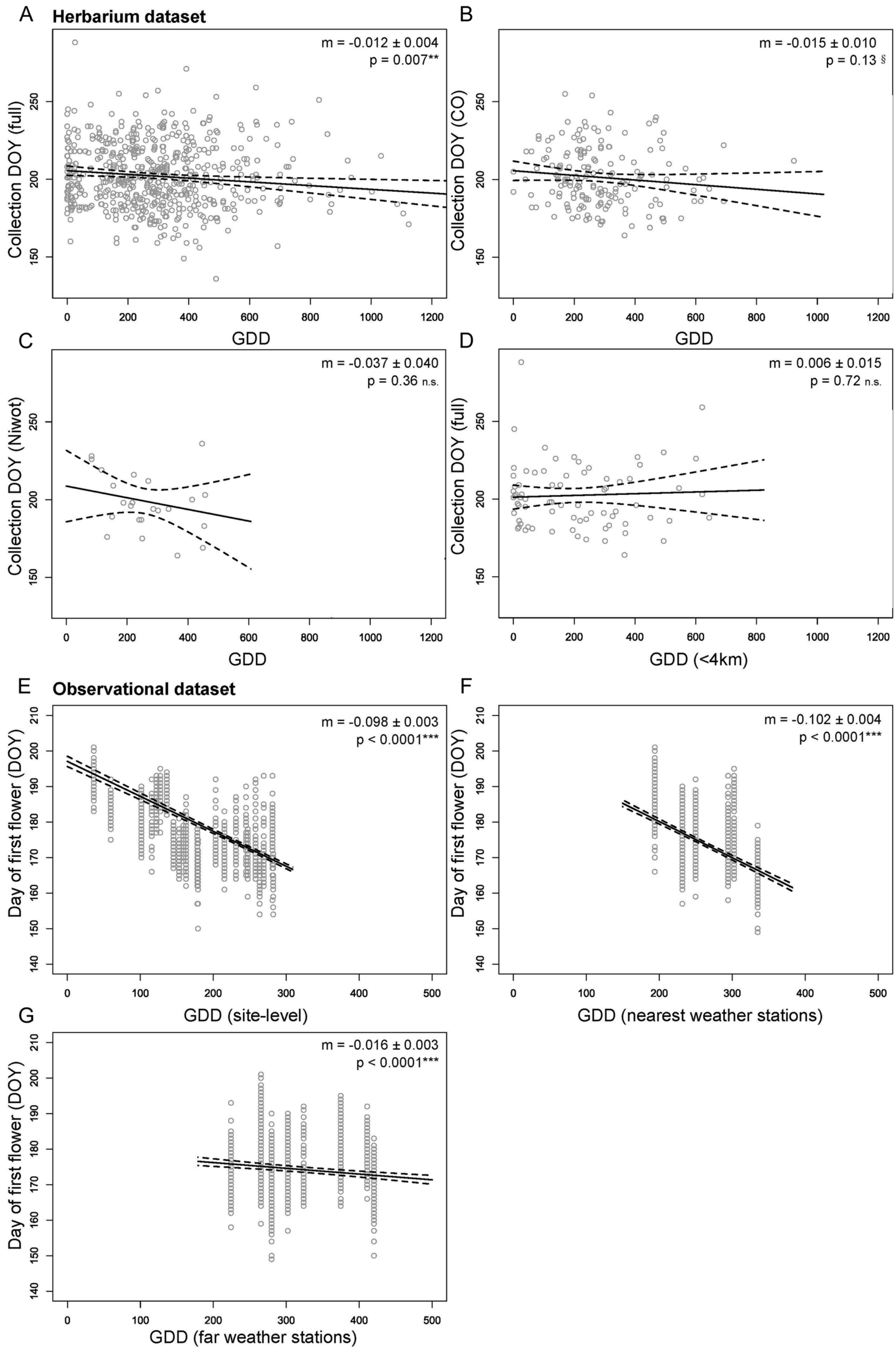

FIGURE 3 Effect of growing degree days (GDD) on flowering phenology in *Silene acaulis*. Top two rows: Effect of GDD on herbarium specimen collection date (day of year [DOY], a proxy for flowering time) in (A) full, (B) Colorado-only (CO), or (C) Niwot Ridge data sets, and (D) using climate data from weather stations within 4 km of collection locations (mirroring the scale of climate data collection in the observational data set). Bottom two rows: Effect of GDD on predicted day of first flower in the observational data set, calculated (E) at the site level, (F) from the nearest weather stations (matching the climate data collection methods used for the herbarium data set), or (G) from weather stations ~13 km from the site (approximate mean distance to weather stations, mirroring the scale of climate data collection in the herbarium data set). Gray circles represent observed data; solid lines represent estimated slopes of phenology against GDD from linear regressions including latitude and longitude as covariates; dashed lines represent 95% confidence intervals. We provide slopes (m) ± SE and associated *p*-values (***$P < 0.0001$; **$P < 0.01$; $^{\$}P < 0.1$; n.s. not significant [$P > 0.1$]) in each panel.

