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Flowering time advances since the 1970s in a sagebrush steppe community: Implications for management and restoration

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Abstract

Climate change is widely known to affect plant phenology, but little is known about how these impacts manifest in the widespread sagebrush ecosystem of the Western United States, which supports a number of wildlife species of concern. Shifts in plant phenology can trigger consequences for the plants themselves as well as the communities of consumers that depend upon them. We assembled historical observations of first-flowering dates for 51 species collected in the 1970s and 1980s in a montane sagebrush community in the Greater Yellowstone Ecosystem and compared these to contemporary phenological observations targeting the same species and locations (2016–2019). We also assembled regional climate data (average spring temperature, day of spring snowmelt, and growing degree days) and tested the relationship between first-flowering time and these variables for each species. We observed the largest change in phenology in early-spring flowers, which, as a group, bloomed on average 17 days earlier, and as much as 36 days earlier, in the contemporary data set. Mid-summer flowers bloomed on average 10 days earlier, nonnative species 15 days earlier, and berry-producing shrubs 5 days earlier, while late summer flowering plants did not shift. The greatest correlates of early-spring and mid-summer flowering were average spring temperature and day of snowmelt, which was 21 days earlier, on average, in 2016–2019 relative to the 1973–1978 observations. The shifts in flowering phenology that we observed could indicate developing asynchronies or novel synchronies of these plant resources and wildlife species of conservation concern, including Greater Sage-grouse, whose nesting success is tied to availability of spring forbs; grizzly bears, which rely heavily on berries for their fall diet; and pollinators. This underscores the importance of maintaining a diverse portfolio of native plants in terms of species composition, genetics, phenological responsiveness to climatic cues, and ecological importance to key wildlife and pollinator species.

Redundancy within ecological niches may also be important considering that species roles in the community may shift as climate change affects them differently. These considerations are particularly relevant to restoration and habitat-enhancement projects in sagebrush communities across western North America.

INTRODUCTION

Around the world, many species are experiencing changes in their phenologies as global and local climates warm (CaraDonna et al., 2014: 2; Deacy et al., 2017; Jones & Daehler, 2018; Inouye, 2008). Shifts in phenology are often the first signs that climate change is impacting natural populations. Changes in plant phenology, in particular, have the potential to affect a wide variety of ecological processes and community dynamics, and understanding these changes is important for informing natural resource management (Enquist et al., 2014; Morellato et al., 2016). For example, phenological data can help identify plant species that are more or less vulnerable to a changing climate, emerging phenological mismatches between plants and interacting species, and potential changes in a community's ability to support the fauna that depend upon it (Morellato et al., 2016).

In the western United States, the sagebrush steppe ecosystem covers millions of acres and is key winter and migration habitat for ungulates such as mule deer, elk, and pronghorn; summer habitat for migratory songbirds and hummingbirds; and year-round habitat for the imperiled Greater Sage-grouse (*Centrocercus urophasianus*; Remington et al., 2021; Ricca & Coates, 2020). Greater Sage-grouse (hereafter "Sage-grouse") are of particular conservation concern given their complete reliance on the sagebrush ecosystem and their high sensitivity to disturbance (Casazza et al., 2011; Chambers et al., 2017; Pyke et al., 2015). Sage-grouse nesting success is closely tied to the availability of spring flowering plant and insect food resources during nesting and brood-rearing periods (Casazza et al., 2011; Gregg et al., 2008). The sagebrush steppe is also an integral part of the Greater Yellowstone Ecosystem (GYE) in the Middle Rockies ecoregion. The GYE supports top predators such as wolves and grizzly bears and is considered one of the most intact ecosystems in the world (Middleton et al., 2020; Noss et al., 2002; Sepulveda et al., 2015).

Changes in plant phenology have the potential to impact all of these species directly and indirectly. Yet, there has been little study of the impact of climate change on the phenology of plants in the sagebrush steppe ecosystem. One study of phenological shifts in rare and endemic plants of the southern Rockies concluded that changes were most pronounced in the inter-basin sagebrush ecosystem rather than the high altitude plant communities, with flowering dates shifting by 42 days since the 1800s (Munson & Sher, 2015). Several studies have shown the effects of warming conditions on a handful of sagebrush ecosystem forb species and their potential implications for nectar provisioning to pollinators (Sherwood et al., 2017; Sprayberry et al., 2017). Others have focused on climate change's impacts on the timing of the "green wave," the progressive spring green up, largely of grasses, from lower to higher elevation, and the consequences for migratory ungulates (Aikens et al., 2017; Merkle et al., 2016; Middleton et al., 2013). Lacking, however, is an understanding of the impacts of climate change on the phenology of the plant community as a whole, particularly the forbs and shrubs that provide essential food resources for many species including Sage-grouse and grizzly bears.

Understanding changes in plant phenology is important for ecosystem management for several reasons. First, it can identify species that may be more vulnerable to the effects of climate change. Although plant phenology is often tied to climatic cues such as temperature and snowmelt timing (CaraDonna et al., 2014, 2018; Inouye & McGuire, 1991; O'Leary et al., 2017; Sherwood et al., 2017; Willis et al., 2008), individual species can vary widely in the degree to which their phenologies track these cues (CaraDonna et al., 2014). In general, species that shift their phenologies in response to temperature may have higher survival under a warming climate than those that do not (Willis et al., 2008). Invasive species, in particular, often have phenologies that are more changeable and responsive to climate cues, and plasticity can give them a competitive advantage over natives (Alexander & Levine, 2019; Wolf et al., 2016).

Second, understanding shifts in plant phenology can help identify developing asynchronies or novel

synchronies between the plants and their pollinators and consumers (Bartomeus et al., 2013; Deacy et al., 2017; Inouye et al., 2000; McKinney et al., 2012). These changes occur when different species respond differently to climate cues or track climate-independent cues such as day length (Coppack et al., 2003; Dawson et al., 2001; Gwinner, 1990). For example, in the northern reaches of the southern Rockies in Colorado, earlier flowering times have resulted in a phenological mismatch where Broad-tailed Hummingbirds, which are arriving at the same time each year, are missing the peak of their traditional nectar sources, which are occurring earlier than in the past (McKinney et al., 2012). Such mismatches can have cascading effects through ecosystems, especially when they involve abundant or otherwise ecologically important species (Butt et al., 2015; Deacy et al., 2017). Management interventions in these cases may focus on ensuring alternative food sources are present when consumers need them most.

Third, the net effect of individual species' phenological changes can add up to whole-community phenological changes. Plant species' phenologies may shift in synchrony, leading to an overall change in the timing of a particular phenological event, such as leaf-out or first flowering. Alternatively, different responses among species in response to the same climatic cues may cause a shuffling of which species flower synchronously. For example, two studies have shown that climate change can cause novel assemblages of co-flowering plants in montane meadow communities (CaraDonna et al., 2014; Theobald et al., 2017). Understanding phenological shifts at a community level is important for assessing whether entire trophic resources are shifting in the timing of their availability and adjusting management practices accordingly.

One approach to understanding how climate change is impacting species' phenologies is to compare current-day phenological events with the timing of those events in historical records to capture changes that may be linked to climate change (Miller-Rushing & Primack, 2008). This approach has been used in a number of locations across North America (Bradley et al., 1999; Miller-Rushing & Primack, 2008; Willis et al., 2008) and worldwide (Hart et al., 2014; Hassall et al., 2007). For example, in eastern Massachusetts, Miller-Rushing and Primack (2008) found that forb communities flowered an average of 7 days earlier from 2004 to 2006 compared to Henry David Thoreau's and Alfred Hosmer's historic notes spanning 1852–1902.

We located and built on historical phenology data gathered by ecologist Frank Craighead, Jr. beginning in the 1970s. Over five spring and summer seasons, Craighead collected near-daily observations of phenological events in the sagebrush steppe and adjacent forest understory habitat surrounding his cabin in Grand Teton National Park (GTNP). These data served as the basis of his popular book *For Everything There is a Season* (1994), which gives a week-by-week account of ecological events that are likely to be occurring in the Grand Teton-Yellowstone area. Craighead wrote this book near the end of his 60+ year ecology career and may have foreseen the impending changes, as he wrote: "If the event occurs earlier or later than anticipated from the base data provided in the book, you can try to determine the influencing factors—for everything there is a reason."

Here, we use Craighead's data to do exactly what Craighead himself suggested: to understand the reasons behind changes in plant phenology, primarily first-flowering date, between the 1970s and 2010s. From 2016 to 2019, we made observations of the same plant species in the same locations as Craighead more than 40 years prior. Our primary research questions are: (1) How has plant phenology, on both a species and ecological group level, shifted between the 1970s and 2010s in this montane sagebrush habitat? And (2) what climate variables (e.g., spring temperature, growing degree days [GDD], timing of snowmelt) are most closely correlated with plant flowering? Ultimately, we aim to understand the ecological impacts of these changes for the plants themselves and for the wildlife that depend on them, in order to inform conservation and restoration planning for sagebrush ecosystems across the middle Rockies.

METHODS

Study site

Craighead's historical data and our contemporary observations center around Blacktail Butte, an isolated outcrop of vegetated limestone with elevations ranging from 1990 to 2343 m in GTNP within the middle Rockies, EPA Ecoregion Level III. The plant community at the base of Blacktail Butte is best described as montane sagebrush steppe (Innes & Zouhar, 2019), where mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana*) is the dominant species along with other shrubs including antelope bitterbrush (*Purshia tridentata*), rubber rabbitbrush (*Ericameria nauseosa*), mountain snowberry (*Symphoricarpos oreophilus*), and diverse perennial and annual forbs. Blacktail Butte also harbors patches of mixed conifer or aspen overstory with a native forb and tall shrub understory. There is a moderately used day hiking trail and climbing area at the base of Blacktail Butte, but other human disturbances are minimal, aside from a small homestead site on the northwest flank that was removed in the 1930s. Blacktail Butte is important

habitat for a diversity of wildlife including grizzly bears, black bears, moose, elk, mule deer, wolves, songbirds, raptors, and Sage-grouse.

Historical observations

We retrieved hand-written notes made by Frank Craighead from his family archives containing nearly 800 phenological observations of native and nonnative angiosperms observed in 1974–1979 and 1988 (Figure 1) and entered these into digital form. During each of these years' spring and summer seasons, Craighead typically made two to four observations per week of various phenological events including the timing of plant emergence

and flowering, migratory bird arrivals, mammal behaviors such as bears emerging from hibernation, fish spawning, and weather events. His notes include observations of 258 species of flowering plants, although not every species was observed every year. We categorized plant observations representing first presence of leaves, first presence of buds, first flower, peak flower, and occurrence of fruits or seeds. All data were sorted by species, year, and phenological event. The vast majority of the observations were of first-flowering date, and we have therefore focused our analyses on this phenological phase (phenophase).

We identified 51 species that had at least three first-flowering observations in our historical data set. We reviewed the written locations of each record using the
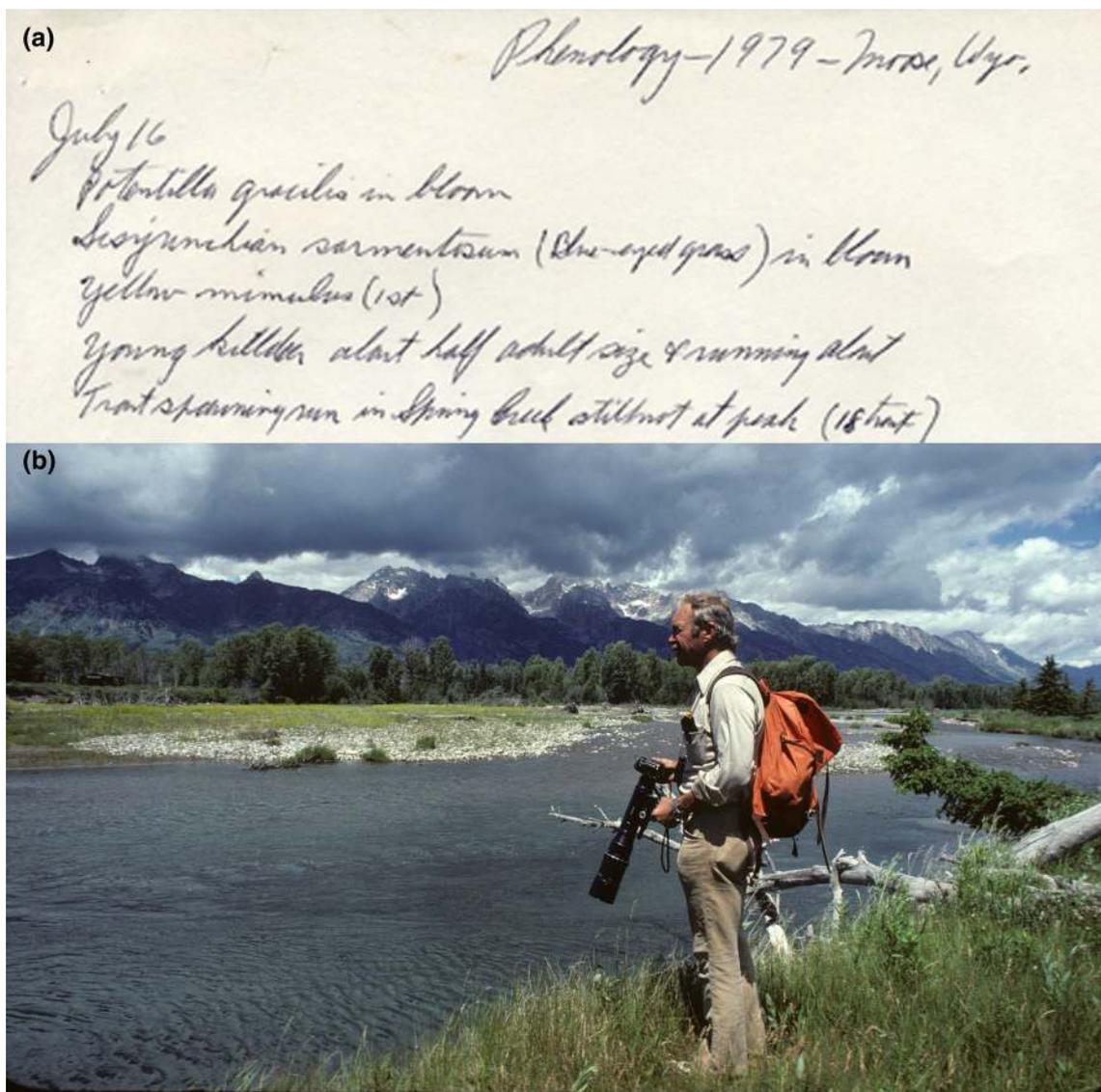

FIGURE 1   (a) An example of the hundreds of detailed records of phenology, handwritten by Frank Craighead in the 1970s. Craighead is pictured in the lower panel (b) near his home in Moose, Wyoming where the majority of the phenology observations were made. Notes courtesy of the Craighead family; photo courtesy of Charlie Craighead

Spatial Analysis Georeferencing Accuracy (SAGA) protocol (Bloom, Flower, & DeChaine,et al. 2018), and identified a 2.7-km trail that Craighead's surviving family members told us he used routinely to make his phenology observations (C. Craighead and S. Craighead, personal communication) and confirmed by his notes. The trail ranges from Craighead's cabin just north of Blacktail Butte and the area along the northwest edge of Blacktail Butte through a gradient of ecosystem types (Appendix S1: Figure S1).

Contemporary observations

In spring 2016, we initiated contemporary observations of the focal 51 species (Appendix S1: Table S1). Our study site was identified to match Craighead's path as best as possible, representing a gradient of ecosystem types, from the dry, exposed mountain sagebrush steppe near Craighead's home, through a mixed conifer forest, across another mountain sagebrush steppe, and into an aspen grove with tall shrub and forb understory. The study site's extent along Craighead's regular walking path was chosen to represent the major ecosystem types that were present, nearby, and collectively contained all the species observed by Craighead. Similar to other studies that have replicated historic phenology observations (Bradley et al., 1999; Jones & Daehler, 2018; Miller-Rushing & Primack, 2008), we made the assumption that Craighead was aware of where along the path he was likely to encounter earliest flowering plants of each species and made his observations at these locations.

During spring, summer, and early fall 2016, 2017, 2018, and 2019 we visited the study site a minimum of twice weekly (every 2 to 4 days), which is considered relatively high frequency (Miller-Rushing et al., 2008), to record the phenophase of our focal species. Although we collected contemporary data on every phenophase, for this paper, we are reporting on first flower, the only phenophase with sufficient historical data to allow direct comparison. For each plant species, we recorded the day of year (DOY; 0–365) for the first flower observed each year. We also grouped species into one of six ecological groups (Appendix S1: Table S2) based on average first flower date for the entire study period (1974–2019) and species' ecology. We categorized most species into groups that split the flowering season approximately into thirds (April–early September) based on the average first-flowering date of the entire data set (contemporary and historic data), a common practice in phenology studies (Arfin Khan et al., 2018; Moore & Lauenroth, 2017; Pearson, 2019). We defined early-spring flowers as having an average first flower before 15 June, mid-summer

between 16 June and 31 July, and late as any species with an average first flower date after 31 July. To explore other ecological patterns, we also defined shrubs that produce berries edible to bears and birds as "berries" and species that are not native to the region as "nonnative," the smallest group since there were few nonnative species in the historical record.

Climate data

We assembled several sets of climate data in order to (1) quantify changes in climate variables relevant to flowering over the study period and (2) test the relationships between these variables and observed changes in first-flowering date for individual species and across different ecological groups. Data were derived from both the Moose Weather Station (National Oceanic and Atmospheric Administration, 2020) and the Parameter elevation Regression on Independent Slopes Model (PRISM; PRISM Climate Group, 2020).

The Moose Weather Station is located at the GTNP headquarters less than 1.5 km from the base of Blacktail Butte and is managed by the National Park Service. This weather station has been continuously recording daily temperatures and daily snow depth from 1958 to the present within a 100-m area. Unfortunately, data were missing for April 1979 and could not be related to first-flowering time for this particular year. For all other years, we derived spring temperature, snowmelt timing, and GDDs. Spring temperature was defined for each year as the mean of the mean daily temperatures for all days in the months of March, April, and May. Snowmelt timing was defined as the first day of the spring where snow depth reached zero (following methods used by Billings & Bliss, 1959; Harpold et al., 2012). Over the entire study period, snow depth always reached zero after 1 March. We also calculated GDD using a threshold temperature of 5.0°C (Anderson et al., 1986; Richardson et al., 1975). Since snowpack insulates the soil surface (Inouye & McGuire, 1991; Lundquist & Lott, 2008), we calculated GDD accumulated beginning from the date of snowmelt timing for each year.

To complement the fine temporal and spatial resolution from the Moose Weather Station data, we also derived temperature data from PRISM (Daly et al., 1997). PRISM data were used to help validate the Moose Weather Station data. The use of a single station is often questioned, as there can be variation in instruments over time, and often these stations move locations while maintaining the same name. Although the Moose station has not been moved significantly and is close to our study site, its data still carry some of the limitations of being derived from just one station.

PRISM data are derived from multiple climate observations from a wide range of networks overlayed on Digital Elevation Models to develop sophisticated spatial climate data sets, which are considered very accurate and widely used (Bloom, Flower, & DeChaine, 2018; Bloom, Flower, Medler, et al., 2018; Buban et al., 2020; Daly et al., 1997). Using PRISM data focused on a 4-km grid cell centered on Blacktail Butte, we averaged monthly spring (March, April, and May) minimum, mean, and maximum temperatures from 1970 to present. Because PRISM only provides monthly temperatures, we could only source GDD and snowmelt timing from the Moose Weather Station, which provides daily temperatures.