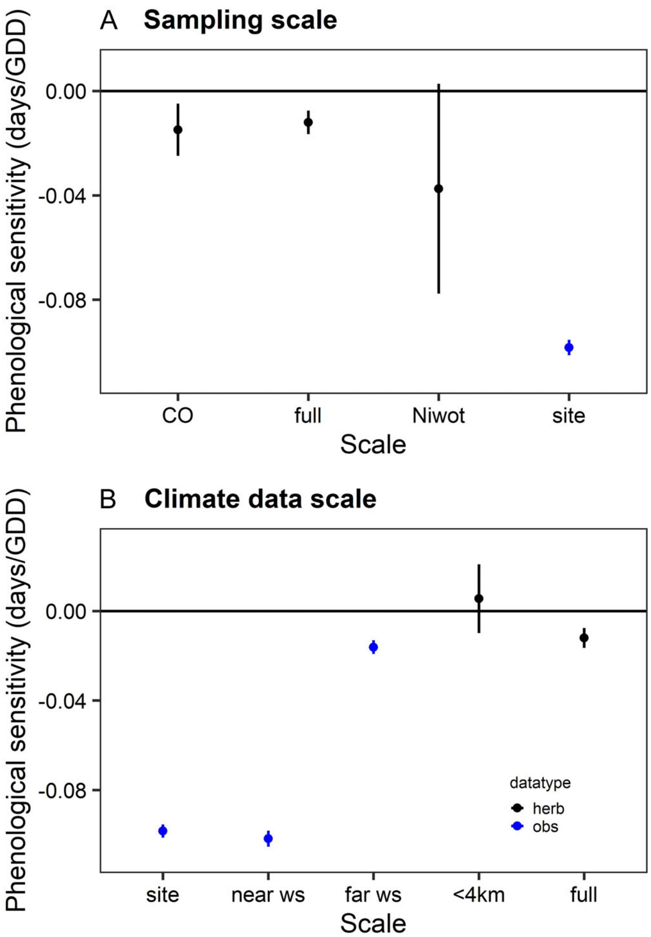

FIGURE 4 Phenological sensitivity in *Silene acaulis* (number of days by which the first flowering date shifts per growing degree day [GDD]) across spatial scales of (A) sampling and (B) climate data collection. Black and blue points are estimates from the herbarium ("herb") and observational ("obs") data sets, respectively. In A, herbarium data were collected at three spatial scales of sampling: the full data set spanning the United States and Canada ("full"), the Colorado-only data set ("CO"), and the Niwot Ridge data set ("Niwot"). We compared these estimates to sensitivity in the site-specific observational data set from Niwot Ridge ("site"). In B, climate data for the observational data set was collected at three spatial scales: at the site level, from the nearest weather station (matching climate data collection methods used for the herbarium data set) ("near ws"), and from weather stations ~13 km from the site (approximate mean distance to weather stations, mirroring the scale of climate data collection in the herbarium data set) ("far ws"). We compared these estimates to sensitivity in the herbarium data set only using climate data from weather stations within 4 km of collection locations (mirroring the scale of climate data collection in the observational data set) ("<4 km") and the full herbarium data set (which used weather stations within 50 km). Values are estimated slopes ± SE. The line at zero indicates no phenological shift in response to GDD; negative values indicate advanced phenology.

study. Data sets across broad spatial scales may average over different phenological sensitivities across multiple, possibly locally adapted populations, weakening estimates of an overall response. The herbarium data set also averages across elevational and range-wide differences in phenological sensitivity. For example, high-elevation populations or those in colder areas of a species range may demonstrate greater phenological sensitivity to climate than lower-elevation or warmer populations (Alexander, 2010; Prevéy et al., 2017). Elevation was collinear with latitude in our herbarium data set and removed from analyses, but most (408/620) specimens were collected 3000–4000 m a.s.l. (median elevation = 3369 m a.s.l.; Appendix S10), close to the elevation of the observational data set (3574 m a.s.l.). Future work in this system should test whether herbarium and observational data sets result in similar predictions if collected at the same spatial scale by gathering observational data from additional, geographically widespread populations. For instance, Ramirez-Parada et al. (2022) found agreement in both direction and magnitude of peak flowering time shifts between herbarium- and field-based data sets spanning a broad geographic range.