Data analysis

To quantify changes over time in patterns of phenology, we conducted paired t tests to look at differences in the average date of first flower for each ecological group between the contemporary and historical data sets. Data were paired by species. We omitted data from 1988 to isolate the era of the 1970s to compare to the era 2016–2019. We calculated standard deviation from the mean for each ecological group for the 1970's historical dataset (SD70s), and 2000's contemporary dataset (SD00's). We did not test for difference in first flower between historic and contemporary observations for each individual species, or across individual years, because of small sample sizes leading to low power to detect differences. However, to enable visualization of these differences, we calculated and plotted the mean and range of first-flowering dates for each species within each era.

We used linear regressions to analyze change in climate variables over time and the relationships between these climate variables and first-flowering dates. We separately regressed minimum, mean, and maximum spring air temperature and snowmelt DOY as a function of year continuously from 1974 through 2019, using climate data for each spring. To explore potential climatic drivers of phenology, we built separate regression models for each species, in which first flower date across all years (historical and contemporary) is modeled as a function of one of four predictor variables: PRISM mean spring temperature, Moose Weather Station mean spring temperature, GDD, and snowmelt timing. We did not analyze first flower date as a function of multiple predictor variables given constraints of sample size and some collinearity of variables. We interpret the R^2 value of the resulting models as a measure of the relative influence of each climate variable on the first-flowering date of each species. We repeated this analysis for the average first flower DOY for each ecological group as a function of each predictor variable individually. Using the $\alpha = 0.05$ level for significance, we acknowledge the 5%

risk of type-1 error for each test used under this approach. All analyses and plotting were performed in R (R Core Team, 2018) using the *plyr* and *ggplot2* packages (Wickham, 2016; Wickham et al., 2019).

RESULTS

Climate trends

Climate data from our study area reveal a gradual, yet variable, increase in spring temperature since the 1970s of approximately 2.0°C (Figure 2a). Using data from the Moose Weather Station, there was a statistically significant increase in maximum ($\beta = 0.044$°C/year, $R^2 = 0.070$, $p = 0.042$), mean ($\beta = 0.041$°C/year, $R^2 = 0.098$, $p = 0.019$), and minimum ($\beta = 0.038$°C/year, $R^2 = 0.105$, $p = 0.016$) temperatures from 1973 to 2019. Using data derived from PRISM, there was no detectible increase in maximum temperatures ($\beta = 0.004$°C/year, $R^2 = -0.021$, $p = 0.806$), a marginal increase in average temperatures ($\beta = 0.021$°C/year, $R^2 = 0.03$, $p = 0.121$) and a statistically significant increase in minimum temperatures ($\beta = 0.038$°C/year, $R^2 = 0.153$, $p = 0.004$).
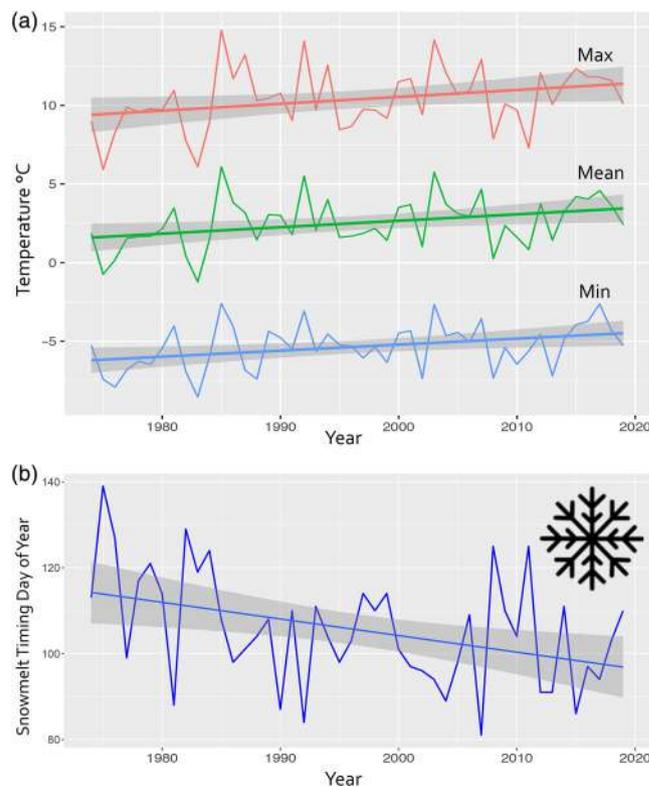

FIGURE 2 Trends from 1975 to 2019 in (a) average maximum, mean, and minimum daily spring temperature (March, April, and May) and (b) snowmelt timing (defined as the first day of year [DOY] with a snow depth of zero). All data derived from the Moose Weather Station 1974–2019

Snowmelt timing (DOY) showed a negative trend over time (Figure 2b), with snowmelt day approximately 20 days earlier in 2016–2019 than in the 1970s ($\beta = -0.387$ days/year, $R^2 = 0.136$, $p = 0.007$).

Changes in phenology and their relation to climate variables

Nearly all species flowered weeks earlier in 2016–2019 than in the 1970s (Figure 3). The greatest shift was observed in an early-spring flower, hooded phlox (*Phlox hoodii*), for which flowering time advanced by ~36 days between the two eras. Although there was variation among species within each ecological group, there was a clear overall pattern of early-flowering species showing a larger advance in first-flowering date than the later-flowering species (Figure 3).

Early-spring flowering species, such as yellowbells (*Fritillaria pudica*) and arrowleaf balsamroot (*Balsamorhiza sagittata*), showed the largest change in mean first-flowering date of all the ecological groups, advancing by 16.8 days ($t = -9.18$, $n = 16$, $p = 0.001$, SD70s = 14.8 days, SD00s = 12.4 days). All but one of the 16 species had a mean contemporary flowering date >11 days earlier than the historical flowering date. Mid-summer flowers, which included sticky geranium (*Geranium viscosissimum*) and green gentian (*Frasera speciosa*), bloomed on average 10.3 days earlier ($t = -4.85$, $n = 21$, $p = 0.001$, SD70s = 10.5 days, SD00s = 11.8 days), and the pattern of earlier flowering date was consistent for most of the species in this group. Nonnative species bloomed on average 14.5 days earlier today ($t = -13.3$, $n = 3$, $p = 0.005$, SD70s = 39.2 days, SD00s = 37.3 days), but the total sample size was small and there was a high degree of interspecies variation. The greatest shift in this group was in the noxious weed, musk thistle (*Carduus nutans*), which flowered an average of 16.2 days earlier. Berries, such as Canada buffaloberry (*Shepherdia canadensis*) and Oregon grape (*Mahonia repens*), bloomed on average 4.9 days earlier than in the 1970s ($t = -1.87$, $n = 6$, $p = 0.079$, SD70s = 13.6 days, SD00s = 20.7 days). For this ecological group as well, the overall sample size was low and interspecies variation was large, which likely explains why the difference for this ecological group was not statistically significant at the $\alpha = 0.05$ level. Four of the berry-producing shrubs (*S. canadensis*, *M. repens*, *Amelanchier alnifolia*, and *Lonicera utahensis*) showed substantially earlier flowering dates in the contemporary era compared to the historical era, whereas the other two species (*Prunus virginiana* and *Rosa woodsii*) did not (Figure 3). Late-season flowers as an ecological group did not appear to have changed much (2.3 days earlier) with respect to first flower timing

($t = -0.650$, $n = 5$, $p = 0.276$, SD70s = 3.2 days, SD00s = 7.1 days). At an individual species level, three of the five species in this group showed an earlier first-flowering date, with the greatest shift in Northern bedstraw (*Galium boreale*) at 11.5 days earlier.

There was substantial variation in the strength and direction of the linear regressions between first-flowering date of 51 species of interest and the four climate variables used in this analysis (Figures 4 and 5). For example, first-flowering date for shooting star (*Dodecatheon pulchellum*, $R^2 = 0.890$, $n = 8$, $p < 0.005$), and early yellow violet (*Viola nuttallii*, $R^2 = 0.92$, $n = 8$, $p < 0.005$) both had tight linear regressions with mean spring temperature for both Moose and PRISM data sets. In contrast, other species such as prairie star (*Lithophragma parviflorum*, $R^2 = 0.890$, $n = 8$, $p < 0.002$) and yellow potentilla (*Potentilla gracilis*, $R^2 = 0.97$, $n = 8$, $p < 0.001$) showed stronger relationships with snowmelt timing. Some species such as green gentian (*Frasera speciosa*) showed a strong relationship with both average spring temperature ($R^2 = 0.81$, $n = 8$, $p < 0.05$) and snowmelt timing ($R^2 = 0.940$, $n = 8$, $p < 0.005$). Some species, mostly late flowering, showed moderate relationships with GDD, as exemplified by yampah (*Perideridia gairdneri*, $R^2 = 0.67$, $n = 6$, $p < 0.05$). Other species, including chokecherry (*Prunus virginiana*, $n = 6$) and the parasitic orchid, striped coral root (*Corallorhiza striata*, $n = 6$), had first-flowering dates that did not show a strong regression with any climate variable.

Across ecological groups, some general patterns are apparent. Average spring temperatures and snowmelt timing were most strongly correlated with first-flowering dates for most, but not all, early-spring and mid-summer flowering species. In contrast, flowering for later species was better correlated with GDD, with high variability among species in the strength of these correlations. Timing for three of the five late-summer flowers showed a stronger regression with accumulated GDD than other climate variables, but none of the species showed very strong regressions with climate variables. Berries differed in their responses, and only one species showed a significant ($p < 0.05$) relationship with a single climate variable: Utah honeysuckle (*L. utahensis*) and GDD ($R^2 = 0.98$, $p = 0.001$). Similarly, results for nonnatives were less clear, although dandelion (*Taraxacum officinale*; $R^2 = 0.48$, $p = 0.056$) and salsify (*Tragopogon dubius*; $R^2 = 0.68$, $p = 0.043$) showed moderate relationships with snowmelt timing.

Statistics and expected errors

This study benefits from a very large amount of data. Thousands of observations from hundreds of days
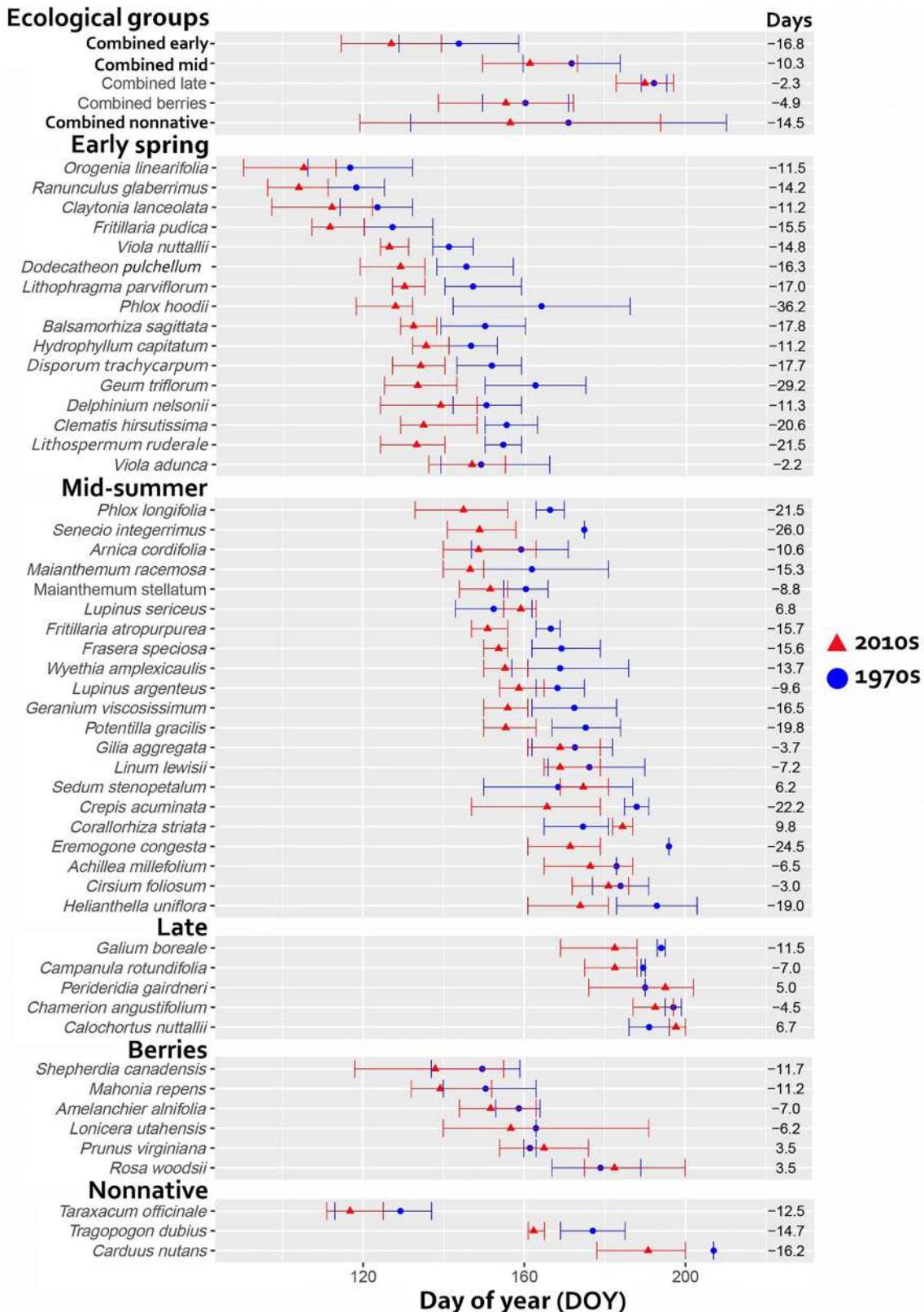
FIGURE 3 Comparison of first-flowering dates from 2016 to 2019 (red triangles) versus 1974–1979 (blue dots) at the same location in Grand Teton National Park. Far right column notes the difference between the two means for each era. Whiskers for ecological groups display one standard deviation from the mean, whereas whiskers for individual species display the entire range of first-flowering dates for each era. Ecological groups with statistically significant differences ($p < 0.05$) between the means are shown in boldface type
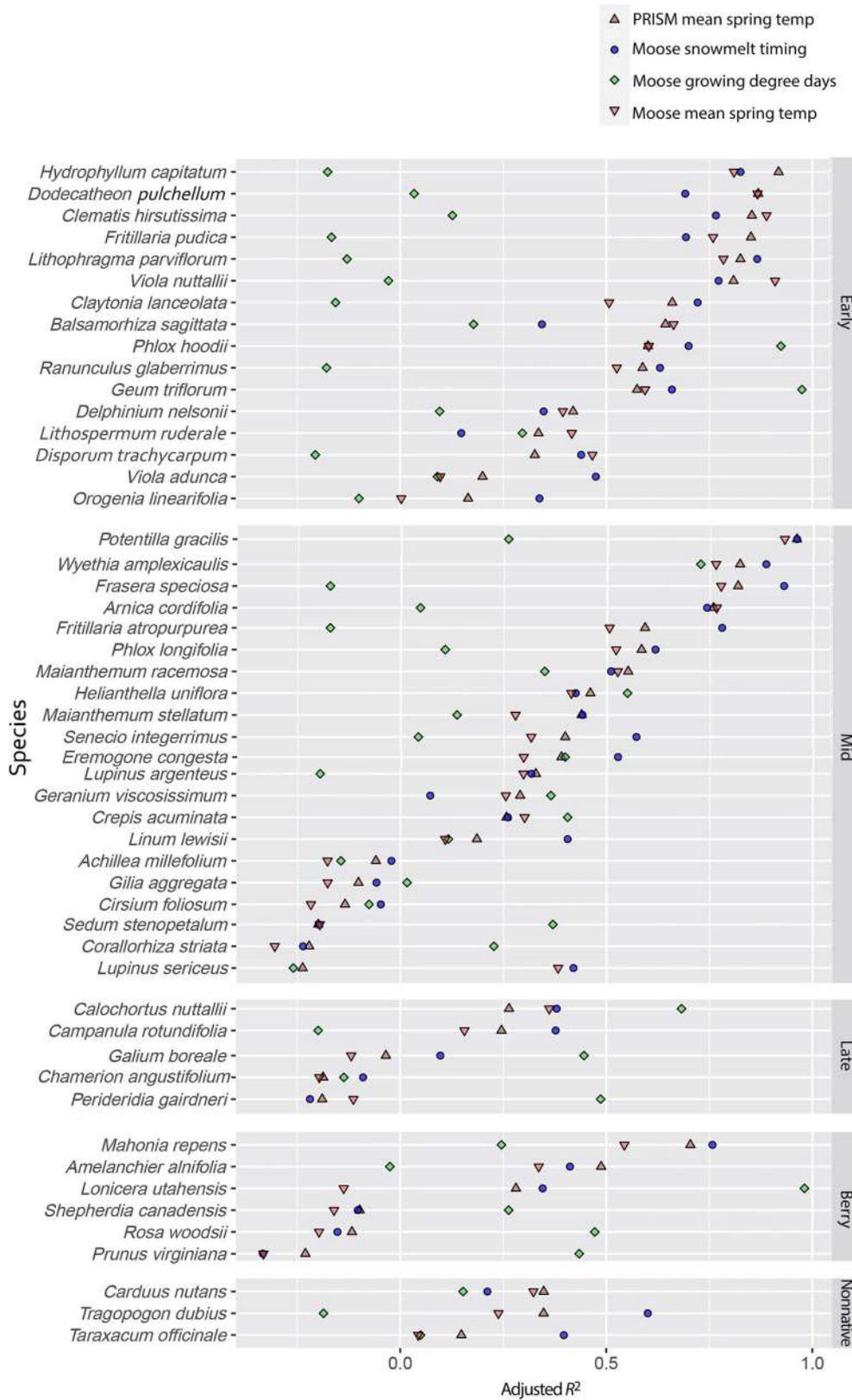
FIGURE 4 Model fit (adjusted R^2) for first flower date as a function of four predictor variables: average spring temperatures (March, April, and May) from both Parameter elevation Regression on Independent Slopes Model (PRISM) and Moose Weather Station and growing degree days, and snowmelt timing derived from Moose Weather Station
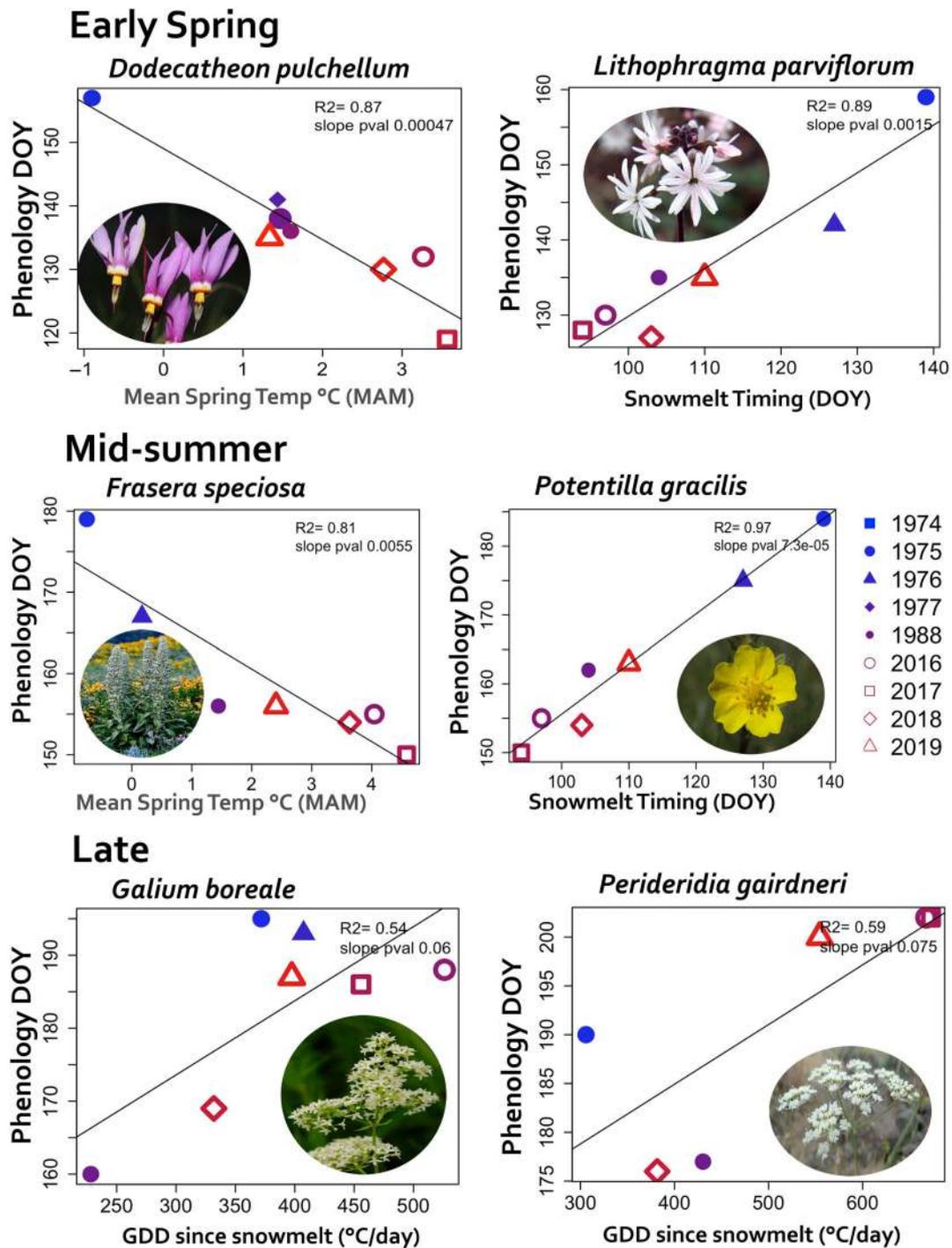
FIGURE 5 Date of first flower, phenology day of year (DOY), as a function of different climatic variables: mean spring temperature (March, April, and May), growing degree days (GDDs), and snowmelt timing for representative species in three ecological groups: early-spring, mid-summer, and late-summer flowering species. Observations by Craighead (1974–1979, and 1988) are indicated by solid symbols, and observations made by the authors are hollow (2016–2019). Mean spring temperatures were derived from Parameter elevation Regression on Independent Slopes Model (PRISM); GDDs and snowmelt timing were derived from the Moose Weather Station