We found more mixed results when exploring the effects of climate data source on estimates of phenological sensitivity. First, estimates of phenological sensitivity in the observational data set were similar when using climate estimates at the site level or from nearby (<4 km away) weather stations. This suggests that climate data collected from nearby weather stations are suitable for quantifying local populations' phenological responses to warming, although plants can also respond to microsite environmental variation better captured by local-scale climate data (Oldfather and Ackerly, 2018; Denney et al., 2020). By contrast, using broader-scale climate data from more distant weather stations (~13 km away), mirroring the average availability of weather stations in the herbarium data set, results in lower estimates of sensitivity, comparable to those obtained in the herbarium analysis. This result likely occurs because increased noise in the climate data will necessarily reduce the slope of a regression coefficient. However, it also suggests that average availability of weather stations, commonly used to correlate phenology with climate, may be insufficient to accurately capture the climate conditions driving phenology, potentially contributing to underestimates of phenological sensitivity in studies without locally measured climate or nearby weather station data. Additionally, even short distances can translate to different climates in alpine environments, so coarser climate resolution could bias estimates of phenological sensitivity in alpine species through increased spatial climatic heterogeneity (Park and Davis, 2017; Cheng et al., 2021). Downscaled historical data sets (e.g., ClimateNA, PRISM, or WorldClim) could offer a potential solution to these problems in systems where monthly climate aggregates are strong predictors of phenology. In our system, daily climate data (used to calculate GDD) is better able to predict phenology than monthly climate aggregates, such as average temperature in May or June (M. Zettlemoyer et al., unpublished data). However, future analyses could use such spatially continuous climate data sets to further explore the effect of spatial and climate resolution on estimates of phenological sensitivity. For example, Ramirez-Parada et al. (2022) found strong correspondence between phenological sensitivity estimates in herbarium vs. observational data sets when using downscaled monthly climate normals obtained from ClimateNA (Wang et al., 2016) for both data sets.

Limiting the herbarium data set to only specimens with nearby weather station data resulted in reduced power to detect phenological shifts and did not improve estimates of phenological sensitivity. The large geographic and temporal scope of herbarium specimens may result in underestimates of phenological sensitivity in comparison to local observational or experimental studies, regardless of climate data source, potentially because herbarium data sets average responses across many populations and/or reflect geographic variation in the importance of other potential phenological cues, such as snowfall (Bjorkman et al., 2015), winter temperatures (Cook et al., 2012; Zettlemoyer et al., 2021), photoperiod (Meng et al., 2021), precipitation (Cui et al., 2017), fertilization (Wang and Tang, 2019), or burning (Richardson and Wagenius, 2022). However, pruning herbarium data sets too strongly on the basis of weather station availability can exacerbate biases in geographic sampling or sample size limitations. For example, almost half of the herbarium specimens in our data set were excluded from climate analyses because the nearest weather station was >50 km away, and this particularly impacted older specimens and specimens in remote, sparsely populated parts of North America. Our study species is limited to arctic and alpine tundra habitats with lower population density and weather station availability, and may be particularly susceptible to climate data limitations. For example, limiting this criterion to weather stations within 4 km left us with only 82 specimens, and we were no longer able to detect a significant effect of GDD on phenology.