spanning many years allow for a robust and in-depth statistical analysis. The known type-1 error rate for a test at the $\alpha = 0.05$ level is by definition 5%, meaning that we expect to see ~10 "false positive" models indicating a statistically significant relationship even if there were no

true relationship between first-flowering data and any of the climate variables tested. While an expected 10 errors are a substantial amount of "noise" in our signal, we found 62 statistically significant correlations between a species' first-flowering date and one of the climate

variables tested, with strong, clear trends in particular groups that support previous findings. Therefore, we suggest that while about one-sixth of the individual correlation tests may be insignificant due to known test error, we remain confident that the overall themes described in the results are robust and consistent with previous studies.

DISCUSSIONS

The sagebrush steppe ecosystems, both the montane and basin forms, cover vast regions of the American West. To date, there has been little research documenting the impacts of climate change on the phenology of the sagebrush community's plants, which support the region's diverse wildlife. Through comparing ecologist Frank Craighead's observations (1974–1979, 1988) with contemporary patterns (2016–2019), we found that many species, mostly native perennial forbs and shrubs, are flowering significantly earlier now than in the past. These species are important forage resources for a variety of species of conservation concern from grizzly bears to Sage-grouse, and our findings highlight a potential need for active management to ensure successful sagebrush habitat management and restoration.

Earlier spring flowering

While nearly all of our study species showed evidence of change in first-flowering date over the last 40 years, the magnitude of this change varied by species group. For early-spring species, the onset of flowering has advanced approximately 17 days since the 1970s (3.4 days/decade), with some species emerging more than a month earlier. For most early-season species, flowering DOY is tightly correlated with increased spring temperatures and earlier snowmelt timing, suggesting that climatic changes are driving the observed earlier flowering date. The few non-native species in our study are flowering over 2 weeks earlier than in the 1970s (2.9 days/decade). Mid-summer species are flowering on average 10 days earlier (2 days/decade), and berry-producing shrubs are flowering anywhere from 0 to 12 days earlier (0–2.4 days/decade). Late-summer flowering species, on the other hand, have not shifted very much in terms of their first-flowering time (only 2.3 days earlier or 0.46 days/decade).

Our results corroborate findings from other phenological studies that have compared historical with contemporary data, all of which have found evidence of earlier flowering times across North America (CaraDonna et al., 2014; Gallinat et al., 2018; Inouye, 2008; Miller-Rushing & Primack, 2008). In one of the most comprehensive historical-contemporary comparisons, Miller-Rushing and Primack (2008) found that 43 common species flowered an average of 7 days earlier in 2004–2006 than 1856–1902 near Walden Pond in Concord, Massachusetts, and this was directly correlated with a 2.4°C increase in temperature. Similar to our findings, they found first-flowering date for spring flowers was correlated with mean temperatures in the month or two before flowering, whereas summer flowers showed more interannual variation and less correlation with mean spring temperatures.

The nearly 3 weeks' advance in spring flowering we observed far exceeds the 1-week advancement observed by Miller-Rushing and Primack in the eastern U.S. near sea level and is strikingly similar to findings from a montane meadow system in the Rocky Mountains of Colorado. Using a continuous data set of phenology observations for over 120 species from 1974 to 2012, CaraDonna et al. (2014) found a 20.7-day shift in the timing of spring peak floral abundances and a 12.9-day shift in summer peak floral abundances. Although several authors (CaraDonna et al., 2014; Inouye et al., 2019) caution that first-flowering date may not correlate well with peak flowering, the close similarity between the magnitude of shift in peak flowering that CaraDonna et al. observed and the shift in first flowering that we observed suggests the possibility of some generalities in how flowering plants are responding to climate across the Rocky Mountain region. The much greater impact of climate change on plant phenology at these two montane sites compared to findings from near sea level supports the idea that the phenology of high-elevation plants may be disproportionally affected by climate change (Bloom, Flower, Medler, et al., 2018; Schmid et al., 2017; Xu et al., 2020).

Similar to other studies in systems where snowpack accumulates over winter, we found that snowmelt timing was an equally or more important correlate of phenology than temperature for many species (Inouye, 2008; Inouye & McGuire, 1991; O'Leary et al., 2017; Sherwood et al., 2017). Snowmelt timing has advanced substantially (on average, approximately 21 days earlier) in our study system over the last 40 years. This may explain why we found that early-spring flowers, which emerge soon after the snow melts, have shifted their flowering dates much more than plants that bloom later in the summer. Late summer flowers, in general, had a stronger relationship with GDDs than other climate variables. Other potential drivers of phenology not explored in this study and potentially impacting some of our study species include day length, precipitation as rain, soil moisture, vapor pressure deficit, and grazing by herbivores (Arfin Khan et al., 2018; Geremia et al., 2019; Moore & Lauenroth, 2017; Notaro et al., 2019; Wolf et al., 2017).

Although most species showed pronounced shifts in first-flowering time since the 1970s, there was substantial variation among species, and some showed little overall change. This degree of variation is consistent with studies in other regions (Arfin Khan et al., 2018; CaraDonna et al., 2014; Miller-Rushing & Primack, 2008; Willis et al., 2010). Species whose phenologies shift more in response to warming conditions may be less vulnerable to climate change and potential local extinction (Cleland et al., 2007, 2012; Willis et al., 2008, 2010). They may even benefit from an extended growing season, depending on moisture conditions, or avoided competition (Alexander & Levine, 2019). However, there is also evidence that earlier phenology can reduce plant fitness by exposing plants to stresses such as early-season herbivory or frost events (Block et al., 2020; Inouye, 2008), or by causing phenological mismatches with pollinators (Kudo & Ida, 2013; Miller-Rushing et al., 2010).

An important caveat to our study is that first-flowering date is an imperfect measure of plant phenology. First-flowering date of any observed individual in a population captures the leading edge of individual plant variation and thus may overestimate the effects of climate change on other, more ecologically important phenological indicators (Inouye et al., 2019). For example, CaraDonna et al. (2014) found that first-flowering date advanced more than other indicators for 56% of their 60-species data set. Further, only 17% of species had a uniform response across first-flowering date, peak flowering date, and last flowering date. First-flowering date does not shed light on how a warming climate affects the whole distribution of a population's flowering time, nor the myriad other ways in which climate change can affect a plant population (Inouye et al., 2019). Further, first-flowering date may be more sensitive to inter-annual variation in temperature than other metrics of plant phenology (Inouye et al., 2019). To best capture a species' phenological sensitivity to warming temperatures, it is recommended that researchers collect data on multiple phenological stages, multiple different plants within the population, and with repeat measurements on the same individuals over time (Inouye et al., 2019).We suggest that longer-term research in the sagebrush system should follow the preceding study design suggestions and focus on species such as *Viola adunca* and *Lupinus sericeus*, which showed little change in flowering time, as well as species such as *P. hoodii* and *Geum triflorum*, which showed the greatest advance in flowering date, in order to further our understanding of how phenological responsiveness to climate change relates to population vulnerability in the long-term. Further, there is a broader need to understand whether the vulnerability–responsiveness relationship depends on ecological contexts such as whether the plant is an early- versus late-emerging species or the climate cues with which it is most closely correlated.

Community implications

The GYE and several other regions of the sagebrush ecosystem are notable in supporting a complete community of large mammals, including top predators, as well as some of the most intact long-distance ungulate migrations in the world (Middleton et al., 2013, 2020; Noss et al., 2002). The broader sagebrush ecosystem is home to myriad sagebrush dependent species, including the declining Greater Sage-grouse, which has been considered for protection under the Endangered Species Act. These and other species may be impacted by the changes in plant phenology that have already occurred and are likely to accelerate in the decades to come.

The substantial shift in phenology we observed among early-spring forbs could have important implications for Sage-grouse in particular. Sage-grouse hens and chicks rely heavily on early-season forbs and the associated insect community as high-protein diet items during pre-laying, nesting, and brood-rearing, and the availability of these food items may ultimately determine nest success rates (Barnett & Crawford, 1994; Casazza et al., 2011; Crawford et al., 2004; Dumroese et al., 2015; Gregg et al., 2008). Some of the key forbs that Sage-grouse consume during this life stage include genera we observed to be flowering significantly earlier than in the past, such as *Crepis* spp., *Delphinium* spp., *Ranunculus* spp., and *Phlox* spp. Although our data are limited to first-flowering date, (which may be more sensitive to climate change than other metrics, as discussed above), it is possible that first leaf-out and peak green biomass of these forb species are also occurring earlier now than in the past and may not be synchronizing optimally with Sage-grouse breeding phenology. There may also be a shift in the availability of the invertebrates that are dependent on this flora, which are key food sources along with the forbs themselves for Sage-grouse (Dumroese et al., 2015). Whether, and to what extent, a phenological mismatch between Sage-grouse and their spring dietary needs is developing depends on (1) whether sage-grouse breeding phenology is static or also shifting to an earlier date and (2) patterns of change in phenology of insects and/or other forb species that may provide dietary alternatives to early-season forbs. Further work is necessary to address these questions and ascertain whether change in early-season forb phenology is limited to first-flowering date or also corresponds to changes in phenological metrics (such as first or peak leaf out) that most impact the forage resources available to sage-grouse.

Little research has addressed the impacts of climate change on sagebrush forbs; our results suggest that the impacts could be substantial and potentially consequential for a wildlife species of high conservation concern.

Earlier flowering could also cause phenological mismatches between flowers and pollinators, which could result in population declines among both (Kudo & Ida, 2013). It is possible that the phenology of certain plants, especially early-spring flowers, is no longer lining up in timing with other important ecological events such as the arrival of migratory birds, pollination habits of insects, and foraging of large mammals, as has been seen elsewhere (Debinski et al., 2014; Mayor et al., 2017; McKinney et al., 2012; Singer & Parmesan, 2010). For example, Broadtail Hummingbirds in the southern Rockies are arriving the same time each year while flowers are blooming earlier (McKinney et al., 2012); thus, hummingbirds are missing peak nectar availability, resulting in reduced brooding success. Since the patterns we observed in early-spring flowering are consistent with patterns found in the southern Rockies, this suggests that similar phenological mismatches between hummingbirds or other taxa and flowering plants may be occurring, or may occur in the future, in the middle Rockies and neighboring sagebrush basins.

Grizzly bears are another species of concern that may be impacted by shifts in plant phenology. Bears rely heavily upon berry-producing shrubs during hyperphagia, the crucial period of time in the fall when they consume excess calories to fatten up for hibernation. Body-fat percentage entering hibernation is correlated with survival and fecundity (Hertel et al., 2016; Stenset et al., 2016). We found that six berry-producing shrub species are flowering on average 5 days earlier now than in the 1970s, but there was substantial variation among species. For example, the first-flowering date of Canada buffaloberry (*S. canadensis*) has advanced by nearly 12 days, whereas the flowering time of the ecologically similar wild rose (*R. woodsii*) has shown little to no change. Although we did not have historical fruiting data to compare to contemporary patterns, other studies have shown that flowering time is related to fruiting time and shifts in fruiting time are likely greater than observed shifts in first flower (Laskin et al., 2019). Laskin et al. (2019) predicted that buffaloberry flowering will advance approximately 13 days and fruiting up to 20 days by 2100 in the Canadian Rockies, due to the increased accumulation of GDDs as summer progresses. Given that we have already observed a 12-day shift in the first-flowering time of buffaloberry, we infer that fruiting may be occurring nearly 3 weeks earlier than in the 1970s. If that is the case (and if first-flowering date correlates with peak flowering date), this could be leading to a widening gap between the availability of this key food and the time when bears' caloric needs are greatest. Wild rose, which showed little change in first-flowering date, may be a more reliable food source for bears in the future, unless its lack of phenological response indicates an overall greater vulnerability of this species to climate change. The ramifications of these species' responses to climate change merits future attention given that climate change is also threatening other important late-season bear foods, such as white bark pine (Loehman et al., 2011; Mattson et al., 1991), and that bear–human conflict rates may increase if bears have increasingly fewer food sources during hyperphagia and humans continue to colonize current bear habitat.

As we have noted, there are important limitations and caveats to what we can infer from first-flowering data alone. In addition to over-estimating population-level changes, first-flowering date is rarely the most ecologically relevant metric for understanding the community implications of phenological shifts (Inouye et al., 2019). Changes in peak flowering and fruiting dates, as well as overall duration of the flowering and fruiting season, may be more consequential for consumers and pollinators than first-flowering date. Moreover, the full consequences may also depend on whole-community parameters such as changes in aggregate (all species) peak floral abundance, aggregate duration of flowering, duration of flower-to-fruit transition (Sethi et al., 2020), rearrangements of which species are co-flowering (CaraDonna et al., 2014), microsite variation in phenology, and synchrony or asynchrony of flowering and fruiting among species that have similar ecological niches or provide similar forage resources to consumers. Untangling this complexity of potential phenological changes will be important for understanding their full ramifications in the community.

Management recommendations

Despite these caveats, our findings that climate change is strongly affecting first-flowering date among sagebrush forb and shrub species suggests that it may also be causing advances and other changes in these species' phenologies, with potential impacts for other taxa. Given the strong relationship between snowmelt timing and/or mean spring temperature and first-flowering date for most of our study species, we can expect that these species' phenologies will shift more in the future. The community consequences, particularly for fauna that consume plant resources, are difficult to fully predict. However, it is clear that maintaining phenological diversity, both within and across species, will be critical to

maintaining adequate and appropriately timed floral and forage resources for wildlife in the face of a warming climate (Bartomeus et al., 2013; Isbell et al., 2015).

We urge land managers to continue conservation efforts that maintain a diverse portfolio of native plant species in terms of species composition, genetics, phenological responsiveness to climatic cues, and ecological importance to key wildlife and pollinator species. Redundancy within ecological niches may also be important to allow that those species' roles in the community may shift as climate changes affects them differently. These considerations are particularly relevant to restoration and habitat-enhancement projects. It may be wise to source native seeds for restoration projects from local as well as more distant geographic ranges (Williams & Dumroese, 2013) and include seeds from a range of climatic and altitudinal gradients. Diverse seed sourcing can increase the duration of floral and forage resources for wildlife and the adaptive capacity of plants to survive in warmer or drier climates, therefore increasing overall community resilience to long-term climate trends (Bernazzani et al., 2012) as well as short-term extreme weather events (Isbell et al., 2015).

Early-spring forbs in the sagebrush system are particularly important food resources for Sage-grouse, yet they are rarely considered in sagebrush plant restoration projects. Our results indicate that these species may be changing rapidly in terms of phenology, with possible ramifications for Sage-grouse and other fauna. It is therefore important to include these forbs in habitat management and restoration planning, including promoting phenological diversity within and across species. Future research can support management by furthering our understanding of how climate change is impacting other sagebrush plant phenophases, such as the onset and duration of the vegetative stage, fruiting, and senescence, and how these individual species changes are playing out in the larger community context. Further research will benefit from collecting phenological data on traits that are chosen to address specific management questions (Inouye et al., 2019), for example, by quantifying the temporal distribution of phenological events over multiple individual plants and multiple Sage-grouse nests to better test for temporal mismatches between these birds and their key spring forage resources.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Corinna Riginos and Trevor D. S. Bloom conceived of the study; Trevor D. S. Bloom collected field data; Trevor D. S. Bloom, Donal S. O'Leary and Corinna Riginos analyzed the data; Trevor D. S. Bloom and Corinna Riginos wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data (Bloom et al., 2021) are available in Dryad at https://doi.org/10.5061/dryad.tmpg4f50r.

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REFERENCES

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. "The Greenscape Shapes Surfing of Resource Waves in a Large Migratory Herbivore." *Ecology Letters* 20: 741–50.

Alexander, J. M., and J. M. Levine. 2019. "Earlier Phenology of a Nonnative Plant Increases Impacts on Native Competitors." *Proceedings of the National Academy of Sciences USA* 116: 6199–204.

Anderson, J. L., E. A. Richardson, and C. D. Kesner. 1986. "Validation of Chill Unit and Flower Bud Phenology Models for "Montmorency" Sour Cherry." *Acta Horticulturae* 184: 71–8.

Arfin Khan, M. A. S., C. Beierkuhnlein, J. Kreyling, S. Backhaus, S. Varga, and A. Jentsch. 2018. "Phenological Sensitivity of Early and Late Flowering Species under Seasonal Warming and Altered Precipitation in a Seminatural Temperate Grassland Ecosystem." *Ecosystems* 21: 1306–20.