We obtained stronger estimates of phenological sensitivity from observational data than from herbarium records, regardless of climate data source or geographic scale. Several other aspects could contribute to these different estimates of phenological sensitivity in herbarium vs. observational data sets. First, herbarium specimens represent a snapshot of phenology, whereas we were able to estimate first and peak flowering dates in the observational data set from complete flowering time curves. In the herbarium data set, the collection date for any specimen including an open flower was used as a proxy for flowering time. This method can result in variable estimates of phenology because it combines individuals at earlier and later stages of flowering (Panchen and Gorelick, 2017). Because they often include open, mature flowers, herbarium specimens may instead reflect peak or late flowering times (Schmidt-Lebuhn et al., 2013). Indeed, our estimates of flowering time in the herbarium data set were generally later than those from the observational data set. For example, we used our analysis of the full herbarium data set to predict flowering time given the latitude, longitude, and year of the observational study; this prediction (day 202.57) was substantially later than our observed mean day of first flower (day 175.99 ± 8.82). However, *S. acaulis* has a very small flowering window, with flowers persisting only for 1–2 weeks in the summer, so the collection date on our herbarium samples should be relatively similar to flowering time in the field. Indeed, we found similar results when using the day of peak flowering as the response variable in analyses, which suggests that the differences we see between herbarium and observational data sets are not simply due to variation in how phenology is quantified. However, future work should investigate whether these patterns hold in species with longer flowering periods. In particular, small phenological shifts may be difficult to detect via herbarium specimens if species have long flowering duration in relation to the magnitude of flowering shift. Some studies estimate phenology along a continuum from herbarium specimens by counting reproductive structures (e.g., Moussus et al., 2010; Panchen and Gorelick, 2017; Zettlemoyer et al., 2021). This approach was not possible in our system, as *S. acaulis* specimens are usually only small chunks of the overall cushion (Figure 1B). Additionally, it was difficult to distinguish between buds and fruits on older specimens. However, in systems where this is possible it could result in more precise estimates of phenological sensitivity from herbarium specimens. Second, the time span represented in herbaria corresponds with greater climatic variation than observational data sets (Davis et al., 2015) and may reflect longer-term responses to climate including evolutionary change. Here, our observational data set spans 6 yr while our herbarium data set spans 149 yr (1872–2021). However, *S. acaulis* is extremely long lived; past demographic studies have estimated the age of first reproduction to be >24 yr, and individuals may live up to hundreds of years (Morris and Doak, 1998). Even the much longer timescale of herbarium specimens is unlikely to represent substantial evolutionary effects on flowering phenology in this system.

Our results are consistent with those of a previous study by Davis et al. (2015) that found qualitatively similar responses (e.g., advancing phenology with warming) in herbarium and observational data sets. However, we highlight the important impacts of spatial sampling scale and climate data resolution on quantitative estimates of the magnitude of phenological sensitivity for a given species, *S. acaulis*. For example, in our system, we would reach similar qualitative conclusions—that *S. acaulis* is advancing its phenology in response to climate change—regardless of the data set. However, if our primary interest were in the magnitude of this shift, such as whether *S. acaulis* is advancing its phenology sufficiently rapidly to keep pace with climate change, our two data sets could result in different answers. Future work should examine whether similar patterns emerge when comparing range-wide observational studies on a single species as well as across multiple species. Accurate predictions of phenological shifts will likely require considering methods that span a variety of spatiotemporal scales, including explicit consideration of the effects of geographic extent and resolution of climate data. This has important implications for studies that seek to quantitatively compare or synthesize estimates of phenological sensitivity obtained from different approaches, climate sources, and spatial scales. We can improve estimates of phenological sensitivity to climate change by contributing to herbarium specimens, improving the workflow for extracting phenological data from herbarium specimens (Pearson et al., 2020), expanding observational and citizen science networks, and standardizing both phenological and climate measurements across studies.

AUTHOR CONTRIBUTIONS

M.Z. and M.D. conceived the study. M.Z. and J.W. collected the herbarium data. M.Z. and M.D. performed statistical analyses. All authors contributed to writing the manuscript.

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DATA AVAILABILITY STATEMENT

The data and code for this study are available in the Figshare Data Repository. Herbarium data set and code: https://doi.org/10.6084/m9.figshare.19083239.v3. Observational data set: https://doi.org/10.6084/m9.figshare.17136419.v1.

ORCID

Meredith A. Zettlemoyer http://orcid.org/0000-0002-8203-7207
Megan L. DeMarche http://orcid.org/0000-0002-5010-2721

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of herbaria.

Appendix S2. Distances between specimen collection locations and weather stations.

Appendix S3. Growing degree days calculated at different spatial and climate scales.

Appendix S4. Effect of year and growing degree days on flowering phenology in the herbarium data sets.

Appendix S5. Effect of growing degree days on first flowering day in the observational data set.

Appendix S6. Effect of growing degree days on peak flowering day in the observational data set.

Appendix S7. Growing degree days over time.

Appendix S8. Effect of growing degree days on flowering phenology in the herbarium data set, using weather stations within 4 km of collection locations.

Appendix S9. Collection day over time in Colorado and Niwot Ridge.

Appendix S10. Effect of GDD on collection day across elevations.

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