Barnett, J. K., and J. A. Crawford. 1994. "Pre-Laying Nutrition of Sage Grouse Hens in Oregon." *Rangeland Ecology & Management/Journal of Range Management Archives* 47: 114–8.

Bartomeus, I., M. G. Park, J. Gibbs, B. N. Danforth, A. N. Lakso, and R. Winfree. 2013. "Biodiversity Ensures Plant–Pollinator Phenological Synchrony against Climate Change." *Ecology Letters* 16: 1331–8.

Bernazzani, P., B. A. Bradley, and J. J. Opperman. 2012. "Integrating Climate Change into Habitat Conservation Plans under the U.S. Endangered Species Act." *Environmental Management* 49: 1103–14.

Billings, W. D., and L. C. Bliss. 1959. "An Alpine Snowbank Environment and its Effects on Vegetation, Plant Development, and Productivity." *Ecology* 40: 388–97.

Block, S., J. M. Alexander, and J. M. Levine. 2020. "Phenological Plasticity Is a Poor Predictor of Subalpine Plant Population Performance Following Experimental Climate Change." *Oikos* 129: 184–93.

Bloom, T. D., A. Flower, and E. G. DeChaine. 2018. "Why Georeferencing Matters: Introducing a Practical Protocol to Prepare Species Occurrence Records for Spatial Analysis." *Ecology and Evolution* 8: 765–77.

Bloom, T. D., A. Flower, M. Medler, and E. G. DeChaine. 2018. "The Compounding Consequences of Wildfire and Climate Change for a High-Elevation Wildflower (*Saxifraga austromontana*)." *Journal of Biogeography* 45: 2755–65.

Bloom, T., D. O'Leary, and C. Riginos. 2021. "Flowering Time Advances Since the 1970s in a Sagebrush Steppe Community: Implications for Management and Restoration." Dryad, data set. https://doi.org/10.5061/dryad.tmpg4f50r.

Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. "Phenological Changes Reflect Climate Change in Wisconsin." *Proceedings of the National Academy of Sciences* 96: 9701–4.

Buban, M. S., T. R. Lee, and C. B. Baker. 2020. "A Comparison of the US Climate Reference Network Precipitation Data to the Parameter-Elevation Regressions on Independent Slopes Model (PRISM)." *Journal of Hydrometeorology* 21: 2391–400.

Butt, N., L. Seabrook, M. Maron, B. S. Law, T. P. Dawson, J. Syktus, and C. A. McAlpine. 2015. "Cascading Effects of Climate Extremes on Vertebrate Fauna through Changes to Low-Latitude Tree Flowering and Fruiting Phenology." *Global Change Biology* 21: 3267–77.

CaraDonna, P. J., J. L. Cunningham, and A. M. Iler. 2018. "Experimental Warming in the Field Delays Phenology and Reduces Body Mass, Fat Content and Survival: Implications for the Persistence of a Pollinator under Climate Change." *Functional Ecology* 32: 2345–56.

CaraDonna, P. J., A. M. Iler, and D. W. Inouye. 2014. "Shifts in Flowering Phenology Reshape a Subalpine Plant Community." *Proceedings of the National Academy of Sciences USA* 111: 4916–21.

Casazza, M. L., P. S. Coates, and C. T. Overton. 2011. "Linking Habitat Selection and Brood Success in Greater Sage-Grouse. Ecology, Conservation, and Management of Grouse." *Studies in Avian Biology* 39: 151–67.

Chambers, J. C., J. D. Maestas, D. A. Pyke, C. S. Boyd, M. Pellant, and A. Wuenschel. 2017. "Using Resilience and Resistance Concepts to Manage Persistent Threats to Sagebrush Ecosystems and Greater Sage-Grouse." *Rangeland Ecology & Management* 70: 149–64.

Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. "Phenological Tracking Enables Positive Species Responses to Climate Change." *Ecology* 93: 1765–71.

Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. "Shifting Plant Phenology in Response to Global Change." *Trends in Ecology & Evolution* 22: 357–65.

Coppack, T., F. Pulido, M. Czisch, D. P. Auer, and P. Berthold. 2003. "Photoperiodic Response May Facilitate Adaptation to Climatic Change in Long-Distance Migratory Birds." *Proceedings of the Royal Society of London B: Biological Sciences* 270: S43–6.

Crawford, J. A., R. A. Olson, N. E. West, J. C. Mosley, M. A. Schroeder, T. D. Whitson, R. F. Miller, M. A. Gregg, and C. S. Boyd. 2004. "Ecology and Management of Sage-Grouse and Sage-Grouse Habitat." *Rangeland Ecology & Management* 57: 2–19.

Daly, C., G. H. Taylor, and W. P. Gibson. 1997. "The PRISM Approach to Mapping Precipitation and Temperature." In *Proceedings of the 10th AMS Conference on Applied Climatology.* 20–3. Citeseer. Corvallis, Oregon: Oregon State University.

Dawson, A., V. M. King, G. E. Bentley, and G. F. Ball. 2001. "Photoperiodic Control of Seasonality in Birds." *Journal of Biological Rhythms* 16: 365–80.

Deacy, W. W., J. B. Armstrong, W. B. Leacock, C. T. Robbins, D. D. Gustine, E. J. Ward, J. A. Erlenbach, and J. A. Stanford. 2017. "Phenological Synchronization Disrupts Trophic Interactions between Kodiak Brown Bears and Salmon." *Proceedings of the National Academy of Sciences USA* 114: 10432–7.

Debinski, D. M., K. Szcodronski, and M. Germino. 2014. "Simulating Expected Changes in Pollinator Resources as a Function of Climate Change." University of Wyoming National Park Service Research Center Annual Report 37: 29–33.

Dumroese, R. K., T. Luna, B. A. Richardson, F. F. Kilkenny, and J. B. Runyon. 2015. "Conserving and Restoring Habitat for Greater Sage-Grouse and Other Sagebrush-Obligate Wildlife: The Crucial Link of Forbs and Sagebrush Diversity." *Native Plants Journal* 16: 276–99.

Enquist, C. A. F., J. L. Kellermann, K. L. Gerst, and A. J. Miller-Rushing. 2014. "Phenology Research for Natural Resource Management in the United States." *International Journal of Biometeorology* 58: 579–89.

Gallinat, A. S., L. Russo, E. K. Melaas, C. G. Willis, and R. B. Primack. 2018. "Herbarium Specimens Show Patterns of Fruiting Phenology in Native and Invasive Plant Species across New England." *American Journal of Botany* 105: 31–41.

Geremia, C., J. A. Merkle, D. R. Eacker, R. L. Wallen, P. J. White, M. Hebblewhite, and M. J. Kauffman. 2019. "Migrating Bison Engineer the Green Wave." *Proceedings of the National Academy of Sciences USA* 116: 25707–13.

Gregg, M. A., J. K. Barnett, and J. A. Crawford. 2008. "Temporal Variation in Diet and Nutrition of Preincubating Greater Sage-Grouse." *Rangeland Ecology & Management* 61: 535–42.

Gwinner, E. 1990. "Circannual Rhythms in Bird Migration: Control of Temporal Patterns and Interactions with Photoperiod." In *Bird Migration*, edited by E. Gwinner, 257–68. Berlin, Heidelberg: Springer.

Harpold, A., P. Brooks, S. Rajagopal, I. Heidbuchel, A. Jardine, and C. Stielstra. 2012. "Changes in Snowpack Accumulation and Ablation in the Intermountain West." *Water Resources Research* 48: W11501.

Hart, R., J. Salick, S. Ranjitkar, and J. Xu. 2014. "Herbarium Specimens Show Contrasting Phenological Responses to Himalayan Climate." *Proceedings of the National Academy of Sciences USA* 111: 10615–9.

Hassall, C., D. J. Thompson, G. C. French, and I. F. Harvey. 2007. "Historical Changes in the Phenology of British Odonata Are Related to Climate." *Global Change Biology* 13: 933–41.

Hertel, A. G., S. M. J. G. Steyaert, A. Zedrosser, A. Mysterud, H. K. Lodberg-Holm, H. W. Gelink, J. Kindberg, and J. E. Swenson. 2016. "Bears and Berries: Species-Specific Selective Foraging on a Patchily Distributed Food Resource in a Human-Altered Landscape." *Behavioral Ecology and Sociobiology* 70: 831–42.

Innes, R. J., and K. Zouhar. 2019. "Fire Regimes of Mountain Big Sagebrush Communities." Fire Effects Information System. Missoula, MT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory.

Inouye, D. W. 2008. "Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers." *Ecology* 89: 353–62.

Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye. 2000. "Climate Change Is Affecting Altitudinal Migrants and Hibernating Species." *Proceedings of the National Academy of Sciences USA* 97: 1630–3.

Inouye, B. D., J. Ehrlén, and N. Underwood. 2019. "Phenology as a Process Rather than an Event: From Individual Reaction Norms to Community Metrics." *Ecological Monographs* 89: e01352.

Inouye, D. W., and A. D. McGuire. 1991. "Effects of Snowpack on Timing and Abundance of Flowering in *Delphinium nelsonii* (Ranunculaceae): Implications for Climate Change." *American Journal of Botany* 78: 997–1001.

Isbell, F., D. Craven, J. Connolly, M. Loreau, B. Schmid, C. Beierkuhnlein, T. M. Bezemer, C. Bonin, H. Bruelheide, and E. De Luca. 2015. "Biodiversity Increases the Resistance of Ecosystem Productivity to Climate Extremes." *Nature* 526: 574–7.

Jones, C. A., and C. C. Daehler. 2018. "Herbarium Specimens Can Reveal Impacts of Climate Change on Plant Phenology; A Review of Methods and Applications." *PeerJ* 6: e4576.

Kudo, G., and T. Y. Ida. 2013. "Early Onset of Spring Increases the Phenological Mismatch between Plants and Pollinators." *Ecology* 94: 2311–20.

Laskin, D. N., McDermid, G. J., Nielson, S. E., Marshall, S. J., Roberts, D. R., and Montaghi, A. 2019. Advances in Phenology are Conserved Across Scale in Present and Future Climates. *Nature Climate Change* 9: 419–25. https://www.nature.com/articles/s41558-019-0454-4

Loehman, R. A., A. Corrow, and R. E. Keane. 2011. Modeling Climate Changes and Wildfire Interactions: Effects on Whitebark Pine (Pinus Albicaulis) and Implications for Restoration, Glacier National Park, Montana, USA. In The Future of High-Elevation, Five-Needle White Pines in Western North America: Proceedings of the High Five Symposium. 28–30 June 2010; Missoula, MT. Proceedings RMRS-P-63, edited by R. E. Keane, D. F. Tomback, M. P. Murray, and C. M. Smith, 176–189. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Lundquist, J. D., and F. Lott. 2008. "Using Inexpensive Temperature Sensors to Monitor the Duration and Heterogeneity of Snow-Covered Areas." *Water Resources Research* 44: W00D16.

Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. "Food Habits of Yellowstone Grizzly Bears, 1977–1987." *Canadian Journal of Zoology* 69: 1619–29.

Mayor, S. J., R. P. Guralnick, M. W. Tingley, J. Otegui, J. C. Withey, S. C. Elmendorf, M. E. Andrew, S. Leyk, I. S. Pearse, and D. C. Schneider. 2017. "Increasing Phenological Asynchrony between Spring Green-Up and Arrival of Migratory Birds." *Scientific Reports* 7: 1902.

McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. "Asynchronous Changes in Phenology of Migrating Broad-Tailed Hummingbirds and their Early-Season Nectar Resources." *Ecology* 93: 1987–93.

Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. "Large Herbivores Surf Waves of Green-Up during Spring." *Proceedings of the Royal Society B: Biological Sciences* 283: 20160456.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. "Animal Migration Amid Shifting Patterns of Phenology and Predation: Lessons from a Yellowstone Elk Herd." *Ecology* 94: 1245–56.

Middleton, A. D., H. Sawyer, J. A. Merkle, M. J. Kauffman, E. K. Cole, S. R. Dewey, J. A. Gude, D. D. Gustine, D. E. McWhirter, and K. M. Proffitt. 2020. "Conserving Transboundary Wildlife Migrations: Recent Insights from the Greater Yellowstone Ecosystem." *Frontiers in Ecology and the Environment* 18: 83–91.

Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. "The Effects of Phenological Mismatches on Demography." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3177–86.

Miller-Rushing, A. J., D. W. Inouye, and R. B. Primack. 2008. "How Well Do First Flowering Dates Measure Plant Responses to Climate Change? The Effects of Population Size and Sampling Frequency." *Journal of Ecology* 96: 1289–96.

Miller-Rushing, A. J., and R. B. Primack. 2008. "Global Warming and Flowering Times in Thoreau's Concord: A Community Perspective." *Ecology* 89: 332–41.

Moore, L. M., and W. K. Lauenroth. 2017. "Differential Effects of Temperature and Precipitation on Early- vs. Late-Flowering Species." *Ecosphere* 8: e01819.

Morellato, L. P. C., B. Alberton, S. T. Alvarado, B. Borges, E. Buisson, M. G. G. Camargo, L. F. Cancian, et al. 2016. "Linking Plant Phenology to Conservation Biology." *Biological Conservation* 195: 60–72.

Munson, S. M., and A. A. Sher. 2015. "Long-Term Shifts in the Phenology of Rare and Endemic Rocky Mountain Plants." *American Journal of Botany* 102: 1268–76.

National Oceanic and Atmospheric Administration. 2020. "Moose, WY US Station Details NOAA." National Centers for Environmental Information. https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00486428/detail.

Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. "A Multicriteria Assessment of the Irreplaceability and Vulnerability of Sites in the Greater Yellowstone Ecosystem." *Conservation Biology* 16: 895–908.

Notaro, M., K. Emmett, and D. O'Leary. 2019. "Spatio-Temporal Variability in Remotely Sensed Vegetation Greenness across Yellowstone National Park." *Remote Sensing* 11: 798.

O'Leary, D. S., J. L. Kellermann, and C. Wayne. 2017. "Snowmelt Timing, Phenology, and Growing Season Length in Conifer Forests of Crater Lake National Park, USA." *International Journal of Biometeorology* 62: 273–85.

Pearson, K. D. 2019. "Spring- and Fall-Flowering Species Show Diverging Phenological Responses to Climate in the Southeast USA." *International Journal of Biometeorology* 63: 481–92.

PRISM Climate Group 2020. "PRISM Climate Group, Oregon State University." https://prism.oregonstate.edu

Pyke, D. A., J. C. Chambers, M. Pellant, S. T. Knick, R. F. Miller, J. L. Beck, P. S. Doescher, E. W. Schupp, B. A. Roundy, and M. W. Brunson. 2015. Restoration Handbook for Sagebrush Steppe Ecosystems with Emphasis on Greater Sage-Grouse Habitat—Part 1. Concepts for Understanding and Applying Restoration. U.S. Geological Survey Circular 1416. https://doi.org/10.3133/cir1416.

R Core Team (2018). "R: A language and environment for statistical computing." Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/.

Remington, T. E., P. A. Deibert, S. E. Hanser, D. M. Davis, L. A. Robb, and J. L. Welty. 2021. *Sagebrush Conservation Strategy—Challenges to Sagebrush Conservation*. Reston, VA: USGS Numbered Series, U.S. Geological Survey.

Ricca, M. A., and P. S. Coates. 2020. "Integrating Ecosystem Resilience and Resistance into Decision Support Tools for Multi-Scale Population Management of a Sagebrush Indicator Species." *Frontiers in Ecology and Evolution* 7: 493.

Richardson, E. A., S. D. Seeley, D. R. Walker, J. L. Anderson, and G. L. Ashcroft. 1975. "Pheno-Climatology of Spring Peach Bud Development." *HortScience* 10: 236–7.

Schmid, S. F., J. Stöcklin, E. Hamann, and H. Kesselring. 2017. "High-Elevation Plants Have Reduced Plasticity in Flowering Time in Response to Warming Compared to Low-Elevation Congeners." *Basic and Applied Ecology* 21: 1–12.

Sepulveda, A. J., M. T. Tercek, R. Al-Chokhachy, A. M. Ray, D. P. Thoma, B. R. Hossack, G. T. Pederson, A. W. Rodman, and T. Olliff. 2015. "The Shifting Climate Portfolio of the Greater Yellowstone Area." *PLoS One* 10: e0145060.

Sethi, M. L., E. J. Theobald, I. Breckheimer, and J. HilleRisLambers. 2020. "Early Snowmelt and Warmer, Drier Summers Shrink Postflowering Transition Times in Subalpine Wildflowers." *Ecology* 101: e03171.

Sherwood, J. A., D. M. Debinski, P. C. Caragea, and M. J. Germino. 2017. "Effects of Experimentally Reduced Snowpack and Passive Warming on Montane Meadow Plant Phenology and Floral Resources." *Ecosphere* 8: e01745.

Singer, M. C., and C. Parmesan. 2010. "Phenological Asynchrony between Herbivorous Insects and their Hosts: Signal of Climate Change or Pre-Existing Adaptive Strategy?" *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3161–76.

Sprayberry, J., R. Defino & M. E. Dillon 2017. "Flowering Phenology and Bumblebee Activity in Early Summer in Grand Teton National Park." University of Wyoming National Park Service Research Center Annual Report. Laramie, Wyoming: University of Wyoming.

Stenset, N. E., P. N. Lutnæs, V. Bjarnadóttir, B. Dahle, K. H. Fossum, P. Jigsved, T. Johansen, et al. 2016. "Seasonal and Annual Variation in the Diet of Brown Bears *Ursus arctos* in the Boreal Forest of Southcentral Sweden." *Wildlife Biology* 22: 107–16.

Theobald, E. J., I. Breckheimer, and J. HilleRisLambers. 2017. "Climate Drives Phenological Reassembly of a Mountain Wildflower Meadow Community." *Ecology* 98: 2799–812.

Wickham, H. 2016. "plyr: Tools for Splitting, Applying and Combining Data." https://cran.r-project.org/web/packages/plyr/plyr.pdf

Wickham, H., W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, H. Yutani and RStudio. 2019. "ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics." https://ggplot2.tidyverse.org/reference/ggplot2-package.html

Williams, M. I., and R. K. Dumroese. 2013. "Preparing for Climate Change: Forestry and Assisted Migration." *Journal of Forestry* 111: 287–97.

Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. "Phylogenetic Patterns of Species Loss in Thoreau's Woods Are Driven by Climate Change." *Proceedings of the National Academy of Sciences USA* 105: 17029–33.

Willis, C. G., B. R. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. "Favorable Climate Change Response Explains Non-native species' Success in Thoreau's Woods." *PLoS One* 5: e8878.

Wolf, A. A., E. S. Zavaleta, and P. C. Selmants. 2017. "Flowering Phenology Shifts in Response to Biodiversity Loss." *Proceedings of the National Academy of Sciences USA* 114: 3463–8.

Wolf, A., N. B. Zimmerman, W. R. Anderegg, P. E. Busby, and J. Christensen. 2016. "Altitudinal Shifts of the Native and Introduced Flora of California in the Context of 20th-Century Warming." *Global Ecology and Biogeography* 25: 418–29.

Xu, S., Z. Yu, D. P. Lettenmaier, T. R. McVicar, and X. Ji. 2020. "Elevation-Dependent Response of Vegetation Dynamics to Climate Change in a Cold Mountainous Region." *Environmental Research Letters* 15: 094005.

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